

Spatial and environmental determinants of plant species diversity in a temperate desert

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Abstract

Aims

Deserts are one of the ecosystems most sensitive to global climate change. However, there are few studies examining how changing abiotic and biotic factors under climate change will affect plant species diversity in the temperate deserts of Asia. This study aimed to: (i) characterize species distributions and diversity patterns in an Asian temperate desert; and (ii) to quantify the effects of spatial and environment variables on plant species diversity.

Methods

We surveyed 61 sites to examine the relationship between plant species diversity and several spatial/environmental variables in the Gurbantunggut Desert. Spatial and environmental variables were used to predict plant species diversity in separate multiple regression and ordination models. Variation in species responses to spatial and environmental conditions was partitioned by combining these variables in a redundancy analysis (RDA) and by creating multivariate regression trees (MRT).

Important Findings

We found 92 plant species across the 61 sites. Elevation and geographic location were the dominant environmental factors

underlying variation in site species richness. A RDA indicated that 93% of the variance in the species–environment relationships was explained by altitude, latitude, longitude, precipitation and slope position. Precipitation and topographic heterogeneity, through their effects on water availability, were more important than soil chemistry in determining the distribution of species. MRT analyses categorized communities into four groups based on latitude, soil pH and elevation, explaining 42.3% of the standardized species variance. Soil pH strongly influenced community composition within homogeneous geographic areas. Our findings suggest that precipitation and topographic heterogeneity, rather than edaphic heterogeneity, are more closely correlated to the number of species and their distributions in the temperate desert.

Keywords: Gurbantunggut Desert, ephemerals, redundancy analysis, species richness, soil pH

Received: 8 May 2014, Revised: 2 July 2015, Accepted: 4 July 2015

INTRODUCTION

Deserts are an important component of terrestrial ecosystems. However, compared to forests and grassland ecosystems, relatively little is known about potential abiotic and biotic influences on desert plant diversity (Bertiller *et al.* 2009; Bisigato *et al.* 2009; Miriti *et al.* 2007; Wang *et al.* 2013; Ward and Olsvig-Whittaker 1993; Wu and Yang 2013). Analyses of changes in species distributions and diversity are crucial for protecting biodiversity in deserts (Baez and Collins 2008; Berry *et al.*

2006; Butterfield *et al.* 2010; Munson *et al.* 2012). As global climate warming continues, desert plant communities may become less stable as interspecific interactions lead to declines in biodiversity (Baez and Collins 2008; Wassenaar *et al.* 2007). Interactions among species composition, community structure and their controlling factors within ecosystems are the product of ecological processes operating over a wide range of spatial and temporal scales (Ohmann and Spies 1998).

The distribution and diversity of plant species within desert communities have most often been related to climatic,

geographic and edaphic heterogeneity factors (Enright *et al.* 2005; Guisan and Thuiller 2005). Regional climate (precipitation and temperature) and geographic factors (altitude, geological substrate, latitude and longitude) can play decisive roles in shaping community structure and large scale species distributions (Chesson 2000; Gaston 2000; Peters *et al.* 2012; Sánchez-gonzález and López-mata 2005). In contrast, local environmental factors, including disturbances (anthropogenic and natural), habitat heterogeneity, soil chemistry and species interactions may affect microhabitats (Bhattarai and Vetaas 2003; Guo 1998; Moser *et al.* 2005; Williams *et al.* 2005). Additionally, the availability of soil nutrients may affect species richness and distributions, as only a few species are adapted to extremely nutrient poor conditions (Venterink 2003). Among the factors influencing species distributions, precipitation may be an especially important limiting factor in the desert; hence, changes in precipitation regimes may lead to substantial alterations in community composition and ecosystem structure (Adler and Levine 2007).

The Gurbantunggut Desert is located in northwestern China. Compared to other deserts in Central Asia, such as the KumTag, Qaidam and Taklamakan, the Gurbantunggut has extremely diverse plant communities (Li *et al.* 2010; Zhang and Chen 2002). In the last 30 years, precipitation in Central Asia has increased substantially (Qian and Zhu 2001; Wei *et al.* 2003), yet little is known about how species diversity is responding to this change. Previous studies of plant diversity in the Gurbantunggut have focused on community composition (Chen *et al.* 1983) and floristic geography (Zhang and Chen 2002). Although Qian *et al.* (2008) recorded vegetation patterns in the Gurbantunggut, their analysis was limited by a small number of sample sites. Also, they did not fully characterize the relationship between plant species diversity and the environment.

In this study, our goal was to characterize spatial patterns of plant diversity in the Gurbantunggut Desert and to uncover the spatial and environmental determinants of these patterns. Species diversity and community structure were investigated by comparing community composition and species distributions among 61 sites using a stratified random sampling design. Specifically, the following two aims were addressed in this study: (i) to characterize plant species diversity and community composition across a range of sites varying in several environmental variables; and (ii) to quantify the effects of these environmental variables, as well as spatial factors, on plant species richness and the distributions of individual species.

MATERIALS AND METHODS

Study area

The Gurbantunggut Desert is the second largest desert in China, after the Taklamakan, and has an area of 48 800 km², 97% of which is comprised of fixed and semi-fixed sand ridges. Elevation ranges from 250 to 700 m above sea level

and increases traveling from west to east. Annual precipitation ranges from 80 to 160 mm, mean annual temperature is 6°C and annual evaporation exceeds 2000 mm (Qian *et al.* 2008; Zhang and Chen 2002; Zhang and Liu 2012). Significant rainfall occurs in the spring and snowfall in the winter, whereas the summer is dry and hot. Many ephemeral plant species occur in this region due to this seasonal variation in precipitation (Zhang and Chen 2002). The dominant species in this region include the perennial shrubs *Haloxylon ammodendron* and *Haloxylon persicum*, various annual herbs and several other ephemeral plant species (Zhang and Liu 2012).

Field surveys

In this study, we sampled in the National Conservation Area of the Gurbantunggut Desert; the Conservation Area is located far away from any desert roads and is minimally impacted by human activity. We created 10 m × 100 m transects perpendicular to the dunes at each sample site and divided each transect into 10 quadrats (10 m × 10 m). A total of 610 vegetation survey quadrats were assessed along 61 transects at sample sites throughout the Gurbantunggut Desert (Fig. 1). The distance between adjacent sites was ~10 km. In order to reduce any confounding effects of latitude, longitude or elevation on species richness, we studied the effects of precipitation over several transects located at the same latitude, longitude and elevation. To ensure the accuracy of species identifications, we performed preliminary investigations in June 2007 and June 2008 in which all plant species in the study area were collected. Plant specimens were identified and deposited at the Shihezi University Herbarium. Plant specimens were identified to the species level. The survey work itself was performed in June 2009. Species numbers, canopy widths and plant heights were documented for each quadrat.

Explanatory variables

Precipitation is a key determinant of species richness and of the distributions of desert plants. Significant differences in precipitation occur between the eastern and western desert (Qian *et al.* 2008), however, there are no weather stations located in the central desert, and hence no precipitation data. Therefore, we interpolated climatic data from the Global Precipitation Climatology Center using methods proposed by Adler *et al.* (2003) and Nezhlin *et al.* (2005). We acquired 30 years of precipitation data for each field site. A global positioning system was used to record latitude, longitude and elevation at each site. Slope was recorded at five positions (one at the top, two at the middle and two at the bottom) along each transect. Soil samples were collected at a depth of 0–10 cm (with three replicates) at each slope position and mean values were calculated. We measured soil organic matter (SOM), total soil nitrogen (TN), total soil phosphorus (TP), available phosphorus (AP), available potassium (AK), sodium (Na⁺), sulfate (SO₄²⁻), pH, chloride (Cl⁻), calcium (Ca²⁺), magnesium (Mg²⁺), carbonate (CO₃²⁻), bicarbonate (HCO₃³⁻) and electrolytic conductivity (EC) using the methods described by Zhao *et al.* (2010).

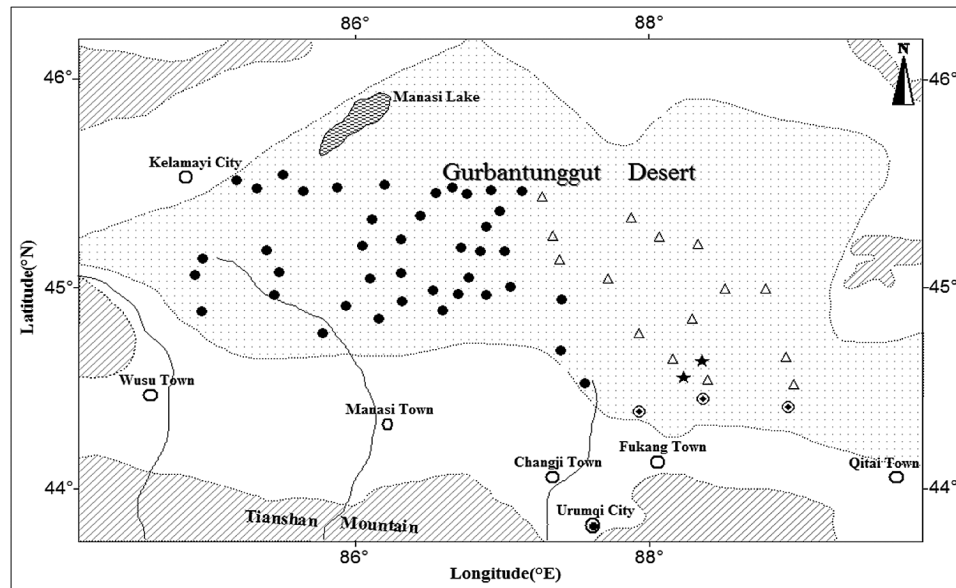


Figure 1: map of the 61 sample sites in the southern Gurbantunggut Desert, where solid circle represents group A, triangle represents group B, pentagram represents group C and empty circle represents group D. (Groups were identified using MRT analyses, see Table 1.)

Table 1: results of MRT analysis and indicator species for the four groups

Group	Environment	No. of sites	No. of species	ID species	DLI
A	Latitude ≥ 44.46 , Soil pH ≥ 7.295 , Elevation < 447	41	79	<i>Stipagrostis pennata</i>	39
				<i>Corispermum lehmannianum</i>	32
				<i>Haloxylon ammodendron</i>	27
				<i>Echinops sphaerocephalus</i>	21
				<i>Calligonum leucocladum</i>	20
				<i>Anabasis aphylla</i>	17
B	Latitude ≥ 44.46 , Soil pH ≥ 7.295 , Elevation ≥ 447	15	74	<i>Malcolmia africana</i>	58
				<i>Nnoea caspica</i>	56
				<i>Agriophyllum squarrosum</i>	55
				<i>Tetracme recurvata</i>	49
				<i>Kochia odontoptera</i>	48
				<i>Eremosparton songoricum</i>	46
C	Latitude ≥ 44.46 , Soil pH < 7.295	2	53	<i>Nepeta micrantha</i>	96
				<i>Horaninowia ulicina</i>	95
				<i>Cancrinia discoidea</i>	92
				<i>Erodium oxyrrhynchum</i>	91
				<i>Lepechinella lasiocarpa</i>	87
				<i>Plantago minuta</i>	81
D	Latitude < 44.46	3	61	<i>Chamaesphacos ilicifolius</i>	98
				<i>Silene nana</i>	84
				<i>Alyssum desertorum</i>	69
				<i>Koelpinia linearis</i>	66
				<i>Eremurus inderiensis</i>	61
				<i>Schismus arabicus</i>	60

MRT analysis defining communities (92 species) in terms of environmental variables across 61 sites. (See Fig. 1 for group locations and see online supplementary material, Appendix 1 for species in groups). Only the six species with the highest DLIs (i.e. indicator values) in each group are listed. ID species are the indicator species.

Statistical analyses

Ordination methods are useful for partitioning spatial and environmental components of variation and for analyzing spatial dependence at the community level (Wagner 2003). Species distribution data were used in de-trended correspondence analysis (DCA) to identify the proper ordination method. In these analyses, the length of the longest gradient was used as an estimate of beta-diversity in the data set. When the longest gradient is greater than 4 SD of beta-diversity, unimodal ordination methods [DCA or canonical correspondence analysis (CCA)] are indicated, while with a longest gradient of less than 3 SD, linear methods [principal components analysis (PCA) and redundancy analysis (RDA)] can be used; when the longest gradient is between 3 and 4 SD, both unimodal and linear methods can work reasonably well (Leps and Smilauer 2003; Rao 1964). In this study, a DCA revealed that the longest gradient was less than 3 SD and hence RDA was used.

Multivariate regression trees (MRT; De'ath 2002) were used to further explore the influence of the environmental variables on species composition. The explanatory variables were randomly split in such a way as to minimize the variation in species composition within groups (or clusters) of sites. The optimal combination of explanatory variables, that produced a best-sized tree maximizing the amount of variation among groups with the fewest possible nodes (following the principal of parsimony), can be found automatically using cross-validation and tree pruning techniques. Indicator values (DLIs; Dufrene and Legendre 1997) were calculated for each species for each node of the tree. The DLI is defined for a given species and group, as the product of the mean species abundance occurring in the MRT group divided by the sum of the mean abundances in all other groups, times the proportion of sites within the group where the species occurs, multiplied by 100. Species with high DLIs were used as characteristic members of each community and the spatial extent of the group indicated the region where the species was predominantly found.

The RDA was performed using Canoco 4.5 for Windows, while all other analyses were performed in R 2.12.1 (R Development Core Team 2011) using the *vegan* (Oksanen et al. 2010), *mvpart* (De'ath 2010) and *mgcv* packages (Wood 2011).

RESULTS

Overall species composition and diversity

We identified 92 species across the 61 sites, including 71 genera from 22 families (see online [supplementary material, Appendix 1](#)). The dominant angiosperm families were Chenopodiaceae (20 species, 14 genera), Compositae (15 species, 14 genera), Brassicaceae (10 species, 7 genera), Poaceae (5 species, 5 genera) and Leguminosae (9 species, 4 genera). These families accounted for 62% of all genera and 64.1% of all species. The dominant species were *Calligonum leucocladum*,

Corispermum ehmannianum, *Haloxylon persicum*, *Salsola praecox* and *Schismus arabicus*.

Of the 92 species, 40, or 43.5% of the total, were ephemerals (including both annuals and perennials); these accounted for 54% of the total plant cover in our study sites (typical open shrub land). Most of the ephemerals were members of either the Boraginaceae, Brassicaceae, Leguminosae, Liliaceae, or Poaceae (see online [supplementary material, Appendix 1](#)). Fifty-six genera were represented by only one species. Twenty-three species exhibited site occurrence frequencies of more than 50% (see online [supplementary material, Appendix 1](#)). Among these 23 species, 21 were herbaceous plants. Seventy-five species of herbs were identified (82% of all species), including 51 annuals and 24 perennials.

Spatial patterns in species richness and cover

In the Gurbantungut Desert, site species richness varied more with latitude, longitude and elevation than with any other measured environmental variables (Fig. 2a–c). As latitude increased, the number of species decreased significantly (Fig. 2a). A steep decline in richness was observed with increasing longitude before 86°E, but this pattern then reversed after 86°E (Fig. 2b). Site species richness peaked around 88°E of longitude. Species number increased with elevation (going from west to east) (Fig. 2c).

Plant percent cover also varied with latitude, longitude and elevation (Fig. 2e–g). Plant cover decreased with increasing latitude ($R^2 = 0.225$, $P < 0.001$), but to a lesser degree than species richness (Fig. 2e). Estimated plant cover was lowest in the northern part of the study region and highest in the southern region. As with species richness, plant cover first decreased with longitude before roughly 86°E (Fig. 2f); however, while it then increased between 86°E and 87.4°E, it decreased again after 87.4°E. Unlike richness, cover increased slightly from west to east (Fig. 2g) and peaked at an elevation of 600 m above sea level.

Site species richness and cover varied with latitude, longitude and elevation and were also greatly influenced by precipitation. Comparing across sites of the same latitude, longitude and elevation, species richness increased with increasing precipitation. However, species richness only increased up to 200 mm of rainfall before plateauing with more rainfall (Fig. 2d), whereas coverage increased consistently with precipitation (Fig. 2h).

Species–environment relationships

We excluded 32 species that had relative frequencies (across the surveyed sites) of <10% from the RDA analysis ($N = 60$ species). A total of 93% of the variance was explained by the first two RDA axes (Fig. 3), with species–environment correlations of 0.30 and 0.29 for the first and second axes, respectively. Precipitation and latitude were negatively correlated ($r = -0.74$, $P < 0.001$), whereas longitude and altitude were positively correlated ($r = 0.51$ and $r = 0.3$, respectively, $P < 0.001$). At a small, local-scale, slope significantly influenced species distributions, while longitude, latitude, altitude

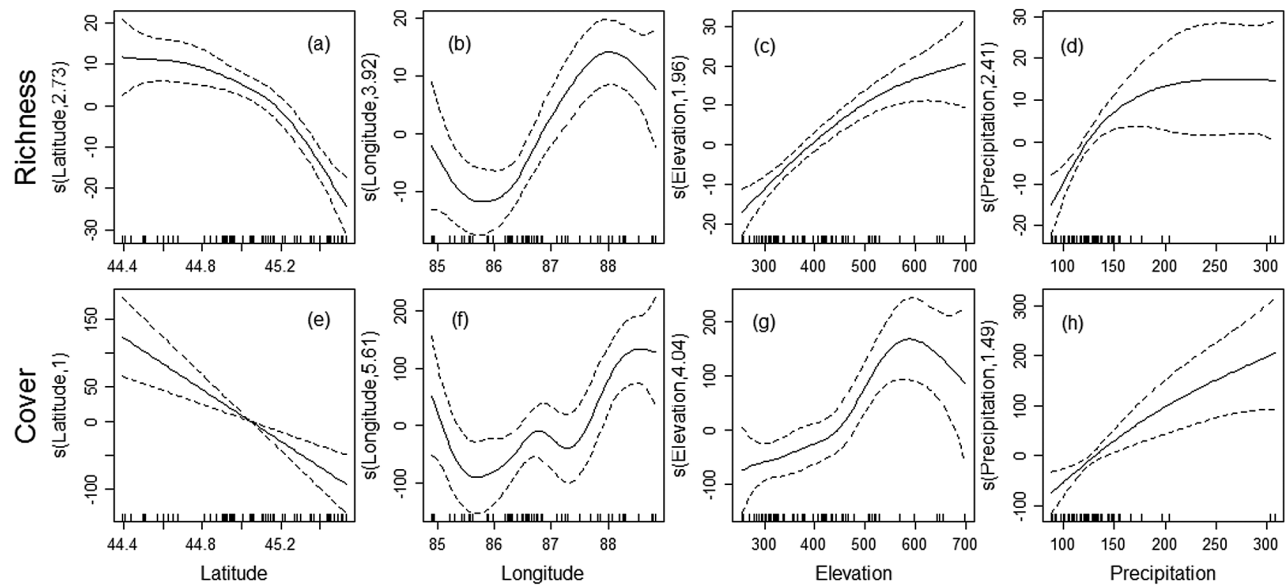


Figure 2: site species richness and cover versus relative latitude (in degrees; **a** and **e**), longitude (in degrees; **b** and **f**), elevation (in m; **c** and **g**) and precipitation (in mm; **d** and **h**). Plots show the partial effects of smoothed trend lines based on linear regression models. All effects were significant for richness and cover ($P < 0.001$). The short dashed lines along the x -axis indicate sample site locations.

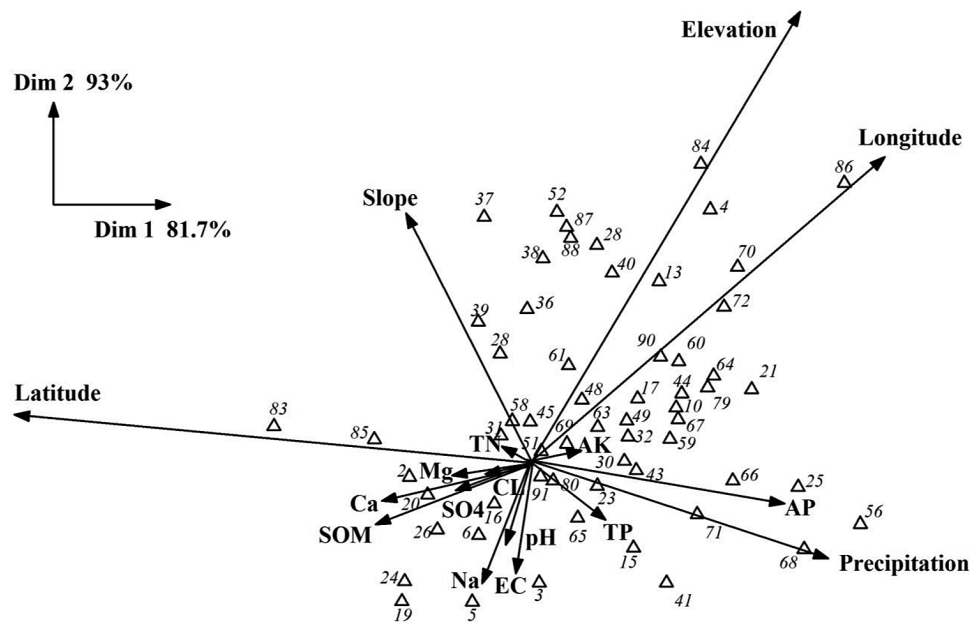


Figure 3: RDA of abundance data for 60 plant species with occurrence frequencies $>10\%$. Species names are listed in see online [supplementary material, Appendix 1](#). The first two axes or dimensions (Dim 1 and Dim 2) explained 93% (cumulative percentage) of the variance in the species–environment relationships. The species–environment correlation values were 0.30 and 0.29 for Dim 1 and Dim 2, respectively. SOM, soil organic matter; TN, total soil nitrogen; TP, total soil phosphorus; AP, available phosphorus; AK, available potassium; Na⁺, sodium; SO₄²⁻, sulfate; Cl⁻, chloride; Ca²⁺, calcium; Mg²⁺, magnesium; CO₃²⁻, carbonate; HCO₃⁻, bicarbonate and EC, electric conductivity.

and precipitation were important determinants of species richness at the regional scale.

The distribution of some study species was controlled by a single dominating environmental or spatial factor. For example the distributions of *Agriophyllum squarrosum* and *Ephedra distachya* were primarily correlated with latitude, whereas the

distributions of *Schismus arabicus* and *Silene nana* correlated with precipitation. Longitude was the driving factor behind the distribution of *Carex physodes*. Some narrow-ranged species, such as *Nitraria sphaerocarpa*, *Petrosimonia sibirica*, *Suaeda microphylla* and *Tragopogon ruber* were restricted to unique habitats, such as areas of high salt concentration. Distributions of some species

(e.g. *Hyalea pulchella*) were closely related to AP; these species occurred at low frequencies across the 61 study sites (see online supplementary material, Appendix 1).

MRT analyses identified four major groups of study sites [group A (latitude ≥ 44.46 , soil pH ≥ 7.295 and elevation < 447 m), B (latitude ≥ 44.46 , soil pH ≥ 7.295 and elevation ≥ 447), C (latitude ≥ 44.46 and soil pH < 7.295) and D (latitude < 44.46)] based on 3 of the 18 explanatory variables in the model (Table 1), explaining 42.3% of the standardized species variance. The four groups (A–D) were split by latitude, soil pH and elevation. The top-ranking indicator species (Table 1) in each of the four groups was *Stipagrostis pennata*, *Malcolmia Africana*, *Nepeta micrantha* and *Chamaesphacos ilicifolius*, respectively. Although three of these four species were observed in all the groups (*C. ilicifolius* was absent from group C) and adjacent communities were similar in species composition, species abundances and relative frequencies differed substantially between the groups. Group B had a faster rate of species accumulation than group A (Fig. 4). Although there were twice as many sites in group A (41 sites) as in group B (15 sites), species richness was lower in group A. The low mean site richness of group B was due to poor representation of taxa at individual sites, rather than sample area size. Cumulative species richness in groups C and D did not form an asymptote.

DISCUSSION

With a total of 92 plant species recorded (see online supplementary material, Appendix 1), the Gurbantunggut Desert, which comprises a relatively small geographical area, had a higher number of plant species than the Taklamakan Desert, but a similar richness to the deserts in Iran, Syria and Turkestan (Zhao et al. 2010). However, species richness of the Gurbantunggut is relatively low compared to high

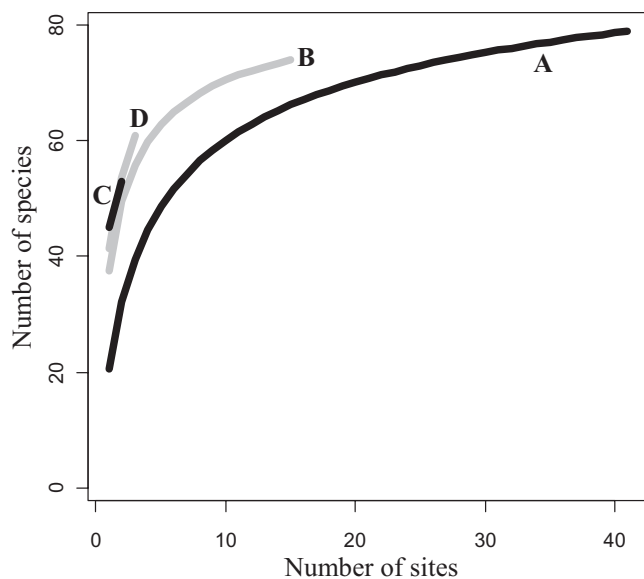


Figure 4: species accumulation curves for the four community groups as determined by MRT analysis.

diversity deserts (e.g. the Negev Desert in Israel and the succulent Karoo communities of South Africa). For example plant species richness can be in excess of 100 species per 0.1 ha in the Karoo (Ward et al. 1993). What is unique about the Gurbantunggut Desert is the high density of ephemeral plants; these evolved in the late Tertiary and early Quaternary periods, after the retreat of the ancient Mediterranean (Mao and Zhang 1994). We found 40 species of ephemerals in our survey, a similar number to that of Zhang and Chen (2002) and of Qian et al. (2008). Ephemerals accounted for 54% of the total percent cover, significantly more than shrubs (see online supplementary material, Appendix 1). This is an important finding to consider in re-vegetation planning (Peltzer et al. 2010) for arid and desertified areas.

Changes in the amount of annual precipitation are expected to strongly impact plant communities, owing to the influence of precipitation on the recruitment, survival and persistence of dominant species (Peters et al. 2012). In this study, species richness increased with precipitation up to a plateau at 200 mm (Fig. 2d), but the dominant species between groups (e.g. groups C and D) could be very different (Table 1), even with similar amounts of precipitation. Complex patterns in plant distributions are often interpreted as reflecting patterns of species coexistence and varying niche requirements (Ricklefs et al. 1999; Silvertown 2004; van der Maarel and Sykes 1993). Among the four plant community groups we identified, there was a strong overlap in species composition and little variation in soil chemistry (with the exception of AP), indicating broad environmental tolerances for most species. Therefore, differences in geographical conditions affecting water availability are likely more important in driving observed vegetation patterns in this desert environment than are successional processes.

Increasing precipitation can not only increase plant species diversity in arid regions, but can also lead to greater interspecific competition (Chesson 2000; Rosenfeld et al. 2001). Ephemeral plant species were more sensitive to changes in precipitation than shrubs, here in the Gurbantunggut. In a previous study, we found that the number of ephemerals increased with increasing precipitation, but shrub species richness did not change (Zhang and Liu 2012). Additionally, ephemerals with shallow root systems have been found to obtain more water and nutrients than shrubs, which have deep roots (van der Maarel and Sykes 1993). As precipitation in the Gurbantunggut Desert is predicted to gradually increase (Qian and Zhu 2001), fundamental changes in plant communities are expected, especially for ephemeral species, which are key determinants of changes in desert community structures.

Soil pH plays an important role in determining community composition within otherwise homogeneous geographic areas. Tilman (1994) and Chytrý et al. (2007) have both suggested that soil pH is strongly related to species richness and distributions. One possible explanation for this causal relationship is related to the historical processes in which the evolution and formation of modern floras took place. Plants cannot tolerate either too low or too high pH, therefore soil pH values need to

be compatible with plant forms. In extremely high pH habitats (e.g. group A in our study), species richness may be reduced, and *H. ammodendron* communities may be degraded (Liu *et al.* 2010). In this study, we found the lowest values of species richness and plant cover near 86°E, where pH was highest.

It was not possible to obtain data to accurately quantify the impact of historical human activities on species distributions and diversity in the Gurbantunggut Desert. While a conservation area was set up in 2000 to protect the Gurbantunggut and help maintain the natural vegetation, there are no historical data available with which to analyze changes in species diversity. Although our sample sites were distantly located from roads and oil fields, in order to reduce the confounding effects of anthropogenic activities, excessive cutting, overgrazing, road construction, oil exploration and drilling before the area was protected may have reduced species abundances and altered vegetation patterns. Native *H. ammodendron* communities may have been particularly impacted by these disturbances (Liu *et al.* 2010; Zhang and Liu 2012). Resolving this issue would require combining high resolution remote-sensing data, to quantify the influence of human activity, with our ground data.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

FUNDING

Joint funding by Natural Science Foundation of China-Xinjiang (U1130304) and the National Science Foundation of China (41061004 and 31260099).

ACKNOWLEDGEMENTS

We are grateful to our anonymous reviewers for their constructive comments that improved this manuscript. We would also like to thank Emily Drummond at the University of British Columbia for her assistance with English language and grammatical editing of the manuscript.

Conflict of interest statement. None declared.

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