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RESEARCH ARTICLE

Spatial patterns and associations of dominant woody species in desert–oasis ecotone of South Junggar Basin, NW China

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Spatial patterns and associations of plant species are important for revealing how species interact with each other and with the environment, and hence have important implications for the understanding of species interaction and underlying ecological processes with apparent patterns in temperate desert vegetation. In this paper, the function $g(r)$ was used to characterize the spatial patterns and associations of four dominant woody species in three 1-ha desert plant plots in the desert–oasis ecotone of South Junggar Basin, NW China. The complete spatial randomness null model showed four species exhibited significant aggregations at small scales (<20 m). *Anabasis aphylla* and *Nitraria roborowskii*, *Haloxylon ammodendron* and *Reaumuria songarica* were spatially positive associations at small scales with the independent null model, while *A. aphylla* and *H. ammodendron*, *A. aphylla* and *R. songarica*, *R. songarica* and *N. roborowskii* species pairs exhibited negative associations at small or moderate scales (20–60 m) in our study. The random labeling null model showed that dead standing plants of *A. aphylla* were largely determined by the combined effects of intra- and interspecific competition. In addition, the results also indicated that the two main factors of habitat heterogeneity and sandy desertification play important roles in determining spatial distribution patterns and associations of woody species in the desert–oasis ecotone of South Junggar Basin. Thus, the differences of species features in spatial patterns and associations should be paid more attention when planning afforestation and developing conservation strategies.

Keywords: spatial pattern; spatial association; habitat heterogeneity; desert–oasis ecotone; South Junggar Basin

Introduction

Spatial patterns of plants are important characteristics of vegetation and play a significant role in ecological processes, including competitive coexistence and transmission of mortality, and have impacts that scale up to ecosystem-level processes (Alekseev & Zherebtsov 1995; Arévalo & Fernández-Palacios 2003). However, many factors play important roles in determining the spatial patterns of tree species distribution in a plant community. In general, biotic and abiotic factors may influence the distribution of species and potentially control their abundance and promote coexistence (Zhang et al. 2010; Schleicher et al. 2011). Furthermore, many species also exhibited ecological habitat preferences, although species richness and associations are different among sites (Bazzaz 1991; Cheng et al. 2014). In addition, theoretical models also confirmed the coexistence of plant species based on habitat heterogeneity (Tilman & Pacala 1993).

Both intra- and interspecific competition should be considered to understand the dynamics of the component species (He & Duncan 2000; Nishimura et al. 2005). Conversely, the spatial patterns of plants affect competition (Duncan 1991; Hara et al. 1995; Kubota & Hara 1995). Regular patterns have been historically viewed as the result of intense competition for limited resources, such as available water or soil resources (King &

Woodell 1973; Phillips & MacMahon 1981; Skarpe 1991). Intraspecific aggregation has been attributed to environmental heterogeneity (Schenk et al. 2003; Perry et al. 2009), seed dispersal (Schurr et al. 2004), and plant interactions (Phillips & MacMahon 1981; Tirado & Pugnaire 2003). In most arid communities, interspecific aggregation of forbs, grasses, and juvenile woody plants around bigger shrubs and trees is often interpreted as evidence of facilitation (Brooker et al. 2008; Rayburn & Wiegand 2012; Wang et al. 2013).

Desert–oasis ecotone is an important constituent of oasis ecosystem and has a vital role in maintaining the stability of oasis (Li et al. 2007; Su et al. 2007). Meanwhile, the desert–oasis ecotone is more sensitive to disturbance than its adjacent ecosystems (Su et al. 2007). When it is disturbed during exploration or utilization, the ecotone has a potential trend to evolve into the desertified land or shifting sand dunes (Ding & Zhang 2006; Wang et al. 2013). Due to severe sandy desertification and water stress in the desert–oasis ecotone of South Junggar Basin, the community composition is simple, and the richness and species diversity are very low. Now, there are few reports on the interspecific associations and the coexistence mechanisms of the desert species, while some studies on spatial pattern and intraspecific association of the monospecific stands have been recently conducted in the desert–oasis ecotone of South Junggar Basin (Liu et al. 2008;

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Song et al. 2010). In this study, we analyze the spatial patterns and associations of four dominant woody species in the desert–oasis ecotone of South Junggar Basin, NW China. Three main questions are addressed: (1) Do the four dominant woody species in oasis–desert ecotone show an aggregated spatial distribution? (2) Is the habitat occupied by the four dominant woody species associated with the sandy desertification? (3) Do dead standing plants of *Anabasis aphylla* have relation to interspecific competition in consideration of massive mortality?

Materials and methods

Study site

The study area was located on the desert–oasis ecotone spanning an elevation range of 258–265 m in South Junggar Basin, NW China (45°22′43.4″N, 84°50′32.5″E), from July 2010 to September 2010, which is a transitional zone from the oasis to the desert. Geological substrates of the study site include aeolian deposits sandy soil and highly eroded diluvial soil. The mean temperature varies from 5°C to 9°C, minimum winter temperatures from –30°C to –41°C, and maximum summer temperatures from 30°C to 40°C. Snow melts at the end of winter, together with the rainfall, amounts to an annual precipitation of 100–150 mm.

Three typical sample plots (3 ha) were laid out in an area with ecotone or hierarchical distribution between diluvial and sandy soil. The microtopography of three plots is complicated and heterogeneous. The sandy soil area takes up 55–70% and sand layer is 5–35 cm deep. The sand burial depth has different spatial distribution according to the Kriging (Figure 1). The sand burial changes limited water distribution. The mean soil water

content under sand bed was 4.55%, more than bare land (0.81%) in April. In the study area, vegetation cover ranges between 10% and 35%, dominated by *A. aphylla*, *Haloxylon ammodendron*, *Reaumuria songarica*, and *Nitraria roborowskii* (Table 1). Other woody plant species in the area include *Lycium ruthenicum*, *Halostachys caspica*, *Halocnemum strobilaceum*, and *Tamarix ramosissima*.

Data collection

Each plot (100 × 100 m) was divided into 400 contiguous 5 × 5 m quadrates, as the basic unit of vegetation survey, using the DQL-1 forest compass (Harbin Optical Instrument Factory, China). All woody plants, including living and dead standing ones, were investigated. The species names, relative location of each individual, height, crown width (the greatest diameter of the vertical projection of the crown in two directions, i.e. north–south or east–west), and microhabitat (e.g. soil surface, depression patch) were recorded.

Data analysis

The examination of spatial point patterns is often carried out using the second moment function K to test the null hypothesis that a point pattern is spatially random (Diggle 2003). Ripley's K -function is a cumulative function of the points within a distance r , i.e. each bigger radius includes points of a smaller radius, and it is possible that information from two different scales may interfere with each other. The pair correlation function $g(r)$, also known as the O -ring statistic (Wiegand & Moloney 2004), is an alternative statistic that estimates the number of points within concentric rings at the

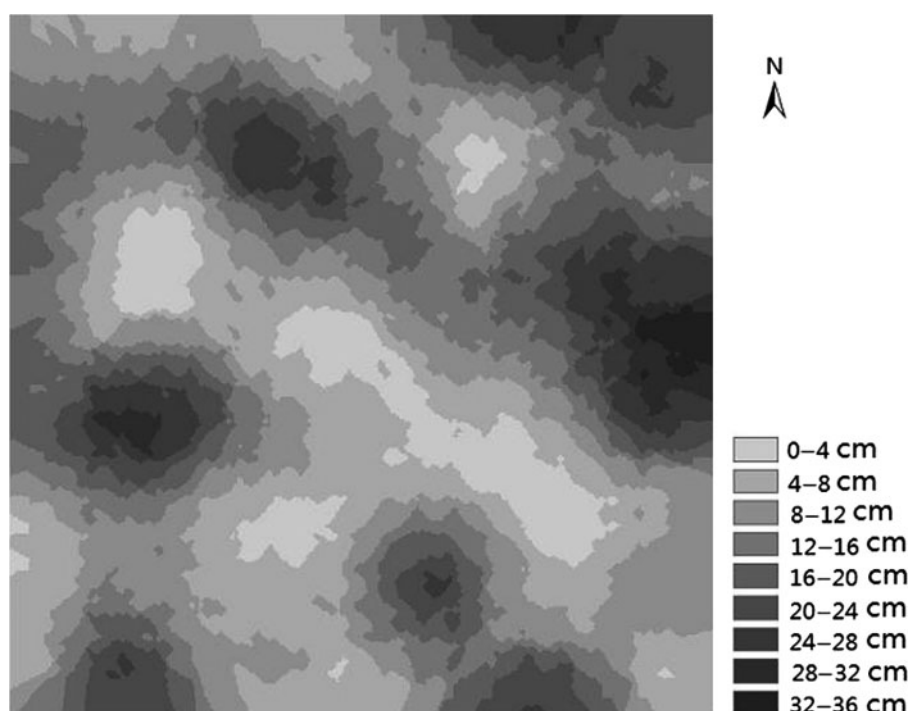


Figure 1. Distribution map of sand burial depth in the 100 × 100 m plot.

Table 1. Basic feature of woody plants in the study plot.

Species	Mean height (cm)	Mean canopy (cm)	Living plants density (individual/ha)	Dead standing plants density (individual/ha)
<i>A. aphylla</i>	47.7	55.3	4372	1372
<i>H. ammodendron</i>	88.2	107.5	1262	106
<i>R. songarica</i>	44.6	46.5	237	17
<i>N. roborowskii</i>	49.2	87.8	276	8
Others	53.1	43.6	108	23

distance r rather than within a radius. The accumulative K -function can detect aggregation or regularity up to a given distance r and is therefore appropriate if the process in question (e.g. the negative effect of competition) may work only up to a certain distance, whereas the function $g(r)$ can detect aggregation or regularity at a given distance r . The function $g(r)$ has the additional advantage that it is a probability density function with the interpretation of a neighborhood density, which is more intuitive than an accumulative measure (Stoyan & Penttinen 2000).

In this study, the univariate function $g(r)$ was used to analyze the spatial patterns of different species, and the bivariate function $g(r)$ was adopted to analyze the spatial associations among different species in the plots. For the univariate analyses, we used the null model of complete spatial randomness (CSR) as a null hypothesis (Wiegand & Moloney 2004; Getzin et al. 2008), because the spatial distributions of plants in the three plots seem to be affected significantly by drought stress and habitat heterogeneity (e.g. soil patch and micro topography). We examined the spatial association between the two species with the independent null model (Wiegand & Moloney 2004). For univariate analysis, if $g(r)$ above the upper confidence limit indicates aggregation, while $g(r)$ below the lower confidence limit indicates regularity. For bivariate analysis, if at a given distance r , $g_{12}(r)$ is above the upper (or below the lower) limit of the confidence envelope, it indicates that species 2 is positively (or negatively) associated with species 1 at the distance r . Function $g_{12}(r)$ is within the confidence intervals, which indicates that there is no interaction between species 1 and 2.

Contrary to the two spatial approaches, we investigated the spatial relation between the distributions of dead standing and living plants, and the random labeling null model was used to detect possible differences in the spatial distribution of dead standing plants compared with the distribution of living plants regardless of the underlying first-order process (Wiegand & Moloney 2004). Random labeling has not been frequently used in forestry research, but it has been implicitly used to assess 'random mortality', considering labels as the living and dead standing plants categories (Kenkel 1988). We used the case-control design with living plants of four species as pattern 1 (control pattern) and *A. aphylla* dead standing plants as pattern 2 (cases). Thus, a difference of $g_{12}(r)$ and $g_{11}(r)$ provides insights

into the spatial distribution of *A. aphylla* dead standing plants around living plants of four species in relation to the spatial distribution of living plants to each other (Getzin et al. 2008; Schleicher et al. 2011). The second comparison, $g_{12}(r) - g_{11}(r)$, can be used to evaluate the spatial distribution of dead standing plants. For example, a positive deviation would mean that dead standing plants exhibited an aggregated spatial distribution in comparison to adult plants (Getzin et al. 2006, 2008; Schleicher et al. 2011). To perform the random labeling analysis, the spatial position of all plants in the plot remained fixed, but the labels of the points (living plants or dead standing plants) were randomly assigned to the overall pattern (Bailey & Gatrell 1995).

In addition, the intensity of spatial patterns or spatial associations is defined as the magnitude of the deviation from randomness or independence (Rebertus et al. 1989). All analyses were conducted in the Programita software package (Wiegand & Moloney 2004). The distance r represents spatial scales within 100 m in the present paper. In all analyses, we used a 1-m cell size, which is a fine enough resolution to answer our questions, and a ring width of one cell. We calculated the statistics up to a scale r of 100 m (100 cells) taking into account plot size. Ninety-nine Monte Carlo simulations were used to generate 99% confidence envelopes.

Results

Stand structure

The total number of woody plants in the plot was 7781 individuals (6255 living and 1526 dead standing), consisting of eight species, eight genus, and three families. *A. aphylla* population was in possession of the dominance of spatial occupation capacity before sandy desertification in the plot, since 5744 individuals or 73.8% were *A. aphylla* (4372 living and 1372 dead standing) (Table 1). *H. ammodendron* (1262 living and 106 dead standing) was the main associated plant species of *A. aphylla*. *R. songarica* and *N. roborowskii* made up 3.3% and 3.6% of the total number, respectively. The other four species together occupied only 1.7% of the total number. *H. ammodendron* was the most abundant canopy species and showed the largest mean canopy (107.5 cm) and largest mean height (88.2 cm). The largest plant height measured in the plot was for *H. ammodendron* (3.2 m).

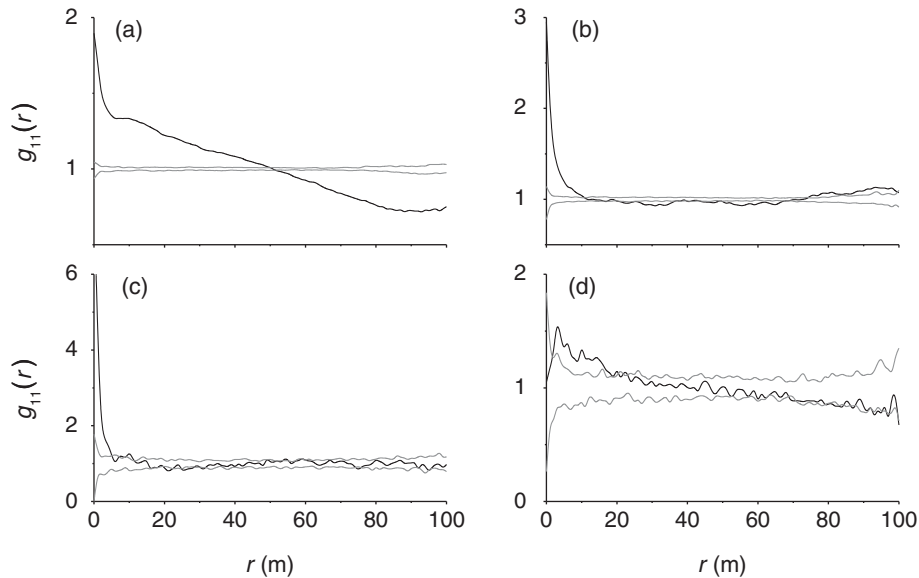


Figure 2. Spatial patterns of four in the study plots analyzed by the univariate function $g(r)$ with the null model of CSR. (a) *A. aphylla*; (b) *H. ammodendron*; (c) *R. songarica*; and (d) *N. roborowskii*.

Spatial patterns

The spatial distribution of the four dominant woody species was analyzed by the living plants (Figure 2). *A. aphylla* was distributed all over the plot. Analysis of the spatial pattern of *A. aphylla* showed that the population was significantly aggregated at all distances between 0 m and 52 m (Figure 2a). *H. ammodendron* population was significantly aggregated at 0–12 m and tended to regular spatial distribution at 12–74 m (Figure 2b). *R. songarica* population showed significantly aggregated distribution at 0–6 m and tended to random spatial distribution at scales >12 m (Figure 2c). *N. roborowskii* population was significantly aggregated at 2–20 m and tended to random spatial distribution at other scales (Figure 2d).

Spatial associations

In the plots, *A. aphylla* significantly had a negative association at 0–3 m, 7–17 m, 32–34 m, 39–41 m, and 42–53 m with *H. ammodendron* (Figure 3a). *A. aphylla* and *R. songarica* was spatially negative association at 0–41 m (Figure 3b). *A. aphylla* and *N. roborowskii* was spatially no association within 1 m scales, and was a positive association at 1–60 m (Figure 3c). *H. ammodendron* and *R. songarica* showed positive association at 0–3 m, and negative association at 11–13 m and 15–26 m (Figure 3d). *H. ammodendron* and *N. roborowskii* had spatially positive association at 19–60 m, but at <19 m scales, they were spatially independent (Figure 3e). *H. ammodendron* and *N. roborowskii* were spatially

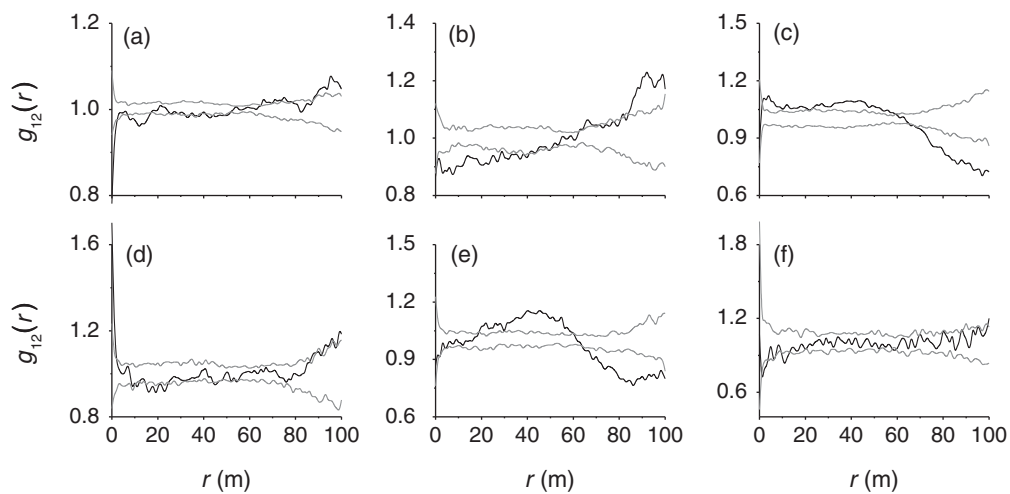


Figure 3. Spatial association between species in the study plots with the null model of independence. (a) *A. aphylla*–*H. ammodendron*; (b) *A. aphylla*–*R. songarica*; (c) *A. aphylla*–*N. roborowskii*; (d) *H. ammodendron*–*R. songarica*; (e) *H. ammodendron*–*N. roborowskii*; and (f) *R. songarica*–*N. roborowskii*.

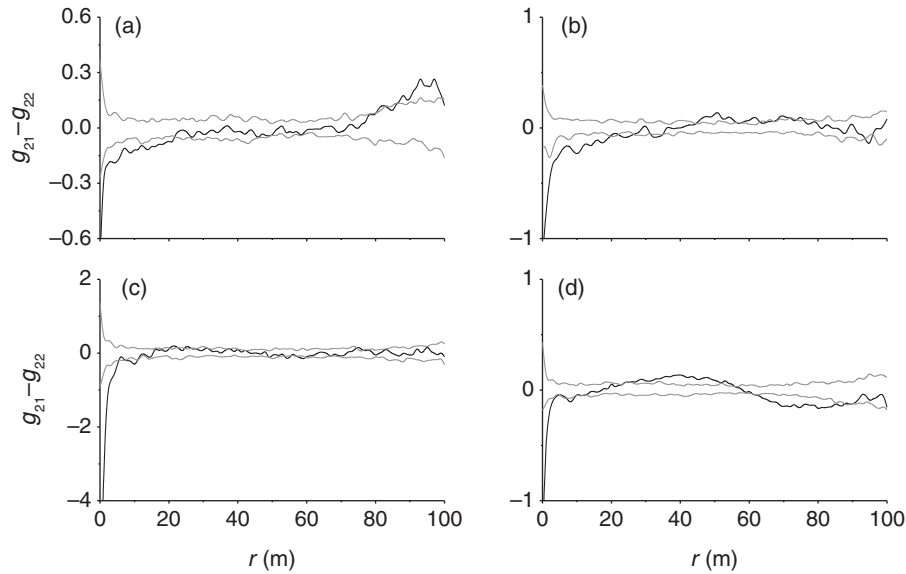


Figure 4. Spatial association between dead standing plants of *A. aphylla* and living plants in the three study plots with the null model of random labeling. (a) *A. aphylla*–dead standing plants of *A. aphylla*; (b) *H. ammodendron*–dead standing plants of *A. aphylla*; (c) *R. songarica*–dead standing plants of *A. aphylla*; and (d) *N. roborowskii*–dead standing plants of *A. aphylla*.

negative association at 2–5 m and 9–14 m; they were spatially independent at other scales (Figure 3f).

For dead standing plants of *A. aphylla* in the plots, the test statistic $g_{21}(r) - g_{22}(r)$ differed significantly from the random labeling null model at 0–23 m, indicating an additional aggregation of dead standing plants of *A. aphylla* independent of *A. aphylla* plants pattern (Figure 4a). Similarly, the test statistic $g_{21}(r) - g_{22}(r)$ revealed strong departures from random labeling pointing to an aggregation mechanism of dead standing plants of *A. aphylla* independent of *H. ammodendron* plants pattern at 0–21 m, 22–26 m, and 32–35 m (Figure 4b). In addition, there was a very strong aggregation among dead standing plants independent from dead standing plants of *A. aphylla* and *R. songarica* plants relation at 0–6 m and 8–12 m, and dead standing plants of *A. aphylla* and *N. roborowskii* plants were spatially positive association at 0–5 m and 8–13 m (Figure 4c and 4d).

Discussion

Aggregated pattern of desert woody species

Aggregated distribution in species is a widespread pattern in nature (Prentice & Werger 1985; Wang et al. 2013; Cheng et al. 2014). This issue also is especially relevant and common in arid and semi-arid shrub lands (Prentice & Werger 1985). In our study, four dominant desert woody species mainly showed aggregated patterns as well at small scales (<20 m) in the desert–oasis ecotone of South Junggar Basin, NW China. Similarly, the spatial aggregation distribution of *H. ammodendron* plants at small scales was exhibited in four soil textures by Song et al. (2010). Aggregation can often be explained simply in terms of regeneration near to seed sources, habitat heterogeneity, or perhaps in safe sites associated with older, larger individuals of one's own or

other species (Zhang et al. 2010, 2013; Myster 2013). In the study sites, the microtopography, such as depression, runnel, and sandy mound, leads to the high habitat heterogeneity of community. There can be no doubt that these seed traps played a role in the maintenance of the aggregated structure. In the plots, we found that variation in depression corresponded closely with the distribution of *A. aphylla* seedling number. The relative depression, representing the gradients of microhabitat conditions such as water and salt, was one of the most important variables for predicting the ecesis condition of the species. Moreover, in the sand texture, there should be more plant available water than in finer-textured clay soils due to the high infiltration rate, deep percolation, and less evaporation of capillary water in coarse soil (McAuliffe 1994; Zou et al. 2010). For example, *H. ammodendron* subtrees developed more feeder roots in sandy compared with heavy textured soil, showing that plants at coarse soil have a greater need to develop more roots (Zou et al. 2010). It is worth mentioning that water is often the most limiting resource in semi-arid and arid area (Sheng et al. 2004). Small-scale variation in vegetation, soil surface cover, and soil texture alters the amount of water available to plants (Whitford 2003; Zou et al. 2010). Therefore, we inferred that habitat heterogeneity is considered to be the most likely factor that leads to water assemble and population aggregation.

Spatial associations and competition of desert woody species

As an important natural selection pressure of plant distribution in desert areas, desertification plays an important role on the community succession (Maun 1998; Peng et al. 2012; Xu et al. 2012). Some studies showed that sand burial can enhance the seed germination and seedling emergence of the sand burial-tolerant shrubs

(Zhang et al. 2010; Wang et al. 2013). During the process of wind and sand disturbance in woody plant communities of Junggar Basin, strongly sand burial-tolerant subtree *H. ammodendron* plays a expand role after sand invasion, and moderate sand burial-tolerant shrub *R. songarica* and *N. roborowskii* can maintain growth in the early sandy desertification, while the occurrence of weakly sand burial-tolerant subshrub *A. aphylla* is gradually reduced and die. Therefore, this difference in density of the species can be caused by (1) niche differences, with *H. ammodendron* preferring sandy soil and *A. aphylla* preferring diluvial soil and (2) a competitive effect, in which *H. ammodendron* subtrees may be a stronger competitor on the sandy soil than *A. aphylla*, *R. songarica*, and *N. roborowskii*.

A. aphylla and *N. roborowskii*, *H. ammodendron* and *R. songarica* showed spatially positive associations at smaller scales, indicating that they prefer the similar habitats. However, spatial negative associations between species provide indirect evidence of habitat differentiation (He et al. 1997; Bunyavejchewin et al. 2003). *A. aphylla* and *H. ammodendron*, *A. aphylla* and *R. songarica*, *R. songarica* and *N. roborowskii* species pairs exhibited negative associations at small or moderate scales in our study, suggesting the importance of soil habitat differentiation. Habitat specialization based on niche differentiation of resources could be the reason that different tree species are best suited to different habitats (Harms et al. 2001). In the plots, the dominant woody species therefore coexist and are strongly associated with various habitats that require for survival and recruitment. Some studies have revealed the importance of topographical variations in determining the species coexistence (Sri-ngernyuang et al. 2003; Yamada et al. 2006). Our study results showed that the soil variations in the desert and oasis transition belt determine the co-occurrence of woody species after sandy desertification.

Cao et al. (2005) reported that the niche breadths of most original species decreased and those of psammophytic species increased accordingly in the process of desertification. This process weakens the plant growth and can affect some plant survival (Maun & Lapierre 1986; Zhang & Maun 1990; Yu et al. 2001). The random labeling null model showed that the aggregation of dead standing plants of *A. aphylla* was strong around *A. aphylla*, *H. ammodendron*, *R. songarica*, and *N. roborowskii* plants, indicating intense intra- and interspecific competition after sandy desertification. Intraspecific and interspecific interactions determine the structure and dynamics of ecological communities and their responses to environmental change (Mangla et al. 2011). Results indicated that the dead standing plants of *A. aphylla* mainly caused by inter- and intraspecific competition in changing harsh environments (desertification).

Conclusions

We suggested that habitat heterogeneity and sand burial were two primary driving forces for spatial patterns and

associations of woody plant community in the desert-oasis ecotone of South Junggar basin, NW China. Spatial pattern analyses showed that the aggregated patterns of woody plant community may be formed by the habitat heterogeneity such as microtopography and limited water distribution. Meanwhile, sand burial seems to be the main force driving community succession. This process causes the species with weakly sand burial tolerance to degenerate and psammophytic species to expand. Such studies could contribute to the understanding of species interaction and underlying ecological processes with apparent patterns in temperate desert vegetation.

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