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RESEARCH ARTICLE

Spatial patterns of soil nutrients, plant diversity, and aboveground biomass in the Inner Mongolia grassland: before and after a biodiversity removal experiment

Fei Yuan · Jianguo Wu · Ang Li · Helen Rowe · Yongfei Bai · Jianhui Huang · Xingguo Han

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Abstract
Context Spatial heterogeneity is ubiquitous in ecological systems, and has important effects on biological diversity and ecological processes.
Objectives Does spatial heterogeneity affect the relationship between biodiversity and ecosystem functioning (BEF)? To help address this question, this study investigated how the spatial patterns of key BEF variables changed before and after the biodiversity removal during a BEF experiment in China.
Methods Our analysis was based on data from the Inner Mongolia grassland removal experiment (IMGRE) which was conducted in the Xilingol Steppe, Inner Mongolia, China. We quantified the spatial patterns of key variables of BEF, and examined the spatial relationships among these variables, using biodiversity indices and spatial statistical methods (autocorrelation and semivariance analysis).
Results Our results show that the variables of BEF in the Inner Mongolian grassland had various spatial patterns, most of which were spatially correlated to each other. Removal treatments had significant effects on these spatial structures and correlations. These effects were diverse in terms of both their kinds and magnitudes because of different removal protocols and treatments.
Conclusions The differences in spatial patterns of plant and soil variables and their correlations before and after the biodiversity manipulation do not necessarily imply that the results from BEF experiments like IMGRE are invalid, but they do suggest that the possible effects of spatial heterogeneity on the BEF relationship should be further scrutinized in future studies.

Keywords Biodiversity and Ecosystem Functioning (BEF) · Removal experiments · Spatial heterogeneity · Pattern analysis · Disturbance · Inner Mongolia grassland

F. Yuan
School of Life Sciences, Arizona State University, Tempe, AZ 85287, USA

J. Wu · H. Rowe
School of Life Sciences and Global Institute of Sustainability, Arizona State University, Tempe, AZ 85287, USA

J. Wu
Sino-US Center for Conservation, Energy, and Sustainability Science, Inner Mongolia University, Hohhot 010021, China

A. Li (✉) · Y. Bai · J. Huang · X. Han
State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China
e-mail: lyons@ibcas.ac.cn; jinglewuaz@gmail.com

X. Han
Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, China

Introduction

A number of studies have demonstrated that the loss of biodiversity (species richness, evenness and composition) may significantly alter the structure and functions of ecosystems, and degrade ecosystem services (Loreau et al. 2002; Naeem et al. 2009; Wu 2013). The influences of biodiversity loss include the following: (1) altered species traits and thus ecosystem processes, (2) reduced plant utilization efficiency for water, nutrients and solar energy, (3) simplified food web structures and its associated components (nutrient structure), and (4) modified disturbance regimes of various ecosystems (the frequency, intensity, and range of disturbances) (Chapin et al. 1997, 2000). The relationship between biodiversity and ecosystem functioning (BEF) has become a central topic in ecological research during the recent decades (Loreau et al. 2002; Naeem et al. 2009, 2012; Cardinale et al. 2012).

Plant removal experiments have been used to understand how non-random losses of target species or plant functional types (PFTs) may affect ecosystem processes in natural systems (McLellan et al. 1997; Wardle et al. 1999; Diaz et al. 2003; Gundale et al. 2010). Removing vegetation increases light levels, creates root gaps and nutrient release zones (Silver and Vogt 1993; Schroeer et al. 1999), and increase patchiness in the litter layer and soil (Guo et al. 2002). Regenerated vegetation patches usually interact with soil nutrient distributions which are altered by vegetation losses (Wu and Levin 1994; Keitt et al. 2002). Plant removal treatments inevitably modify or destroy existing spatial patterns of both vegetation and soil nutrients, which may consequently change the relationship among biodiversity and ecosystem variables.

Conceivably, a first step towards understanding the effects of spatial heterogeneity on the BEF relationship is to quantify the spatial patterns of key variables of BEF. However, little is known about the spatial relationship among soil nutrients, plant diversity, and biomass production during and after BEF experiments. Statistical methods do exist for such analysis, though. For example, geostatistical techniques have been widely used to study spatial patterns of environmental factors and ecological properties (Rossi et al. 1992; Fortin and Dale 2005). Especially, semivariogram modeling is suitable to quantify spatial structures of physical and biological variables and detect the characteristic scales of spatial heterogeneity (Robertson and Gross 1994; Burrough 1995; Meisel and Turner 1998; Vasques et al. 2012; Foster et al. 2013).

In this study, therefore, we used the semivariogram method to compare the spatial patterns of soil nutrients, such as total carbon (TC) and total nitrogen (TN), biodiversity measures, and aboveground biomass (AGB) before and after plant removal treatment during a BEF field experiment in Inner Mongolia, China. We examined how a selected set of variables representing plant BEF are spatially structured and related to each other before and after removal treatments. Specifically, we tested the following two hypotheses: (1) removal of PFTs results in distinct changes of spatial patterns of variables relevant to BEF, and (2) spatial correlations among soil nutrients, plant diversity and AGB will change due to different plant removal treatments.

Methods and materials

Data acquisition

All the data used in this analysis were obtained from the Inner Mongolia grassland removal experiment (IMGRE), a biodiversity removal experiment designed to test how grassland ecosystem processes respond to biodiversity loss and grazing by grasshoppers and livestock (see Wu et al. 2015 for an overview of the IMGRE project). The study site is located in the Xilingol River Basin (116°42′E, 43°38′N), and characterized by a semiarid climate (Wu and Loucks 1992; Bai et al. 2010; Li et al. 2012). The mean annual temperature is about 3 °C, and the mean annual precipitation is about 340 mm. Roughly 70 % of rainfall takes place between June and August. The dominant species of the local plant communities are *Leymus chinensis* and *Stipa grandis*, and common species include *Achnatherum sibiricum*, *Cleistogenes squarrosa*, *Koeleria cristata*, *Agropyron cristatum* and *Allium tenuissimum*. There are 86 species in the study area, which fall into 5 PFTs based on their life forms: perennial rhizomes (PRs), perennial bunchgrasses (PBs), perennial forbs (PFs), annuals and biennials (ABs), and shrubs and semi-shrubs (Bai et al. 2004; Wu et al. 2015).

The IMGRE experiment had 32 treatments, each having 16 replicates, and a total of 512 plots (see detail in Wu et al. 2015). Baseline data were collected in 2005 before the biodiversity removal treatments started in 2006. Plant biodiversity removal was done using two parallel protocols: complete removal and partial removal. The former removed all the plant species within a target functional type, whereas the latter removed the targeted functional types until approximately 50 % of the total plant cover in the treatment plot was eradicated—attempting to keep the level of physical disturbance in all treatment plots roughly equal (see Wu et al. 2015).

Plants and soil were sampled in late August, the timing corresponding to the peak of annual aboveground net primary production in this temperate grasslands. Specific measurements included species richness (the number of species in a specified area), the AGB of individual species, TC, and TN. Soil samples were collected in evenly distributed plots across the same research site. Three soil samples, which formed a triangle around each plot center, were collected using a 3-cm diameter soil auger to a depth of 20 cm immediately after plant harvesting and removal of surface litter. Samples from the same plot were mixed as one composite sample and air-dried in a ventilation room, cleared of roots and organic debris, and passed through 2-mm sieves for further chemical analysis.

Data analysis

Biodiversity indices

Three measurements of species diversity of plant community were computed. First, species richness (S) is simply the number of species in a plant community (or a sampling area). Second, the Shannon–Weaver index (H) was used, which is the most frequently used species or PFT diversity index:

$$H = -\sum_{i=1}^{s} (P_i \ln P_i), \tag{1}$$

where S is the total number of species or PFTs in the plot, and P_i is the biomass proportion of the ith species or PFT. For a given number of species or PFTs in a community, the more even the relative abundance among the species or the PFT is, the higher the value of H will be. In our study, we used the relative AGB (the percentage of a PFT AGB relative to the total AGB of all PFTs) to represent the relative abundance of a PFT in the community. There is no upper bound to the values of this index.

Third, evenness (E) is a measure of how similar the abundance of different species or PFTs is in a community. The Shannon evenness index is computed as:

$$E = \frac{H}{H_{\max}} = \frac{H}{\ln\ S}, \tag{2}$$

where H is the Shannon–Weaver index calculated as shown above. When the proportions of all species or PFTs are similar, evenness is close to one. When the abundances of different species or PFTs are quite dissimilar (e.g., some rare and some common), the value of evenness will be much larger than one. Since the data for the number of species in 2008 were not available, we only calculated the biodiversity index and evenness index at the level of PFTs.

Spatial statistical methods

Semivariance analysis is a common geostatistical method which can be employed to quantify spatial autocorrelation and spatial dependence of ecological patterns (Rossi et al. 1992). The semivariance is calculated as:

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [z(x_i) - z(x_i + h)]^2, \tag{3}$$

where $N(h)$ is the number of pairs of data at each distance interval h, and $z(x_i)$ and $z(x_i + h)$ are measurements at sampling points separated by a lag of h.

The semivariogram is plotted as $\gamma(h)$ against lag distances, and the shape of the plot shows how the degree of autocorrelation changes in space. To identify spatial structure in the observational data, we fitted and compared spherical, exponential, linear, and Gaussian models using the GS+ package, version 7.0 (Gamma Design Software, Plainwell, MI, USA). The "best fit" model was identified as the one with the least residual sums of squares (RSSs). Five semivariogram parameters were derived in the analysis, including: (1) range (A_0), separation distance at which spatial dependence is apparent, (2) nugget variance (C_0), random variation which is attributed to measurement error and within-sampling area variability,

(3) structural variance (C), variation caused by spatial heterogeneity, (4) sill ($C_0 + C$), overall spatial variability of the system, and (5) $C/(C_0 + C)$, the proportion of variance due to spatial structure, which is also called the spatial heterogeneity percentage (Robertson et al. 1993; Gross et al. 1995; Li and Reynolds 1995).

Moran's I, a global measure of spatial autocorrelation was also used to identify the degree of spatial dependence on variables over distances in our study (Moran 1948). Moran' I is calculated with the following formula:

$$I = \frac{n \sum_{i=1}^{n} \sum_{j=1}^{n} \omega_{ij}(x_i - \bar{x})(x_j - \bar{x})}{\left(\sum_{i=1}^{n} \sum_{j=1}^{n} \omega_{ij}\right) \sum_{i=1}^{n} (x_i - \bar{x})^2}, \tag{4}$$

where x_i and x_j refer to the measured sample values at i and j, respectively, x_j is the average value of x, is the weighted matrix value, and is the number of pairs of data. Values of range between −1 and 1 with positive values corresponding to positive autocorrelation, 0 indicating randomness, and negative values representing negative autocorrelation. Calculating this index for a variety of lag distances yields Moran's I correlograms which were generated by GS+ package.

Semivariance and Moran's I are complementary for evaluating the spatial structure of data. In our study, the minimum lag distance was 7 m, which corresponds to the minimal distance between sampled plots, while the maximum lag distance was extended to 186 m (approximately equals 50 % of the distance between the largest lag pair; Rossi et al. 1992). For spatial pattern analysis, we selected several variables that are relevant to the BEF relationship, including: spatial variability of soil nutrients (TC and TN), PFT diversity index (H_{PFT}), PFT evenness index (E_{PFT}), and AGB at the organizational levels of PFT and the whole community of each plot.

We identified the variable pairs whose relationship varied significantly between 2005 and 2008, for soil nutrients, biodiversity measures, and AGB. Seventy-nine plots were sampled for variables in TC and TN in both 2005 and 2008, 490 plots for variables in biodiversity measures and AGB. The independence of samples could not be guaranteed at such a fine scale, so the modified t test was used to correct the degree of freedom, based on the amount of autocorrelation in the data (Clifford et al. 1989). The modified t-test was performed using PASSaGE (V. 2.0) software (http://www.passagesoftware.net/). After the modified t-test, we identified those variable pairs from biodiversity measures and AGB, the relationship of which varied significantly between 2005 and 2008 (e.g., from positive to negative, from positive to random, and etc.). We did Pearson's correlation analysis for such variable pairs under the different complete and partial treatments. The Pearson's correlation was analyzed using SAS Version 9.2.

Results

Summary statistics of BEF variables in 2005 and 2008

From 2005 to 2008, TC decreased by 57.57 %, from 45.91 ± 1.09 g kg^{-1} averaged over a total of 79 sampled plots to 19.76 ± 0.38 g kg^{-1} over a total of the same 79 sampled plots (Table 1). From 2005 to 2008, TN decreased only by 14.34 %. Coefficients of variations (CVs) of H_{PFT} and E_{PFT} decreased significantly by 29.87 and 27.54 % from 2005 to 2008, respectively (Table 1). AGB at the levels of PFTs and the whole community also varied dramatically, especially for AB. We did not conduct analysis for the ABs functional type in 2005 due to too small a sample size. In 2008 AB was abundant, and the mean value of AGB of this functional type was 1.74 ± 2.43 g m^{-2} (Table 1). Large differences in CVs of AGB between 2005 and 2008 were also found, ranging from 25.97 to 78.87 % for PF in 2005 and from 43.69 to 3,097.13 % for AB in 2008 (Table 1).

Spatial patterns of soil nutrients, plant diversity, and biomass

We quantified spatial autocorrelation among sample points within the field. The spherical model provided the best fit for TC and TN in 2008 (Table 2). Range values were 13 and 75 m for TC and TN in 2008 (Table 2). TC showed lower spatial autocorrelation and higher spatial heterogeneity percentage in 2008 than in 2005 (Table 2). The semivariogram for TN in 2008 exhibited a smaller nugget effect than in 2005 (Fig. 1). Correlograms showed that TC in 2008 had a fluctuating autocorrelation pattern: a positive correlation within 60 m, a negative correlation at lag distances between 60 and 70 m, and a repeated pattern with further increasing lag distances (Fig. 2).

Table 1 Summary statistics of variables of soil nutrients, plant diversity, and aboveground biomass in 2005 and 2008

Variables	2005				2008			
	Mean	SE	CV (%)	Number of samples	Mean	SE	CV (%)	Number of samples
TC (g kg^{-1})	45.91	1.09	21.59	79	19.76	0.38	17.16	79
TN (g kg^{-1})	4.60	0.11	21.09	79	3.94	0.05	10.91	79
H_{PFT}	0.77	0.01	23.38	490	0.54	0.01	61.11	490
E_{PFT}	0.69	0.01	23.19	490	0.50	0.01	56.00	490
PR (g m^{-2})	26.81	0.69	56.58	490	22.59	2.16	211.69	490
PB (g m^{-2})	69.77	1.04	32.87	490	62.26	2.62	93.19	490
PF (g m^{-2})	12.26	0.44	78.87	490	2.18	0.36	366.97	490
AB (g m^{-2})	–	–	–	–	1.74	2.43	3,097.13	490
AGB (g m^{-2})	109.30	1.28	25.97	490	132.53	2.62	43.69	490

PR perennial rhizomes, *PB* perennial bunchgrasses, *PF* perennial forbs, *AB* annuals and biennials, *AGB* the aboveground biomass at the community level, *CV* coefficient of variation defined as the ratio of the standard deviation to the mean

Table 2 Semivariogram parameters for soil variables, biodiversity measures and aboveground biomass of the Inner Mongolia grassland BEF site in 2005 and 2008

Years	Variables	Models	Range (m)	Nugget	Sill	RSS	r^2	$C/(C_0 + C)$ (%)
2005	TC	Spherical	76.90	52.70	131.40	1,886.00	0.88	60
	TN	Spherical	102.30	0.31	1.14	0.50	0.71	73
	H_{PFT}	Exponential	26.60	1.41E−2	4.80E−2	3.44E−5	0.97	70
	E_{PFT}	Exponential	28.20	1.29E−2	0.04	2.19E−5	0.97	67
	PR	Exponential	9.30	28.00	383.80	5.17E+3	0.78	93
	PB	Exponential	7.80	52.00	435.30	1.37E+4	0.49	88
	PF	Exponential	42.70	52.70	105.50	5.35E+2	0.85	50
	AB	Linear	–	3.66E−2	3.66E−2	1.11E−4	0	0
	AGB	Exponential	6.90	105.00	735.10	4.16E+4	0.37	86
2008	TC	Spherical	13.10	0.41	10.96	15.00	0.15	96
	TN	Spherical	74.80	0.09	0.19	1.43E−3	0.87	54
	H_{PFT}	Exponential	14.20	0.011	0.118	2.39E−3	0.60	91
	E_{PFT}	Exponential	4.90	0.008	0.083	8.65E−4	0.13	91
	PR	Exponential	2.00	220.00	2,226.00	130,534	0.005	90
	PB	Exponential	2.60	272.00	3,292.00	965,008	0.02	92
	PF	Linear	185.76	63.18	63.18	270.00	0.58	0
	AB	Exponential	1.90	399.00	2,770.00	4,914,012	0	86
	AGB	Exponential	3.50	340.00	3,553.00	1,556,343	0.05	90

PR perennial rhizome, *PB* perennial bunchgrasses, *PF* perennial forbs, *AB* annuals and biennials, *AGB* the aboveground biomass at the community level

The plant removal treatment had a significant effect on the spatial structure of biodiversity measures at the level of PFTs in 2008 (Table 2; Fig. 3). Both H_{PFT} and E_{PFT} exhibited stronger spatial structure in 2008 with a much higher spatial heterogeneity percentage of 91 %, compared to 67–70 % in 2005 (Table 2). The correlograms of biodiversity measures revealed similar patterns between 2005 and 2008; H_{PFT} and E_{PFT} were positively autocorrelated within the lag distance of 70 m in 2008 and within 75 m in 2005 (Fig. 4).

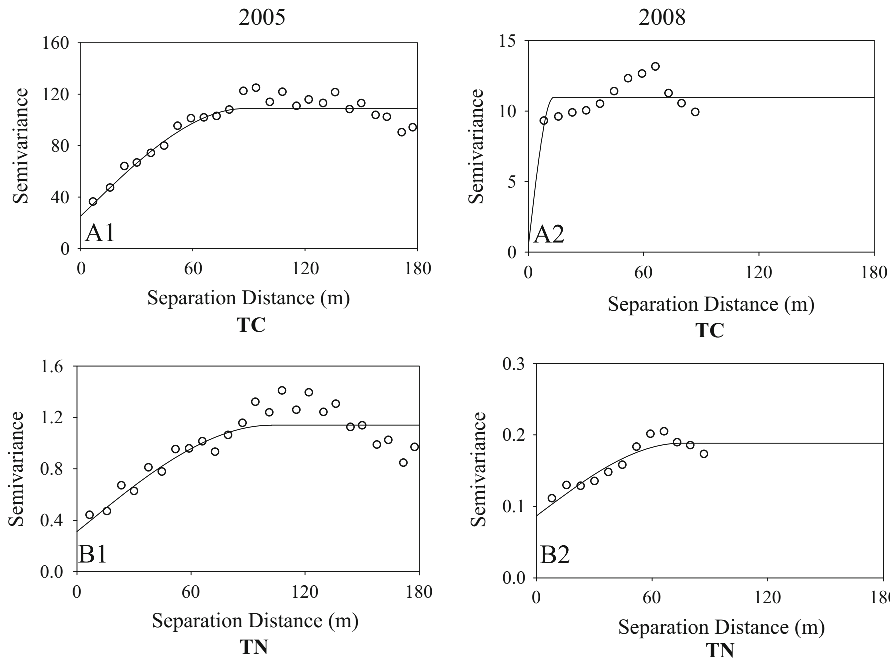

Fig. 1 Semivariograms of TC and TN of the Inner Mongolia grassland BEF site in 2005 (**A1**, **B1**) and 2008 (**A2**, **B2**)

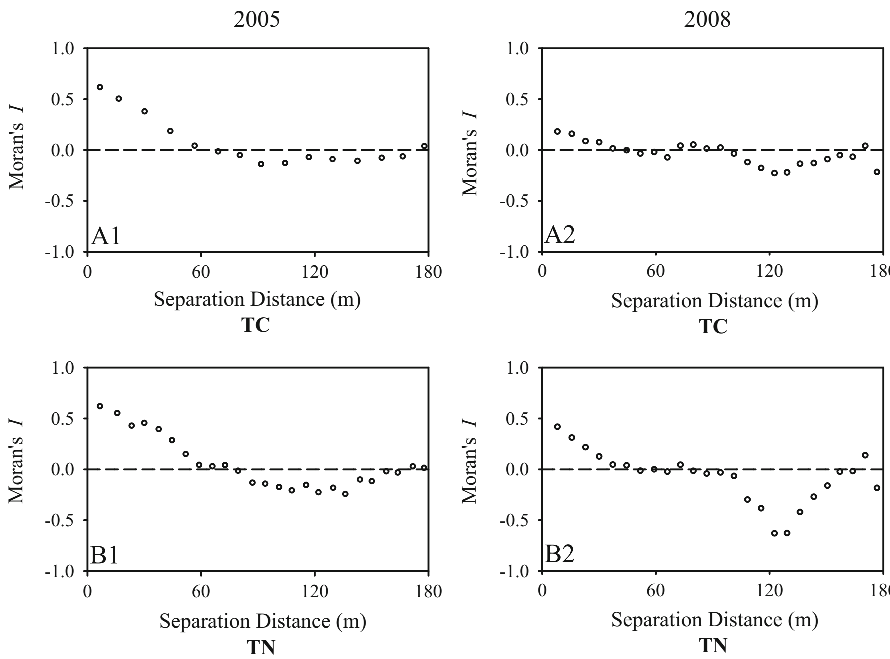

Fig. 2 Correlograms of TC and TN of the Inner Mongolia grassland BEF site in 2005 (**A1**, **B1**) and 2008 (**A2**, **B2**)

For both 2005 and 2008, the exponential model was the best fit to the semivariograms for most AGB of PFTs, with the exception of PF fit by the linear model in 2008 (Table 2). The range values for the variables in AGB sampled in 2008 decreased (except PF), ranging from 1.90 m for AB to 185.76 m for PF, in comparison to the range values of 6.90 m for AGB to 42.70 m for PF derived from variables of AGB sampled in 2005 (Table 2). In 2008, PF did not show any spatial structure with the value of spatial

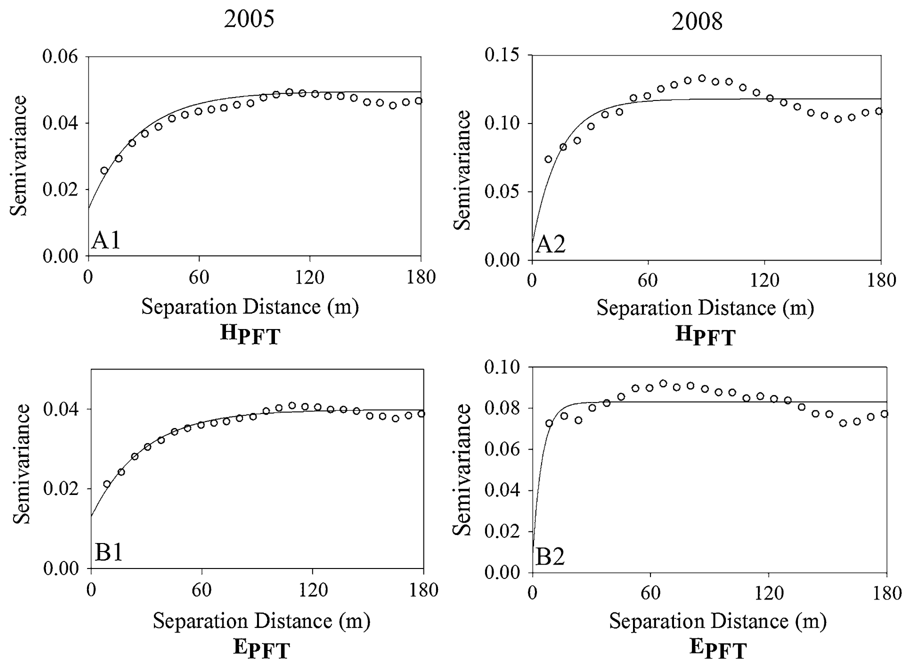

Fig. 3 Semivariograms of H_{PFT} and E_{PFT} of the Inner Mongolia grassland BEF site in 2005 (**A1**, **B1**) and 2008 (**A2**, **B2**)

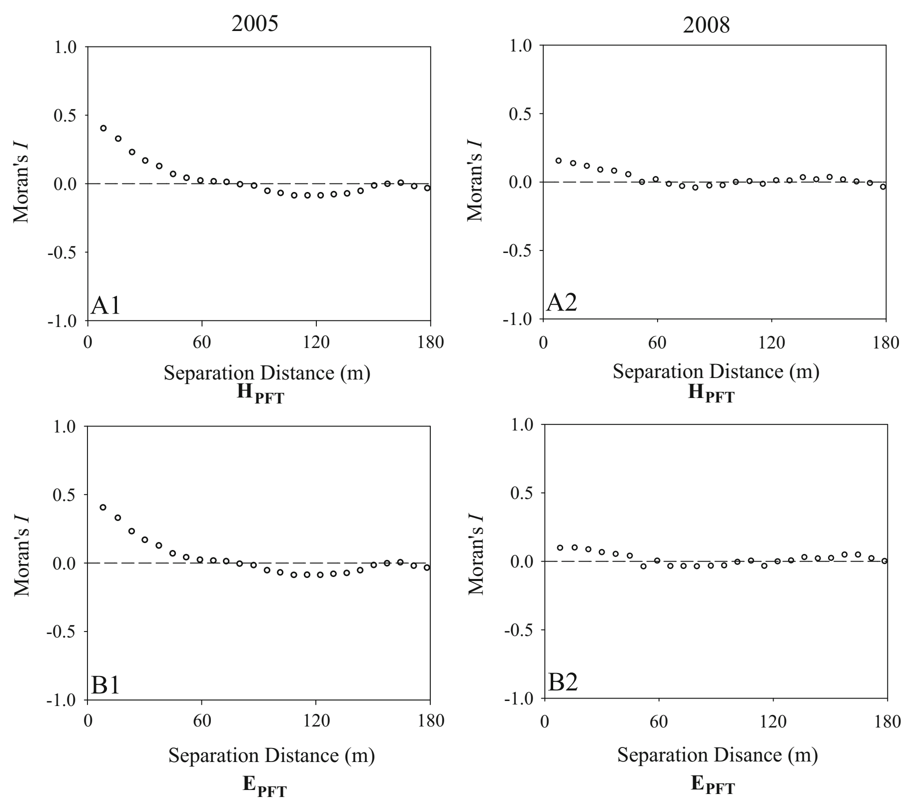

Fig. 4 Correlograms of H_{PFT} and E_{PFT} of the Inner Mongolia grassland BEF site in 2005 (**A1**, **B1**) and 2008 (**A2**, **B2**)

heterogeneity percentage at 0 %, whereas AB exhibited high spatial structure with the value of spatial heterogeneity percentage at 86 % (Table 2; Fig. 5).

The correlograms showed that there was a random autocorrelation for each of the variables in AGB at the level of PFT after the removal treatments in 2008, which was quite different from the pattern showing that each of those variables in 2005 prior to the removal treatments exhibited a positive autocorrelation within short distances apart (Fig. 6).

Correlations among BEF variables

Most of correlations among variables of soil nutrients, biodiversity measures, and AGB showed significant

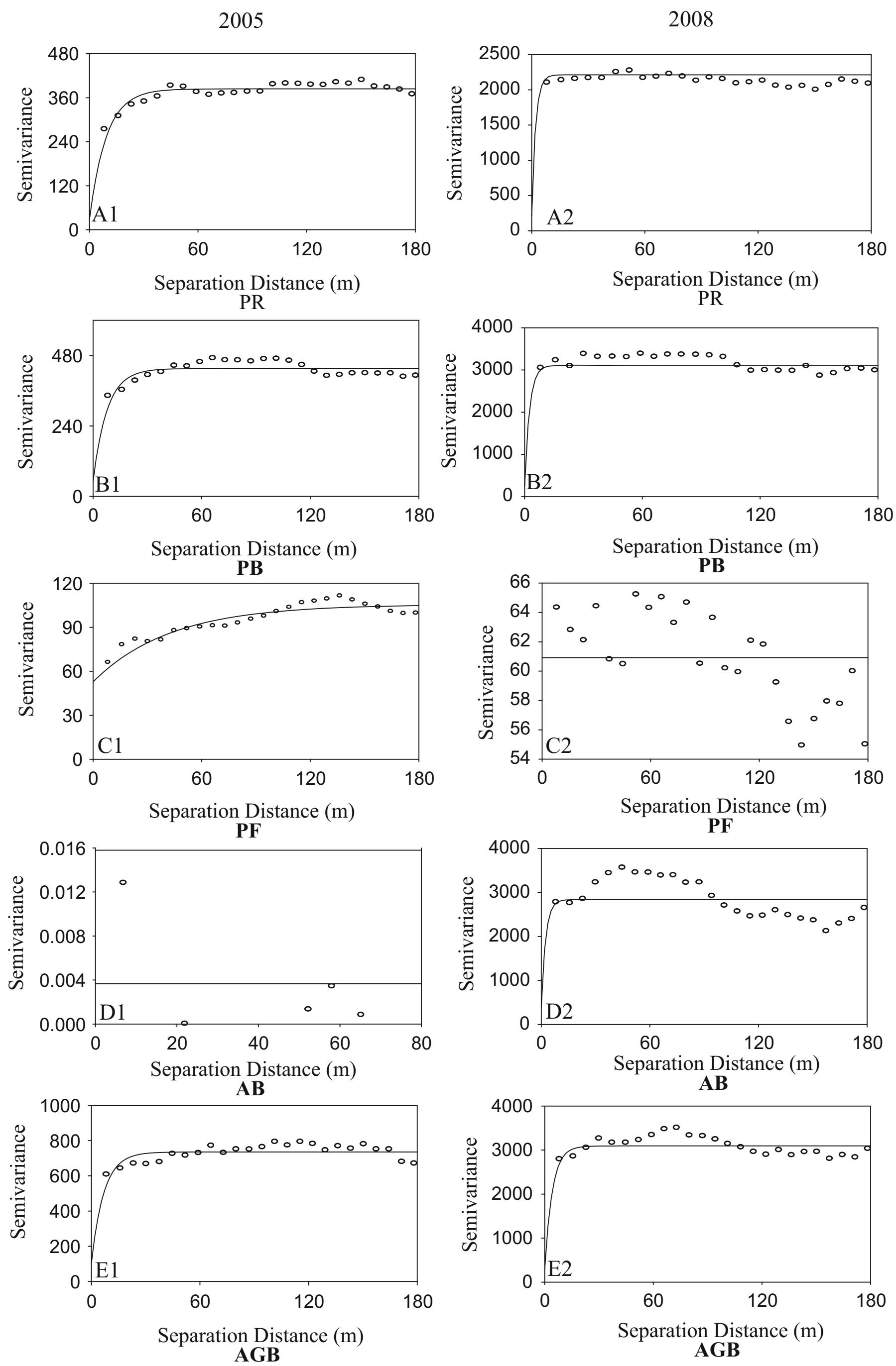

Fig. 5 Semivariograms of PR, PB, PF, AB and AGB of the Inner Mongolia grassland BEF site in 2005 (**A1**, **E1**) and 2008 (**A2**, **E2**). *PR* perennial rhizomes, *PB* perennial bunchgrasses, *PF* perennial forbs, *AB* annuals and biennials, *AGB* the aboveground biomass at the community level

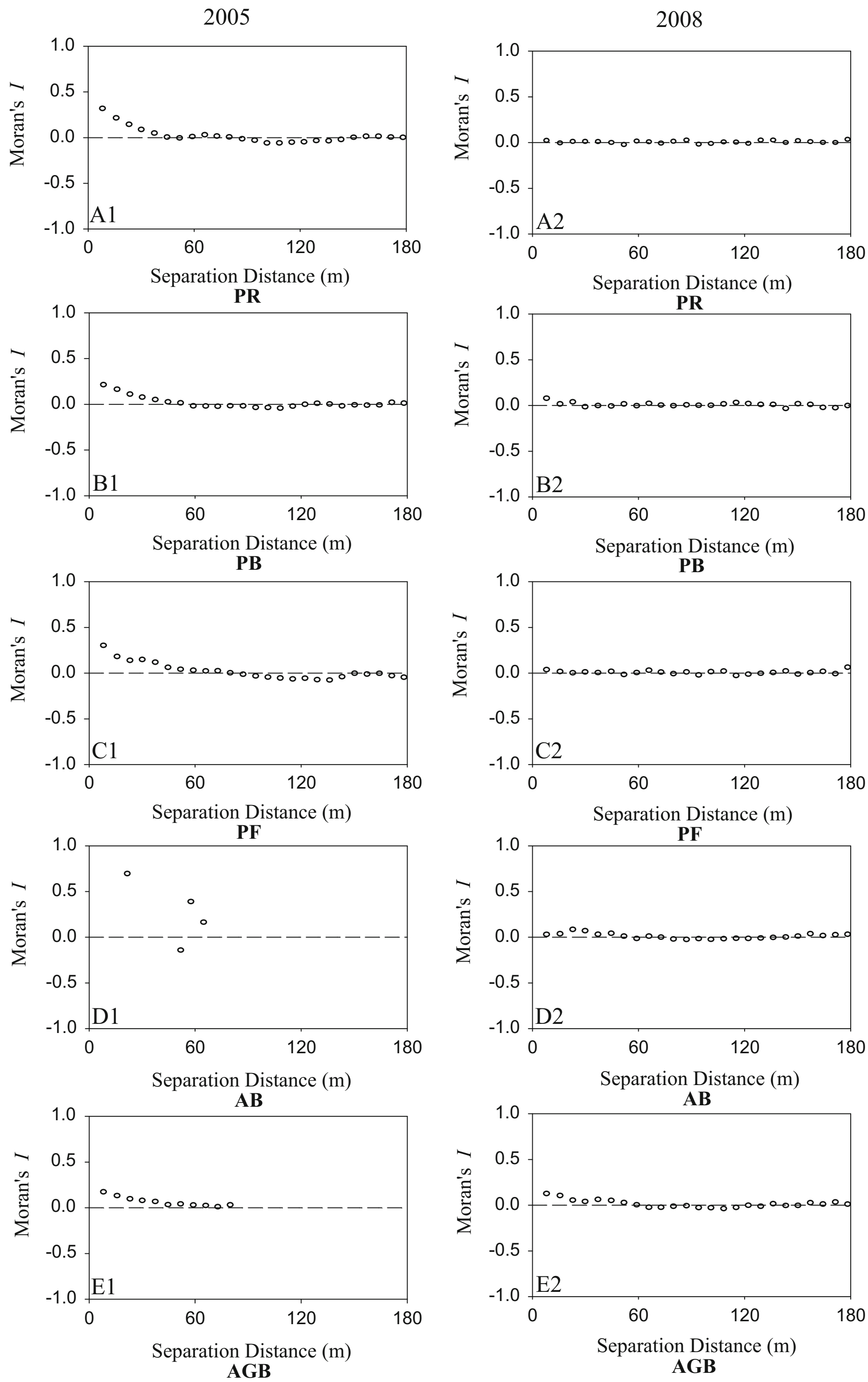

Fig. 6 Correlograms of PR, PB, PF, AB and AGB of the Inner Mongolia grassland BEF site in 2005 (**A1**, **E1**) and 2008 (**A2**, **E2**)

positive relationships in 2005, except between PB and TC (Table 3). However, the removal treatments had a significant effect on the relationships between variables in 2008. Some significant positive relationships were weakened due to the removal treatments (Table 3).

We also found that the relationships between H_{PFT} and AGB, H_{PFT} and PB, PF and AGB, and PR and PF

Table 3 Correlation coefficient matrix for soil nutrients, plant biodiversity, and aboveground biomass of the Inner Mongolia grassland BEF site in 2005 and 2008

Years	Variables	TC	TN	H_{PFT}	E_{PFT}	PR	PB	PF	AB	AGB
2005	TC	1								
	TN	0.918**	1							
	H_{PFT}	0.339**	0.314**	1						
	E_{PFT}	0.339**	0.314**	1.000**	1					
	PR	0.238**	0.231**	0.601**	0.601**	1				
	PB	−0.030	0.005	−0.538**	−0.538**	−0.421**	1			
	PF	0.222*	0.188*	0.707**	0.707**	0.393**	−0.300**	1		
	AB	–	–	–	–	–	–	–	1	
	AGB	0.228	0.234	0.283**	0.283**	0.572**	0.324**	0.415**	–	1
2008	TC	1								
	TN	0.829**	1							
	H_{PFT}	−0.023	−0.019	1						
	E_{PFT}	−0.012	−0.004	0.892**	1					
	PR	0.183	0.181	0.155**	0.150**	1				
	PB	0.033	0.122	0	−0.033	−0.434**	1			
	PF	−0.155	−0.215	0.226**	0.257**	0.057	−0.154**	1		
	AB	−0.049	−0.027	−0.184**	−0.161**	−0.182**	−0.285**	−0.049	1	
	AGB	0.117	0.217	−0.012	−0.023	0.230**	0.357**	−0.014	0.488**	1

Dashes (–) indicate no correlations found due to few samples for AB in 2005. Sample size $n_1 = 79$ for TC and TN, and $n_2 = 490$ for PR, PB, PF, AB and AGB

PR perennial rhizomes, *PB* perennial bunchgrasses, *PF* perennial forbs, *AB* annuals and biennials, *AGB* the aboveground biomass at the community level

* *P*-value <0.05; ** *P*-value <0.01

have changed significantly from 2005 to 2008 (Table 4). These changes varied depending on the different removed targets. For example, the complete removal of PF erased the significant negative correlation between H_{PFT} and PB ($r = -0.291$, *P*-value <0.01 and $n = 16$), and the complete removals of AB, PR + AB changed the relationship from randomness in 2005 to significant negative correlations in 2008 (Table 4). For most complete removal treatments, there was no relationship between H_{PFT} and PR in 2008 (Table 4). Several partial removals also decoupled the relationships between H_{PFT} and PB (Table 4). On the other hand, the effects of complete removal and the partial removals on the relationships between variables of interest were different. For example, H_{PFT} and PB had no relation in 2005, but became significantly negatively correlated in 2008 ($r = -0.862$, *P*-value <0.01, and $n = 15$) after the complete removal of PR + AB. On the other hand, H_{PFT} and PB were negatively correlated in 2005, but had no significant correlation in 2008 for most partial removal treatments. The complete removals of PFTs under any treatments did not change the relationship between PR and PF significantly, but the partial removal did (Table 4).

Discussion

Spatial patterns of BEF variables as influenced by biodiversity removal

We demonstrated that the spatial autocorrelation patterns of most BEF variables would be quite different before the biodiversity manipulation (2005) and after it (2008). The average patch sizes of TC and TN decreased in 2008, with TC exhibiting a higher degree of spatial autocorrelation and a higher spatial

Table 4 Pearson correlations between H_{PFT} and AGB, H_{PFT} and PB, PF and AGB, and PR and PF, respectively, in 2005 and 2008 for the same plots under different treatments

Treatments (removed functional types)	H_{PFT} and AGB		H_{PFT} and PB		PF and AGB		PR and PF		*n*
	2005	2008	2005	2008	2005	2008	2005	2008	
Complete									
Control (no removal)	0.567*	−0.477	−0.728**	−0.771**	0.564*	−0.149	0.566*	0.214	15
PR	0.666**	−0.05	−0.38	−0.454	0.678**	0.005	0.675**	–	15
PB	0.104	−0.064	−0.499*	–	0.267	0.185	0.494	0.065	16
PF	0.584*	−0.211	−0.291**	−0.359	0.465	–	0.066	–	16
AB	0.343	0.701	−0.205	−0.663**	0.662**	0.141	0.117	0.32	14
PR + PB	−0.149	0.857**	−0.607*	–	0.016	−0.318	−0.064	–	15
PR + PF	0.397	0.087	−0.618*	−0.633*	0.152	–	−0.066	–	15
PR + AB	0.287	−0.318	−0.465	−0.862**	0.313	−0.018	0.233	–	15
PB + PF	−0.171	0.173	−0.424	–	0.131	–	−0.073	–	15
PB + AB	0.177	−0.376	−0.347	–	0.681**	0.281	0.699**	0.101*	16
PF + AB	0.313	0.092	−0.752**	−0.528*	0.05	–	0.374	–	16
PR + PB + PF	0.431	–	−0.309	–	0.568*	–	0.029	–	15
PR + PB + AB	0.187	0.587*	−0.47	–	0.511*	0.271	0.41	–	16
PR + PF + AB	0.156	0.267	−0.337	−0.26	0.641*	–	0.261	–	15
PB + PF + AB	0.44	0.032	0.627**	–	0.437	–	0.223	–	16
PR + PB + PF + AB	0.217	–	−0.451	–	−0.031	–	0.547*	–	16
Partial									
Control (no removal)	0.259	−0.015	−0.747	−0.575*	0.417	0.563*	0.586*	0.744**	16
PR	0.049	−0.23	−0.869**	−0.590*	−0.068	−0.08	−0.01	0.359	16
PB	0.077	−0.156	−0.708**	0.533	0.297	0.294	0.056	0.754**	16
PF	0.454	−0.186	−0.692**	−0.347	0.607*	0.633*	0.759**	0.1	14
AB	0.192	−0.073	−0.587*	−0.295	0.415	0.15	0.627**	0.295	16
PR + PB	0.475	−0.331	−0.783**	−0.061	0.817**	0.166	0.884**	0.36	14
PR + PF	0.352	−0.549*	−0.686**	−0.723**	0.256	0.056	0.223	0.219	16
PR + AB	0.319	−0.401	−0.882**	−0.569*	0.792	0.318	0.767**	0.137	15
PB + PF	0.298	0.258	−0.739**	0.556*	0.478	−0.348	0.601*	−0.106	14
PB + AB	0.502	−0.083	0.1	0.572*	0.348	0.641	0.151	0.710**	15
PF + AB	0.261	−0.104	−0.534*	−0.418	0.505*	0.496	0.096	0.662	16
PR + PB + PF	0.504	−0.18	−0.48	0.529*	0.478	−0.038	0.286	0.505	15
PR + PB + AB	0.567*	−0.574*	0.708**	−0.850**	0.738**	0.04	0.691**	0.261	16
PR + PF + AB	0.34	−0.376	−0.697**	−0.586*	−0.868	−0.325	0.620*	0.615*	15
PB + PF + AB	0.653**	0.006	−0.714**	0.790**	0.838**	0.822**	0.436	0.786**	15
PR + PB + PF + AB	0.561*	−0.376	−0.791**	−0.762**	0.577*	0.570*	0.602*	0.282	15

PR perennial rhizomes, *PB* perennial bunchgrasses, *PF* perennial forbs, *AB* annuals and biennials, *AGB* the aboveground biomass at the community level

"–" indicates no correlations between the variable pairs

* *P*-value <0.05; ** *P*-value <0.01

heterogeneity percentage in 2008 than in 2005. Biodiversity measures and AGB at the levels of PFTs and the community in 2008 also decreased in their average patch size and increased in the degree of spatial structure. Shannon index and evenness index showed quite similar patterns in our analysis, and their similarity may be explained from their mathematical formulations. Shannon index consists of the richness and evenness of PFTs. Because the total number of PFTs was only four, much of the variability in Shannon index was actually that of evenness.

For the two dominant PFTs we examined, PR and PB, the spatial dependence of AGB did not appear to be affected by the removal treatment. However, for non-dominant PFTs, PF and AB, spatial dependence was strongly affected by the removal treatment. With the exception of PF, the average patch size of PFTs, in terms of AGB and indicated by range values of semivariograms, decreased from 2005 to 2008 because of destructive biodiversity removal treatment. More studies are needed to determine how long these changes caused by biodiversity removal last.

A number of studies have attempted to explain spatial patterns in plant and soil properties (e.g., Robertson et al. 1988; Jackson and Caldwell 1993b; Schlesinger et al. 1996; Saetre 1999) because spatial pattern may indicate important ecological mechanisms (Levin 1992; Legendre and Fortin 1989; Wu and Loucks 1995). For example, the spatial pattern of soil nutrients in desert ecosystems, known as "islands of fertility", is a result of the interactions between shrubs and local environmental factors, including wind, water, and soil erosion, which drives patterns of nitrogen cycling, soil respiration, and other ecosystem properties (Robertson et al. 1988; Saetre 1999). Also, spatial patchiness of vegetation can influence the degree to which soil nutrients are spatially structured (Jackson and Caldwell 1993a, b; Mueller et al. 2008). In the IMGRE project, biodiversity removal, both complete and partial, certainly created much spatial patchiness in vegetation, resulting in wide-ranging changes in the spatial patterns of BEF variables. In addition, the root decay of the removed species may also have affected soil TC and TN and likely contributed to the decreased patch sizes for both TC and TN.

Changing relationships among BEF variables due to removal treatments

As expected, the removal treatments also changed species composition and relative plant abundance, as well as the relationships among most of the BEF variables that we examined. For example, the average AGB of AB was much higher in 2008 than in 2005, and this functional type appeared much more frequently in the sampled plots across the study site in 2008. The species of AB only germinate after rainfall events, have a short lifespan, and produce a large amount of small seeds. In an undisturbed mature *L. chinensis*-dominant community, AB is an inferior competitor to PR and PB. However, the removal of their dominant competitors created new open habitat for AB plants to thrive.

In 2005, there was a significant positive correlation in AGB between PR and PF, partly explained by their relatively high demands for soil water, but these two PFTs were no longer correlated in 2008 after complete removal treatments. However, this positive association between PR and PF remained statistically significant in 2008 under several partial removal treatments (e.g., removals of PB, PB + AB, PB + PF + AB). Also, the negative correlation between H_{PFT} and the AGB of PB found in 2005 was no longer existent in 2008 after complete removal treatments. The positive correlation in AGB between PF and the whole community in 2005 also disappeared in 2008. In addition, our correlation analysis indicated strong compensatory growth of PB in response to the removal of PR (also see Bai et al. 2004). PB plants were highly productive and tented to inhibit establishment and growth of PF.

Implications for BEF research

BEF field experiments involve direct manipulations of biodiversity levels commonly through either removal of existing plants or systematic re-seeding after eradicating existing vegetation and topsoil. In so doing, experimental plots with different diversity levels are created, and ecosystem functioning variables are subsequently measured along the biodiversity gradient. All these experiments assume that spatial heterogeneity in plants and soil resources is either insignificant or can be averaged out by having replicates. Our study, however, indicates that the spatial patterns of plant and soil variables in natural grassland communities may be quite different from those in BEF treatment plots. The relationships between these variables may also be substantially different. As all BEF experiments inevitably change the spatial patterns of, and correlations between, plant and soil variables, the potential confounding effects of spatial pattern on the BEF relationship should be examined explicitly.

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