

Cross-spatial-scale patterns in the facilitative effect of shrubs and potential for restoration of desert steppe

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ABSTRACT

Facilitation (positive plant–plant interactions) is a potential means to accelerate vegetation restoration in arid areas. Shrubs can accelerate vegetation recovery by means of soil amelioration, but this effect has not been evaluated at large spatial scales or across scales. Here, we examined the facilitative function of shrub change across spatial scales at a desert steppe in Mongolia. Using a high-resolution satellite image, we established five 2500 m² plots in each of three shrub density classes (low, moderate, high) in a desert steppe in Mongolia. To evaluate the facilitative functions of shrubs at multiple spatial scales, we recorded the total number of plant species at three nested spatial scales in each plot: 25, 400, and 2500 m². The facilitative effect of shrubs on plant species richness was more pronounced at larger scales. Denser shrub communities increased plant species diversity at a larger scale. However, the increased taxonomic diversity was not clearly related to increased functional diversity in this system. This scale dependency in species diversity can be explained by the degree to which spatial heterogeneity of habitats within the plots increased as plot size increased. These results support the hypothesis of scale-dependent changes in the balance between facilitation and competition. Therefore, transplanting shrub saplings at high-density and a larger scale could potentially improve the success of vegetation restoration in arid regions.

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1. Introduction

Degradation in arid–semiarid ecosystems is impairing the ability of local peoples to effectively use the biological, physiological, and ecological resources of this land (Wezel and Rath, 2002), but also has serious consequences like poverty at a global scale. Human activities in arid areas depend strongly on the ecosystem services provided by arid–semiarid ecosystems, including the provision of food, foliage resources, and soil stabilization. It is therefore necessary to restore the ecosystem functions provided by these ecosystems and ensure sustainable management so that local peoples can continue to enjoy ecosystem services while striking a balance between sustainable production and preventing degradation.

Facilitation, an ecological term that describes positive plant–plant interactions, has received considerable attention as a tool to accelerate vegetation restoration processes, particu-

larly in arid areas (Flores and Jurado, 2003; Padilla and Pugnaire, 2006; Brooker et al., 2008). Planting of trees or shrubs in sandy land to control desertification and provide a more favorable environment for other species is an example of this approach (Zhang et al., 2004). Shrub establishment increases the content of fine soil particles, soil moisture, and seed density in the soil. Furthermore, it enhances the accumulation of organic C and increases total N, and decreases pH in proximity to the shrubs (Facelli and Temby, 2002; Su and Zhao, 2003; Zhao et al., 2007). This soil amelioration results in greater diversity, density, height, cover, and above-ground and belowground biomass of herbaceous species (Facelli and Temby, 2002; Su and Zhao, 2003; Zhang et al., 2004; Zhao et al., 2007). In addition, grazing-sensitive plants growing close to shrubs can be protected from herbivory, particularly if the shrub species have spines, toxic fruits or leaves (Rebollo et al., 2002). Consequently, the species richness of understory plants is related to the size of the individual shrubs according to a simple power relationship for a wide array of species (Maestre and Cortina, 2005). The facilitative effects of planted shrubs generally increase as the shrubs develop, but after a certain point of development the effectiveness eventually diminishes due to competition for light and other resources (Reisman-Berman, 2007). To fully benefit

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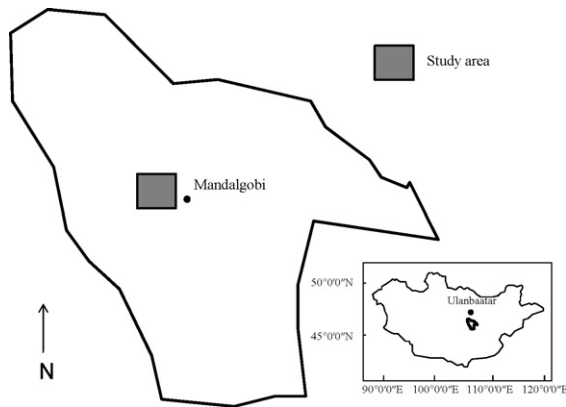


Fig. 1. Overview of the study area, inset: location of the Saintsagaan soum (country) in the Mongolia.

from the facilitative action of shrubs, tall plants must be able to avoid competition with the shrubs for light and other resources such as water (Pihlgren and Lennartsson, 2008).

The relative importance of the parameters that control ecological processes appears to vary with the spatial scale (Bissonette, 1997; Gascoigne et al., 2005), and this can alter the nature or magnitude of the facilitative effect. In sandy grasslands in eastern Asia, individual shrubs trap wind-blown sands, and soil mounds develop beneath the shrub canopy. As the mounds grow, the overall surface roughness of a site increases, and the wind velocity and sand transport rate both decrease (Li et al., 2002; He et al., 2008). These environmental changes can promote vegetation recovery at larger spatial scales through ecological processes that differ from those that function at the scale of individual shrubs. Nevertheless, most studies of shrub facilitation effects have been conducted at a single small scale, as in studies of the relationship between shrubs and their neighbors (Zhao et al., 2007; Tewksbury and Lloyd, 2001). Studies that have evaluated the function of shrubs at large scales or across spatial scales remain scant. Thus, in the present study, we examined whether the facilitative function of shrubs changed across spatial scales, and whether such changes had implications for enhancing sustainable use of Mongolian rangelands. Our hypothesis was that the facilitation effect would be enhanced at larger scales.

Species diversity is commonly used as an indicator of ecosystem function and therefore of the services provided by an ecosystem and its health (including the recovery processes it is undergoing). However, unless the taxonomic and functional diversity are strongly correlated, taxonomic diversity cannot serve as a surrogate for functional diversity (Naeem, 2002; Micheli and Halpern, 2005). The degree to which taxonomic and functional diversity are correlated has not been reported for most ecosystems (Naeem, 2002). In Mongolian rangeland ecosystems, plant communities generally exhibit functional redundancy (Sasaki et al., 2009); that is, two or more species often serve similar functions. We therefore compared not only species richness but also functional richness.

2. Materials and methods

2.1. Site description

Our study area was situated near Mandalgobi (45°46'N, 106°16'E) in Mongolia, which is in the country's steppe and desert steppe ecological zones (Fig. 1). Summer and winter temperatures average around 19 and -14°C , respectively. Annual rainfall averages around 170 mm (coefficient of variance = 28%), most of which is received during the summer. Vegetation on sandy soil in the area

is characterized by a mixture of patchily distributed shrubs and herbs. The shrub species found most frequently in the study area are *Caragana* spp. (Fabaceae, *Caragana microphylla*, *C. leucophloea*, and *C. pygmaea*), and it is assumed that the region's sandy soil, which is dominated by large particles, is suitable for their establishment (Sasaki et al., 2008). The study area has a long history (centuries) of grazing by domestic livestock under nomadic or semi-nomadic patterns of land use.

2.2. Satellite image and ground truthing

We designed the present study to test the hypothesis that shrub density at a large spatial scale would affect ecological processes at that scale and would thereby affect vegetation recovery. However, we found it difficult to estimate shrub density at a large scale in the field. To solve this problem, we obtained a panchromatic imagery with a spatial resolution of 0.7 m captured by a QuickBird satellite in the summer (July 14th) of 2008 (Fig. 2). An object-oriented classification was performed on the imagery that covers 64 km² study area, using eCognition professional 4.0 (Definiens Imaging GmbH). Pixels were identified as shrubs or non-shrub cover through a series of segmentation and classification after the workflow of Laliberte et al. (2004). We also randomly located fifteen 400 m² ground truthing plots in the study area, measured shrub areas and density manually, and compared shrub cover/density from the classification of the QuickBird image with those ground-based measurements. After confirming that the positions were correct, we selected a total of 15 areas, with 5 areas at each of the three levels (low, moderate, high) of shrub density. At the center of each area, we established a 2500-m² (50 × 50 m) plot (Fig. 2). To avoid spatial autocorrelation between plots, the plots were separated by at least 1000 m, but remained within the same general landscape position.

2.3. Field survey

In mid-August 2008, we counted the number of *Caragana* shrubs within the 15 plots. To formulate a description of shrub and mound structure, we measured the major axis (the longest diameter of shrub viewed from above), minor axis (the shortest diameter of shrub viewed from above), shrub height, and mound height for each shrub. We also systematically established ten 1 × 1 m quadrats within each plot and collected the aboveground vegetation sample on each quadrat. These vegetation samples were dried in a forced-air oven at 70 °C for 48 h to determine the plant biomass. Because facilitative effects can be altered by grazing intensity (Smit et al., 2007), we estimated the grazing intensity based on the density of livestock dung. We counted the number of sheep and goat dung on the ten quadrats. To evaluate the facilitative functions of the shrubs at multiple spatial scales, we recorded the total number of plant species at three nested spatial scales in each plot: 25 m² (5 × 5 m extent), 400 m² (20 × 20 m extent), and 2500 m² (50 × 50 m extent).

To investigate the soil texture, we extracted five paired core samples (10-cm diameter × 15-cm depth) from mounds and inter-mound sample points in each plot. For each plot, we homogenized the mound samples into one bulk sample, and did the same for the inter-mound samples. In the laboratory, we determined the soil particle size distribution (coarse sand, fine sand, and the silt and clay contents) of each homogenized sample using the criteria of ISSS (1994).

2.4. Data analysis

Because the shrubs were either round or elongated, we calculated the canopy size of each shrub based on the assumption that

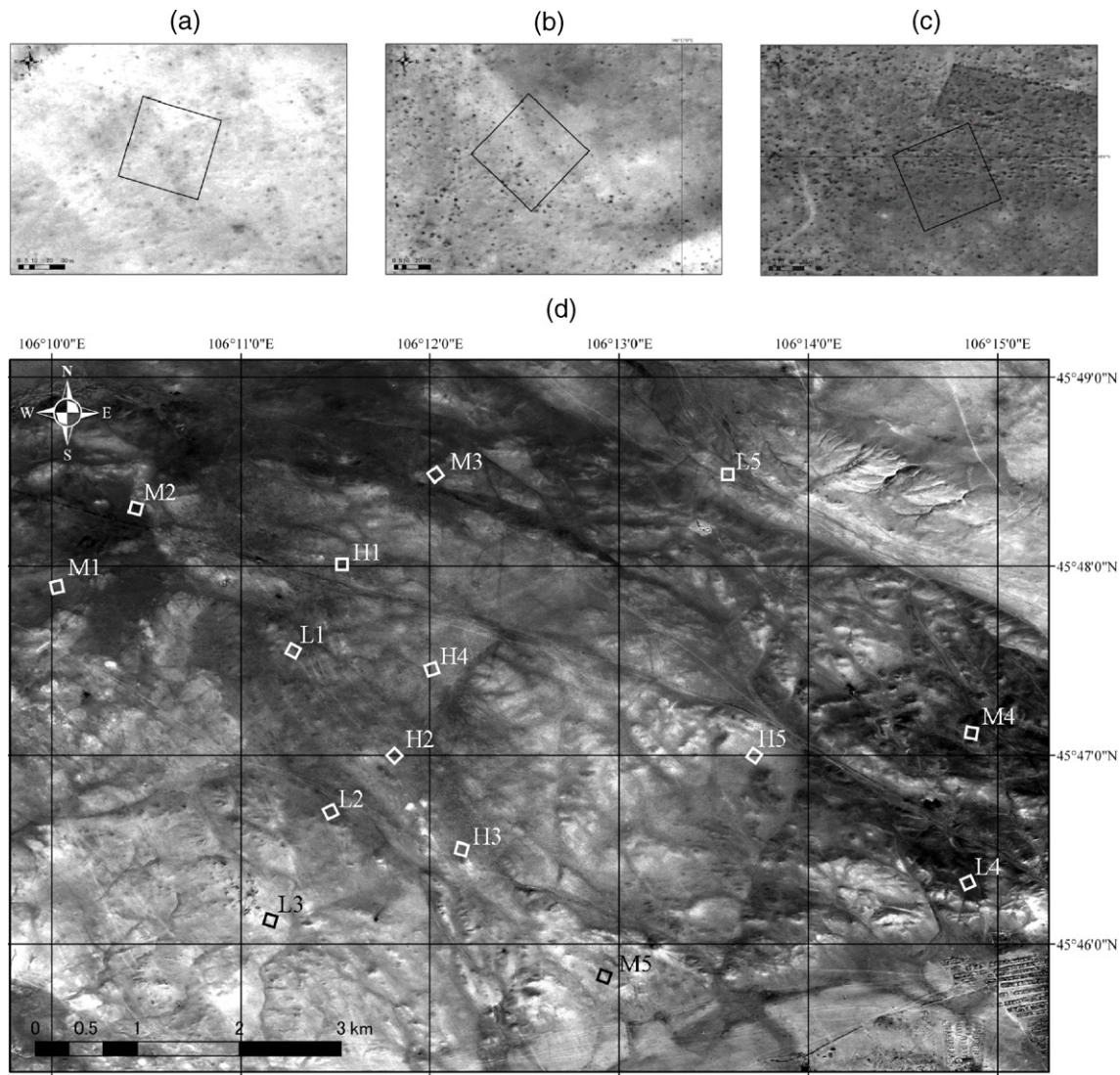


Fig. 2. QuickBird panchromatic images (0.7-m resolution) showing (a–c) enlarged images of the study plots and (d) the overall study site in western Mandalgobi, with the locations of individual plots indicated. (a) Plot L3 (low-density shrubs), (b) plot M4 (moderate-density shrubs), and (c) plot H1 (high-density shrubs). Based on ground truthing, the dark dots in (a) and (b) were confirmed to be mostly shrubs, and the undulating surfaces and dark areas in (c) are mostly shrub mounds and their shadows. Boxes represent the 2500-m² study plots where the field survey was conducted.

the canopy could be modeled as an ellipse, and used the major and minor axes to calculate the area. We further calculated the total shrub area within a plot as the mean canopy size × the number of shrubs, and the shrub cover as the total shrub area × 100/plot area (Table 1).

We selected several functional traits of species that are considered key to determining their role within an ecosystem (Sasaki et al., 2009), for a total of 33 categories of 8 plant functional traits (Table 2). We compiled this trait data from an existing reference on Mongolian flora (Grubov, 1982), supplemented with information

Table 1
Structural characteristics of the shrubs and soil mounds in each density level.

Shrub density		Number of shrubs	Shrub size						
			Major axis (cm)	Minor axis (cm)	Canopy size (cm ²)	Shrub area (m ² /plot)	Cover (% of plot area)	Shrub height (cm)	Mound height (cm)
Low	Mean	60.4	53.7	37.4	1596	8.0	0.3	14.0	5.5
	SD (within plots)	–	31.1	15.8	1876	–	–	5.9	5.2
	SD (between plots)	61.2	16.8	16.2	1535	7.9	0.3	8.0	3.6
Moderate	Mean	157.2	63.0	48.4	3550	55.5	2.2	18.2	6.5
	SD (within plots)	–	42.7	32.3	5278	–	–	7.2	6.8
	SD (between plots)	65.1	15.7	13.7	1977	32.0	1.3	1.9	2.1
High	Mean	461.2	92.2	70.4	7866	361.4	14.5	21.1	17.1
	SD (within plots)	–	70.1	52.6	12,884	–	–	9.6	14.6
	SD (between plots)	75.9	7.5	6.4	1513	79.6	3.2	2.0	3.4

Table 2
Plant functional traits and the related categories used in our analyses. “Multiple membership” defines whether a species can belong to more than one category for a trait.

	Plant functional trait	Trait categories	Multiple membership
1	Growth form	Grass; forb; sub-shrub (only woody at the base); shrub	No
2	Life history	Annual; biennial; herbaceous perennial; woody perennial	Yes
3	Lateral spread	Erect (solitary); tussock; branched; prostrate	Yes
4	Phylogenetic group	Monocotyledon; dicotyledon	No
5	Leaf margin	Entire; toothy; revolute; thorny	Yes
6	Leaf shape	Linear; lanceolate; elliptical; ovate or obovate; oblong; round	Yes
7	Leaf form	Entire; lobed; pinnatisect; pinnate; multipinnate	Yes
8	Leaf attachment	Opposite; alternate; decussate; fasciculate	Yes

provided by Jigjidsuren and Johnson (2003), and validated these data with field observations.

We analyzed differences in dung density and plant biomass among the treatments using univariate ANOVA after confirming the assumption of homogeneity of variance. Species and functional richness were analyzed using two-way ANOVA to examine the interaction terms between shrub density and spatial scale. *Post hoc* comparisons using the least-significant-difference (LSD) test were performed to test for statistically significant differences between shrub density levels. We conducted principal components analysis (PCA) on the correlation matrix at the plot level to find relationship between shrub density and soil particle size distribution, using the PC-ORD software (version 4.0; McCune and Mefford, 1999). We used LSD test to compare statistically the contents of coarse and fine particles in soil samples among the mounds and inter-mound at three shrub density levels. These analyses were performed using the Statistica 6.0J software (Systat Inc.).

3. Results

We found a mean of 6.66 (SD=4.17) pieces of dung per m² across all the study plots, indicating that grazing intensity was relatively low. There were no significant differences in dung density between the shrub density levels ($F=2.13$, $P=0.160$, d.f. = 2). Species richness showed a significant density \times scale interaction ($F=2.73$, $P=0.044$, d.f. = 4, Fig. 3). However, functional richness showed no density \times scale interaction ($F=1.85$, $P=0.138$, d.f. = 4, Fig. 3). Species richness did not differ significantly among shrub densities at a 5 \times 5 m scale ($P=0.236$) or at a 20 \times 20 m scale ($P=0.950$), but was significantly higher in the high-density plots at the 50 \times 50 m scale ($P=0.040$). Shrub density had no significant effect on functional richness at the 5 \times 5 m scale ($P=0.057$), the 20 \times 20 m scale ($P=0.433$), or the 50 \times 50 m scale ($P=0.338$).

There was no obvious difference in the composition of functional traits (based on the functions in Table 2) among shrub densities, but the abundance of late-successional species such as *Stipa* increased as shrub density increased; this species was present in 2 of 5 plots at low shrub density, 3 of 5 plots at moderate density, and 5 of 5 plots at high density. Plant biomass did not differ significantly among density levels ($F=2.62$, $P=0.114$, d.f. = 2), although biomass in the moderate-density plots (16.3 ± 6.1 g/plot, mean \pm SD) and the high-density plots (13.2 ± 4.3 g/plot) were about 2 and 1.5 times the biomass in the low-density plots (9.4 ± 3.4 g/plot).

The soil particle size distribution also differed between the three shrub densities and between positions (Fig. 4). Soil collected from the mounds beneath shrubs showed a significantly greater content of coarse sand than soil from the samples between mounds in each shrub density, but showed no significant difference in clay content (Fig. 5). The difference increased in magnitude with increasing shrub density, and the difference was significant for coarse sand, indicating that the spatial heterogeneity of soil particle size was greater within the high-density plots.

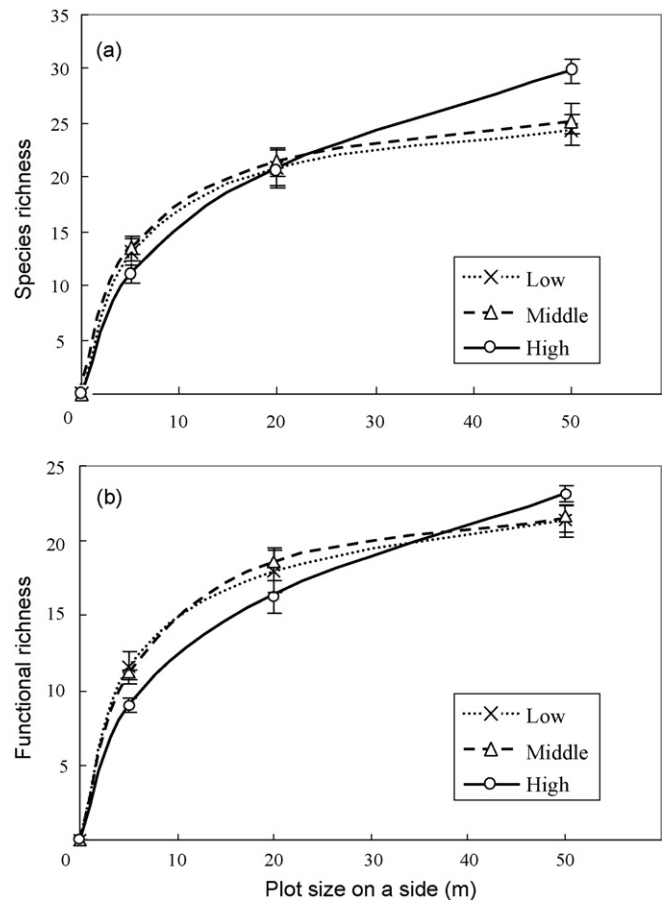


Fig. 3. The (a) species richness and (b) functional richness of plant species as a function of spatial scale at each shrub density. (Values represent means \pm SD.) The curves connect the mean values at the three spatial scales.

4. Discussion

One major finding was that the facilitative effect of shrubs on plant species richness depended on the spatial scale, and the effect was most pronounced at the largest scale. The extent of the facilitation by shrubs, which we represented by the species richness, thus showed a drastic change at a certain shrub density; the dense shrubs increased species diversity at a larger scale. However, this increase in taxonomic diversity was not clearly associated with a comparable increase in functional diversity in this system; although functional diversity increased with increasing scale, the difference among shrub densities was not significant. Sasaki et al. (2009) demonstrated the existence of functional redundancy in plant communities in Mongolian rangelands similar to the one in our study. Plant biomass was positively correlated with the abundance of shrubs, but did not respond to the shrub density in a simple

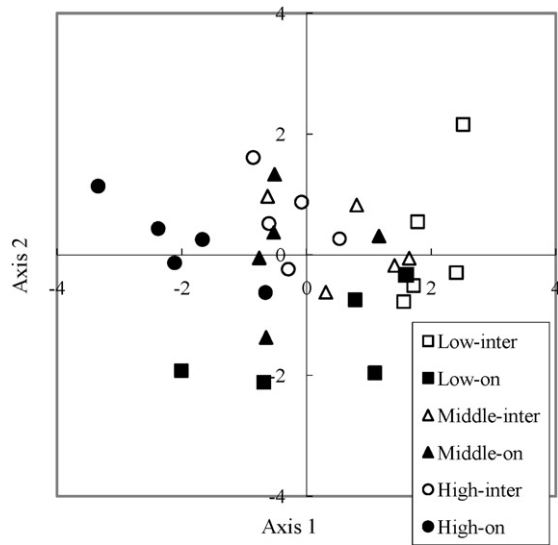


Fig. 4. Principal components analysis (PCA) of the soil particle size taken between the mounds that collected below shrubs (inter-mound) and samples collected from these mounds (on-mound) at each shrub density level.

manner. However, given that the proportion of late-successional plants was the highest in the dense shrub communities, the net effect of shrubs on Mongolian rangeland ecosystems appears to be positive.

There is growing evidence that both positive (i.e., facilitation) and negative (i.e., competition) interactions occur simultaneously between interacting plants (Brooker et al., 2008). Clarifying the mechanisms responsible for the balance between positive and negative interactions in plant communities is a central topic in ecology,

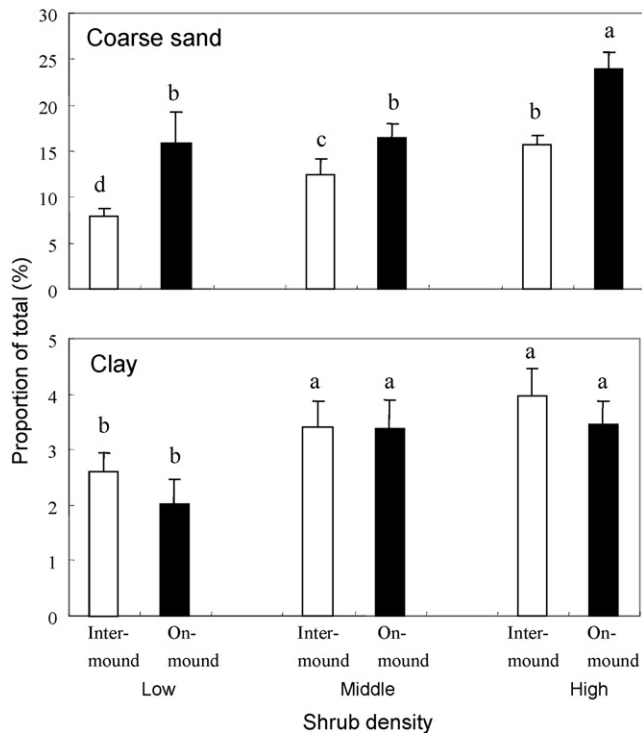


Fig. 5. Proportions of coarse and fine particles in soil samples taken from inter-mounds and on-mounds at each shrub density level. Bars within a particle size class labeled with different letters differ significantly ($P < 0.05$, LSD test). Range bars indicate the standard error of the mean.

thus a number of empirical and theoretical studies have examined this challenging topic. Numerous regulatory factors potentially relevant to these interactions have been proposed. Among the most important factors that have been recently proposed are aspects related to the degree of environmental severity (Callaway et al., 2002), such as water availability (Michalet, 2006; Kikvidze et al., 2006), and the relative resource demands of nurse and protégé plants, including their respective relative growth stages (Miriti, 2006; Reisman-Berman, 2007), the height of the protégé plants (Pihlgren and Lennartsson, 2008), and the relatedness of their taxa (Valiente-Banuet and Verdu, 2008). Our results suggest a shift from negative or neutral interactions at small scales to positive interactions (i.e., increased species and functional richness) at a large scale, even though our field survey was conducted at comparable topographic positions for each scale, suggesting that scale is another key factor that regulates these interactions.

It is difficult to define facilitative versus competitive interactions between plants, because the nature of the interaction varied among the estimators of plant performance that were used to describe the interactions (Gomez-Aparicio et al., 2005). In the present study, we analyzed species and functional richness at multiple spatial scales. Therefore, our results should be interpreted with caution because of the limited number of estimators (species and function). Nonetheless, the differences revealed by our approach suggest that a multi-spatial approach for other estimators of plant performance deserves more attention.

The mean species richness in the high-density plots was lowest at the smallest spatial scale and highest at the largest scale. Because soil nutrient properties between on-mounds and inter-mound areas were comparable (Sasaki et al., 2010), both the spatial heterogeneity of soil particle size and the measurement scale may have determined this pattern. In the high-density plots, the 5×5 m measurement scale contained one or a few mounds, and the mounds that were characterized by coarse particles favored a limited number of sand-dune-specific species (e.g., *Bassia dasyphylla*). The 50×50 m measurement scale contained not only a range of shrub and mound sizes and shapes but also many inter-mound areas, and the inter-mound areas, which were characterized by a higher proportion of fine particles (Fig. 5), favored different species than those that became established on the mounds. Moreover, the increased roughness of the land and increasing amount of spatial heterogeneity of shade at high shrub density may have facilitated the coexistence of species by partitioning the available space into more niches for different plant species (Reisman-Berman, 2007). In contrast, the plots with few shrubs were more physically homogeneous, and exhibited a slower increase in species richness with increasing spatial scale. Interestingly, a similar pattern was seen on and between the mounds created by rodents as a result of the disturbances caused by their burrowing activity (Yoshihara et al., 2009). They established a 50×50 m plot without marmot burrows, and a same-sized plot including burrows in Mongolian grasslands. Each plot was subdivided into 625 adjacent 2×2 m square quadrats. In each quadrat, they recorded the area of ground covered by each species. Due to the spatial heterogeneity created by the mounds, plant species richness in marmot colonies was lower at the 2×2 m scale and higher at the 50×50 m scale than in the plot without burrows.

However, at moderate shrub densities, the facilitative effects on diversity were not clearly expressed compared with the effects at high shrub density. This relationship presumably arises from lower spatial heterogeneity in the moderate-density plots (Table 1). The smaller shrub size in the moderate-density plots may be another reason for this difference. In a previous study, the species richness of protégé plants was related to the area covered by sprouting shrubs (Maestre and Cortina, 2005).

Given that dense shrubs appear to have accelerated the succession process by increasing species diversity, conservation of these shrubs should be a priority for management of ecosystems in this region. Understanding the relationship between facilitation and spatial scale and determining the spatial scale at which the facilitative effect will be maximized will provide guidance for conservation and restoration management. If we had used larger plots than those in the present study, the scale dependency of the diversity pattern would probably increase because both the species richness and the functional richness in the high-density shrub plots had not reached a plateau, even at the 50 × 50 m scale (Fig. 3). Therefore, transplanting shrubs at larger scales and higher densities could potentially improve vegetation restoration in arid regions. However, as for other field experiments, the causal relationship between shrub density and taxonomic diversity is not proved in this study. A manipulative experiment where shrub density is manipulated is needed before take any conclusion related to the causal relationships between shrub density and taxonomic diversity. Once the causal relationship is proved, stronger management recommendations can be given. In addition, in transplanting shrubs we must not ignore the possibility that increasing shrub density beyond the level that can be sustained by the available moisture may actually have adverse effects on vegetation diversity if evapotranspiration by the shrubs lowers the water table excessively, making the surface soils unable to support herbaceous vegetation.

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