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Impact of established shrub shelterbelts around oases on the diversity of ground beetles in arid ecosystems of Northwestern China

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Abstract. 1. Oases in arid regions of northwestern China are main sites for agriculture and human settlement. Conservation of these important oasis habitats involves establishing shrub shelterbelts around the oases. We investigated how different types of shrub shelterbelts affect the diversity of ground beetles.

2. We sampled carabid and tenebrionid assemblages with pitfall traps in spring and summer and measured key environmental variables in four habitats of the arid region: planted stands of pure and mixed plantations of two long-lived shrubs (*Haloxylon ammodendron* and *Tamarix ramosissima*) and natural grassland (NG) from which planted systems were converted.

3. Beetle abundance and species richness reduced significantly in the pure plantations but the mixed plantation had similar abundance and higher richness in spring and lower richness in summer relative to NG. We found differences in response between functional groups of beetles. The pure plantations resulted in reduced abundance and richness of herbivores and detritivores and increased predator abundance in spring and reduced predator abundance in summer. The mixed plantation resulted in increased detritivore richness in spring and reduced detritivore richness in summer as well as increased herbivore abundance in spring and reduced herbivore and predator abundance and richness in summer. The beetle community was largely determined by shrub cover and herbaceous plant diversity.

4. We conclude that the pure shrub plantations reduce beetle diversity, whereas the mixed shrub plantation has less adverse effect on beetle diversity. Shrub mixtures can therefore be a practical measure to minimise the negative impacts of shrub shelterbelts on beetles.

Key words. Activity abundance, beetle assemblages, land use change, shrub mixtures, shrub monocultures, species diversity.

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Introduction

Habitat alteration or loss resulting from changes in land use or land cover is a major cause of reduced biodiversity in many terrestrial ecosystems (Krauss *et al.*, 2010; Koellner & Geyer, 2013; Vergnes *et al.*, 2014; Souza *et al.*, 2015). Understanding the extent of biodiversity loss associated with land use/land cover changes at different spatial scales is a crucial research issue in biodiversity conservation (Garcia-Tejero *et al.*, 2013). While the impacts of land use/cover changes on above- and belowground biodiversity have been well documented in many parts of the world (Perner & Malt, 2003; Garnier *et al.*, 2007; Nielsen *et al.*, 2010; Garcia-Tejero *et al.*, 2013; Sweaney *et al.*, 2015), detailed studies are rare so far in the temperate arid regions in northwestern China (Li *et al.*, 2014; Feng *et al.*, 2015), which are facing the serious challenge of rapid landscape transformation due to large-scale afforestation programmes (Cao, 2011) and land reclamation for urban and agricultural development (Chen, 2008; Wang *et al.*, 2010).

China's temperate arid regions distribute mainly in the northwestern three provinces, including Xingjian, Gansu and Inner Mongolia. They occupy approximately two million km^2 and are inhabited by about 70 million people (Chen, 2008). Artificial oases, which account for approximately 5% of the arid land, are the major sites for agriculture and human settlement (Wang & Liu, 2013). Conservation of these ecologically fragile oasis habitats generally involves establishing protective shrub shelterbelts (500–1000 m wide) around the human-inhabited oases (Chang *et al.*, 2014). Over the last half century, the implementation of oasis conservation planning throughout the arid regions has converted natural grassland at the margins of many oases into structurally simple shrub shelterbelts (Pan & Chu, 2012). These shrub shelterbelts play important ecological roles in maintaining the stability and sustainability of the oasis ecosystems (Chang *et al.*, 2014).

The conversion from natural grassland to shrub shelterbelts significantly alters vegetation type, cover and plant community composition and diversity, which in turn cause changes in microclimatic conditions, soil properties and resource availability. These changes can affect, directly or indirectly, the patterns of abundance, species richness and composition of beetle communities (Stapp, 1997; Schweiger *et al.*, 2005; Woodcock *et al.*, 2010; Pakeman & Stockan, 2014), which could have important consequences for beetle-mediated ecosystem services, such as pollination (Steffan-Dewenter *et al.*, 2001), pest control (Suenaga & Hamamura, 2001; Zaller *et al.*, 2009), seed dispersal (Andresen & Feer, 2005) and decomposition of dung and dead plant material (Wu & Sun, 2010). Previous studies have addressed the effects of converting natural grassland to irrigated cropland or tree plantations on the structure and diversity of ground arthropod communities (Li *et al.*, 2014; Feng *et al.*, 2015). Nevertheless no studies have investigated how different types of shrub shelterbelts established around oases will affect the abundance, species richness and community composition of ground beetles, a dominant group of arthropods in China's arid ecosystems (Ren & Yu, 1999; Liu *et al.*, 2012).

To address this knowledge gap, we conducted a field study to investigate the activity abundance, species richness and community composition of ground beetle (Carabidae and Tenebrionidae) assemblages and measure key environmental variables known to affect beetle activity and distributions, including shrub cover, shrub height, herbaceous plant biomass, herbaceous species richness, soil pH, texture and salinity, in four habitats of the northwestern arid region: planted stands of pure and mixed plantations of two long-lived shrub species [*Haloxylon ammodendron* (Mey.) Bunge. and *Tamarix ramosissima* Ledeb.], as well as natural grassland from which planted systems were converted. The aim of this study was to evaluate the effects of established shrub plantations on the composition and diversity of the ground carabid and tenebrionid beetle assemblages and identify the determinants of beetle diversity and community composition. We predicted that the establishment of shrub plantations will result in loss of beetle species diversity in the desert landscape, but the magnitude of diversity loss may be greater in pure than mixed shrub plantations. We also predicted that land conversion-induced alterations in soil and vegetation conditions will both contribute to variation in beetle diversity and community composition, but vegetation change may play a more important role in structuring beetle communities than soil change.

Materials and methods

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 mean annual temperature of 7.6 °C (mean monthly temperature ranging from −10.4 °C in January to 23.9 °C in July) and mean annual precipitation of 117 mm, 12.6%, 28.4%, 19.1% and 16.6% of which occur in June, July, August and September respectively (data from the meteorological station of the Linze Inland River Basin Research Station, Chinese Ecosystem Research Network during the period 1995–2014). The mean annual pan-evaporation is approximately 2390 mm, 20 times more than the annual precipitation. The 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 & Shao, 2014).

Study system

The study site is a centuries-old artificial oasis zone (called 'Linze oasis') of approximately 6000 km^2. The Linze oasis zone consists of several small, isolated oases, three of which were chosen for the study. Areas of these three oases ranged from 600 to 800 km^2. To investigate the effects of established shrub plantations on ground beetles, the four land-cover types (Fig. 1) were selected at the margins of each oasis, including planted stands of pure *H. ammodendron* plantation (HAP; 21 years old), pure *T. ramosissima* plantation (TRP; 20 years old) and mixed

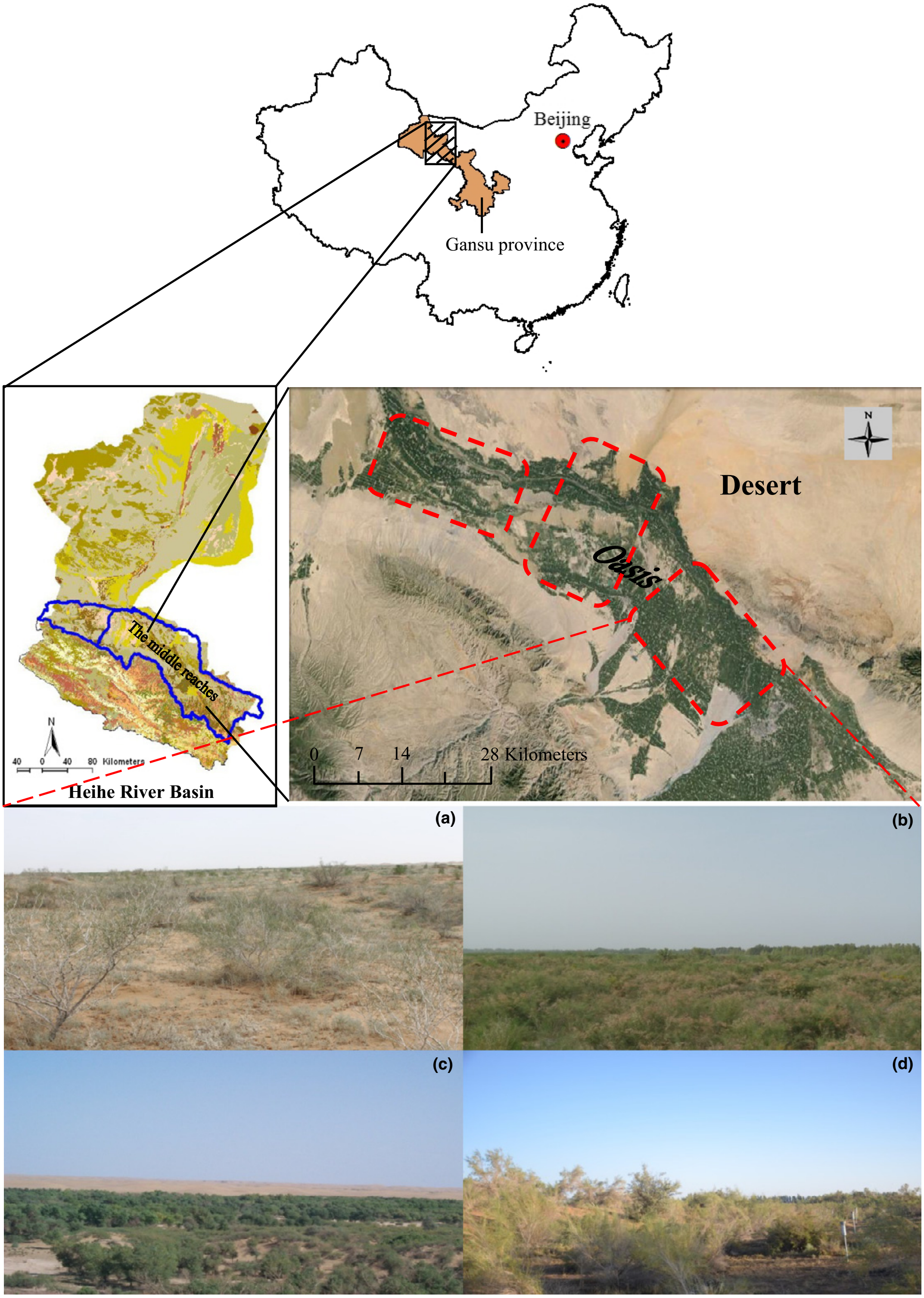

Fig. 1. The study site is located in the middle reaches of the Heihe River Basin in the western Gansu Province, northwestern China. Pictures show the real landscapes of four land-cover types: (a) natural grassland, (b) planted pure *Tamarix ramosissima* plantation, (c) planted pure *Haloxylon ammodendron* plantation, and (d) planted mixed plantation of *T. ramosissima and H. ammodendron*.

plantation of these two shrub species (MP; 20–21 years old) as well as natural grassland (NG) from which planted systems were converted. Distances between the four habitats in each oasis ranged from 500 to 1000 m.

The NG patches sampled were dominated by 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 HAP stands sampled were planted with seedlings from the local nursery, irrigated for 3 years after planting, and then received no further irrigation. Once established, these deep-rooted shrubs can survive depending on current-year precipitation and shallow groundwater (Tian *et al.*, 2014). Species in the herbaceous layer were mainly *B. dasyphylla*, *Halogeton arachnoideus*, *Salsola ruthenica*, *Chloris virgata* and *A. squarrosum*. The TRP stands sampled were planted with seedlings from the local nursery, irrigated for 3 years after planting, and then received no further irrigation. Similarly, established seedlings of these deep-rooted shrubs can survive depending on current-year precipitation and shallow groundwater (Zhang *et al.*, 2011). Species in the herbaceous layer were mainly *Onopordum acanthium*, *H. arachnoideus*, *B. dasyphylla*, *Peganum harmala*, *Atriplex centralasiatica*, *Mulgedium tataricum* and *Cynanchum chinense*. The MP stands sampled were planted with seedlings, irrigated for 3 years after planting, and then received no further irrigation. Species in the herbaceous layer were mainly *H. arachnoideus*, *S. ruthenica*, *B. dasyphylla*, *Eragrostis minor*, *C. virgate*, *Corispermum hyssopifolium*, *Echinops gmelinii*, *Phragmites australis*, *Chenopodium album*, *A. squarrosum*, *Artemisia desterorum* and *C. chinense*.

Sampling of ground beetles

Ground beetles were sampled with pitfall traps. In each oasis, three 30 × 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 beneath the shrubs (five traps) and in the open areas (five traps) between shrubs, resulting in a total of 90 traps per habitat and a total of 360 traps across four habitats. Each trap consisted of two cups, an outer permanent cup made of PVC pipe (8.5 × 20 cm) buried flush with the soil surface and a removable plastic cup inside the PVC pipe. In 2012, trapping was undertaken in spring (May 8–15, day and night) and also in summer (August 10–17, day and night). This sampling strategy was used to assure that local beetle populations were not over-captured due to frequent sampling (Liu *et al.*, 2010). These traps were emptied at the end of each sampling period and preserved specimens in a jar with a rubber seal, filled with 70% ethanol.

The captured beetles were counted and identified to species or genus level based on the keys (Ren & Yu, 1999; Zheng & Gui, 2004; Wang *et al.*, 2008; Ren & Ba, 2010). Although more than 10 beetle families were recorded, we considered only two families, Carabidae and Tenebrionidae, which were well represented by pitfall trapping (Spence & Niemela, 1994) and excluded the remaining families in the analysis. Species of carabids and tenebrionids were further assigned into 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 & Yu, 2000; Zhang, 2005; Ren & Ba, 2010).

Measurements of environmental variables

A suite of environmental variables known to affect beetle distributions were measured in all 36 plots of the four habitats across the three oases in late-August 2012, which peaked at biomass and diversity of plant communities (Liu *et al.*, 2010). The cover of shrubs in each plot was determined using the line intercept method (Mueller-Dombois & Ellenberg, 1974). Shrub height was determined by measuring the height of five randomly selected shrubs in each plot, from the ground surface to the highest point on the plant. Average canopy sizes [(long canopy diameter + short canopy diameter)/2] of the same shrubs were determined by measuring their long and short canopy diameters (Li *et al.*, 2005). The cover of the understory herbaceous layer in each plot was estimated visually using five 1-m^2 subplots located ≥8 m apart to each other. Species richness of herbaceous plants in these subplots was determined by identifying and counting the number of species. Herbaceous plant biomass was determined by clipping plants at a height of 2–3 cm above the ground. The harvested samples were oven-dried at 80 °C for 24 h and then weighed for dry mass.

After the aboveground plant materials were removed, soil cores were taken at a depth of 10 cm using a 5-cm diameter soil auger. Five soil cores from each plot were pooled and mixed thoroughly to form one composite sample. The roots and stones were removed by sieving with 2-mm mesh and these composite samples were used for analyses of soil pH, particle size distribution, electrical conductivity, soil organic carbon (SOC) and soil total nitrogen (TN). Soil pH was determined in 1:2.5 soil-water solutions using a Mettler Toledo 320-S pH meter (Mettler-Toledo Instruments Co. Ltd., Shanghai, China). Electrical conductivity was determined in 1:5 soil-water solutions using a conductivity meter (DDSJ-308A; INESA Scientific Instrument Co. Ltd., Shanghai, China). Particle size distribution was determined with a Microtrac S3500 Particle Size Analyzer (Microtrac Inc., Florida, USA) by dividing the soil into three size classes: coarse sand (2–0.25 mm), fine sand (0.25–0.05 mm), and silt plus clay (<0.05 mm), which were expressed as percentages of air-dried soil weight. SOC was determined with a TOC Analyzer (Elementar, Frankfurt, Germany). TN was determined by the Kjeldahl method (DK Heating Digester, UDK140 Automatic Steam Distilling Unit, Titroline

96, Milan, Italy). A summary of the measured environmental variables is given in Appendix S1.

Statistical analysis

A two-way repeated measures analysis of variance (ANOVA) was performed to test for the effects of habitat type, sampling season and their possible interaction on the performance of the beetle community and the three functional groups and eight dominant species whose number of individuals accounted for approximately 1% of the total. One-way ANOVA was also used to test for the effects of habitat type on the measured environmental variables. A Tukey's post hoc test was performed for multiple comparisons (with a significance level of $P < 0.05$). Data were log $(x + 1)$-transformed prior to analysis to meet the assumptions of ANOVA (Sokal & Rohlf, 1995). These analyses were conducted using the SPSS 17.0 software package.

A two-way PERMANOVA (PRIMER v6 software; Anderson *et al.*, 2008) was performed to determine the effects of habitat type, sampling season and their interaction on the species composition of the beetle community. Since a significant interaction between habitat type and sampling season was detected, one-way PERMANOVA was conducted for each of the two sampling seasons to determine differences in species composition (using Bray–Curtis similarity) between habitats. The pair-wise permutation tests of the statistical significance were based on 999 permutations of the log $(x + 1)$-transformed data. Data were transformed to reduce the influence of highly abundant beetle species.

Canonical correspondence analysis (CCA) was used to explore the relationships between the species composition of the beetle community and the explanatory variables using a data matrix consisting of 16 species and the selected seven environmental variables, including four plant-related parameters [shrub cover (SC), shrub height (SH), herbaceous plant biomass (HPB) and herbaceous species richness (HSR)] and three soil-related parameters [soil pH (pH), sand (coarse plus fine sand) fraction content (SFC; as a proxy of soil texture) and electrical conductivity (EC; as a proxy of soil salinity)]. The matrix was first analysed by detrended correspondence analysis, showing that CCA is an appropriate ordination approach in our case (length of gradient <3). To assess the relative importance of the seven explanatory variables in determining beetle species composition, a partial CCA (pCCA) was performed to quantify the relative contribution of each explanatory variable to the variation in species composition, which was depicted by the inertia from the conditional effect. The inertia value indicates the magnitude of additional explanatory power each explanatory variable contributes when it is added to the model (Lepš & Šmilauer, 2003). The pCCA and the Monte Carlo permutation tests were conducted using the CANOCO 5.0 software package to calculate the inertia values of the seven explanatory variables when controlling for the effects of other explanatory variables. Data were log $(x + 1)$ transformed before analysis. Simple linear regressions were used to examine relationships between the activity density and species richness of the beetle community and the statistically significant explanatory variables identified by the pCCA model.

Results

Changes in activity abundance, species richness and composition of beetle communities

A total of 20 589 carabids and tenebrionids belonging to 16 species were captured during the survey across the four habitats (Appendix S2). The activity abundance (number of individuals per trap) and species richness (number of species per trap) of the beetle community were significantly affected by habitat type, but effects varied between seasons because of a significant interaction between habitat type and sampling season (Table 1). Beetle activity abundance and species richness in HAP and TRP were significantly lower in spring and summer, whereas MP had similar activity abundance across the season and higher species richness in spring (+24%) and lower species richness in summer (−65%) relative to NG (Fig. 2). Moreover, MP had significantly higher numbers of beetles and beetle species than in HAP and TRP in spring and summer.

The PERMANOVAS showed significant effects of habitat type ($F_{3,71} = 54.48$, $P < 0.001$), sampling season ($F_{1,71} = 23.68$, $P < 0.001$) and their interaction ($F_{3,71} = 15.91$, $P < 0.001$) on the species composition of the beetle community. There were significant differences in communities between NG and HAP in spring ($t = 7.32$, $P < 0.001$) and summer ($t = 5.85$, $P < 0.001$), between NG and TRP in spring ($t = 7.15$, $P < 0.001$) and summer ($t = 7.99$, $P < 0.001$), and between NG and MP in spring ($t = 2.74$, $P = 0.002$) and summer ($t = 3.65$, $P < 0.001$). When pooling two sampling seasons together, communities were similar between NG and MP ($t = 1.20$, $P = 0.208$), but varied between NG and HAP ($t = 6.74$, $P < 0.001$) and between NG and TRP ($t = 6.29$, $P < 0.001$) respectively.

Changes in the performance of beetle functional groups

The activity of beetle functional groups was significantly affected by habitat type, but effects varied between seasons (Table 1). In spring, predator activity abundance was significantly higher in HAP and TRP and remained unchanged in MP, whereas in summer predator activity abundance was significantly lower in HAP and MP and remained unchanged in TRP relative to NG (Fig. 3). HAP and TRP significantly reduced activity abundance of herbivores and detritivores in spring and summer and increased predator activity abundance in spring and reduced predator activity abundance in summer. Herbivore activity abundance in MP was higher in spring and

Table 1. The statistical significance of the effects (*F* ratio and *P* value) of habitat type, sampling season and their interaction on performance measures of the beetle community and the three functional groups and eight dominant species.

	Habitat type		Sampling season		Habitat × season	
Variables	$F_{3,719}$	P	$F_{1,719}$	P	$F_{3,719}$	P
Community						
Activity abundance	283.75	0.001	155.17	0.006	13.62	0.004
Species richness	38.16	0.001	63.46	0.015	21.88	0.001
Functional groups						
Predatory beetles						
Activity abundance	3.63	0.084	8.40	0.101	57.51	0.001
Species richness	6.89	0.023	24.17	0.039	106.98	0.001
Relative proportion	24.28	0.001	14.87	0.061	61.77	0.001
Herbivorous beetles						
Activity abundance	35.27	0.001	181.56	0.005	57.59	0.001
Species richness	37.66	0.001	429.94	0.001	43.74	0.001
Relative proportion	3.87	0.075	134.38	0.007	18.28	0.002
Detritivorous beetles						
Activity abundance	599.52	0.001	186.93	0.005	17.84	0.002
Species richness	70.70	0.001	58.98	0.017	18.68	0.002
Relative proportion	101.70	0.001	81.72	0.012	67.41	0.001
Activity abundance of dominant species						
Anatolica sp.	123.42	0.001	284.69	0.003	287.97	0.001
Blaps gobiensis	0.54	0.672	9.55	0.091	2.48	0.158
Blaps caraboides	5.31	0.040	12.94	0.069	16.57	0.003
Harpalus pallidipennis	2.56	0.151	0.34	0.620	10.85	0.008
Mantichorula semenowi	174.69	0.001	238.52	0.001	174.69	0.001
Microdera sp.	4.39	0.059	73.79	0.013	4.96	0.046
Sternoplax setosa	36.46	0.001	80.23	0.012	145.13	0.001
Tentyria sp.	1704.47	0.001	189.34	0.005	50.55	0.001

lower in summer, whereas detritivore activity abundance in MP resembled that of NG in spring and summer. Compared to HAP and TRP, MP had lower predator activity abundance in spring and summer and higher herbivore and detritivore activity abundance in spring (Fig. 3).

Species richness of the functional groups was also significantly affected by habitat type, but the magnitude of these effects varied between seasons (Table 1). Predator richness increased from NG to HAP and TRP in spring, but it decreased from NG to HAP and MP and remained unchanged in TRP in summer (Fig. 3). Species richness of herbivores and detritivores was significantly lower in HAP and TRP than in NG in spring and summer, whereas that of herbivores and detritivores in MP was similar in spring and lower in summer relative to NG. Compared to HAP and TRP, MP had significantly higher detritivore richness in spring and summer and higher herbivore richness and lower predator richness in spring (Fig. 3).

The proportion of individuals in each of the three functional groups was significantly affected by habitat type, but effects varied with season (Table 1). Converting NG to MP did not alter the relative abundance of predators and detritivores in spring and summer, but significantly increased that of herbivores in spring and decreased that of herbivores in summer (Fig. 3). Converting NG to HAP and TRP significantly increased the relative abundance of predators and herbivores and decreased that of detritivores in spring, while converting NG to HAP increased the relative abundance of predators and converting NG to TRP increased that of predators and decreased that of herbivores and detritivores in summer (Fig. 3).

Changes in activity abundance of dominant species

The eight dominant beetle species responded differently to the conversion of NG to shrub plantations. In particular, the responses of these species were remarkably inconsistent across the season (Table 1). In spring, five response groups were identified. Group one included *Anatolica* sp. and *Mantichorula semenowi*, showing a consistent decline in activity abundance from NG to MP, HAP and TRP. Group two included *Blaps caraboides* and *Blaps gobiensis* whose activity abundance significantly increased in MP and remained unchanged in HAP and TRP relative to NG. Group three included *Sternoplax setosa* and *Tentyria* sp. whose activity abundance significantly increased in MP and decreased in HAP and TRP. Group four included one species (*Microdera* sp.) whose activity abundance significantly increased in HAP and MP and remained unchanged in TRP. Group five included one species (*Harpalus pallidipennis*) whose activity abundance significantly increased in HAP and TRP and remained unchanged in MP (Table 2).

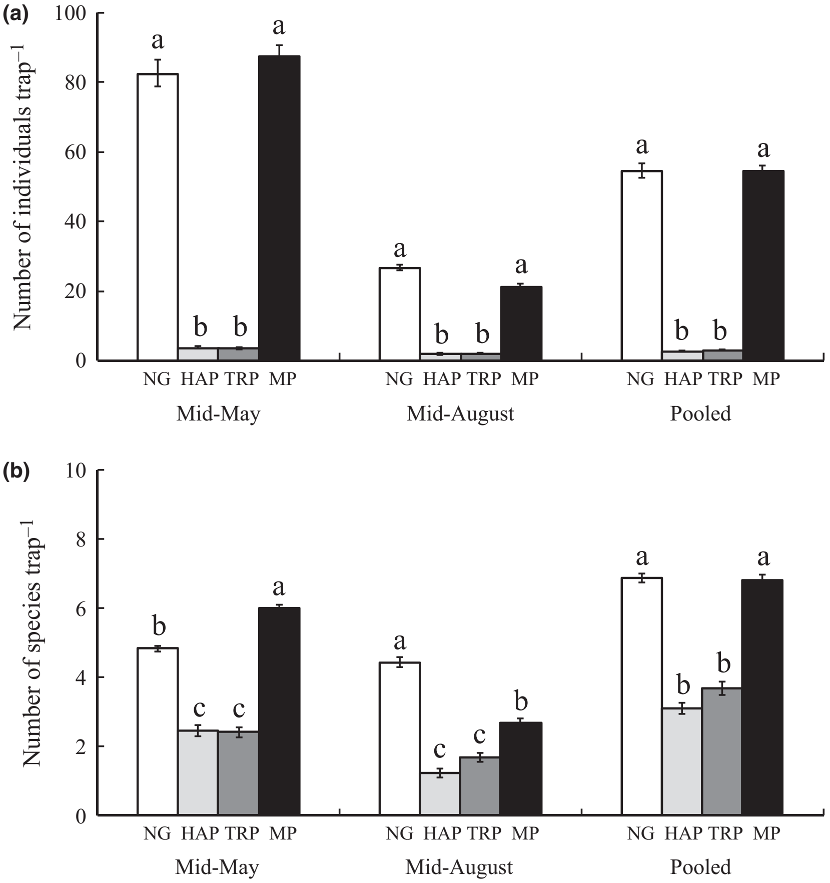

Fig. 2. Effects of converting natural grassland (NG) to planted pure *Haloxylon ammodendron* plantation (HAP), pure *Tamarix ramosissima* plantation (TRP), and mixed plantation (MP) of these two shrub species on activity abundance (a) and species richness (b) of the carabid and tenebrionid beetle community. The data are analysed for each of the two sampling seasons, and for both sampling seasons pooled. Means (±standard error) with different letters indicate significant differences among habitats ($P < 0.05$).

In summer, six response groups were identified. Group one included *Anatolica* sp. and *S. setosa*, which showed a consistent decline in activity abundance in all three shrub plantations. Group two included *Tentyria* sp, whose activity abundance showed a sharp decline in HAP and TRP and remained unchanged in MP. Group three included *Microdera* sp. whose activity abundance showed a decline in HAP and TRP and an increase in MP. Group four included *B. caraboides* and *B. gobiensis* whose activity abundance showed a significant decline in TRP and MP and remained unchanged in HAP. Group five included *H. pallidipennis* whose activity abundance increased in TRP and MP and decreased in HAP relative to NG. Group six included *M. semenowi* whose activity abundance did not differ among habitats (Table 2).

Relative importance of environmental variables in structuring beetle communities

The CCA model explained 74.6% of the variation in beetle species composition of which 55.1% and 11.2% were explained by axis 1 and 2 respectively (Fig. 4). The pCCA analysis revealed that the relative contributions of the seven explanatory variables varied considerably. Of the seven variables, only the conditional effects of HPB, SC, HSR and EC were statistically significant in the Monte Carlo permutation test ($P < 0.01$), explaining 47.4% (HPB), 11.1% (SC), 10.2% (HSR) and 2.9% (EC) of the variation in the data, respectively, whereas only 3.0% of the variation in the data was explained by the remaining variables that were not statistically significant in the Monte Carlo permutation test ($P > 0.05$; Table 3). Therefore, HPB, SC and HSR were the major drivers of community composition, particularly in HPB being the most important predictor. The biplot revealed that beetle species like *Opatrum* sp., *Carabidae* sp1, *Carabidae* sp2 and *Harpalus* sp. were much more abundant in the TRP site than the other sites, whereas beetle species like *H. pallidipennis* was found only in the HAP and TRP sites. Beetle species such as *Anatolica* sp., *M. semenowi*, *S. setosa* and *Tentyria* sp. were much more abundant in the NG and MP sites than in the HAP and TRP sites (Fig. 4).

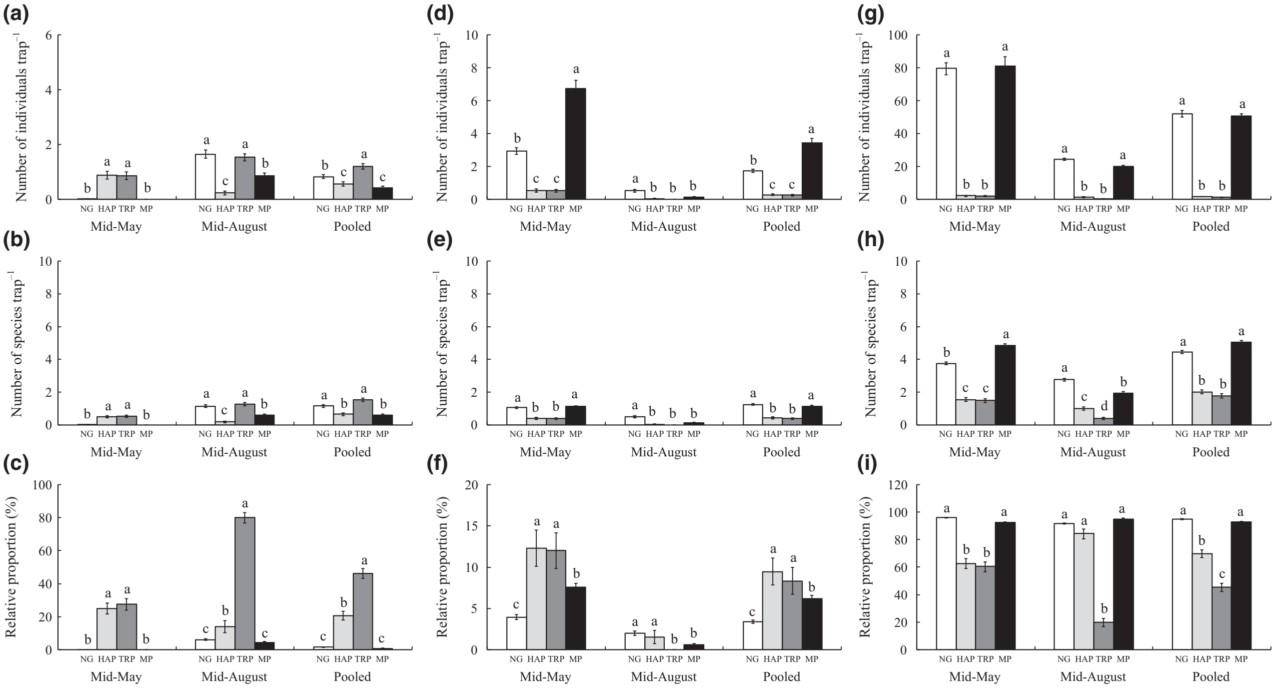

Fig. 3. Effects of converting natural grassland (NG) to planted pure *Haloxylon ammodendron* plantation (HAP), pure *Tamarix ramosissima* plantation (TRP), and mixed plantation (MP) of these two shrub species on activity abundance, species richness, and relative proportion of predatory beetles (a–c), herbivorous beetles (d–f), and detritivorous beetles (g–i). The data are analysed for each of the two sampling seasons, and for both sampling seasons pooled. Means (±standard error) with different letters indicate significant differences among habitats ($P < 0.05$).

Simple regression models showed that beetle activity abundance was positively correlated with HPB and HSR and negatively correlated with SC and EC, whereas beetle species richness was negatively correlated with SC and EC (Fig. 5).

Discussion

Effects of shrub shelterbelts on beetle diversity and community composition

Our results provide the evidence for strong effects of established shrub shelterbelts on beetle diversity and community composition, and also show that the magnitude of these effects varied across different types of shrub plantations. The establishment of pure shrub plantations irrespective of shrub species significantly reduced the abundance and diversity of the investigated carabid and tenebrionid beetle assemblages. This is consistent with previous studies at the same site, in which conversion of natural grassland to irrigated cropland or pure poplar and pure pine plantations significantly decreased activity abundance and taxon richness of ground-active arthropod communities (Li *et al.*, 2014; Feng *et al.*, 2015). Sweaney *et al.* (2015) also found that replacement of agricultural pastures by pure pine plantations resulted in significantly decreased species richness of ground-active beetle assemblages.

The effects of established pure shrub plantations on beetle communities were remarkably inconsistent across the sampled seasons (spring and summer). Beetle activity abundance measured in HAP and TRP was 4.4% and 4.2% of the levels in NG in spring and 6.7% and 7.7% of the levels in NG in summer while measured beetle species richness in HAP and TRP was 50.9% and 50.1% of the levels in NG in spring and 28.0% and 38.1% of the levels in NG in summer. These data suggest that converting NG to either of the two pure shrub plantations resulted in a larger decline in beetle activity abundance in spring than in summer and a larger decline in beetle species diversity in summer than in spring. In addition, our results also show that converting NG to pure shrub plantations regardless of shrub species substantially altered the species composition of the beetle community. The compositional variation was not only associated with replacement or altered dominance of a few species, but also associated with changes in the number of beetle species.

In contrast to the negative effects of pure shrub plantations, the observed effects of mixed shrub plantation on beetle diversity and community composition were quite complex. For instance the establishment of mixed shrub plantation did not have a significant effect on beetle overall abundance in either spring or summer, but it resulted

Table 2. Effects of converting natural grassland (NG) to planted stands of pure *Haloxylon ammodendron* plantation (HAP), pure *Tamarix ramosissima* plantation (TRP), and mixed plantation (MP) of these two shrub species on the activity abundance (number of individuals per trap) of eight dominant beetle species.

Species	Sampling season	NG	HAP	TRP	MP
Anatolica sp.	Mid-May	19.84 ± 1.32a	0.00 ± 0.00c	0.00 ± 0.00c	10.30 ± 0.49b
	Mid-August	3.17 ± 0.29a	0.00 ± 0.00b	0.00 ± 0.00b	0.03 ± 0.02b
	Pooled	11.51 ± 0.72a	0.00 ± 0.00c	0.00 ± 0.00c	5.17 ± 0.25b
Blaps caraboides	Mid-May	0.16 ± 0.04b	0.22 ± 0.05b	0.20 ± 0.05b	0.74 ± 0.11a
	Mid-August	0.22 ± 0.05a	0.21 ± 0.05a	0.02 ± 0.02b	0.09 ± 0.03ab
	Pooled	0.19 ± 0.03b	0.22 ± 0.04b	0.11 ± 0.03b	0.42 ± 0.06a
Blaps gobiensis	Mid-May	0.46 ± 0.07b	0.78 ± 0.11ab	0.76 ± 0.11ab	1.09 ± 0.15a
	Mid-August	0.43 ± 0.07ab	0.54 ± 0.09a	0.08 ± 0.03c	0.24 ± 0.06b
	Pooled	0.44 ± 0.05b	0.66 ± 0.08a	0.42 ± 0.06b	0.67 ± 0.08a
Harpalus pallidipennis	Mid-May	0.00 ± 0.00b	0.79 ± 0.14a	0.73 ± 0.13a	0.00 ± 0.00b
	Mid-August	0.19 ± 0.04b	0.06 ± 0.02b	0.77 ± 0.10a	0.73 ± 0.10a
	Pooled	0.09 ± 0.02c	0.42 ± 0.07b	0.75 ± 0.08a	0.37 ± 0.05b
Mantichorula semenowi	Mid-May	12.62 ± 0.85a	0.00 ± 0.00c	0.00 ± 0.00c	6.97 ± 0.40b
	Mid-August	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a	0.00 ± 0.00a
	Pooled	6.31 ± 0.42a	0.00 ± 0.00c	0.00 ± 0.00c	3.48 ± 0.20b
Microdera sp.	Mid-May	0.56 ± 0.17c	0.84 ± 0.09b	0.77 ± 0.09bc	4.38 ± 0.45a
	Mid-August	0.63 ± 0.09b	0.32 ± 0.06c	0.06 ± 0.03c	1.00 ± 0.12a
	Pooled	0.59 ± 0.09b	0.58 ± 0.06b	0.41 ± 0.04c	2.69 ± 0.26a
Sternoplax setosa	Mid-May	2.83 ± 0.21b	0.24 ± 0.07c	0.24 ± 0.07c	6.56 ± 0.53a
	Mid-August	0.31 ± 0.05a	0.02 ± 0.02b	0.00 ± 0.00b	0.11 ± 0.03b
	Pooled	1.57 ± 0.10b	0.13 ± 0.04c	0.12 ± 0.04c	3.33 ± 0.27a
Tentyria sp.	Mid-May	45.9 ± 2.1b	0.31 ± 0.07c	0.36 ± 0.07c	57.43 ± 2.17a
	Mid-August	19.97 ± 0.51a	0.41 ± 0.15b	0.09 ± 0.03b	18.68 ± 0.77a
	Pooled	32.93 ± 1.13a	0.36 ± 0.08b	0.22 ± 0.04b	38.06 ± 1.35a

The data are analysed for each of the two sampling seasons (mid-May and mid-August), and for both sampling seasons pooled. Means (± standard error) with different letters within each species indicate significant differences among habitats ($P < 0.05$; see Table 1 for statistical analyses).

Table 3. Partial canonical correspondence analysis (CCA) for quantifying the relative contributions of the seven key environmental variables to the variation in species composition of the sampled carabid and tenebrionid beetle assemblages.

Variable	Inertia conditional effects	MCR (%)	*F*	*P*
Shrub cover	0.077	11.05	8.78	<0.001
Shrub height	0.01	1.43	1.61	0.123
Herbaceous species richness	0.071	10.19	10.34	<0.001
Herbaceous plant biomass	0.33	47.35	30.56	<0.001
Soil pH	0.009	1.29	1.45	0.203
Sand fraction content	0.003	0.43	0.55	0.718
Electrical conductivity	0.02	2.87	3.08	0.014
Total	0.52	74.61		

Inertia from the conditional effects is used to derive the multivariate correlation ratio (MCR), which represents the proportion of variation explained by each environmental variable. The sum of all unconstrained eigenvalues = 0.697.

in increased beetle species richness in spring and reduced species richness in summer. These observations confirmed that a mixture of two shrub species had little impact on beetle activity patterns, but showed significant impacts on beetle diversity patterns in our study system. This highlights that the mixed plantation provides habitat that is more favourable for beetle species during the spring season, whereas the natural grassland habitat is more favourable for beetle species during the summer season. Therefore, preserving these two habitats is crucial for the maintenance of the carabid and tenebrionid assemblages. Furthermore, we found evidence that establishment of mixed shrub plantation did not cause a substantial shift in the species composition of the beetle community.

The mixed plantation harboured greater numbers of beetles and beetle species than either of the two pure shrub plantations, thus suggesting that shrub mixtures will have a greater conservation value of beetle species diversity. The enhanced conservation potential of shrub mixtures may result from greater structural complexity of the vegetation (Gardner *et al.*, 1995; Axmacher *et al.*, 2009; Gardiner *et al.*, 2010; Araújo *et al.*, 2013; Duan *et al.*, 2015) as well as higher plant diversity and productivity (Siemann, 1998; Brose, 2003; Woodcock & Pywell,

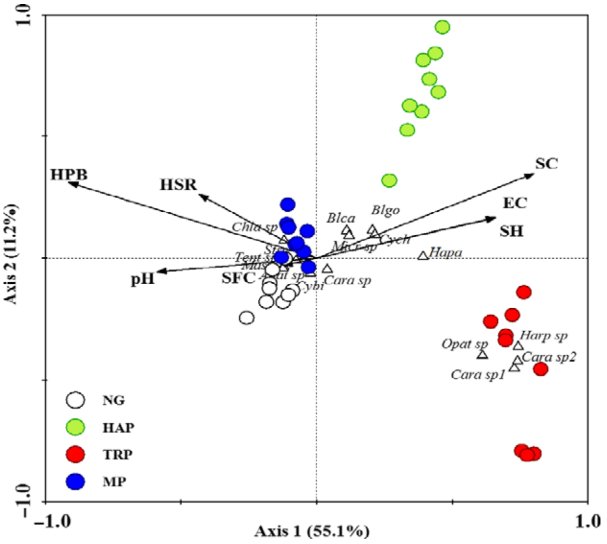

Fig. 4. Canonical correspondence analysis (CCA) ordination diagrams of the first two axes showing the relationships between beetle community composition and the environmental variables as well as the distribution of all 36 plots in the four habitats [hollow circles: natural grassland (NG), green circles: planted pure *Haloxylon ammodendron* plantation (HAP), red circles: planted pure *Tamarix ramosissima* plantation (TRP), and blue circles: planted mixed plantation of these two shrub species (MP)]. Beetle species are represented by hollow triangles: *Blaps gobiensis* (Blgo), *Blaps caraboides* (Blca), *Cyphogenia chinensis* (Cych), *Sternoplax setosa* (Stse), *Mantichorula semenowi* (Mase), *Anatolica* sp. (Anat sp), *Tentyria* sp. (Tent sp), *Microdera* sp. (Micr sp), *Opatrum* sp. (Opat sp), *Carabus* sp. (Cara sp), *Harpalus pallidipennis* (Hapa), *Cymindis binotata* (Cybi), *Harpalus* sp. (Harp sp), *Chlaenius* sp. (Chla sp), *Carabidae* sp1 (Cara sp1), and *Carabidae* sp2 (Cara sp2). Degree of the correlation of the environmental variables (SC, shrub cover; SH, shrub height; HPB, herbaceous plant biomass; HSR, herbaceous species richness; pH, soil pH; SFC, sand fraction content; EC, electrical conductivity) with the axes are shown as vectors. Vector length and angle are proportional to the direction and degree of their correlation with the plot ordination scores.

2009). Our results showed that the mixed plantation had significantly higher herbaceous plant biomass and species richness compared with the pure shrub plantations (Appendix S1). Although studies comparable to ours are lacking, a study investigating the effects of pure and mixed plantations of spruce and beech trees on ground-active spider and carabid communities found that there were no significant differences in the structure and diversity of the ground-active spider and carabid communities between the pure and mixed stands of spruce and beech (Oxbrough *et al*., 2012).

Effects of shrub shelterbelts on beetles functional groups

The effects of shrub shelterbelts on the abundance and diversity of the beetle functional groups varied across different types of shrub plantations and across the sampled seasons. The establishment of mixed plantation of two shrub species did not affect detritivore activity and diversity patterns across the season, but significantly increased activity abundance of herbivores in spring and decreased activity abundance and species richness of predators and herbivores in summer. This suggests that the mixed plantation provides habitat that favours herbivorous beetles during the spring season and does not favour predatory and herbivorous beetles during the summer season. Nevertheless, the pure shrub plantations were found to have a positive effect on predator abundance and diversity during the spring season, but a consistent negative influence on the abundance and diversity of herbivores and detritivores across the season and the abundance and diversity of predators during the summer season. This stands in contrast to a study in a semiarid region in Inner Mongolia of northern China, in which replacement of degraded natural sandy grassland with pure shrub plantations had little impact on the activity abundance and taxon richness of ground-active detritivorous arthropods, but resulted in increased taxon richness of ground-active herbivorous arthropods (Liu *et al*., 2015a).

Reduced abundance of herbivores in the pure shrub plantations was due mainly to decreased abundance of one species, *S. setosa*, whereas reduced abundance of detritivores in these pure shrub plantations was due mainly to decreased abundance of three dominant species, such as *Anatolica* sp., *M. semenowi* and *Tentyria* sp. *S. setosa* is a dominant herbivorous species in the desert ecosystem and its adults are pollinators (Zhang, 2005). A remarkable decline in *S. setosa* abundance will likely have a negative influence on pollination function (Kremen *et al*., 2007). *Anatolica* sp., *M. semenowi* and *Tentyria* sp. are the three most abundant species within the detritivorous assemblage in our study system (Liu *et al*., 2012). The disappearance of populations in *Anatolica* sp. and *M. semenowi* and the remarkable decline in abundance of *Tentyria* sp. in the pure shrub plantations would be

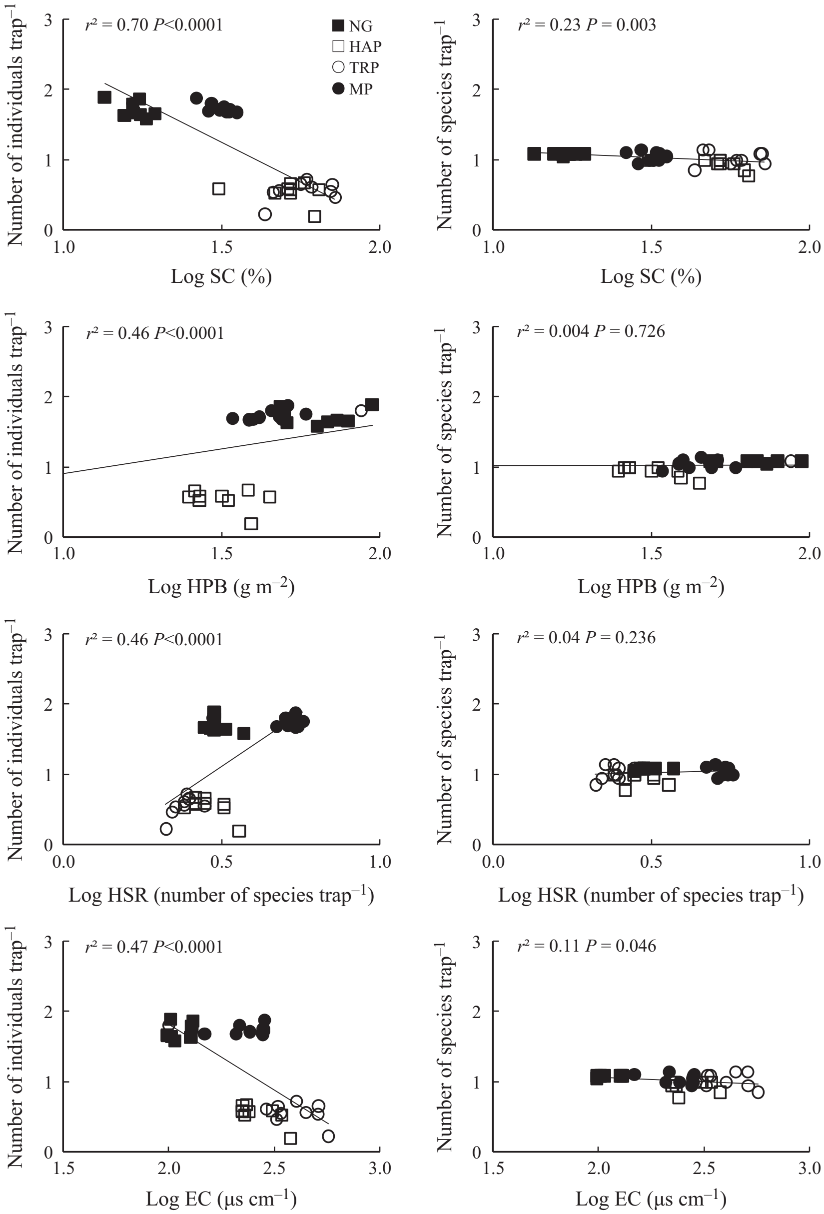

Fig. 5. Relationships between the activity abundance and species richness of the beetle community and the four statistically significant environmental variables, including shrub cover (SC), herbaceous plant biomass (HPB), herbaceous species richness (HSR), and electrical conductivity (EC). All data were log $(x + 1)$-transformed. The four habitat types are shown on the graphs.

expected to have important consequences for the delivery of ecosystem services that these species provide.

Key drivers of beetle diversity and species composition

Our variance partitioning analyses demonstrate that the relative roles of soil and vegetation variables in shaping the species composition of the investigated carabid and tenebrionid beetle assemblages varied considerably. The fact that the vegetation variables accounted for 51.3% of the variation, whereas the soil variables explained only 5.1% of the variation in the beetle community composition suggests that vegetation change exerted a stronger bottom-up control on the beetle community structure than soil change. Variance partitioning analyses also reveal that herbaceous plant biomass, herbaceous species richness and shrub cover were the most important predictors of beetle community composition at the local scale. This is consistent with previous experimental and observational studies (Andow, 1991; Siemann, 1998; Brose, 2003; Harvey *et al.*, 2008; Wenninger & Inouye, 2008; Axmacher *et al.*, 2009; Scherber *et al.*, 2010; Borer *et al.*, 2012; Liu *et al.*, 2015b).

Across all four habitats, we observed significant positive relationships between beetle activity abundance and species richness and herbaceous plant biomass and species richness and significant negative relationships between beetle activity abundance and shrub cover. This is consistent with a study in a temperate forest in Jilin Province of northern China (Zou *et al.*, 2013). The positive response of beetle activity to increased herbaceous plant diversity and the negative response of beetle activity to increased shrub cover suggest that the investigated beetle assemblages prefer open habitats with lower shrub cover and higher herbaceous plant diversity. Several previous studies have demonstrated that ground beetles usually prefer open, sunny habitats interspersed with bare sandy areas (Fattorini, 2010; Olsson & Ödman, 2014; Olsson *et al.*, 2014). For example, a study in arid and semiarid ecosystems in Israel found that ground beetles prefer shrub patches in an arid ecosystem with low cover (~25%) of shrubs, but prefer open patches between shrubs in a semi-arid ecosystem with high cover (~42%) of shrubs (Shelef & Groner, 2011). The observed positive relationship between beetle activity and herbaceous plant diversity and the negative relationship between beetle activity and shrub cover may explain why the abundance and diversity of ground beetles reduced significantly in the two pure shrub plantations. The average shrub cover was 51% in the *H. ammodendron* plantation and 57% in the *T. ramosissima* plantation, which greatly exceed the presumed value of shrub cover where the preferred microhabitat for ground beetles is open patches (Shelef & Groner, 2011).

In conclusion, this study contributes to a better understanding of the ecological impact of established shrub shelterbelts on beetle diversity and community composition and the functional consequences of altered beetle diversity and species composition patterns for beetle-mediated ecosystem services. The most striking finding from this study is that the establishment of pure shrub plantations regardless of shrub species can result in large loss of beetle taxonomic and functional diversity, whereas establishment of mixed shrub plantation has much less effect on beetle diversity and community composition. These findings can help develop an effective management framework for beetle diversity conservation in this desert ecosystem. We highlight that shrub mixtures should be a key management objective in future oasis conservation planning for mitigating the negative impact of shrub monocultures on beetle diversity. Further work should focus on selecting the appropriate shrub species combinations and evaluating their conservation potential experimentally.

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/icad.12152:

Appendix S1. Summary of the measured environmental variables in the studied four habitats.

Appendix S2. Number of captured individuals of 16 beetle species belonging to two families (Carabidae and Tenebrionidae) by pitfall traps in the studied four habitats during the two sampling periods combined.

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