

Shrubs and species identity effects on the distribution and diversity of ground-dwelling arthropods in a Gobi desert

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Received: 14 March 2012 / Accepted: 12 July 2012 / Published online: 21 July 2012
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Abstract Disentangling the relationship between shrub vegetation and ground-dwelling arthropods at multiple levels of taxonomic resolution is essential to developing a suitable management strategy for the conservation of shrub-associated arthropod biodiversity in shrubland ecosystems. Using Gobi desert (dominated by shrub species *Nitraria sphaerocarpa* and *Reaumuria soongorica*) occurring widely in inland arid areas of northwest China as a model system, we sampled ground-dwelling arthropods by pitfall trapping method under canopies of both shrubs and in intershrub bare areas during spring, summer and autumn. Our aim was to determine whether the presence and species identity of shrubs influence the distribution of ground-dwelling arthropods and whether the influence of shrub presence and species identity differs among trophic and taxonomic groups. At the community level, total arthropod abundance and species richness were significantly greater under shrubs than in intershrub bare habitats, whereas more arthropods were captured under *N. sphaerocarpa* than under *R. soongorica*. At the trophic group level, the abundance of predator and decomposer arthropods was significantly greater under shrubs than in intershrub bare habitats, whereas herbivore and decomposer arthropods were more abundant under *N. sphaerocarpa* than under *R. soongorica*. At the family level, the abundance of Carabidae, Gnaphosidae, Karschiidae, Tenebrionidae and Thomisidae was consistently much greater under shrubs

than in intershrub bare habitats, whereas that of Formicidae, Philodromidae and Tettigoniidae did not differ between the shrub microhabitats and the intershrub bare habitats. However, the abundance of Curculionidae under *R. soongorica* and the abundance of Geotrupidae under *N. sphaerocarpa* were significantly lower than that in intershrub bare habitats. *N. sphaerocarpa* was commonly preferred by arthropods in the families of Curculionidae and Tenebrionidae, whereas *R. soongorica* was commonly preferred by arthropods in the family Geotrupidae, but shrub species identity did not affect the abundance of the remaining families. Our results suggest that shrubs and species identity play important roles in structuring ground-dwelling arthropod communities, but the response of arthropods differed among trophic or taxonomic groups. This study may have important implications for the conservation of invertebrate biodiversity in Gobi desert ecosystems.

Keywords Desert shrubland · Ground arthropod diversity · Microhabitat selection · Shrub–arthropod relationship · Trophic and taxonomic groups

Introduction

Shrubland is a widely distributed biome type in arid and semiarid areas across the globe (Aguiar and Sala 1999). Shrub vegetation is a leading dominant component of shrubland ecosystems. Shrubs, as primary producers and providers of resources as well as builders of microhabitats for above- and below-ground arthropods (Shachak et al. 2008; Cushman et al. 2010), are thought to be the important and immediate drivers of soil and ground-dwelling arthropod communities (Mazía et al. 2006; Bezemer et al. 2010). Therefore, disentangling the ecological role of shrub

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vegetation in structuring soil and ground-dwelling arthropod communities is essential to understanding the relationship between shrub vegetation and soil/ground-dwelling arthropod composition and diversity and to developing a suitable management strategy for arthropod conservation (Sylvain and Wall 2011).

Over the past few decades, a considerable effort has been spent on examining the role of shrubs as a source of spatial heterogeneity in abiotic environment (e.g., microclimate, soil water and nutrient availability) in arid and semiarid ecosystems (Charley and West 1975; Barth and Klemmedson 1978; Garner and Steinberger 1989; Rosagno et al. 1991; Gutiérrez et al. 1993; Haworth and McPherson 1995; Su et al. 2004; López-Pintor et al. 2006). In recent years, a number of studies have also explored the role of shrubs as a source of spatial variation in herbaceous plant community composition and diversity as well as soil seed bank composition and abundance under their canopies in arid and semiarid ecosystems (Vetaas 1992; Callaway 1992; Moro et al. 1997; Pugnaire and Lázaro 2000; Shumway 2000; Facelli and Temby 2002; Li et al. 2005, 2009a; Li 2008). More recently, animal ecologists have focused on the role of shrubs as a driver of spatial distribution in soil fauna communities (Peterson et al. 2001; Pen-Mouratov et al. 2004; Doblás-Miranda et al. 2009; Liu et al. 2011) and ground beetle communities in arid and semiarid ecosystems (Rogers et al. 1988; Stapp 1997; Mazía et al. 2006). These studies provided empirical evidence suggesting that shrub vegetation plays a key role in determining the distribution, abundance and composition of soil/ground fauna communities, but the patterns of responses differed among trophic and taxonomic groups because of differences in their biological and functional traits (Bezemer et al. 2010; Nielsen et al. 2010). To our knowledge, however, no studies have investigated explicitly the influence of shrubs and their species identity on the distribution, abundance and composition of ground-dwelling arthropod communities in Gobi desert, northwest China.

Gobi desert in northwest China, which is characterized by coarsely textured soil, sparse vegetation, low species diversity, severe solar radiation and very rare rainfall (Zhou et al. 2010), is a widely distributed biome type in inland arid regions, with mean annual precipitation less than 250 mm (Li et al. 2009b). In the Gobi desert, shrublands (dominated by a few xerophytic shrub species such as *Reaumuria soongarica*, *Nitraria sphaerocarpa* and *Salsola passerine*) are the dominant natural vegetation and are primarily subject to livestock grazing (Zhou et al. 2011). Since 1970s, rapid increase in the number of livestock in order to meet the growing demand for livestock products has led to widespread degradation in desert shrubland, which is reflected primarily in declining shrub cover,

biomass and species diversity (Zhou et al. 2010). The degradation of shrub vegetation caused by livestock overgrazing may have a significant impact on the growth, recruitment and survival of ground-dwelling arthropods by altering the physical environment and resource availability in the ecosystem (Ren and Yu 1999). As such, there is a need for exploring the responses of ground-dwelling arthropods to shrub cover and species identity at different levels of biological organization in this important biome.

In this study, we chose two native dominant shrub species, *N. sphaerocarpa* (Zygophyllaceae) and *R. soongarica* (Tamaricaceae), occurring widely in the Gobi desert as a model system. We sampled the communities of ground-dwelling arthropods using pitfall traps under canopies of both shrub species (hereafter referred to as ‘microhabitats under shrubs’) and in open bare areas between shrubs (hereafter referred to as ‘intershrub bare habitats’) during spring, summer and autumn corresponding to the main period of arthropod activity in the study area (Liu et al. 2010). The main aims of this study were to determine how shrubs and their species identity influence the spatial distribution of ground-dwelling arthropods, and to assess whether the response of arthropods to the presence and species of shrubs differed among trophic and taxonomic groups. We tested two hypotheses: (1) the presence of shrubs will have a significant influence on the distribution of ground-dwelling arthropods by altering the biotic and abiotic environments, and (2) different shrub species will differ in their influence on the arthropod community and trophic and taxonomic groups of the assemblage. Answers to these questions will help resource managers formulate a rational invertebrate conservation planning aimed at maintaining ecosystem health and function.

Materials and methods

Study system

This study was conducted in a typical Gobi desert located in the middle reaches of the Heihe River (39°24'N, 100°07'E; 1,350 m a.s.l.), the second largest inland river basin (135,000 km²) in the arid regions of northwest China (Li et al. 2009b). This area is characterized by a temperate continental climate, with long cold winters and warm summers. The mean annual precipitation is approximately 117 mm, most of which occurs between June and September. The mean annual air temperature is 7.6 °C, varying from −10.7 °C in January (coldest) to 23.8 °C in July (warmest). The mean annual pan evaporation is 2,390 mm over the past 30 years. The soil is classified as gray brown desert soil according to the Chinese Soil Taxonomy

classification (Chen and Li 1998). Vegetation at the study site is dominated by a few xerophytic shrub species such as *Nitraria sphaerocarpa*, *Reaumuria soongorica* and *Salsola passerine*, along with several herbaceous plant species such as *Suaeda glauca*, *Artemisia scoparia*, *Allium mongolicum* and *Zygophyllum mucronatum*. In the unprotected (grazed) areas, the cover of the shrub communities is between 5 and 8 %, and the cover of the herbaceous communities is between 1 and 3 % during the peak plant community biomass (Liu et al. 2010).

Sampling of ground-dwelling arthropods

To explore the influence of two most abundant native shrubs (*N. sphaerocarpa* and *R. soongorica*) on the distribution and diversity of ground-dwelling arthropods, four sampling plots (30 m × 30 m) were established in a 5-year-old fenced (ungrazed) area that has been used as a permanent vegetation monitoring plot by the Linze Inland River Basin Research Station, Chinese Ecosystem Research Network, with at least 150 m between plots (Ziesche and Roth 2008). In the fenced plot, the density and percentage cover of the shrub *N. sphaerocarpa* were 740 ± 560 plants ha^{-1} and 3.0 ± 1.9 %. The density and percentage cover of the shrub *Z. mucronatum* were 1680 ± 800 plants ha^{-1} and 4.5 ± 1.2 %. The percentage cover of herbaceous communities was 3.2 ± 2.1 %. In each sampling plot, four adult individuals of *N. sphaerocarpa* of similar sizes (41.6 cm ± 3.1 cm in plant height and 166.0 cm ± 12.9 cm in canopy diameter) and four adult individuals of *R. soongorica* of similar sizes (27.8 cm ± 2.3 cm in plant height and 61.0 cm ± 4.4 cm in canopy diameter), as well as four open bare-ground sites between shrubs were selected. The distance between the shrubs that were sampled within a plot was >6 m in order to avoid autocorrelation between the traps (Mazía et al. 2006). Pitfall traps (8 cm diameter, 10 cm deep) filled with approximately 70 ml of 70 % ethanol solution were buried flush with the ground surface under canopies of the two shrubs, as well as in the intershrub bare sites (the distance to the nearest shrub sampled was >5 m). We thus had 16 traps from each microhabitat type, and a total of 48 traps from the three microhabitat types. Sampling was conducted in spring (6–20 May), summer (4–18 July) and autumn (8–22 September), respectively, which corresponds to the main period of ground-dwelling arthropod activity in our study system (Liu et al. 2010). Each of the three sampling periods consisted of 15 consecutive days (day and night). All traps were checked every 3 days during the 15-day sampling period. Captured arthropod specimens (preserved in 75 % ethyl alcohol) were counted and identified to the family level as per Ren and Yu (1999) and Yin (2000).

Measurements of plant characteristics and environmental variables

To evaluate the differences between the two shrubs in the quantity and quality of resources that they provide, plant characteristics of both shrubs were measured. In each sampling plot, shrub cover was measured using the line-intercept method (Mueller-Dombois and Ellenberg 1974) with 15 interception lines (2 m between lines for a total line length of 450 m) in each plot. Four adult individuals of each shrub species were randomly selected in each sampling plot for determining plant height (from the soil surface to the highest point in the plant) and canopy diameter (average of the longest and shortest crown diameters). Then, one of the four individuals of each shrub species was cut off at ground surface for measuring biomass of leaves and current-year shoots per plant as well as leaf nitrogen (N) content (an important indicator of plant quality). Leaf N content was determined by the Kjeldahl method (DK Heating Digester, UDK140 Automatic Steam Distilling Unit, Titroline 96, Italy). In addition to this, we also monitored phenological period characteristics of both shrub species.

To determine the differences among three microhabitat types in their abiotic conditions, the physical and hydrological properties of surface soil (20 cm depth) in the three microhabitat types were measured following vegetation investigation. In each sampling plot, four soil cores (5-cm diameter, 20-cm depth) were taken using an auger from each of the three microhabitats (under *N. sphaerocarpa*, under *R. soongorica* and in intershrub bare habitat). These four cores were bulked and mixed thoroughly to form one composite soil sample (a total of 4 composite samples from each microhabitat type) for analyzing soil texture. Soil texture was determined by the dry sieve method (Li et al. 2009c) dividing the soil into three particle sizes: coarse sand (>2 mm), fine sand (2–0.05 mm) and silt plus clay (<0.05 mm), which were expressed percentage of soil weight. Time domain reflectometry (TRIME-FM, IMKO Micromodultechnik GmbH, Ettlingen, Germany) was used to measure soil moisture content at a depth of 20 cm in each of the three microhabitat types. Daily maximum temperatures at the ground surface in these three microhabitats were also measured at 14:00 with a geothermometer. Measurements of soil moisture and ground temperature were conducted for three consecutive days during each sampling period.

Data analysis

A total of 8,101 individual arthropods were collected in pitfall traps from the three microhabitat types across the three sampling periods, which included 15 taxonomic taxa

(families) in two classes: seven families belonging to Arachnida and eight families to Insecta. All 15 families were further classified into one of four trophic groups based on their feeding habits, namely predators (Carabidae, Gnaphosidae, Karschiidae, Nesticidae, Phalangiidae, Philodromidae, Salticidae and Thomisidae), herbivores (Curculionidae, Scarabaeidae and Tettigoniidae), detritivores (Geotrupidae, Silphidae and Tenebrionidae) and omnivores (Formicidae). At the community level, we calculated total abundance (the total number of arthropods per trap averaged over the four traps per plot) and total taxonomic richness (the total number of families in the ground-dwelling arthropods, which was the sum of families found in the four traps per plot), and Shannon's indices of species diversity and evenness (H and J, respectively; Begon et al. 2006) using a mean of the four traps per plot. At the trophic group level, we calculated the abundance of the three main trophic groups of predators, herbivores and decomposers (detritivores + omnivores). At the family level, we calculated the abundance of the ten dominant families (Carabidae, Curculionidae, Formicidae, Geotrupidae, Gnaphosidae, Karschiidae, Philodromidae, Tenebrionidae, Tettigoniidae and Thomisidae). We performed a two-way ANOVA using SPSS 16.0 for Windows (SPSS Inc, Chicago, Illinois) to determine the effects of microhabitat type (under *R. soongorica*, under *N. sphaerocarpa* and in intershrub bare habitat) and season or sampling period (spring, summer and autumn) and their interactions on total abundance, total taxon richness, diversity and evenness indices of the ground-dwelling arthropod community, and the abundance of the three trophic groups and the ten dominant families. Tukey's (HSD) post hoc tests were used to compare differences in these response variables among seasons and microhabitat types. We also performed one-way ANOVA and Tukey's (HSD) post hoc tests to determine differences in the measured environmental variables (soil moisture, ground temperature, coarse sand content, fine sand content and silt plus clay content) among microhabitat types. Student's paired *t* tests were used to determine differences in plant characteristics (plant height, canopy diameter, shoot biomass per plant, leaf biomass per plant and leaf N content) between the two shrub species. To meet the requirements for normality and homogeneity of variance, percentage data were arcsine square root-transformed and non-percentage data were $\log(x + 1)$ -transformed prior to analysis. Means (\pm standard error) presented in text and figures were calculated using non-transformed data.

To explore differences in the community composition of ground-dwelling arthropods among three microhabitat types within seasons, we compared the arthropod communities found in the intershrub bare habitat with those in the microhabitats under both shrubs using the Sørensen

index, which is a measure of proportional similarity, ranging from 0 (no similarity) to 1 (identical).

Ordination techniques were used to identify arthropod microhabitat choice and the relationship between arthropod community composition and environmental factors. Redundancy analysis (RDA) on the family abundance data using CANOCO software for Windows 4.5 (Microcomputer Power, Ithaca, USA) was chosen to determine the relative contribution of the measured environmental variables to the community composition. The data were first analysed by detrended correspondence analysis (DCA) suggesting that RDA is an appropriate approach (length of gradient < 3). The relative contribution of each environmental variable to the explained variation in the data was determined by the inertia from the conditional (or partial) effects, which show the amount of additional variation each variable contributes when it is added to the model (Lepš and Šmilauer 2003). Partial RDA and the Monte Carlo permutation test were performed to determine the conditional effect of ground temperature with the other variables as covariables, that of soil moisture content with the other variables as covariables, that of coarse sand content with the other variables as covariables, that of fine sand content with the other variables as covariables, and that of silt plus clay content with the other variables as covariables.

Results

Physical environment and plant characteristics

The physical environment differed among the three microhabitat types. Mean coarse sand content in surface soil (0–20 cm) was significantly ($P < 0.05$) greater in the intershrub bare habitat than in the microhabitats under both shrubs, whereas no differences were found among microhabitat types in mean contents of fine sand and silt plus clay (Fig. 1), indicating that the intershrub bare habitat had a more coarsely textured soil. Mean content of soil moisture across the growing season was lower in the intershrub bare habitat than in the microhabitats under both shrubs, especially significantly ($P < 0.05$) lower than that under *R. soongorica*. In contrast, the mean daily ground maximum temperature across the growing season was significantly ($P < 0.05$) greater in the intershrub bare habitat than in the microhabitats under both shrubs (Fig. 1).

On average, plant height, canopy diameter, biomasses of shoots and leaves per plant and leaf N content were consistently greater in *N. sphaerocarpa* than in *R. soongorica*. In particular, canopy diameter, leaf biomass and leaf N content were significantly ($P < 0.05$) greater in *N. sphaerocarpa* than in *R. soongorica* (Fig. 2). Both

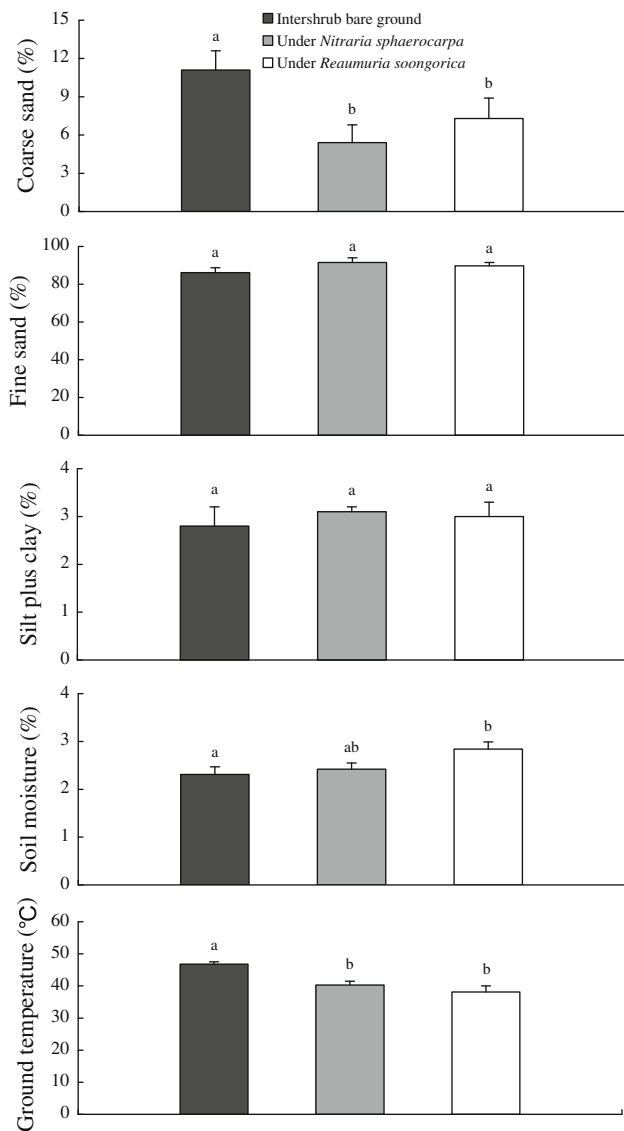


Fig. 1 The measured environmental variables of the three microhabitats (under *Nitraria sphaerocarpa*, under *Reaumuria soongorica* and intershrub bare habitat) in a Gobi desert. Means (\pm SE) with different letters within each variable indicate significant differences among microhabitats ($P < 0.05$ from one-way ANOVA followed by Tukey’s HSD tests)

shrub species also differed in their phenological period characteristics. The main phenological stages of *N. sphaerocarpa* occur: bud germination: 6–12 April; leaf expansion: 15–28 April; initial flowering stage: 9–11 May; full-bloom stage: 12–23 May; fructicative period: 20 May to 18 June; and defoliation period: 28 October to 9 November. The main phenological stages of *R. soongorica* occur: bud germination: 8–18 April; leaf expansion: 25 April to 3 May; initial flowering stage: 11–26 July; full-bloom stage: 2–15 August; fructicative period: 15 August to 22 October; and defoliation period: 5–11 November.

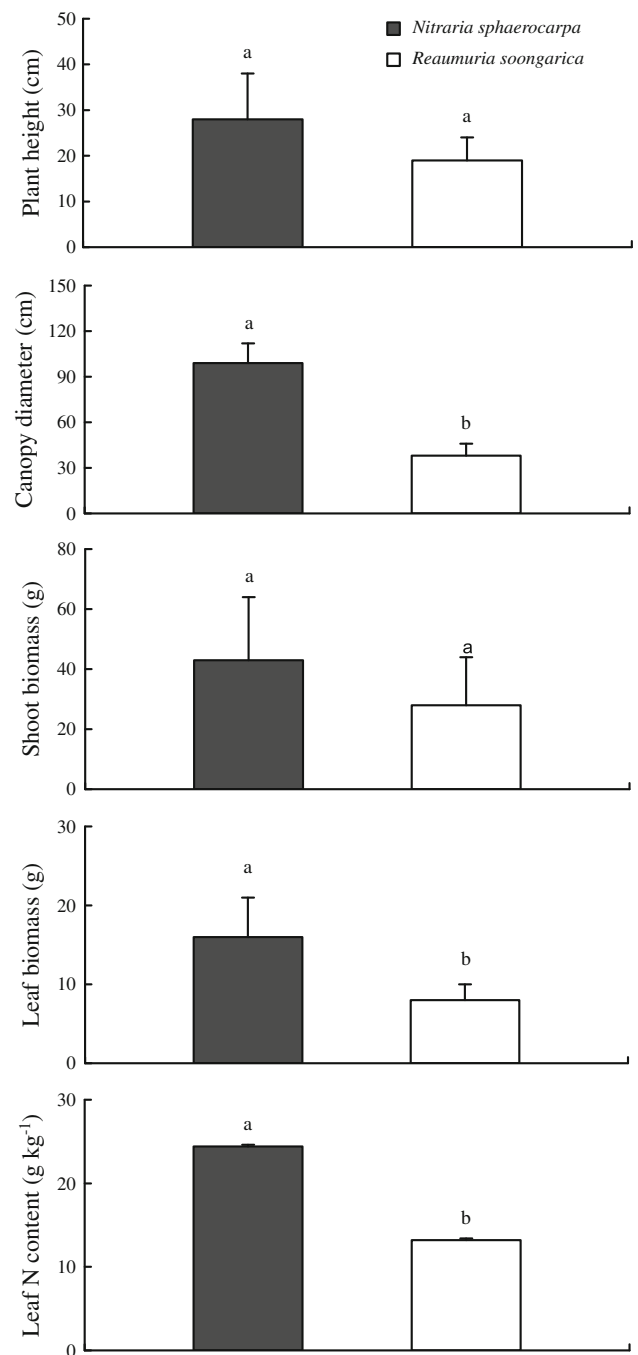


Fig. 2 Plant characteristics of two shrub species studied in a Gobi desert. Means (\pm SE) with different letters indicate significant differences between the two shrub species ($P < 0.05$ from Student’s paired t tests)

Community-level responses to shrub presence and species identity

Results from a two-way ANOVA showed that microhabitat type had a significant effect on the abundance, taxon richness and evenness index of ground-dwelling arthropods, but did not affect the diversity index (Table 1).

Table 1 Results of two-way ANOVAs for the effects of season (spring, summer and autumn) and microhabitat type (under *Nitraria sphaerocarpa*, under *Reaumuria soongorica* and intershrub bare ground) and their interactions on the abundance, taxon richness,

diversity and evenness indices of ground-dwelling arthropods as well as the abundance of the three trophic groups and the ten dominant families

	Season ($F_{2, 24}$)	Microhabitat ($F_{2, 24}$)	Season \times microhabitat ($F_{4, 24}$)
Community level			
Total abundance	34.70***	18.42***	7.11***
Taxon richness	1.94n.s.	17.34***	8.33***
Diversity index	103.46***	1.31n.s.	2.69*
Evenness index	100.07***	3.93*	3.33*
Abundance of trophic groups			
Predators	40.83***	47.23***	5.19**
Herbivores	57.58***	6.39**	6.47***
Decomposers	134.35***	17.70***	9.35***
Abundance of dominant families			
Carabidae	29.93***	8.03***	6.05***
Curculionidae	67.99***	6.79***	4.65**
Formicidae	3.94*	0.98n.s.	0.94n.s.
Geotrupidae	22.87***	3.61*	2.17n.s.
Gnaphosidae	15.61***	14.62***	1.75n.s.
Karschiidae	7.01***	3.37*	2.93*
Philodromidae	0.50n.s.	1.49n.s.	1.14n.s.
Tenebrionidae	132.03***	17.58***	5.99***
Tettigoniidae	4.54*	0.24n.s.	0.08n.s.
Thomisidae	24.64***	3.38*	3.01*

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; n.s., not significant

Averaged over the three seasons, total arthropod abundance and taxon richness were significantly greater in the microhabitats under shrubs than in the intershrub bare habitat, whereas in contrast the evenness index was significantly lower under shrubs than in intershrub bare habitats (Fig. 3). However, there were significant interactions between microhabitat type and season on the abundance, taxon richness and indices of species diversity and evenness of ground-dwelling arthropods, indicating that the effect of microhabitat type varied across seasons (Table 1). Separate ANOVAs for each season showed that the positive effect of shrubs on arthropod abundance was found only in the spring and summer samplings, whereas shrub presence effects on arthropod taxon richness were observed only in the summer. The identity of shrub species had a significant effect on arthropod abundance, but did not affect the richness and indices of diversity and evenness of ground-dwelling arthropods. Averaged over the three seasons, more arthropods were captured under *N. sphaerocarpa* than under *R. soongorica*, but this pattern occurred only in the spring (Fig. 3).

The Sørensen similarity analysis showed that the community composition of ground-dwelling arthropods under *N. sphaerocarpa* was more similar to that under *R. soongorica* in all three seasons. However, the communities in

the microhabitats under both shrubs differed markedly from those in the intershrub bare habitats in the spring and summer, whereas similarity in the communities between the shrub microhabitats and the intershrub bare habitats increased significantly in the autumn (Table 2).

Trophic group-level responses to shrub presence and species identity

The influence of shrub presence and species identity on the distribution of ground-dwelling arthropods differed between trophic groups. The two-way ANOVA showed that microhabitat type had a significant effect on the abundance of predator, herbivore and decomposer arthropods (Table 1). Averaged over the three seasons, the abundance of both predator and decomposer arthropods was significantly greater under both shrubs than in intershrub bare habitats, whereas the abundance of herbivore arthropods under *R. soongorica* was significantly lower than that in the intershrub bare habitat (Fig. 4). Both herbivore and decomposer arthropods were much more abundant under *N. sphaerocarpa* than under *R. soongorica*, whereas we found no differences in the abundance of predator arthropods between the two shrub species (Fig. 4).

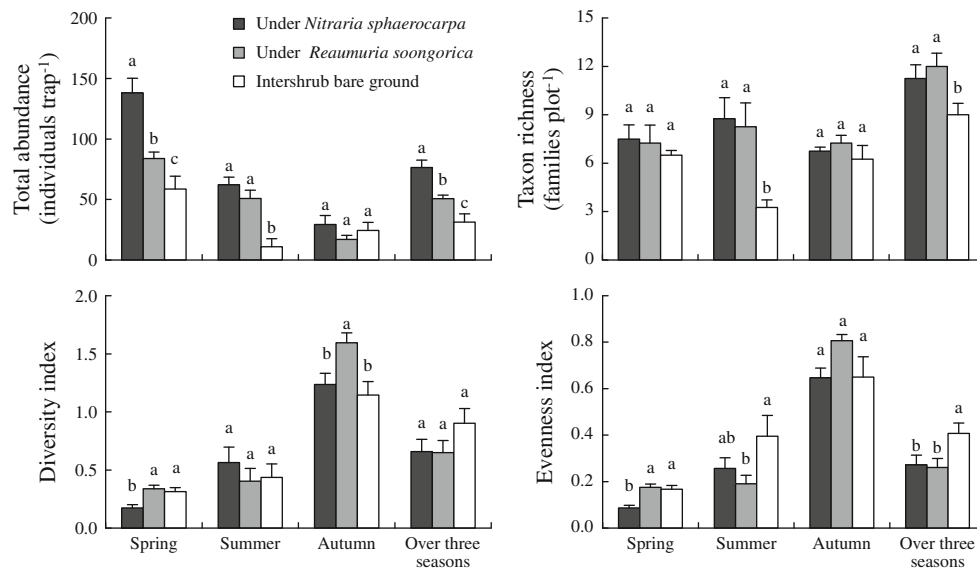


Fig. 3 The total abundance, taxon richness, diversity and evenness indices of ground-dwelling arthropods in the three microhabitat types (under *Nitraria sphaerocarpa*, under *Reaumuria soongorica* and intershrub bare habitat) in a Gobi desert. Means (\pm SE) with different

letters within each season indicate significant differences among microhabitats ($P < 0.05$ from one-way ANOVA followed by Tukey’s HSD tests)

Table 2 The Sørensen similarity index values for comparing community composition of ground-dwelling arthropods among microhabitat types within seasons

Microhabitat type	Under <i>Nitraria sphaerocarpa</i>	Under <i>Reaumuria soongorica</i>	Intershrub bare ground
Spring			
Under <i>Nitraria sphaerocarpa</i>	1	0.95	0.74
Under <i>Reaumuria soongorica</i>		1	0.80
Intershrub bare ground			1
Summer			
Under <i>Nitraria sphaerocarpa</i>	1	0.96	0.63
Under <i>Reaumuria soongorica</i>		1	0.59
Intershrub bare ground			1
Autumn			
Under <i>Nitraria sphaerocarpa</i>	1	0.93	0.93
Under <i>Reaumuria soongorica</i>		1	0.98
Intershrub bare ground			1
Across three seasons			
Under <i>Nitraria sphaerocarpa</i>	1	0.96	0.80
Under <i>Reaumuria soongorica</i>		1	0.85
Intershrub bare ground			1

There were significant interactions between microhabitat type and season on the abundance of predator, herbivore and decomposer arthropods (Table 1). Separate ANOVAs for each season showed that shrub presence effects on the abundance of predator arthropods were observed in all three seasons, whereas shrub presence effects on the abundance of decomposer arthropods were significant only in the spring (in *N. sphaerocarpa*) and

summer (Fig. 4). There was a significant difference between the two shrub species in the abundance of herbivore arthropods in the summer and autumn, but the significant difference between shrub species in the abundance of decomposer arthropods was found only in the spring. In all cases, greater numbers of herbivore and decomposer arthropods were captured under *N. sphaerocarpa* than under *R. soongorica* (Fig. 4).

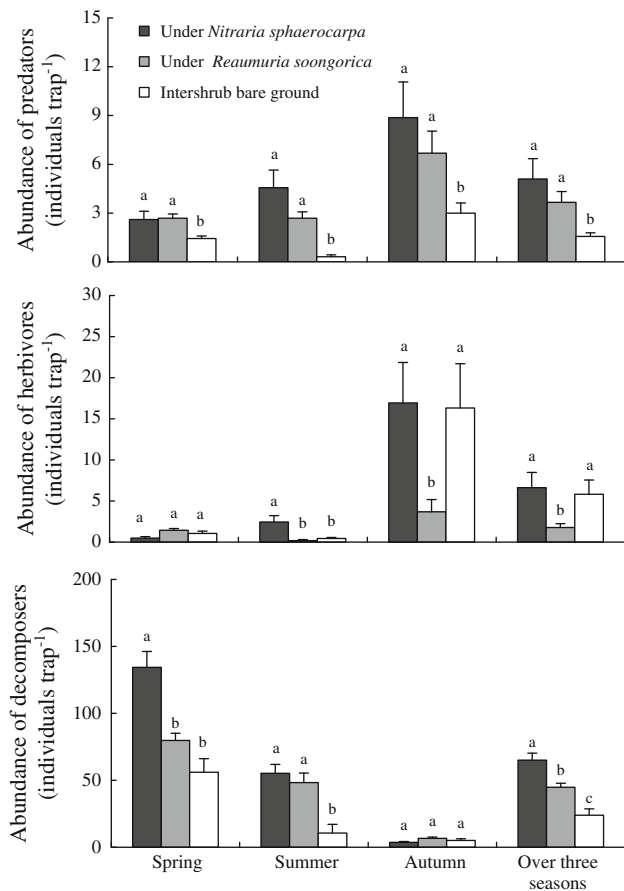


Fig. 4 The abundance of three trophic groups in the ground-dwelling arthropod community across the three microhabitat types (under *Nitraria sphaerocarpa*, under *Reaumuria soongorica* and intershrub bare habitat) in a Gobi desert. Means (\pm SE) with different letters within each season indicate significant differences among microhabitats ($P < 0.05$ from one-way ANOVA followed by Tukey's HSD tests)

Taxon-level responses to shrub presence and species identity

The influence of shrub presence and species identity on the distribution of ground-dwelling arthropods differed among families. The two-way ANOVA showed that microhabitat type had significant effects on the abundance of Carabidae, Curculionidae, Geotrupidae, Gnaphosidae, Karschiidae, Tenebrionidae and Thomisidae, but did not affect the abundance of Formicidae, Philodromidae and Tettigoniidae (Table 1). Averaged over the three seasons, the abundance of Carabidae, Gnaphosidae, Karschiidae, Tenebrionidae and Thomisidae was consistently much greater in the microhabitats under both shrubs than in the intershrub bare habitat (Fig. 5), indicating a positive response of these five families to shrub cover. The abundance of Curculionidae and Tenebrionidae was significantly greater under *N. sphaerocarpa* and under *R. soongorica*, whereas in contrast the

abundance of Geotrupidae was significantly lower under *N. sphaerocarpa* than under *R. soongorica* (Fig. 5). There were significant interactions between microhabitat type and season on the abundance of Carabidae, Curculionidae, Karschiidae, Tenebrionidae and Thomisidae (Table 1), indicating that the influence of microhabitat type on these five families varied across seasons.

Redundancy analysis

Redundancy analysis (RDA) was used to determine the relative importance of the measured environmental variables in the arthropod community composition in this Gobi desert (Fig. 6). The five environmental variables (ground temperature, soil moisture, coarse sand, fine sand and silt plus clay) together explained 57.8 % of the total variation in the data, with axes 1 and 2 explaining 34.4 and 19.9 % of the total variation, respectively. Partial RDA showed that different environmental variables differed in their influence on the community composition (Table 3). Of the five variables, the conditional effect of ground temperature was significant under the Monte Carlo permutation test ($P = 0.047$) and that of silt plus clay content was also marginally significant under the Monte Carlo permutation test ($P = 0.079$), whereas that of the remaining three variables was not significant under the Monte Carlo permutation test (in all cases $P > 0.05$). Of the total 57.8 % variation explained by the RDA, 21.3 % was explained by ground temperature, 18.2 % by silt plus clay content and the rest (18.3 %) by variables that were not significant under the Monte Carlo permutation test (Table 3), indicating that ground temperature and silt plus clay content were the most important explanatory variables.

Discussion

This study provides the first investigation into the influence of shrub presence and species identity on the distribution and diversity of ground-dwelling arthropod communities in a Gobi desert of northwestern China. Our results demonstrate that two dominant shrubs, *N. sphaerocarpa* and *R. soongorica*, in the Gobi desert play an important role in shaping the patterns of ground-dwelling arthropod composition and diversity, in accordance with our first hypothesis. The significantly greater abundance and species richness of ground-dwelling arthropods in the microhabitats under shrubs than in the intershrub bare habitats suggest that the presence of shrubs had a facilitative (i.e. positive) effect on recruitment of ground-dwelling arthropod populations and communities. This positive relationship between shrub vegetation and ground-dwelling arthropod community highlights the importance of shrubs

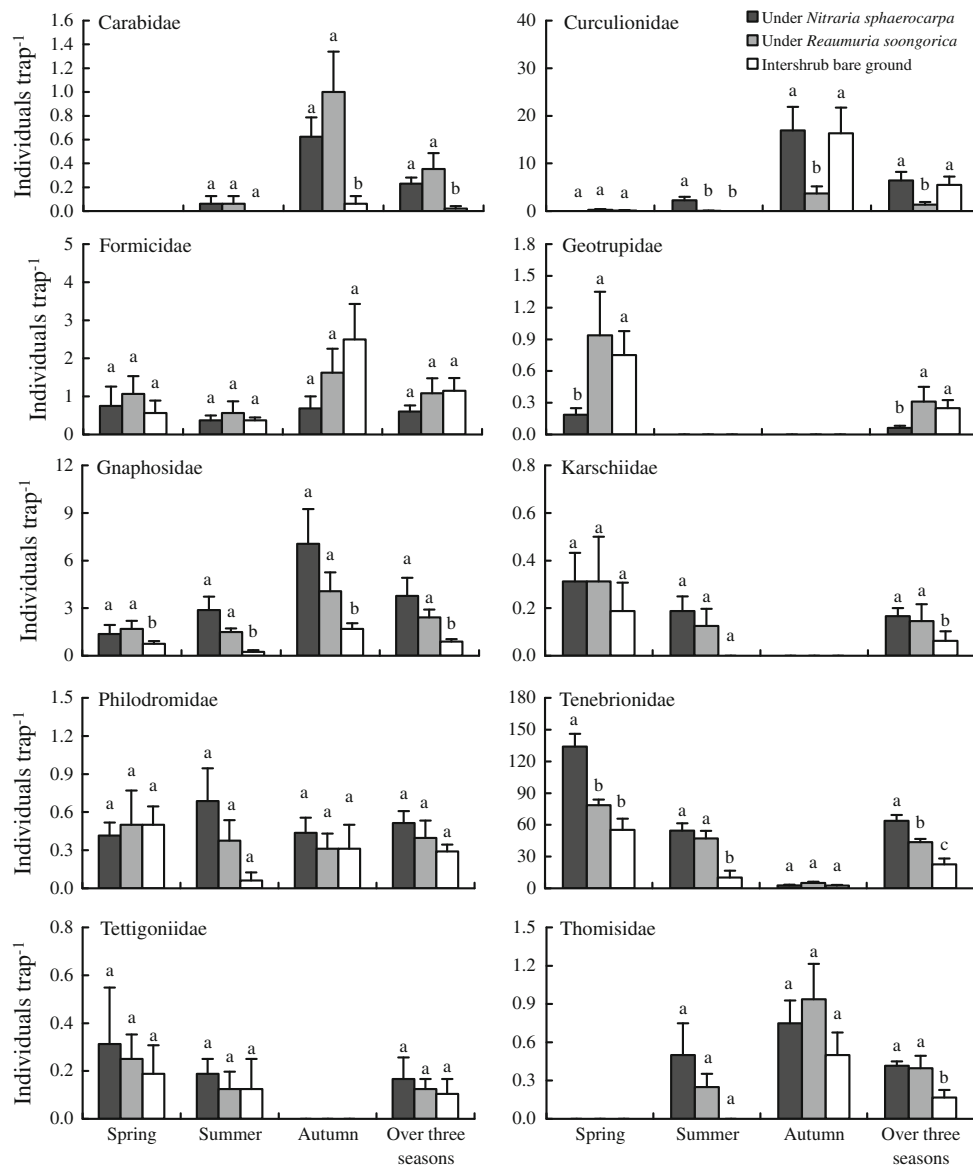


Fig. 5 The abundance of ten dominant families in the ground-dwelling arthropod community across the three microhabitat types (under *Nitraria sphaerocarpa*, under *Reaumuria soongorica* and intershrub bare habitat) in a Gobi desert. Means (\pm SE) with different

letters within each season indicate significant differences among microhabitats ($P < 0.05$ from one-way ANOVA followed by Tukey's HSD tests)

for the maintenance of arthropod assemblage diversity in the Gobi desert system. This result is consistent with studies from other shrubland ecosystems demonstrating a facilitative effect of shrub cover on the abundance, biomass and species richness of ground-dwelling beetles (Rogers et al. 1988; Stapp 1997; Mazía et al. 2006). Nevertheless, evidence of the significantly lower arthropod evenness index in the microhabitats under shrubs than in the intershrub bare habitats suggests that shrubs appeared to have reduced arthropod evenness, as a consequence of increased dominance by a few taxa. Thus, shrub-driven changes in ground-dwelling arthropod communities are associated

with changes in arthropod dominance, abundance and richness, with the consequences of increased arthropod abundance and richness and reduced arthropod evenness as we observed.

The observed positive effects of shrubs on ground-dwelling arthropods could be attributed to multiple ecological roles of shrubs as primary producers and providers of resources as well as important modulators of microhabitats (Shachak et al. 2008; Cushman et al. 2010; Gabay et al. 2012). With this study, at least four possible effect pathways allowed shrubs to alter profoundly the microenvironment and the availability of resources for ground-

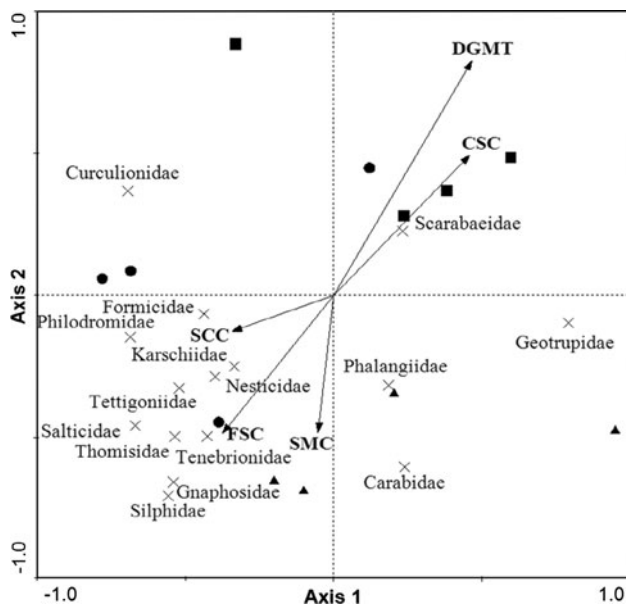


Fig. 6 RDA two-dimensional ordination diagram of the first two axes showing the relationship between the community composition of ground-dwelling arthropods and environmental variables. The arthropod families are represented by \times . Three microhabitat types are represented by circles (under *Nitraria sphaerocarpa*), triangles (under *Reaumuria soongorica*) and squares (intershrub bare habitat). Environmental variables (*SMC* soil moisture content, *DGMT* daily ground maximum temperature, *CSC* coarse sand content, *FSC* fine sand content, *SCC* silt plus clay content) were represented as arrows and the strength of their impact was directly proportional to the length of the arrow lines

dwelling arthropods. First, shrubs can have a shading effect, thereby reducing soil temperature extremes beneath their canopies, as indicated by our observations and other studies (Valiente-Banuet and Ezcurra 1991; Doblás-Miranda et al. 2009). Second, shrub canopies can intercept rainfall (Mauchamp and Janeau 1993; Li et al. 2008), thus allowing more rainwater to be stored in the soil beneath shrub canopies (Wang et al. 2011; as indicated by our observations). Third, the deposition of leaf litter and by trapping wind-blown litter and seeds from the open area around shrubs (Bullock and Moy 2004; Li 2008) may

provide essential food sources for herbivore and decomposer arthropods. These ecological functions combine to create a favorable microhabitat with relatively mild microclimates, more secure oviposition sites, high resource availability and shelter (Parmenter et al. 1989; Stapp 1997; Titus et al. 2002), thereby promoting the activity and colonization of ground-dwelling arthropods in areas under shrubs (Slobodchikoff 1983; Stapp 1997).

The two shrub species with contrasting plant and life-history characteristics differed in their impact on the distribution of ground-dwelling arthropods. Averaged over the three seasons, our data indicate that shrub species identity had a significant influence on the abundance of ground-dwelling arthropods, but did not affect the richness, diversity and evenness of ground-dwelling arthropods. These results suggest that arthropod abundance is more responsive than arthropod richness, diversity and evenness to the identity of the shrub species. Evidence that arthropods were more abundant under *N. sphaerocarpa* than under *R. soongorica* suggests that arthropods prefer *N. sphaerocarpa* more than *R. soongorica*, indicating that the *N. sphaerocarpa* community is more important than the *R. soongorica* community for the persistence of arthropod assemblages in the studied system. The large difference between the two shrub species in their influence on arthropod abundance could be simply explained by differences in resource quantity and quality that they provide (Wardle et al. 2004; Wilder et al. 2011). Both shrubs differ markedly in the following aspects that generally reflect the differences in resource quantity and quality of the two shrubs. First, an adult individual of *N. sphaerocarpa* is generally larger in size than that of *R. soongorica*. Larger sized plants may contribute more resources (leaf and litter) to herbivore and decomposer arthropods, and at the same time may also provide greater numbers of secure oviposition sites for female arthropods than smaller sized plants (Stapp 1997). Second, *N. sphaerocarpa* has a greater leaf production than does *R. soongorica*, and at the same time leaf nitrogen content is also significantly greater in *N. sphaerocarpa* than in *R. soongorica*. Research has

Table 3 Redundancy analysis (RDA) on the family abundance data for quantifying the conditional effects of the measured environmental variables on the arthropod community composition using forward selection with Monte Carlo permutation test

Variables	Inertia conditional effects	MCR (%)	F	P
Ground temperature (°C)	0.213	21.3	2.69	0.047
Soil moisture (%)	0.060	6.0	0.86	0.503
Coarse sand (%)	0.049	4.9	0.6	0.606
Fine sand (%)	0.074	7.4	0.89	0.451
Silt plus clay (%)	0.182	18.2	2.64	0.079
Total		57.8		

The inertia from the conditional effects is used to calculate the multivariate correlation ratio (MCR), representing the proportion of variation explained by the individual environmental variables

shown that leaf nitrogen content is an important indicator of leaf quality (de Sassi et al. 2012) and that leaf quality of host plants can have strong effects on the abundance and performance of insect herbivores (Barber and Marquis 2011). Third, both shrubs differed considerably in their phenological period characteristics. For example, *N. sphaerocarpa* germinates in mid April, blossoms in mid May, and fruits in June, whereas *R. soongorica* germinates in late April, blossoms in late July, and fruits in mid August. This phenological period contrast may reflect differences in growth patterns of the shrubs with regard to the seasonal dynamics of leaf biomass and quality. Thus, the large plant size, the high leaf production and the high leaf N content of the shrub *N. sphaerocarpa* may explain why *N. sphaerocarpa* is commonly preferred by most arthropods in our system.

Furthermore, we found evidence that the influence of shrub presence and species identity differed among trophic and taxonomic groups of ground arthropods, supporting our second hypothesis. For the three trophic groups under study, the abundance of both predator and decomposer arthropods was significantly greater under shrubs than in intershrub bare habitats, suggesting a consistent positive response of these two trophic groups to shrub cover. This result also suggests a positive relationship between shrubs and predator and decomposer arthropods. However, we found no evidence of a positive response between shrubs and herbivore arthropods, as herbivore arthropod abundance under *N. sphaerocarpa* was similar to that in the intershrub bare habitat while herbivore arthropod abundance under *R. soongorica* was significantly lower than that in the intershrub bare habitat. A possible explanation for the lack of a positive correlation between shrubs and herbivore arthropods may partly be due to potential predation effects (Wise 1985; Barber and Marquis 2011). In our study, the significantly greater number of predator arthropods under shrubs than in intershrub bare habitats may suggest a greater predator pressure in areas under shrubs than in shrub-free bare areas. In consequence, a greater number of herbivore arthropods would be consumed by predator arthropods in areas under shrubs than in shrub-free bare areas. However, whether predation is a key factor responsible for the lack of a positive correlation between shrubs and herbivore arthropods needs further verification. In addition, shrub species identity had a significant influence on the abundance of both herbivore and decomposer arthropods but not of predator arthropods. This suggests that herbivore and decomposer arthropods were more responsive than predator arthropods to the identity of the shrub species. Evidence that more herbivore and decomposer arthropods were captured in traps under *N. sphaerocarpa* than under *R. soongorica* suggests that these two trophic groups prefer *N. sphaerocarpa* more than

R. soongorica, highlighting that *N. sphaerocarpa* is more important than *R. soongorica* for persistence of the herbivore and decomposer arthropod communities.

For the ten dominant arthropod families under study, the abundance of Carabidae, Gnaphosidae, Karschiidae, Tenebrionidae and Thomisidae was consistently much greater under shrubs than in intershrub bare habitats. This suggests a consistent positive response of these five taxa to shrub cover and highlights the importance of shrubs on population persistence of these five taxa. In contrast, there were no differences in the abundance of Formicidae, Philodromidae and Tettigoniidae between the shrub microhabitats and the intershrub bare habitats, indicating that these three arthropod taxa are relatively insensitive to the identity of the microhabitat. A similar finding was reported by Peterson et al. (2001) that the abundance of ants (Formicidae) under shrubs was similar to that in shrub-free bare areas. These results suggest the power of using the abundance of Carabidae, Gnaphosidae, Karschiidae, Tenebrionidae and Thomisidae as indicators of shrub cover change. The two shrub species also differed in their influence on ten dominant arthropod families. Evidence that more arthropods of the two families Curculionidae and Tenebrionidae were captured under *N. sphaerocarpa* than under *R. soongorica* suggests that these two taxa prefer to use *N. sphaerocarpa*. In contrast, more arthropods in the family Geotrupidae were captured under *R. soongorica* than under *N. sphaerocarpa*, suggesting that *R. soongorica* is preferred by this arthropod taxa. However, we found no differences between the two shrub species in the abundance of Carabidae, Formicidae, Gnaphosidae, Karschiidae, Philodromidae, Tettigoniidae and Thomisidae, suggesting that these seven taxa were not significantly affected by the identity of the shrub species. Such family-specific habitat preferences provide evidence suggesting that a high diversity of shrub species is of great importance for the maintenance of a diverse arthropod community, supporting the general notation that there is a positive relationship between habitat diversity and biotic community diversity (Sylvain and Wall 2011; Rosin et al. 2012). Also, these results illustrate the power of using the abundance of Curculionidae, Tenebrionidae and Geotrupidae as indicators of natural or human-induced changes in shrub species composition. The large difference in the extent of response to shrub species identity between the three trophic groups and the ten dominant families can be explained by differences in their ecology and biology (Lövei and Sunderland 1996; Coleman et al. 2004; Nielsen et al. 2010).

Using redundancy analysis (RDA), we assessed the relative importance of the measured environmental factors in structuring ground-dwelling arthropod communities in the Gobi desert. RDA illustrates that the five environmental factors (i.e. ground temperature, soil moisture, coarse sand,

fine sand and silt plus clay content) together explained 57.8 % of the total variation in the arthropod community composition. This suggests that some other factors that are not considered in this study may also contribute to the unexplained variation. Partial RDA further indicates that factors that most strongly influenced the distribution and composition of ground-dwelling arthropods were ground temperature and soil texture, consistent with other studies suggesting that soil texture, soil moisture and ground temperature have important impacts, both directly and indirectly, on the distribution of ground-dwelling beetle communities (Slobodchikoff 1983; Stapp 1997; Antvogel and Bonn 2001; Ziesche and Roth 2008).

In conclusion, the current study considerably advances our understanding of the ecological roles of shrubs as drivers of ground-dwelling arthropod community composition and diversity patterns. Our results provide empirical evidence suggesting the positive relationship between the shrub communities and the arthropod communities and highlighting the importance of shrubs for the maintenance of invertebrate assemblages. Over the past several decades, prolonged overgrazing disturbances have caused extensive degradation of Gobi desert ecosystems in northwest China, resulting in significant reductions in the cover, biomass and species richness of shrub communities. This degradation is likely to have an adverse impact on the invertebrate fauna (Blight et al. 2011). Thus, the implementation of large-scale restoration programs for degraded Gobi desert ecosystems via livestock control and planting of native shrubs is the key for successful conservation of shrubland-associated invertebrate assemblage diversity. Our findings provide valuable information supporting the development of a regional conservation planning.

Acknowledgments We thank two anonymous referees for helpful comments on an earlier version of this manuscript. We also thank all technicians for assistance in the field. This work was supported by the grants 31170496 and 91025021 from the National Natural Science Foundation of China and the grant 41125002 from the National Science Foundation for Distinguished Young Scholars of China.

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