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A positive correlation between plant diversity and productivity is indirectly caused by environmental factors driving spatial pattern of vegetation composition in semiarid sandy grassland

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Abstract

Although patterns between plant diversity and ecosystem productivity have been much studied, a consistent relationship has not yet emerged. Several different patterns have been observed both naturally and experimentally, likely caused by spatial variability of environmental factors and vegetation composition. In this study, we measured the vegetation cover, plant diversity, productivity, soil properties and site characteristics along an environment gradient of natural sandy grasslands (mobile dune, semi-fixed dune, fixed dune, dry meadow, wet meadow and flood plain grassland) in a semiarid area of Northern China. We used multivariate analysis to examine the relationships between environment factors, vegetation composition, plant diversity and productivity. We found a positive correlation between plant diversity and productivity. Vegetation composition had also a significantly positive correlation with plant diversity and productivity. Environment gradients in relation to soil properties and topography features affected the distribution patterns of species diversity, vegetation composition and productivity. However, environment gradients are a better determiner for vegetation composition and productivity than for species diversity. The analysis from optimization model of structural equation suggests that environmental factors determine vegetation composition, which in turn drives independently both plant diversity and productivity. Thus the positive correlation between plant diversity and productivity is not direct, but indirectly driven by the spatial pattern of vegetation composition determined by environment gradients in soil and topography.

1 Introduction

Diversity–productivity relationships have shown several different patterns in ecology over the last decades (Grace et al., 2007; Pärtel et al., 2007, 2010; Xiao et al., 2010). Numerous studies have reported the five different diversity–productivity patterns: positive, negative, hump-shaped, U-shaped or no relationship (Hector et al., 2010; Ma et al., 2010). However, there are different mechanisms that explain the variation in diversity–productivity relationships in grassland ecosystems include complementary species interactions (Gross et al., 2007; van Ruijven and Berendse, 2009), plant density (He et al., 2005), dispersal limitation (Pärtel and Zobel, 2007), evolutionary history (Pärtel et al., 2007; Venail et al., 2008), disturbance and management history (Wilsey and Polley, 2003; Zhou et al., 2006; Gross et al., 2009; Marriott et al., 2009), temporal and spatial scale (Horner-Devine et al., 2003; van Ruijven and Berendse, 2005), soil fertility (Guo and Berry, 1998; Fornara and Tilman, 2009), and climate change (Kahmen et al., 2005b; Laughlin and Moore, 2009; Ma et al., 2010).

In the past decade theoretical and experimental studies have greatly increased our knowledge of how plant diversity influences ecosystem productivity. Specifically, manipulative experiments changing plant diversity by drawing plant species from a random species pool have shown that increasing species diversity frequently increase productivity (Tilman et al., 1997, 2001; Hector, 1998; Hector et al., 1999). These experiments studies are often performed in uniform environments with well mixed species pools (Zhou et al., 2006). However, studies in natural ecosystems report the different patterns of diversity-productivity, because field observations typically involve one or several environmental gradients (Cardinale et al., 2000; Zuo et al., 2011).

Some studies have shown that environment gradient is thought to be an important factor influencing both species richness and the distribution of biomass in natural ecosystems (Maestre et al., 2006; Fornara and Tilman, 2009; Ma et al., 2010). In Chinese natural grasslands, a positive correlation between plant diversity and productivity is also formed due to the changes of climate and soil (Bai et al., 2007; Ma et al., 2010). This raises the question that if a positive relationship of diversity-productivity exists in natural ecosystems, how environmental factors influence species diversity and productivity (Waide et al., 1999; Cardinale et al., 2004).

Secondly, apart from species diversity, ecosystem productivity can also be strongly influenced by biotic attributes of plant communities such as species composition and evenness (Hooper et al., 2005). Within a given community, species number at the local scale may vary due to spatial stability of community compositions (Weigelt et al., 2008). To further understand the mechanism driving the diversity-productivity relationships, it is necessary to consider all components of diversity, species richness and evenness (Isbell et al., 2008). In addition, in order to test the diversity–productivity relationship in grassland ecosystem, it is also necessary to consider the characteristics, structures and compositions of vegetation in specific regions (Cardinale et al., 2004; Ma et al., 2010). Previous study has also suggested that species compositions of plant communities may influence productivity independently of plant diversity (Kahmen et al., 2005a).

Thus a further study is called to assess how important environmental factors and vegetation composition is in influencing the diversity-productivity relationships (Chapin et al., 2000; Loreau et al., 2001; Kahmen et al., 2005a), in order to manage and restore natural grassland ecosystems with the goal of improving diversity, productivity and sustainability. Our previous study suggests that a combination of soil properties and topography features determines the vegetation pattern and composition along the environment gradient in sandy grasslands (mobile dune, semi-fixed dune, fixed dune, dry meadow, wet meadow and flood plain grassland) (Zuo et al., 2011). Here we use a multivariate model that examines and controls environmental variables statistically to determine the effects of vegetation composition and environment factors on the relationship of plant diversity-productivity in sandy grassland. We tested two hypotheses that 1) a positive correlation between plant diversity and productivity is along the environment gradient in sandy grassland; and 2) environment factors control the distributions and compositions of plant communities, which in turn control the pattern of species diversity and productivity.

2 Materials and methods

2.1 Study area description

The study was conducted in the south-western part (42°55′ N, 120°42′ E; 360 m elevation) of Horqin Sandy Land, Inner Mongolia, China. The region, about 50 600 km^2, is located in transitional zone between agriculture and pasture and is an important commodity grain production base in China. The climate is temperate, semi-arid continental and monsoonal, receiving 360 mm in precipitation annually, with 75 % of the precipitation in the growing season of June to September. The annual mean open-pan evaporation is about 1935 mm. The annual mean temperature is around 6.4 °C, with the minimum monthly mean temperature of −13.1 °C in January and the maximum of 23.7 °C in July. The annual mean wind velocity is in the range of 3.2 to 4.1 m s^{-1}, and the prevailing wind direction is northwest in winter and spring (Liu et al., 1996; Zhang et al., 2005).

Horqin Sandy Land consists of a mixture of flood plain grasslands, lowland grasslands, sand dunes, woodlands and farmlands (Liu et al., 1996, 2007). Soils are of three different types; marsh soil present in wetland and flood plain grassland, meadow soil in meadow habitat and sandy soil in sandy dune habitat (Liu et al., 1996). The sandy soil is highly vulnerable to wind erosion. The species composition of the sandy grassland consists of native plants, including grasses (e.g. *Leymus chinensis Cleistogenes squarrosa*, *Setaria viridis*, *Phragmites australis*, *Digitaria ciliaris*,), forbs (*Mellissitus ruthenicus*, *Salsola collina*, *Agriophyllum squrrosum*, *Artemisia scoparia*, *Typha orientalis*,*Carex dispalata*), shrubs (e.g. *Caragana microphylla*, *Lespedeza davurica*), and subshrubs (e.g. *Artemisia halodendron*, *Artemisia frigida*).

2.2 Experiment design

Vegetation survey in 60 sites were carried out in August and were selected from six typical vegetation types in the area of 20 × 50 km, including sand dunes (mobile dune, semi-fixed and fixed dune) and grasslands (dry meadow, wet meadow and flood plain grassland). At each site, a 30 × 30 m plot was established. Three random quadrats (1 × 1 m) were placed in each plot to measure plant height (maximum), species abundance and plant cover. In each quadrat, the peak aboveground biomass, as a proxy for annual productivity was estimated by clipping all vegetation at ground level. The aboveground biomass was dried at 60° for 48 h.

For each site a soil profile (20 cm in depth) was excavated to identify the soil type. Using a 3 cm diameter soil auger, one soil sample was collected within each quadrat at 0–20 cm depth for laboratory analysis. With the same auger at the same time, three additional samples were taken in each plot to measure soil water content (SW) at depths of 0–20, 20–40 and 40–60 cm.

Soil samples were hand-sieved through a 2-mm screen to remove roots and other debris. Soil particle size was determined by the pipette method in a sedimentation cylinder, using sodium hexametaphosphate as the dispersing agent (ISSCAS, 1978). Soil pH and electrical conductivity (EC) were measured in a 1 : 1 soil-water slurry and in a 1 : 5 soil-water aqueous extract, respectively. Soil organic carbon (C) was measured by the dichromate oxidation method of Walkey and Black (Nelson and Sommers, 1982) and total nitrogen (N) was determined by the Kjeldahl procedure (ISSCAS, 1978).

2.3 Data analysis

2.3.1 Plant diversity measures

The importance value of species (IV) in each plot was calculated using the formula IV = (relative abundance + relative height + relative cover of the plant)/3 (Zhang et al., 2005; He et al., 2007; Zuo et al., 2009). From the importance value of species, species diversity was calculated by the species richness, Shannon-Wiener index, Simpson ecological dominance index and Evenness index (Zhang et al., 2005).

2.3.2 Aggregation of vegetation compositions and environment factors

To determine the effect of vegetation compositions and environmental factors on plant diversity and productivity, the ordination techniques of principal component analysis (PCA) and non-metric multidimensional scaling (NMDS) were used to aggregate environment factors and vegetation composition (Kahmen et al., 2005a). Using these approaches for 60 sites, we constructed the data matrixes of plant cover, soil properties and site characteristics. We used a square-root transformation data of plant cover and environment factor to improve normality of measured variables for the PCA and NMDS analyses.

As a first step, using the PCA method, we aggregated soil properties and site characteristics data (ter Braak and Smilauer 2002). PCA is a method that reduces data dimensionality by performing a covariance analysis between factors. This procedure summarizes the information of the variables as four major axes of a standardized PCA, and creates composite independent variables (Kahmen et al., 2005a). PCAs were performed separately for soil properties and site characteristics. From each PCA, the axes explaining most of the total variance were extracted to form the new PCA-derived variables. These new PCA-derived variables were used in all consecutive analyses as independent parameters. Intra-set correlations from the PCA are used to assess the importance of soil properties and site characteristics.

As a next step, the compositional differences among plant communities for the 60 investigated sites were analyzed using NMDS, with Bray-Curtis coefficient as distance measure (Kahmen et al., 2005a; Spiegelberger et al., 2006). NMDS is commonly regarded as the best and most robust unconstrained ordination method in community ecology (Minchin, 1987). The scores of the NMDS axes were used as parameters for vegetation composition (Kahmen et al., 2005a). To determine which species are mainly responsible for the compositional changes within the investigated communities (along the extracted NMDS axes), the linear regressions of each plant cover versus the scores of the NMDS axes were performed.

2.3.3 Relationship among plant diversity, productivity, vegetation compositions and environmental factors

As a third step, least squares linear regressions were used to analyze the relationships between plant diversity measures (species richness, Shannon-Wiener index, Simpson ecological dominance index and Evenness index) and productivity, between plant diversity and vegetation compositions (NMDS axes), and between vegetation composition and productivity. In addition, multiple regression analyses were also performed separately for each diversity measure, vegetation composition and productivity, with one of the PCA constructed variable groups, soil variables and site characteristics (Kahmen et al., 2005a). Subsequently, we used a multiple stepwise regressions to test whether the PCA-derived variables were significant predictors for plant diversity, vegetation composition and productivity. For each dependent variable (diversity measures, NMDS1, NMDS2 and productivity), separated regression models were calculated for each parameter group, soil properties and site characteristics, respectively.

2.3.4 Influence of vegetation composition and environment factors on plant diversity and productivity

In a final path analysis, we used structural equation modeling (SEM) to examine the relationship between plant diversity and productivity, the influence of soil properties and site characteristics on vegetation composition, plant diversity and productivity, and the influence of vegetation composition on plant diversity and productivity. Starting from the most complex model that included all significant variables from the analyses of multiple stepwise regressions, model simplification was based on the significance of the regression weights. The competing models were compared by using the Chi-square test, Akaike information criterion (AIC), Browne-Cudeck criterion (BCC) and the squared multiple correlation (SMC) (Arbuckle, 2008; Kahmen et al., 2005a). Considering the complexity of structural equation modeling, the model postulated that diversity and productivity is response variable, having no effect on environmental variables or vegetation composition.

The descriptive statistical parameters, variance (ANOVA) procedures and Tukey's test, and regression analyses were performed using SPSS 16.0 software. PCA were performed using the CANOCO 4.5 software (ter Braak and Smilauer 2002). NMDS ordination techniques were applied using the program PC-ORD 5.0 software (McCune and Mefford 2006). The structural equation modeling was applied using AMOS 17.0 software (Arbuckle, 2008).

3 Results

3.1 The relationship between vegetation patterns and environment factors

Ordination of the 60 plant communities using NMDS is depicted in Fig. 1. Based on plant species compositions, the 60 plots can be classified into six vegetation types in order of increasing species richness, Shannon-Wiener index and biomass: mobile dune, semi-fixed dune, fixed dune, dry meadow, wet meadow and flood plain grassland (Table 1, all $P < 0.01$). Our results showed that along a habitat gradient from mobile dune to flood plain grassland, mean species richness increased from 3 to 15 species per m^2, and aboveground biomass increased from 31 to 391 g m^{-2}. NMDS also showed that a two-dimensional solution was sufficient to achieve low stress values (first axis/dimension = 49.13, $R^2 = 0.28$, $P = 0.004$; second axis/dimension = 31.66, $R^2 = 0.42$, $P = 0.004$) to explain vegetation composition (Fig. 1).

From the intra-set correlations of environmental factors with the first two axes of NMDS (Table A1), the first axis correlated significantly with soil type, soil organic C, total N, C/N, pH, EC and latitude ($P < 0.01$), and the second axis correlated significantly with soil type, soil organic C, total N, EC, soil water contents at three depths, very fine sand content and altitude ($P < 0.01$). These results explained 70 % of the species-environment relationship, indicating that environment gradients in relation to soil and topographic factors (i.e. soil type, soil organic C, total N, C/N, pH, EC, soil water content, very fine sand content and altitude) are the key factors determining the distribution patterns of plant communities.

Based on this strong vegetation-environment relationship, we used the scores of the first two axes as parameters for plant species compositions (NMDS1 and NMDS2) in sandy grassland. The correlation analysis showed that plant diversity was correlated with species compositions (NMDS1) (Table A2). Several dominant plant species, such as *Agriophyllum squarrosum*, *Artemisia halodendrom*, *Calamagrostis pseudophragmites*, *Carex dispalata*, *Digitaria ciliaris*, *Lespedeza davurica*, *Plantago asiatica*, *Potentilla bifurca*, *Salsola collina* and *Typha orientalis*, showed a strong positive or negative relation with the NMDS1 and NMDS2, indicating that vegetation composition is closely related to the dominant species in plant communities (Table A3).

3.2 Changes of environmental factors

Soil organic C, total N, C/N, pH, EC, very fine sand and soil water contents (0–20, 20–40 and 40–60 cm) differed among six vegetation types (Table 1, all $P < 0.01$). Soil organic C, total N and soil water contents increased from the mobile dune to the flood plain grassland, but there were no significant differences in soil organic C and total N among dry meadow, wet meadow and flood plain grassland ($P > 0.05$) and were no significant differences in soil water contents among mobile dune, semi-fixed dune and the fixed dune ($P > 0.05$). There were differences in fine sand and altitude among six vegetation types (Table 1, $P < 0.05$), but not for coarse sand, silt and clay (all $P > 0.05$). Except for pH, soil properties had a high coefficient of variation (CV), indicating that the spatial distribution of soil properties is highly variable in the study area.

3.3 Aggregation of environmental factors

Four axes explaining 94.7 % of the total variance of all soil properties were extracted as independent variables from the PCA and labeled soil1-soil4 (Table A4). Soil1 accounted for 68.80 % of the total variance and was significantly positive correlated to soil type, soil C, total N, C/N, pH, EC, soil water contents at three depths, very fine sand and silt + clay ($P < 0.01$), and significantly negative correlated to coarse sand and fine sand ($P < 0.01$). Soil2 accounted for 15.40 % of the total variance and was significantly positive correlated with very fine sand and silt + clay ($P < 0.01$), and significantly negative correlated to coarse sand ($P < 0.01$). Soil3 explained 6.00 % of the total variance and was significantly positive correlated with coarse sand ($P < 0.01$), and significantly negative correlated to fine sand ($P < 0.01$). Soil4 explained 4.50 % of the variance and was significantly positive correlated with total N, silt + clay ($P < 0.01$), and significantly negative correlated to coarse sand ($P < 0.01$).

Two axes (site 1–2) were extracted from the PCA, explaining 100 % of the total site variation (Table A4). Site1 was significantly positive correlated to latitude and altitude ($P < 0.01$), which account for 99 % of the total variance of site characteristics. Site2 was significantly positive correlated to longitude and latitude ($P < 0.01$), which account for 1 % of the total variance of site characteristics.

3.4 The relationship between plant diversity and productivity

Overall, we found a positive correlation between plant diversity and productivity in sandy grassland (Fig. 2). Species richness and the Shannon-Wiener diversity index were significantly positive correlated to productivity ($P < 0.01$), and Simpson dominance index was significantly negative correlated to productivity ($P < 0.01$). Vegetation compositions represented as NMDS1 and NMDS2 were significantly positive correlated to productivity ($P < 0.001$, Fig. 2).

3.5 Relationships among environmental factors, plant diversity, vegetation composition and productivity

We found that environmental factors were correlated to plant diversity, vegetation composition and productivity in sandy grassland. Using multiple stepwise regression models, we also found that all explanations of soil parameter for the total variability in vegetation composition and productivity are over 43 % which is double than that for species diversity (Table 2). The parameter soil1 explained 20.9 % of the total variability in species richness (Table 2). Soil1 and soil4 explained 43.9 % of the total variability in NMDS1 and soil1, soil3 and soil4 explained 56.1 % of the total variability in NMDS2. In the regressions with either site characteristics as independent variables, the parameters site2 explained 31.0 % and 19.3 % of the variation in species richness and NMDS1 scores, respectively (Table 2). In addition, 11.4 % of the total variation in NMDS2 was explained by site1. For productivity, 62.7 % of total variation was explained by soil1, soil2 and soil3, and 22.5 % by site1 and site2 (Table 2).

3.6 Structural equation modeling (path analysis)

We used structural equation modeling to examine the direct and indirect correlations among plant diversity, productivity and environmental factors. Note that we only used species richness as a diversity measure, because this was the only variable which was significantly correlated to the soil and site parameters ($P < 0.01$). We used soil1, soil2, soil3, soil4, site1 and site2 as independent variables, and NMDS1, NMDS2, plant diversity and productivity as dependent variables (Table 2), to determine the initial structural equation modeling (Fig. 3a). Considering the effect of environment factors on plant diversity, vegetation composition and productivity, the initial model consisted of PCA-derived soil and site parameters that were significantly correlated with the variables of plant diversity, NMDS1, NMDS2 and productivity in the multiple regression analyses (Table 2). Productivity and diversity were also hypothesized to be dependent on soil1, soil2, soil3, soil4, site1, site2, NMDS1 and NMDS2, and we structured the model including paths from those variables to plant diversity and productivity.

This initial model was simplified by removing variables and paths according to the measures of fitting model (Table 3). All of the tested models were significant. The optimization model of structural equation with the best AIC and BCC values included variables soil1, soil4, site1, site2, NMDS1, NMDS2 and productivity, but excluded the relationship of soil1 with diversity, and of site1 with productivity, and of regression site2 with productivity (Table 3, Fig. 3b). The paths from soil1 and soil4 to vegetation compositions, from site2 to plant diversity, and from vegetation composition to plant diversity and productivity were significant ($P < 0.01$). Using this approach, however, the paths from plant diversity to productivity and from productivity to plant diversity were not significant ($P > 0.05$). Thus, according to the regression weights along paths, the relationship between diversity and productivity was a positive correlation, but was indirectly driven by vegetation composition.

4 Discussion

4.1 Positive correlation between plant diversity and productivity in sandy grassland

We found a positive correlation between plant diversity and ecosystem productivity in sandy grassland, which is consistent with the finding from other experimental studies both in synthesized assemblages (Tilman et al., 1997, 2001; Hector, 1998; Hector et al., 1999; Bai et al., 2007) and in natural grassland ecosystem (Bai et al., 2007; Ma et al., 2010). The multivariate regression analysis indicates that environmental factors and vegetation composition control both plant diversity and productivity (Table 2, Fig. 2.). However, the optimization model of structural equation indicates that vegetation composition rather than environmental factors influence both diversity and productivity in this sandy grassland system (Fig. 3b). Environment variables influence plant diversity and productivity, mostly via their direct effects on vegetation composition in sandy grassland. Our studies suggest that plant diversity and productivity both depending on vegetation composition increase consistently along the habitat gradient in sandy grassland which is closely correlated to the differences in soil properties and topographic features.

This study supports a positive, rather than a humped-shaped pattern of diversity-productivity (Mittelbach et al., 2001; Gillman and Wright, 2006; Bai et al., 2007; Gross et al., 2009; Ma et al., 2010). An unimodal relationship between diversity-productivity, is often found in the temperate ecosystems, and the positive relationship is often found in tropical ecosystems (Pärtel et al., 2007). A meta-analysis also has supported the unimodal shape relationship from local to landscape scales, whereas a positive linear relationship is common at large spatial scale (Mittelbach et al., 2001). In Northern American grassland, Guo and Berry (1998) showed that, when the environmental gradients extend from extremely "poor" microhabitats to extremely "rich" microhabitats, a hump-shaped relationship can develop. However, other studies from semiarid grasslands in Europe and China contradict this hump-shaped relationship, and show that at the regional scale, the relationship between diversity-productivity is a positive pattern which is driven by an environmental gradient of climate and soil fertility (Hector et al., 1999; Bai et al., 2007; Ma et al., 2010). So there are the more positive patterns of diversity-productivity in grasslands, likely because of the effect of natural environment gradients at larger spatial scales.

4.2 Environmental factors explain the positive correlation between plant diversity and productivity

The positive pattern of diversity-productivity can occur when environmental conditions change from a small scale to a region scale and can promote species coexistence rather than competitive exclusion (Cardinale et al., 2000). At a Eurasian continent scale, a spatial gradient related to annual precipitation and soil nitrogen is thought to contribute to a positive relationship of plant diversity-productivity in grassland (Bai et al., 2007). Our results also suggest that environment factors are a better determiner for vegetation composition and productivity than for species diversity (Table 2). In our study system, spatial patterns of soil and topography may reinforce species compositions at small scales, and spatial changes of habitats may result in the more homogeneous field-level productivity. The important gradient of soil properties that we found from mobile dune to flood plain grassland may determine the distribution patterns of plant communities (Zuo et al., 2011). So the particular pattern of vegetation composition contributes to the positive linear relationship in diversity-productivity at this region scale. This pattern also supports the findings of previous studies demonstrating that environmental factors are important drivers of species dissimilarity with increasing productivity (Chase and Leibold, 2002).

The effect of habitat change may also be important at regional scale, and is an alternative explanation of variations in diversity-productivity relationships among grasslands (Foster et al., 2007; Guo, 2007). Previously we have found that plant diversity and ecosystem productivity increased with the restoration of degraded vegetation in dune stabilization (Guo et al., 2008). In addition, the vegetation restoration of mobile dune also significantly enhances topsoil development by increasing the accumulation of carbon and total nitrogen (Li et al., 2009; Zuo et al., 2009). Thus, once species-poor habitats (e.g. mobile dune) have been gradually transformed into diverse natural habitats such as semi-fixed dune and fixed dune, vegetation restoration may cause an increase in plant diversity and ecosystem productivity in sandy grassland.

4.3 Vegetation composition drives the positive correlation between plant diversity and productivity

Some studies have indicated that vegetation composition, in addition to species diversity, can strongly influence ecosystem productivity in grasslands (Cardinale et al., 2000; Hooper et al., 2005; Kahmen et al., 2005a; Ma et al., 2010). In our study, the gradient of soil properties drives vegetation composition, which in turn drives patterns in plant diversity and productivity. Our study is consistent with finding from other studies that vegetation composition is an important driver of ecosystem functioning in grassland ecosystems (Hooper et al., 2005; Kahmen et al., 2005a; Maestre et al., 2006).

Not surprisingly, we found that species compositions in plant communities changed from the pioneer plant species on mobile dune to hygrophytes in the flood plain grassland and that vegetation composition strongly varied with environmental conditions.

Clearly, the occurrence of plant species at a site depends on the presence of suitable habitat, and local diversity and vegetation composition is strongly influenced by the number of habitat types, i.e. environmental heterogeneity. Therefore, niche differentiation between species may increase the collective performance of plant community across the habitat types, which further driving patterns of plant diversity and productivity. This is specifically indicated by that spatial heterogeneity that allows environmental resources to be used in spatially complementary ways utilized by different plant species (Cardinale et al., 2000). Thus, it is conceivable that the habitat variations caused by differences in soil properties and topography features, may affect species distributions and compositions in plant communities, and vegetation composition further drive plant diversity and productivity in the same positively correlated direction.

Our study demonstrates that vegetation composition, plant diversity and productivity changed consistently along an environment gradient in soil and topography in sandy grasslands. Although soil properties and topographic features are highly important basic factors for plant diversity and ecosystem functioning, their influences on plant diversity and productivity are indirect via driving the vegetation composition, supporting that vegetation composition of grassland ecosystem are an important parameter that is greatly driving the plant diversity and productivity. Thus to understand ecosystem functioning, we need to examine spatial patterns of plant diversity, vegetation composition and environment factors and how these factors influence productivity. In addition, to maintain the diversity and productivity in grassland ecosystem in semiarid area, it is necessary to conserve the sandy grassland habitats and promote the restoration succession of degraded vegetation by improvement of environment conditions.

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References

Arbuckle, J. L.: AMOS 17.0 user's guide, Amos Development Corporation, Crawfordville, F. L., 2008.

Bai, Y. F., Wu, J. G., Pan, Q. M., Huang, J. H., Wang, Q. B., Li, F. S., Buyantuyev, A., and Han, X. G.: Positive linear relationship between productivity and diversity: evidence from the Eurasian Steppe, J. Appl. Ecol., 44, 1023–1034, 2007.

Cardinale, B. J., Nelson, K., and Palmer, M. A.: Linking species diversity to the functioning of ecosystems: on the importance of environmental context, Oikos, 91, 175–183, 2000.

Cardinale, B. J., Ives, A. R., and Inchausti, P.: Effects of species diversity on the primary productivity of ecosystems: extending our spatial and temporal scales of inference, Oikos, 104, 437–450, 2004.

Chapin, F. S., Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., Hooper, D. U., Lavorel, S., Sala, O. E., Hobbie, S. E., Mack, M. C., and Diaz, S.: Consequences of changing biodiversity. Nature, 405, 234–242, 2000.

Chase, J. M. and Leibold, M. A.: Spatial scale dictates the productivity-biodiversity relationship, Nature, 416, 427–430, 2002.

Chase, J. M. and Ryberg, W. A.: Connectivity, scale-dependence, and the productivity-diversity relationship, Ecol. Lett., 7, 676–683, 2004.

Fornara, D. A. and Tilman, D.: Ecological mechanisms associated with the positive diversity-productivity relationship in an N-limited grassland, Ecology, 90, 408–418, 2009.

Foster, B. L., Murphy, C. A., Keller, K. R., Aschenbach, T. A., Questad, E. J., and Kindscher, K.: Restoration of prairie community structure and ecosystem function in an abandoned hayfield: a sowing experiment, Restor. Ecol., 15, 652–661, 2007.

Gillman, L. N. and Wright, S. D.: The influence of productivity on the species richness of plants: A critical assessment, Ecology, 87, 1234–1243, 2006.

Grace, J. B., Anderson, T. M., Smith, M. D., Seabloom, E., Andelman, S. J., Meche, G., Weiher, E., Allain, L. K., Jutila, H., Sankaran, M., Knops, J., Ritchie, M., and Willig, M. R.: Does species diversity limit productivity in natural grassland communities?, Ecol. Lett., 10, 680–689, 2007.

Gross, N., Suding, K. N., Lavorel, S., and Roumet, C.: Complementarity as a mechanism of coexistence between functional groups of grasses, J. Ecol., 95, 1296–1305, 2007.

Gross, N., Bloor, J. M. G., Louault, F., Maire, V., and Soussana, J. F.: Effects of land-use change on productivity depend on small-scale plant species diversity, Basic Appl. Ecol., 10, 687–696, 2009.

Guo, Q. F.: The diversity-biomass-productivity relationships in grassland management and restoration, Basic Appl. Ecol., 8, 199–208, 2007.

Guo, Q. F. and Berry, W. L.: Species richness and biomass: dissection of the hump-shaped relationships, Ecology, 79, 2555–2559, 1998.

Guo, Y. R., Zhao, H. L., Zuo, X. A., Drake, S., and Zhao, X. Y.: Biological soil crust development and its topsoil properties in the process of dune stabilization, Inner Mongolia, China, Environ. Geol., 54, 653–662, 2008.

He, J. S., Wolfe-Bellin, K. S., Schmid, B., and Bazzaz, F. A.: Density may alter diversity-productivity relationships in experimental plant communities, Basic Appl. Ecol., 6, 505–517, 2005.

He, M. Z., Zheng, J. G., Li, X. R., and Qian, Y. L.: Environmental factors affecting vegetation composition in the Alxa Plateau, China. J. Arid Environ., 69, 473–489, 2007.

Hector, A.: The effect of diversity on productivity: detecting the role of species complementarity, Oikos, 82, 597–599, 1998.

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M. C., Diemer, M., Dimitrakopoulos, P. G., Finn, J. A., Freitas, H., Giller, P. S., Good, J., Harris, R., Hogberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Korner, C., Leadley, P. W., Loreau, M., Minns, A., Mulder, C. P. H., O'Donovan, G., Otway, S. J., Pereira, J. S., Prinz, A., Read, D. J., Scherer-Lorenzen, M., Schulze, E. D., Siamantziouras, A. S. D., Spehn, E. M., Terry, A. C., Troumbis, A. Y., Woodward, F. I., Yachi, S., and Lawton, J. H.: Plant diversity and productivity experiments in European grasslands, Science, 286, 1123–1127, 1999.

Hector, A., Hautier, Y., Saner, P., Wacker, L., Bagchi, R., Joshi, J., Scherer-Lorenzen, M., Spehn, E. M., Bazeley-White, E., Weilenmann, M., Caldeira, M. C., Dimitrakopoulos, P. G., Finn, J. A., Huss-Danell, K., Jumpponen, A., Mulder, C. P. H., Palmborg, C., Pereira, J. S., Siamantziouras, A. S. D., Terry, A. C., Troumbis, A. Y., Schmid, B., and Loreau, M.: General stabilizing effects of plant diversity on grassland productivity through population asynchrony and overyielding, Ecology, 91, 2213–2220, 2010.

Hooper, D. U., Chapin, F. S. I., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setäla, H., Symstad, A. J., Vandermeer, J., and Wardle, D. A.: Effects of biodiversity on ecosystem functioning: a consensus of current knowledge, Ecol. Monogr.,75, 3–35, 2005.

Horner-Devine, M. C., Leibold, M. A., Smith, V. H., and Bohannan, B. J. M.: Bacterial diversity patterns along a gradient of primary productivity, Ecol. Lett., 6, 613–622, 2003.

Institute of Soil Sciences, CAS.: Physical and Chemical Analysis Methods of Soils, Shanghai Science Technology Press, Shanghai, 1978 (in Chinese).

Isbell, F. I., Losure, D. A., Yurkonis, K. A., and Wilsey, B. J.: Diversity-productivity relationships in two ecologically realistic rarity-extinction scenarios, Oikos, 117, 996–1005, 2008.

Kahmen, A., Perner, J., Audorff, V., Weisser, W., and Buchmann, N.: Effects of plant diversity, community composition and environmental parameters on productivity in montane European grasslands, Oecologia, 142, 606–615, 2005a.

Kahmen, A., Perner, J., and Buchmann, N.: Diversity-dependent productivity in semi-natural grasslands following climate perturbations, Funct. Ecol., 19, 594–601, 2005b.

Laughlin, D. C. and Moore, M. M.: Climate-induced temporal variation in the productivity-diversity relationship, Oikos, 118, 897–902, 2009.

Li, Y. L., Cui, J. Y., Zhang, T. H., Okuro, T., and Drake, S.: Effectiveness of sand-fixing measures on desert land restoration in Kerqin Sandy Land, Northern China, Ecol. Eng., 118–127, 2009.

Liu, X. M., Zhao, H. L., and Zhao, A. F.: A Wind-sandy Environment and Vegetation in the Horqin Sandy Land, Chinda, Science Press, Beijing, 1996 (in Chinese).

Liu, Z., Yan, Q., Liu, B., Ma, J., and Luo, Y.: Persistent soil seed bank in Agriophyllum squarrosum (Chenopodiaceae) in a deep sand profile: Variation along a transect of an active sand dune, J. Arid Environ., 71, 236–242, 2007.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., Hooper, D. U., Huston, M. A., Raffaelli, D., Schmid, B., Tilman, D., and Wardle, D. A.: Ecology – biodiversity and ecosystem functioning: Current knowledge and future challenges, Science, 294, 804–808, 2001.

Ma, M.: Species richness vs evenness: independent relationship and different responses to edaphic factors, Oikos, 111, 192–198, 2005.

Ma, W. H., He, J. S., Yang, Y. H., Wang, X. P., Liang, C. Z., Anwar, M., Zeng, H., Fang, J. Y., and Schmid, B.: Environmental factors covary with plant diversity-productivity relationships among Chinese grassland sites, Global Ecol. Biogeogr., 19, 233–243, 2010.

Maestre, F. T., Bradford, M. A., and Reynolds, J. F.: Soil heterogeneity and community composition jointly influence grassland biomass, J. Veg. Sci., 17, 261–270, 2006.

Marriott, C. A., Hood, K., Fisher, J. M., and Pakeman, R. J.: Long-term impacts of extensive grazing and abandonment on the species composition, richness, diversity and productivity of agricultural grassland, Agr. Ecosyst. Environ., 134, 190–200, 2009.

Mittelbach, G. G., Steiner, C. F., Scheiner, S. M., Gross, K. L., Reynolds, H. L., Waide, R. B., Willig, M. R., Dodson, S. I., and Gough, L.: What is the observed relationship between species richness and productivity?, Ecology, 82, 2381–2396, 2001.

Pärtel, M. and Zobel, M.: Dispersal limitation may result in the unimodal productivity-diversity relationship: a new explanation for a general pattern, J. Ecol., 95, 90–94, 2007.

Pärtel, M., Laanisto, L., and Zobel, M.: Contrasting plant productivity-diversity relationships across latitude: the role of evolutionary history, Ecology, 88, 1091–1097, 2007.

Pärtel, M., Zobel, K., Laanisto, L., Szava-Kovats, R., and Zobel, M.: The productivity-diversity relationship: varying aims and approaches, Ecology, 91, 2565–2567, 2010.

Spiegelberger, T., Matthies, D., Muller-Scharer, H., and Schaffner, U.: Scale-dependent effects of land use on plant species richness of mountain grassland in the European Alps, Ecography, 29, 541–548, 2006.

ter Braak, C. J. F. and Smilauer, P.: CANOCO Releases 4.5 Reference Manual and User's Guide to Canoco for Windows, Microcomputer Power, Ithaca, NY, 2002.

Tilman, D., Lehman, C. L., and Thomson, K. T.: Plant diversity and ecosystem productivity: Theoretical considerations, P. Natl. Acad. Sci. USA., 94, 1857–1861, 1997.

Tilman, D., Reich, P. B., Knops, J., Wedin, D., Mielke, T., and Lehman, C.: Diversity and productivity in a long-term grassland experiment, Science, 294, 843–845, 2001.

van Ruijven, J. and Berendse, F.: Diversity-productivity relationships: Initial effects, long-term patterns, and underlying mechanisms, P. Natl. Acad. Sci. USA, 102, 695–700, 2005.

van Ruijven, J. and Berendse, F.: Long-term persistence of a positive plant diversity-productivity relationship in the absence of legumes, Oikos, 118, 101–106, 2009.

Venail, P. A., MacLean, R. C., Bouvier, T., Brockhurst, M. A., Hochberg, M. E., and Mouquet, N.: Diversity and productivity peak at intermediate dispersal rate in evolving metacommunities, Nature, 452, 210–214, 2008.

Waide, R. B., Willig, M. R., Steiner, C. F., Mittelbach, G., Gough, L., Dodson, S. I., Juday, G. P., and Parmenter, R.: The relationship between productivity and species richness, Ann. Rev. Ecol. S., 30, 257–300, 1999.

Weigelt, A., Schumacher, J., Roscher, C., and Schmid, B.: Does biodiversity increase spatial stability in plant community biomass?, Ecol. Lett., 11, 338–347, 2008.

Wilsey, B. J. and Polley, H. W.: Effects of seed additions and grazing history on diversity and productivity of subhumid grasslands, Ecology, 84, 920–931, 2003.

Xiao, S., Zobel, M., Szava-Kovats, R., and Partel, M.: The effects of species pool, dispersal and competition on the diversity-productivity relationship, Global Ecol. Biogeogr., 19, 343–351, 2010.

Zhang, J., Zhao, H., Zhang, T., Zhao, X., and Drake, S.: Community succession along a chronosequence of vegetation restoration on sand dunes in Horqin Sandy Land, J. Arid Environ., 62, 555–566, 2005.

Zhou, Z., Sun, O. J., Huang, J., Gao, Y., and Han, X.: Land use affects the relationship between species diversity and productivity at the local scale in a semi-arid steppe ecosystem, Funct. Ecol., 20, 753–762, 2006.

Zuo, X. A., Zhao, H. L., Zhao, X. Y., Guo, Y. R., Yun, J. Y., Wang, S. K., and Miyasaka, T.: Vegetation pattern variation, soil degradation and their relationship along a grassland desertification gradient in Horqin Sandy Land, Northern China, Environ. Geol., 58, 1227–1237, 2009a.

Zuo, X. A., Zhao, X. Y., Zhao, H. L., Zhang, T. H., Guo, Y. R., Li, Y. Q., and Huang, Y. X.: Spatial heterogeneity of soil properties and vegetation-soil relationships following vegetation restoration of mobile dunes in Horqin Sandy Land, Northern China, Plant Soil, 318, 153–167, 2009b.

Zuo, X. A., Zhao, X. Y., Zhao, H. L., Zhang, T. H., Li, Y. L., Wang, S. K., and Li, W. J., and Powers, R.: Scale dependent effects of environmental factors on vegetation pattern and composition in Horqin Sandy Land, Northern China, Geoderma, doi:10.1016/j.geoderma. 2011.10.003, 2011.

Table 1. Descriptive statistics of productivity, biodiversity parameters, soil variables and site characteristics.

	Mobile dune	Semi Fixed dune	Fixed dune	Dry meadow	Wet meadow	Flood plain grassland	Coefficient of variation	*F*	*P*
Species richness	4.22 ± 1.92^{a}	9.29 ± 4.39^{b}	14.44 ± 3.57^{c}	14.33 ± 3.37^{c}	12.56 ± 3.91^{c}	15.57 ± 4.2^{c}	44.91	30.58	0.000
Shannon-Wiener	0.9 ± 0.47^{a}	1.66 ± 0.42^{b}	2.27 ± 0.29^{c}	2.06 ± 0.27^{c}	1.82 ± 0.37^{bc}	2.17 ± 0.31^{c}	31.08	12.42	0.000
Evenness	0.62 ± 0.27^{a}	0.79 ± 0.05^{b}	0.86 ± 0.06^{b}	0.78 ± 0.06^{bc}	0.73 ± 0.07^{c}	0.80 ± 0.06^{bc}	17.05	16.93	0.000
Simpson	0.53 ± 0.23^{e}	0.25 ± 0.09^{ad}	0.13 ± 0.05^{ac}	0.18 ± 0.05^{ab}	0.26 ± 0.11^{bd}	0.16 ± 0.06^{ab}	63.35	4.35	0.002
Biomass ($g\,m^{-2}$)	31.35 ± 20.54^{a}	118.81 ± 58.39^{b}	121.69 ± 43.8^{b}	$187.33 \pm 81.3b^{c}$	315.68 ± 59.27^{d}	390.96 ± 89.40^{e}	79.20	38.74	0.000
Soil C ($g\,kg^{-1}$)	0.52 ± 0.22^{a}	1.79 ± 1.87^{b}	3.34 ± 0.84^{c}	4.68 ± 1.25^{d}	5.75 ± 4.12^{d}	6.50 ± 2.44^{d}	80.81	11.06	0.000
Total N ($g\,kg^{-1}$)	0.09 ± 0.05^{a}	0.15 ± 0.09^{b}	0.26 ± 0.06^{c}	0.34 ± 0.08^{d}	0.43 ± 0.23^{d}	0.40 ± 0.13^{d}	62.40	12.54	0.000
C/N	6.28 ± 2.43^{a}	10.22 ± 3.85^{b}	12.81 ± 2.1^{b}	14.02 ± 2.01^{c}	12.52 ± 4.69^{bc}	16.17 ± 1.65^{e}	35.32	10.89	0.000
pH	7.86 ± 0.33^{a}	8.04 ± 0.38^{b}	8.10 ± 0.25^{bc}	8.20 ± 0.24^{c}	8.84 ± 0.42^{d}	8.69 ± 0.59^{d}	5.91	9.82	0.000
Electrical conductivity ($\mu s\ cm^{-1}$)	14.22 ± 6.04^{a}	23.79 ± 11.28^{b}	39 ± 11.38^{bc}	47.42 ± 21.6^{c}	116.89 ± 93.07^{d}	187.71 ± 76.61^{d}	113.93	17.84	0.000
Soil water content (0–20 cm, %)	3.36 ± 0.43^{a}	3.72 ± 1.29^{a}	4.10 ± 0.63^{a}	4.03 ± 1.68^{a}	6.60 ± 3.42^{b}	22.55 ± 5.53^{c}	100.67	68.69	0.000
Soil water content (20–40 cm, %)	3.61 ± 0.56^{a}	3.45 ± 0.76^{a}	4.13 ± 0.83^{a}	4.44 ± 2.21^{a}	7.45 ± 3.72^{b}	22.02 ± 4.80^{c}	95.88	67.83	0.000
Soil water content (40–60 cm, %)	3.66 ± 0.63^{a}	3.61 ± 0.96^{a}	3.83 ± 0.7^{a}	6.08 ± 5.50^{b}	7.00 ± 3.59^{b}	20.78 ± 6.70^{c}	95.95	25.11	0.000
Coarse sand (2–0.25 mm, %)	34.13 ± 13.02^{a}	35.28 ± 10.81^{a}	34.13 ± 11.8^{a}	30.61 ± 17.63^{a}	33.34 ± 15.47^{a}	24.06 ± 15.87^{a}	43.16	0.70	0.625
Fine sand (0.25–0.1 mm, %)	51.18 ± 16.1^{ab}	48.38 ± 10.24^{ab}	57.8 ± 11.9^{a}	43.56 ± 14.46^{b}	42.04 ± 10.27^{bc}	33.01 ± 22.38^{bc}	32.74	2.97	0.019
Very fine sand (0.1–0.05 mm, %)	6.05 ± 6.53^{ab}	9.45 ± 8.24^{ab}	4.42 ± 4.02^{a}	13.5 ± 11.25^{b}	14.33 ± 17.32^{b}	32.98 ± 26.08^{c}	120.37	4.76	0.001
Silt + clay (< 0.05 mm, %)	8.71 ± 7.36^{ac}	7.06 ± 2.88^{ac}	3.74 ± 2.66^{b}	12.08 ± 11.07^{c}	10.19 ± 6.94^{c}	9.58 ± 8.78^{c}	86.04	1.63	0.169
Longitude (°)	120.62 ± 0.11^{a}	120.65 ± 0.1^{a}	120.63 ± 0.09^{a}	120.7 ± 0.07^{a}	120.62 ± 0.08^{a}	120.64 ± 0.18^{a}	0.09	0.85	0.519
Latitude (°)	43.03 ± 0.13^{a}	43.04 ± 0.12^{a}	42.98 ± 0.08^{a}	42.97 ± 0.08^{a}	43.01 ± 0.09^{a}	43.02 ± 0.13^{a}	0.24	0.70	0.628
Altitude (m)	359.33 ± 16.31^{a}	351.44 ± 16.94^{a}	357.1 ± 14.18^{a}	353.65 ± 11.97^{a}	347.85 ± 15.03^{b}	335.51 ± 16.96^{b}	4.59	2.42	0.040

Different letters in vegetation characteristics and environment factors indicate statistical difference among different vegetation types at $P < 0.01$.

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Table 2. Multiple stepwise regression models for species richness, NMDS1, NMDS2 and productivity. Separate regressions were calculated for the parameter groups of soil and site characteristics.

Dependent variable	Independent parameter group	Details of multiple regression model				Model summary	
		Variable	b	P	R^2	R^2	P
Species richness	Soil					0.215	0.009
		Soil1	2.347	0.000	0.209		
	Site					0.314	0.000
		Site2	–2.857	0.000	0.310		
Shannon-Wiener	Soil					0.148	0.062
		Soil1	0.201	0.004	0.131		
	Site					0.215	0.001
		Site2	–0.257	0.000	0.463		
Simpson	Soil					0.104	0.187
		Soil1	–0.047	0.024	0.085		
	Site					0.140	0.002
		Site2	0.060	0.002	0.138		
NMDS1	Soil					0.439	0.000
		Soil1	0.406	0.000	0.338		
		Soil4	0.183	0.013	0.406		
	Site					0.191	0.002
		Site2	–0.305	0.001	0.190		
NMDS2	Soil					0.561	0.000
		Soil1	0.463	0.000	0.419		
		Soil3	0.132	0.048	0.535		
		Soil4	–0.205	0.003	0.501		
	Site					0.133	0.017
		Site1	0.241	0.008	0.114		
Productivity	Soil					0.627	0.000
		Soil1	95.80	0.000	0.555		
		Soil2	–25.98	0.015	0.598		
		Soil3	22.271	0.036	0.627		
	Site					0.225	0.001
		Site1	37.95	0.003	0.225		
		Site2	–46.88	0.013	0.136		

Table 3. Fitted measures for the competing structural equation models tested using the bootstrapping procedure implemented in AMOS. The most complex starting model (model A) is shown in Fig. 3a. Model G is the best-fitting model based on AIC, BCC and the SMC of variable productivity (Fig. 3b).

Model	Model details	χ^2	AIC	BCC	SMC diversity	SMC productivity
Model A	Full model (Fig. 3a)	24.20	94.20	110.24	0.56	0.74
Model B	Regression soil1 on diversity excluded	24.21	92.21	107.79	0.56	0.74
Model C	Regression soil1 on diversity excluded, regression site1 on productivity excluded;	25.04	91.04	106.17	0.56	0.75
Model D	Regression soil1 on diversity excluded, regression site1 on productivity excluded, regression site2 on productivity excluded	25.37	89.37	104.03	0.57	0.75
Model E	Regression soil1 on diversity excluded, regression site1 on productivity excluded, regression site2 on productivity excluded, soil2 excluded	12.82	68.82	80.24	0.55	0.76
Model F	Regression soil1 on diversity excluded, regression site1 on productivity excluded, regression site2 on productivity excluded, soil2 excluded, regression soil3 on NMDS2 excluded	14.63	68.63	79.65	0.55	0.76
Model G	Regression soil1 on diversity excluded, regression site1 on productivity excluded, regression site2 on productivity excluded, soil2 excluded, regression soil3 on NMDS2 excluded, soil3 excluded (Fig. 3b)	12.87	60.88	69.52	0.55	0.75
Model H	Regression soil1 on diversity excluded, regression site1 on productivity excluded, regression site2 on productivity excluded, soil2 excluded, regression soil3 on NMDS2 excluded, soil3 excluded, regression soil1 on productivity excluded	15.31	61.30	69.59	0.53	0.75

χ^2, Chi-square test, The Browne-Cudeckcriterion (BCC), the Akaike information criterion (AIC), the consistent AIC, the squared multiple correlation (SMC) of the variable diversity (species richness), the SMC of variable productivity.

Table A1. Intra-set correlations of the environmental variables and cumulative percentage variance for the first two axes of NMDS in sandy grasslands.

	NMDS1	NMDS2
Soil type	0.55^b	0.74^b
Soil C	0.65^b	0.39^b
Total N	0.72^b	0.37^b
C/N	0.55^b	0.17
pH	0.56^b	0.36^b
EC	0.49^b	0.65^b
Soil water content (0–20 cm)	0.29^a	0.74^b
Soilwater content (21–40 cm)	0.32^a	0.77^b
Soil water content (41–60 cm)	0.32^a	0.68^b
Coarsesand (2–0.25 mm)	–0.15	–0.11
Fine sand (0.25–0.1 mm)	–0.17	$–0.33^a$
Very fine sand(0.1–0.05 mm)	0.23	0.37^b
Silt + clay (< 0.05 mm)	0.16	0.13
Longitude	0.16	–0.05
Latitude	$–0.34^b$	0.08
Altitude	–0.04	$–0.34^b$
Cumulative percentage variance (%)	28.20	69.90

[a] $P < 0.05$
[b] $P < 0.01$

Table A2. Correlation analyses among species richness, Shannon-Wiener index, Evenness index, Simpson index, NMDS1and NMDS2 in sandy grasslands.

	Species richness	Shannon-Wiener	Evenness	Simpson	NMDS1	NMDS2
Species richness	1					
Shannon-Wiener	0.92[b]	1				
Evenness	0.44[b]	0.69[b]	1			
Simpson	–0.79[b]	–0.95[b]	–0.83[b]	1		
NMDS1	0.69[b]	0.68[b]	0.32[a]	–0.62[b]	1	
NMDS2	0.11	–0.05	–0.23	0.14	0.12	1

[a] $P < 0.05$;
[b] $P < 0.01$

Table A3. Relative presence and average cover of those plant species in all 60 sites that explain $>8\,\%$ of the variance of the non-metric multidimensional scaling (NMDS) axis and $>7\,\%$ of variability in productivity in simple linear regressions. + and − signs represent the direction of the relationship.

	Presence (%)	Average cover (%)	NMDS1 (R^2)	NMDS2 (R^2)	Productivity (R^2)
Agriophyllum squarrosum	20	1	0.69[b](−)		0.44[b](−)
Artemisia halodendrom	33	5.07	0.43[b](−)	0.41[b](−)	0.27[a](−)
Calamagrostis Pseudophragmites	15	1		0.57[b](+)	0.53[b](+)
Caragana microphylla	22	2.13		0.41[b](−)	
Carex dispalata	13	3.37		0.69[b](+)	0.55[b](+)
Chloris virgata	33	3.49	0.30[a](+)		0.33[a](+)
Cleistogenes squarrosa	28	2.6	0.35[a](+)		
Corispermum elongatum	50	2.18		0.40[b](−)	
Digitaria ciliaris	27	1	0.34[b](+)		
Lespedeza davurica	38	1.16		0.38[b](−)	
Phragmites communis	33	3.62	0.27[a](+)	0.30[a](+)	0.37[b](+)
Plantago asiatica	15	1		0.66[b](−)	0.50[b](+)
Potentilla bifurca	13	2		0.47[b](+)	0.33[a](+)
Salsola collina	45	1.09	0.33[a](+)	0.32[b](−)	
Typha orientalis	10	4.12		0.68[b](−)	0.62[b](+)

[a] $P < 0.05$;
[b] $P < 0.01$

Table A4. Eigenvalues and eigenvector coefficients (loadings) of a standardized principal component analysis (PCA). PCA was performed separately for edaphic factors, site characteristics and management parameters.

PCA	Axis1	Axis2	Axis3	Axis4
Soil factors	Soil1	Soil2	Soil3	Soil4
Eigenvalue	0.69	0.15	0.06	0.05
Cumulative percentage variance (%)	68.80	84.20	90.20	94.70
Soil Type	0.79[b]	–0.08	0.17	–0.12
Soil C	0.72[b]	–0.13	0.06	0.29[a]
Total N	0.70[b]	–0.19	0.01	0.36[b]
C/N	0.53[b]	–0.04	0.11	0.11
pH	0.73[b]	–0.15	0	0.22
EC	0.98[b]	–0.18	–0.03	0.08
Soil water content (0–20 cm)	0.82[b]	–0.16	0.04	–0.45[b]
Soil water content (21–40 cm)	0.84[b]	–0.17	0.11	–0.44[b]
Soil water content (41–60 cm)	0.72[b]	–0.18	0.16	–0.55[b]
Coarse sand (2–0.25 mm)	–0.50[b]	–0.38[b]	0.64[b]	0.12
Fine sand (0.25–0.1 mm)	–0.51[b]	–0.7	–0.66[b]	–0.03
Very fine sand (0.1–0.05 mm)	0.63[b]	0.74[b]	0.07	–0.11
Silt + Clay (< 0.05 mm)	0.41[b]	0.68[b]	0.03	0.40[b]
Site characteristics	Site1	Site2	Site3	Site4
Eigenvalue	0.99	0.01	0	0
Cumulative percentage variance (%)	99	100		
Longitude	0.04	–0.90[b]		
Latitude	0.82[b]	0.50[b]		
Altitude	1.00[b]	0		

[a] $P < 0.05$;
[b] $P < 0.01$

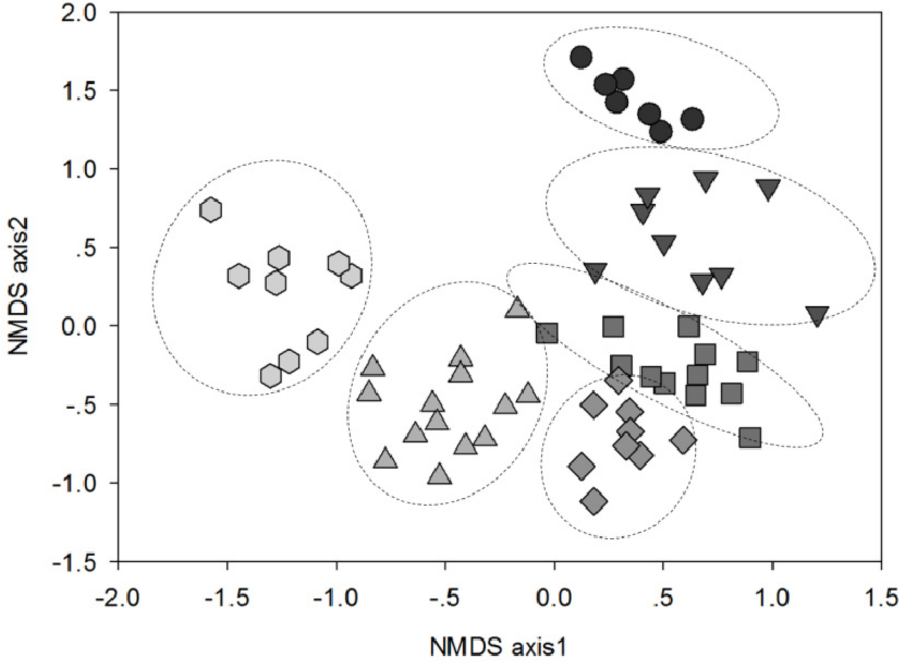

Fig. 1. Non-metric multidimensional scaling (NMDS) ordination of the 60 sandy grassland sites (minimum stress values first axis/dimension = 49.13, $R^2 = 0.28$, $P = 0.004$; second axis/dimension = 31.66, $R^2 = 0.42$, $P = 0.004$). ⬡, Mobile Dune; ▲, Semi Fixed Dune; ◆, Fixed Dune; ■, Dry Meadow; ▼, Wet Meadow; ●, Flood Plain Grassland.

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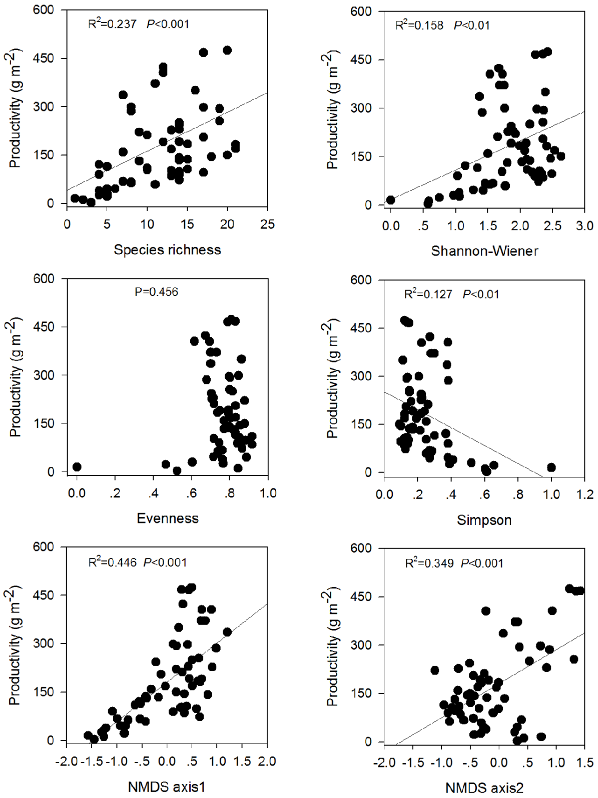

Fig. 2. Relationships of different plant diversity measures and community composition to productivity in sandy grasslands ($n = 60$).

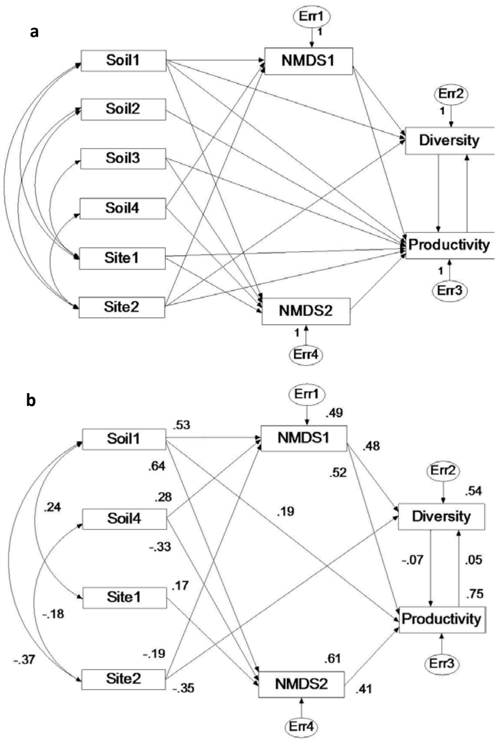

Fig. 3. Structural equation modeling. **(a)**, Initial model. Single-headed arrows indicate paths. Double-headed arrows show the covariance included in the model based on modifications proposed by AMOS (procedure modification indices). The exogenous unobserved variables Err1, Err2, Err3 and Err 4 account for the unexplained error in the estimation of NMDS1, NMDS2, diversity (species richness) and productivity, respectively. Their regression weights were a priori set to unity. **(b)**, Standardized regression weights (along paths), correlations (along double-headed arrows) and squared multiple correlations (beside the boxes of NMDS1, NMDS2, diversity and productivity) for the best-fitting model G (Table 3).