Contents lists available at ScienceDirect

Catena

journal homepage: www.elsevier.com/locate/catena

Spatial characteristics of two dominant shrub populations in the transition zone between oasis and desert in the Heihe River Basin, China



^a Linze Inland River Basin Research Station, Chinese Ecosystem Research Network, Key Laboratory of Eco-Hydrology of Inland River Basin, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, Lanzhou 730000, China

^b University of Chinese Academy of Sciences, Beijing 100049, China

ARTICLE INFO

Keywords: Transition zone Population characteristics Spatial pattern Spatial heterogeneity Summer precipitation

ABSTRACT

Changes in spatial patterns of vegetation and their underlying hydrological mechanisms has significant implications for landscape ecological researches. However, empirical studies which test the relationships between vegetation spatial pattern and hydrology are scarce. Based on an in situ investigation and on geostatistical analysis, we described spatio-temporal changes in population characteristics in two shrub populations in the transition zone between oasis and desert in the Heihe River Basin, northwestern China. Our results showed that the density and cover of two dominant species were significantly greater in 2016 than in 2002. Total species richness also increased with time. N. sphaerocarpa population was distributed in small strips in 2002 and in big strips in 2016. R. soongorica population exhibited uniform distribution in 2002, and big-strip distribution pattern in 2016. The results of a semi-variogram analysis showed that the nugget/sill ratio of the two populations was 0.077 to 0.116 in 2002, and 0.066 to 0.144 in 2016. This indicated that the random variance of spatial heterogeneity occupied 7.7-11.6% of total spatial heterogeneity in 2002, and 6.6-14.4% in 2016. In 2002, the range values (A_0) , respectively for density and cover, were 33.09 and 14.7 m for N. sphaerocarpa, and 24.9 and 25.2 m for R. sphaerocarpa. In 2016, these values increased to 37.2 and 30.3 m for N. sphaerocarpa, and 57.3 and 75 m R. sphaerocarpa. This indicated that the scale of spatial heterogeneity for density and cover of the two dominant species increased from 2002 to 2016. Correlation analysis showed that summer precipitation and soil water content significantly related to total species richness. We concluded that summer precipitation was a key factor which affected population characteristics and spatial patterns. The mechanism driving this was a rise in summer precipitation leading to an increase in soil water content and, eventually, to a change in the spatial patterns of plants.

1. Introduction

Spatial patterns of plant communities have been an important topic in ecology because they are critical to the understanding of the functions and processes of ecosystems across variable scales (Condit et al., 2000; Rietkerk et al., 2004; Perry et al., 2012). Vegetation in arid and semiarid landscapes is commonly distributed in patches within a matrix of bare ground and low vegetation cover (Bautista et al., 2007). Vegetation patterns include banded vegetation in the Chihuahuan desert (Aguiar and Sala, 1999), stripes and labyrinths of bushy vegetation in the Niger (Rietkerk et al., 2002; Barbier et al., 2006), and spots and gap vegetation in the Niger (Rietkerk et al., 2002, 2004). The spatial structure of vegetation is typically described in terms of source-sink systems, with bare soil and vegetation patches acting, respectively, as sources and sinks of vital resources (Mayor et al., 2008). Plant spatial patterns have been shown to be related to key variables such as biodiversity, thought to affect many ecosystem processes and services (Maestre, 2004). Soil properties such as soil water condition and soil biota also affect ecosystem processes (Belnap et al., 2005). Therefore, evaluation of the spatial patterns of vegetation is critical to the understanding of the functions and processes of ecosystems across variable scales (Rietkerk et al., 2004; Perry et al., 2012).

Disturbances, such as grazing, significantly affected spatial patterns of some plants (Deangelis, 2012; Komac et al., 2011), but a response of spatial patterns to grazing exclusion was detected only at patch size (Deangelis, 2012). Slope gradient and rainfall also controlled spatial patterns of vegetation in some systems (Bautista et al., 2007; Perry et al., 2012). For example, in semi-arid regions, when slope gradient is < 0.2% and mean annual rainfall ranges from 200 to 550 mm per year, vegetation patterns include spots, labyrinths, and gaps,

https://doi.org/10.1016/j.catena.2018.06.020





CATENA



^{*} Corresponding author. E-mail address: zhaowzh@lzb.ac.cn (W. Zhao).

Received 13 September 2017; Received in revised form 9 April 2018; Accepted 22 June 2018 0341-8162/ © 2018 Elsevier B.V. All rights reserved.

respectively with diameters from 5 to 20 m, from 10 to 50 m, and from 5 to 20 m, were observed (Couteron and Lejeune, 2001). However, when slope > 0.2% in arid regions, the main vegetation pattern was regular-banded with band width in the range of a few tens of meters (d'Herbes et al., 2001). Further, species functional traits related to their spatial distribution at the landscape level, but site effects were as important as functional traits in determining the spatial pattern at fine scales (Perry et al., 2012). Irrespective of the origin, site-to-site variation in environmental conditions influenced spatial patterning through habitat selection (Getzin et al., 2008; Burton et al., 2011). Under some conditions, spatial patchiness of vegetation may be sufficient to precipitate sudden changes in ecosystems (Pascual and Guichard, 2005). Given the complexity of these interactions, a better understanding of the factors which determine the formation of vegetation spatial patterns is still greatly needed.

In water limited systems, landscapes can generally be described as mosaics of vegetation and bare-soil patches of various forms (Zelnik et al., 2013). A substantial body of empirical evidence indicated that this type of vegetation patchiness is a self-organization phenomenon which can occur in different physical environments (Rietkerk et al., 2002; Deblauwe et al., 2008; Zelnik et al., 2013). These self-organized vegetation patterns are very important for maintaining productivity in arid ecosystems (Noy-Meir, 1973; Rietkerk et al., 2002). The main mechanism of spatial self-organization is a positive feedback between plant growth and availability of water, because water infiltrates faster into vegetated ground (due to root penetration) than into bare soil (due to shading), leading to a net displacement of surface water to vegetated patches (Rietkerk et al., 2004; Deangelis, 2012). The formation of selforganized patchiness in arid brush-lands was related to the redistribution of surface runoff, driven by differences in water infiltration at a scale of 10 m (Rietkerk et al., 2002).

Geostatistical techniques are useful tools for quantify the spatial characteristics of arid landscapes. They assist in sampling design, and in defining the spatial resolution for remote sensing, thereby enabling the monitoring of desert vegetation (He and Zhao, 2006). Geostatistics comprise a group of spatial statistical techniques which evaluate autocorrelation commonly observed in spatial data; in autocorrelation, data values associated with proximal locations are more similar to each other than data values associated with locations that are further apart (i.e., statistical variation in the data is a function of distance) (Isaaks and Srivastava, 1989). The spatial structures of different plant communities could characterized by nugget, range and sill parameters of geostatistical models such as spherical or exponential model variograms (He and Zhao, 2006). Therefore, geostatistical models were often used in quantify the spatial characteristics and explore the succession process of different plant communities (He and Zhao, 2006; He et al., 2007).

The main vegetation type in the transition zone between oasis and desert in northwestern China is desert vegetation dominated by several super-xerophytic shrubs such as Reaumuria soongorica and Salsola passerina. These shrubs exhibit strong adaptability to drought and sand habitats, and have important roles in soil water conservation and wind prevention. Although the vegetative structures are relativity simple and species composition is very poor, vegetation in the transition zone between oasis and desert plays a very important conservation role for the oases in northwestern China (He and Zhao, 2004). Rainfall is almost the only source of soil water in this extremely arid environment, and the importance of hydrological behavior for the spatial pattern of vegetation is widely acknowledged (Li et al., 2013). However, there is little empirical work addressing the relationships between vegetation spatial pattern and hydrology. We address this research gap by focusing here on answering the following questions. 1) What are the changes of density and cover of dominant populations in the transition zone between oasis and desert over time? 2) What are the drivers of change in spatial patterns and heterogeneity of the dominant populations?

Table 1

Nutrient concentrations and texture of soil in the study site (sampling depth of soil layer was 0–50 cm, the number of samples was 35; He et al., 2007).

Soil properties	Average	Minimum	Maximum	Standard deviation
Soil organic matter content (%)	0.23	0.17	0.34	0.07
Total				
N (%)	0.041	0.021	0.087	0.05
P (%)	0.092	0.045	0.112	0.07
K (%)	2.17	1.97	2.56	0.24
Readily available				
N (%)	0.003	< 0.001	0.007	0.001
P (%)	0.001	< 0.001	0.003	0.001
K (%)	0.015	0.008	0.023	0.002
PH	8.31	8.10	8.63	0.21
Quadrat content of 0.25–0.05 mm (%)	86.2	74.5	90.7	4.5
Average depth of groundwater (m)	12.6	11.2	13.8	1.5

2. Methods

2.1. Study site

The study was conducted in the transition zone (39°20'N, 100°08'E) between desert and oasis near the Linze Inland River Basin Research Station of the Chinese Academy of Sciences, located in central Gansu province in northwestern China. Average annual rainfall is 117 mm, of which 65% is distributed mainly in summers as short-duration showers. Precipitation events can be characterized as rainfall pulses with discontinuous, highly variable, and largely unpredictable frequency and intensity (Zhao and Liu, 2010). Mean annual temperature is 7.6 °C. There is a mean number of 165 days with freezing temperatures which occur mainly in December and January.

The selected sites are located within an alluvial plain with relatively flat topography; elevation is about 1250 m. Vegetation is a xerophytic scrub. Vegetation patterns can be described as patches of dense scrub (for example, an association of *Nitraria sphaerocarpa* Maxim. and *Reaumuria soongorica* (Pall.) Maxim.) surrounded by bare areas with vegetation cover of < 10%. Soils exhibit sandy and sandy loam texture with low nutrient levels (Table 1). Groundwater depth is between 11 m and 13 m, and soil moisture content is very low, about 3% (He et al., 2007).

2.2. Sampling design and data collection

One plot of 500 m × 500 m was selected subjectively in the transition zone between oasis and desert. A hill is located 2 km west of the plot, and desert is north of the plot. East and south edges are bordered by the oasis at a distance from plot edge of 1.5 and 0.5 km, respectively. The plot was divided into 2500 quadrats of 10 m × 10 m. In each quadrat, the number, percent cover, and spatial position (the position of each plant in each quadrat) of two dominant species (*Nitraria sphaerocarpa* and *Reaumuria soongorica*) were assessed visually, and with a ruler. Then, twenty 10 m × 10 m quadrats were selected for examination of species composition and abundance in the plot. Species composition and number were recorded in each quadrat in June of every year during 2012 to 2016.

The density of each population was defined as the total number of each species in the area of $10 \times 10 \text{ m}^2$. The cover was obtained by measuring the scrub-projection area, and then calculating the percent of scrub projection area within each quadrat area. The spatial position of each species distribution was determined by recording the x and y coordinates of each quadrat (He et al., 2007).

Depth of groundwater table was automatically measured using a water sensor (HOBO water level logger, Onset Computer Corporation,

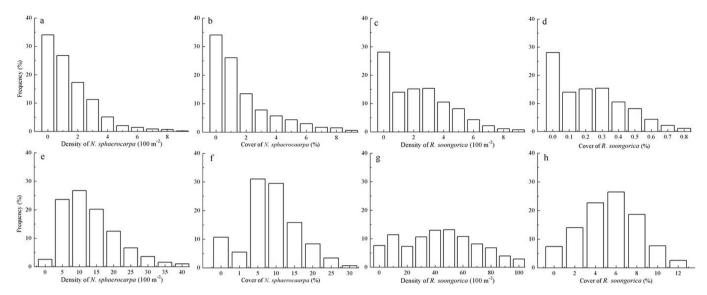
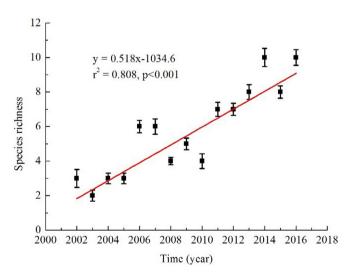


Fig. 1. Frequency distributions of population characteristics of two dominant species in 2002 and 2016 (a and b, density and cover of *N. sphaerocarpa* in 2002; c and d, density and cover of *R. sphaerocarpa* in 2002; e and f, density and cover of *N. sphaerocarpa* in 2016; f and g, density and cover of *R. sphaerocarpa* in 2016).

Table 2
Descriptive statistics of two dominant-species populations at different time periods ($n = 2500$).

	Nitraria sphaerocarpa				Reaumuria soongorica				
	Density (clump/100m ²)		Cover (%)		Density (ind./100m ²)		Cover (%)		
	2002	2016	2002	2016	2002	2016	2002	2016	
Mean	1.52	11.95	1.56	8.13	2.34	42.6	0.23	4.48	
Standard deviation	1.76	9.88	2.34	6.64	2.18	31.4	0.22	2.84	
Sample variance	3.11	97.62	5.47	44.11	4.74	986.38	0.05	8.06	
Minimum value	0	0	0	0	0	0	0	0	
Maximum value	18	112	18	67.38	13	243	1.32	23.87	
Skewness	2.07	2.56	2.34	1.54	0.87	0.82	0.87	0.40	



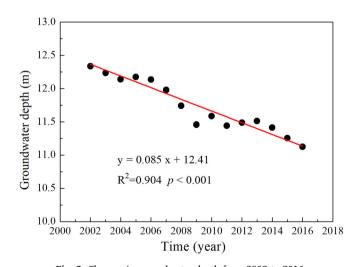


Fig. 3. Changes in groundwater depth from 2002 to 2016.

Fig. 2. Changes in species richness from 2002 to 2016.

Electronics, Dallas, TX, USA).

Pocasset, MA, USA); data were recorded every ten days in June during 2002 to 2016. Five observation wells, 5-cm in diameter, were made of polyvinyl chloride, fitted with sensors, and installed in the plot. Soil water content was measured every 10 days in June of 2002 to 2016 using the oven-drying method with 20 replicates. Soil samples were collected every 0.2 m between 0 and 1.5 m. Soil samples were oven-dried (105 °C) for 48 h prior to analysis. Precipitation was measured with a tipping-bucket rain gauge (model TE525, metric; Texas

2.3. Data analysis

2.3.1. Correlation analysis

We used Pearson's correlation to explore the relationships between vegetation (species richness) and hydrological parameters (soil water content of different layers, groundwater depth, and precipitation).

Table 3

Pearson's coefficients of bivariate correlations between vegetation and hydrological variables (SWC = soil water content).

	SWC (10 cm)	SWC (50 cm)	SWC (100 cm)	SWC (150 cm)	Groundwater depth	Total precipitation	Summer precipitation	Species richness
SWC (10 cm)	1							
SWC (50 cm)	0.690**	1						
SWC (100 cm)	0.705**	0.996**	1					
SWC (150 cm)	0.831**	0.668**	0.675**	1				
Groundwater depth	-0.823**	-0.874**	-0.870**	-0.781**	1			
Total precipitation	0.037	0.026	0.035	-0.144	-0.098	1		
Summer precipitation	0.601*	0.558*	0.591*	0.529*	-0.232	0.366	1	
Species richness	0.862**	0.814**	0.839**	0.854**	-0.802**	0.051	0.582*	1

* Significant correlation at the p < 0.05 level

** Significant correlation at the p < 0.01 level (n = 15).

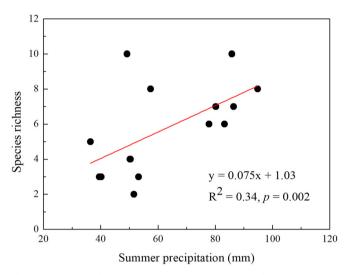


Fig. 4. The relationship between summer precipitation and species richness.

Table 4

Semivariogram models (exponential) and characteristics of two dominant species populations in two time periods.

	Nitraria	sphaeroca	rpa		Reaumuria soongorica				
	Density (clump/ 100m ²)		Cover (%)		Density (ind./ 100m ²)		Cover (%)		
	2002	2016	2002	2016	2002	2016	2002	2016	
C_0 $C + C_0$ A_0 $C_0/(C + C_0)$ R^2 D	0.346 3.096 33.09 0.116 0.733 1.964	6.1 92.3 37.2 0.066 0.551 1.962	0.410 5.313 14.7 0.077 0.237 1.987	5.9 45 30.3 0.131 0.780 1.980	0.37 4.615 24.9 0.080 0.758 1.977	185 1283 57.3 0.144 0.900 1.945	0.004 0.046 25.2 0.081 0.758 1.977	1.4 75 75 0.019 0.964 1.932	

Differences obtained at the level of p < 0.05 were considered significant. Regression analysis was used to determine the relationships between species richness, hydrological parameters and time periods. Time periods were independent variables. Data were transformed for normality before analysis, when necessary. All analysis were conducted with SPSS 16.0 (SPSS, Chicago, IL, USA).

2.3.2. Spatial pattern analysis

Geostatistical analysis involves two main steps: (1) defining the degree of autocorrelation among the measured data points, and (2) interpolating values between measured points based on the degree of autocorrelation encountered (He and Zhao, 2006). Autocorrelation is evaluated with semi-variograms r(h), calculated for each specific distance or time interval h in a data set such that:

$$\mathbf{r}(\mathbf{h}) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [z(x_i) - z(x_{i+h})]^2$$

Where $z(x_i)$ is a measured sample value at point x_i , $z(x_{i+h})$ is the sample value at point x_{i+h} , and N(h) is the total number of sample point contrasts or couples for an interval in question. The resulting plot of r(h) versus all evaluated h is the semi-variogram; the shape of this plot describes the degree of autocorrelation present. The parameters of the modeled variogram include (1) the distance over which data are correlated (the range A_0); (2) the level of random variation within the data (the nugget C_0); and (3) the total variation present (the sill $C_0 + C$). By definition, the value of the variogram at a distance of 0 is equal to 0 (i.e., data at the same location are identical). The nature of the spatial variability of the data is depicted by the overall shape of the variogram (Isaaks and Srivastava, 1989; Webster and Oliver, 1990). All these parameters of the semivariogram were calculated by software of Geostatistic Analysis (GS⁺) (He et al., 2007).

3. Results

3.1. Changes in distribution characteristics of dominant species over time

The distribution frequency of density and cover of *N. sphaerocarpa* in 2002 exhibited power functions. About 35% of quadrats were bare land, and the density and cover of *N. sphaerocarpa* in > 80% of quadrats was smaller than 5 clump/100m² and 5%, respectively (Fig. 1a, b). However, frequency of density and cover of *N. sphaerocarpa* in 2016 exhibited normal distribution. Density of *N. sphaerocarpa* in 71.5% of quadrats was between 5 and 10 clump/100m². Cover of *N. sphaerocarpa* in 76.4% of quadrats was between 5% and 15% (Fig. 1e, f). Again, about 28.1% of quadrats were bare land, and the density and cover of *R. soongorica* in > 83.2% of quadrats were smaller than 5 clump/100m² and 0.5%, respectively, in 2002 (Fig. 1c, d). In 2016, the density of *R. soongorica* in 37.5% of quadrats was between 30 and 50 clump/100m². Cover of *R. soongorica* in 67.8% of quadrats was between 4% and 6% (Fig. 1g, h).

3.2. Changes in plant and environmental characteristics of dominant species over time

The density of two dominant species increased between 2002 and 2016 from $1.52 / 100 \text{ m}^{-2}$ to $11.95 / 100 \text{ m}^{-2}$ for *N. sphaerocarpa*, and from 1.56% to 8.13% for *R. soongorica*. The cover increased between 2002 and 2016 from $2.34 / 100 \text{ m}^{-2}$ to $42.6 / 100 \text{ m}^{-2}$ for *N. sphaerocarpa*, and from 0.23% to 4.48% for *R. soongorica* (Table 2). Total species richness increased over time (Fig. 2). The depth of groundwater significantly decreased from 2002 to 2016, while annual precipitation changed with a quadratic function (Fig. 3). Soil water content of different layers increased from 2002 to 2016 (Fig. 5). Correlation analysis shows that there were strong positive correlations between soil water

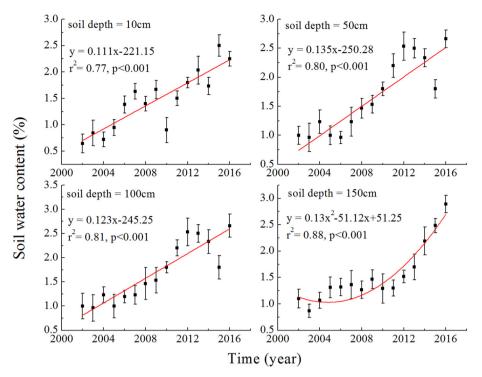


Fig. 5. Changes in soil water content with different layers from 2002 to 2016.

content and species richness, and strong negative correlation between soil water content and the depth of groundwater (Table 3). The correlation between the depth of groundwater and species richness was also strong negative (Table 3). And there were no significantly correlations between total precipitation and soil water content, groundwater depth, species richness (Table 3). But species richness was positive related to summer precipitation (Table 3, Fig. 4).

3.3. Spatial heterogeneity and patterns of dominant species in 2002 and 2016

Some parameters of the semi-variogram models of two dominant species populations differed greatly between the two time periods (Table 4, Fig. 6). The nugget value (C_0), sill ($C + C_0$), and range (A_0) of density and cover of *N. sphaerocarpa* increased rapidly between 2002 and 2016. Changes in C_0 , ($C + C_0$), and A_0 of density and cover of *R. sphaerocarpa* exhibited the same tendency as *N. sphaerocarpa* (Table 4). The nugget-sill ratio of the semi-variogram of the two populations was 0.077–0.116 in 2002, and 0.066–0.144 in 2016. This indicated that the spatial heterogeneity occupied 7.7% -11.6% in 2002, and 6.6% - 14.4% in 2016. In 2002, the range value (A_0) of density and cover was 33.09 m and 14.7 m for *N. sphaerocarpa*, and 24.9 m and 25.2 m for *R. sphaerocarpa*, respectively. In 2016, A_0 of density and cover was 37.2 m and 30.3 m for *N. sphaerocarpa*, and 57.3 m and 75 m for *R. sphaerocarpa*, respectively (Table 4).

Spatial patterns of the two dominant species changes significantly over time (Fig. 7). *N. sphaerocarpa* population exhibited strip distribution in 2002, with a direction of south to north and small strips (Fig. 7a). However, the number and area of strips significantly increased, while the direction remained the same in 2016 (Fig. 7b). *R. soongorica* population exhibited uniform distribution in 2002 (Fig. 7e); in 2016, the uniform pattern changed to a big-strip distribution with a direction of south to north (Fig. 7f).

4. Discussion

4.1. Changes in population characteristics of dominant species over time

Theoretically, the density of populations and species will increase continuously if the resources such as soil water, nutrition, light, and space are sufficient (Harper, 1977). In reality, however, population density will reach a stable value because resources in every habitat are limited (Harper, 1977; Vospernik and Sterba, 2015). When resources are no longer adequate to support normal growth of all species, growth of some species will decrease, and some species will eventually die (Burkhart and Tomé, 2012). Under these conditions, the strong competition effect may restrict the growth and development of some species (Weigelt et al., 2005; Mason et al., 2012), leading in turn to a decrease in density and cover of less-competitive species, some of which will eventually disappear from the community (Chesson et al., 2004; Suttle et al., 2007). In this study, we found that the density and cover of two dominant species and the total species number of the whole community increased significantly between 2002 and 2016 (Table 2, Fig. 1). This indicated that resources, especially soil water and space, were abundant for the two dominant species. Additionally, we found numerous small seedlings of both, N. sphaerocarpa and R. sphaerocarpa, in 2016. We concluded that the two populations were still at a growth stage, and that their densities and cover would continue to increase.

Patch size, cover, and diversity of zonal vegetation are highly related to depth of groundwater, and precipitation (He and Zhao, 2004). Species composition and spatial pattern differed significantly across a precipitation gradient from semi-desert to extremely arid regions (Zhao and Cheng, 2001; He and Zhao, 2006). In arid and semiarid ecosystems, vegetation cover is a suitable ecological indicator as it is closely related to soil water content and ground water depth (Cui and Shao, 2005). Our study also found strong correlations between soil water content and species richness, and the cover of dominant species (Table 3). Soil water content of different layers was significantly positively related to groundwater depth and summer precipitation (Table 3). Species richness was increased with the increase of summer precipitation (Fig. 4). The explanation was that rainfall events in our study area can be

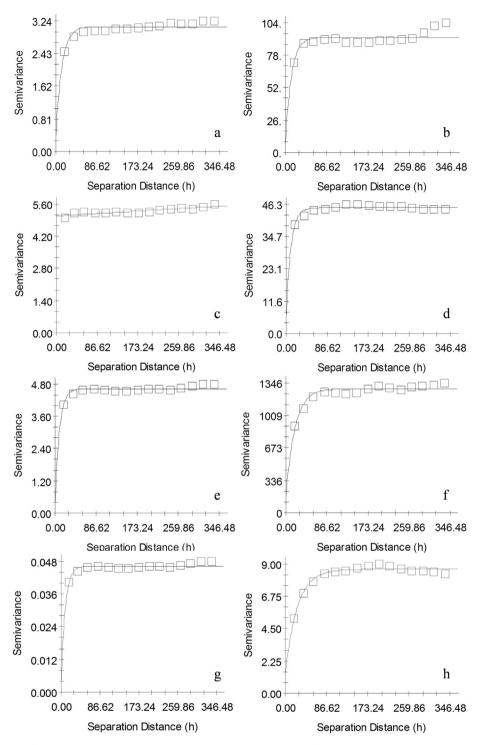


Fig. 6. Semivariogram for spatial continuous data layers (a, density of *N. sphaerocarpa* in 2002; b, density of *N. sphaerocarpa* in 2016; c, cover of *N. sphaerocarpa* in 2002; d, cover of *N. sphaerocarpa* in 2016; e, density of *R. sphaerocarpa* in 2002; f, density of *R. sphaerocarpa* in 2016; g, cover of *R. sphaerocarpa* in 2002; h, cover of *R. sphaerocarpa* in 2002; h, cover of *R. sphaerocarpa* in 2016; e, density of *R. sphaerocarpa* in 2002; f, density of *R. sphaerocarpa* in 2016; g, cover of *R. sphaerocarpa* in 2002; h, cover of *R. sphaerocarpa* in 2016; g, cover of *R. sphaerocarpa* in 2002; h, cover of *R. sphaerocarpa* in 2016; g, cover of *R. sphaerocarpa* in 2002; h, cover of *R. sphaerocarpa* in 2016; g, cover of *R. sphaerocarpa* in 2002; h, cover of *R. sphaerocarpa* in 2016; g, cover of *R. sphaerocarpa* in 2002; h, cover of *R. sphaerocarpa* in 2016; g, cover of *R. sphaerocarpa* in 2002; h, cover of *R. sphaerocarpa* in 2016; g, cover of *R. sphaerocarpa* in 2016; g, cover of *R. sphaerocarpa* in 2002; h, cover of *R. sphaerocarpa* in 2016; g, cover of *R. sphaerocar*

characterized as rainfall pulses with discontinuous and highly variable which can trigger a cascade of ecosystem responses that affect plant water utilization and soil water cycling (Li et al., 2013; Zhou et al., 2017). > 62.5% of precipitation was concentrated in summer (Li et al., 2013). Shallow soil water was mainly supplemented by large precipitation event in summer and autumn while deep soil water was supplemented by groundwater (Li et al., 2013; Zhou and Zhao, 2015; Zhou et al., 2017). For example, one 24.8 mm rain event can significantly increase soil water content with the depth about 1.5 m, but one 8.0 mm rain event can only change water content of surface layer with the depth of 20 cm (Zhou and Zhao, 2016; Zhou et al., 2017). The root distribution patterns of adults of both *N. sphaerocarpa* and *R. sphaerocarpa* were similarly, about 70.6% and 90.2% proportion of root were distributed between the soil depth of 0–50 cm, and only 4.02% and 3.2% were under the depth of 1.5 m (Yang et al., 2013; Zhou, 2016). Thus, their main water sources was shallow soil water which mainly supplied by summer precipitation. On the other hand, although soil water content and species richness were significantly related to

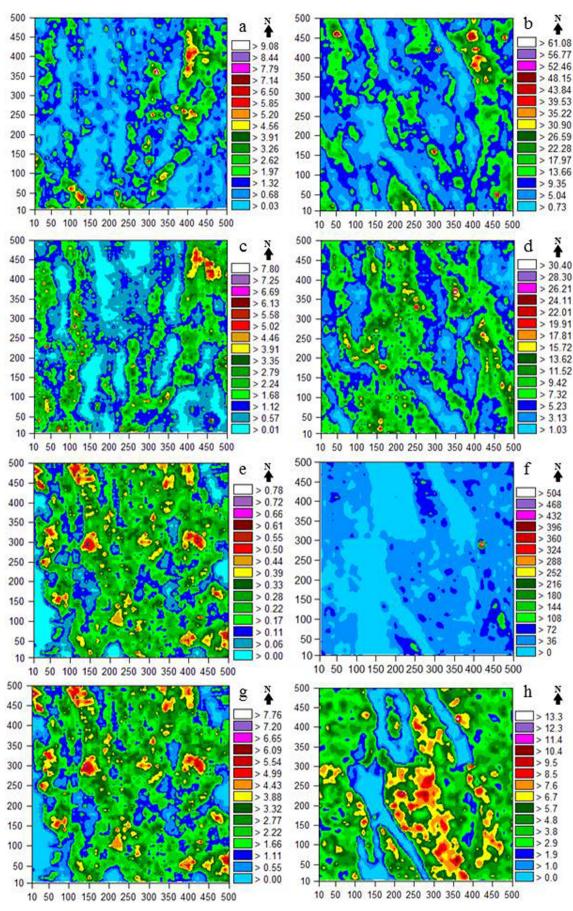
61.08

N

26.21

N

Å



⁽caption on next page)

Fig. 7. Spatial pattern of density and cover of two dominant species population using Kriging interpolation method (X and Y axes are in m, density is in clump/ $100m^2$, and cover is in %; and b, density of *N. sphaerocarpa* in 2002 and 2016; c and d, cover of *N. sphaerocarpa* in 2002 and 2016; e and f, density of *R. sphaerocarpa* in 2002 and 2016; g and h, cover of *R. sphaerocarpa* in 2002 and 2016).

groundwater depth according to statistical analysis, but both the shrubs and herbs could not absorb groundwater because the groundwater table was too depth (about 11 m). This indicated that in this region, population characteristics of dominant species were controlled by soil water content which was closely related to summer precipitation.

4.2. Spatial pattern of dominant species over time

Climatic conditions, soil properties, and plant communities are specific in arid and semi-arid ecosystems (Baird and Wilby, 1999). For example, plant communities have a specific spatial pattern in desert regions because rainfall events are discontinuous, highly variable, and largely unpredictable (Noy-Meir, 1973). Plant-soil dynamics and differential water availability in the soil can be the cause of particular vegetation patterns (Vincenot et al., 2016). A previous study indicated that vegetation spatial patterns and the ratio of precipitation (P) and potential evaporation (Ep) were strongly correlated; thus, across regions where P/Ep > 1 to regions P/Ep < 0.3, vegetation patterns changed from continuous forest and meadow, to patchy vegetation (Baird and Wilby, 1999). In our research area, the P/Ep = 0.05 (average annual precipitation = 117.1 mm and average annual potential evaporation = 2390 mm), and the vegetation pattern was discontinuous patchy (Fig. 6).

Plant spatial patterns are the result of processes operating at different spatial scales, and they may respond to changes in conditions such as water availability (Couteron and Lejeune, 2001; Rietkerk et al., 2002; Alados et al., 2004). For example, vegetation spatial pattern and total runoff produced by the largest rain events were strongly related (Bautista et al., 2007). Increasing plant diversity had a positive effect on soil and water availability, and changed the spatial pattern of vegetation (Bautista et al., 2007). We found that *N. sphaerocarpa* was distributed in small patches, and *R. sphaerocarpa* in long belts in both 2002 and 2016 (Fig. 6). The areas of patches and belts in 2016 were larger than those in 2002 (Figs. 5, 6). More of the *N. sphaerocarpa* and *R. sphaerocarpa* were distributed in the south and east directions, close to the oasis. The main reason is that some part of the study area was closed to grazing, thus more seedlings were saved. And as a result, patch areas and density were increased.

4.3. Spatial heterogeneity of dominant species over time

According to the principles of geostatistics, the value of nugget (C_0) represents the level of random variation. The value of sill $(C_0 + C)$ represents the level of total variation, with higher numbers indicating a higher degree of spatial heterogeneity. The value of (A_0) represents the distance over which data are correlated. The value of $C_0 / (C_0 + C)$ is the ratio of random to total spatial heterogeneity, which consists of random and autocorrelated spatial heterogeneity (Trangmar et al., 1985; Li and Reynolds, 1995; Robertson et al., 1997; He et al., 2007). We found that for N. sphaerocarpa, the C_0 of density increased from 0.346 in 2002 to 6.1 in 2016, and cover from 0.410 in 2002 to 5.90 in 2016, with the density and cover of *R. sphaerocarpa* exhibiting a similar trend (Table 4). This indicated that the degree of random variation in density and cover of the two populations increased from 2002 to 2016. The values of density and cover for both populations in 2002 were significantly higher than those in 2016 (Table 4), which indicated that the degree of total spatial heterogeneity of both populations significantly increased between 2002 and 2016. In 2002, the value of C_0 / $(C_0 + C)$ of density and cover of both populations was between 0.077 and 0.116, indicating that the random variance of spatial heterogeneity was 7.7–11.6% and autocorrelated spatial heterogeneity was

88.4–92.3% of total spatial heterogeneity. Similarly, in 2016, the random variance of spatial heterogeneity occupied 1.6–13.1%, and autocorrelated spatial heterogeneity occupied 86.9–98.4% of total spatial heterogeneity.

Spatial heterogeneity is a function of scale (Cressie, 1991; Li and Reynolds, 1995), and the degree of spatial correlation in population characters differs across scales (He et al., 2007). Spatial correlation existed when the scale was less than A_0 , but disappeared when the scale was larger than A_0 (Li and Reynolds, 1995; He et al., 2007). We found that in 2002, the A_0 of density and cover of both populations in our study were between 14.7 m and 33.09 m, indicating that the scale of spatial correlation was 33.09 m. In 2016, the A₀ of density and cover of both populations were between 30.2 m and 75 m, indicating that the scale of spatial correlation was 75 m. Our results confirmed earlier ones in that the scales of spatial correlation changed with time or habitats (Dickinson and Norton, 2011). However, if the scale was smaller then, the environmental factors which affect spatial heterogeneity of populations cannot be completely inclusive. And the data between sampling quadrats has significant difference, and the difference is enough to cover up the difference which causing by spatial station. Thus, the parameters of spatial heterogeneity cannot reflect the real spatial patterns of populations. On the other hand, if the scale was too large, the data between sampling quadrats trend in homogeneous and the degree of heterogeneity will decrease. Thus, those data cannot reflect the real spatial patterns of populations either (Li and Reynolds, 1995; He et al., 2007). Selection of a suitable scale is critical for revealing real spatial patterns of plant communities.

5. Conclusions

Based on an in situ investigation and geo-statistical theory and methods, we described temporal changes in population characteristics, and in spatial patterns and heterogeneity of density and cover of two shrub populations in the transition zone between oasis and desert. We concluded that the total species number of the whole community, and the density and cover of two dominant species significantly increased between 2002 and 2016. Spatial patterns of two dominant species also significantly changed. Summer precipitation was the key factor affecting population characteristics. The likely mechanism included a rise in summer precipitation that led to an increase in soil water content and finally, to changes in the spatial patterns of plants.

Acknowledgments

We would like to thank Dr. Kathryn B. Piatek (kbpiatek@gmail. com), a US-based forest ecologist, for her assistance with English language editing and valuable comments on this article. We gratefully acknowledge the journal's anonymous reviewers for their valuable comments on our manuscript. This study was supported by the National Natural Science Foundation of China subsidization project (Grant No. 41471435).

References

- Aguiar, M.R., Sala, O.E., 1999. Patch structure, dynamics and implications for the functioning of arid ecosystems. Trends Ecol. Evol. 14 (7), 273–277.
- Alados, C.L., Elaich, A., Papanastasis, V.P., Ozbek, H., Navarro, T., Freitas, H., et al., 2004. Change in plant spatial patterns and diversity along the successional gradient of mediterranean grazing ecosystems. Ecol. Model. 180 (4), 523–535.
- Baird, A., Wilby, R., 1999. Eco-hydrology: Plants and Water in Terrestrial and Aquatic Environments. Routledge.
- Barbier, N., Couteron, P., Lejoly, J., Deblauwe, V., Lejeune, O., 2006. Self-organized vegetation patterning as a fingerprint of climate and human impact on semi-arid

W. Luo et al.

ecosystems. J. Ecol. 94 (3), 537-547.

- Bautista, S., Mayor, A.G., Bourakhouadar, J., Bellot, J., 2007. Plant spatial pattern predicts hillslope runoff and erosion in a semiarid Mediterranean landscape. Ecosystems 10 (6), 987–998.
- Belnap, J., Phillips, S.L., Sherrod, S.K., Moldenke, A., 2005. Soil biota can change after exotic plant invasion: does this affect ecosystem processes? Ecology 86 (11), 3007–3017.
- Burkhart, H.E., Tomé, M., 2012. Modeling Forest Trees and Stands. Springer Netherlands.
- Burton, J.I., Mladenoff, D.J., Clayton, M.K., 2011. The roles of environmental filtering and colonization in thefine-scale spatial patterning of ground-layer plant communities in northtemperate deciduous forests. J. Ecol. 99 (3), 764–776.
- Chesson, P., Gebauer, R.L.E., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M.S.K., et al., 2004. Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. Oecologia 141 (2), 236–253.
- Condit, R., Ashton, P.S., Baker, P., Bunyavejchewin, S., Gunatilleke, S., Gunatilleke, N., et al., 2000. Spatial patterns in the distribution of tropical tree species. Science 288 (5470), 1414–1418.
- Couteron, P., Lejeune, O., 2001. Periodic spotted patterns in semi-arid vegetation explained by a propagation-inhibition model. J. Ecol. 89, 616–628.
- Cressie, N.A.C., 1991. Statistics for Spatial Data. John Wiley and Sons, New York. Cui, Y.L., Shao, J.L., 2005. The role of ground water in arid/semiarid ecosystems,
- Northwest China. Ground Water 43 (4), 471–477. Deangelis, D.L., 2012. Self-organizing processes in landscape pattern and resilience: a
- review. In: International Scholarly Research Notices, 2012, pp. 4–6.
- Deblauwe, V., Barbier, N., Couteron, P., Lejeune, O., Bogaert, J., 2008. The global biogeography of semi-arid periodic vegetation patterns. Glob. Ecol. Biogeogr. 17, 715–723.
- d'Herbes, J.M., Valentin, C., Tongway, D.J., 2001. Banded vegetation patterns and related structures. In: Tongway, D.J., Valentin, C., Seghieri, J. (Eds.), Banded Vegetation Patterning in Arid and Semiarid Environments; Ecological Processes and Consequences for Management. Springer, Heidelberg, pp. 1–19.
- Dickinson, Y., Norton, D.A., 2011. Divergent small-scale spatial patterns in New Zealand's short tussock grasslands. N. Z. J. Ecol. 35, 76–82.
- Getzin, S., Wiegand, T., Wiegand, K., He, F., 2008. Heterogeneity influences spatial patterns and demographics in forest stands. J. Ecol. 96 (4), 807–820.
- Harper, J.L., 1977. Population Biology of Plants. Academic Press, London/New York.
- He, Z.B., Zhao, W.Z., 2004. Spatial pattern of two dominant shrub populations at transitional zone between oasis and desert of Heihe River Basin. Chin. J. Appl. Ecol. 15 (6), 947–952.
- He, Z.B., Zhao, W.Z., 2006. Characterizing the spatial structures of riparian plant communities in the lower reaches of the Heihe River in China using geostatistical techniques. Ecol. Res. 21 (4), 551–559.
- He, Z.B., Zhao, W.Z., Chang, X.L., 2007. The modifiable areal unit problem of spatial heterogeneity of vegetation communities in the transitional zone between oasis and desert. Acta Phys. Sin. 28 (5), 616–622.
- Isaaks, E.H., Srivastava, R.M., 1989. An Introduction to Applied Geostatistics. Oxford University Press, New York, pp. 520–561.
- Komac, B., Alados, C.L., Bueno, C.G., Gómez, D., 2011. Spatial patterns of species distributions in grazed subalpine grasslands. Plant Ecol. 212, 519.
- Li, H., Reynolds, J.F., 1995. On definition and quantification of heterogeneity. Oikos 73 (2), 280–284.
- Li, F., Zhao, W., Liu, H., 2013. The response of aboveground net primary productivity of desert vegetation to rainfall pulse in the temperate desert region of Northwest China. PLoS One 8 (9), e73003.

Maestre, F.T., 2004. On the importance of patch attributes, environmental factors and

past human impacts as determinants of perennial plant species richness and diversity in mediterranean semiarid steppes. Divers. Distrib. 10 (1), 21–29.

- Mason, T.J., French, K., Russell, K., 2012. Are competitive effects of native species on an invader mediated by water availability? J. Veg. Sci. 23 (4), 657–666.
- Mayor, Á.G., Bautista, S., Small, E.E., Dixon, M., Bellot, J., 2008. Measurement of the connectivity of runoff source areas as determined by vegetation pattern and topography: a tool for assessing potential water and soil losses in drylands. Water Resour. Res. 44 (10), 2183–2188.
- Noy-Meir, I., 1973. Desert ecosystems: environment and producers. Annu. Rev. Ecol. Syst. 4, 25–51.
- Pascual, M., Guichard, F., 2005. Criticality and disturbance in spatial ecological systems. Trends Ecol. Evol. 20, 88–95.
- Perry, G.L.W., Enright, N.J., Miller, B.P., Lamont, B.B., 2012. Do plant functional traits determine spatial pattern? A test on species-rich shrublands, Western Australia. J. Veg. Sci. 24 (3), 441–452.
- Rietkerk, M., Boerlijst, M.C., Van, L.F., Hillerislambers, R., Jv, D.K., Kumar, L., Prins, H.H.T., de Roos, A.M., 2002. Self-organization of vegetation in arid ecosystems. Am. Nat. 160 (4), 524.
- Rietkerk, M., Dekker, S.C., de Ruiter, P.C., Van, d.K.J., 2004. Self-organized patchiness and catastrophic shifts in ecosystems. Science 305 (5692), 1926–1929.
- Robertson, G.P., Klingesmith, K.M., Klug, M.J., et al., 1997. Soil resources, microbial activity, and primary production across an agricultural ecosystem. Ecol. Appl. 7, 158–170.
- Suttle, K.B., Thomsen, M.A., Power, M.E., 2007. Species interactions reverse grassland responses to changing climate. Science 315 (5812), 640–642.
- Trangmar, B.B., Yost, R.S., Uehara, G., 1985. Application of geostatistics to spatial studies of soil properties. Adv. Agron. 38, 44–94.
- Vincenot, C.E., Carteni, F., Mazzoleni, S., Rietkerk, M., Giannino, F., 2016. Spatial selforganization of vegetation subject to climatic stress-insights from a system dynamicsindividual-based hybrid model. Front. Plant Sci. 7, 636.
- Vospernik, S., Sterba, H., 2015. Do competition-density rule and self-thinning rule agree? Ann. For. Sci. 72 (3), 379–390.
- Webster, R., Oliver, M.A., 1990. Statistical Methods in Soil and Land Resource Survey. Oxford University Press, New York, pp. 146–176.
 Weigelt, A., Steinlein, T., Beyschlag, W., 2005. Competition among three dune species:
- Weigelt, A., Steinlein, T., Beyschlag, W., 2005. Competition among three dune species: the impact of water availability on below-ground processes. Plant Ecol. 176 (1), 57–68.

Yang, H.T., Li, X.R., Liu, L.C., Jia, R.L., Wang, Z.R., Li, X.J., Li, G., 2013. Biomass allocation patterns of four shrubs in desert grassland. J. Desert Res. 33 (5), 1340–1348.

Zelnik, Y.R., Kinast, S., Yizhaq, H., Bel, G., Meron, E., 2013. Regime shifts in models of dry land vegetation. Phil. Trans. R. Soc. A 371, 20120358.

- Zhao, W.Z., Cheng, G.D., 2001. Review of several problems on the study of eco-hydrological processes in arid zones. Chin. Sci. Bull. 46 (22), 1851–1857.
- Zhao, W.Z., Liu, B., 2010. The response of sap flow in shrubs to rainfall pulses in the desert region of China. Agric. For. Meteorol. 150, 1297–1306.
- Zhou, H., 2016. Root distribution and water use strategies of typical desert shrubs in an oasis edge of Hexi corridor. In: PhD Thesis. University of Chinese Academy of Sciences.
- Zhou, H., Zhao, W.Z., 2015. Root distribution of *Nitraria sibirica* with seasonally varying water sources in a desert habitat. J. Plant Res. 128, 613–622.
- Zhou, H., Zhao, W.Z., 2016. Response of soil moisture to precipitation pulse by stable isotope in desert area of the Hexi Corridor. J. Desert Res. 36 (6), 1637–1645.
- Zhou, H., Zhao, W.Z., Zhang, G.F., 2017. Varying water utilization of *Haloxylon ammodendron* plantations in a desert-oasis ecotone. Hydrol. Process. 31, 825–835.