

Patterns of shrub species richness and abundance in relation to environmental factors on the Alxa Plateau: Prerequisites for conserving shrub diversity in extreme arid desert regions

LI XinRong[†], TAN HuiJuan, HE MingZhu, WANG XinPing, LI XiaoJun

Shapotou Desert Research and Experiment Station, Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences, Lanzhou 730000, China

Shrub species are considered the dominant plants in arid desert ecosystems, unlike in semiarid steppe zones or in grassland ecosystems. On the Alxa Plateau, northern China, sparse vegetation with cover ranging from 15% to 30% is characterized mainly by multifarious shrubs because herbaceous species are strongly restricted by the extreme drought climate, wind erosion, overgrazing and sand burial. Patterns in shrub species richness and species abundance in relation to environmental conditions were examined by DCA (detrended correspondence analysis) and interpreted by a biplot. The relationships between species diversity and environmental factors were examined using regression analyses. Our results show that the distributions of the shrub species in response to environmental conditions can be grouped into four ecological types, corresponding with the biological traits of the shrubs and their responses to the gradients of soil texture and soil water content. Patterns in species richness and species abundance were mainly determined by the deeper soil water content, instead of the soil texture as hypothesized by numerous studies in semiarid grasslands. With exception of the deeper soil water content, soil organic matter and total N content were positively correlated with species abundance, while pH was negatively correlated with it. These findings imply that it is vital for current shrub diversity conservation to reduce agricultural water use in the middle reaches of the Heihe River, which supplies water for the lower reaches in the western parts of the plateau, and to reduce the amount of groundwater exploitation and urban and oasis water use, to increase the water supply from Helan Mountain to the eastern desert of the Alxa Plateau.

biodiversity conservation, shrub species richness, abundance, Alxa Plateau, desert ecosystems

Currently, most ecosystems are experiencing loss of biodiversity associated with the activities of human expansion, raising the issue of whether the functions and processes of ecosystems will be impaired by this loss of species^[1,2]. In particular, for arid desert ecosystems, numerous studies suggest that it is necessary to understand species richness patterns in relation to the environment before drawing conclusions about the effects of biodiversity loss in ecosystem processes^[3,4]. As desert ecosystems commonly have a sparse vegetation cover and

are characterized by a distinct patchiness comprised of shrubs and herbaceous plants, especially annual plants growing on a soil mound^[5], the importance of the correlations between the patterns of shrub species and annual plants and environmental conditions such as the soil

Received April 4, 2008; accepted October 14, 2008

doi: 10.1007/s11430-009-0054-7

[†]Corresponding author (email: Lxinrong@lzb.ac.cn)

Supported by National Key Technology R & D Program (Grant Nos. 2007BAD46B03, 2006BAD26B0201) and National Natural Science Foundation of China (Grant No. 40825001)

type has long been documented^[6–9]. With respect to these studies, except on the effects of species richness on inter-specific and extra-specific competition and interactions^[10], most researchers focused on the relationship between the distribution of species (woody vs. herbaceous plants) and soil properties^[11–15], as well as the response of species patterns to environmental gradients^[8,16], site heterogeneity^[17–19], scales^[20,21] and disturbances^[22,23]. Most of these studies of species richness in relation to environmental gradients were mainly single-factor studies, although the distribution of species richness is commonly governed by more environmental gradients^[8,24,25]. Previous studies emphasized that heterogeneity created opportunities for species to coexist and increased species diversity because it increased habitat diversity and resource variability^[26,27], leading to the prevention of competitive exclusion between plant species^[28]. In addition, the responses of species richness to different disturbances such as grazing^[29], fire^[30], improving soil fertility^[31] and soil disturbance^[22] have been largely documented. Although the influences of the above environmental factors on patterns of plant species richness in desert ecosystems have been emphasized, few studies have specifically addressed how such influences are affected by varying environmental features on a regional scale, and almost all the above relationships have been tested in herbaceous communities, so studies on shrub species richness are rare^[22,32,33]. Furthermore, few data are available to explain why shrub diversity is conserved under the extreme environmental stress of arid desert ecosystems, even under the strong influence of human activities such as overgrazing.

Shrubs are the dominant plants in the arid desert regions of China^[34,35]. Their presence has long been theorized to contribute to the ecological restoration of degraded desert ecosystems^[12]. In comparison with herbaceous species, shrubs are more tolerant and better adapted to wind erosion, sand burial, grazing disturbance and drought stress, and have lower requirements for soil nutrients^[9]. In the arid desert regions of China, the propagation of herbaceous plants is strongly limited by overgrazing, sand burial and the drought climate^[36]. Therefore, we hypothesize that the pattern of shrub species richness reflects the result of the long-term integration of both interactions between climatic and environmental factors and human activities such as overgrazing and ecological processes in arid desert regions. Hence,

the objectives of this study are to draw out the main factors governing the coexistence of shrubs and further analyze how shrub species diversity is maintained in an extremely arid desert. This study will provide basic knowledge for biodiversity conservation in arid regions.

1 Materials and methods

1.1 Study area

The Alxa Plateau occupies 0.25 million square kilometers of the Inner Mongolia excluded area of Helan Mountain, where the Tengger Desert, Badain Jaran Desert and Ulan Buh Desert are located. It is one of the regions with very serious desertification in China^[37]. Geographically, the Alxa vegetation falls in the Alxa desert province in the central Asian desert sub-zone (Gobi desert sub-zone) in the easternmost part of the Asian desert plant region. In general, the vegetation can be distinguished as four sub-types^[36], namely, typical desert vegetation, steppified desert vegetation, desert steppe vegetation and psammophytic vegetation (Figure 1). The corresponding soils, climatic features, distribution areas and vegetative characteristics are listed in Table 1.

1.2 Investigative design and sampling

(1) Vegetation survey. Field investigations were conducted in the autumns of 2005 and 2006. A total of 133 sampling plots were selected to represent the variability of environmental conditions and plant species composition in the different vegetation subzones (Figure 1). The plot size for vegetation investigation was 10 m × 10 m. For each plot, the species richness (number of species per plot), abundance (total number of each species per plot), height, shrub cover and herbaceous cover were recorded. The shrub canopy cover as a percentage of the ground surface was determined by the method described by Lu and Li^[38]. The sum of the relative density, relative frequency and relative cover gave the important value (*IV*) of each shrub species^[33].

(2) Soil sampling. Soil samples were taken from the topsoil of each plot at a soil depth of 0–10 cm with three replications. Each sample was air-dried, crushed, and passed through a 2 mm sieve. The following parameters were determined: particle size as determined by the pipette method^[39]; soil bulk density was determined by inserting metallic core (0.05 m in depth and diameter) into the soil^[38]; pH was determined with a soil suspen-

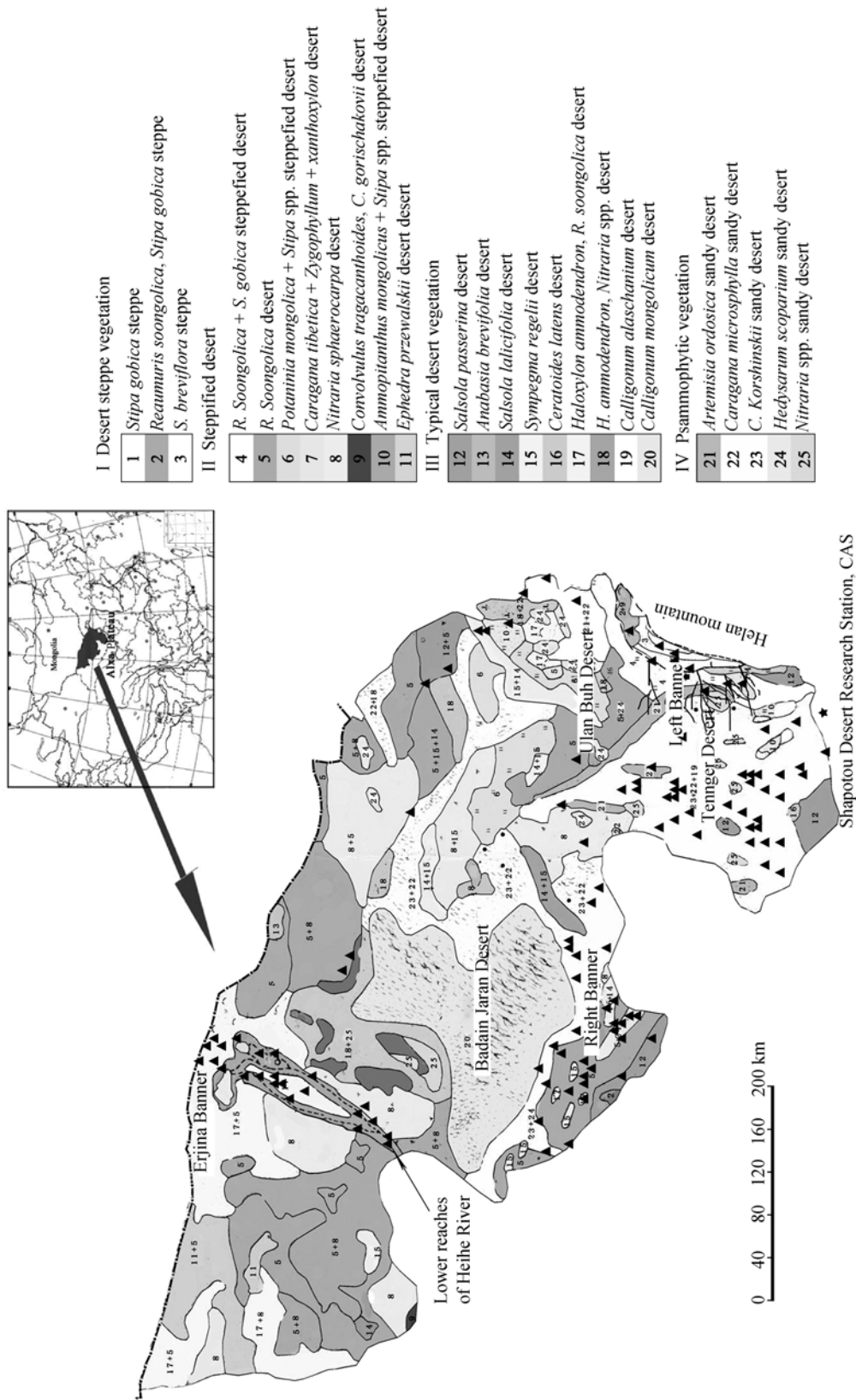


Figure 1 The distribution of vegetation and investigative plots (black triangle marks) on the Alxa Plateau, northern China.

Table 1 Descriptions of the study sites on the Alxa Plateau

Vegetation type	Distribution area of vegetation	Dominant species	Climatic condition		Soil type
			Annual mean temperature (°C)	Annual precipitation (mm)	
Typical desert vegetation	North region of the Helan Mountains, the Tengger Desert and west of the Ulan Buh Desert	<i>Reaumuria soongolica</i> , <i>Pataninia mongolica</i> , <i>Salsola passerina</i> , <i>Ephedra przewalskii</i> , <i>Sympegma regelii</i> and <i>Haloxylon ammodendron</i>	2–7	150–250	Brown soil, mountain gray-cinnamonic soil and chestnut soil of coarse texture
Steppified desert vegetation	Alluvial fan between the Helan Mountains and the Tengger Desert and the low-mountain areas	<i>Salsola passerina</i> , <i>Reaumuria soongolica</i> , <i>Nitraria sphaerocarpa</i> , <i>Zygophyllum xanthoxylum</i> , <i>Caragana tibetica</i> and <i>Oxytropis aciphylla</i>	6–8	100–150	Gray desert soil with surface wind erosion
Desert steppe vegetation	Low-mountain areas of Tao-hua Mountain and Longshou Mountain	<i>Caragana microphylla</i> , <i>C. stenophylla</i> , <i>Ceratoides latens</i> , <i>Kalidium cuspidatum</i> , <i>Nitraria tangutorum</i> and <i>Oxytropis acciphylla</i>	7–8.2	50–100	Gray-brown desert soil, blown sand soil and saline soil
Psammophytic vegetation	Badain Jaran Desert, Tengger Desert and Ulan Buh Desert	<i>Artemisia desertorum</i> , <i>Psammochloa villosa</i> , <i>Hedysarum scoparium</i> and <i>Haloxylon ammodendron</i>	8.3–9.4	80–180	Wind-eroded soil

sion of soil-water in the ratio of 1:5 by a calibrated pH meter (PHS-4, made in China); soil organic matter (OM) was measured by the $K_2Cr_2O_7$ method^[38]; total N was measured by a Kjeltac System 1026 Distilling Unit (Teccator AB, Sweden); and total phosphorus and potassium was measured by the methods described by Knudsen et al.^[40] and Olsen Sommers^[41], respectively. To measure soil water contents, soil samples were collected manually by a soil core sampler during investigative periods and dried at 105°C for 24 h^[38]. Soil samples were taken from above different plots with 3 replicates at 15 different depths: 0.2, 0.4 m, and therefore at every 0.4 to 3.0 m.

(3) Statistical analysis. The differences in plant species richness, abundance and soil parameters among the different sites/plots were studied by using variance analysis (one-way ANOVA). A stand-species data matrix was classified using the *IV* of species by means of two-way indicator species analysis using TWINSpan^[42]. The shrub species responses to environmental conditions were examined by DCA, and a biplot of species diversity was described using CCA (canonical correspondence analysis) combining vegetation and soils, performed using CANOCO^[43]. The relationships between species diversity and environmental factors were examined using regression analyses. These procedures were performed on Windows-based SPSS 10th edition software (Chicago, USA).

2 Results

2.1 Shrub species diversity and its distribution on the Alxa Plateau

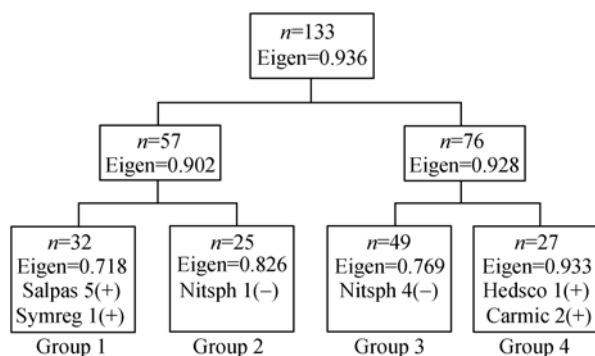
Our investigation shows that 70 varieties of shrub and sub-shrub species occur on the Alxa Plateau. Among them are rare evergreen shrubs such as *Ammopiptanthus mongolicus*; ancient relict species, i.e., *Potania mongolica*, a national protected species, and *Helianthemum songoricum* and *Tetraena mongolica*, national second-class protected species; superior forages, i.e., *Caragana stenophylla*, *C. intermedia*, *C. microphylla*, *C. korshinskii* and *C. roborovskyi* of the bean family, as well as *Ceratoides latens* of the goosefoot family; and valuable medicinal shrubs, i.e., *Prinsepia uniflora*, *Potentilla fruticosa* and *Rosa xanthina* of the rose family, and *Berberis caroli* of the Berberidaceae. However, most of the shrubs occur at a frequency of less than 5% in all the 133 plots as their distribution is confined and limited by sand burial and human activities. Only 33 shrub species with a frequency of more than 5% (Table 2) were considered for TWINSpan classification. Figure 2 indicates that the distribution of these 33 shrubs on the Alxa Plateau was grouped into four site groups.

Group 1 is represented by the *Salsola passerina*-*Sympegma regelii*-*Reaumuria soongolica*-*Caragana stenophylla* steppified desert shrub community type, with a higher shrub abundance (Table 3). In this group of shrub communities, soil properties such as the proportions of

Table 2 The frequency of main shrub species (>5%), occurring in the total investigative plots (n=133)^{a)}

Shrub species	Frequency	Abbreviation
<i>Alhagi sparsifolia</i> Shap. ex Keller et Shap	5.05	Alhspa
<i>Ammopiptanthus mongolicus</i> Cheng	7.01	Ammon
<i>Amygdalus mongolica</i> Ricker	5.07	Amymon
<i>Artemisia ordosica</i> Krasch	13.02	Artord
<i>Atraphaxis bracteata</i> ex Keller et Shap	5.22	Atrbra
<i>Calligonum alaschanicum</i> A. Los.	5.66	Calala
<i>Calligonum mongolicum</i> Turcz.	7.26	Calmog
<i>Caraga korshinskii</i> Kom.	10.77	Carkor
<i>Caragana microphylla</i> Lam.	7.01	Carmic
<i>Caragana pygnaea</i> (L.) DC. Prodr.	8.27	Carpyg
<i>Caragana stenophylla</i> Pojark.	8.51	Carste
<i>Caragana tibetica</i> Kom.	6.26	Cartib
<i>Ceratoides latens</i> Reveal et Holmgren	11.52	Cerlat
<i>Convolvulus gortschakovii</i> Schrenk	11.52	Congor
<i>Ephedra przewalskii</i> Stapf	7.01	Ephprz
<i>Haloxylon ammodendron</i> Bge.	6.26	Halamm
<i>Hedysarum scoparium</i> Fisch. & Mey.	9.26	Hedsco
<i>Kalidium cuspidatum</i> (Ung.-Sternb.) Grub.	7.01	Kalcul
<i>Kalidium gracile</i> Fenzl	5.12	Kalgra
<i>Nitraria sphaerocarpa</i> Maxim.	10.02	Nitsph
<i>Nitraria sibirica</i> Pall.	5.05	Nitsib
<i>Nitraria tangutorum</i> Bobr.	7.76	Nittan
<i>Oxytropis aciphylla</i> Ledeb.	21.29	Oxyaci
<i>Potania mongolica</i> Maxim.	7.01	Potmon
<i>Reaumuria soongolica</i> (Pall.) Maxim.	21.29	Reasoo
<i>Salsola passerina</i> Bge.	10.02	Salpas
<i>Salsola laricifolia</i> Turcz.	6.26	Sallar
<i>Sympegma regelii</i> Bge.	7.01	Symreg
<i>Tamarix chinensis</i> Lour.	7.51	Tamchi
<i>Tetraena mongolica</i> Maxim.	7.01	Tetmon
<i>Zygophyllum xanthoxylum</i> Maxim.	19.79	Zyghan

a) The species with frequency less than 5% were omitted.

**Figure 2** Dendrogram of TWINSpan for shrub communities on the Alxa Plateau (species abbreviations are shown in Table 2).

silt and clay, total N, soil organic matter and soil water content were relatively higher than in the soils of the other three groups. Most of the plots were distributed in the typical desertified steppe subzone of the southern fringe and middle parts of the Alxa Plateau (Figure 1).

Group 2 is represented by the *Nitraria sphaerocarpa*-

Kalidium cuspidatum community type, most of which is distributed in soil with a strongly alkaline pH value and a relatively high soil water content. Plots were located in the southern fringe of the Tengger Desert and the western part of the Alxa Plateau.

Group 3 is represented by the communities dominated by *Nitraria tangutorum* and *Calligonum alaschanicum*, with a lower shrub species richness and abundance, which occurs in the semi-fixed sand dunes of the Tengger, Ulan Buh and Badain Jaran deserts, as well as in the transitional zone between desert and steppified desert. The soil was coarse in texture, with a higher pH and bulk density and a lower total N and OM content.

Group 4 is represented by the psammophytic shrub communities, characterized by *Hedysarum scoparium*, *Caragana korshinskii*, *C. microphylla* and *Artemisia ordosica*, which are distributed on the semifixed dunes or sandland with a coarse texture and poor total N and OM contents, as well as lower soil water content.

2.2 Responses of the patterns of shrub diversity to environmental gradients

In Figure 3, the shrub species composition of the plots was evaluated by DCA. The first two DCA axes account for a total of 92% of the variance in species data (total n of species: 33). The first axis mainly represents a gradient of soil texture, in which the silt and clay content increases gradually from the left to the right of the axis. Xerophytic shrubs such as *Salsola passerina*, *Haloxylon ammodendron*, *Tamarix chinensis* and *Reaumuria soongorica* show higher scores on the first axis, while the psammophytic shrubs *Artemisia ordosica*, *Hedysarum scoparium* and *Calligonum mongolicum* have lower scores. The second axis indicates the increase in the water content of the deeper soil layer of the plots. On this axis the extra-arid desert shrub *Salsola laricifolia* shows

a low score, while *Nitraria sphaerocarpa*, *Nitraria sibirica*, *Caragana pygmaea* and *Sympegma regelii* have high scores. As indicated in Figure 3, most of these species occur in plots with higher soil moisture.

The results of the DCA indicated that most shrubs are distributed between the scores of 300 and 500 on the second axis; this means that the soil water content is significant in determining shrub species richness. In comparison with soil water, however, the response of shrub species richness to other environmental factors is unclear. For species abundance, there is an unclear tendency with the first two axes of the DCA. However, the biplot of the CCA analysis combining environmental variables suggested that species abundance in group 1 was correlated with most soil parameters such as OM, silt and clay, as well as the soil water content at both

Table 3 Shrub species richness and abundance and environmental properties (mean \pm s.e.) in different groups by TWINSpan

Shrub group	Species richness	Species abundance	Sand (%)	Silt (%)	Clay (%)	Bulk density ($\text{g} \cdot \text{cm}^{-3}$)	pH	Total N ($\text{g} \cdot \text{kg}^{-2}$)	OM ($\text{g} \cdot \text{kg}^{-2}$)	Water (0–0.4 m, %)	Water (0.4–3 m, %)
1	3.38 \pm 1.19	116.84 \pm 86.02	47.35 \pm 26.56	43.30 \pm 23.21	9.30 \pm 4.09	1.25 \pm 0.17	8.53 \pm 0.31	0.07 \pm 0.04	0.65 \pm 0.37	1.33 \pm 0.62	2.46 \pm 0.77
2	3.28 \pm 1.76	96.84 \pm 98.86	74.28 \pm 19.98	20.82 \pm 16.73	4.65 \pm 4.10	1.28 \pm 0.17	8.72 \pm 0.27	0.04 \pm 0.04	0.34 \pm 0.38	1.18 \pm 0.32	2.08 \pm 0.62
3	2.68 \pm 1.28	70.62 \pm 123.33	80.36 \pm 15.64	15.26 \pm 14.03	4.34 \pm 3.22	1.44 \pm 0.20	8.85 \pm 0.23	0.02 \pm 0.02	0.29 \pm 0.18	0.98 \pm 0.66	2.07 \pm 0.78
4	2.58 \pm 1.64	48.12 \pm 48.15	86.50 \pm 8.55	9.55 \pm 6.35	3.99 \pm 3.24	1.42 \pm 0.11	8.80 \pm 0.27	0.02 \pm 0.02	0.23 \pm 0.14	0.89 \pm 0.43	1.89 \pm 0.70

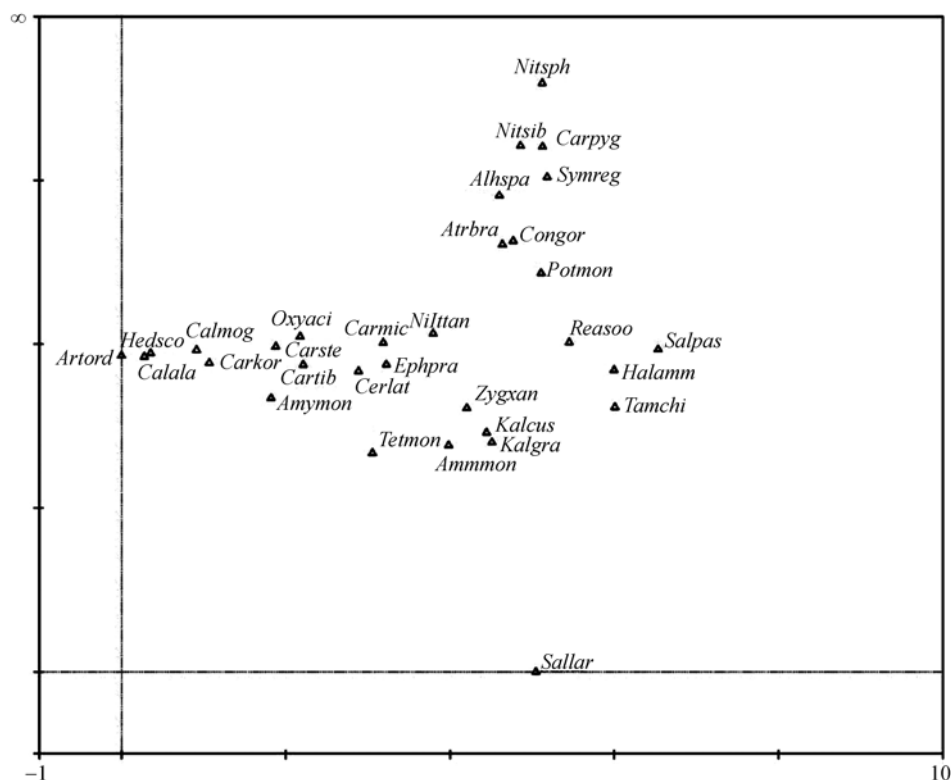


Figure 3 DCA ordination diagram of 33 shrub species scores on axes 1 and 2 (only species with a frequency of more than 5% in the sampling plots are considered).

shallow and deep depth. The species abundance in group 2 was correlated with sand content and soil pH, while it was correlated with soil bulk density in group 3. However, the relationship between species abundance and environmental variables was unclear for shrubs in group 4; the abundances of some species, such as *Artemisia ordosica* and *Hedysarum scoparium*, were correlated with sand content, pH and bulk density (Figure 4).

2.3 Relationships between soil properties and patterns of species richness and abundance

The pattern of species richness differs from the abundance in terms of their correlations with soil parameters on the Alxa Plateau. While shrub species richness was not significantly correlated with different soil properties in most cases, it was positively correlated with sand content and deeper soil water content, and was nega-

tively correlated with OM, all at the 5% level of significance (Figure 5). No significant relationship was found between species richness and the other measured properties such as clay, silt, bulk density, topsoil water content, total N and pH. All of the soil properties were significantly correlated with species abundance (Figure 6, $P < 0.05$). A positive correlation was found between species abundance and the silt, clay, topsoil water content, deeper soil water content and OM, while a negative relationship was found between species abundance and sand content, bulk density and pH. Figures 5 and 6 also show that most of these relationships were relatively stronger for species abundance.

The results of the stepwise regression indicate that shrub species richness was mainly correlated with deeper soil water content on the Alxa Plateau (Table 4). Shrub abundance was mainly related to deeper soil wa-

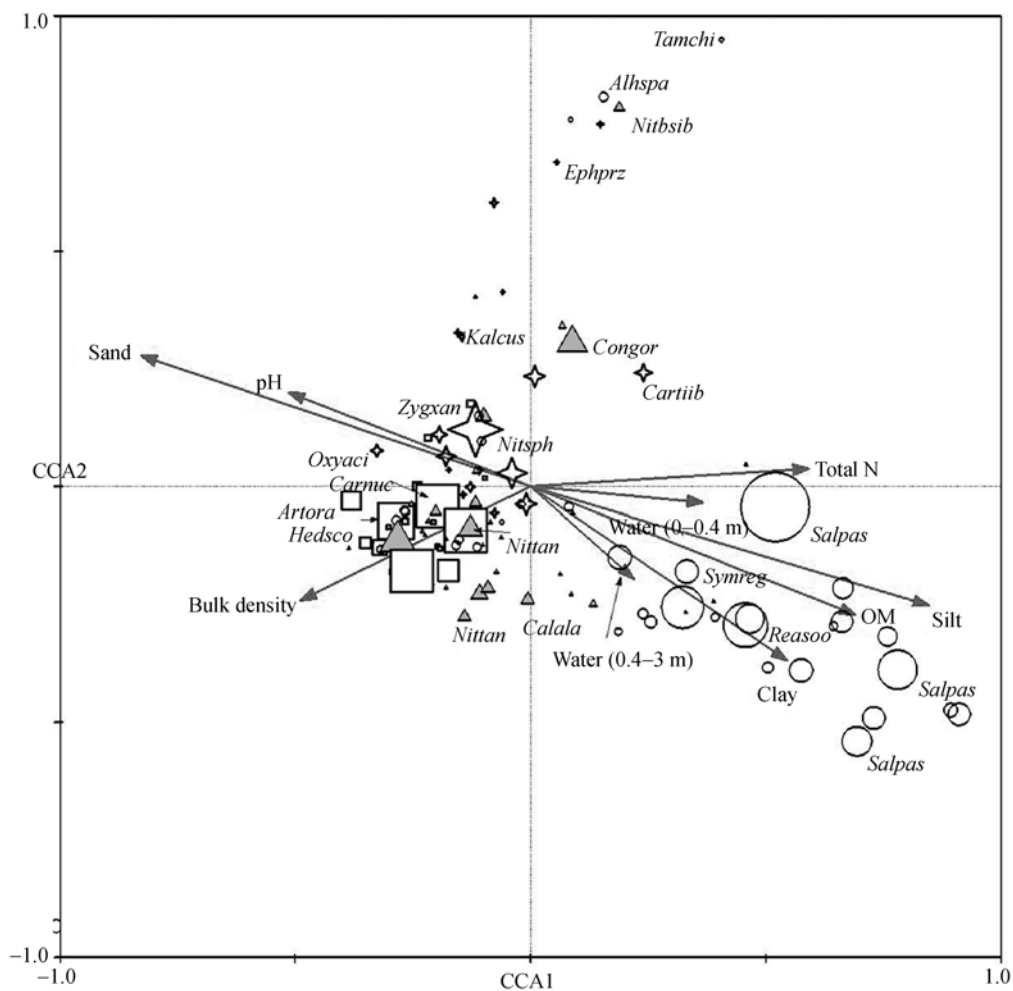


Figure 4 Biplot of shrub species abundance and environmental factors on the Alxa Plateau (Pearson correlation coefficients between axes and environmental factors are represented by the length and direction of arrows; the size of different symbols represents the values of species abundance, the circle symbol represents plots with dominant shrub species in group 1 of TWINSpan; the star represents plots with dominant species in group 2; the up-triangle plots of group 3 and the square symbol plots of group 4, abbreviation of shrub species see Table 1).

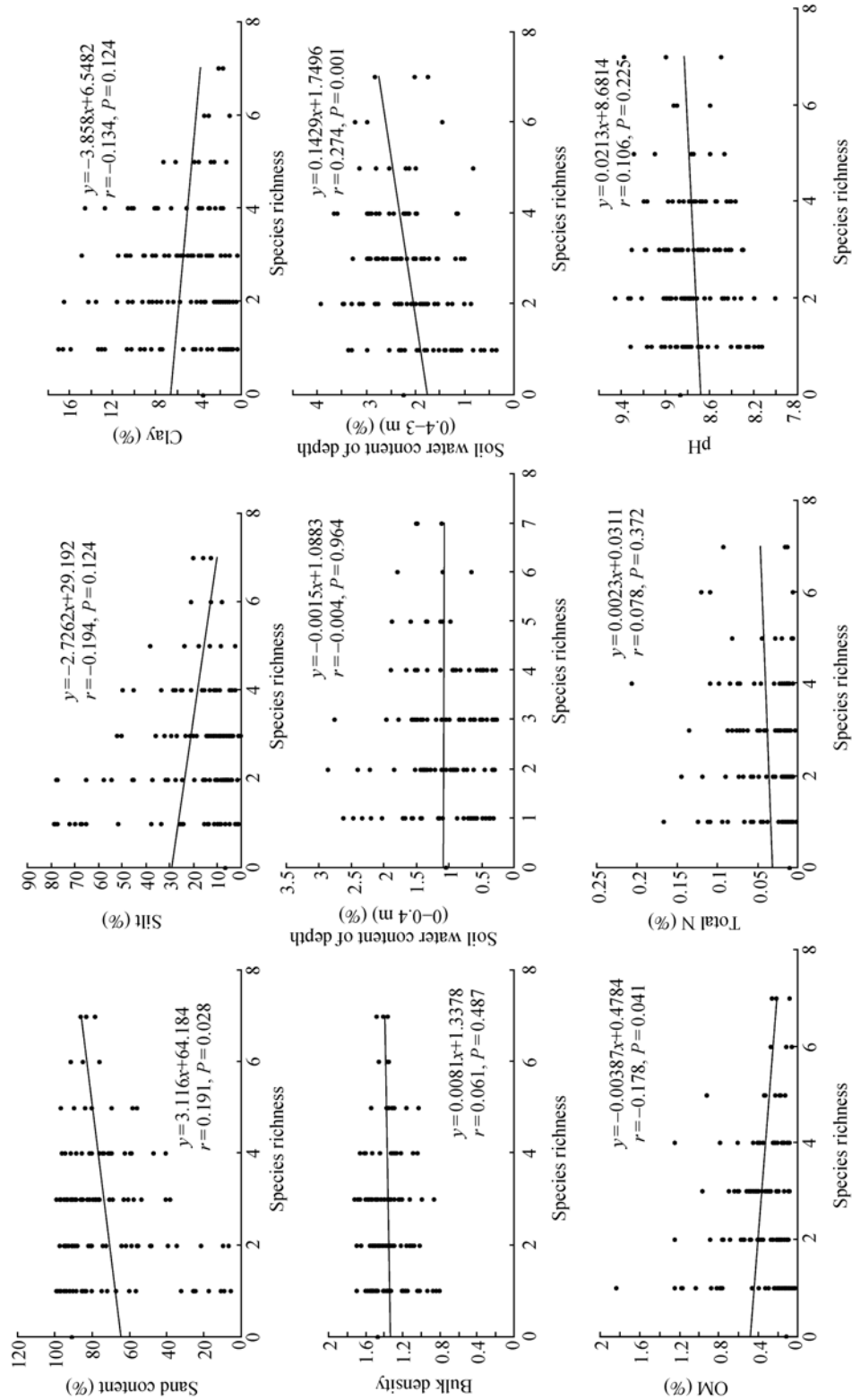


Figure 5 Relationships between shrub species richness and soil parameters in the steppe desert of the Alxa Plateau, Northwest China (n=133).

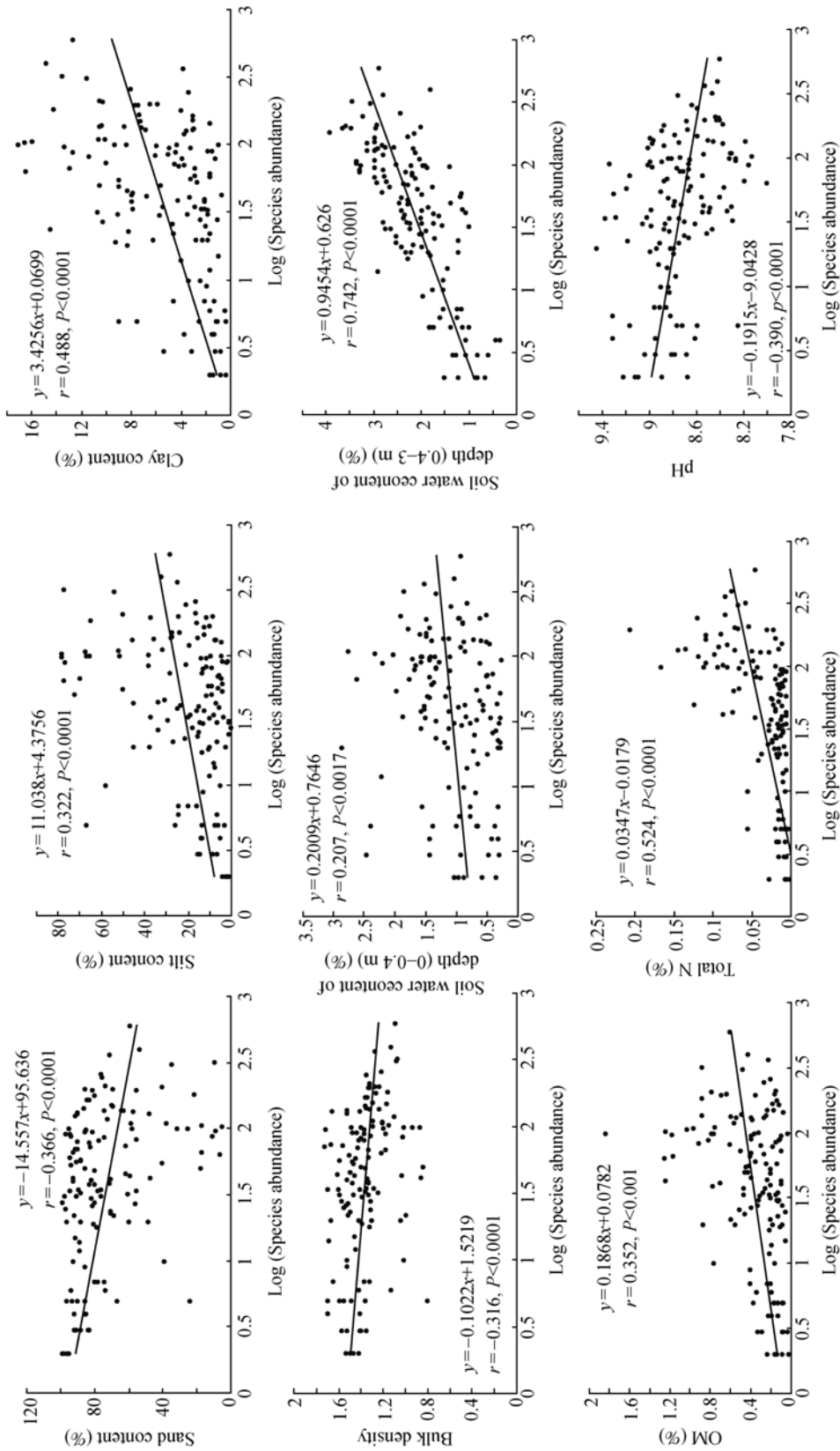


Figure 6 Relationships between shrub species abundance and soil parameters in the steppe desert of the Alxa Plateau, Northwest China ($n=133$).

Table 4 The equations using the stepwise regression method between species richness and abundance of shrub species and soil parameters

Equation	R^2	Level of significance
Richness = $1.543 + 0.525$ Soil water content _(0.4–3 m)	0.750	$P < 0.0001$
Abundance = $0.339 + 0.501$ Soil water content _(0.4–3 m) + 4.842 TN	0.640	$P < 0.0001$

ter content and total N ($R^2=0.64$, $P < 0.0001$). The models explained 75% of the variation in species richness and 64% of the variation in species abundance. This implied that drought stress is the main factor limiting biodiversity in the arid desert regions of China.

3 Discussion

It is recognized that species with similar biological traits have similar responses to changes in habitat conditions^[44]. Therefore, species can be grouped into “response types” in terms of their response to an environmental factor such as availability of resources^[45]. The results of the TWINSPLAN classification of 133 plots on the Alxa Plateau showed that the four groups of shrub species differed in their responses to soil properties. For most of the xerophytic shrubs, such as *Salsola passerina* and *Sympegma regelii* (group 1), their pattern of species abundance was determined by the soil water, organic matter, clay and silt content as well as total N, due to their distribution on fixed dunes and alluvial fans in the sub-zone of the steppified desert of the Alxa Plateau. Species abundance was positively correlated with these soil properties. In other words, shrub abundance was determined by multiple factors, and was negatively correlated with coarse soil texture. This suggested that the distribution of shrub diversity in the steppified desert of the Alxa Plateau could not support the hypothesis that the dominance of shrubs or grasses is related to soil texture as in semiarid grassland^[13,15]. In addition, some shrub communities, which were governed by a unique and extreme habitat, such as *Nitraria sphaerocarpa*, *Kalidium cuspidatum*, *Haloxylon ammodendron*, *Kalidium gracile* and *Nitraria tangutorum* distribute commonly in alkaline soils with a higher pH. In this case, all components of the community were required to adapt to this habitat, which reduced the possibility for other species to establish and coexist with these unique species. Similarly, for psammophytic communities characterized by shrubs such as *Hedysarum scoparium*, *Caragana korshinskii*, *Caragana microphylla*, *Calligonum mongolicum* and *Artemisia ordosica*, species diversity was limited by wind erosion and the habitat of the semi-moving

dunes. Shrubs have a higher tolerance to sand burial, and the coarse soil texture favored the growth of shrub and semishrub species rather than grasses and forbs^[9]. In this case, the patterns of the different life-form species supported the hypothesis of Sala et al.^[13]. However, for some shrubs with a relatively large ecological amplitude in arid desert ecosystems, such as *Oxytropis aciphylla*, it was difficult to interpret the effects of soil properties on species diversity due to their occurrence in different habitats.

The results of DCA and the biplot successfully described the distribution pattern of the main shrub species on the Alxa Plateau and their response to environmental variables. In this study, we did not consider the effects of climatic factors on shrub species diversity because there were no significant differences in the main climatic factors such as annual precipitation, annual mean temperature and evaporation between the steppified desert subzone and the desert subzone for shrub species, whereas differences may exist for the growth of grass and herbaceous species^[36]. This suggests that the contribution of conservation of soil habitat, such as reducing sand burial, maintaining the soil available water content and soil structure and controlling salinization, is more vital to species abundance than it is to species richness. This can be attributed to the fact that a stable soil habitat can maintain available ecological niches for populations of each species and reduce the probability of species loss. In general, soil water was the main limiting factor on the Alxa Plateau. In fact, for a given quantity of water, the amount actually available to the plant varies according to the soil properties. Therefore, the soil characteristics may be the key factors determining shrub diversity in an extremely arid desert ecosystem.

Using multi-regression analyses is an effective approach for examining the relationships between species diversity and environmental factors^[46]. Our results indicated that the relationships between shrub species richness and measured environmental factors were not clear, except for soil water content at 0.4–3.0 m depth. This supported numerous hypotheses that soil water is the predominant factor in desert ecosystems. Water avail-

ability not only governs productivity but also limits the distribution and abundance of many species and thus restricts plant associations^[1]. The reason for the greater importance of the deeper soil water content compared with the shallower soil water content can be partially explained by the distribution of the root systems of the shrubs, namely most shrubs had deeper roots within the 0.4–3.0 m soil layer. In this study we failed to find a significant relationship between shrub species diversity and soil texture. This means that the deeper soil water content controls the distribution of shrub species in desert or steppified desert ecosystems, rather than soil texture as in semiarid grassland.

With regard to shrub species abundance, the deeper soil water content was a key factor supporting shrubs on the Alxa Plateau. Additionally, the soil total N was positively correlated with shrub species abundance (Table 4). Therefore, maintaining a relatively stable water content in deeper soils is vital for conservation of shrub diversity. However, the western parts of the Alxa Plateau are in the lower reaches of the Heihe River (Figure 1), and agricultural water use in the oasis of the middle reaches results in a long-term cutting off the water supply for the western desert of the Alxa Plateau. Dune movement and sand burial from the Tengger and Badain Jaran deserts lower the groundwater in the parts of the middle of the

Alxa Plateau, while water replenishment from the Helan Mountain to the eastern parts of the Alxa Plateau is reduced by the extension of the urban and oasis areas^[47]. On the other hand, most of the limited rainfall events, an important fresh water source, are less than 10 mm, and weakly infiltrate to deeper soil due to stronger evaporation^[47]. Hence, it is a challenge for both ecologists and land managers to preserve shrub diversity in this extremely arid desert zone.

4 Conclusions

The significance of shrub species diversity in arid desert ecosystems is greater than in steppe ecosystems because of the predominant role of shrubs. The distribution patterns of shrub species are not only associated with a series of environmental factors such as soil texture, soil pH and soil water content, but are correlated with their biological traits. The response of shrub species diversity to environmental factors is not significant except for soil water, while the pattern of shrub species abundance is correlated with most of the measured soil properties, such as deeper soil water content, soil OM, total N and soil pH. Maintaining the current water content in deeper soils on the Alxa Plateau has been suggested as an optimal way of counteracting the current loss of shrub diversity.

- 1 Polis G A. Desert communities: An overview of patterns and processes. In: Polis G A, ed. *The Ecology of Desert Communities*. Tucson: University of Arizona Press, 1991
- 2 Naeem S, Thompson L J, Lawler S P, et al. Declining biodiversity can alter the performance of ecosystems. *Nature*, 1994, 368: 734–736
- 3 Huston M A. Hidden treatments in ecological experiments: Evaluating the ecosystem function of biodiversity. *Oecologia*, 1997, 110: 449–460
- 4 Whitford W G. *Ecology of Desert Ecosystems*. New York: Academic Press, 2002
- 5 Shachak M, Lovett G M. Atmospheric deposition to a desert ecosystem and its implications for management. *Ecol App*, 1998, 18: 455–463
- 6 MacMahon J A, Wagner F H. The Mojave, Sonoran and Chihuahuan Deserts of North America. In: Evanari M, Noy-Meir I, Goodall D W eds. *Hot Deserts and Arid Shrublands: Ecosystems of the World*. New York: Elsevier New York, 1985
- 7 Ludwig J A, Reynolds J F. *Statistical Ecology: A Primer on Methods and Computing*. New York: John Wiley & Sons, 1988
- 8 Tielborger K, Kadmon R. Relationships between shrubs and annual communities in a sandy desert ecosystem: A three-year study. *Plant Ecol*, 1997, 130: 191–201
- 9 Li X R, Zhang Z S, Zhang J G, et al. Association between vegetation patterns and soil properties in the Southeastern Tengger Desert, China. *Arid Land Res Manag*, 2004, 18: 369–383
- 10 Nunez-Olivera E, Martinez-Abaigar J, Escuderero J C, et al. Comparative study of *Cistus ladanifer* shrublands in Extremadura (CW Spain) on the basis of woody species composition and cover. *Vegetatio*, 1995, 117: 123–132
- 11 Noy-Meir I. Desert ecosystems: Environment and producers. *Annual Rev Ecol System*, 1973, 4: 25–51
- 12 Garner W, Steinberger Y. A proposed mechanism for the formation of “fertile islands” in the desert ecosystem. *J Arid Environ*, 1989, 16: 257–262
- 13 Sala O E, Lauenroth W K, Golluscio R A. Plant functional types in temperate semiarid regions. In: Smith T M, Shugart H H, Woodward F I, eds. *Plant Functional Types*. Cambridge: Cambridge University Press, 1997
- 14 Schlesinger W H, Raikes J A, Hartley A E, et al. On the spatial pattern of soil nutrients in desert ecosystems. *Ecology*, 1996, 77: 364–374
- 15 Dodd M B, Lauenroth W K, Burke I C, et al. Association between vegetation patterns and soil texture in the shortgrass steppe. *Plant Ecol*, 2002, 158: 127–137
- 16 Holzapfel C, Tielborger K, Parag H A, et al. Annual plant-shrub in-

- teractions along an aridity gradient. *Basic Appl Ecol*, 2006, 7: 268–279
- 17 Williams M, Shimabukuro Y E, Herbert D A, et al. Heterogeneity of soils and vegetation in an Eastern Amazonian rain forest: Implications for scaling up biomass and production. *Ecosystems*, 2002, 5: 692–704
- 18 Lundholm J T, Larson D W. Relationships between spatial environmental heterogeneity and plant species diversity on a limestone pavement. *Ecography*, 2003, 26: 715–722
- 19 Kumar S, Stohlgren T J, Chong G W. Spatial heterogeneity influences native and nonnative plant species richness. *Ecology*, 2006, 87: 3186–3199
- 20 Pickett S T A, Cadenasso M L. Landscape ecology: Spatial heterogeneity in ecological systems. *Science*, 1995, 269: 331–334
- 21 Kie J G. Landscape heterogeneity at differing scales: Effects on spatial distribution of mule deer. *Ecology*, 2002, 83: 530–544
- 22 Boeken B, Lipchin C, Gutterman Y. Annual plant community responses to density of small-scale soil disturbances in the Negev Desert of Israel. *Oecologia*, 1998, 114: 106–117
- 23 Oztas T, Koc A, Comakli B. Changes in vegetation and soil properties along a slope on overgrazed and eroded rangelands. *J Arid Environ*, 2003, 55: 93–100
- 24 Pausas J G. Species richness patterns in the understorey of Pyrenean *Pinus sylvestris* forest. *J Vege Sci*, 1994, 5: 517–524
- 25 Austin M P, Pausa J G, Nicholls A O. Patterns of tree species richness in relation to environment in south-eastern New South Wales. *Aus J Ecol*, 1996, 21: 154–164
- 26 Huston M A. *Biodiversity: The Coexistence of Species in Changing Landscapes*. Cambridge: University Press, 1994
- 27 Pausas J G, Austin M P. Patterns of plant species richness in relation to different environments: An appraisal. *J Veg Sci*, 2001, 12: 153–166
- 28 Tilman D. *Resource Competition and Community Structure*. Princeton: Princeton University Press, 1982
- 29 Sternberg M, Gutman M, Perevolotsky A, et al. Vegetation response to grazing management in a Mediterranean herbaceous community: A functional group approach. *J Appl Ecol*, 2000, 37: 1–15
- 30 Higgins S I, Bond W J, Trollope S W. Fire, resprouting and variability: A recipe for grass-tree coexistence in savanna. *J Ecol*, 2000, 88: 213–229
- 31 Henkin Z, Sternberg M, Seligman No'am G, et al. Species richness in relation to phosphorus and competition in a Mediterranean dwarf-shrub community. *Agr Ecosys Environ*, 2006, 113: 277–283
- 32 Inouye R S. Population biology of desert annual plants. In: Polis G A, ed. *The Ecology of Desert Communities*. Tucson: University of Arizona Press, 1991
- 33 Ludwig J A, Gunningham G L, Whitson P D. Distribution of annual plants in North American deserts. *J Arid Environ*, 1998, 15: 221–227
- 34 Zhang X S. Principles and optimal model for development of Maowusu sandy grassland (in Chinese). *Acta Phytocool Sin*, 1994, 18: 1–16
- 35 Li X R. Study on shrub community diversity of Ordos Plateau, Inner Mongolia, Northern China. *J Arid Environ*, 2001, 47: 271–279
- 36 Integrative Investigation Team for Vegetation of Inner Mongolia, CAS. *Vegetation of Inner Mongolia* (in Chinese). Beijing: Science Press, 1985
- 37 Zhu Z D, Chen G Q. *Sandy Desertification in China* (in Chinese). Beijing: Science Press, 1994
- 38 Lu Q, Li X R, Xiao H L. *The Observation Methods for Desert Ecosystems* (in Chinese). Beijing: Chinese Environmental Science Press, 2004
- 39 Loveland P J, Walley W R. Particle size analysis. In: Simth K A, Mullins C E, eds. *Soil and Environmental Analysis, Physical Methods*. 2nd ed. New York: Marcel Dekker Inc, 2001
- 40 Knudsen D, Peterson G A, Pratt P F. Lithium, sodium and potassium. In: Page A L, Miller R H, Keeney D R, eds. *Methods of Soil Analysis Part 2: Chemical and Microbiological Properties*. 2nd ed. Madison WI: American Society of Agronomy, Soil Science Society of America, 1982
- 41 Olsen S R, Sommers L E. Phosphorus. In: Page A L, Miller R H, Keeney D R, eds. *Methods of Soil Analysis Part 2: Chemical and Microbiological Properties*. 2nd ed. Madison, WI: American Society of Agronomy, Soil Science Society of America, 1982
- 42 Hill M O, Smilauer P. *TWINSPAN for Windows version 2.3*. Centre for Ecology and Hydrology & University of South Bohemia, Huntingdon & Ceské Budejovice, 2005
- 43 ter Braak C J F, Smilauer P. *CANOCO Reference Manual and CanoDraw for Windows User's guide: Software for Canonical Community Ordination (Version 4.5)*. Microcomputer Power, Ithaca N Y USA. 2002
- 44 Gitay H, Nobe I R. What are functional types and how should we seek them? In: Smith T M, Shugart H H, Woodward F I, eds. *Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change*. Cambridge: Cambridge University Press, 1997
- 45 Díaz S, Cabido M. Vive la différence: Plant functional diversity matters to ecosystem processes. *Trends Ecol Evol*, 2001, 16: 646–655
- 46 Hardtle W, Redecker B, Assmann T, et al. Vegetation responses to environmental conditions in floodplain grasslands: Prerequisites for preserving plant species diversity. *Basic Appl Eco*, 2006, 7: 280–288
- 47 Liu W N. *The Classification of Agro-meteorological Resource in the Left Banner of Alxa league* (in Chinese). Huhehot: Huhehot People's Publishing House of Inner Mongolia, 1994