

Effect of desert shrubs on fine-scale spatial patterns of understory vegetation in a dry-land

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Abstract In arid and semiarid ecosystems, shrubs usually play an important role in determining vegetation pattern and landscape diversity. By exerting multiple effects on microhabitat, shrubs can modulate the performances, species assemblages, and spatial patterns of their understory plants. Both positive and negative interactions act simultaneously, and the balance between them shifts at different spatial locations. To better understand shrub–herb interaction and its possible mechanisms, we chose three common shrub species in a dry-land of Hexi desert region and examine their effects on microhabitat and understory vegetation among different locations. Results showed that the understory vegetation can benefit from the presence of *Calligonum mongolicum*, as a result of modified drought stresses, increased soil nutrients and more available seeds. However, understory vegetation

exhibited better performances at the peripheral location of *Nitraria sphaerocarpa* patches, which can be explained by the balance between resources improvement and seeds limitation. It has been also found that the higher salt contents (e.g., Na^+ , K^+ , Cl^- , and SO_4^{2-}) on vegetation patches beneath *Haloxylon ammodendron* may interfere with herbaceous performances and thus modified their spatial pattern. Our study revealed that the multiple effects of shrubs on microhabitat are species specific and at a fine scale, which may result in various fine-scale spatial patterns of vegetation in response to different shrub species.

Keywords Competition · Arid land · Facilitation · Shrub–herb interaction · Spatial pattern · Vegetation patch

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Introduction

Shrub–herb interactions are well documented and numerous interactive mechanisms have been demonstrated (Maestre et al. 2009; Segoli et al. 2012; Rayburn and Schupp 2013; Poulos et al. 2014). Negative interactions, such as competition, interference, and predation, have long been considered as the major processes structuring plant communities. However, the experimental and theoretical studies over the last few decades have indicated that the understory species can also benefit from woody plants, especially

in stressful environments (Bertness and Callaway 1994; Maron and Connors 1996; Maestre et al. 2003; Michalet et al. 2006; Callaway 2007; Giladi et al. 2007; Armas and Pugnaire 2009; He et al. 2012). This positive interaction was suggested to play a role in the survival, growth, and reproduction of understory vegetation (Callaway et al. 2002; Cavieres et al. 2006) and have important implications for species coexistence and community diversity (Bruno et al. 2003; Brooker et al. 2008).

Shrubs have multiple effects on their understory microhabitats (Ludwig et al. 2004; Reisman-Berman 2007; Kidron 2011; Wang et al. 2011). Soil moisture pattern beneath shrubs can be modulated by canopy interception, stem flow, and runoff (Mauchamp and Janeau 1993; Kidron and Gutschick 2013). Meanwhile, soil temperature and available radiation under shrubs will be changed as a result of canopy shading (Moro et al. 1997; Zhang and Zhao 2015). Shrubs were also reported to have the ability to improve soil properties beneath them, due to the capture of wind-dispersed particles, arthropod activities increasing, litter deposition, and nitrogen fixation (Davies et al. 2007; Wang et al. 2011; Travers and Eldridge 2012). Additionally, it has been showed that salt contents and animal grazing may be also reduced by the presence of mature shrubs (Veblen 2008; He et al. 2012). Under combined impacts from these effects, vegetation beneath shrubs can thus exhibit corresponding responses (Segoli et al. 2012). For understory plants, changes in some factors have positive effect, while others exert negative effect (Giladi et al. 2007, 2013). At the same time, the magnitude of shrub effects also varies among different factors, such as rainfall distribution, canopy identity, and patch size (Zhang et al. 2015; Zhang and Zhao 2015). Thus, integrated functions of multiple effects in response to changing environments can result in the final balance between facilitation and competition among plants, which should be considered in studies of plant–plant interaction.

In terrestrial ecosystems, woody plants are one of the most primary landscape modulators (Callaway 1995). By creating a spotted two-phase mosaic formed by vegetation patch and bare soil, shrubs have the ability to alter landscape diversity and species diversity (Maestre and Cortina 2005; Segoli et al. 2012). Many previous studies about the relationship between shrubs and their understory vegetation were conducted by comparing plant performances between shrub patch and open area.

However, it has been shown that microhabitats on vegetation patches are not completely independent from open areas; instead, they are arranged spatially in the form of continuous variable (Caballero et al. 2008; Giladi et al. 2013). Water condition, soil nutrient, light interception, grazing pressure, and seed rain are not constant among different positions beneath canopies, which might create corresponding changes in both facilitative and positive effects on their understory plants (Bertiller et al. 2009). But only recently have researchers considered the effect of nurse plants using microsites with a finer resolution than the commonly used canopy–interspace classification (Soliveres et al. 2015). For example, Li et al. (2010) found that the maximal vegetation productivity appeared at locations connecting shrub patch and open area using the distance to nurse plant as a continuous variable, resulting in the balance between light interception and drought ameliorating. Similar variations in the performance of understory vegetation were also reported by Pescador et al. (2014), in which multiple target species were measured. Woody–herbaceous interaction was spatially heterogeneous within and immediately adjacent to vegetation patch due to seed assembling, canopy shading, and water regime (Segoli et al. 2012). The improvement of soil attributes with proximity to the trunk of woody plants can also partially attributes to species richness and community composition across subcanopy microsites (Soliveres et al. 2015). The most recent study have also found that community assembly in a semiarid dwarf shrub land can be explained mainly by interspecific accumulations at fine scales (<30 cm), which suggested the positive interaction within plants as one of main drivers of vegetation patterns (Chacón-Labela et al. 2016). Therefore, it is critical to clarify the relationship between the effects of subcanopy positions and the responses of both microhabitats and understory plants at a fine scale in order to understand how overstory shrub influences vegetation pattern and community composition.

Our study was conducted at a dry-land of Hexi desert region in northwest China. Due to scattered vegetation and violent wind, this region has become one of major sources of dust-storm in Chinese inland. Here, shrub-dominated vegetation patches are the most important landscape modulator in stabilizing sand surface, reducing wind erosion and maintaining biological diversity (Zhang et al. 2015). The present study focused on the effect of shrubs on their surrounding microhabitats and understory vegetation.

We selected three most common shrub species in this region as research targets, including two native shrubs (*Calligonum mongolicum* and *Nitraria sphaerocarpa*) and a nonnative shrub species (*Haloxyton ammodendron*) introduced no more than four decades. During the experimental investigation and data analysis, the two-phase mosaic including vegetation patch and open area was classified as four different fine-scale locations, such as (a) core location under shrubs, (b) inner periphery of shrub patch, (c) outer periphery of shrub patch, and (d) open area at shrub interspaces. The overall objectives of our study were to explore (1) how the shrubs modulate microhabitat at a fine spatial scale from under-shrub site to open area, (2) whether the balance between facilitation and interference shows spatial heterogeneity at a fine scale, and (3) is the relationship between shrubs and understory vegetation species specific?

Materials and methods

Study area

The study area is located in the Linze Inland River Basin Research Stations, Chinese Academy of Sciences, one of Chinese Ecosystem Research Network Stations located at the southern edge of the Badain Jaran Desert (between 39°22'N and 39°23'N, and between 100°07'E and 100°08'E). The altitude is about 1380 m above sea level. The annual rainfall averages 116.8 mm; about 60 % of the total precipitation with low rainfall intensity is received during July–September (Zhao and Liu 2010). But the potential evaporation is about 2390 mm per year (1965–2015). The mean daily temperature is about 7.6 °C, with the lowest temperature (−27.3 °C) in January and the highest temperature (39.1 °C) in July. Due to multiple stresses, such as low precipitation, high evaporation, and violent wind, vegetation cover in our study area only ranges from 5 to 7 %.

Study species

Calligonum mongolicum (Turcz.), *Nitraria sphaerocarpa* (Maxim.) and *Haloxyton ammodendron* (Bunge.) are common perennial shrub species in our study site. They distribute widely on the flat desert, sand dune, and inter-dune lowland of desert at the periphery of oases, are important species for the formation of vegetation

landscape in this region. They belong to Polygonaceae, Zygophyllaceae, and Chenopodiaceae, respectively. Their growing season is generally from May to October. *C. mongolicum* and *H. ammodendron* are common erect shrubs, while *N. sphaerocarpa* is a dwarf shrub species (Table 1). In our study site, *C. mongolicum* and *N. sphaerocarpa* are mainly natural vegetation. Yet, in addition to a small amount of natural distribution, most *H. ammodendron* shrubs were introduced during 1980s and 1990s in last century. The common annual species in this region include *Bassia dasyphylla*, *Salsola collina*, *Chloris virgata*, *Agriophyllum squarrosum*, *Halogeton arachnoideus*, and *Corispermum lehmannianum*. Their growth periods are generally from June to September.

Sampling methods

In 2013, we randomly selected 20 shrubs of each species to study the shrubs' effect on abiotic environmental condition and understory vegetation. The distance between any two shrub individuals was no less than 10 m to insure the independence of the sample. All samples were selected within 4 km². On the basis of fine-scale locations under and around shrubs, four different subcanopy positions were defined, which were core location under shrubs (Core), inner periphery of shrub patch (I.P.), outer periphery of shrub patch (O.P.), and open area at shrub interspaces (Open). Core location is close to the base of shrubs or in the central area of shrub canopy's vertical projection. I.P. is an approximate circular ring extending from vertical projection periphery of shrub canopy to 50 cm inside the projection line. O.P. is a ring strip extending from vertical projection periphery of shrub canopy to 50 cm outside the projection line. Open area is located in the shrub interspaces extending from 4 to 10 m outside shrub patches.

Environmental measurements

To evaluate the effect of shrub species on microhabitats, we measured soil moisture and temperature, soil nutrition, salt concentration, and available photosynthetically active radiation (PAR) at different fine-scale locations.

Soil moisture, soil temperature, and PAR were measured in early August 2013. Soil moisture was measured once, while temperature and PAR were measured for four times among different days. We

collected cylindrical soil cores (5 cm diameter; 5–15 cm depth) from different fine-scale locations. The soil water content was determined gravimetrically by oven-dried for 48 h at 110 °C. Soil temperature in different locations under shrubs were measured at 10–15 cm depth below ground surface from 10:00 to 14:00 on clear days with the 6310 soil thermometer (Spectrum, Technologies, Inc., US). In each location of shrub samples, we measured PAR values under canopies with Field Scout Light Meters (Spectrum, Technologies, Inc., US) from 10:00 to 12:00 and from 14:00 to 16:00 on clear days. The probe was placed north–south direction, and the values were recorded at 5 cm above soil surface.

To measure soil nutrient and salt concentration, we randomly selected ten shrubs from the samples in each shrub species and collected three soil cores (5 cm diameter, 5–15 cm depth) from each fine-scale location in early August 2013. Three soil samples from the same location of each shrub were mixed and put into a plastic bag. Before chemical properties analysis in labs, all soil samples were air dried for 30 days and passed through a 2 mm sieve to remove plant fragments and stones. Soil organic C, total N, and total P were measured by the dichromate oxidation method (Kalembasa and Jenkinson 1973), the Kjeldahl digestion method (Jackson 1973), and molybdenum antimony-ascorbic acid colorimetric method (Olsen and Sommers Olsen 1982), respectively. Na^+ and K^+ were measured by the flame photometry method, Ca^{2+} was measured by the EDTA complex titration method, Cl^- was measured by the AgNO_3 titration method, and SO_4^{2-} was measured by the EDTA indirect titration method (Bao 1999).

Understory vegetation measurements

The plant measurements were carried out in late August 2013. The basic characteristics of selected shrubs ($N = 80$), including canopy size, shrub height, canopy depth (distance between top and bottom of canopy), and shrub biomass, were measured and recorded. Then we placed two plots ($30 \times 30 \text{ cm}^2$) in each location of a selected shrub to study shrub effect on the performances and spatial patterns of understory vegetation. All herbaceous plants in plots were counted and recorded for each species. The above-ground part of herbaceous plant in a plot was harvested to measure biomass using an electronic balance, after oven-drying

at 80 °C for 48 h. The data of two plots in each location of shrub sample were pooled before analyses.

Soil seed bank measurements

In mid-May 2013, we randomly collected three soil cores (5 cm diameter; 0–12 cm depth) in each fine-scale location of selected shrub samples. Three soil samples from the same location of each shrub were mixed and put into a cloth bag, placed for 15 days of direct exposure, then sieved through 2 mm mesh sieves to remove plant fragments and stones. We used the direct germination method of Thompson and Grime (1979) to assess the germinable seed species (Ma et al. 2010). In early June, soil samples were spread evenly in plastic germination trays (30 cm diameter) over a 10 cm layer sterilized sand that had been oven-dried at 140 °C for 48 h. Control trays with only sterilized sand ($N = 20$) were added into the experiment to detect potential contamination by wind-dispersed seeds (no seedling germinated in control trays). The trays were watered regularly every 2 days. Germinating seedlings were monitored weekly. All emerging seedlings were identified and then removed immediately in order to encourage maximum germination. In early August, we carefully turned over the soil samples to facilitate new germination (Roberts 1981). The whole observation lasted until mid-October.

Data analysis

A linear mixed-effects model ANOVA fitted by restricted maximum likelihood estimation was used to measure the effects of fine-scale locations on environmental variables and understory plant performances. In order to analyze the effect of shrubs on soil temperature and PAR, the mixed-effect models took the form: response variable \sim location \times time, random = ~ 1 shrub. Here, the soil temperature and PAR were included as the response variable, in which fine-scale locations were nested in sampling times, with location and time as fixed terms and shrub individual sample as random terms.

To analyze the effect of shrubs on soil properties and understory plant performances, the mixed-effect model took the form: response variable \sim location, random = ~ 1 shrub. Here, the soil nutrients, iron contents, biomass, density, richness, and seed number

were included as the response variable, with fine-scale location as fixed terms and shrub individual sample as random terms. The ‘lme’ function in nlme package in R was used to perform the mixed-effects model ANOVA (Galecki and Burzykowski 2013).

These fitted models were examined using graphical and numerical summarizes to assess assumptions of normally distributed and homogeneous residuals for both within-group and random errors (Pinheiro and Bates 2000). Where necessary, the ‘varIdent’ variance function structure was used as a weights argument in ‘lme’ function to allow different residuals for each level of factors and fit heteroscedastic models (Pinheiro and Bates 2000; Galecki and Burzykowski 2013). The ‘glht’ function in multcomp package in R was used to perform Tukey’s post hoc analysis at 0.05 level.

The relative interaction intensity (RII) was used to quantify responses of herbaceous species to shrub effect. We calculated the RII values based on above-ground biomass, plant density, and species richness respectively, as follows: $RII = (X_U - X_I)/(X_U + X_I)$. X_U and X_I are performances of plants growing beneath/around shrub canopies and in shrub interspaces, respectively. RII values were calculated both for each microhabitat beneath/around canopies (e.g., Core, I.P., O.P.) and for total microhabitats under shrub’s influence (the data of three microhabitats were pooled). RII is symmetrical around zero, with positive values indicating facilitation, negative values indicating competition, and zero values indicating no significant interaction. Using RII, we can directly compare plant performances among different shrub species. Mann–Whitney test was performed to compare RII values pairwise among different spatial locations, in which groups’ and blocks’ factors give fine-scale location and shrub individual sample, respectively.

Whittaker index, one of β -diversity indices, was used to qualitatively analyze the variation trend of

identities of plant communities beneath shrub canopy among different locations. We calculated the Whittaker indices based on species abundance of understory herbaceous, as follows: $\beta_W = (S_T/S_a) - 1$. S_T is the total number of herbaceous species within the sample composed of plots ($N = 80$) in each shrub species; S_a is the average species richness of the sample plots ($N = 20$) in each location. The Whittaker indices can clearly reflect the relationship between biodiversity and species abundance, which analyze their variation tendencies of β -diversity among different locations based on plant communities with the similar habitats.

Results

Characters of studied shrubs

Nitraria sphaerocarpa has larger canopies than *C. mongolicum* and *H. ammodendron*. *H. ammodendron* has the largest height, while *N. sphaerocarpa* was lowest. The mean of canopy depth was smallest for *N. sphaerocarpa*, but largest for *H. ammodendron*. The biomass density of shrub canopies decreased from *N. sphaerocarpa* to *C. mongolicum* (Table 1).

Soil physical and chemical properties

Soil moisture (Fig. 1; Table 2) and temperature (Table 3) varied significantly among different fine-scale locations. Under-shrub sites had higher soil moisture than shrub interspaces (Fig. 1). Soil temperature decreased significantly from core location under shrubs to open area in shrub interspaces. There is no significant interactive effect between spatial location and sampling period for all shrub species (Table 3). Shrubs also have significant effects on soil nutrients among different locations (Table 2). The content of soil

Table 1 Statistic parameters of the shrub samples

| Shrub species | <i>N</i> | Canopy length (m) | Canopy width (m) | Canopy height (m) | Canopy depth (m) | Canopy biomass (g m ⁻²) |
|------------------------|----------|---------------------------|---------------------------|---------------------------|---------------------------|-------------------------------------|
| <i>C. mongolicum</i> | 20 | 1.86 ± 0.227 ^a | 1.54 ± 0.209 ^a | 1.50 ± 0.195 ^b | 1.13 ± 0.173 ^b | 711.9 ± 154.15 ^a |
| <i>N. sphaerocarpa</i> | 20 | 3.95 ± 0.650 ^b | 3.58 ± 0.719 ^b | 0.50 ± 0.083 ^a | 0.46 ± 0.074 ^a | 1103.5 ± 328.67 ^b |
| <i>H. ammodendron</i> | 20 | 1.83 ± 0.266 ^a | 1.64 ± 0.195 ^a | 1.86 ± 0.304 ^c | 1.31 ± 0.291 ^b | 828.1 ± 301.9 ^a |

Data are mean ± SD. Letters (a, b, c) show Tukey’s post hoc analysis between different shrub species with ANOVA, means with the same letter are not significantly different at $P > 0.05$ level

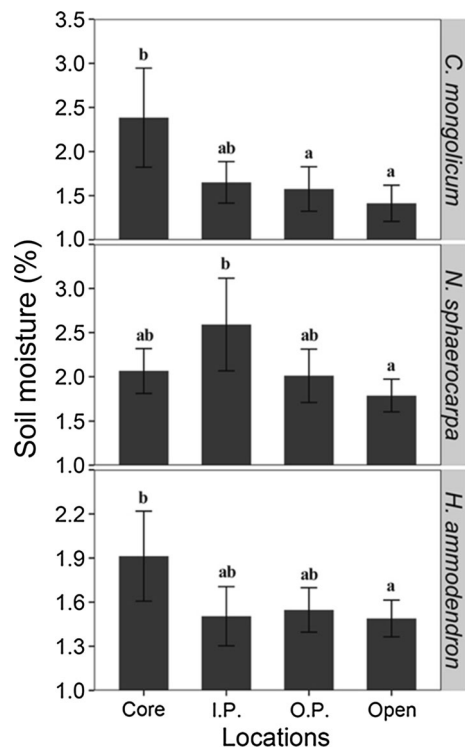


Fig. 1 Soil moisture (%) among different patch locations. Letters show Tukey's post hoc multiple comparisons of the data between locations in each shrub species with mixed models ANOVA, means with the same letter are not significantly different at $P > 0.05$ level. Data are mean \pm SE. $N = 20$

organic carbon significantly decreased from core location to open area (Table 4). The total nitrogen and phosphorus contents also showed similar decreases for *C. mongolicum*, *N. sphaerocarpa*, and *H. ammodendron* (Table 4), although some variations were not significant (Tables 2, 4). Mixed models ANOVA showed that *C. mongolicum* and *N. sphaerocarpa* have no significant effect on salt contents among different locations at a fine scale (Table 2). On the contrary, K^+ , Na^+ , Cl^- , and SO_4^{2-} in the soil can be influenced significantly by the presence of *H. ammodendron* shrubs (Table 2), which increased from the open area in shrub interspaces to core location under shrubs (Fig. 2).

Light conditions

The available PAR under canopies varied significantly among different spatial locations for all shrub species

(Table 3). For *C. mongolicum* and *H. ammodendron*, the lowest PAR values were found in core location under shrubs, while PAR did not vary significant between core location and inner periphery of *N. sphaerocarpa* patches (Fig. 3).

Seed abundance

Seed abundance in the soil varied significantly among fine-scale locations (Table 2). Seed abundance decreased gradually from core location to open area for *C. mongolicum*, while increased for *H. ammodendron* (Fig. 4). For *N. sphaerocarpa*, seed abundance was largest at open area and outer periphery of patches, while the lowest value appears at core location (Fig. 4).

Herbaceous performances

Above-ground biomass, individual density and species richness of herbaceous plants showed remarkable fine-scale spatial patterns (Table 2). These change trends in vegetation patterns also differed among overstory shrub species (Figs. 5, 6). At core locations under *C. mongolicum*, herbaceous species performed better than at open area (Figs. 5, 6). For *N. sphaerocarpa*, the above-ground biomass was lowest in plots under canopies, but highest at outer periphery location of shrub patches (Fig. 5). Meanwhile, the herbaceous density and richness at both inner and outer periphery were larger than both core location and open area (Fig. 6). Similarly, the core location under *H. ammodendron* canopies negatively affects the performances of their understory vegetation (Figs. 5, 6).

RII values

The RII values of biomass and richness decreased from core location to outer periphery of *C. mongolicum* patches, and the net positive shrub effects significantly shifted to neutral ones (Fig. 7). Under *N. sphaerocarpa* canopy, however, the positive effects appeared at outer periphery and shifted significantly into negative effect at core location (Fig. 7). Similarly, *H. ammodendron* exerted significant negative effect on herbaceous plants at core location, while showed neutral effect at periphery sites of patches (Fig. 7).

Table 2 Results of mixed models ANOVA showing the effects of spatial location on SWC, soil nutrients, iron concentration, and understory plant performances

| Variables | <i>C. mongolicum</i> | | <i>N. sphaerocarpa</i> | | <i>H. ammodendron</i> | |
|---|----------------------|------------------|------------------------|------------------|-----------------------|------------------|
| | <i>F</i> | <i>P</i> | <i>F</i> | <i>P</i> | <i>F</i> | <i>P</i> |
| SWC (%) | 4.278 | 0.009 | 3.793 | 0.015 | 2.193 | 0.099 |
| SOC (g kg ⁻¹) | 7.873 | <0.001 | 7.540 | <0.001 | 14.554 | <0.001 |
| TN (g kg ⁻¹) | 6.412 | <0.001 | 7.534 | <0.001 | 1.635 | 0.205 |
| TP (g kg ⁻¹) | 11.816 | <0.001 | 1.583 | 0.217 | 3.773 | 0.022 |
| Na ⁺ (c mol kg ⁻¹) | 1.164 | 0.342 | 0.423 | 0.738 | 36.313 | <0.001 |
| K ⁺ (c mol kg ⁻¹) | 2.266 | 0.104 | 1.656 | 0.200 | 3.983 | 0.018 |
| Ca ²⁺ (c mol kg ⁻¹) | 0.473 | 0.703 | 2.206 | 0.110 | 2.560 | 0.076 |
| Cl ⁻ (c mol kg ⁻¹) | 2.575 | 0.075 | 0.892 | 0.455 | 5.094 | 0.006 |
| SO ₄ ²⁻ (c mol kg ⁻¹) | 1.724 | 0.186 | 1.172 | 0.339 | 3.842 | 0.021 |
| Biomass (g m ⁻²) | 15.092 | <0.001 | 23.970 | <0.001 | 25.668 | <0.001 |
| Density (m ⁻²) | 10.641 | <0.001 | 10.530 | <0.001 | 3.910 | 0.013 |
| Richness (m ⁻²) | 6.470 | <0.001 | 14.636 | <0.001 | 7.201 | <0.001 |
| Seeds (m ⁻³) | 11.332 | <0.001 | 28.743 | <0.001 | 5.022 | 0.007 |

SWC soil water content, SOC soil organic content, TN total N content, TP total P content. *P* values at < 0.05 level are in bold. In mixed models ANOVA, SWC, biomass, density, richness, and seeds have three numerator and 57 denominator degrees of freedom; SOC, TN, TP, Na⁺, K⁺, Ca²⁺, Cl⁻, and SO₄²⁻ have three numerator and 27 denominator degrees of freedom

Table 3 Results of mixed models ANOVA showing the effects of spatial location and sampling period on soil temperature and PAR

| Variables | Factors | <i>C. mongolicum</i> | | <i>N. sphaerocarpa</i> | | <i>H. ammodendron</i> | |
|---|------------------------|----------------------|------------------|------------------------|------------------|-----------------------|------------------|
| | | <i>F</i> | <i>P</i> | <i>F</i> | <i>P</i> | <i>F</i> | <i>P</i> |
| Soil temperature (°C) | L _{3,108} | 5.437 | 0.002 | 5.393 | 0.002 | 2.996 | 0.034 |
| | T _{3,36} | 1.760 | 0.172 | 2.593 | 0.068 | 1.595 | 0.208 |
| | L × T _{9,108} | 1.253 | 0.272 | 1.352 | 0.219 | 0.797 | 0.619 |
| PAR (μmol m ⁻² s ⁻¹) | L _{3,108} | 60.256 | <0.001 | 159.282 | <0.001 | 92.521 | <0.001 |
| | T _{3,36} | 2.768 | 0.056 | 1.978 | 0.135 | 2.759 | 0.058 |
| | L × T _{9,108} | 0.877 | 0.549 | 0.552 | 0.834 | 1.325 | 0.233 |

P values at < 0.05 level are in bold. For fixed factors, *L* means fine-scale location and *T* means sampling times. Two subscripts in factor terms show numerator and denominator degrees of freedom in mixed models, respectively

7 β-diversity indices

As showed in Fig. 8, the variation of β-diversity from core location to open area was species specific. *W_β* index declined with increasing distance from the core site for *C. mongolicum*, but increased for *H. ammodendron*. However, for *N. sphaerocarpa*, *W_β* decreased from core location to outer periphery of shrub patch, but increased again from outer periphery to open area.

Discussion

In arid and semiarid ecosystems, the net effects of woody plant on their understory species usually shift between facilitation and interference depending on environmental conditions (Reisman-Berman 2007; Bertiller et al. 2009). The present study on shrub–herbs interactions in a dry-land aimed at clarifying whether the balance between facilitation and interference shows spatial pattern under a canopy, and

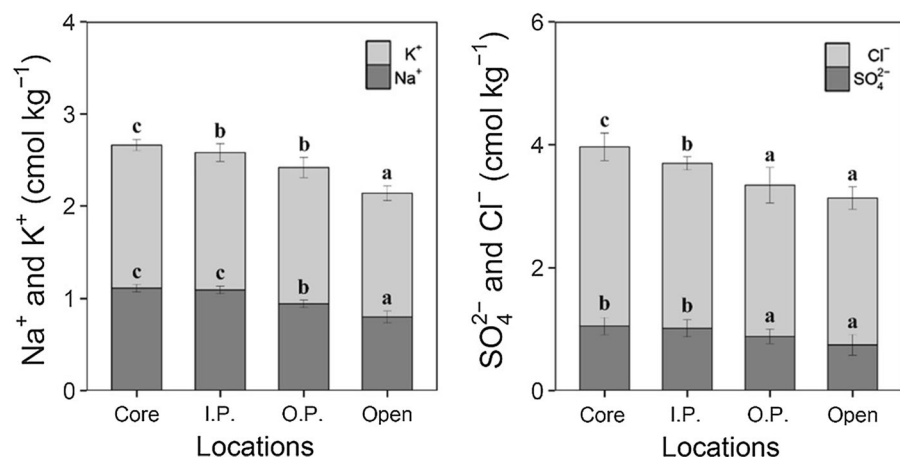
Table 4 Soil nutrient contents (g kg^{-1}) among different patch locations

| Species | Locations | SOC (g kg^{-1}) | TN (g kg^{-1}) | TP (g kg^{-1}) |
|------------------------|-----------|----------------------------|---------------------------|---------------------------|
| <i>C. mongolicum</i> | Core | 1.49 ± 0.289^c | 0.20 ± 0.033^b | 0.60 ± 0.082^c |
| | I. P. | 1.28 ± 0.320^{bc} | 0.15 ± 0.035^a | 0.55 ± 0.030^{bc} |
| | O. P. | 1.13 ± 0.311^{ab} | 0.14 ± 0.049^a | 0.51 ± 0.045^{ab} |
| | Open | 0.94 ± 0.229^a | 0.18 ± 0.048^{ab} | 0.47 ± 0.048^a |
| <i>N. sphaerocarpa</i> | Core | 2.03 ± 0.200^c | 0.25 ± 0.028^b | 0.41 ± 0.012^a |
| | I. P. | 1.87 ± 0.439^c | 0.25 ± 0.063^b | 0.42 ± 0.051^a |
| | O. P. | 1.37 ± 0.179^b | 0.20 ± 0.052^{ab} | 0.44 ± 0.055^a |
| | Open | 1.03 ± 0.118^a | 0.19 ± 0.040^a | 0.48 ± 0.123^a |
| <i>H. ammodendron</i> | Core | 1.68 ± 0.276^c | 0.17 ± 0.065^a | 0.44 ± 0.014^b |
| | I. P. | 1.25 ± 0.157^b | 0.17 ± 0.040^a | 0.43 ± 0.016^b |
| | O. P. | 1.19 ± 0.135^{ab} | 0.21 ± 0.074^a | 0.43 ± 0.017^{ab} |
| | Open | 1.00 ± 0.226^a | 0.22 ± 0.072^a | 0.41 ± 0.023^a |

SOC soil organic carbon, TN total N content, TP total P content. Data are mean \pm SD. Letters (a, b, c) show Tukey's post hoc multiple comparisons of the data between locations in each shrub species with mixed models ANOVA, means with the same letter are not significantly different at $P > 0.05$ level. $N = 10$

Fig. 2 The concentration of salt iron (cmol kg^{-1}) in the soil among different patch locations of *H.*

ammodendron. Letters show Tukey's post hoc analysis between different locations in the same shrub species with mixed models ANOVA, means with the same letter are not significantly different at $P > 0.05$ level. Data are mean \pm SE. $N = 10$



exploring its potential relationship with spatial heterogeneity of available resources and environmental severity. Our data provide evidence that overstory shrubs can affect microhabitats at a fine scale, which result in the spatially heterogeneous performances of herbaceous plants under canopies. Meanwhile, these effects by shrubs are species specific.

Microhabitats and herbaceous performances

The relative high soil moisture beneath shrubs was in agreement with other studies reported from arid and

semiarid ecosystems (Armas et al. 2012; Kidron and Gutschick 2013). A number of researches have already proven that understory vegetation could benefit from better water conditions (Maestre et al. 2008; Li et al. 2010). By shading the ground surface from direct solar radiation, shrubs have the ability to decrease potential evaporation and soil temperature (Kidron and Gutschick 2013; Zhang and Zhao 2015), which may contribute to the higher moisture at under-shrub sites. As noted by Armas and Pugnaire (2005), the high moisture can also result from better physical conditions due to the accumulation of soil organic matter under shrubs. Hydraulic lift of woody plants may be another possible explanation (Armas et al. 2012). Yet,

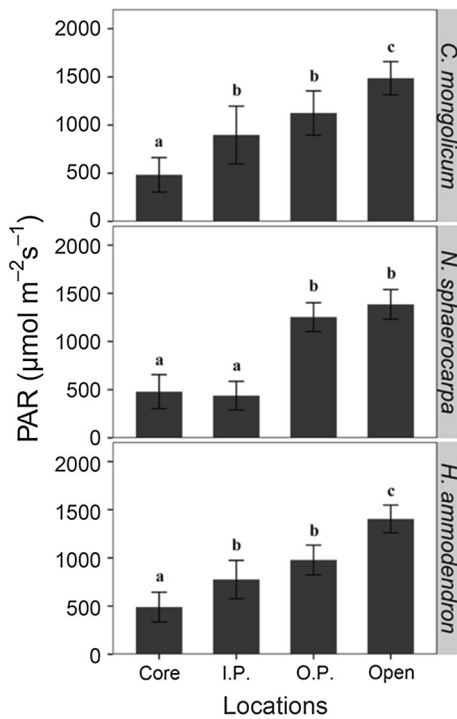


Fig. 3 The available photosynthetically active radiation ($\mu\text{mol m}^{-2} \text{s}^{-1}$) at 5 cm above soil surface among different patch locations. Letters show Tukey’s post hoc analysis between different locations in the same shrub species with models ANOVA, means with the same letter are not significantly different at $P > 0.05$ level. Data are mean \pm SE. $N = 40$

we do not find any related report about this effect in our studied shrub species.

It should be noted that results of soil moisture in the present study probably have some limitations, because it was measured only once and lack of replications in sampling periods (although we have 20 plots in each location). Results of our two previous studies (Zhang and Zhao 2015; Zhang et al. 2015) in the same region have indicated that *C. mongolicum* and *N. sphaerocarpa* shrubs (which have similar canopy/patch size with the present study) could improve soil moisture conditions under their canopies. Meanwhile, Li et al. (2010) have also reported a similar positive effect by *H. ammodendron* shrubs on soil moisture in the understory. Therefore, we can conclude safely that the presence of these three shrub species will facilitate soil moisture improvement on their patches. However, due to temporally unpredictable rainfall in hot summer, the relative values of soil moisture among core location,

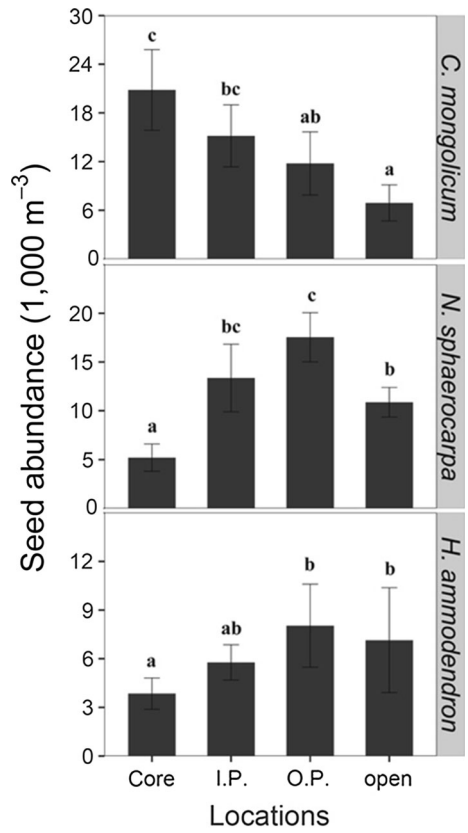


Fig. 4 Seed abundance (1000 m^{-3}) showed from soil seed bank among different patch locations. Letters show Tukey’s post hoc multiple comparisons of the data between locations in each shrub species with mixed models ANOVA, means with the same letter are not significantly different at $P > 0.05$ level. Data are mean \pm SE. $N = 20$

inner periphery, and outer periphery under canopy might be somewhat different from our results.

Overstory vegetation can also change light conditions, which in turn modulates plant growth and species assemblage of understory vegetation (Reisman-Berman 2007; Zhang et al. 2015). For example, shrub canopies can facilitate understory plants via protecting them from fatal photoinhibition (Moro et al. 1997). However, heavy shading by canopies was also reported to limit photosynthetic activity of understory species (Hautier et al. 2009), which impair their establishment, growth, and reproduction (Schramm and Ehrenfeld 2010; Holmgren et al. 2012). It has been shown that the facilitation effects by arid land shrubs are in some cases more important for nonresource factors, such as light and temperature, than water resources, which, however, may be

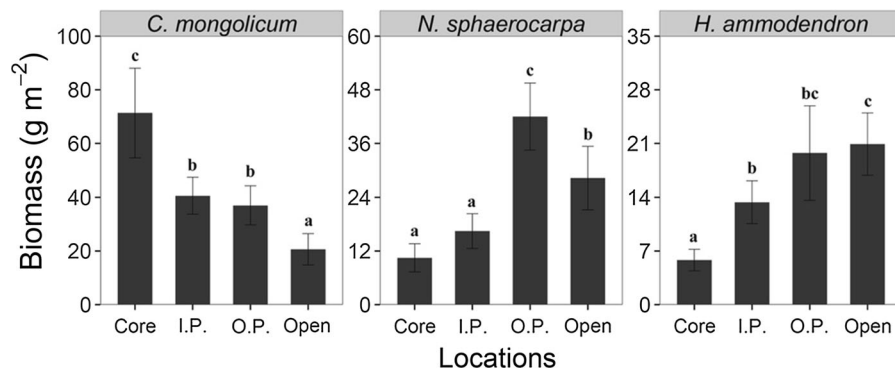
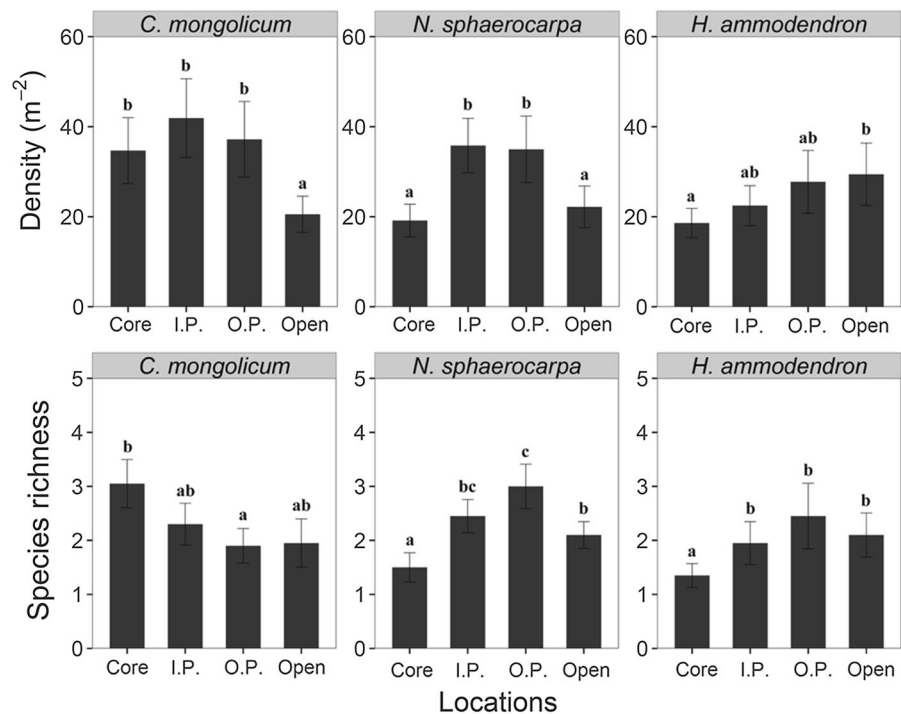


Fig. 5 Biomass (g m^{-2}) of herbaceous plants among different patch locations. Letters show Tukey's post hoc multiple comparisons of the data between locations in each shrub species

with mixed models ANOVA, means with the *same letter* are not significantly different at $P > 0.05$ level. Data are mean \pm SE. $N = 20$

Fig. 6 Density and richness of herbaceous plants among different patch locations. Letters show Tukey's post hoc analysis between different fine-scale locations with mixed models ANOVA, means with the *same letter* are not significantly different at $P > 0.05$ level. Data are mean \pm SE. $N = 20$



suppressed due to competition under severe drought conditions (Jankju 2013). Meanwhile, changes to soil temperature and moisture through shading have the potential to influence the density of seedling germinating from the seed bank (Weedon and Facelli 2008). Therefore, the variation of PAR due to canopy shading in our study probably generates a spatial heterogeneity of microhabitats beneath shrubs, which is likely to modulate the relative intensity of

facilitation and interference between shrubs and herbaceous plants at a fine scale.

Shrubs can significantly improve soil nutrient contents, such as organic C, total N, and total P, in our study site. Similar results have been reported in some other ecosystems (Turner and Knapp 1996; Cavieres et al. 2007; Wang et al. 2011). Following water condition in dry-land, nutrients are considered to be the second limiting factor for plant growth. But it

Fig. 7 RII values of the biomass, density and richness among different shrub species and among different microhabitats. Letters show pairwise comparison between different habitats for each shrub species with Mann–Whitney test; means with the same letter are not significantly different at 0.05 levels. Significances of RII were analyzed with one-sample Wilcoxon signed-rank test; **represents RII significantly different from zero at $P < 0.01$; * represents significant at $0.01 < P < 0.05$; *n.s.* not significant at 0.05 levels. Data are mean \pm SE. $N = 20$

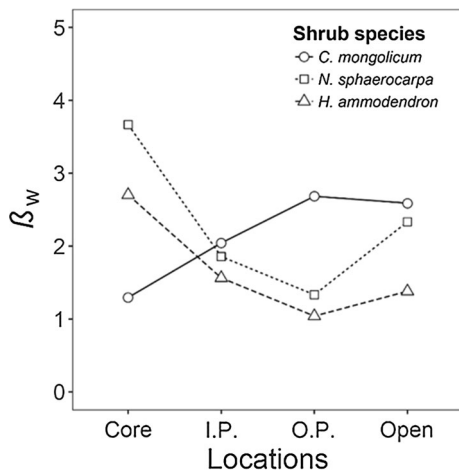
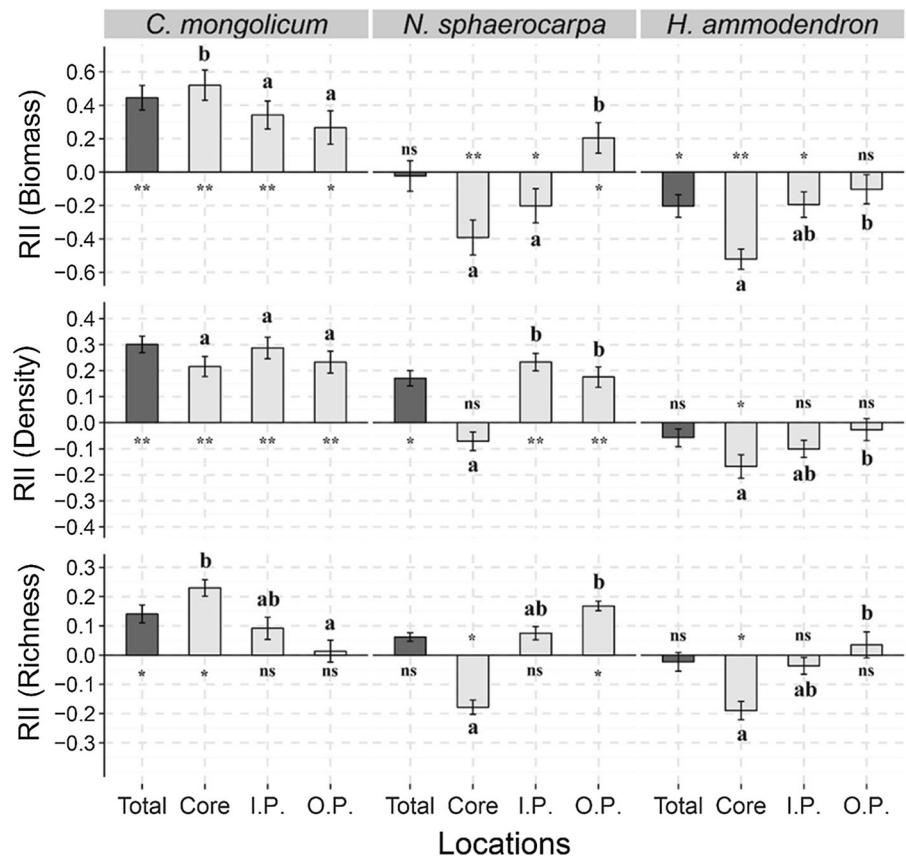


Fig. 8 Whittaker β -diversity indices (β_w) among fine-scale locations in each shrub species

has been proven that the nutrient accumulation beneath shrubs has positive effect on their neighbor plants (Walker et al. 2001). It was also reported that the improved soil properties can promote biomass

production on shrub island (Turner and Knapp 1996); Soliveres et al. (2015) even found that nurse effects are mostly unrelated to prevailing environmental conditions in their study sites, but are only partially driven by effects of soil properties.

However, it is important to note that soil salt contents can also be changed by the presence of *H. ammodendron*. In our study site, the core location under *H. ammodendron* has higher salt concentration (e.g. Na^+ , K^+ , Cl^- , and SO_4^{2-}), compared with shrub interspaces. It has been shown that high salt concentrations in the environment can inhibit plant growth, due to possible osmotic stress, nutritional imbalance, or ion toxicity (Munns and Tester 2008). Therefore, by changing soil salinity, *H. ammodendron* can modulate the environmental stress at a fine scale under the canopy, which possibly contributes to the spatial pattern of understory vegetation. A similarly lower biomass production at core location under *H. ammodendron* was also reported by Li et al. (2010) in Gurbantunggut Desert. They suggested that vegetation

patterns beneath *H. ammodendron* may be due to the balance between modified drought stress and increased above-ground competition. But our data indicated that salt accumulation under canopies may also play a role. This phenomenon of changing plant–plant interaction due to indirectly biochemical processes is not rare in communities. As reported by Arroyo et al. (2015), an allelopathic dwarf shrub may have complex facilitative and interferential effects on subcanopy diversity and species assemblage. Although this shrub acted as a diversity repellers, there are more perennial grass species in the local neighborhood than expectation, suggesting some tolerance of subcanopy species to its “chemical neighbor” (Arroyo et al. 2015).

Soil seed bank

The spatial pattern of soil seeds beneath shrubs may also play a role in determining vegetation pattern and community assemblage (Eccles et al. 1999). Similar to abiotic environmental factors, the soil seed bank also exhibits an obvious spatial pattern on vegetation patches. Results showed that *C. mongolicum* has higher seed density in core location compared to open area, which concurs with the spatial pattern of subcanopy density in line with the finding of Facelli and Temby (2002). This may be as a result of better seed retention or higher seed production under shrubs. By increasing surface roughness, the accumulation of leaf litter can trap more seeds beneath canopy (Flores and Jurado 2003). Additionally, the greater biomass of herbaceous layer may also result in the higher seed production, which in turn has positive effect on herbaceous performances.

Although *H. ammodendron* has similar canopy structure as *C. mongolicum* shrubs, it shows a totally opposite effects on spatial pattern of seed density. We suspect that it may be related to the formation of physical crust on their patches, which is likely to hinder the vertical movement of seeds in soil, and thus negatively affect seed abundance. *N. sphaerocarpa* has the highest seed abundance at the periphery of shrub patches, which is different from *C. mongolicum*. Similar spatial pattern of seeds was also reported in other dry-land (Giladi et al. 2007). As suggested by Giladi et al. (2013), the low canopy of dwarf shrubs can function as a barrier to block seed movement toward the core location and function simultaneously as a trap to accumulate seeds at the

periphery site of shrub patches. Therefore, the net effect of shrubs on spatial pattern of seed abundance may be species specific and determined by canopy structures.

Spatial pattern of understory vegetation

By separating different mechanisms of plant–plant interaction, Weedon and Facelli (2008) suggested that shrub-understory interactions can be mediated via more than one limiting resource or condition with the result depending on the balance between them. Similarly, our results also demonstrated that shrubs could exert multiple influences on microhabitats, such as water, temperature, light, nutrient, and salt contents. Increases in some environmental factors are sometimes followed by decreases in some of others (Malkinson and Tielbörger 2010). In our study, for example, soil moisture and nutrient improvements with proximity to core site of shrub patch were accompanied by decreases in available light and soil temperature. These complex variations may generate a new two-phase mosaic habitat with multiple resource and stress layers (Shachak et al. 2008), and thus determine the net result of shrub–herbs interactions among different locations.

In evaluating relationships between shrubs and their understory plants, many traditional researches commonly use the canopy-open classification. However, the spatial pattern of understory vegetation richness, density, and productivity in our study indicates that shrub–herbs interactions actually shift at a much finer scale. Although traditional sampling method has greater effectiveness in describing plant–plant relationship, it might overlook some important information (Fig. 7). For example, the periphery of *N. sphaerocarpa* patch has the better plant performances than both core and open area. Meanwhile, species richness and vegetation productivity of plots beneath *C. mongolicum* declined from core location to periphery site, but enhanced at *H. ammodendron* patches. Some recent studies have also reported similar fine-scale variations (Li et al. 2010; Giladi et al. 2013) and noticed its importance for understanding ecosystem functioning in arid land (Segoli et al. 2012).

Although the spatial pattern of vegetation has been proven to be mainly determined by the heterogeneity of microhabitats beneath shrubs or trees, the possible effect of plant–plant interaction

among herbaceous species could not be ignored either. As reported by Amat et al. (2015), changing effects on the performance of a target plant can result from different subcanopy locations, which, however, may be also caused by indirect interactions with other species beneath shrub canopy. Other findings in shrub–herbaceous interaction have shown that the balance between positive and negative effects are density-dependent, rather than driven by the variation in only abiotic factor across subcanopy locations (Dickie et al. 2005). In the latter study, facilitative effects are reported to prevail in microhabitats with low plant density under shrubs, while high density of understory plants are more favorable for competition among them.

Our results suggest that the effect of shrubs on fine-scale spatial pattern of understory vegetation is species specific, which is probably related to different canopy structures and physiological processes among shrub species. However, many studies have proven that the direction and magnitude of plant–plant interactions was closely related to ontogeny traits of different understory species (Sthultz et al. 2007; Armas and Pugnaire 2009). It was also reported that adaptive strategies (e.g., stress tolerance and competitive ability) of herbaceous species might determine their net relationships with overstory plants among stressful environments (He et al. 2012). Additionally, the height of woody plants was also considered to be important factors potentially mediating their relationship with understory species at a fine scale (Moustakas et al. 2013). Therefore, more investigations about species-specific variations in spatial pattern of understory vegetation are needed, which may contribute to predict the plant–plant interaction in communities and the vegetation pattern under changing environments.

Additionally, *H. ammodendron* is the most extensively introduced sand-fixing plants in Hexi desert region, which has been replacing native shrubs (e.g., *C. mongolicum* and *N. sphaerocarpa*) as the dominant species in shrub land communities. As shown in our results, *H. ammodendron* shrubs can change subcanopy soil texture and salt content, and interfere with seed accumulation, individual growth, and spatial pattern of their understory plants. It may produce some unpredictable impacts on vegetation composition and community stability in the long run.

Conclusion

In arid lands, water is always considered as the major factor in regulating plant–plant interactions (Franco and Nobel 1988; Callaway 1995; Kidron and Gutschick 2013). But our present study demonstrated that other environmental factors (e.g., temperature, nutrients, salt contents, and available light) can also play important roles. These combining effects of shrubs determine their net relationships with understory vegetation. The variation in microhabitat shows a gradual shift from under-shrub sites to shrub interspaces, which thus results in a fine-scale spatial pattern of understory vegetation. Although it has been proven that shrubs in stressful environment commonly have positive effect on their understory species (Bruno et al. 2003; Brooker et al. 2008; Xu et al. 2010), the present study indicated that the effect of shrubs is species specific according to different morphological characteristics and physiological processes among shrub species. By studying the spatial pattern of understory vegetation, we can better understand the possible mechanisms underlying the shrub–herbs interaction and evaluate the importance of different shrub species on the vegetation process in communities.

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