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Effects of *Juniperus sabina* coverage on plant community structure in semiarid areas of China

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Abstract
Plant interactions are one of the fundamental processes shaping the structure and function of plant communities and help create species diversity. Species diversity affects the current functioning of ecosystems and their resistance and resilience to future climate change. In harsh environments such as drylands, positive plant–plant interactions are important in promoting species diversity. *Juniperus sabina* is an evergreen shrub that is native to the semiarid areas of northern China. Because *J. sabina* can modify some harsh environmental conditions in its role as a nurse plant, it is expected to facilitate species diversity, although it may exhibit allelopathic inhibition. Previous research has only examined effects of *J. sabina* coverage onα-diversity in a single-year, and its effects on the β-diversity of the plant community structure in the local ecosystem are still unclear. We compared environmental conditions and plant species composition inside and outside of 11 J. *sabina* patches to evaluate the effects of its coverage on the species diversity of the understory community structure through modifying microhabitat conditions. Water and nutrient conditions were higher inside the patches, whereas light conditions were higher outside. More perennial herbs and C3 plants were found inside and more annual herbs and C4 plants were found outside. There were different trends in α-diversity each year, while β-diversity was consistently greater inside the patches. This research suggests that the coverage of *J. sabina* can drive different community structures by providing heterogeneous environmental conditions, and would increase plant species diversity in the local ecosystem.

Keywords Nurse plant · Plant species diversity · Plant species coexistence · Plant–plant interactions · Mu Us sandy land

Introduction

“Desertification” equates to land degradation in arid, semiarid and dry sub-humid areas resulting from various factors, including climatic variations and human activities (UNCCD 1994). Desertification has a significant impact on the local natural environment, society and economy (UNCCD 1994). It can lead to continuous deterioration of the ecological environment and reduce the carrying capacity of the land, and even has a substantial adverse impact on productivity and life in surrounding areas (Cai 2023). China has implemented large-scale land conservation and restoration programs since approximately 1980 to combat desertification, undertaking extensive afforestation using non-native species (Li et al. 2021). However, non-native species use more groundwater than native species (Wilske et al. 2009; Song et al. 2020), and activities associated with restoration and conservation projects, such as afforestation, can impose

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substantial pressure on water resources (Cao 2008; Deng et al. 2016; Li et al. 2021). A study found that, by 2015, 45.8% of China's drylands had experienced notable land improvement, but 11.4% had undergone desertification (Li et al. 2021). Therefore, it is crucial to prevent the expansion of desertified land and to rehabilitate ecosystems through the conservation of native plant communities and revegetation using native plant species (Deng et al. 2016).

Species diversity in community structures affects the current functioning of ecosystems as well as their resistance and resilience to future climate change (Chapin III 2000). It also affects an ecosystem's resistance to desertification (Maestre et al. 2012). Communities form in patchy environments; spatial heterogeneity and the ability to disperse within larger habitats composed of multiple small patches are the key to species coexistence (Fahrig 1992; Kadowaki 2016). Thus, understanding how species composition varies among sites across space or time (i.e., β-diversity) is a key focus in ecology (Svenning et al. 2011; da Silva et al. 2018; Zeng et al. 2022). The increased interest in β-diversity comes from the recognition of its important role in revealing community assembly mechanisms (Zellweger et al. 2017; Soininen et al. 2018), and helping guide conservation practices (reviewed in Socolar et al. 2016).

Interactions between plants are among the fundamental processes that shape the structure and functioning of plant communities, creating species diversity (Arroyo 2015). Plant interactions refer to the effects of one plant on the growth or survival of another plant. These include not only negative effects through competition, but also positive effects (facilitation effects) (Miller 1994; Callaway 2007). In harsh environments such as drylands, net interactions generally have facilitating effects (nursery effects) and shrub species often function as nurse plants (Gómez-Aparicio 2009; Soliveres et al. 2011; He et al. 2013; Danet et al. 2024). Therefore, interactions mediated by shrub species are important ecological processes forland restoration (Padilla and Pugnaire 2006).

Juniperus sabina L. (family Cupressaceae, Synonyms: *Sabina vulgaris* Antoine) is the only native evergreen shrub species in northern China and is one of the main revegetation species in the semiarid areas of the region (Hirobe et al. 2001; Ohte et al. 2003). This species has prostrate stems and grows radially to cover the ground surface, forming a dense patch with a canopy that is more than several meters in diameter (Zhang et al. 1997; Hirobe et al. 2001; Ning et al. 2013). The species is effective in protecting wind as a windbreak and preventing aeolian sand erosion and transport (Zhang et al. 1997; Song et al. 2003). *J. sabina* afforestation is also beneficial for restoring soil physicochemical properties (Nan et al. 2024) and it has substantial environmental modification effects, including redistributing water to the soil surface (Ohte et al. 2003; Yang et al. 2014; Miki et al. 2016, 2018) and nutrient accumulation (Hirobe et al. 2001). However, it may also inhibit the establishment of other shrub species through resource competition (Matsumoto et al. 2015) and/or allelopathy (Qin et al. 2021; Semerdjieva et al. 2022). Although a previous study in Mu Us Sandy Land showed that the plant species and environment conditions were different at the center, inner edge and outside of *J. sabina* patches and that some species were facilitated inside the patch (Ning et al. 2013), the effects of *J. sabina* coverage on the β-diversity of the plant community structure in the local ecosystem are still unclear. It is crucial to clarify the effects of this species on the community structure (species diversity) of ecosystems to maximize its potential use in combating desertification and restoring ecosystem.

In this study, we compared environmental conditions and plant species composition inside and outside *J. sabina* patches to evaluate the effects of *J. sabina* coverage on the α- and β-diversity of the understory community structure through modifying microhabitat conditions. Given the limited water availability at this study site, coverage by *J. sabina* may enhance the diversity in plant community under its canopy by mitigating environmental conditions and enhancing the spatial heterogeneity of environmental conditions. Thus, *J. sabina* may contribute to the conservation of plant species diversity in desertified land.

Materials and methods

Study site

The survey was conducted in the Mu Us Sandy Land, a semiarid area located in the center of the Ordos Plateau, Inner Mongolia Autonomous Region of China. In this area, fixed, semi-fixed, and shifting sand dunes, and interdune lowlands are distributed in a mosaic pattern. In fixed and semi-fixed sand dunes, communities of the shrub *J. sabina*, belonging to the Cupressaceae family, can cover the surface of the dunes. In addition to *J. sabina*, there are widespread communities of *Artemisia ordosica*, Asteraceae family (Fig. 1). A natural community of *J. sabina* on fixed and semi-fixed sand dunes several kilometers northeast of the Mu Us Developmental Research Center (38°59′ N, 109°09′ E; 1300 m a.s.l.) was selected as the study site. The 15-year mean of annual precipitation and monthly temperature (January–December) from 2003 to 2017 were 342.1 mm (maximum: 567.6 mm, minimum: 164.3 mm) and 7.1 °C (monthly maximum: 28.9 °C, monthly minimum: -19.0 °C), respectively, at the Wushenzhao Meteorological Station 18 km northwest of the research site. In 2016 and 2017, when the study was conducted, the annual precipitation

Fig. 1 Fixed sand dunes in the Mu Us Sandy Land

was 567.6 mm and 280.1 mm, the precipitation during the growing season from April to October in both years was 542.8 mm and 256.0 mm, respectively and the annual mean temperature was 7.4 °C and 7.7 °C, respectively. Since the early 2000s, grazing has been restricted in the study site under government policy to restore vegetation conditions, and therefore little effect from grazing was observed (Liu 2010; Bryan et al. 2018; Wang et al. 2023; Yong et al. 2025).

Methods

Belt transects

Eleven similar-sized patches of *J. sabina* (patch diameter 10-20 m) were selected for our research. A belt transect (1 m × 11 m) was set for each patch from the center to the outside, so that approximately half the transect was inside the patch and half was outside (Fig. 2). The distance from the belt transect to the surrounding patches was > 5 m. All the belt transects were oriented toward the north. The belt transects were divided into 1 m × 1 m squares and one square was selected every other meter as subplots for our survey (total of six subplots for each belt transect, three inside *J. sabina* patches and three outside) (Fig. 2b).

Vegetation survey

In each survey subplot, the species name and the number of individuals were recorded for all species. Each plant species was identified according to Flora of China (http://www.iplant.cn/foc) and Ordos Plant List (2007). Individuals that were less than 1 cm or just germinated, where the species was hard to identify, were not counted in this survey. For clonal plants (*Carex duriuscula*) and vines (*Clematis aethusifolia, Cynanchum chinese, Rubia cordifolia*), the number of main stems that appeared on the ground was counted as the number of individuals. The survey was conducted twice: September 2016 and, August to September 2017.

Using the number of species and individuals in each subplot, the Shannon–Wiener diversity index (H') and Shannon's evenness index were calculated. The Shannon–Wiener diversity index (H') is obtained from the number of species (S) in the community and the relative abundance of the i species (*pi*) as follows (Colwell 2009):

$$H' = -\sum_{i}^{S} p_i \ln p_i$$

H' has a higher value as S increases and has the maximum value when the number of individuals and the coverage of all species are equal (Sasaki et al. 2015). The Shannon's evenness index (Pielou 1969) stems from the Shannon–Wiener diversity index (H') and the maximum value of the diversity index (H' max). The calculation is as follows:

$$\text{Shannon's evenness } \left(\text{Pielous}' J\right) = \frac{H'}{H'_{max}} = \frac{H'}{\ln \text{S}}$$

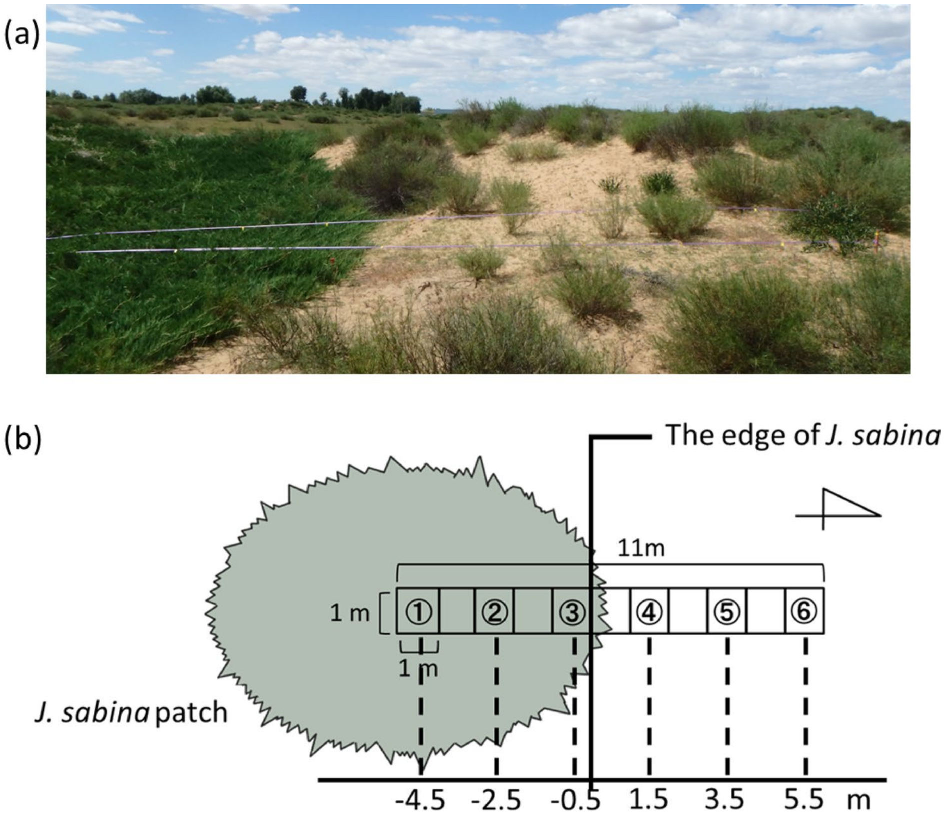

Fig. 2 **a** Overview of a belt transect; **b** schematic diagram of a belt transect and the distance between the subplots and the edge of the *J. sabina* patch

The Shannon's evenness index takes a value from 0 to 1, with values closer to 1 indicating higher evenness (Sasaki et al. 2015).

The life form (herbaceous [annual, perennial] or shrub) was determined according to the Ordos Plant List (2007). The life cycle of annual herbaceous species is usually one year but sometimes it can be 2 years, depending on the growth environment. These species were analyzed as annual herbaceous plants in this study. The photosynthetic pathway (C3, C4 and CAM) of each plant species was also identified according to previous studies (Hesla et al. 1982; Yin and Li 1997; Tang and Liu 2001; Wang 2003, 2004, 2005; Li et al. 2004, 2006; Choi et al. 2005; Huang et al. 2005; Feng et al. 2012; Zhao et al. 2019).

Measurement of environmental conditions

To investigate whether the environmental conditions inside and outside the *J. sabina* patches were different, we measured several environmental factors that reflected aspects such as light (coverage of *J. sabina*, relative photosynthetic photon flux density), water (volumetric water content, distance from the water table, soil hardness) and nutrient conditions (soil electrical conductivity reflecting soil salinity, soil carbon and nitrogen content).

(1) Coverage of J. sabina

The edge of the *J. sabina* patch in each subplot was sketched on 1 mm graph paper (scale of 1:10), and the coverage per subplot was calculated using image analysis software (ImageJ Java1.6.0_24, https://imagej.nih.gov/ij/download.html). Measurements were taken in September 2016.

(2) Relative photosynthetic photon flux density

At the four corners and the center of each subplot (30 points per belt transect), and at one point in the bare ground near the patch, the photosynthetic photon flux density (PPFD) was measured on the soil surface using light meters (Model LI-189 and Model LI-250, LI-COR, Nebraska, USA). Each point in the belt transect was measured synchronously on the bare ground to calculate the relative values of PPFD (rPPFD). The mean rPPFD values in each subplot (five points) were used for analysis. Measurements were taken in August 2016.

(3) Volumetric water content

At the four corners of each subplot (24 points per belt transect), the volumetric water content (VWC) of the soil was measured using a soil moisture meter (Theta Probe ML 2x, Delta-T Devices Ltd, Cambridge, UK). At each point, the organic material layer on the soil surface was removed and measurements were taken at both depths of 0–5 cm and 10–15 cm where many roots of *J. sabina* are distributed (Zhang et al. 1999; Ohte et al. 2003). The mean values in each subplot (four points) were used for analysis. Measurements were taken twice: on 28 Aug 2016 and 1 Sep 2017. To evaluate differences in soil water conditions within and between patches, measurements were taken on the fifth day after rainfall in both years, avoiding the immediate post-rain period.

(4) Soil electrical conductivity

At the four corners of each subplot (24 points per belt transect), the organic layer on the soil surface was removed and mineral soil was collected using a 100 cm^3 soil column. After air drying in a room for several days, the soil was dried at 40 °C for 2 days using a forced convection dryer (DO-600FA, AS ONE Corporation, Osaka, Japan) to obtain an air-dried soil sample. A mixture of the air-dried soil sample (5 g) and ion-exchange water (25 ml) was stirred in a falcon tube for 1 h. The soil electrical conductivity (EC) was measured using an electrical conductivity meter (ES-14, HORIBA, Kyoto, Japan). The mean values of each subplot (four points) were used for analysis. Measurements were made in August 2016.

(5) Soil nutrient content (total soil nitrogen and carbon content)

After removing large and small organic matter, 5 g air-dried soil samples were crushed in a pestle. The total carbon (C) and nitrogen (N) content in the ground samples were measured using a macro coder (JM1000CN, J-SCIENCE LAB Co., Ltd., Kyoto, Japan). The mean values of each subplot (four points) were used for analysis.

(6) Percentage of micro soil particles (< 100 μm)

The air-dried soil samples were dried at 105 °C for over 48 h using a natural convection dryer (EOP-450B, AS ONE Corporation, Osaka, Japan) to obtain a completely dry soil sample. A 5 g sample of the completely dried soil was sieved through a 100 μm sieve for approximately 20 min. The percentage of micro soil particles (< 100 μm) was calculated by weight as the ratio of the micro soil particles (< 100 μm) to the total soil particles. The measurement method was basically based on Hirobe et al. 2001. The mean values of each subplot (four points) were used for analysis.

(7) Soil hardness

At the four corners of each subplot (24 points per belt transect), after removing the organic layer on the soil surface, the soil hardness was measured using a soil hardness tester (Yamanaka type, Fujiwara Seisakusho Co., Ltd., Tokyo, Japan). The mean values of each subplot (four points) were used for analysis. Measurements were taken in August 2016.

(8) Distance from the water table

For each belt transect, we selected one position within 10 m of the transect and measured the distance from the groundwater surface to the ground surface by digging a hole. Then, the relative height between every corner of each subplot (24 points per belt transect) and the dug point was measured using a laser rangefinder (Tru Pulse 360°, Laser Technology Inc., Colorado, USA). On the basis of the relative height, the distance from the soil surface to the water table was calculated for each point (assuming that the groundwater level was constant within each transect). The mean values of each subplot (four points) were used for analysis. Measurements were made in August 2016.

Statistical analysis

In each belt transect, the edge of the *J. sabina* patch was set as the 0 m point, and the value of the distance from the 0 m point to the center point of each subplot was defined as the "distance from the edge of *J. sabina* patch". The subplots inside the patch of *J. sabina* were set to negative values, and the subplots outside were set to positive values (Fig. 2b). These values were used in all statistical analyses. All statistical analyses were conducted using the statistical software R (ver. 4.3.3, R Development Core Team 2024).

The relationship between the distance from the edge of *J. sabina* patch and the understory community structures (number of individuals, number of species) or the environmental conditions (coverage of *J. sabina*, rPPFD, percentage of micro soil particles, soil hardness, VWC, distance from the water table, soil EC, soil C and N content) were tested using generalized linear mixed models (GLMMs) in each year. Then, the vegetation and environmental data were used as response variables. The distance from the edge of the *J. sabina* patch was used as an explanatory variable. The error distribution of response variables and link functions were set as follows: Poisson distribution and log link function for numbers of individuals and species; Gaussian distribution and identity link function for all environmental conditions. The ID of each belt transect was set as the random effect. We decided on the best fitting model (compared with the Null model) of the explanatory variables using Akaike's Information Criterion (Johnson and Omland 2004). The regression lines are shown on the graphs only for the explanatory variable selected by the likelihood ratio test. All GLMMs were conducted using the glmer function in the lme4 package (Bates et al. 2015). A one-sample t-test was used compare the differences between the two years at each distance from the edge of the *J. sabina* patch.

Permutational multivariate analysis of variance (PERMANOVA) was used to evaluate the multiple-site plant community composition inside and outside the *J. sabina* patches (among belt transects). The adonis2 function of the vegan package (Oksanen et al. 2025) was used for this analysis. The Jaccard distance was used and the permutations were set to 999. The tests of homogeneity of dispersion (PERMDISP) were performed to evaluate the multiple-site plant community dispersion inside and outside *J. sabina* patches (β-diversity) (Anderson 2006). The betadisper function of the vegan package was used for this analysis. The Jaccard distance was used and the permutations were set to 999. We evaluated Simpson-based multiple-site dissimilarity (β_{SIM}), nestedness-resultant multiple-site dissimilarity (β_{NES}) and Sørensen-based multiple-site dissimilarity (β_{SOR}) using the betapart package (Baselga et al. 2005).

Non-metric multidimensional scaling (NMDS) was used to visualize differences in the plant community structure inside and outside the *J. sabina* patches. The metaMDS function of the vegan package and the Jaccard distance matrix were used for this analysis. The influence of environmental conditions in each subplot was reflected on the graph of NMDS using the env.fit function of the vegan package.

Results

Among the environmental conditions, the coverage of *J. sabina* was consistently higher inside the patches than outside, and therefore rPPFD was lower inside the patches than outside (Fig. 3a, b). The percentage of micro soil particles (< 100 µm), VWC (0–5 cm, 10–15 cm depth), soil EC, and soil nutrient content (total C and N) was higher inside *J. sabina* patches, and there were large variations between belt transects inside the patches (Fig. 3c–h). The soil hardness and the distance from the water table were almost constant, irrespective of the distance from the edge of the *J. sabina* patch (Fig. 3i, j). In addition, the VWC did not differ between 2016 and 2017 (Fig. 3c, d), indicating that there was no critical difference in soil water availability despite the high precipitation in 2016.

The total number of individuals in 2016 and 2017 was 10,190 and 7969, respectively; however, no significant difference between the corresponding subplot was shown between the two years (Fig. 4a). The total number of individuals was positively related to the distance from the edge of the *J. sabina* patch in both years (Fig. 4a). The number of species was 64 in 2016 and 50 in 2017, and the number of species inside the patches showed greater annual variation than outside (Fig. 4b, Table S1 available as Supplementary Data). In 2016, the number of species was negatively related to the distance from the edge of the *J. sabina* patch, while the inverse relationship was found in 2017 (Fig. 4b).

For annual herbs, the number of species was positively related to the distance from the edge of the *J. sabina* patch (Fig. 5a), whereas the perennial herbs showed a negative relationship (Fig. 5b). The number of species of C4 plants was positively related to the distance from the edge of the *J. sabina* patch (Fig. 5c), whereas the number of C3 plant species was negatively related (Fig. 5d). For annual herbs and C4 plants, the number of species inside patches was larger in 2016, and showed significant differences between the two years (Fig. 5a, c).

The diversity and evenness indices were higher inside the *J. sabina* patches than outside in both years (Table 1). The community structure clearly differed inside and outside the *J. sabina* patches in both 2016 and 2017 (Fig. 6; stress values in 2016 and 2017 = 0.23 and 0.19). The variation in community structure among subplots and transects was also larger inside *J. sabina* patches. In 2016 especially, community structure was clearly separated between inside and outside along NMDS 1 (Fig. 6). For the effects of environmental conditions, the direction of arrows in VWC, soil N content and rPPFD was directed along NMDS 1. The VWC and soil N content had positive effects on the variation of community structure inside, while rPPFD had positive effects outside. In both 2016 and 2017, there were significant differences on community dispersion (β-diversity) (PERMDISP; Table 2), as well as on community composition (PERMANOVA; Table 2)inside and outside the patches. The β_{SIM}, β_{NES} and β_{SOR} showed little difference inside and outside the patch (Table 3).

Discussion

In arid environments, shrub coverage can often modify microhabitat environments (Garcia-Moya and Mckell 1970; Hastwell and Facelli 2003; Kidron 2009). Indeed, in our study, the VWC, soil nutrient content, soil EC and percentage of micro soil particles tended to be higher inside the *J. sabina* patches (Fig. 3c–h), whereas the rPPFD tended to be higher outside (Fig. 3b). In previous studies, dense *J.*

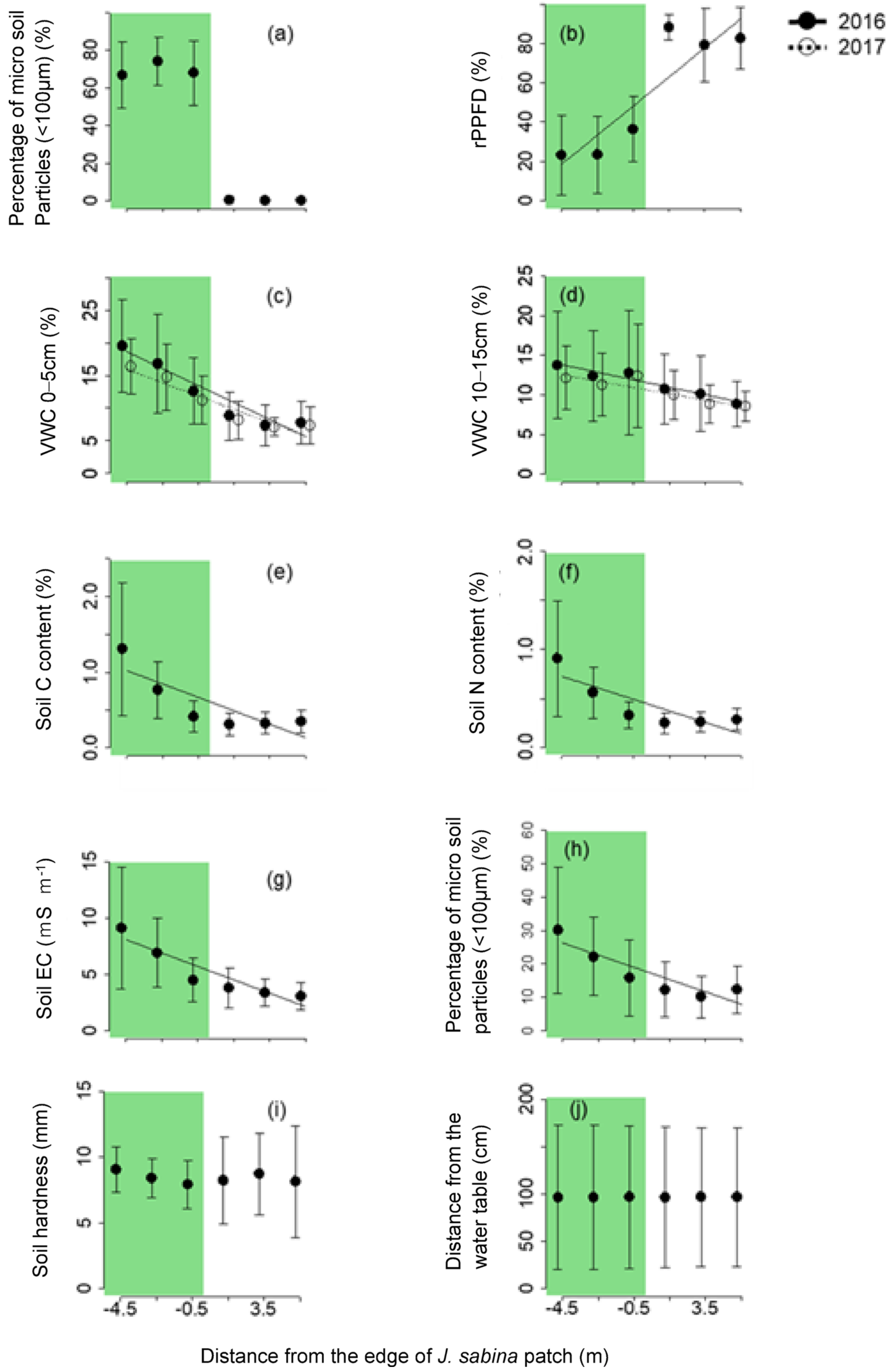

Fig. 3 Values of environmental conditions. **a** Coverage of *J. sabina*; **b** relative photosynthetic photon flux density; **c** volumetric water content 0–5 cm; (d) volumetric water content 10–15 cm; **e** soil nitrogen content; **f** soil carbon content; **g** soil electrical conductivity; **h** percentage of micro soil particles; **i** soil hardness; **j** distance from the water table. Values are the means ± SEs. The colored parts correspond to inside the *J. sabina* patch. The regression lines are shown on the graphs only for the explanatory variables selected by the likelihood ratio test

sabina patches that include many prostrate stems (Zhang et al. 1997) were found to cause environment modifications, such as providing a windbreak and fixing sand movement (Hong 2006), redistributing water from the deep soil to the surface (Yang et al. 2014; Miki et al. 2016, 2018), and accumulating nutrients (Hirobe et al. 2001). Therefore, our results, showing that the coverage of *J. sabina* mitigated the harsh conditions in the semiarid area and resulted in different environmental parameters inside and outside the patches (Fig. 3), support previous research.

Different plant community structures also clearly formed inside and outside the *J. sabina* patches (Fig. 6). Several

Fig. 4 Total number of **a** individuals; **b** species. Values are the means ± SEs. The colored parts correspond to inside the *J. sabina* patch. * $P < 0.05$, t-test. The regression lines are shown on the graphs only for the explanatory variables selected by the likelihood ratio test

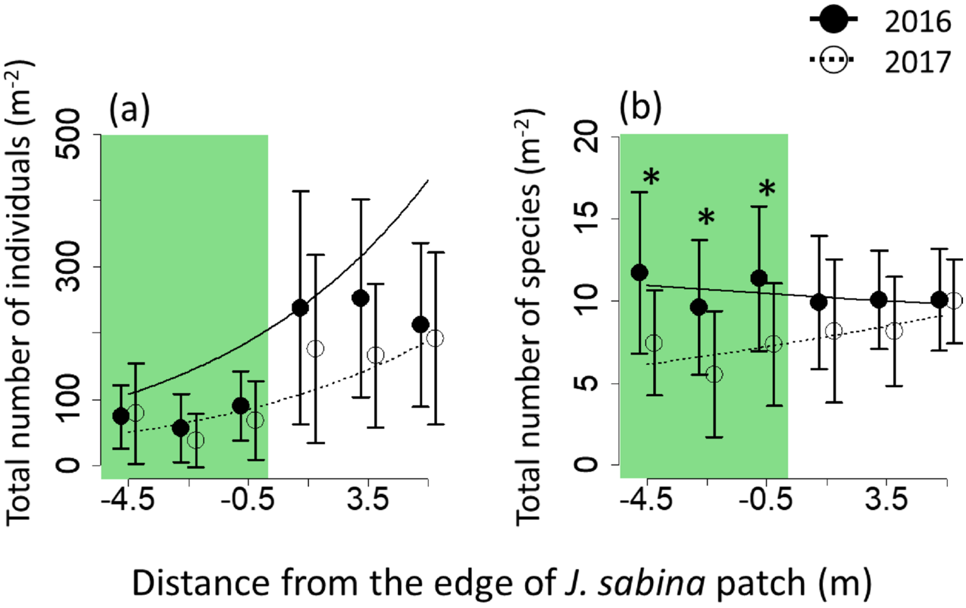

Fig. 5 Number of species of **a** annual herbs; **b** perennial herbs; **c** C3 plants; **d** C4 plants. Values are the means ± SEs. The colored parts correspond to inside the *J. sabina* patch. * $P < 0.05$, t-test. The regression lines are shown on the graphs only for the explanatory variables selected by the likelihood ratio test

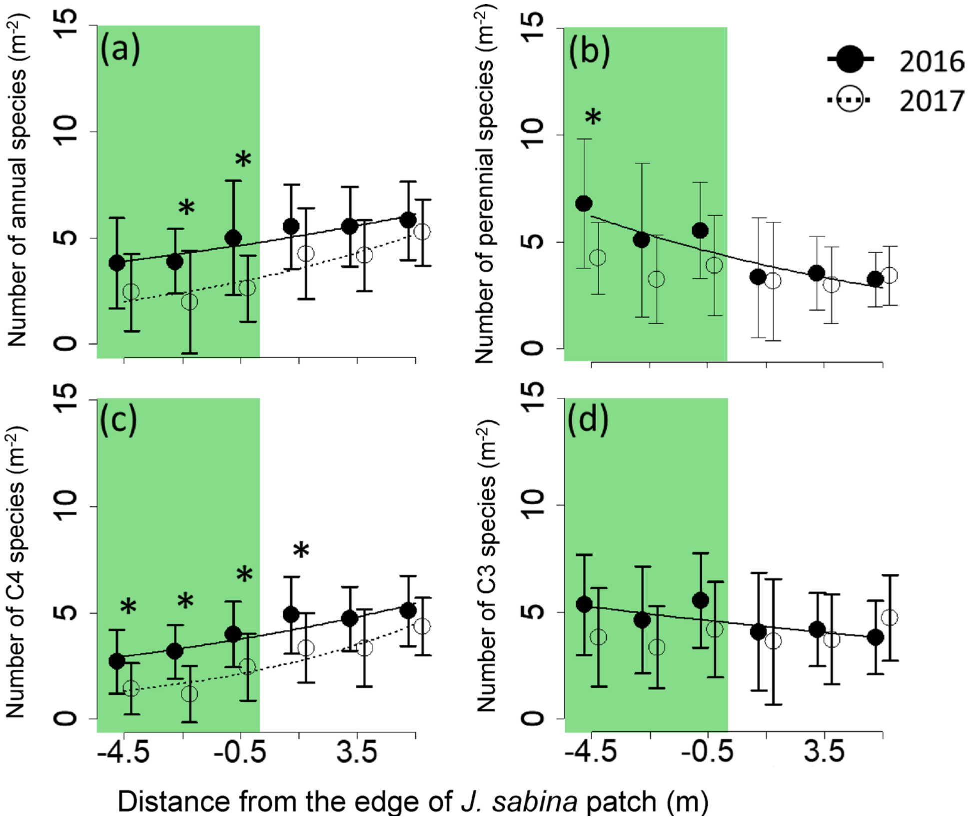

Table 1 The Shannon–Wiener diversity index and Shannon's evenness index inside and outside patches of *J. sabina*. Values are the means ± (SEs)

	Diversity Index		Evenness Index	
	Inside	Outside	Inside	Outside
2016	3.11 (±0.09)	1.99 (±0.05)	0.77 (±0.02)	0.52 (±0.02)
2017	2.98 (±0.07)	2.07 (±0.08)	0.71 (±0.03)	0.50 (±0.03)

studies in arid areas showed that seedlings from some species tended to grow under the canopies of other tree species (Franco and Nobel 1988, 1989). *J. sabina* exhibits allelopathic inhibition against some species (Qin et al. 2021; Semerdjieva et al. 2022); however, this effect would be species selective (Qin et al. 2021), owing to the species selective inhibitory effects of allelochemical, monoterpenoids (sabinene, α-pinene and β-myrcene) (Williamson et

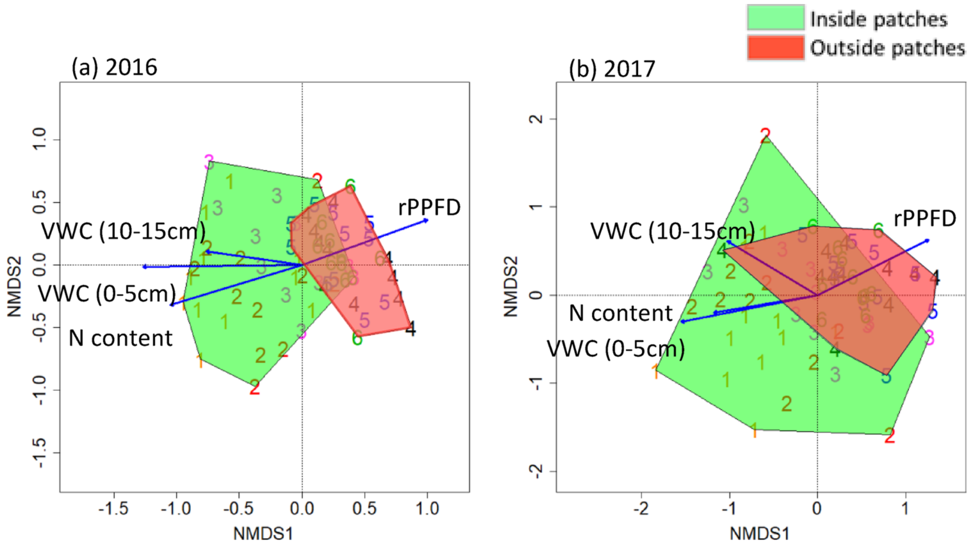

Fig. 6 NMDS analysis of differences in community structure inside and outside *J. sabina* patches using the Jaccard index: **a** 2016; **b** 2017. The numbers represent each subplot in belt transects, with 1–3 being subplots located inside the patch and 4–6 being subplots located outside the patch. The direction of arrows in VWC, soil N content, and rPPFD coincided with the direction of arrows in the community structure variation

Table 2 The results of PERMANOVA and PERMDISP analysis using the Jaccard index

	PERMANOVA				PERMDISP			
	DF	Sum sq	F-value	*p*-value	DF	Sum sq	F-value	*p*-value
2016	1	1.910	7.481	0.001	1	0.082	17.337	0.001
2017	1	2.319	7.713	0.001	1	0.195	21.659	0.001

Table 3 The results of multiple-site dissimilarity (β_{SIM},β_{NES} and β_{SOR}) using the Jaccard index

		β_{SIM}	β_{NES}	β_{SOR}
2016	Inside	0.876	0.044	0.921
	Outside	0.846	0.053	0.899
2017	Inside	0.887	0.045	0.932
	Outside	0.844	0.061	0.905

al. 1992; Abrahim et al. 2000; Vokou et al. 2003; Loi et al. 2008). The coverage of *J. sabina* mitigated harsh conditions in the semiarid area, which meant that *J. sabina* was the nurse plant for some species.

More individuals were found outside the patches (Fig. 4a), which reflected the same trends as the study of Ning et al. (2013). However, the total number of species was negatively related to the distance from the edge of the *J. sabina* patch in 2016, while the inverse relationship was found in 2017 (Fig. 4b). Ning et al. (2013) did a one-year survey and found the same trends as our result in 2017. The number of species of annual herbs and C4 plants inside the patches was significantly larger in 2016 than in 2017 (Fig. 5a, c). The total number of species was also significantly larger in 2016 than in 2017, which might be related to the increase in the number of annual herbs and C4 plant species. In annual herbaceous plants of dryland, fluctuations in populations responding to rainfall have often been reported (Bagstad et el. 2005; Angert et al. 2007), suggesting that population fluctuations associated with rainfall variability in annual herbs may be one reason. Although the reason was not clear directly, these variables may be influenced by annual factors such as fluctuation of rainfall.

More annual herbs and C4 plants were found outside the patches (Fig. 5a, c), whereas more perennial herbs and C3 plants were found inside the patches (Fig. 5b, d). Perennial herbs have a relatively larger individual size compared with annual herbs, they distribute more nutrients to underground rhizomes and they have higher N requirements (Bloom et al. 1985; Bazzaz et al. 1987; Joffre 1990). In contrast, the annual herbs have a lower distribution of nutrients in the underground rhizomes than the perennial herbs, they produce more seeds and their N requirements are lower than perennials (Joffre 1990). Seeds have much higher viability under dry conditions than tubers (Rajjou and Debeaujon 2008; Smolikova et al. 2021). Environmental conditions in drylands include not only water-limited conditions but also substantial water variability (Sala and Lauenroth 1982; Schwinning and Sala 2004). Annual herbs may be able to survive better in such harsh environments in the form of seeds (Poppenwimer et al. 2023). Furthermore, the C4 photosynthesis pathway has a higher CO_2 fixation efficiency than the C3 photosynthesis pathway and can maintain a high photosynthesis rate by reducing the loss of water from evaporation (Taiz and Zeiger 2002; Gowik and Westhoff 2011). Thus, C4 plants have higher water use efficiency and can grow in strong light and arid conditions (Guidi et al. 2019; Leakey et al. 2019). Inside the patches of *J. sabina*, there is higher soil nutrient content owing to the accumulation of litter and fine material (Hirobe et al. 2001). The soil moisture content inside patches is also high because evapotranspiration is reduced by shade (Yamanaka et al. 2000) and because of the hydraulic redistribution of water from deeper soil to surface soil (Yang et al. 2014; Miki et al. 2016, 2018). These factors explain why perennial herbs and C3 plants were more abundant inside the *J. sabina* patches, while annual herbs and C4 plants were more abundant outside the patches.

The variation of the community structure was larger inside the *J. sabina* patches, and the direction of arrows in VWC and soil N content showed positive effects on its variation inside (Fig. 6, Tables 1, 2). This indicated that the formation of different community structures was affected by the different environments in the *J. sabina* patches. Ning et al. (2013) analyzed the number of individuals (density) and species (α-diversity) and found that increasing soil water and nitrogen resources were associated with the facilitative effects of *J. sabina*, which reflected the same trends as our study (Figs. 3, 4). In addition to the α-diversity, we analyzed the variations among the belt transects (β-diversity) (Fig. 6, Tables 2, 3). The fluctuations in environmental conditions such as moisture and nutrients tended to be larger inside the *J. sabina* patches than outside (SE in Fig. 3), and the variations in community structure were also larger inside. The β-diversity inside and outside the *J. sabina* patches also showed differences—the β-diversity inside the *J. sabina* patches was significantly greater than outside the patches (PERMDISP; Table 2, Fig. 6). The β-diversity reflects the spatial distribution pattern of species, which involves several ecological processes, including species turnover, nestedness, checkerboard (competitive exclusion) and randomness (Leibold and Mikkelson 2002; Almeida-Neto et al.2007; Ulrich and Gotelli 2013). Species turnover and nestedness components were unlikely to be the main drivers explaining differences in β-diversity inside and outside patches (Table 3). Therefore, the main drivers of differences in β-diversity were likely to be checkerboard (competitive exclusion) and/or random components. In other words, the β-diversity found inside *J. sabina* patches was probably related to niche partitioning caused by the variation in environmental conditions owing to differences in site location and canopy density (spatial heterogeneity of environmental conditions) in each patch and/or might be associated with the differences in probability of wind-blown seeds being trapped in each patch. Inside patches, α-diversity may vary because of factors that fluctuate annually, such as rainfall, but β-diversity would remain a stable property.

In conclusion, these results in two years with different rainfall amounts suggest that the patchy cover of *J. sabina* resulted in different environmental conditions inside and outside the patches, thereby forming different plant community structures. Inside the patches, there were more perennial herbs and C3 plants, and various species that created diverse communities. In contrast, there were more annual herbs and C4 plants outside the patches, and the smaller number of species formed similar communities. Therefore, it is considered that the coverage of *J. sabina* patches can modify the environmental conditions, providing heterogeneity in environmental conditions and thereby increasing the β-diversity of the community inside the patches. Hence, regardless of annual fluctuations in rainfall, *J. sabina* can contribute to the improvement of plant species diversity in local ecosystems of fixed and semi-fixed sand dunes in Mu Us Sandy Land. Revegetation with *J. sabina* species may lead to more successful ecosystem restoration in arid environments.

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Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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