



## Indirect drivers of plant diversity-productivity relationship in semiarid sandy grasslands

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**Abstract.** Although patterns between plant diversity and ecosystem productivity have been much studied, a consistent relationship has not yet emerged. Differing patterns between plant diversity and productivity have been observed in response to spatial variability of environmental factors and vegetation composition. In this study, we measured vegetation cover, plant diversity, productivity, soil properties and site characteristics along an environmental gradient (mobile dune, semi-fixed dune, fixed dune, dry meadow, wet meadow and flood plain grasslands) of natural sandy grasslands in semiarid areas of northern China. We used multivariate analysis to examine the relationships between environmental factors, vegetation composition, plant diversity and productivity. We found a positive correlation between plant diversity and productivity. Vegetation composition aggregated by the ordination technique of non-metric multidimensional scaling had also a significantly positive correlation with plant diversity and productivity. Environmental gradients in relation to soil and topography affected the distribution patterns of vegetation composition, species diversity and productivity. However, environmental gradients were a better determinant of vegetation composition and productivity than of plant diversity. Structural equation modeling suggested that environmental factors determine vegetation composition, which in turn independently drives both plant diversity and productivity. Thus, the positive correlation between plant diversity and productivity is indirectly driven by vegetation composition, which is determined by environmental gradients in soil and topography.

### 1 Introduction

Diversity-productivity relationships have shown several patterns in ecology over the last decades (Grace et al., 2007; Pärtel et al., 2007; Pärtel et al., 2010; Xiao et al., 2010). Numerous studies have reported five diversity-productivity patterns: positive, negative, hump-shaped, U-shaped and no relationship (Hector et al., 2010; Ma et al., 2010). Differing explanations have been given for the variation in diversity-productivity relationships in grassland ecosystems, including 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), limited temporal and scale of studies (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).

Theoretical and experimental studies have greatly increased our knowledge of how plant diversity influences ecosystem productivity in the past decades. Specifically, manipulative experiments in which plant diversity is changed by drawing plant species from a random species pool have shown that increasing species diversity frequently enhances productivity (Tilman et al., 1997; Hector, 1998; Hector et al., 1999; Tilman et al., 2001). These experimental studies are often performed in a uniform environment with

well-mixed species (Zhou et al., 2006). However, studies in natural ecosystems report differing patterns of diversity-productivity, because field observations typically involve one or several environmental gradients (Cardinale et al., 2000; Zuo et al., 2012).

Many studies have shown that environmental gradients are important factors, influencing both species richness and biomass in natural ecosystems (Maestre et al., 2006; Fornara and Tilman, 2009; Ma et al., 2010). In Chinese natural grasslands, a positive relationship between plant diversity and productivity has been ascribed 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, what is the role of environmental factors in this relationship (Waide et al., 1999; Cardinale et al., 2004)?

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

We therefore assessed how important environmental factors and vegetation composition are in influencing diversity-productivity relationships (*sensu* Chapin et al., 2000; Loreau et al., 2001; Kahmen et al., 2005a) in order to manage natural grassland ecosystems for improved species diversity, productivity and sustainability. Our previous study suggests that a combination of soil properties and topography determines the vegetation pattern and composition along an environmental gradient (mobile dune, semi-fixed dune, fixed dune, dry meadow, wet meadow and flood plain grasslands) in sandy grasslands (Zuo et al., 2012). Here, we use a multivariate model that examines and controls environmental variables statistically to determine effects of vegetation composition and environmental factors on the relationship of plant diversity-productivity in sandy grasslands. We tested two hypotheses that (1) plant diversity and productivity are influenced by both environmental factors and community composition in sandy grasslands; and (2) environmental factors determine the distribution and composition 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 climate is temperate, semiarid 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<sup>-1</sup>, and the prevailing wind direction is northwest in winter and spring (Liu et al., 1996; Zhang et al., 2005).

The region, about 50 600 km<sup>2</sup>, is located in a transitional zone between croplands and pastures and is an important commodity grain production base in China. Horqin Sand Land is one of the most severely desertified regions of China. However, owing to the annual precipitation of 350–500 mm, the degraded vegetation could be gradually and naturally restored after excluding fuel wood gathering and grazing. Due to vegetation restoration, sandy desertification in this region has been reversed since 2000 (Wang et al., 2004). This region consists of a mixture of flood plain grasslands, lowland grasslands, sand dunes, woodlands and farmlands (Liu et al., 1996; Liu et al., 2007). Soils are of three different types: marsh soil present in wetland and flood plain grasslands, 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 grasslands consists of native plants, including grasses (e.g. *Leymus chinensis*, *Cleistogenes squarrosa*, *Setaria viridis*, *Phragmites australis*, *Digitaria ciliaris*), forbs (*Melissitus ruthenicus*, *Salsola collina*, *Agriophyllum squarrosum*, *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 surveys in 60 fenced sites, excluding land use, were carried out in mid August (the peak time of biomass) 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 grasslands). At each site, a 30 × 30 m plot was established. Three random quadrats (1 × 1 m) were placed in each plot, giving a total of 180 quadrats to measure plant height (maximum), species abundance and plant cover. Abundance was defined as individual density. Plant cover was visually estimated as percent canopy

cover. Plant height was measured with a ruler on those culms. Maximum aboveground biomass was selected as a proxy for annual productivity. Therefore, in each quadrant all vegetation was clipped at ground level. The leaves and current-year twigs of each shrub species in each quadrat were collected to estimate its annual productivity. The aboveground biomass was dried at 60 °C 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 cm, 20–40 cm 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 (ISS-CAS, 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  $IV = (RC + RA + RH)/3$ , where RC is the relative cover of the species (species cover/total cover for all species  $\times 100$ ), RA is the relative abundance (species density/total density for all species  $\times 100$ ), and RH is the relative height (species height/total height for all species  $\times 100$ ) (Zhang et al., 2005; He et al., 2007; Zuo et al., 2009). Indices of species diversity were calculated from the importance value of species, including species richness, Shannon–Wiener index, Simpson ecological dominance index and evenness index (Zhang et al., 2005).

### 2.3.2 Aggregation of vegetation compositions and environmental factors

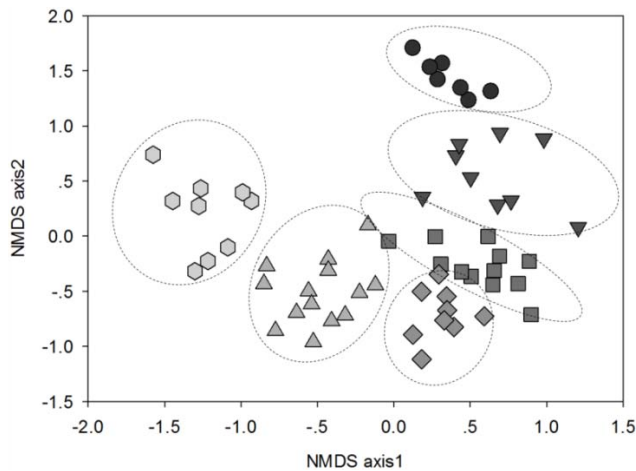
To determine the effect of vegetation compositions and environmental factors on plant diversity and productivity, the ordination techniques of principal component analysis (PCA) and non-metric multidimensional scaling (NMDS) were used to aggregate environmental factors and vegetation composition (Kahmen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



**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 Grasslands.

### 2.3.4 Influence of vegetation composition and environmental 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 are response variables, 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. PCAs 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 environmental factors

Based on the ordination analysis of 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 grasslands (Fig. 1, Table 1 and all  $P < 0.01$ ). Our results showed that along a habitat gradient from mobile dune to flood plain grasslands, 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 (Appendix Table 1), 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 environmental 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 grasslands. The correlation analysis showed that plant diversity was correlated with species compositions (NMDS1) (Appendix Table 2). 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 (Appendix Table 3).

### 3.2 Changes of environmental factors

Soil organic C, total N, C/N, pH, EC, very fine sand and soil water contents (0–20 cm, 20–40 cm 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 grasslands, but there were no significant differences in soil organic C and total N

**Table 1.** Descriptive statistics of diversity parameters, productivity, soil variables and site characteristics (mean  $\pm$  SD).

	Mobile Dune	Semi-fixed Dune	Fixed Dune	Dry Meadow	Wet Meadow	Flood Plain Grassland	Coefficient of Variation (%)	<i>F</i>	<i>P</i>
Species richness	4.22 $\pm$ 1.92 <sup>a</sup>	9.29 $\pm$ 4.39 <sup>b</sup>	14.44 $\pm$ 3.57 <sup>c</sup>	14.33 $\pm$ 3.37 <sup>c</sup>	12.56 $\pm$ 3.91 <sup>c</sup>	15.57 $\pm$ 4.2 <sup>c</sup>	44.91	30.58	0.000
Shannon-Wiener	0.90 $\pm$ 0.47 <sup>a</sup>	1.66 $\pm$ 0.42 <sup>b</sup>	2.27 $\pm$ 0.29 <sup>c</sup>	2.06 $\pm$ 0.27 <sup>c</sup>	1.82 $\pm$ 0.37 <sup>bc</sup>	2.17 $\pm$ 0.31 <sup>c</sup>	31.08	12.42	0.000
Evenness	0.62 $\pm$ 0.27 <sup>a</sup>	0.79 $\pm$ 0.05 <sup>b</sup>	0.86 $\pm$ 0.06 <sup>b</sup>	0.78 $\pm$ 0.06 <sup>bc</sup>	0.73 $\pm$ 0.07 <sup>c</sup>	0.80 $\pm$ 0.06 <sup>bc</sup>	17.05	16.93	0.000
Simpson	0.53 $\pm$ 0.23 <sup>c</sup>	0.25 $\pm$ 0.09 <sup>ad</sup>	0.13 $\pm$ 0.05 <sup>ac</sup>	0.18 $\pm$ 0.05 <sup>ab</sup>	0.26 $\pm$ 0.11 <sup>bd</sup>	0.16 $\pm$ 0.06 <sup>ab</sup>	63.35	4.35	0.002
Biomass (g m <sup>-2</sup> )	31.35 $\pm$ 20.54 <sup>a</sup>	118.81 $\pm$ 58.39 <sup>b</sup>	121.69 $\pm$ 43.8 <sup>b</sup>	187.33 $\pm$ 81.3b <sup>c</sup>	315.68 $\pm$ 59.2 <sup>d</sup>	390.96 $\pm$ 89.40 <sup>e</sup>	79.20	38.74	0.000
Soil C (g kg <sup>-1</sup> )	0.52 $\pm$ 0.22 <sup>a</sup>	1.79 $\pm$ 1.87 <sup>b</sup>	3.34 $\pm$ 0.84 <sup>c</sup>	4.68 $\pm$ 1.25 <sup>d</sup>	5.75 $\pm$ 4.12 <sup>d</sup>	6.50 $\pm$ 2.44 <sup>d</sup>	80.81	11.06	0.000
Total N (g kg <sup>-1</sup> )	0.09 $\pm$ 0.05 <sup>a</sup>	0.15 $\pm$ 0.09 <sup>b</sup>	0.26 $\pm$ 0.06 <sup>c</sup>	0.34 $\pm$ 0.08 <sup>d</sup>	0.43 $\pm$ 0.23 <sup>d</sup>	0.40 $\pm$ 0.13 <sup>d</sup>	62.40	12.54	0.000
C/N	6.28 $\pm$ 2.43 <sup>a</sup>	10.22 $\pm$ 3.85 <sup>b</sup>	12.81 $\pm$ 2.1 <sup>b</sup>	14.02 $\pm$ 2.01 <sup>c</sup>	12.52 $\pm$ 4.69 <sup>bc</sup>	16.17 $\pm$ 1.65 <sup>e</sup>	35.32	10.89	0.000
pH	7.86 $\pm$ 0.33 <sup>a</sup>	8.04 $\pm$ 0.38 <sup>b</sup>	8.10 $\pm$ 0.25 <sup>bc</sup>	8.20 $\pm$ 0.24 <sup>c</sup>	8.84 $\pm$ 0.42 <sup>d</sup>	8.69 $\pm$ 0.59 <sup>d</sup>	5.91	9.82	0.000
Electrical conductivity ( $\mu$ s cm <sup>-1</sup> )	14.22 $\pm$ 6.04 <sup>a</sup>	23.79 $\pm$ 11.28 <sup>b</sup>	39 $\pm$ 11.38 <sup>bc</sup>	47.42 $\pm$ 21.6 <sup>c</sup>	116.89 $\pm$ 93.07 <sup>d</sup>	187.71 $\pm$ 76.61 <sup>d</sup>	113.93	17.84	0.000
Soil water content (0–20 cm, %)	3.36 $\pm$ 0.43 <sup>a</sup>	3.72 $\pm$ 1.29 <sup>a</sup>	4.10 $\pm$ 0.63 <sup>a</sup>	4.03 $\pm$ 1.68 <sup>a</sup>	6.60 $\pm$ 3.42 <sup>b</sup>	22.55 $\pm$ 5.53 <sup>c</sup>	100.67	68.69	0.000
Soil water content (20–40 cm, %)	3.61 $\pm$ 0.56 <sup>a</sup>	3.45 $\pm$ 0.76 <sup>a</sup>	4.13 $\pm$ 0.83 <sup>a</sup>	4.44 $\pm$ 2.21 <sup>a</sup>	7.45 $\pm$ 3.72 <sup>b</sup>	22.02 $\pm$ 4.80 <sup>c</sup>	95.88	67.83	0.000
Soil water content (40–60 cm, %)	3.66 $\pm$ 0.63 <sup>a</sup>	3.61 $\pm$ 0.96 <sup>a</sup>	3.83 $\pm$ 0.7 <sup>a</sup>	6.08 $\pm$ 5.50 <sup>b</sup>	7.00 $\pm$ 3.59 <sup>b</sup>	20.78 $\pm$ 6.70 <sup>c</sup>	95.95	25.11	0.000
Coarse sand (2–0.25 mm, %)	34.13 $\pm$ 13.02 <sup>a</sup>	35.28 $\pm$ 10.81 <sup>a</sup>	34.13 $\pm$ 11.8 <sup>a</sup>	30.61 $\pm$ 17.63 <sup>a</sup>	33.34 $\pm$ 15.47 <sup>a</sup>	24.06 $\pm$ 15.87 <sup>a</sup>	43.16	0.70	0.625
Fine sand (0.25–0.1 mm, %)	51.18 $\pm$ 16.1 <sup>ab</sup>	48.38 $\pm$ 10.24 <sup>ab</sup>	57.8 $\pm$ 11.9 <sup>a</sup>	43.56 $\pm$ 14.46 <sup>b</sup>	42.04 $\pm$ 10.27 <sup>bc</sup>	33.01 $\pm$ 22.38 <sup>bc</sup>	32.74	2.97	0.019
Very fine sand (0.1–0.05 mm, %)	6.05 $\pm$ 6.53 <sup>ab</sup>	9.45 $\pm$ 8.24 <sup>ab</sup>	4.42 $\pm$ 4.02 <sup>a</sup>	13.5 $\pm$ 11.25 <sup>b</sup>	14.33 $\pm$ 17.32 <sup>b</sup>	32.98 $\pm$ 26.08 <sup>c</sup>	120.37	4.76	0.001
Silt + Clay (<0.05 mm, %)	8.71 $\pm$ 7.36 <sup>ac</sup>	7.06 $\pm$ 2.88 <sup>ac</sup>	3.74 $\pm$ 2.66 <sup>b</sup>	12.08 $\pm$ 11.07 <sup>c</sup>	10.19 $\pm$ 6.94 <sup>c</sup>	9.58 $\pm$ 8.78 <sup>c</sup>	86.04	1.63	0.169
Longitude (°)	120.62 $\pm$ 0.11 <sup>a</sup>	120.65 $\pm$ 0.1 <sup>a</sup>	120.63 $\pm$ 0.09 <sup>a</sup>	120.7 $\pm$ 0.07 <sup>a</sup>	120.62 $\pm$ 0.08 <sup>a</sup>	120.64 $\pm$ 0.18 <sup>a</sup>	0.09	0.85	0.519
Latitude (°)	43.03 $\pm$ 0.13 <sup>a</sup>	43.04 $\pm$ 0.12 <sup>a</sup>	42.98 $\pm$ 0.08 <sup>a</sup>	42.97 $\pm$ 0.08 <sup>a</sup>	43.01 $\pm$ 0.09 <sup>a</sup>	43.02 $\pm$ 0.13 <sup>a</sup>	0.24	0.70	0.628
Altitude (m)	359.33 $\pm$ 16.31 <sup>a</sup>	351.44 $\pm$ 16.94 <sup>a</sup>	357.1 $\pm$ 14.18 <sup>a</sup>	353.65 $\pm$ 11.97 <sup>a</sup>	347.85 $\pm$ 15.03 <sup>b</sup>	335.51 $\pm$ 16.96 <sup>b</sup>	4.59	2.42	0.040

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

among dry meadow, wet meadow and flood plain grasslands ( $P > 0.05$ ) and were no significant differences in soil water contents among mobile dune, semi-fixed dune and the fixed dune ( $P > 0.05$ ). There were also differences in fine sand and altitude among six vegetation types (Table 1,  $P < 0.05$ ). 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 (Appendix Table 4). Soil1 accounted for 68.8 % of the total variance, and was significantly positive correlated to soil type, soil C, total N, C/N, pH, EC, soil water contents, 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 15.4 % 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 % 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 4.5 % 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 (Appendix Table 4). 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 corre-

lated 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 grasslands (Fig. 2). Species richness and the Shannon-Wiener diversity index were significantly positive correlated to productivity ( $P < 0.01$ ), and the 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

Environmental factors were correlated to plant diversity, vegetation composition and productivity in sandy grasslands. Using multiple stepwise regression models, 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

**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	<i>P</i>	<i>R</i> <sup>2</sup>	<i>R</i> <sup>2</sup>	<i>P</i>
Species richness	Soil	Soil1	2.347	0.000	0.209	0.215	0.009
		Soil2	−2.857	0.000	0.310	0.314	0.000
	Site						
Shannon-Wiener	Soil	Soil1	0.201	0.004	0.131	0.148	0.062
		Soil2	−0.257	0.000	0.463	0.215	0.001
	Site						
Simpson	Soil	Soil1	−0.047	0.024	0.085	0.104	0.187
		Soil2	0.060	0.002	0.138	0.140	0.002
	Site						
NMDS1	Soil	Soil1	0.406	0.000	0.338	0.439	0.000
		Soil4	0.183	0.013	0.406	0.191	0.002
	Site	Site1	−0.305	0.001	0.190		
		Site2					
NMDS2	Soil	Soil1	0.463	0.000	0.419	0.561	0.000
		Soil3	0.132	0.048	0.535		
		Soil4	−0.205	0.003	0.501		
		Soil2					
	Site	Site1	0.241	0.008	0.114	0.133	0.017
Productivity	Soil	Soil1	95.80	0.000	0.555	0.627	0.000
		Soil2	−25.98	0.015	0.598		
		Soil3	22.27	0.036	0.627		
	Site	Site1	37.95	0.003	0.225	0.225	0.001
		Site2	−46.88	0.013	0.136		

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 that 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 environmental factors on plant diversity, vegetation composition and pro-

ductivity, 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 the fitting model (Table 3). All of the tested models were significant. The optimal structural equation model 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

**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	X <sup>2</sup>	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

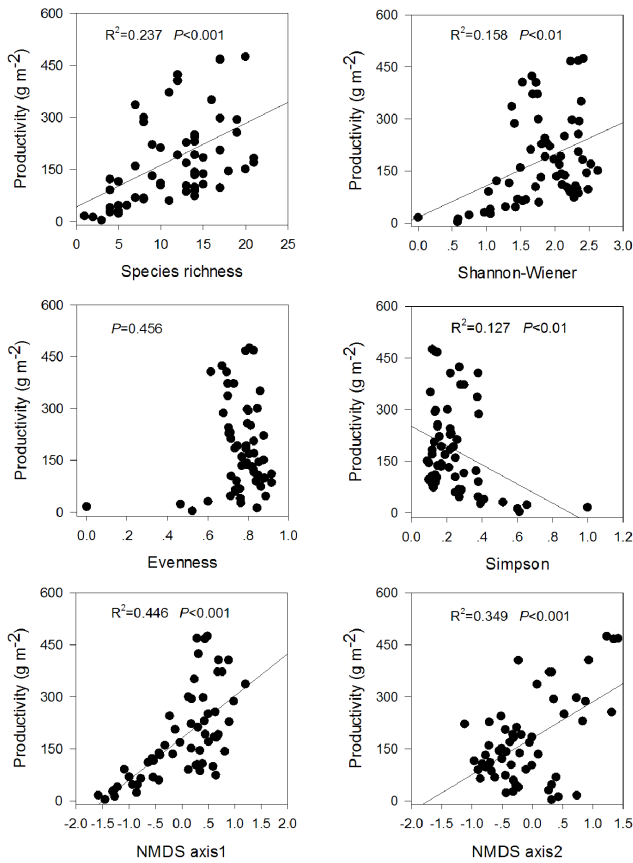
X<sup>2</sup>, chi-square test, The Browne-Cudeck criterion (BCC), the Akaike information criterion (AIC), the consistent AIC, the squared multiple correlation (SMC) of the variable diversity (species richness), the SMC of variable productivity.

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

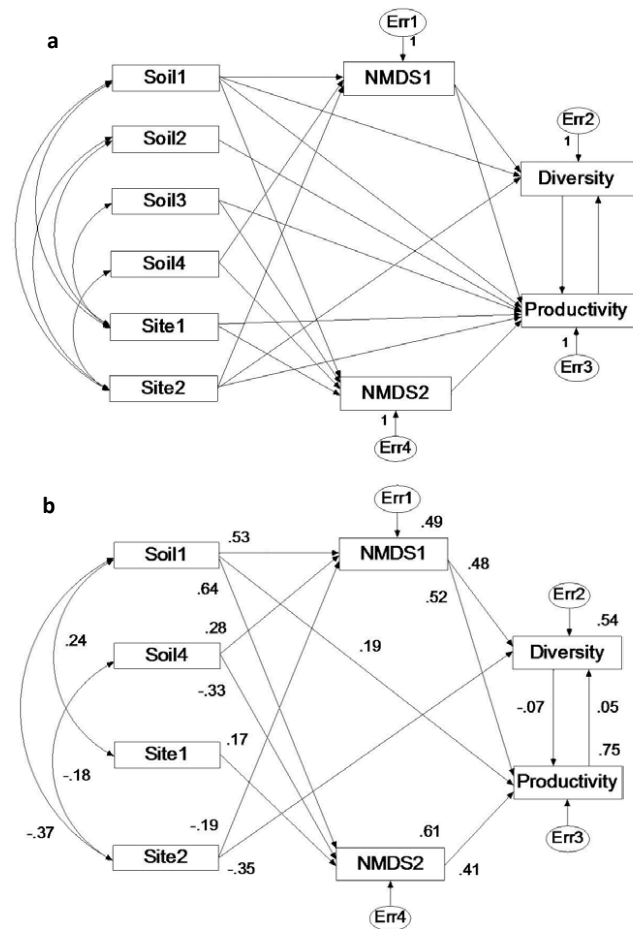
We found a positive correlation between plant diversity and ecosystem productivity in sandy grasslands, which is consistent with other studies both in synthesized experimental ecosystems (Tilman et al., 1997; Hector, 1998; Hector et al., 1999; Tilman et al., 2001) and natural grassland ecosystems (Bai et al., 2007; Ma et al., 2010). Some studies have shown that environmental factors determine both species richness and biomass in natural ecosystems (Maestre et al., 2006; Fornara and Tilman 2009; Ma et al. 2010), and may cause increasing species dissimilarity (Chase and Leibold, 2002). In our study soil water, nutrients and other properties positively influenced plant diversity and productivity, consistent with other grassland studies (Sala et al., 1988; Bai et al., 2007).





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

At the regional scale, vegetation composition is primarily determined by environmental factors such as climate, soil fertility and topography (Whittaker et al., 2001; Huerta-Martínez et al., 2004; Jafari et al., 2004). Among different environmental factors, soil is very important for plant growth and distribution, because it is a function of climate, soil biota, topography, parent material and time (Jafari et al., 2004). In our study area, climate difference is relatively small, so vegetation composition in sandy grasslands may be potentially affected by the gradient of soil properties and topography. Our previous studies have shown that the vegetation restoration of mobile dunes also significantly enhances topsoil development, and conversely, the spatial variation of soil properties is likely to determine the plant distribution in dune ecosystem (Li et al., 2009; Zuo et al., 2009). Topography can also partly affect the redistribution of soil water content, nutrient and soil particles, thereby indirectly impacting plant distribution at the dune scale (Zuo et al., 2009). In addition, the spatial variation of soil water content is also particularly important, because it determines the regional distribution of an ecosystem (Ma et al., 2004). One previous study has also shown that soil water content affected by altitude is one of



**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 D (Table 3).

the important factors affecting the vegetation composition in grassland habitats (Zuo et al., 2012).

This study supports a positive, rather than a humped-shaped pattern of diversity-productivity (e.g. Mittelbach et al., 2001; Gillman and Wright, 2006; Bai et al., 2007; Gross et al., 2009; Ma et al., 2010). A unimodal relationship between diversity-productivity is often found in temperate ecosystems, and a positive relationship is often found in tropical ecosystems (Pärtel et al., 2007). A meta-analysis has also supported the unimodal shape relationship from local to landscape scales, whereas a positive linear relationship is



common at the continental scale (Mittelbach et al., 2001). In Northern American grasslands, 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 more positive patterns of diversity-productivity in grasslands, likely because of the effect of natural environmental gradients at larger spatial scales.

The positive relationship between diversity and productivity can occur when environmental conditions change from a small scale to a regional 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 generate a positive relationship between plant diversity and productivity in grasslands (Bai et al., 2007). In addition to explanations of environmental conditions at different scales, spatial changes of habitats also determine the vegetation composition, plant diversity and productivity (Zuo et al., 2009; 2012). The effect of habitat change is very important at the regional scale and is an alternative explanation of variation 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). Thus, once species-poor habitats (e.g. mobile dune) have been gradually transformed into diverse natural habitats such as a semi-fixed dune and fixed dune, vegetation restoration may cause an increase in plant diversity and ecosystem productivity in sandy grasslands.

Not surprisingly, we found that species compositions in plant communities changed from the pioneer plant species on mobile dunes to hygrophytes in the flood plain grasslands and that vegetation composition strongly varied with environmental conditions. Clearly, the occurrence of plant species at a site is determined by the presence of a suitable habitat, and local diversity; vegetation composition is also strongly influenced by the number of habitat types, i.e. environmental heterogeneity. Therefore, niche differentiation between species may increase the collective performance of plant communities across the habitat types, further driving patterns of plant diversity and productivity. This is specifically indicated by the spatial heterogeneity of habitat, allowing 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 vegetation composition, and vegetation composition may further drive plant diversity and productivity in the same direction.

Our study demonstrates that vegetation composition, plant diversity and productivity changed consistently along an environmental gradient in soil and topography in sandy grasslands. Although soil properties and topographic features are highly important factors for plant diversity and ecosystem functioning, their influences on plant diversity and productivity are indirect via driving vegetation composition. Our results support that vegetation composition of grassland ecosystems is 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 environmental factors and how these factors influence productivity. In addition, to maintain the diversity and productivity in grassland ecosystems in semiarid areas, it is necessary to conserve the sandy grassland habitats and promote the restoration succession of degraded vegetation by improvement of environmental conditions.

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

\*  $P < 0.05$ ; \*\*  $P < 0.01$ .**Table A2.** Correlation analyses among species richness, Shannon-Wiener index, evenness index, Simpson index, NMDS1 and NMDS2 in sandy grasslands.

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

\*  $P < 0.05$ ; \*\*  $P < 0.01$ .**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 ( $R^2$ )
<i>Agriophyllum squarrosum</i>	20	1	0.69**(-)		0.44**(-)
<i>Artemisia halodendrom</i>	33	5.07	0.43**(-)	0.41**(-)	0.27*(-)
<i>Calamagrostis Pseudophragmites</i>	15	1		0.57**(+)	0.53**(+)
<i>Caragana microphylla</i>	22	2.13		0.41**(-)	
<i>Carex dispalata</i>	13	3.37		0.69**(+)	0.55**(+)
<i>Chloris virgata</i>	33	3.49	0.30*(+)		0.33*(+)
<i>Cleistogenes squarrosa</i>	28	2.6	0.35*(+)		
<i>Corispermum elongatum</i>	50	2.18		0.40**(-)	
<i>Digitaria ciliaris</i>	27	1	0.34**(+)		
<i>Lespedeza davurica</i>	38	1.16		0.38**(-)	
<i>Phragmites communis</i>	33	3.62	0.27*(+)	0.30*(+)	0.37**(+)
<i>Plantago asiatica</i>	15	1		0.66**(-)	0.50**(+)
<i>Potentilla bifurca</i>	13	2		0.47**(+)	0.33*(+)
<i>Salsola collina</i>	45	1.09	0.33**(+)	0.32*(-)	
<i>Typha orientalis</i>	10	4.12		0.52**(+)	0.46**(+)

\*  $P < 0.05$ ; \*\*  $P < 0.01$ .

**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**	-0.08	0.17	-0.12
Soil C	0.72**	-0.13	0.06	0.29*
Total N	0.70**	-0.19	0.01	0.36**
C/N	0.53**	-0.04	0.11	0.11
pH	0.73**	-0.15	0	0.22
EC	0.98**	-0.18	-0.03	0.08
Soil water content (0–20 cm)	0.82**	-0.16	0.04	-0.45**
Soil water content (21–40 cm)	0.84**	-0.17	0.11	-0.44**
Soil water content (41–60 cm)	0.72**	-0.18	0.16	-0.55**
Coarse sand (2–0.25 mm)	-0.50**	-0.38**	0.64**	0.12
Fine sand (0.25–0.1 mm)	-0.51**	-0.7	-0.66**	-0.03
Very fine sand (0.1–0.05 mm)	0.63**	0.74**	0.07	-0.11
Silt + Clay (<0.05 mm)	0.41**	0.68**	0.03	0.40**
Site characteristics	Site1	Site2	Site3	Site4
Eigenvalue	0.99	0.01	0	0
Cumulative percentage variance (%)	99	100		
Longitude	0-.04	-0.90**		
Latitude	0.82**	0.50**		
Altitude	1.00**	0		

\*  $P < 0.05$ ; \*\*  $P < 0.01$ .

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