Spatial Relationships among Soil Nutrients, Plant Biodiversity and Aboveground Biomass in the Inner Mongolia Grassland, China

by

Fei Yuan

A Thesis Presented in Partial Fulfillment
of the Requirements for the Degree
Master of Science

Approved June 2011 by the
Graduate Supervisory Committee:

Jianguo (Jingle) Wu, Chair
Helen I. Rowe
Andrew T. Smith

ARIZONA STATE UNIVERSITY

August 2011

ABSTRACT

The relationship between biodiversity and ecosystem functioning (BEF) is a central issue in ecology, and a number of recent field experimental studies have greatly improved our understanding of this relationship. Spatial heterogeneity is a ubiquitous characterization of ecosystem processes, and has played a significant role in shaping BEF relationships. The first step towards understanding the effects of spatial heterogeneity on the BEF relationships is to quantify spatial heterogeneity characteristics of key variables of biodiversity and ecosystem functioning, and identify the spatial relationships among these variables. The goal of our research was to address the following research questions based on data collected in 2005 (corresponding to the year when the initial site background information was conducted) and in 2008 (corresponding to the year when removal treatments were conducted) from the Inner Mongolia Grassland Removal Experiment (IMGRE) located in northern China: 1) What are the spatial patterns of soil nutrients, plant biodiversity, and aboveground biomass in a natural grassland community of Inner Mongolia, China? How are they related spatially? and 2) How do removal treatments affect the spatial patterns of soil nutrients, plant biodiversity, and aboveground biomass? Is there any change for their spatial correlations after removal treatments? Our results showed that variables of biodiversity and ecosystem functioning in the natural grassland community would present different spatial patterns, and they would be spatially correlated to each other closely. Removal treatments had a significant effect on spatial structures

and spatial correlations of variables, compared to those prior to the removal treatments. The differences in spatial patterns of plant and soil variables and their correlations before and after the biodiversity manipulation may not imply that the results from BEF experiments like IMGRE are invalid. However, they do suggest that the possible effects of spatial heterogeneity on the BEF relationships should be critically evaluated in future studies.

ACKNOWLEDGMENTS

First and foremost, I express my appreciation for the guidance and patience provided by my advisor Dr. Jianguo Wu. He is a model advisor and taught me many things. Without his help and support, this thesis could never have been completed.

I would also like to thank my committee members, Dr. Helen Rowe and Dr. Andrew Smith, for their guidance during the development of this research and their comments on earlier draft of this document. Also, I must thank them for agreeing on working on thesis committee in a very short notice, and giving me so much support for completing my thesis work.

For data collection, I would like to express my appreciation to professors and graduate students at Institute of Botany, Chinese Academy of Sciences, who participated in the fieldwork of the IMGRE project, especially Xingguo Han, Yongfei Bai, Jianhui Huang, Xiaotao Lv, Meng Wang, and Qiang Yu. I also thank Ang Li for providing valuable advice for statistical analysis.

I would also like to thank all of my former and current labmates for their encouragement and support during my graduate school years at ASU. They include: Jeff Ackley, Alex Buyantuyev, Christopher M. Clark, Lisa Dirks, Zhibin Jia, Cheng Li, Junxiang Li, Cunzhu Liang, Jennifer Litteral, Fengqiao Liu, Kaesha Neil, Ronald Pope, Guixia Qian, Tracy Shoumaker, Yu Tian, Hong Xiao, Qi Yang, Chengbo Yi, Ge Zhang, Jing Zhang, and Ting Zhou.

Finally, my most emotional thanks go to my parents for their patience and understanding of my study in the US. I could not take care of them much when I was studying here, and I am indebted to them a lot. I love you both forever.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Figure Page

CHAPTER 1: INTRODUCTION

IMPORTANCE OF SPATIAL HETEROGENEITY IN UNDERSTANDING THE RELATIONSHIP BETWEEN BIODIVERSITY AND ECOSYSTEM FUNCTIONING

1 Introduction

Since the beginning of the 20th century, intensive anthropogenic disturbance has spawned the 6th major extinction event in the history of life, leading to changes in species distribution across the world (Chapin et al. 2000). A number of studies have demonstrated that changes in biodiversity (species richness, evenness and composition) caused by global changes may significantly alter the structure and functions of ecosystems, leading to degraded ecosystem services that affect human social and economic activities (Fig. 1). The influences of changes in biodiversity on ecosystem functioning have led to: 1) altered species traits and thus ecosystem processes; 2) reduced utilization efficiency by plants for water, nutrients and solar energy; 3) simplified food web structures and the relationship of 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).

Recent studies have shown that biodiversity affects structure, functioning, and dynamics of ecosystems, and is one of the key factors in controlling stability, productivity, nutrient cycling, and introduction of invasive species of ecosystems (Naeem 1994, Tilman 1996, 1999, 2000, Chapin et al. 2000, Bai et al. 2004, Hooper et al. 2005, Spehn et al. 2005). The maintenance of biodiversity and ecosystem functioning is fundamentally important to the supply of ecosystem goods and services. Therefore, in-depth research on the relationship between biodiversity and ecosystem functioning (hereafter abbreviated BEF) is needed to provide a solid scientific foundation and guiding principles for protecting biodiversity conservation and ecosystem services (Loreau et al. 2002, Hooper et al. 2005, Naeem et al. 2009, Gravel et al. 2011).

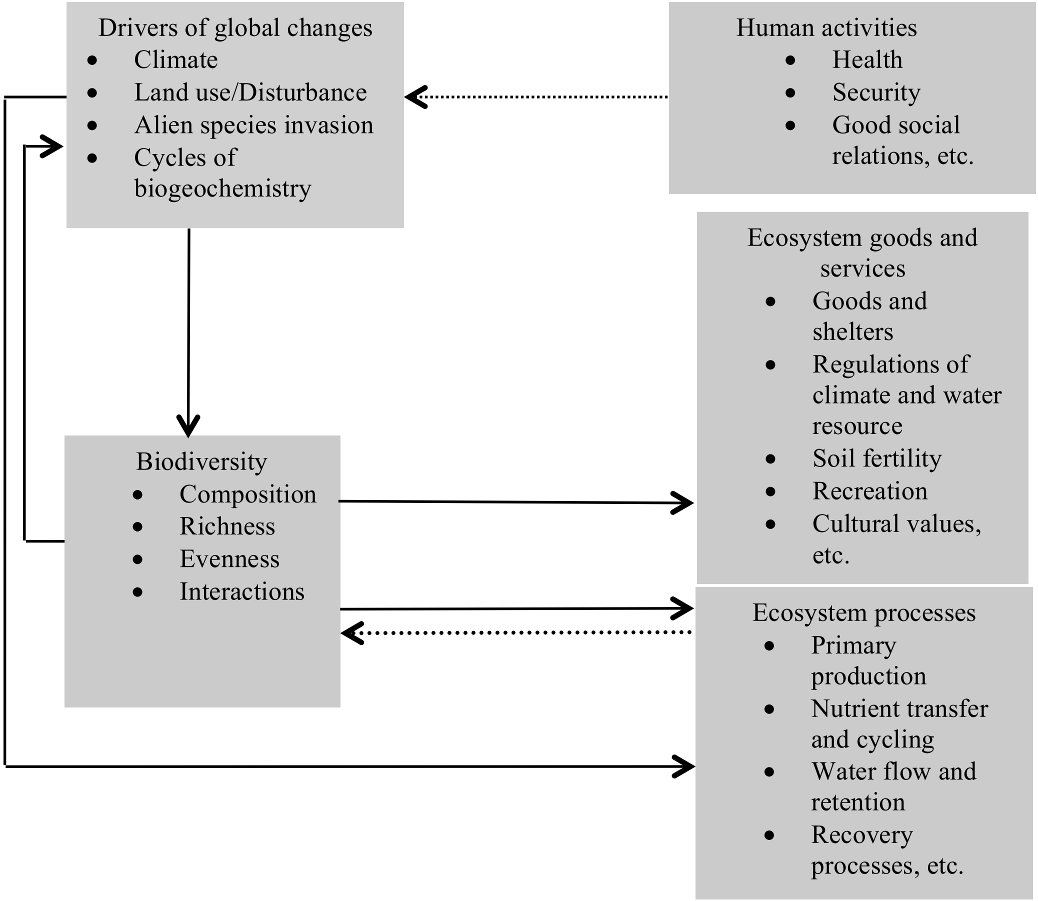

Fig. 1.1 The relationship between biodiversity and global changes (adapted from Chapin et al. 2000). Solid lines denote the direct links between components, and dashed lines denote the indirect links.

2 The relationship between biodiversity and ecosystem functioning

Biodiversity was coined by E. O. Wilson in 1998 by combining the two terms of “biological” and “diversity” (Wilson 1988). There are many definitions for biodiversity, and the most commonly accepted definitions consist of three levels of ecological organization: genetic, species and ecosystems. Biodiversity is the ecological complex of biology and environment, and the sum of all associated ecological processes, including millions of animals, plants, microorganisms, genes, and complicated ecosystems formed by these organisms and their living surroundings (Wilson 1988, 1993, Ma 1993, Gaston 1996, Purvis and Hector 2000, Mooney 2002). Biodiversity is a prerequisite of ecosystem functions and services, which in turn provide the basis for the development and maintenance of human society.

Definitions of ecosystem functioning have been defined from both broad and narrow perspectives. Broadly, ecosystem functions include ecosystem properties, ecosystem goods, and ecosystem services (Christensen et al. 1996). Narrowly, the term refers only to ecosystem functions and properties, including the size of ecosystem components (such as carbon or organic pools) and process rates (such as ecosystem productivity, energy flow, material recycling and information transfer rates, and ecosystem stability) (Hooper et al. 2005). Ecosystem goods are those kinds of ecosystem properties that have direct market value, including food, building materials, medicines, gene products, and recreation. Ecosystem services refers to those properties of ecosystems that have a direct or indirect impact on human beings, such as regulating climate, controlling hydrology, purifying air and water, and maintaining soil nutrient balance (Costanza et al. 1997, Daily et al. 1997).

The relationship between biodiversity and ecosystem functioning has become one of the central research topics in ecology in recent decades (Chapin et al. 1992, Chapin et al. 2000). The US National Science Foundation lists it as one of the eight challenges in Environmental Sciences (Omenn 2006). The main objectives of BEF research are to understand how changes in biodiversity affect ecosystem functioning, and how changes in ecosystem functioning influence biodiversity. To date, the most BEF studies have focused on the effects of changes in species richness and composition on ecosystem functioning (Hooper et al. 2005, Bai et al. 2007).

There are three types of BEF relationships: 1) biodiversity and ecosystem functioning are positively related (e.g., ecosystem functioning increases with increasing biodiversity, or decreases with decreasing biodiversity); 2) biodiversity and ecosystem functioning are negatively related (e.g., ecosystem functioning decreases with increasing biodiversity, or increases with decreasing biodiversity); and 3) biodiversity and ecosystem functioning have no relationship at all (e.g., ecosystem functioning does not change with the change of biodiversity). Existing studies of BEF to date indicate that biodiversity generally enhances ecosystem functioning in both terrestrial and aquatic ecosystems (Loreau et al. 2002, Naeem et al. 2009).

Most BEF studies have been field manipulative experiments in which primary productivity is the focal variable for ecosystem functioning. Primary productivity is a collective variable representing multiple ecosystem processes (e.g., nutrient transfer and cycling, water flow, etc.) and has been one of the most commonly used indicators of ecosystem function in many ecological studies for decades (Whittaker and Levin 1975). Results from numerous BEF experiments to date show that ecosystem productivity is positively related to biodiversity (Hooper et al. 2005). Two primary mechanisms have been offered to explain the positive relationship: first is niche complementarity effect, and second is selection effect or sampling effect. Niche complementarity effect occurs when differences in species resource requirements allow diverse communities to use available resources more completely and efficiently and convert these resources into greater biomass or other functions (Tilman et al. 1997, Loreau 2000, Spehn et al. 2005). Selection effect or sampling effect refers to the phenomenon that increasing biodiversity increases the possibility of species that are competitively superior and functionally important being included in the community (Aarssen 1997, Huston 1997, Tilman 1997, 2001, Loreau 2000, Fox 2005, Spehn et al. 2005). However, the two effects are not mutually exclusive, and both effects can operate simultaneously to affect productivity.

The relationship between biodiversity and stability has been a central issue in the BEF context. Because of the ambiguity in the definitions of biodiversity and stability, and the complexity in the relationship between them, the diversity-stability relationship has long been debated (Wu and Loucks 1995, Tilman 1999). However, several studies suggest that the level of biodiversity plays a key part in keeping the stability of ecosystem. David Tilman and his colleagues began a long-term study to investigate the relationship between biodiversity and stability in plant communities at Cedar Creek History Area, Minnesota, in 1982. They found that diversity within an ecosystem tends to be correlated positively with the stability of plant community (David and Downing 1994, Tilman 1996, Tilman et al. 1996, Tilman et al. 2006). In a grassland of Temple, Texas, Isbell et al. (2009) found that productivity was less variable among years in plots planted with more species. The higher the level of biodiversity for an ecosystem is, the more the number of genes and species there are, thus, the ecosystem can adapt itself better to external stress. On the other side, stability is considered most meaningfully with reference to disturbance or other external events. Disturbance has effects on local diversity. A habitat with a high level of disturbance is extremely unstable and can be tolerated usually only by few specially adapted species (Grime 1973). A habitat with a low level of disturbance is highly stable, but often supports little species richness because competitive exclusion has time to run its course. Accordingly, empirical studies showed that the highest species richness often occurs at intermediate disturbance intensity. Continued research in this area is needed to explore the underlying mechanism behind the relationship between biodiversity and ecosystem stability (Ives and Carpenter 2007).

3 Effects of spatial heterogeneity on the BEF relationships

Numerous studies have been carried out to explore the relationship between biodiversity and ecosystem functioning (BEF) in natural ecosystems (Lechmere-Oertel et al. 2005, Bai et al. 2007, Cheng et al. 2007, Grace et al. 2007). For example, Bai et al. (2007) reported that a positive linear, rather than hump-shaped, form was ubiquitous across all the organizational levels of association type, vegetation type and biome, and spatial scales of local, landscape and regional in Inner Mongolia region of the Eurasian Steppe. A number of mechanisms have been proposed to explain observed BEF relationships, and one of them is spatial heterogeneity (Chesson 2000, Bailey et al. 2007). Spatial heterogeneity, referring to unevenness and complexity of spatial distribution for an ecological attribute (Kolasa and Pickett 1991), is considered as a ubiquitous characterization of ecosystem processes (Pickett and Cadenasso 1995, Hutchings 2000, Hutchings et al. 2000, Wu et al. 2000, Turner and Cardille 2007). Spatial heterogeneity is one of the major drivers behind species coexistence and biodiversity at different scales (Wu and Loucks 1995).

Previous studies on BEF relationships have centered primarily on the effects of species richness on ecosystem functioning at fine-scale and relatively homogeneous communities (Tilman et al. 1996, 1997, Hooper et al 1999), with little attention to the possible effects of spatial heterogeneity (Guo et al. 2006, Duffy 2009). However, spatial heterogeneity may have important influences on the BEF relationships especially on broad scales (Cardinale et al. 2000, Deutschman 2001, Pachepsky et al. 2007, Tylianakis et al. 2008, Duffy 2009). A growing body of BEF literature has documented that the shape and pattern of the BEF relationships can depend critically on spatial heterogeneity in environment (Fridley 2002, Cardinale et al. 2004, Wardle and Zackrisson 2005). For example, resource heterogeneous distribution often strengthens the relationship between plant biodiversity and productivity (Fridley 2002, Zhang and Zhang 2006). Moreover, spatial heterogeneity represented as particular habitat types composing the landscape could change the direction and magnitude of the slope relating biodiversity and ecosystem functioning (Cardinale et al. 2000).

Spatial heterogeneity can have a variety of consequences on key variables of biodiversity and ecosystem functioning. Spatial heterogeneity of environmental conditions can increase the importance of species richness for an ecosystem process (Griffin et al. 2009) and promote ecosystem functioning which could be indicated by productivity (Wacker et al. 2008). A first step toward understanding the effects of spatial heterogeneity on the BEF relationships is to quantify spatial heterogeneity characteristics of key variables of biodiversity and ecosystem functioning, and identify the spatial relationships among these variables. Geostatistics has been a revolutionary tool to examine spatial heterogeneity characteristics of variables of ecological processes in that the parameters derived from the semivariogram model offer an index to quantify the magnitude and scale of spatial heterogeneity for a variable studied (Curran 1988, Meisel and Turner 1998).

In this thesis, I propose to examine how a selected set of variables representing plant biodiversity and ecosystem functioning are spatially structured and related to each other in a natural grassland in Inner Mongolia, China. This study will take advantage of the data produced by the largest grassland BEF field experiment – the Inner Mongolia Grassland Removal Experiment (IMGRE) funded jointly by US NSF and Chinese NSF. The experiment was initiated in 2005 for background information investigation when the study site was in a natural condition, and in the following years through 2006 to 2009, removal treatments of plant functional types were conducted each year. Specifically, my research will focus on the following two overarching research questions:

1. What are the spatial patterns of soil nutrients, plant biodiversity, and aboveground biomass in a natural grassland community of Inner Mongolia, China? How are they related spatially?
2. How do removal treatments affect the spatial patterns of soil nutrients, plant biodiversity, and aboveground biomass? Is there any change for their spatial correlations after removal treatments?

We predicted that soil nutrients, plant biodiversity, and aboveground biomass in the natural grassland community would present different spatial patterns, and they would be spatially correlated to each other closely. Removal treatments will have a significant effect on spatial structures and spatial correlations of variables, compared to those prior to the removal treatments.

These two research questions will be addressed through a series of spatial analyses using traditional and spatial statistics. The field data for this study will include the data from the IMGRE project as well as other studies in the Inner Mongolia grassland region. The findings of our research are expected to provide new insight into the spatial ecology of grasslands, and to help improve our understanding of the BEF relationships and grassland management in the Inner Mongolia grassland.

CHAPTER 2

SPATIAL PATTERNS OF SOIL NUTRIENTS, PLANT DIVERSITY, AND ABOVEGROUND BIOMASS AND THEIR RELATIONSHIPS IN A NATURAL GRASSLAND COMMUNITY IN INNER MONGOLIA, CHINA

1 Introduction

Spatial heterogeneity affects biodiversity as well as population and ecosystem processes across a range of scales (Kolasa and Pickett 1991, Wu and Loucks 1995). While understanding the dynamics and consequence of spatial heterogeneity has been recognized as a central goal of landscape ecology (Turner et al. 2001, Wu and Hobbs 2007), a "spatial" perspective has now become pervasive in population, community, and ecosystem ecology and beyond because heterogeneity is ubiquitous across systems and scales (Wu and Loucks 1995).

Ecosystem functioning in arid and semi-arid ecosystems is strongly controlled by the spatial heterogeneity of soil water and nutrients (Wu and Levin 1994, Schlesinger et al. 1996, Reynolds et al. 1997, Olofsson et al. 2008). Theoretical studies suggest that spatial heterogeneity in soil resources can modulate the strength of BEF relationships (Tilman 1982, 1985). Spatial heterogeneity can promote coexistence among species through resource or niche partitioning (Tilman 1982, 1985). This notion is consistent with niche theory that more species can coexist in a local area if they have complementary ways of acquiring resources (Tilman and Kareiva 1997, Hutchings et al. 2003).

Consequently, higher species diversity will increase the rates of ecological processes (McNaughton 1993).

While the relationship between biodiversity and ecosystem functioning (BEF) has received considerable attention in the past few decades (Loreau et al. 2002, Hooper et al. 2005, Bai et al. 2007, Naeem et al. 2009), the effects of spatial heterogeneity on the BEF relationships are still poorly understood. However, numerous empirical studies suggest that spatial heterogeneity may significantly influence how biodiversity and ecosystem functioning interact in different landscapes. For example, Bai et al. (2007) found that, in the Eurasian steppe region, plant species diversity and grassland net primary productivity both increase along a regional environmental gradient with increasing precipitation, and that the relationship between plant diversity and productivity may vary on fine spatial scales. The BIODEPTH (Biodiversity and Ecological Processes in Terrestrial Herbaceous Ecosystems) project carried out a series of BEF experiments in seven European countries, and found that soil heterogeneity between sites had significant effects on the experimental results (Hector et al. 1999, Hector and Hooper 2002, Hector et al. 2007). One of the major findings from these experiments was that heterogeneity in soil properties across sites had strong effects on the magnitude and variability of the measured effects, such as Aboveground Net Primary Production (ANPP).

Within-site or within-community heterogeneity in environmental resources may also significantly affect biodiversity and ecosystem functioning.

Studies have shown that differences in fine-scale topography and soil resources may have significant effects on plant growth and species diversity (Schlesinger et al. 1996, Reynolds et al. 1997, Olofsson et al. 2008). Zhou et al. (2008) found that plant diversity was positively correlated with spatial heterogeneity of soil nutrients in a semiarid grassland of Inner Mongolia in China. Factors affecting broad-scale patterns of biodiversity and ecosystem processes may be quite different from those on fine scales (Wu and Loucks 1995, Davies et al. 2005). Although fine-scale environmental heterogeneity is likely to influence biodiversity, ecosystem functioning, and their relationship, most BEF experiments have assumed the environment within a biological community is spatially homogeneous. This may potentially be a form of 'hidden treatments' (sensu Huston 1997).

To help improve our understanding of the effects of fine-scale spatial heterogeneity on the BEF relationships, a plausible first step is to quantify the spatial patterns of variables representing biodiversity and ecosystem functioning, and then examine the relationships between these two groups of variables in a particular ecosystem. To do this, geostatistical techniques (Matheron 1963, David 1977) provide an effective approach. In recent decades, these methods have been widely used to study spatial patterns of environmental factors and ecological properties (Rossi et al. 1992, Fortin and Dale 2005). For example, semivariogram modeling is suitable to quantify spatial structures of physical and biological variables and detect the characteristics scales of spatial heterogeneity (Turner et al. 1991, Robertson and Gross 1994, Burrough 1995, Kareiva and Wennergren 1995, Meisel and Turner 1998). Semivariograms can also be used in developing sampling schemes that avoid the problems of spatial autocorrelation or pseudo-replication (Legendre and Fortin 1989, Turner et al. 1991, Meisel and Turner 1998).

The main goal of this study was, therefore, to understand the spatial patterns of abiotic and biotic variables relevant to biodiversity and ecosystem functioning as well as their relationships, based on an existing BEF field experiment in the Inner Mongolia grassland, China. We applied geostatistical methods to examine the spatial patterns of soil nutrients, plant diversity, and aboveground biomass at three organizational levels - the individual species, plant functional types (PFTs), and the whole plant community. Two research questions were addressed: 1) What are the spatial patterns of soil nutrients, plant biodiversity and aboveground biomass? and 2) How are these variables related to each other spatially and across the different levels of organization?

2 Materials and methods

2.1 Study site and experimental design

This study was based on the ongoing field manipulative experiment on the biodiversity-ecosystem functioning relationship in the Inner Mongolia grassland in northern China - the Inner Mongolia Removal Experiment (IMGRE). The study site is located in a *L. chinensis*-dominant community in the Xilin River

Basin of Inner Mongolia Autonomous Region of China (116°42′E, 43°38′N). The long-term annual mean air temperature is 0.6 ºC. The coldest month (January) is characterized by the mean temperature of -21.6 ºC, and the mean temperature of the warmest month (July) is 19.0 ºC. Topographic relief exhibits little variation, with elevation ranging from 1,250-1,260 m at the experimental site. Mean annual precipitation is 346.1 mm with 60-80% occurring during the growing season from May to August. Main soil type is chestnut soils with similar physiochemical properties throughout the site. Vegetation of the region consists of the dominant species *Leymus chinensis* (LC) and *Stipa grandis* (SG), and five non-dominant species *Achnatherum sibiricum* (AS), *Cleistogenes squarrosa* (CS), *Koeleria cristata* (KC), *Agropyron cristatum* (AC) and *Allium tenuissimum* (AT), etc. There are 86 species in the plant community, which fall into five plant functional types based on their life forms: perennial rhizome (PR), perennial bunchgrasses (PB), perennial forbs (PF), annuals and biennials (AB), and shrubs and semi-shrubs (SS) (Bai et al. 2004).

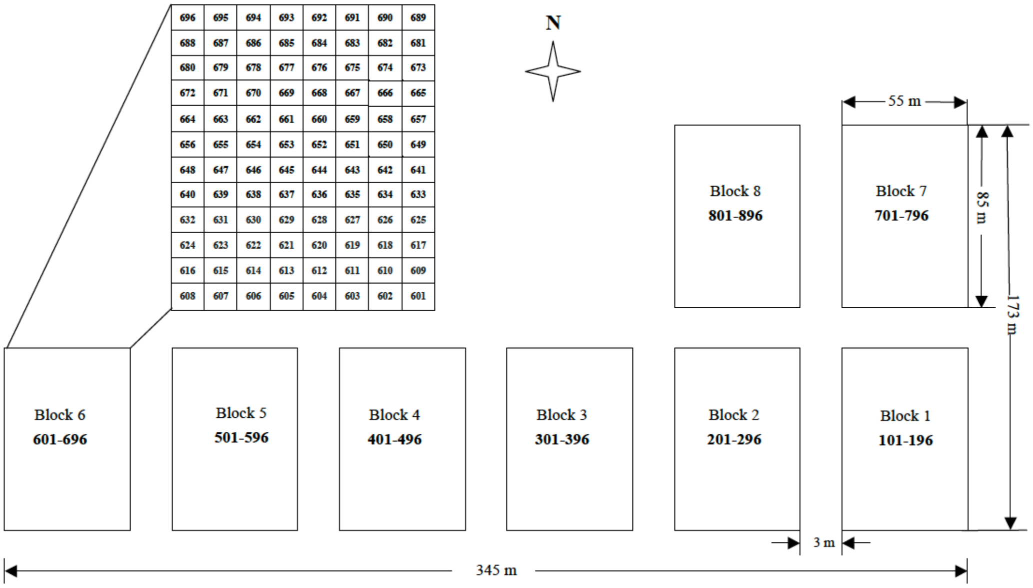

Fig. 2.1 Plot layout of the Inner Mongolia Grassland Removal Experiment (IMGRE). Eight 55 m X 85 m blocks each contain 96 plots. Aboveground biomass was sampled in each plot, whereas soil nutrients were measured only in a set of randomly chosen plots.

The IMGRE experiment was initiated in 2005 at a site located 3 km from Inner Mongolia Grassland Research Station. It has eight 55 m X 85 m blocks separated by 3 m (Fig. 2.1). Blocks were arranged horizontally in a topographically uniform area to avoid the effects of anisotropy (directional dependence) in subsequent spatial analyses of data. Each block was divided into 96 plots which formed a pattern of 8 X 12 spatial grids. Plots were separated by a 1-m wide path and sets of plots by a 2-m wide walking path. Each plot was further divided into 16 1 m X 1 m quadrats which were separated by 40 cm from each other to avoid edge effects. Plants and soil were sampled in one of these 16 quadrats in late August 2005. The timing corresponds to the peak of annual aboveground net primary production (ANPP) in temperate grasslands (Sala and Austin 2000, Bai et al. 2004). Specific measurements included species richness (the number of species in a specified area), the aboveground biomass of individual species, total carbon (TC), total nitrogen (TN), and total phosphorous (TP).

2.2 Vegetation sampling and measurements

We clipped the stem of live plant at the ground level of live plants in one of the 16 quadrates in each plot (768 plots in total) and sorted material by species. All samples were oven-dried to a constant mass at 65 °C for a minimum of 48 h. Aboveground biomass (g) was measured by plant species and then grouped into categories of plant functional types.

The species diversity of a plant community can be measured in three ways. First, species richness (S) is simply the number of species in a plant community (or a sampling area). Second, information theoretic indices are often used to capture the diversity of species in terms of both their richness (the number of species) and relative abundances (evenness). The most frequently used species or plant functional type diversity index is the Shannon-Weaver index (*H*):

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

where *S* is the total number of species or plant functional types in the plot, and P_i is the biomass proportion of the *i*th species or plant functional type. For a given number of species in a community, the more even the relative abundance among the species is, the higher the value of H will be. In our study, we used the relative aboveground biomass (the percentage of a species' aboveground biomass relative to the total aboveground biomass of all species) to represent the relative abundance of a species in the community. There is no upper bound to the values of this index.

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

$$E = \frac{H}{H_{\max}} = \frac{H}{\ln S} \qquad (2)$$

where H is the Shannon-Weaver index calculated as shown above. When the proportions of all species are similar, evenness is close to one. When the abundances of different species are quite dissimilar (e.g., some rare and some common), the value of evenness will be much larger than one.

2.3 Soil sampling and measurements

Soil samples were collected in evenly distributed plots across the same research site. Three soil samples, which form 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. Total carbon (TC) was analyzed following a modified Meius method, total nitrogen (TN) - by the Kjeladahl digestion procedure, and total phosphorus (TP) - by the digestion of soil samples with perchloric acid.

All the sampling and measurements for vegetation and soil properties were done by the IMGRE research team, including a large number of faculty and graduate students from Institute of Botany of the Chinese Academy of Sciences and School of Life Sciences, Arizona State University.

2.4 Data analysis

Several variables were selected in our analysis based on their relevance to the BEF relationships. These include: spatial variability of soil nutrients (TC, TN, and TP) in sampled plots, plant biodiversity measures (number of species (N_{SP}), species diversity index (H_{SP}), species evenness index (E_{SP}), plant functional type diversity index (H_{PFT}), and plant functional type evenness index (E_{PFT})), and aboveground biomass at the organizational levels of individual species, plant functional type and the whole community of each plot.

Spatial autocorrelation analysis provides a quantitatively unbiased estimate of the spatial correlation between sampled values as a function of their lag distances. A common geostatistical method, semivariance analysis, can be employed to quantify spatial autocorrelation and spatial dependence of ecological patterns (Rossi et al. 1992). The semivariance is calculated as:

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

where *N(h)* is the number of pairs of data at each distance interval (lag) *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 (Fig. 2.2), and the shape of the plot shows how the degree of autocorrelation changes in space. Spatial structure is determined by identifying the "best fit" model (the one with the least residual sums of squares (RSS)) to the experimental semivariogram. We fitted spherical, exponential, linear, and Gaussian semivariogram models by using the GS+ package, version 7.0 (Gamma Design Software 1999, Plainwell, MI, USA). Five semivariogram parameters were derived and used in the analysis, including: 1) Range (A_0), separation distance at which spatial dependence is apparent; 2) Nugget variance (C_0), level of random variation which is attributed to either measurement error or spatial variability occurring at intervals of less than the smallest interval sampled; 3) Structural variance (C), the effect of structure variation caused by spatial heterogeneity; 4) Sill (C_0+C), the population variance which indicates the overall spatial variability when the semivariance may rise to some asymptote; and 5) C/(C_0+C), the proportion of variance due to spatial structure, which is called spatial heterogeneity percentage. Semivariograms with a high value of spatial heterogeneity percentage indicate a strong spatial heterogeneity (Robertson et al. 1993, Gross et al. 1995, Li and Reynolds 1995, Schlesinger et al. 1996).

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:

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

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, ω_{ij} is the weighted matrix value, and n is the number of pairs of data. Values of I range between -1 and 1 with positive values corresponding to positive autocorrelation, zero indicating randomness, and negative values representing negative autocorrelation. Calculating this index for a variety of lag distances yields Moran's *I* correlograms. The correlograms were generated by using the 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). We performed block kriging mapping with calculated semivariograms for the aforementioned variables, except the rare plant functional types AB and SS because of too few samples for AB and no samples for SS.

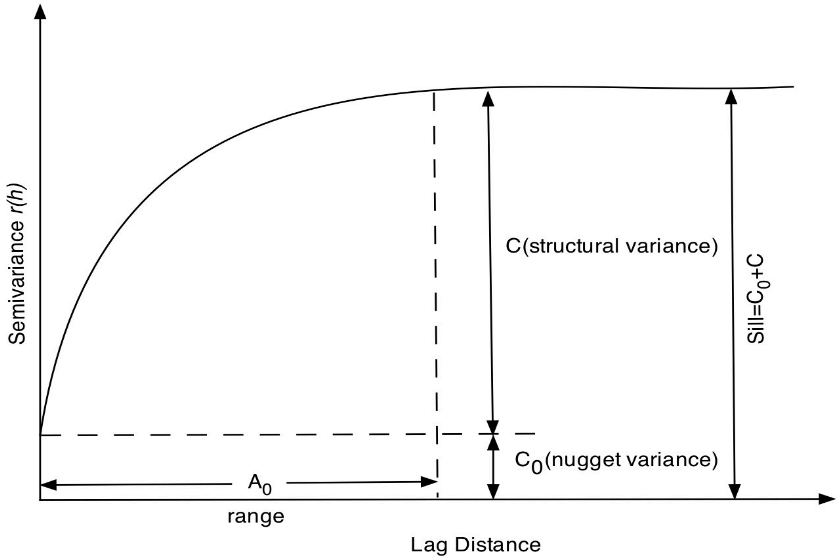

Fig. 2.2 An idealized semivariogram, showing semivariance (γ) increasing with distances between paired samples (lag distances). The curve indicates that samples show spatial autocorrelation over the range (A_0) and become independent beyond that distance. Random measurement errors and spatial variation below the scale of the minimum lag distance comprise the nugget variance (C_0). Spatial variation caused by non-random spatial structure is the structural variance (C). Sill is the sum of C_0 and C, which indicates the total spatial variability.

Correlations between soil nutrients, biodiversity measures, and aboveground biomass were analyzed by the modified t-test. The independence of samples could not be guaranteed at such a fine scale, so the modified t-test correlation 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 software (V. 2.0) (http://www.passagesoftware.net/).

3 Results

3.1 Summary statistics of variables of soil nutrients, plant biodiversity, and aboveground biomass

Averaged over the sampled plots, mean values of TC, TP, and TN were 47.98 ± 0.07 $g \cdot kg^{-1}$, 4.88 ± 0.07 $g \cdot kg^{-1}$, and 7.23 ± 0.10 $g \cdot kg^{-1}$, respectively. Mean species richness was 8 ± 0.05 m^{-2}, species diversity index (H_{sp}) at the plot level was 1.46 ± 0.21, and the plant functional type diversity index (H_{PFT}) was 0.76 ± 0.21 (Table 2.1). The smallest value of aboveground biomass of seven individual species in the study was observed in *A. tenuissimum* (1.45 ± 1.28 $g \cdot m^{-2}$), while *L. chinensis* and *S. grandis* contributed the most to the total aboveground biomass. When grouped by plant functional type, perennial bunchgrasses were the main contributor to the total aboveground biomass (Table 2.1). Coefficients of variation (CV) - which is the ratio of standard deviation to the mean - ranged from 16% for N_{SP} to 130% for the annuals and biennuals functional type (Table 2.1). The coefficients of skewness and kurtosis could be used to describe the shape of the sample distribution. The majority of variables, except TC, TP, E_{SP}, H_{PFT}, E_{PFT} and perennial bunchgrasses, showed positively skewed distributions. Most variables had distributions with positive kurtosis, indicating a "peaked" distribution, while TC, H_{PFT}, E_{PFT}, and *S. grandis* were characterized by relatively smooth distributions owing to the negative kurtosis (Table 2.1).

3.2 Spatial patterns of soil nutrients, plant biodiversity, and aboveground biomass

3.2.1 Soil nutrients

The "best-fit" model to the semivariograms of soil nutrients in our study was spherical model, indicating the presence of spatial autocorrelation within a certain distance defined by the range (Table 2.2, Fig. 2.3 A1-C1). Spatial autocorrelation ranges varied from 69.30 m for TP to 102.30 m for TN. The values of spatial heterogeneity percentage were high, ranging from 73% (TN) to 99% (TP), which suggests high spatial structure. The high values (above 50%) of spatial heterogeneity percentage also suggested that spatially structured variance accounted for a larger proportion of the total sample variance in soil nutrients (Table 2.2). Compared to other soil nutrients, TP had higher r^2 and lower nugget values in the semivariogram model (Table 2.2). All soil nutrient variables were positively autocorrelated within 60 m, and then showed negative autocorrelation at greater lag distances (Fig. 2.3 A2-C2). Kriging maps illustrated that spatial patterns of soil nutrients were considerably correlated with each other (Fig. 2.5 A-C). The island of low values of the three soil variables was apparent in block 1 of the study site. Higher values of soil nutrients were found in blocks 2 and 3 (Fig. 2.5 A-C).

3.2.2 Plant biodiversity

The "best-fit" model for most plant biodiversity measures was exponential model (Table 2.2, Fig. 2.4 A1-E1). The only exception was H_{SP} where spherical model provided the best fit (Table 2.2). The ranges of N_{SP}, H_{SP}, E_{SP}, H_{PFT}, and E_{PFT} were 39.90 m, 118.50 m, 13.20 m, 26.60 m, and 28.20 m, respectively (Table 2.2). All semivariograms of N_{SP}, H_{SP}, E_{SP}, H_{PFT}, and E_{PFT} exhibited distinctive patterns (Fig. 2.4 A1-E1) as indicated by high r^2, low RSS, relatively low nugget values (Table 2.2). From Fig. 2.4, N_{SP}, H_{SP}, and E_{SP} exhibited positive autocorrelations within 80 m, and then showed negative autocorrelations and no correlations with increasing lag distances (Fig. 2.4 A2-C2). H_{PFT} and E_{PFT} were positively autocorrelated within 75 m, and then showed negative autocorrelations and no correlations at greater lag distances (Fig. 2.4 D2-E2). Kriging maps showed higher values of N_{SP} and H_{SP} were concurrent in blocks 1 and 2 (Fig. 2.5 D, E). Moreover, H_{PFT} and E_{PFT} showed appropriately identical spatial patterns (Fig. 2.5 G and H).

Table 2.1 Summary statistics of variables of soil nutrients, plant biodiversity, and aboveground biomass in the study site of the Inner Mongolia grassland of China in 2005

	Variable	Maximum	Minimum	Mean	StDev	Standard Error	CV*(%)	Skewness	Kurtosis	Number of led plots/variables present
Soil nutrients	TC ($g \cdot kg^{-1}$)	69.64	17.97	47.98	1.00	0.07	2.08	-0.28	-0.03	212
	TN ($g \cdot kg^{-1}$)	9.82	2.33	4.88	1.01	0.07	20.70	0.12	2.05	219
	TP ($g \cdot kg^{-1}$)	10.15	3.24	7.23	1.45	0.10	20.05	-0.70	0.08	217
Biodiversity measures	N_{SP} (m^{-2})	13.00	4.00	8.08	1.30	0.05	16.06	0.05	0.25	736
	H_{SP}	2.67	0.72	1.46	0.21	0.01	14.31	0.05	1.30	736
	E_{SP}	1.29	0.00	0.70	0.09	0.003	12.86	-1.01	9.65	733
	H_{PFT}	1.10	0.12	0.76	0.21	0.008	27.63	-0.48	-0.51	736
	E_{PFT}	1.00	0.11	0.69	0.19	0.008	27.54	-0.48	-0.51	736
Aboveground biomass	LC ($g \cdot m^{-2}$)	143.44	0.30	26.02	19.93	0.73	76.59	1.48	3.08	736
	SG ($g \cdot m^{-2}$)	98.23	1.32	40.21	18.07	0.67	44.94	0.35	-0.08	733
	AS ($g \cdot m^{-2}$)	48.28	0.01	5.54	5.70	0.23	102.89	2.09	7.29	606
	CS ($g \cdot m^{-2}$)	81.60	0.02	16.76	11.88	0.44	70.88	0.90	1.11	731
	KC ($g \cdot m^{-2}$)	58.43	0.05	11.09	9.60	0.36	86.56	1.40	2.19	710
	AC ($g \cdot m^{-2}$)	50.11	0.01	8.80	8.21	0.35	93.30	1.55	2.86	540
	AT ($g \cdot m^{-2}$)	9.80	0.01	1.45	1.28	0.05	88.28	1.92	5.53	662
	PR ($g \cdot m^{-2}$)	143.44	0.30	26.02	19.93	0.73	76.59	1.49	3.08	736
	PB ($g \cdot m^{-2}$)	143.20	1.49	70.61	20.66	0.76	29.26	-0.41	0.96	736
	PF ($g \cdot m^{-2}$)	59.22	0.10	12.22	9.62	0.35	78.72	1.36	2.19	736
	AB ($g \cdot m^{-2}$)	0.18	0.0003	0.05	0.07	0.03	130.02	1.25	0.17	6
	SS ($g \cdot m^{-2}$)	-	-	-	-		-	-	-	-
	AGB ($g \cdot m^{-2}$)	374.58	2.41	109.10	26.58	0.98	24.36	0.87	16.28	736

*Coefficient of variation (CV) is calculated as the ratio of standard deviation to the mean.

N_{SP} represents number of species, H_{SP} and E_{SP} represent species diversity and evenness indices, respectively, H_{PFT} and E_{PFT} represent plant functional type diversity and evenness indices, respectively, and AGB indicates aboveground biomass at the community level.
"-" means SS not found in the sampled plots.

LC-*L. chinensis*; SG-*S. grandis*; AS-*A. sibiricum*, CS-*C. squarrosa*, *KC-K. cristata*, AC-*A. cristatum* and AT-*A. tenuissimum*.
PR-perennial rhizomes, PB-perennial bunchgrasses, PF-perennial forbs, AB-annuals and biennials.

3.2.3 Aboveground biomass

Exponential model provided the best fit to semivariograms of all commonly found individual species except *S. grandis*, which was best fit by spherical model (Table 2.3, Fig. 2.6 A1-G1). Most species displayed a range of spatial autocorrelation at 40 m or less (e.g., *L. chinensis*, *A. sibiricum*, *C. squarrosa*, *K. cristata, A. cristatum* and *A. tenuissimum*, see Table 2.3). *S. grandis* was spatially autocorrelated at the ranges of 132 m (Table 2.3). The values of spatial heterogeneity percentage varied from 50% to 93% (Table 2.3). Based on Fig. 2.6 A2-G2, *L. chinensis*, *A. sibiricum* and *K. cristata* were positively autocorrelated at the distance of 50 m or less, beyond which they showed a random distribution (Fig. 2.6 A2, C2, E2). *S. grandis* was positively autocorrelated at 70 m or less, and negatively autocorrelated with the increasing lag distances (Fig. 2.6 B2). A positive autocorrelation was found for both *C. squarrosa* and *A. cristatum* at 80 m or less, and these species displayed a random distribution when the lag distance was greater than 80 m (Fig. 2.6 D2, F2). The correlogram for *A. tenuissimum* showed that it was distributed randomly in this area (Fig. 2.6 G2). As it is indicated by higher r^2 (Table 2.3), the aboveground biomass of *L. chinensis*, *S. grandis*, *C. squarrosa* and *K. cristata* exhibited distinct spatial patterns (Fig. 2.8 A, B, D, E) compared to those of *A. sibiricum*, *A. cristatum* and *A. tenuissimum* (Fig. 2.8 C, F, G). The aboveground biomass of *A. sibiricum*, for example, was mostly uniformly distributed at a moderate level with just a few patches with higher values (Fig. 2.8 C). The aboveground biomass of *S. grandis* was higher in the center of the study site (Fig. 2.8 B).

Table 2.2 Semivariogram parameters for soil variables and biodiversity measures in the study site of the Inner Mongolia grassland of China in 2005

	Model	Range (m)	Nugget	Sill	RSS	r^2	$C/(C_0+C)$ (%)
TC	Spherical	76.90	52.70	131.40	1886	0.88	60
TN	Spherical	102.30	0.31	1.14	0.50	0.71	73
TP	Spherical	69.30	0.03	2.32	2.30	0.76	99
N_{SP}	Exponential	39.90	0.91	1.82	0.18	0.84	50
H_{SP}	Spherical	118.50	2.40E-2	4.90E-2	4.34E-5	0.96	50
E_{SP}	Exponential	13.20	1.82E-3	9.44E-3	9.69E-6	0.57	80
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

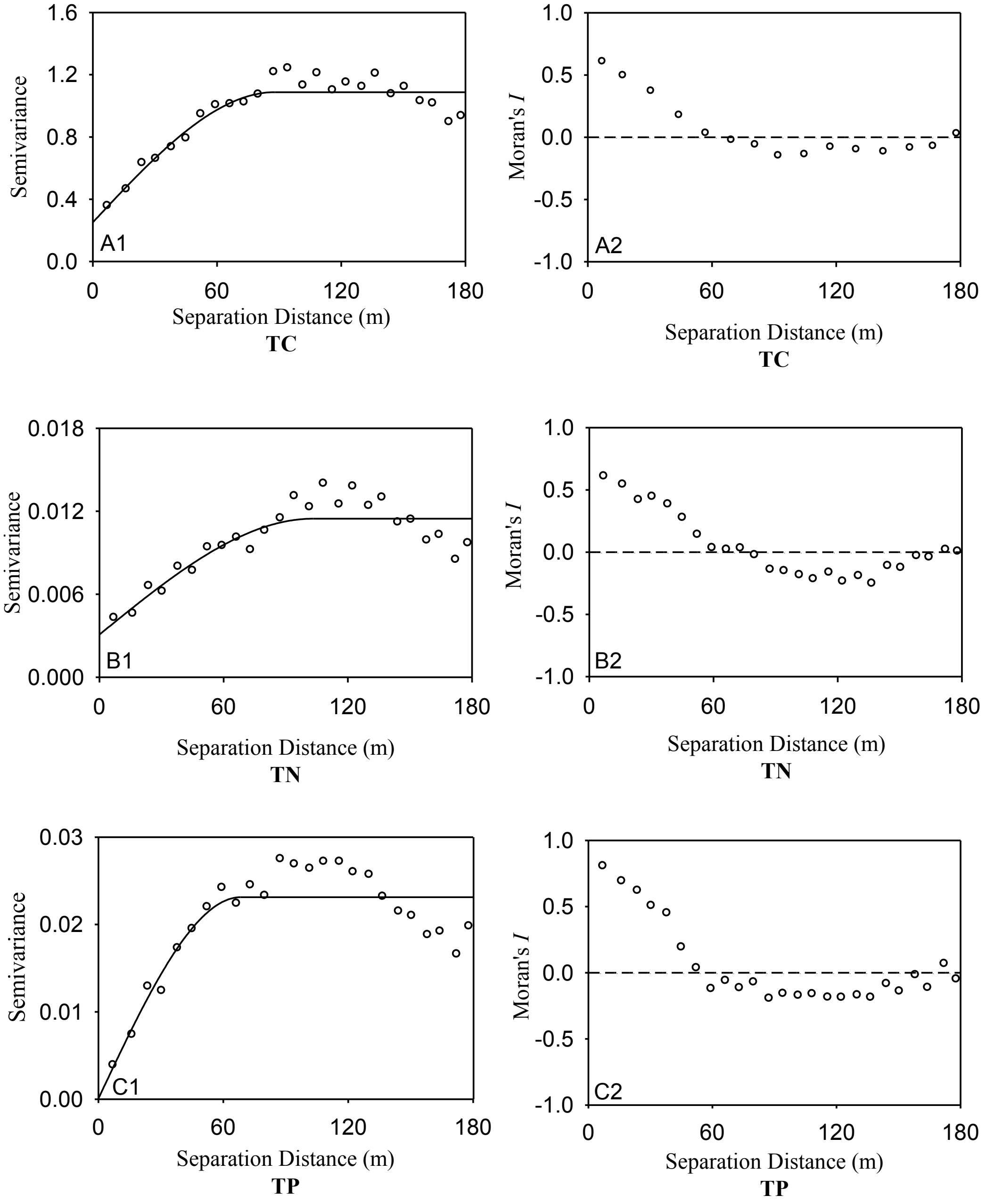

Fig. 2.3 Semivariograms (A1-C1) and correlograms (A2-C2) of TC, TN, and TP in the study site of the Inner Mongolia grassland of China in 2005

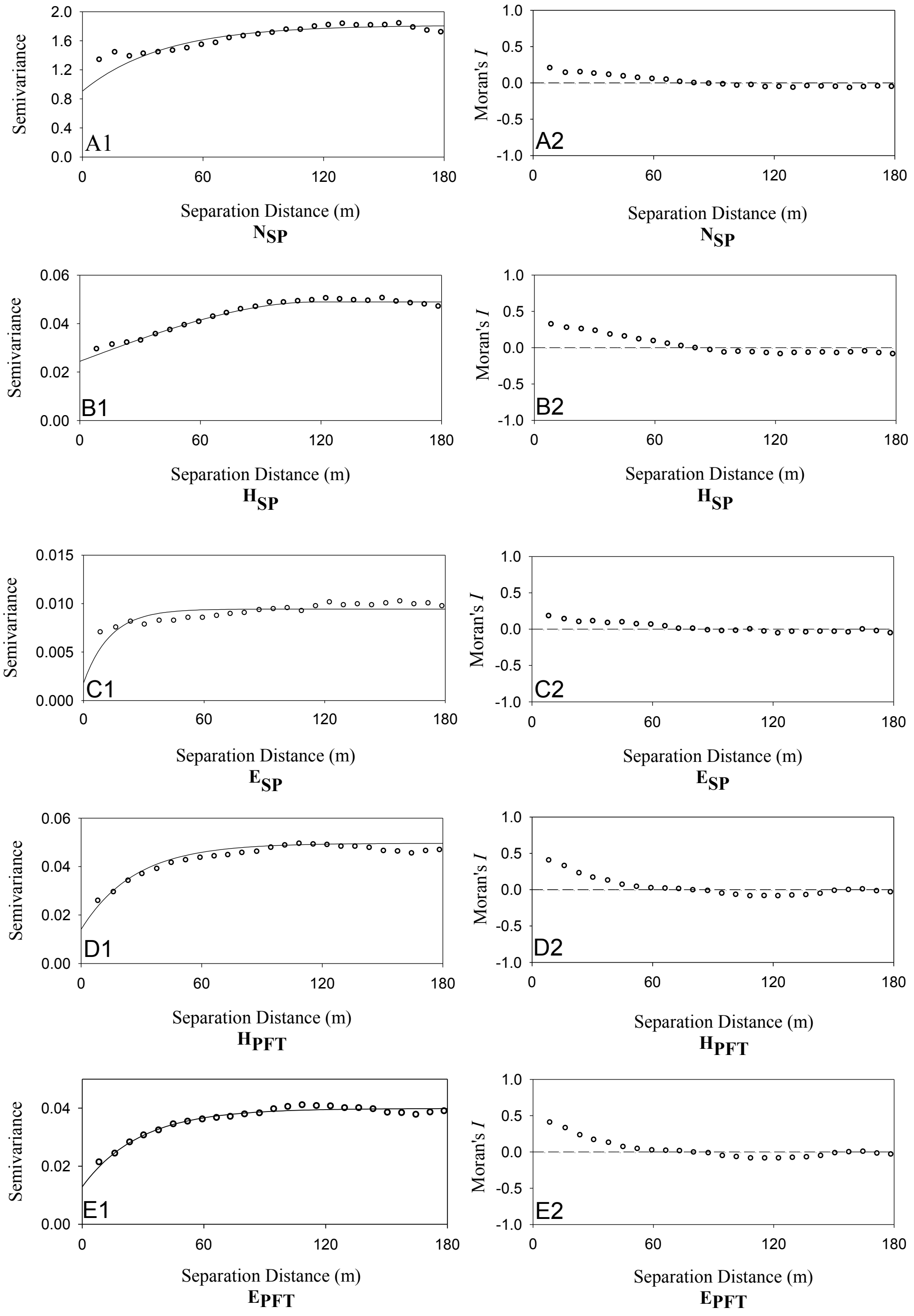

Fig. 2.4 Semivariograms (A1-E1) and correlograms (A2-E2) of N_{SP}, H_{SP}, E_{SP}, H_{PFT}, and E_{PFT} in the study site of the Inner Mongolia grassland of China in 2005

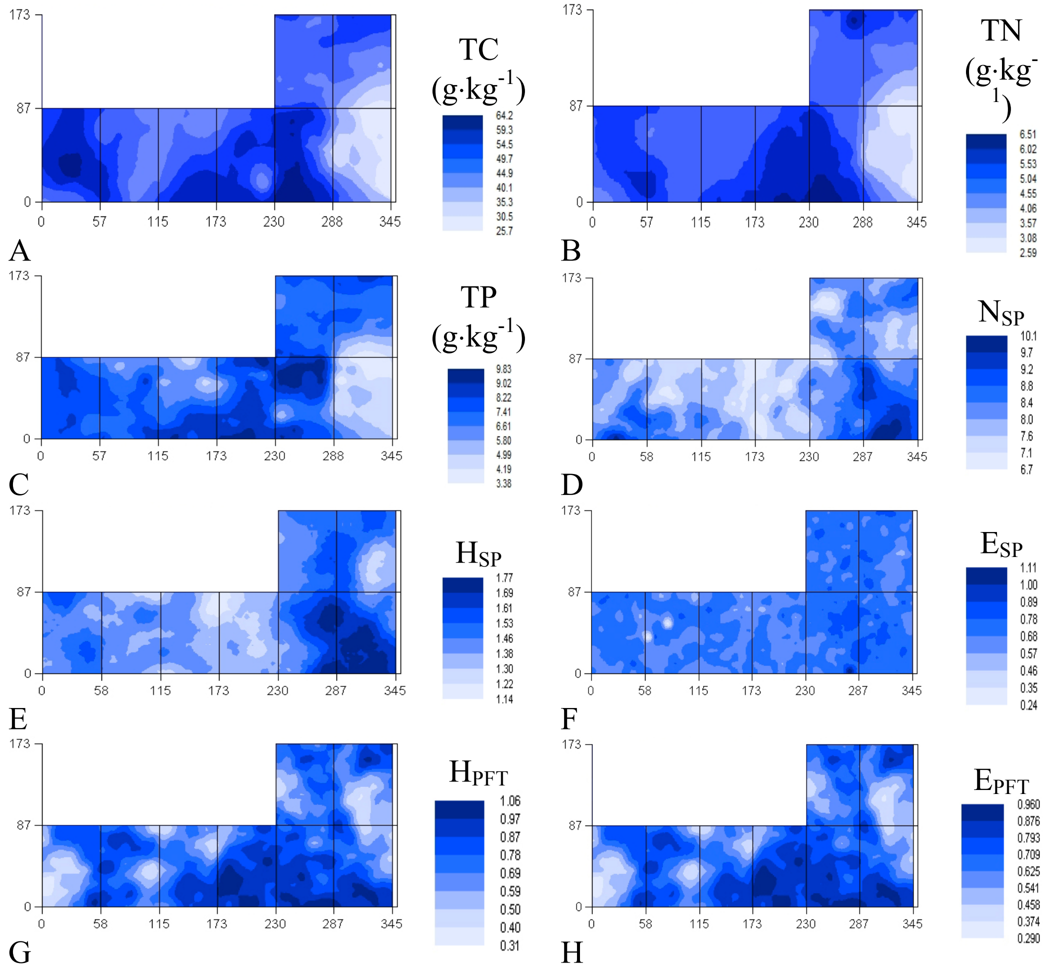

Fig. 2.5 Spatial patterns of TC ($g\cdot kg^{-1}$) (A), TN ($g\cdot kg^{-1}$) (B), TP ($g\cdot kg^{-1}$) (C), N_{SP} (D), H_{SP} (E), E_{SP} (F), H_{PFT} (G), and E_{HPT} (H) derived by using kriging interpolation in the study site of the Inner Mongolia grassland of China in 2005

Exponential model was the best fit to the semivariograms for most aboveground biomass of plant functional types (Table 2.3, Fig. 2.6). The annuals and biennials functional type with only six samples was best fit by linear model (Table 2.3, Fig. 2.6 D). Two dominant plant functional types of perennial rhizome and perennial bunchgrasses displayed ranges of spatial autocorrelation at 9.30 m and 7.80 m, respectively, whereas perennial forbs had the range value of

42.70 m, and annuals and biennials had no range value because of few samples found in the study site (Table 2.3). The values of spatial heterogeneity percentage were above 50% for perennial rhizome, perennial bunchgrasses and perennial forbs, indicating higher spatial structures in these plant functional types (Table 2.3). The aboveground biomass of perennial rhizome and perennial forbs exhibited distinct patchiness (Fig. 2.7 H, J), supported by the high r^2 (Table 2.3). Correlograms showed that perennial rhizome and perennial bunchgrasses were positively autocorrelated within 50 m, and then were randomly distributed with the increasing lag distances (Fig. 2.7 A2, B2). The non-dominant plant functional type of perennial forbs was positively autocorrelated within 80 m, and then negatively autocorrelated between 80 m and 150 m (Fig. 2.7 C2). The perennial bunchgrasses functional type was characterized by high biomass distributed homogenously across the study site (Fig. 2.7 I).

Exponential model provided the best fit to semivariograms of the aboveground biomass at the community level (AGB) (Table 2.3). The range of AGB was 6.90 m, and the value of spatial heterogeneity percentage was 86% at this level. No distinctive patchiness can be found at this level (Fig. 2.7 K), which was also suggested by the low value of r^2 (Table 2.3).

3.3 Correlations among soil nutrients, plant biodiversity, and aboveground biomass

Correlation analysis was performed to explore the relationships among soil nutrients, plant biodiversity measures and the aboveground biomass at the levels of individual species, plant functional type and the whole community (Table 2.4). Note that the correlation between the annuals and biennials functional type and any other variable was not conducted because its sample size was too small. Strongly positive correlations ($0.647 < r < 0.835$ and $P < 0.01$) were found between TC and TN, between TC and TP, and between TN and TP. In terms of plant biodiversity measures, significantly positive correlations ($0.282 < r < 0.791$ and $P < 0.01$) existed between N_{SP} and H_{SP}, between H_{SP} and E_{SP}, H_{PFT}, and E_{PFT}, between E_{SP} and H_{PFT} and E_{PFT}, and between H_{PFT} and E_{PFT}.

TC was significantly positively correlated ($P < 0.01$) to H_{PFT}, E_{PFT}, *L. chinensis*, *K. cristata*, perennial rhizome and perennial forbs, and TN was positively correlated ($P < 0.01$) to H_{PFT}, E_{PFT}, *L. chinensis*, perennial rhizome and perennial forbs. There were no significant correlations between TP and variables of plant biodiversity measures and aboveground biomass.

Table 2.3 Semivariogram parameters for the aboveground biomass at the levels of species, PFT and the whole community in the study site of the Inner Mongolia grassland of China in 2005

	Model	Range (m)	Nugget	Sill	RSS	r^2	$C/(C_0+C)$ (%)
LC	Exponential	9.30	28.00	383.80	5.17E+3	0.78	93
SG	Spherical	132.20	189.70	382.50	5.59E+2	0.99	50
AS	Exponential	5.20	2.57	31.85	6.31E+1	0.32	92
CS	Exponential	11.40	12.20	139.50	4.65E+2	0.89	91
KC	Exponential	39.40	51.90	103.90	5.93E+2	0.82	50
AC	Exponential	5.70	5.30	65.30	2.80E+2	0.31	92
AT	Exponential	2.90	0.16	1.62	5.00E-2	0.08	90
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

LC-*L. chinensis*; SG-*S. grandis*; AS-*A. sibiricum*, CS-*C. squarrosa*, *KC-K. cristata*, AC-*A. cristatum* and AT-*A. tenuissimum.*
PR-perennial rhizome, PB-perennial bunchgrasses, PF-perennial forbs, AB-annuals and biennials.
AGB-the aboveground biomass at the community level.

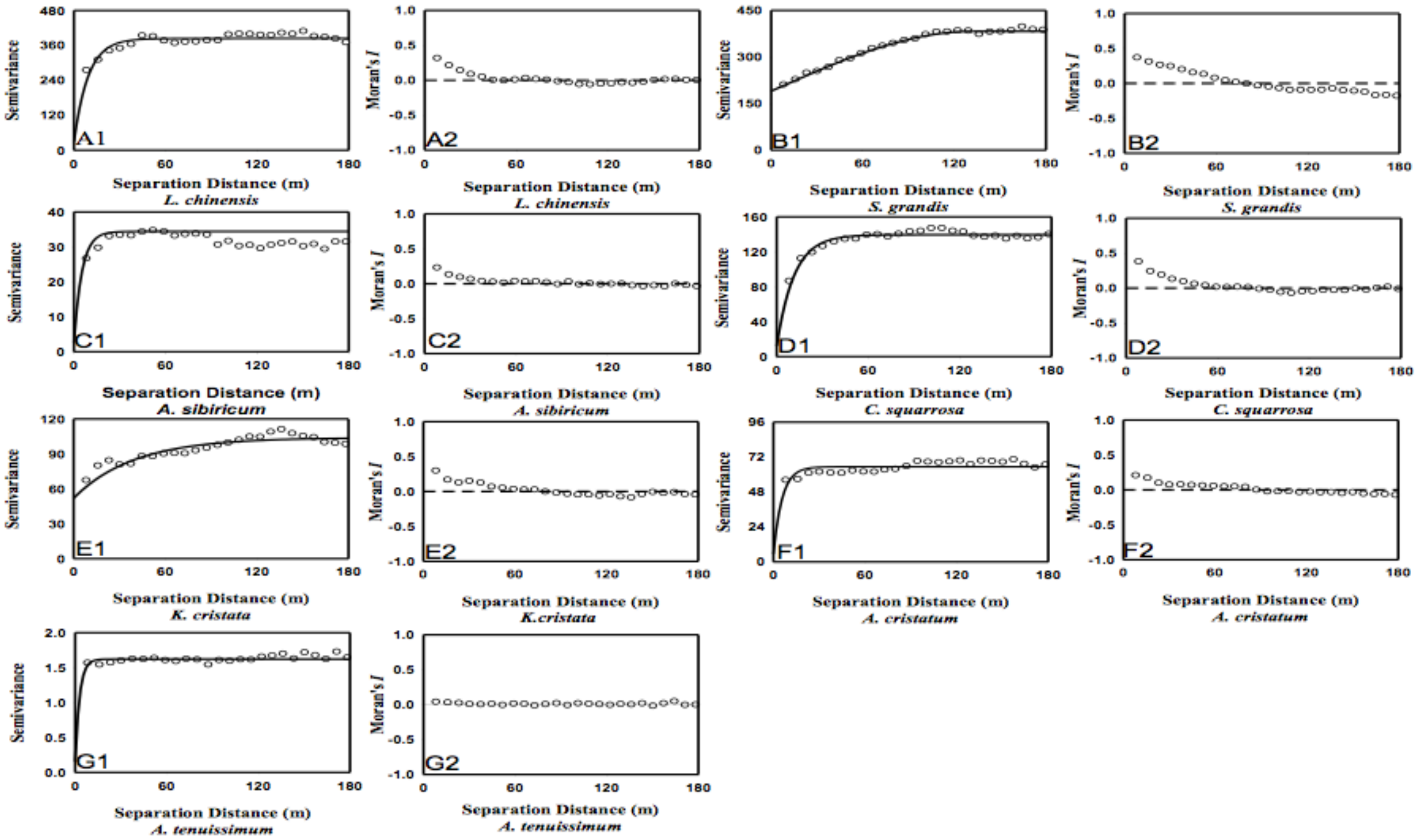

Fig. 2.6 Semivariograms (A1-G1) and correlograms (A2-G2) of *L. chinensis*, *S. grandis*, *A. sibiricum*, *C. squarrosa*, *K. cristata*, *A. cristatum* and *A. tenuissimum* in the study site of the Inner Mongolia grassland of China in 2005

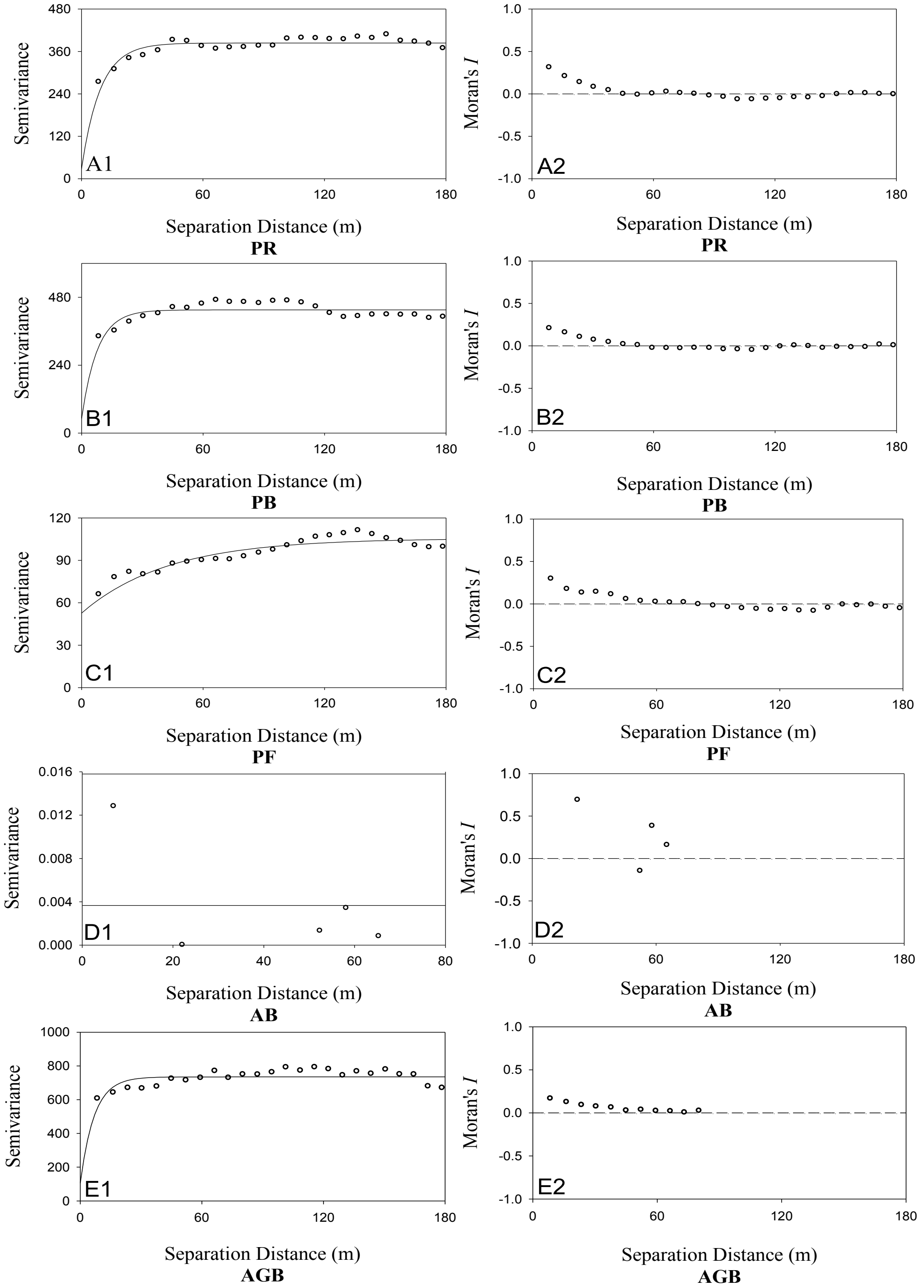

Fig. 2.7 Semivariograms (A1-E1) and correlograms (A2-E2) of the aboveground biomass of PR, PB, PF, and AB, and the aboveground biomass at the community level (AGB) in the study site of the Inner Mongolia grassland of China in 2005

PR-perennial rhizome, PB-perennial bunchgrasses, PF-perennial forbs, AB-annuals and biennials.

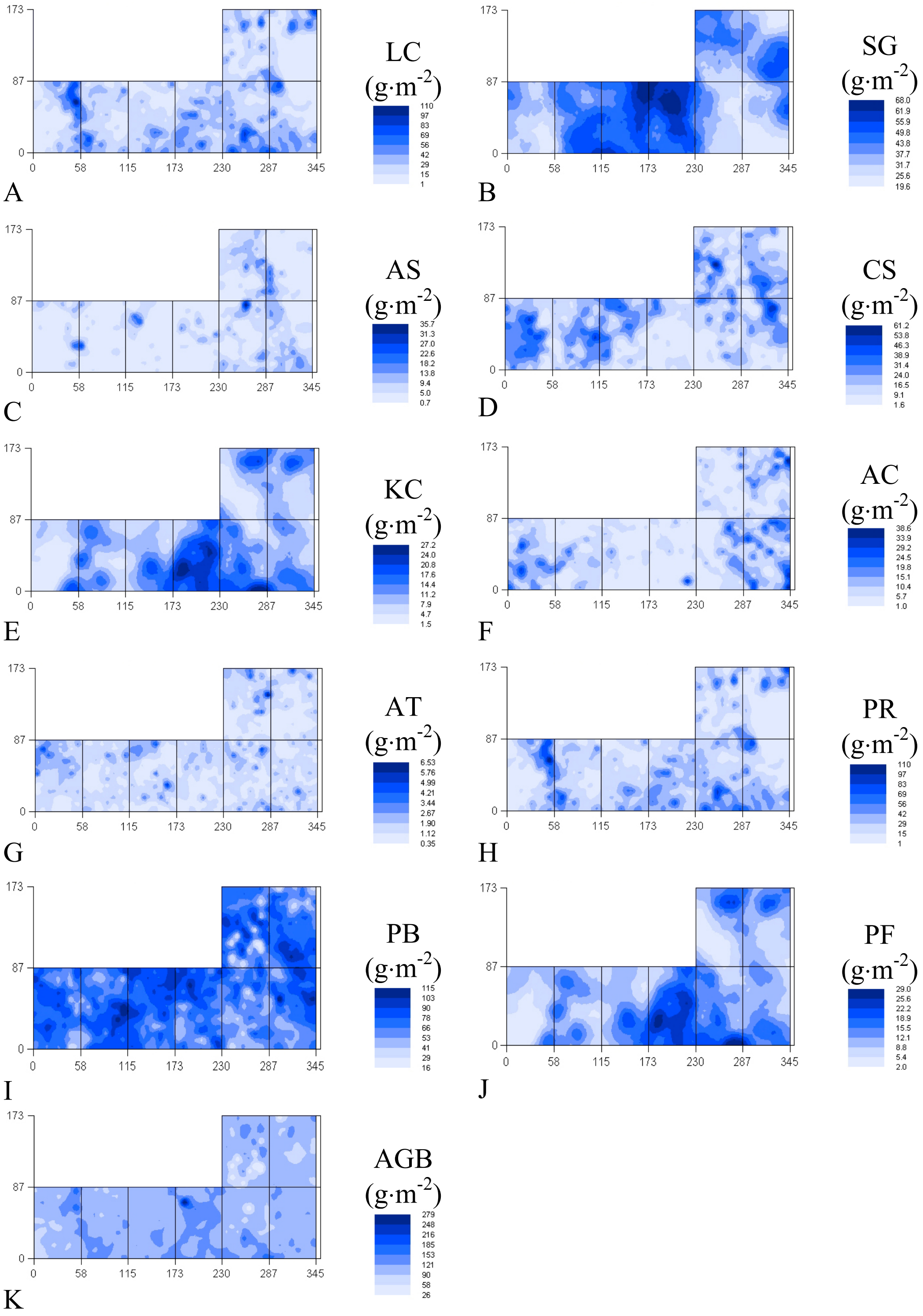

Fig. 2.8 Spatial patterns of LC (g·m^{-2}) (A), SG (g·m^{-2}) (B), AS (g·m^{-2}) (C), CS (g·m^{-2}) (D), KC (g·m^{-2}) (E), AC (g·m^{-2}) (F), AT (g·m^{-2}) (G), PR (g·m^{-2}) (H), PF

(g·m^{-2}) (I), PB (g·m^{-2}) (J) and AGB (g·m^{-2}) (K) derived using kriging interpolation in the study site of the Inner Mongolia grassland of China in 2005

LC-*L. chinensis*; SG-*S. grandis*; AS-*A. sibiricum*; CS-*C. squarrosa*; KC-*K. cristata*; AC-*A. cristatum* and AT-*A. tenuissimum*.
PR-perennial rhizome, PB-perennial bunchgrasses, PF-perennial forbs, AB-annuals and biennials.
AGB-the aboveground biomass at the community level.

For the aboveground biomass of individual species, the dominant species *L. chinensis* was significantly positively correlated ($P < 0.01$) with plant biodiversity measures of H_{PFT} and E_{PFT}, the other dominant species *S. grandis* was significantly negatively correlated ($P < 0.01$) with N_{SP}, E_{SP} and H_{SP}, whereas non-dominant species including *A. sibiricum*, *A. cristatum* and *A. tenuissimum* were significantly positively correlated ($P < 0.01$) with E_{SP} and H_{SP}. With respect to 21 species pairs constructed from the seven species, a significant positive correlation ($P < 0.01$) was found only for one pair (the dominant species *L. chinensis* versus the non-dominant species *K. cristata*), while a negative correlation ($P < 0.01$) was found for six pairs (e.g., *L. chinensis* versus *S. grandis*, *L. chinensis* versus *C. squarrosa*, *L. chinensis* versus *K. cristata*, *S. grandis* versus *A. cristatum*, *A. sibiricum* versus *C. squarrosa*, and *C. squarrosa* versus *K. cristata*). The dominant species, *L. chinensis* and *S. grandis*, were significantly negatively correlated ($P < 0.01$) (Table 2.4).

For the aboveground biomass of plant functional types, the three plant functional types of perennial rhizome, perennial bunchgrasses and perennial forbs were significantly correlated ($P < 0.01$) with H_{PFT} and E_{PFT}, either positively or negatively. A significantly positive correlation ($P < 0.01$) existed between the perennial rhizome functional type and the perennial forbs functional type, and a significantly negative correlation ($P < 0.01$) was found between the perennial bunchgrasses functional type and the perennial forbs functional type. Two dominant plant functional types, the perennial rhizome and the perennial bunchgrasses, were significantly negatively correlated ($P < 0.01$) (Table 2.4).

The aboveground biomass at the community level (AGB) was significantly positively correlated ($P < 0.01$) with the individual species of *L. chinensis*, *S. grandis*, *A. sibiricum*, *K. cristata* and *A. tenuissimum*, and the plant functional types of perennial rhizome, perennial bunchgrasses, and perennial forbs. No statistically significant correlations were found between AGB and N_{SP}, but AGB was significantly positively correlated ($P < 0.01$) with both H_{PFT} and E_{PFT}, and inversely, was significantly negatively correlated ($P < 0.01$) with both H_{SP} and E_{SP} (Table 2.4).

4 Discussion

4.1 Spatial structures of soil nutrients, plant diversity, and aboveground biomass

Geostatistical analysis has been increasingly used to examine spatial variability in abiotic and biotic variables in ecosystems (Cheng et al. 2007, Wang et al. 2007, Zhou et al. 2008, Zuo et al. 2009, Xin et al. 2002, Zawadzki et al. 2005a, Zawadzki et al. 2005b, De Jager and Pastor 2009). In this study, we quantified the spatial patterns of soil nutrients, species richness, species and plant functional type diversity and evenness indices, and the aboveground biomass at the levels of species, plant functional type and the whole community in the Inner Mongolia grassland, China. We found that TC, TN and TP displayed spatial autocorrelation over a range of 102 m or less (Table 2.2). Most studies have demonstrated that the magnitude of spatial autocorrelation varied depending on the system studied. For example, Don (2007) reported that soil organic carbon (SOC) was spatially autocorrelated within a range of 47 m to 131 m in grasslands in Germany, whereas the range of SOC autocorrelation was detected at 3,070 m in a forest ecosystem in North America (Wang et al. 2002). Compared to sill, nugget effect values in our study were relatively small for all the studied soil variables (Table 2.2). Meanwhile, ranges were much longer than the sampling interval of 7 m. Therefore, the current sampling design for soil variables adequately revealed spatial distribution features.

While many studies have quantified the spatial patterns of soil variables (Augustine and Frank 2001, Don 2007, Wang et al. 2007), much less attention has been paid to exploring the spatial patterns of biodiversity measures and aboveground biomass. Biodiversity measures exhibited spatial autocorrelation over ranges of 120 m or less, and most species and plant functional types displayed spatial autocorrelation over ranges of less than 130 m, while the pattern of spatial autocorrelation for several non-dominant species (e.g., *A. sibiricum*, *A. cristatum*, and *A. tenuissimum*) were poorly described by any of the models used in our study, based on the values of RSS and r^2 (Table 2.3). Because different species can respond to environment factors at different scales, these scales may be indicative of the dispersal ranges of the plants under study (Holland et al. 2004). The combined effects of abiotic and biotic processes are expected to regulate the spatial distribution of individual species and plant functional types, and in turn, biodiversity measures.

Compared to Zhou et al. (2008), who conducted their study in an area not far from our site, the values of the semivariogram parameters, such as range, nugget, sill and spatial heterogeneity percentage, were quite different from our study. For example, Zhou et al. (2008) reported that the values of the range varied from 2 m to 31 m for plant functional types (the classification among plant functional types was the same as our study), whereas in our study the values of the range for the plant functional types ranged from 9.30 m to 42.70 m (Table 2.3). This may be explained by differences in sampling intervals selected by these two experiments. In Zhou et al. (2008), variables were sampled at an interval of 1 m within an area of 10 m X 10 m, whereas in this study variables were sampled at 7 m within an area of 173 m X 345 m. These discrepancies may be explained by the fact that range values in semivariograms may depend on the measurement interval as well as the spatial extent of the study area (Meisel and Turner 1998, Oline and Grant 2002, He et al. 2007). Large intervals often filter out spatial variation occurring at scales smaller than the size of sampling units, thus increasing the proportion of the spatially structured component of a larger scale.

The semivariogram calculated from large sampling intervals does not contain any information about spatial structure at the level below the size of the actual sampling interval.

Spatial patterns of biotic variables are believed to reflect spatial heterogeneity in abiotic variables (Robertson et al. 1997). This observation is particularly true for plant species diversity and aboveground biomass. It is also important to note that relationships between environmental factors, such as soil nutrients and ecological processes, change with scale, which requires multi-scale field observations and experiments. Indeed, most ecological patterns and processes are scale-dependent (Levin 1992, Wu and Loucks 1995). Therefore, identifying specific spatial scales at which an ecological variable responds most strongly to spatial patterns is needed. These specific, or characteristic, scales of response may differ among variables (Wu et al. 2006). Geostatistical methods, semivariance analysis in particular, have long been known for their ability to detect characteristic scales (Wu 2004). In our study, different variables demonstrated varying scales of patchiness, which supports the idea that, to explore the relationships among soil nutrients, plant diversity and the aboveground biomass at the levels of individual species, plant functional type and the whole community, studies should be conducted at multiple scales based on the range values derived from the semivariogram.

Although fit by different functions, semivariograms generally exhibited a similar shape with increasing semivariance at small lags and leveling off at longer distances, beyond which no autocorrelation is present, so that samples were assumed independent. Our goal was not to analyze spatial autocorrelation in detail, but to detect commonalities among abiotic and biotic variables.

Two patterns emerge from our analysis. First, autocorrelation patterns change with scale similarly for groups of soil nutrients, biodiversity measures (except H_{SP}), and the aboveground biomass at the level of plant functional type (except for perennial forbs). We found that semivariogram ranges for each group are strikingly similar (Table 2.2 and 2.3). Second, our results showed that spherical and exponential models provided the best fit to empirical semivariograms of most variables with exponential models being the dominant form. The main difference between the two models is that in the exponential model semivariance values increased slowly to approach the sill, while in the spherical model they rose much quicker, which indicates that a variable best fit by spherical model will have greater variability than a variable best fit by exponential model within the average patch size represented by range values, given that the semivariograms of the two models reach the sill at the same level.

4.2 Correlations among soil nutrients, plant biodiversity, and aboveground biomass

We found that correlations between soil variables in our study were significantly positive (Table 2.4), and their spatial patterns were very similar to each other throughout the entire study site (Fig. 2.5 A-C). This result is consistent with previous studies conducted both in Inner Mongolia grasslands and in other places worldwide (Zhang et al. 2007, Okin et al. 2008). Species richness was significantly positively correlated with aboveground biomass of *L. chinensis*, but negatively with that of *S. grandis* (Table 2.4), which is consistent with the findings that species richness was higher in *L. chinensis*-dominant grassland than in *S. grandis*-dominant grassland through a 24-year observation study in Inner Mongolia grassland (Bai et al. 2004). *L. chinensis*, a eurytopic mesophtyic rhizome grass, is widely distributed in habitats with fertile and water-rich soils, whereas *S. grandis*, a xerophyte bunchgrass, grows in habitats with infertile and well-drained soils. Our findings suggest the existence of *S. grandis* may need occupy more niches to obtain nutrients for maintaining its growth, which potentially reduce the possibility of coexistence of other species, and eventually lead to the reduction of species diversity, while the habitats for the development of *L. chinensis* may attract other species to colonize readily because of excellent soil condition (Inner Mongolia-Ningxia Integrative Expert Team of the Chinese Academy of Science, 1985).

The compensatory effect hypothesis proposes that compensatory mechanisms occur in an ecosystem when biomass production between some of its major components, such as species or PFTs, exhibits negative correlations with each other (McNaughton 1977, Tilman and Downing 1994, Naeem and Li 1997, Tilman 1999). The correlation analysis revealed that some species and PFTs were negatively correlated, indicating that compensatory mechanisms could likely operate at both levels, especially among dominant components, such as species and PFTs with high relative biomass. The dominant species pair in our study was *L. chinensis* (22.73% of AGB, when averaged over 736 sampled plots) and *S. grandis* (37.16% of AGB when averaged over 733 sampled plots). The dominant PFTs pair consisted of perennial rhizome (22.73% of AGB averaged over 736 sampled plots) and perennial bunchgrasses (66.44% of AGB averaged over 736 sampled plots). Both the species pair and the PFT pair exhibited a negative correlation which indicates the possibility of compensatory mechanisms. Aboveground biomass of most other species pairs (14 out of 21 pairs) did not show any significant correlations at the $P = 0.01$ level. This is likely the result of statistical averaging effects at the species level. These results generally agree with the findings of Bai et al. (2004) and provide additional evidence for compensatory effects resulted from interactions between dominant plant species in this community.

In previous studies that were conducted in artificially assembled plant communities, a positive correlation between species richness and aboveground biomass were found (Tilman et al. 2001, Hooper et al. 2005, Roscher et al. 2005, Spehn et al. 2005). However, this positive correlation was not corroborated by our study in natural grassland communities of Inner Mongolia (Table 2.4). We found that there was no correlation between species richness and aboveground biomass.

Several reasons are suspected to play a role in this inconsistency. It may be partly explained by differences in sample intervals, since it is increasingly recognized that spatial scale is an important component to consider empirically when investigating the relationship between biodiversity and ecosystem functioning (Mittelbach et al. 2001, Bond and Chase 2002, Chase and Leibold 2002). A hump-shaped relationship between productivity and species richness is the most common at scales below the continental or global scale (Rosenzweig 1995, Waide et al. 1999, Gaston 2000), which means a peak in diversity at the intermediate productivity levels. Rather than a hump-shaped relationship, species richness was found to increase linearly with productivity across local, landscape and regional scales in the Eurasian steppe (Bai et al. 2007). Our experiment was performed in an area of 173 m X 345 m with species richness varying from 4 m^{-2} to 13 m^{-2} in a *L. chinensis*-dominant community. So it may well be that no statistical relationship between species richness and community-level aboveground biomass could be detected at such a fine-scale experimental design.

In our study, we also found that aboveground biomass was significantly negatively correlated with species diversity and species evenness indices, but significantly positively correlated with plant functional type diversity and plant functional type evenness indices (Table 2.4). This suggests that at the plot scale (6 m x 6 m) in our study, functional diversity may be more important for promoting ecosystem functioning (e.g., aboveground biomass) than taxonomic diversity (Naeem and Wright 2003). On broader scales, however, both kinds of plant diversity become important to ecosystem functioning, as shown by numerous studies (Colwell and Coddington 1995, Hooper et al. 2002). Future research, therefore, should consider a multi-scale design and develop a proper scaling approach that would allow for accurate examination of changes in biodiversity and plant production relationship in the *L. chinensis*-dominant community. For example, we can subjectively set four sample size levels at n=50, 100, 200 and 300 by sampling 50, 100, 200 and 300 plots randomly and repeatedly from our sample pool of n = 768. Thus, we can examine the influence of biodiversity on plant production.

Table 2.4 Correlation coefficient matrix of soil nutrients, biodiversity measures, and aboveground biomass at the levels of individual species, PFTs, and the whole community in the study site of the Inner Mongolia grassland of China in 2005

	TC	TN	TP	N_{SP}	H_{SP}	E_{SP}	H_{PFT}	E_{PFT}	LC	SG	AS	CS	KC	AC	AT	PR	PB	PF	AGB
TC	1.000																		
TN	0.835**	1.000																	
TP	0.703**	0.647**	1.000																
N_{SP}	-0.038	-0.070	-0.129	1.000															
H_{SP}	-0.005	-0.041	-0.068	0.512**	1.000														
E_{SP}	0.026	0.000	0.008	-0.052	0.791**	1.000													
H_{PFT}	0.362**	0.383*	0.210	0.125	0.322**	0.282**	1.000												
E_{PFT}	0.362**	0.383*	0.210	0.125	0.322**	0.282**	1.000**	1.000											
LC	0.318**	0.330**	0.149	0.116	-0.050	-0.107	0.630**	0.630**	1.000										
SG	-0.026	0.058	0.061	-0.272**	-0.536**	-0.435**	-0.255*	-0.255*	-0.242**	1.000									
AS	0.142	0.114	-0.009	0.024	0.251**	0.260**	0.154*	0.154*	0.140*	-0.045	1.000								
CS	-0.223*	-0.254*	-0.155	-0.102	-0.061	0.006	-0.617**	-0.617**	-0.455**	0.041	-0.202**	1.000							
KC	0.264**	0.271*	0.179	-0.054	0.036	0.083	0.675**	0.675**	0.406**	-0.019	0.133*	-0.421**	1.000						
AC	-0.215	-0.291	-0.147	0.124*	0.275**	0.206**	-0.202*	-0.202*	-0.116	-0.331**	-0.077	0.106	-0.214**	1.000					
AT	0.049	0.096	0.005	0.049	0.195**	0.192**	0.075	0.075	-0.017	0.065	0.049	0.068	-0.043	-0.029	1.000				

PR	0.318**	0.330**	0.149	0.116	-0.050	-0.107	0.630**	0.630**	1.000**	-0.242**	0.140*	-0.455**	0.406**	-0.116	-0.017	1.000			
PB	-0.185	-0.159	-0.100	-0.088	-0.223**	-0.204**	-0.574**	-0.574**	-0.428**	0.710**	0.094	0.562**	-0.300**	0.143*	0.126**	-0.428**	1.000		
PF	0.257**	0.265*	0.160	0.010	0.093	0.105	0.701**	0.701**	0.401**	-0.009	0.151*	-0.416**	0.985**	-0.203**	0.093*	0.401**	-0.277**	1.000	
AGB	0.187	0.218*	0.090	0.000	-0.227**	-0.247**	0.269**	0.269**	0.557**	0.372**	0.234**	-0.040	0.426**	-0.047	0.109**	0.558**	0.362**	0.445**	1.000

*Correlation is significant at the 0.05 level (2-tailed); **Correlation is significant at the 0.01 level (2-tailed)

LC-*L. chinensis*; SG-*S. grandis*; AS-*A. sibiricum*, CS-*C. squarrosa*, *KC-K. cristata*, AC-*A. cristatum* and AT-*A. tenuissimum*

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

CHAPTER 3

EFFECTS OF BIODIVERSITY REMOVAL ON THE SPATIAL PATTERN OF PLANT AND SOIL VARIABLES AND THEIR RELATIONSHIPS

1 Introduction

Anthropogenic activities are accelerating the rate of species extinctions in many of earth's ecosystems (Wilson 1988), raising the issue of how species loss alters community-level and ecosystem-level attributes and processes (Schulze and Mooney 1993, Hooper et al. 2005). These alterations can be highly variable over time and space, because of the complexity and variability of ecosystem variables such as aboveground biomass and soil nutrients (Li and Reynolds 1995). For instance, N, the most limiting nutrient in ecosystems, plays an important role in limiting ecosystem productivity (Seastedt et al. 1991, Bai et al. 2010), and influencing biogeochemical cycles of other elements dominantly through the process of litter decomposition (Knorr et al. 2005). Soil is the most direct N pool for plants and microbes in terrestrial ecosystems. The heterogeneity of soil resources inevitably affects local N pools, and influences the spatial distribution of vegetation (Wang et al. 2002, Feng et al. 2008), thus contributing greatly to the relationship between biodiversity and ecosystem functioning (BEF) (Hooper 1998, Cardinale et al. 2004).

Plant removal experiments have emerged as a powerful tool to understand how non-random losses of targeted species or plant functional types 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, and creates root gaps and nutrient release zones (Silver and Vogt 1993, Schroeer et al. 1999). Species removal can also increase patchiness in the litter layer and soil, thereby increasing spatial variability in soil moisture and temperature (Guo et al. 2002). Regenerated vegetation patches formed after removal treatments could interact with soil nutrient distributions altered by vegetation losses. Such interactions may lead to a dynamic process in which the spatial structure of re-vegetation is both an independent and dependent variable which affects, and is a product of, soil nutrient heterogeneity (Keitt et al. 2002).

The process of plant removal treatments, for experimental purposes, potentially alters spatial heterogeneity of both vegetation and soil nutrients. However, little quantitative information exists on spatial patterns of soil nutrients, plant diversity and remaining aboveground biomass after the removal of vegetation. Here, we compare spatial patterns of soil nutrients (e.g. total carbon (TC) and total nitrogen (TN)), biodiversity measures, and aboveground biomass before and after plant removal treatment, in an existing BEF field experiment in an Inner Mongolia grassland, China. Specifically, our intention was to test two hypotheses: 1) Removal of plant functional types results in distinct changes of spatial patterns of variables relevant to biodiversity and ecosystem functioning; and 2) Spatial correlations among soil nutrients, plant diversity and aboveground biomass will change due to different plant removal treatments. To test the two hypotheses, we used two data sets, one was collected in 2005 when the removal experiment was initiated for background information investigation (including soil nutrients, biodiversity measures at the levels of plant functional type and aboveground biomass at the levels of plant functional type and the whole community); the other was acquired in 2008 after removal treatments began in 2006 and included the corresponding variables collected in 2005.

2 Methods and materials

2.1 Study area

The study area has been described in Chapter 2.

2.2 Experimental design

The Inner Mongolia Grassland Removal Experiment (IMGRE) was initiated in 2005 and provided initial background information for investigation. Removal treatments were conducted annually from 2006 until 2009. The experiment site is composed of 8 blocks, each with 96 plots measuring 6 m x 6 m which were subdivided into 3 portions (3 x 32 plots). We did removal treatment in two of the three portions of plots, one with complete removal (n = 512), and the other with partial removal (n = 512), leaving the third portion untouched for future investigation.

According to the plant life forms found in the study area, we categorized all plant species into five plant functional types: perennial bunchgrasses (PB), perennial rhizome grasses (PR), perennial forbs (PF), annuals/biennials (AB), and shrubs and semi-shrubs (SS) (Bai et al. 2004). We established a biodiversity gradient by removing 0 to 5 functional types, producing a total of 32 different combinations of removal treatments. In the two selected portions of plots, treatments were assigned on a random basis. However, during the experiment we could not find SS existing in the research area. Thus, there were only 16 different treatments, each implemented in two plots of each block (Table 3.1).

2.3 Biodiversity removal

We conducted the plant removal by pulling species out using two parallel protocols: complete and partial removal. The complete removal protocol removed all targeted plant species within a particular functional type, whereas the partial removal protocol removed the targeted functional types until approximately 50% of the total plant cover in each treatment plot was left. The purpose here was to keep the physical disturbance in each treatment plot at the same level. We conducted the partial removal scheme based on the following rules. If the total cover of the targeted functional types was less than 50% of the vegetation cover of the entire plot, all targeted functional types were removed, and the remaining plants continued to be removed randomly until about 50% of the total vegetation cover was removed. If the total cover of targeted functional types was larger than 50%, then the rare targeted functional type(s) (annuals and biennals, and/or perennial forbs) were removed first, and the dominant functional type(s) (perennial forbs and/or perennial bunchgrasses) were then removed until the 50% vegetation cover requirement was met. The different removal treatments were listed in Table 3.1.

To make sure that the removal treatment completely stopped the growth of the targeted plants (or at least significantly reduced it), we started the removal treatment in early June of 2006, and then conducted follow-up removal in the following three years (2007-2009) when plants started to grow in late May or early June. Timing of plant sampling coincided with the peak biomass. All samples were oven-dried to a constant mass at 65 °C for a minimum of 48 h. Biomass was determined by plant functional types for our further data analysis.

2.4 Soil sampling and measurements

Soil samples were collected in evenly distributed plots across the 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. Total carbon (TC) was analyzed following a modified Meius method, total nitrogen (TN) - by the Kjeladahl digestion procedure.

All the sampling and measurements for vegetation and soil properties were done by the IMGRE research team, including a large number of faculty and graduate students from the Institute of Botany of the Chinese Academy of

Sciences and School of Life Sciences, Arizona State University. To alleviate the effects of the removal treatments on soil nutrient contents, we did not take soil samples in 2006 and 2007, only in 2008. So to test our hypotheses, we compared the data collected in 2005 and 2008.

Table 3.1 Full combinatorial design of the removal experiment

Treatments	Number of plant functional types removed	PR	PB	PF	AB	Replicates
1	0 (no removal)					32
2	1	x				32
3	1		x			32
4	1			x		32
5	1				x	32
6	2	x	x			32
7	2	x		x		32
8	2	x			x	32
9	2		x	x		32
10	2		x		x	32
11	2			x	x	32
12	3	x	x	x		32
13	3	x	x		x	32
14	3		x	x	x	32
15	3	x		x	x	32
16	4	x	x	x	x	32
Total number of removal treatment plots						512

PR-perennial rhizome, PB-perennial bunchgrasses, PF-perennial forbs, AB-annuals and biennials.

2.5 Data analysis

We used both traditional statistics and geostatistics to analyze the spatial characteristics of the measured variables. Traditional statistics, such as mean, standard deviation, and coefficient of variation (CV), were used to examine the degree of overall variation.

Semivariograms were used to quantify the spatial structure of the variables of interest. In a spatial data set, points located closer to each other usually have values more similar than points far apart. As a result, semivariance will increase with distance, until the dissimilarity among data points is no longer distance-dependent. The relationship between semivariance and distance can be fitted with regression models (e.g., spherical, exponential, Gaussian and linear). The fitted curve is called a semivariogram, and several parameters can be derived. The plateau of a semivariogram curve is called sill, the distance from zero to where the sill occurs is called range, the semivariance at zero distance is called nugget. Nuggets are often greater than zero because of sampling error or the lack of observations at very small distances. If a semivariogram does not show autocorrelation (i.e., sill is equal to nugget), it is defined as a nugget effect (Isaaks and Srivastava 1989). In this study, we used spatial heterogeneity percentage (which is defined as 100 (sill−nugget)/sill) to indicate the degree of spatially structured variability (Rossi et al. 1992, Robertson and Gross 1994, Li and Reynolds 1995).

Correlograms generated from Moran's *I* index against lag distances were also used in our study for the purpose of comparison. Moran's *I*, a global measure of spatial autocorrelation, was also used to identify the degree of spatial autocorrelation on variables over distances in our study (Moran 1948). Semivariance and Moran's *I* are complementary for evaluating the spatial structure of data, both of which will be constructed using the GS+ package, version 7.0 (Gamma Design Software 1999, Plainwell, MI, USA). In our study, the minimum lag distance was 7 m, which corresponds to the minimal distance between two adjacent 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).

Correlation comparisons among variables in soil nutrients, biodiversity measures and aboveground biomass collected in 2005 and 2008 were analyzed by the modified t-test. 82 plots were sampled for variables in TC and TN in both 2005 and 2008, 490 plots for variables in biodiversity measures and aboveground biomass. The independence of samples could not be guaranteed at such a fine scale, so the modified t-test correlation 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 aboveground biomass, 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 (SAS Institute Inc. 2008).

3. Results

3.1 Descriptive summary of BEF variables in 2005 and in 2008

From 2005 to 2008, TC decreased by 57.57%, from 45.91 ± 1.09 $g \cdot kg^{-1}$ averaged over a total of 79 sampled plots to 19.76 ± 0.38 $g \cdot kg^{-1}$over a total of the same 79 sampled plots (Table 3.2). TN did not vary very much from 2005 to 2008, which decreased only by 14.34% (Table 3.2). Coefficients of variations (CVs) of H_{PFT} and E_{PFT} increased significantly by 161.80% and 141.48% from 2005 to 2008, respectively (Table 3.2). Aboveground biomass at the levels of PFT and the whole community also varied dramatically, especially for the annuals and biennials functional type. In 2005 we did not conduct statistics for the annual and biennials functional type due to small sample size, whereas in 2008 annuals and biennials showed up greatly, and the mean value of aboveground biomass of this functional type was 1.74 ± 2.43 $g \cdot m^{-2}$ (Table 3.2). Large differences for the aboveground biomass between 2005 and 2008 were also found in CVs, ranging from 25.97% for AGB to 78.87% for perennial forbs in 2005 versus ranging from 43.69% for AGB to 3097.13% for annuals and biennials in 2008 (Table 3.2).

3.2 Comparison of spatial patterns of soil nutrients, plant diversity and aboveground biomass between 2005 and 2008

3.2.1 Soil nutrients

We used spatial autocorrelation analysis to quantify spatial autocorrelation among sample points within the field. For TC and TN contents examined in 2005, the resulting semivariograms demonstrated moderate spatial autocorrelation among sample locations (Table 3.3). The degree of autocorrelation was the strongest for locations within 77 m of one another for TC, and within 102 m for TN (Table 3.3, Fig. 3.1 A1 and B1). The values of spatial heterogeneity percentage were high at 60% and 73% for TC and TN in 2005, suggesting that much of population variance was a function of spatial autocorrelation (Table 3.3). The remaining variance was due either to experimental error or to autocorrelation at the lag distance below 7 m. TC and TN were positively autocorrelated within 60 m, and then showed negative autocorrelation at greater lag distances (Fig. 3.2 A1 and B1).

Spherical model also provided the best fit for TC and TN in 2008 (Table 3.3). Range values were 13 m and 75 m for TC and TN in 2008 (Table 3.3). TC sampled in 2008 showed a higher spatial autocorrelation represented by the value of spatial heterogeneity percentage at 97% (Table 3.3), in contrast to the value of 60% in 2005. The semivariogram for TN in 2008 (Fig. 3.1 B2) exhibited a higher nugget effect compared to TN in 2005 (Fig. 3.1 B1), indicating the variance among points close to one another was no different than variance among points farther apart. Correlograms showed that TC demonstrated a periodic autocorrelation with a positive correlation within 60 m, and a negative correlation at the lag distance between 60 m and 70 m, then repeated this trend with the increasing lag distances (Fig. 3.2 A2 and B2).

3.2.2 Plant diversity

In 2005, the “best-fit” model was exponential model for both H_{PFT} and E_{PFT} (Table 3.3, Fig. 3.3 A1, B1). The ranges were 26.60 m and 28.20 m for H_{PFT} and E_{PFT}, respectively (Table 3.3). The values of spatial heterogeneity percentage showed that both H_{PFT} and E_{PFT} exhibited a moderate spatial structure (< 75%). Correlograms showed that these measures were positively autocorrelated within 75 m, and then showed negative autocorrelations and randomness at greater lag distances (Fig. 3.4 A1, B1).

The plant removal treatment had a significant effect on the spatial structure of biodiversity measures at the level of plant functional type in 2008 (Table 3.3, Fig. 3.3 A2, B2). Exponential model provided the best fit to semivariograms for H_{PFT} and E_{PFT} (Table 3.3). The ranges were 14.20 m and 4.90 m for H_{PFT} and E_{PFT}, respectively (Table 3.3). Both of these two variables exhibited stronger spatial structure in 2008 with the values of spatial heterogeneity percentage at 91% of population variances, compared to the values at 67-70% derived in 2005 (Table 3.3). From the correlograms constructed for biodiversity measures (Fig. 3.4 A2, B2), the pattern for H_{PFT} in 2008 was highly similar to the one for E_{PFT} in 2008 as both of them were positively autocorrelated within the lag distance of 70 m, and negatively autocorrelated at the distance between 70 m and 100 m.

Table 3.2 Summary statistics of variables of soil nutrients, plant diversity and aboveground biomass in 2005 and 2008

	2005							2008						
Variable	Maximum	Minimum	Mean	StDev	Standard error	CV*(%)	Number of samples	Maximum	Minimum	Mean	StDev	Standard error	CV*(%)	Number of samples
TC (g×kg^{-1})	67.93	23.43	45.91	9.91	1.09	21.59	79	31.18	11.08	19.76	3.39	0.38	17.16	79
TN (g×kg^{-1})	6.51	2.33	4.60	0.97	0.11	21.09	79	5.04	2.82	3.94	0.43	0.05	10.91	79
H$_{PFT}$	1.10	0.12	0.77	0.18	0.01	23.38	490	1.31	0	0.54	0.33	0.01	61.11	490
E$_{PFT}$	1.00	0.11	0.69	0.16	0.01	23.19	490	1.00	0	0.50	0.28	0.01	56.00	490
PR (g×m^{-2})	143.44	0.30	26.81	15.17	0.69	56.58	490	224.51	0	22.59	47.82	2.16	211.69	490
PB (g×m^{-2})	143.20	1.49	69.77	22.93	1.04	32.87	490	300.43	0	62.26	58.02	2.62	93.19	490
PF (g×m^{-2})	59.22	0.11	12.26	9.67	0.44	78.87	490	72.76	0	2.18	8.00	0.36	366.97	490
AB (g×m^{-2})	-	-	-	-	-	-	-	434.56	0	1.74	53.89	2.43	3097.13	490
AGB (g×m^{-2})	374.58	4.73	109.30	28.38	1.28	25.97	490	438.63	0.32	132.53	57.90	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.

Table 3.3 Semivariogram parameters for soil variables, biodiversity measures and aboveground biomass in the study site of Inner Mongolia grassland of China in 2005 and 2008

Year	Variable	Model	Range (m)	Nugget	Sill	RSS	r^2	$C/(C_0+C)$ (%)
2005	TC	Spherical	76.90	52.70	131.40	1886.00	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	2226.00	130534	0.005	90
	PB	Exponential	2.60	272.00	3292.00	965008	0.02	92
	PF	Linear	185.76	63.18	63.18	270.00	0.58	0
	AB	Exponential	1.90	399.00	2770.00	4914012	0	86
	AGB	Exponential	3.50	340.00	3553.00	1556343	0.05	90

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

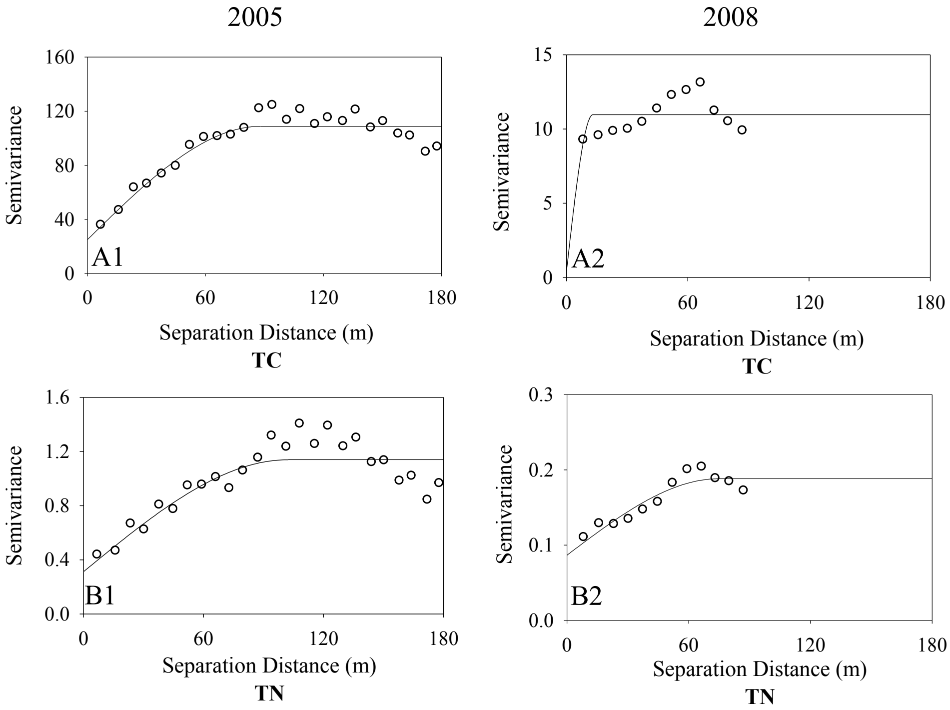

Fig. 3.1 Semivariograms of TC and TN in the study site of the Inner Mongolia grassland of China in 2005 (A1 and B1) and 2008 (A2 and B2)

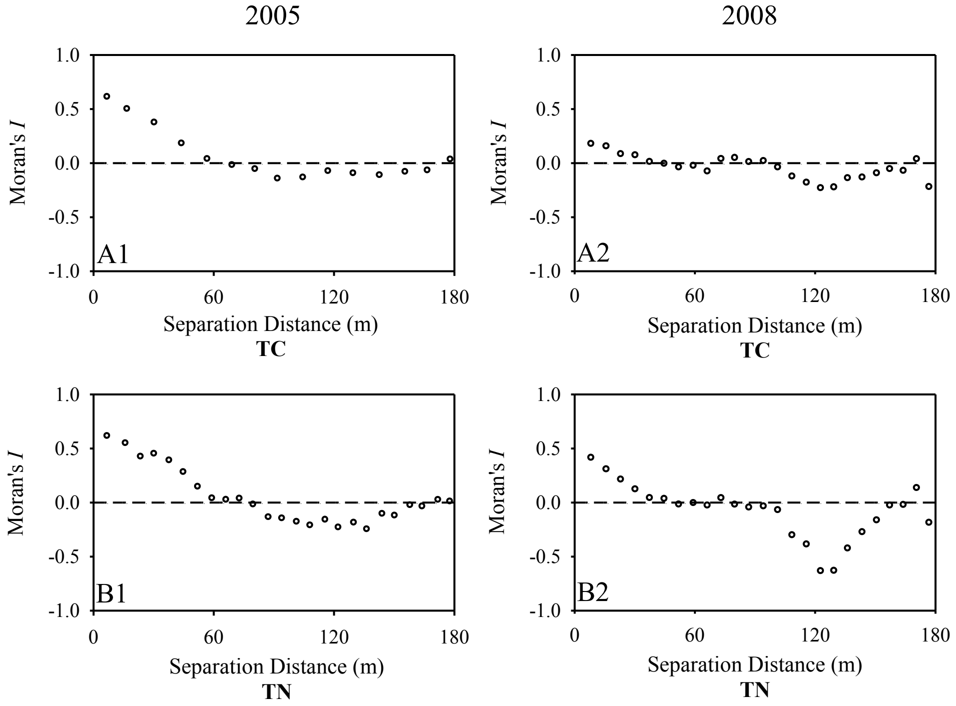

Fig. 3.2 Correlograms of TC and TN in the study site of the Inner Mongolia grassland of China in 2005 (A1 and B1) and 2008 (A2 and B2)

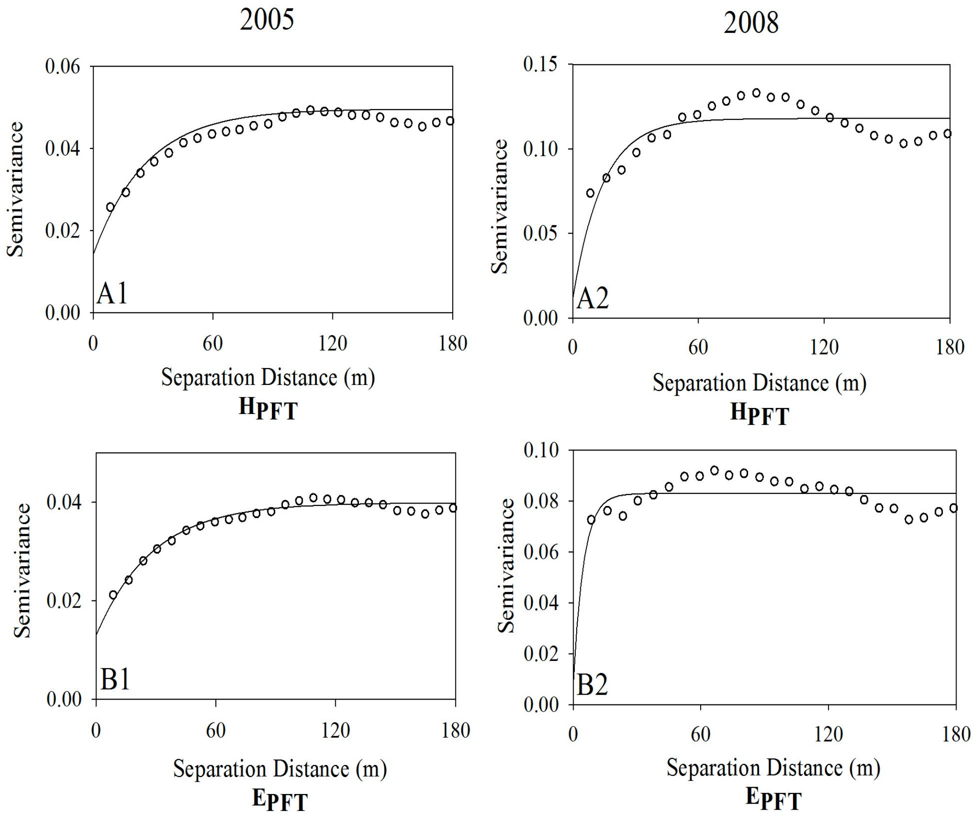

Fig. 3.3 Semivariograms of H_{PFT} and E_{PFT} in the study site of Inner Mongolia grassland of China in 2005 (A1 and B1) and 2008 (A2 and B2)

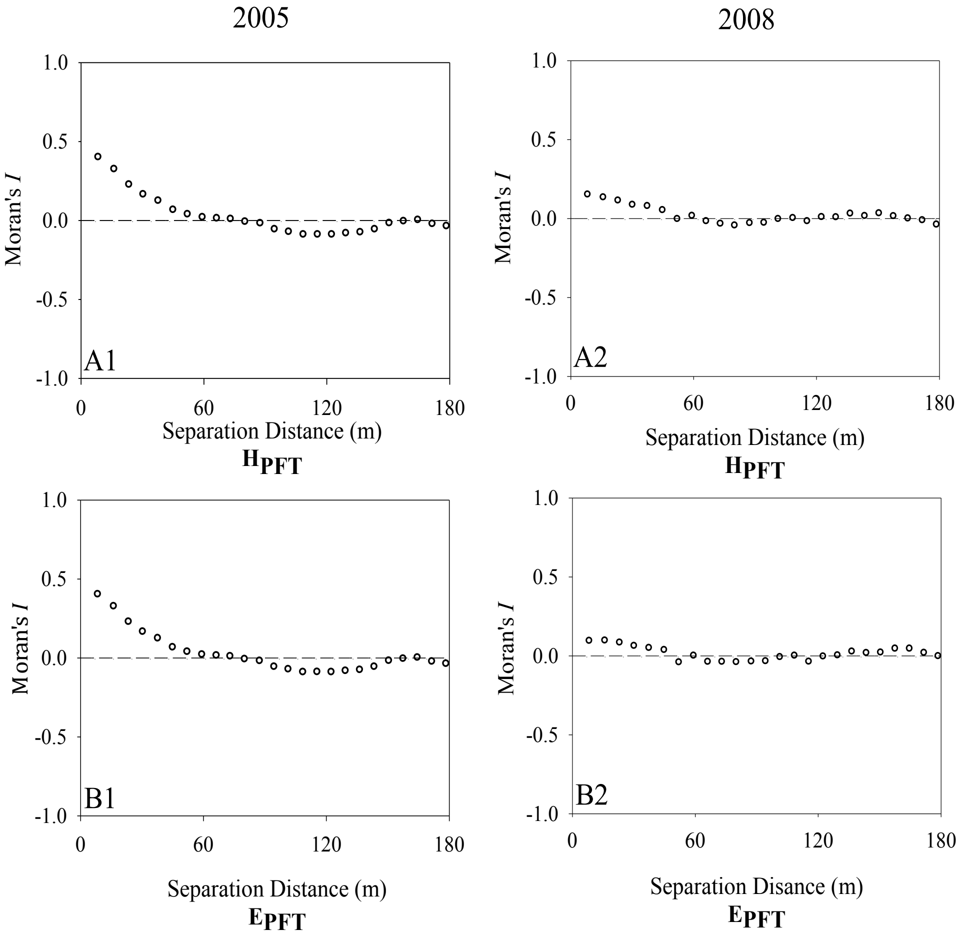

Fig. 3.4 Correlograms of H_{PFT} and E_{PFT} in the study site of Inner Mongolia grassland of China in 2005 (A1 and B1) and 2008 (A2 and B2)

3.2.3 Aboveground biomass

In 2005, exponential model was the best fit to the semivariograms for most aboveground biomass of PFTs (Table 3.3, Fig. 3.5). The PFT of annuals and biennials with only six samples was better fit by linear model with no range value detected (Table 3.3, Fig. 3.5 D1). Two dominant PFTs, perennial rhizome and perennial bunchgrasses, displayed ranges of spatial autocorrelation at 9.30 m and 7.80 m, respectively, whereas the non-dominant PFT, perennial forbs, had the range value of 42.70 m (Table 3.3). The values of spatial heterogeneity percentage were above 50% for perennial rhizome, perennial bunchgrasses and perennial forbs, indicating higher spatial structures in these plant functional types (Table 3.3). Correlograms showed that perennial rhizome and perennial bunchgrasses functional types were positively autocorrelated within 50 m, and then were randomly distributed with the increasing lag distances (Fig. 3.6 A1 and B1). The non-dominant PFT, perennial forbs, was positively autocorrelated within 80 m, and then negatively autocorrelated between 80 m and 150 m (Fig. 3.6 C1). Exponential model provided the best fit to semivariograms of AGB at the community level (Table 3.3). The range of AGB was 6.90 m and the value of spatial heterogeneity percentage was 86% at this level (Table 3.3).

In 2008, exponential model was the best fit to the semivariograms for most aboveground biomass of PFTs, with the exception of perennial forbs fit by linear model (Table 3.3). The range values for the variables in aboveground biomass sampled in 2008 decreased (except PF), ranging from 1.90 m for annuals and biennials to 185.76 for perennial forbs, in comparison to the range values of 6.90 m for AGB to 42.70 m for perennial forbs derived from variables of aboveground biomass sampled in 2005 (Table 3.3). In 2008, perennial forbs did not show any spatial structure with the value of spatial heterogeneity percentage at 0%, whereas annuals and biennials exhibited high spatial structure with the value of spatial heterogeneity percentage at 86% (Table 3.3, Fig. 3.5). The correlograms showed that there was random autocorrelation for each of the variables in aboveground biomass at the level of PFT after the removal treatment in 2008, which was quite different from the pattern showing that those variables in 2005 before removal treatment exhibited a positive autocorrelation within short distances apart (Fig. 3.6).

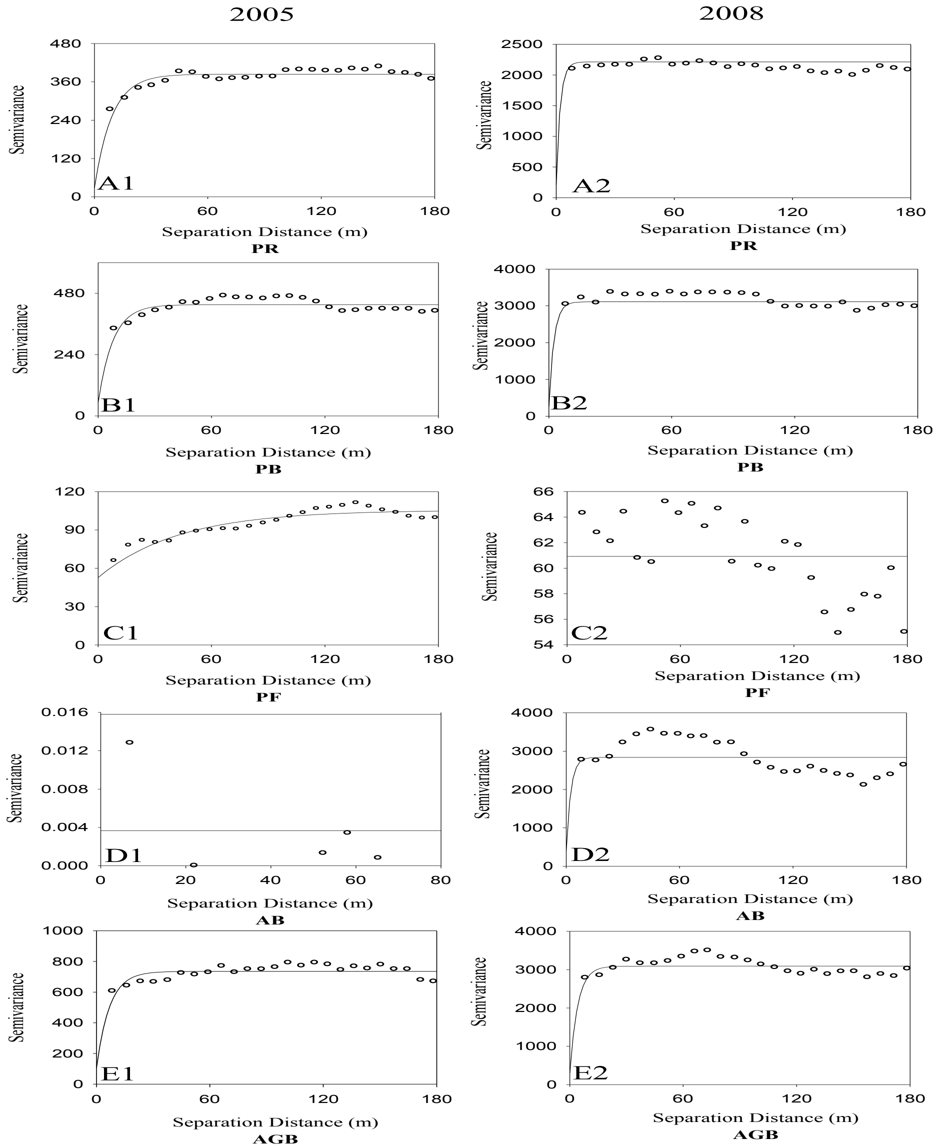

Fig. 3.5 Semivariograms of PR, PB, PF, AB and AGB in the study site of Inner Mongolia grassland of China in 2005 (A1 and E1) and 2008 (A2 and E2)

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

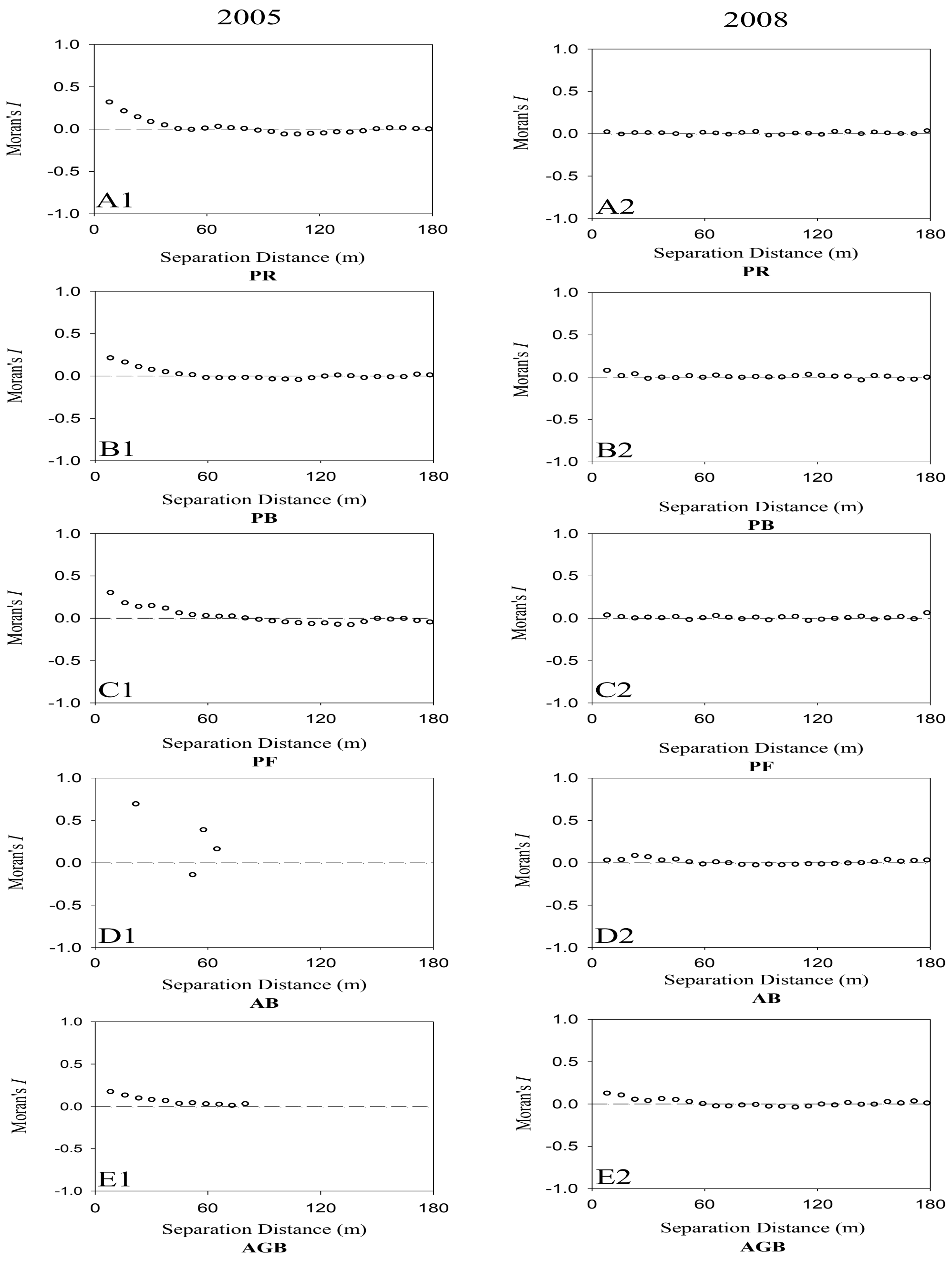

Fig. 3.6 Correlograms of PR, PB, PF, AB and AGB in the study site of Inner Mongolia grassland of China in 2005 (A1 and E1) and 2008 (A2 and E2)

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

3.3 Comparing relationships among soil nutrients, biodiversity measures, and aboveground biomass before and after biodiversity removal

Similar to the relationship between TC and TN found in 2005, the removal treatment did not affect the relationship between these two variables in 2008, with a significantly positive correlation ($r = 0.829$ and $P < 0.01$). Both TC and TN were significantly positively correlated ($0.314 < r < 0.339$; $P < 0.01$) with H_{PFT} and E_{PFT} in 2005, however, no correlations were found between variables in soil nutrients and biodiversity measures in 2008. TC was not correlated with variables of the aboveground biomass at the levels of PFT and the whole community in 2008, which was different from the findings that there had been a strongly positive correlation between TC and perennial rhizome ($r = 0.238$ and $P < 0.01$), and between TC and perennial forbs ($r = 0.222$ and $P < 0.05$) in 2005. For TN, there were no correlations with variables in biodiversity and aboveground biomass in 2008, whereas in 2005 we found that TN was significantly positively correlated to H_{PFT} ($r = 0.314$ and $P < 0.01$), E_{PFT} ($r = 0.314$ and $P < 0.01$), perennial rhizome ($r = 0.231$ and $P < 0.05$), and perennial forbs ($r = 0.188$ and $P < 0.05$). We did not find any correlations between soil nutrients and aboveground biomass at the community level either in 2005 or in 2008 (Table 3.4).

For variables of biodiversity measures, plant functional type diversity (H_{PFT}) was still strongly positively correlated with plant functional type evenness (E_{PFT}) in 2008 ($r = 0.892$ and $P < 0.01$), similar to the correlation between these two variables in 2005 ($r = 1$ and $P < 0.01$). In 2008, H_{PFT} had no correlations with perennial bunchgrasses (r = 0) and AGB (r =-0.012).

Among variables of aboveground biomass at the level of PFT sampled in 2008, we found that strongly negative correlations existed between perennial rhizome and perennial bunchgrasses (r = -0.434 and $P < 0.01$), between perennial rhizome and annuals and biennials (r = -0.182 and $P < 0.01$), between perennial bunchgrasses and perennial forbs (r = -0.154 and $P < 0.01$), and between perennial bunchgrasses and annuals and biennials (r = -0.285 and $P < 0.01$). The phenomenon that no significant correlations were found between perennial rhizome and perennial forbs, and between perennial forbs and AGB in 2008 did not occur in 2005, and significantly positive correlations between perennial rhizome and perennial forbs and between perennial forbs and AGB were detected in 2005 (r = 0.393 and $P < 0.01$, and r = 0.415 and $P < 0.01$, respectively). Among the four functional types, significantly positive correlations were found between perennial rhizome and AGB (r = 0.230 and $P < 0.01$), and between perennial bunchgrasses and AGB (r = 0.329 and $P < 0.01$) in 2008, whereas perennial rhizome, perennial bunchgrasses and perennial forbs all were significantly positively correlated with AGB in 2005 (Table 3.4).

Based on Table 3.4, we found that the relationships between H_{PFT} and AGB, between H_{PFT} and perennial bunchgrasses, between perennial forbs and AGB, and between perennial rhizome and perennial forbs have changed significantly from 2005 to 2008. So, we did Pearson's analysis to investigate the change of the relationship for the above variable pairs under different treatments.

Under the complete removals of perennial rhizome and perennial rhizome + perennial bunchgrasses, and the partial removals of perennial bunchgrasses + perennial forbs + annuals and biennials, the correlation between H_{PFT} and AGB changed significantly in 2008, in comparison to those in 2005. For H_{PFT} and perennial bunchgrasses, the complete removal of perennial forbs made the change from the significantly negative correlation ($r = -0.291$, $P < 0.01$ and $n = 16$) to no correlation, and the complete removals of annuals and biennials, perennial rhizome + annuals and biennials changed the relationship from no correlation in 2005 to significantly negative correlation in 2008.

Because of the complete removal with PB, PR+PB, PB+PR, PB+AB, PR+PB+PF, PR+PB+AB, PB+PF+AB, and PR+PB+PF+AB, there was no relationship between H_{PFT} and perennial rhizome in 2008. Several partial removals also made the change of the relationship between H_{PFT} and perennial bunchgrasses. The partial removals of perennial bunchgrasses, perennial forbs and perennial rhizome + perennial bunchgrasses made the change from the negative correlation in 2005 ($-0.783 < r < -0.692$) to no correlation in 2008 (Table 3.5).

With the complete removal of perennial rhizome + annuals and biennials, the correlation of H_{PFT} and perennial bunchgrasses presented significantly negative ($r = -0.862$ and $P < 0.01$) in 2008, compared to no correlation in 2005. In 2008, the correlation of H_{PFT} and perennial bunchgrasses was nonexistent with the partial removals of perennial bunchgrasses, perennial forbs and perennial rhizome + perennial bunchgrasses, compared to the negative correlation occurring in 2005. The partial removal of perennial rhizome + perennial bunchgrasses + annuals and biennials changed the relationship between H_{PFT} and perennial bunchgrasses from significantly positive in 2005 to significantly negative in 2008, and the partial removal of perennial bunchgrasses + perennial forbs + annuals and biennials inversely changed the relationship, from significantly negative to significantly positive. The complete removals of perennial rhizome, annuals and biennials and perennials bunchgrasses + annuals and biennials and the partial removals of perennial rhizome + perennial bunchgrasses and perennial rhizome + perennials bunchgrasses + annuals and biennials changed the relationship between perennial forbs and AGB from significantly positive in 2005 to no correlation in 2008 (Table 3.5).

The complete removals of plant functional types under any treatments did not change the relationship of perennial rhizome and perennial forbs significantly, with the exception of those treatments either perennial rhizome or perennial bunchgrasses being removed. However, the partial removal changed the correlation of perennial rhizome and perennial forbs significantly. With the partial removals of PB, PB+AB, and PB+PF+AB, the relationship between perennial rhizome and perennial forbs changed from no correlation in 2005 to significantly positive in 2008, and with the partial removals of PF, AB, PR+AB, and PR+PB+AB, the relationship between perennial rhizome and perennial forbs changed from significantly positive to no correlation (Table 3.5).

Table 3.4 Correlation coefficient matrix for soil nutrients, plant biodiversity, and aboveground biomass in 2005 and 2008 in the study site of the Inner Mongolia grassland of China

Year	Variable	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.

* $P < 0.05$; ** $P < 0.01$

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.

Table 3.5 Pearson correlations between H_{PFT} and AGB, between H_{PFT} and PB, between PF and AGB, and between PR and PF 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 (no removal)	2008	2005 (no removal)	2008	2005 (no removal)	2008	2005 (no removal)	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**	-0.050	-0.380	-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	0.320	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*	0.050	-	0.374	-	16
	PR+PB+PF	0.431	-	-0.309	-	0.568*	-	0.029	-	15
	PR+PB+AB	0.187	0.587*	-0.470	-	0.511*	0.271	0.410	-	16
	PR+PF+AB	0.156	0.267	-0.337	-0.260	0.641*	-	0.261	-	15
	PB+PF+AB	0.440	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	-0.230	-0.869**	-0.590*	-0.068	-0.080	-0.010	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**	0.100	14
	AB	0.192	-0.073	-0.587*	-0.295	0.415	0.150	0.627**	0.295	16

PR+PB	0.475	-0.331	-0.783**	-0.061	0.817**	0.166	0.884**	0.360	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	0.100	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	-0.180	-0.480	0.529*	0.478	-0.038	0.286	0.505	15
PR+PB+AB	0.567*	-0.574*	0.708**	-0.850**	0.738**	0.040	0.691**	0.261	16
PR+PF+AB	0.340	-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

"-" indicates no correlations between the variable pairs.

$P < 0.05$; $^{**}P < 0.01$

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

4 Discussion

4.1 Spatial autocorrelation

We hypothesized that the spatial patterns of most variables representing biodiversity and ecosystem functioning would be different before the biodiversity removal (2005) and after (2008). Our results show that the average patch sizes of TC and TN decreased from 2005 to 2008, and that TC exhibited a higher degree of spatial autocorrelation and a higher value of spatial heterogeneity percentage after the biodiversity removal (Table 3.3). Biodiversity measures and aboveground biomass at the levels of plant functional type and the community in 2008 also decreased in the average patch size and increased in spatial patchiness due to the biodiversity manipulation (Table 3.3). These differences were primarily due to the altered spatial patterns of vegetation and soil by the physical removal of plants in 2006. The effects of the spatial distribution of vegetation on the spatial pattern of soil nutrients have been well documented (Jackson and Caldwell 1993a, 1993b, Ryel et al. 1996, Cain et al. 1999). In addition, the physical activity of pulling out plants during the removal manipulation increased the degree of soil fragmentation, resulting in decreased average patch sizes for TC and TN in 2008.

The biodiversity removal had differential effects on plant species of different abundance. The spatial structure of the two dominant PFTs, the perennial rhizome and perennial bunchgrasses, was not significantly affected by the removal treatment. For example, 90% of the population variance ($C+C_0$) for the perennial rhizome was attributable to spatial autocorrelation in 2008, and this value was 93% in 2005 (Table 3.3). For perennial bunchgrasses, the population variance was 92% in 2008 and 88% in 2005. The spatial pattern of non-dominant PFTs (including perennial forbs as well as annuals and biennials), however, was clearly affected by the removal treatment. For example, perennial forbs showed no spatial dependence with 0% of the model sample variance in 2008, but a moderate degree of spatial dependence with 50% of the model sample variance in 2005.

While the degree of spatial dependence for aboveground biomass of dominant PFTs was little affected by the removal treatment, the distance over which this spatial dependence was expressed did change substantially between the two years. With the exception of the perennial forbs, the average patch size represented by the range value of the semivariogram was shorter in 2008 than in 2005 (Table 3.3). The possible explanation for this difference is again the fragmentation effect of the removal treatment.

Various studies have attempted to explain spatial patterns in plant and soil properties because these patterns may be indicative of important ecological mechanisms (Legendre 1993). For example, the spatial pattern of soil nutrients in desert ecosystems known as “island of fertility” reflects the spatial distribution of shrubs (Jackson and Caldwell 1993b, Schlesinger et al. 1996), which drives patterns of nitrogen cycling, soil respiration and other soil properties (Robertson et al. 1988, Saetre 1999). Spatial patterns in plant biomass may also be related to spatial patterns in genotypes (Stratton 1994, Bjørnstad et al. 1995). Our study here indicates that biodiversity removal in BEF studies significantly affect the spatial patterns of plants and soils in several ways. Whether these altered spatial patterns would confound the biodiversity effects on ecosystem functioning deserve future studies.

4.2 Spatial correlations

The removal treatment plays a significant role in changing species composition and spatial correlations at our study site. We found that the average aboveground biomass of the functional type of annuals and biennials increased from 2005 to 2008 (Table 3.2), and this was particularly true in the sampled plots across the study site (Table 3.2). In the mature *L. chinensis*-dominant community, annuals and biennials – r-strategists – are usually inferior to perennial rhizome and perennial bunchgrasses and forbs in terms of competing for water, nutrients, and light. Annuals and biennials only germinate after rainfall events, and complete their life cycle quickly with a large amount of small seeds produced (Chen and Wang 2000, Chen et al. 2001). However, the removal treatment created a great number of openings within the community, which allowed annuals and biennials to flourish. In other words, the life history characteristics (e.g., nutrition use strategy and the reproduction times) of the functional type of annuals and biennials can get adjusted to changing habitat quickly (Yuan et al. 2004). Thus, these r-strategy species responded to the competition-relaxing event strongly, and produced greater biomass than they did prior to the removal treatments. As a result, the aboveground biomass of annuals and biennials in 2008 increased significantly after the removal treatments.

Prior to the removal treatment in 2005, there was a positive correlation between aboveground biomass at the community level (AGB) and plant functional type diversity (H_{PFT}), but this correlation disappeared in 2008 (Table 3.4). This result suggests that, in mature steppe communities without human disturbances, biodiversity and ecosystem productivity are positively correlated – confirming the observation by Bai et al. (2004). However, this positive correlation between diversity and productivity was disrupted by the removal treatment in 2006. For instance, in the plots with the complete removal of perennial rhizome + perennial forbs + annuals and biennials in 2008, only the functional type of perennial bunchgrasses was left untouched and all other plant functional types were removed. As a result, the plant cover of perennial bunchgrasses increased even though the diversity of plant functional types decreased. Therefore, the aboveground biomass of the functional type of perennial bunchgrasses was greater after the biodiversity manipulation, which decoupled the correlation between plant diversity and biomass production ($r = 0.267$).

The relationship between H_{PFT} and the biomass of perennial bunchgrasses was significantly negative in 2005, and this relationship also disappeared in 2008 (Table 3.4). Under different removal treatments, we found that the complete removal treatments of plant functional types had a significant effect on the relationship between H_{PFT} and the functional type of perennial bunchgrasses (Table 3.5). Specifically, because of the complete removal of perennial bunchgrasses, no correlations were found between H_{PFT} and the functional type of perennial bunchgrasses.

There was a positive relationship between the aboveground biomass of perennial forbs and the community-level aboveground biomass in 2005 (Table 3.4). This indicates that the functional type of perennial forbs contributes significantly to the aboveground biomass at the community level in natural conditions. However, the correlation in aboveground biomass between the functional type of perennial forbs and the entire community disappeared in 2008 (Table 3.4). Through the analysis of the correlation between variables under different treatments, we found that removal of the perennial rhizome resulted in a great increase in the aboveground biomass of the perennial bunchgrasses because of the compensatory interactions between these two functional types (Bai et al. 2004). Similarly, there was no correlation between H_{PFT} and the aboveground biomass for the treatment plots with the complete removal of the perennial rhizome (Table 3.5).

In 2005, there was a significantly positive relationship between the aboveground biomass of perennial rhizome and that of perennial forbs (Table 3.4), which may be partly explained by their similar requirements for resources. The functional type of perennial rhizome, comprised of *L. chinensis* only, and perennial forbs both grow better in relatively moist areas in the Inner Mongolia grassland region (Chen and Wang 2000, Chen et al. 2001). In 2008, no correlation was found between perennial rhizome and perennial forbs. This change in the relationship between these two plant functional types is again attributable to the removal of targeted plants and physical disturbances incurred during the removal treatment (Table 3.5).

In addition, we found that, in several partial removal treatment plots (e.g., removals of perennial bunchgrasses, perennial bunchgrasses + annuals and biennials, perennial bunchgrasses + perennial forbs + annuals and biennials), the relationship between the functional types of perennial rhizome and perennial forbs was significantly positive in 2008. This further supports our interpretation that the complete removal treatment altered the correlations between variables of interest in our study. Whether and how these altered correlations between variables would significantly affect the BEF experimental results beg future investigations.

CHAPTER 4 CONCLUSION

1 Major research findings

Understanding the effects of spatial heterogeneity on the relationship between biodiversity and ecosystem functioning (BEF) is important for a number of reasons. Spatial heterogeneity in resources can modulate the strength and shape of the BEF relationships (Cardinale et al. 2000), and heterogeneity has long been recognized to promote species coexistence through resource partitioning (Tilman and Kareiva 1997) and niche regeneration (Wu and Loucks 1995). Also, the BEF relationships are scale-dependent (Bond and Chase 2002, Chase and Leibold 2002, Mouquet and Loreau 2003, Harrison et al. 2006) because heterogeneity itself varies with scale (Weins 1989, Wu and Loucks 1995).

The first step toward understanding the effects of spatial heterogeneity on the BEF relationships is to quantify spatial heterogeneity of key variables of biodiversity and ecosystem functioning, and to identify the spatial relationships among these variables. Toward this end, we used two datasets from the on-going Inner Mongolia Grassland Removal Experiment to explore the problem of spatial heterogeneity in relation to BEF research. Specifically, we addressed the following two research questions:

1) What are the spatial patterns of soil nutrients, plant biodiversity, and aboveground biomass in a natural grassland community of Inner Mongolia, China? How are they related spatially?

2) How do removal treatments affect the spatial patterns of soil nutrients, plant biodiversity, and aboveground biomass? Is there any change for their spatial correlations after removal treatments?

Our results have shown that plants and soil in the typical steppe community of Inner Mongolia had the following spatial patterns before the biodiversity removal treatment (in 2005):

1) Most of the selected variables of biodiversity and ecosystem functioning were spatially autocorrelated. Soil nutrients such as TC, TN and TP were spatially autocorrelated over a range of 102 m or less, biodiversity measures over a range of 120 m or less, and most species and plant functional types over a range of less than 30 m. This suggests that the characteristic scales of spatial patchiness varied with different kinds of variables.

2) TC, TN, and TP were highly correlated with each other;

3) Species diversity was positively correlated with aboveground biomass at both the species and PFT levels; and

4) Dominant species, as well as major PFTs, were negatively correlated with each other, supporting the hypothesis of compensatory interactions (Bai et al. 2004).

However, the biodiversity removal treatment conducted in 2006 significantly altered the spatial patterns of the plant and soil variables and their correlations. Based on available data from 2005 and 2008, we were able to quantify these changes in a comprehensive manner. These changes were not always in the same direction. For example, the degree of spatial autocorrelation increased for TC but decreased for TN from 2005 to 2008. Most variables, however, showed a higher degree of spatial patchiness after the biodiversity removal.

Importantly, the spatial correlations between these variables also changed significantly after the removal treatment. For instance, the functional types of perennial rhizome and perennial forbs showed a strongly positive correlation in 2005 but no relationship in 2008. Similarly, most of the statistically significant correlations between variables that existed in natural conditions were disrupted or destroyed by the complete removal treatment required for the biodiversity manipulation experiment.

2 Significance and implications

2.1 Importance for BEF research

Most studies of the BEF relationships have been based on field experiments, which involve direct manipulations of biodiversity levels. In so doing, plots with different levels of species or functional diversity are created, and variables of ecosystem functioning are subsequently measured along the biodiversity gradient. Then, the relationship between biodiversity and ecosystem functioning can be explored with statistical analysis. 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 be even more different.

Our results challenge the common assumption of homogeneity in BEF experiments. With these findings, we must ask questions about the validity of many previous and ongoing BEF experiments. For example, as all BEF experiments inevitably change the spatial patterns of and correlations between plant and soil variables one way or another, would these changes in spatial heterogeneity be confounded with the effects of biodiversity on ecosystem functioning? If so, how? This thesis work does not provide the direct answers to these questions, but does provide the first direct quantification of these changes in spatial patterns. In addition, it suggests that future BEF experiments should explicitly consider these questions. The specific findings of this study will be considered in the final analysis of the experimental results from the IMGRE project – the largest grassland BEF experiment of the world.

2.2 Implications for grassland management

Spatial heterogeneity is critically important to biodiversity and ecosystem functioning in natural ecosystems, and has been considered fundamental for biological conservation and ecosystem management (Wu and Loucks 1995, Pickett et al. 1997, Wu and Hobbs 2007). Grasslands are inherently heterogeneous because species composition, biodiversity and productivity all vary across multiple scales in addition to grazing activities by herbivores (Wu and Levin 1994, Ludwig and Tongway 1995, Patten and Ellis 1995, Bai et al. 2007, 2008). Studies have shown that grazing can affect the spatial heterogeneity of vegetation (Glenn et al. 1992, Rietkerk et al. 2000, Olofsson et al. 2008) and the spatial patterns of soil nutrients through tramping and wallowing (Knapp et al. 1999).

The results of this study have two major implications for grassland management. The first is that the lost of biodiversity may lead to altered spatial patterns of plants and soil as well as the changed relationships between biodiversity and ecosystem functioning. Previous studies from the region (e.g., Bai et al. 2004, 2007, 2008) have shown that high levels of biodiversity, primary production, and ecosystem stability are positively correlated in the Inner Mongolia steppe communities. Thus, maintaining a high level of plant diversity should be a primary goal of the grassland management in this area. Second, our study shows that the spatial heterogeneity of plants and soil resources in undisturbed mature grasslands in Inner Mongolia has unique patterns which is quite different from that after biodiversity loss or disturbances. This suggests that, to sustain the structure and function of the Inner Mongolia grassland, a second primary goal of management is to maintain the fine-scale patterns of plants and soil.

How can these management goals be achieved? Numerous studies have suggested that managing grazing activities (especially stocking rates) is the key (e.g., Jiang et al. 2006). In the Inner Mongolia grassland, grazing by sheep has been a major activity that influences spatial heterogeneity of plants and soil and in turn strongly affects ecosystem processes. Heavy grazing of sheep can decrease the heterogeneity of plant production and soil nutrients. Thus, maintaining a moderate level of grazing in rangeland management is essential for preserving plant biodiversity and fine-scale heterogeneity of plants and soil resources.

In most natural and managed grasslands, a common management goal is to maintain diversity and productivity (Guo 2007). Although in some grasslands the management goal is to increase productivity only in order to meet increasing human demands, this notion is now changing as more people recognize the importance of nutritional diversity and forage quality (Parton and Risser 1979, Marriott et al. 2004). It has been widely recognized that varying the frequency, intensity, and timing of grazing and fires can often increase habitat productivity and species diversity (Dyer et al. 1991).

REFERENCES

Chapter1

Aarssen, L. 1997. High productivity in grassland ecosystems: Effected by species diveristy or productive species? Oikos 80:183.

Bai, Y., X. Han, J. Wu, Z. Chen, and L. Li. 2004. Ecosystem stability and compensatory effects in the Inner Mongolia Grassland. Nature 431:181-184.

Bai, Y., J. Wu, Q. Pan, J. Huang, Q. Wang, F. Li, A. Buyantuyev, and X. Han. 2007. Positive linear relationship between productivity and diversity: Evidence from the Eurasian Steppe. Journal of Applied Ecology 44:1023-1034.

Bailey, D., R. Billeter, S. Aviron, O. Schweiger, and F. Herzog. 2007. The influence of thematic resolution on metric selection for biodiversity monitoring in agricultural landscapes. Landscape Ecology 22:461-473.

Campbell, V., G. Murphy, and T. N. Romanuk. 2011. Experimental design and the outcome and interpretation of diversity-stability relations. Oikos 120:399-408.

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

Cardinale, B. J., D. S. Srivastava, J. E. Duffy, J. P. Wright, A. L. Downing, M. Sankaran, and C. Jouseau. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature 443:989-992.

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

Chapin, F. S., E.-D. Schulze, and H. A. Mooney. 1992. Biodiversity and ecosystem processes. Trends in Ecology & Evolution 7:107-108.

Chapin, F. S., B. Walker, and R. Hobbs. 1997. Biotic control over the functioning of ecosystems. Science 277:500-504.

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

Cheng, X., S. An, J. Chen, B. Li, Y. Liu, and S. Liu. 2007. Spatial relationships among species, above-ground biomass, N, and P in degraded grasslands in Ordos Plateau, northwestern China. Journal of Arid Environments 68:652-667.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31:343-366.

Christensen, N. L., A. M. Bartuska, J. H. Brown, S. Carpenter, C. D'Antonio, R. Francis, J. F. Franklin, J. A. MacMahon, R. F. Noss, D. J. Parsons, C. H. Peterson, M. G. Turner, and R. G. Woodmansee. 1996. The report of the Ecological Society of America Committee on the scientific basis for ecosystem management. Ecological applications 6:665-691.

Costanza, R., R. d'Arge, R. de Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R. V. O'Neill, J. Paruelo, R. G. Raskin, P. Sutton, and M. van den Belt. 1997. The value of the world's ecosystem services and natural capital. Nature 387:253-260.

Curran, P. J. 1988. The semivariogram in remote sensing: An introduction. Remote Sensing of Environment 24:493-507.

Daily, G. C., S. Alexander, P. R. Ehrlich, L. Goulder, J. Lubchenco, P. A. Matson, H. A. Mooney, S. Postel, S. H. Schneider, D. Tilman, and G. M. Woodwell. 1997. Ecosystem services: Benefits supplied to human societies by natural ecosystems. Issues in Ecology 2.

Deutschman, D. H. 2001. Design and analysis of biodiversity field experiments. Ecological Research 16:833-843.

Duffy, J. E. 2009. Why biodiversity is important to the functioning of real-world ecosystems. Frontiers in Ecology and Environment 7:437-444.

Fox, J. W. 2005. Interpreting the 'selection effect' of biodiversity on ecosystem function. Ecology Letters 8:846-856.

Fridley, J. D. 2002. Resource availability dominates and alters the relationship between species diversity and ecosystem productivity in experimental plant communities. Oecologia 132:271-277.

Gaston, K. J. 1996. Species-range-size distributions: Patterns, mechanisms and implications. Trends in Ecology & Evolution 11:197-201.

Gravel, D., T. Bell, C. Barbera, T. Bouvier, T. Pommier, P. Venail, and N. Mouquet. 2011. Experimental niche evolution alters the strength of the diversity-productivity relationship. Nature 469:89-92.

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

Griffin, J. N., S. R. Jenkins, L. Gamfeldt, D. Jones, S. J. Hawkins, and R. C. Thompson. 2009. Spatial heterogeneity increases the importance of species richness for an ecosystem process. Oikos 118:1335-1342.

Guo, Q., T. Shaffer, and T. Buhl. 2006. Community maturity, species saturation and the variant diversity-productivity relationships in grasslands. Ecology Letters 9:1284-1292.

Hector, A. and R. Bagchi. 2007. Biodiversity and ecosystem multifunctionality. Nature 448:188-190.

Hooper, D. U., F. S. Chapin III, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setala, A. J. Symstad, J. Vandermeer, and D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecological Monographs 75:3-35.

Huston, M. A. 1997. Hidden treatments in ecological experiments: Re-evaluating the ecosystem function and biodiversity. Oecologia 110:449-460.

Hutchings, J. A. 2000. Collapse and recovery of marine fishes. Nature 406:882-885.

Hutchings, M. J., E. A. John, and A. J. A. Stewart. 2000. The Ecological Consequences of Environmental Heterogeneity. Blackwell Science, Cambridge, UK.

Ives, A. R. and S. R. Carpenter. 2007. Stability and diversity of ecosystems. Science 317:58-62.

Kolasa, J. and S. T. A. Pickett, editors. 1991. Ecological Heterogeneity. Springer-Verlag, New York, US.

Lechmere-Oertel, R. G., G. I. H. Kerley, and R. M. Cowling. 2005. Patterns and implications of transformation in semi-arid succulent thicket, South Africa. Journal of Arid Environments 62:459-474.

Loreau, M. 2000. Biodiversity and ecosystem functioning: Recent theoretical advances. Oikos 91:3-17.

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

Loreau, M., A. Downing, M. C. Emmerson, A. Gonzalez, J. Hughes, P. Inchausti, J. Joshi, J. Norberg, and O. E. Sala. 2002. A new look at the relationship between diversity and stability. Pages 79-91 *in* M. Loreau, S. Naeem, and P. Inchausti, editors. Biodiversity and Ecosystem Functioning: Synthesis and Perspectives. Oxford University Press, Oxford, UK.

McCann, K. S. 2000. The diversity-stability debate. Nature 405:228-233.

Meisel, J. E. and M. G. Turner. 1998. Scale detection in real and artificial landscapes using semivariance analysis. Landscape Ecology 13:347-362.

Mooney, H. A. 2002. The debate on the role of biodiversity in ecosystem functioning. Pages 12-17 *in* M. Loreau, S. Naeem, and P. Inchausti, editors. Biodiversity and Ecosystem Functioning. Oxford University Press, New York, US.

Naeem, S., D. E. Bunker, A. Hector, M. Loreau, and C. Perrings, editors. 2009. Biodiversity, Ecosystem Functioning, and Human Wellbeing: An Ecological and Economic Perspective. Oxford University Press, New York, US.

Naeem, S., L. J. Thompson, S. P. Lawler, J. H. Lawton, and R. M. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. Nature 368:734-736.

Omenn, G. S. 2006. Presidential Address: Grand challenges and great opportunities in science, technology, and public policy. Science 314:1696-1704.

Pachepsky, E., J. L. Bown, A. Eberst, U. Bausenwein, P. Millard, G. R. Squire, and J. W. Crawford. 2007. Consequences of intraspecific variation for the structure and function of ecological communities Part 2: Linking diversity and function. Ecological Modelling 207:277-285.

Pickett, S. T. A. and M. L. Cadenasso. 1995. Landscape ecology: Spatial heterogeneity in ecological systems. Science 269:331-334.

Purvis, A. and A. Hector. 2000. Getting the measure of biodiversity. Nature 405:212-219.

Roscher, C., V. M. Temperton, N. Buchmann, and E.-D. Schulze. 2009. Community assembly and biomass production in regularly and never weeded experimental grasslands. Acta Oecologica 35:206-217.

Spehn, E. M., A. Hector, J. Joshi, M. Scherer-Lorenzen, B. Schmid, E. Bazeley-White, C. Beierkuhnlein, M. C. Caldeira, M. Diemer, P. G. Dimitrakopoulos, J. A. Finn, H. Freitas, P. S. Giller, J. Good, R. Harris, P. Hogberg, K. Huss-Danell, A. Jumpponen, J. Koricheva, P. W. Leadley, M. Loreau, A. Minns, C. P. H. Mulder, G. O'Donovan, S. J. Otway, C. Palmborg, J. S. Pereira, A. B. Pfisterer, A. Prinz, D. J. Read, E.-D. Schulze, A.-S. D. Saiamantziouras, A. C. Terry, A. Y. Troumbis, F. I. Woodward, S. Yachi, and J. H. Lawton. 2005. Ecosystem effects of biodiversity manipulations in European grasslands. Ecological Monographs 75:37-63.

Tilman, D. 1996. Biodiversity: Population versus ecosystem stability. Ecology 77:350-363.

Tilman, D. 1999. The ecological consequences of changes in biodiversity: A search for general principles. Ecology 80:1455-1474.

Tilman, D. 2000. Causes, consequences and ethics of biodiversity. Nature 405:208-211.

Tilman, D., C. L. Lehman, and K. T. Thomson. 1997. Plant diversity and ecosystem productivity: theoretical considerations. Proceedings of the National Academy of Sciences (USA) 94:1857-1861.

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

Turner, M. G. and J. A. Cardille. 2007. Spatial heterogeneity and ecosystem processes. Pages 62-77 *in* J. Wu and R. Hobbs, editors. Key Topics in Landscape Ecology. Cambridge University Press, Cambridge, UK.

Wacker, L., O. Baudois, S. Eichenberger-Glinz, and B. Schmid. 2008. Environmental heterogeneity increases complementarity in experimental grassland communities. Basic and Applied Ecology 9:467-474.

Wardle, D. A. and O. Zackrisson. 2005. Effects of species and functional group loss on island ecosystem properties. Nature 435:806-810.

Whittaker and S. A. Levin. 1975. On the reasons for distinguishing "Niche, habitat, and ecotope". America Nature 109:79-82.

Wilson, E. O. 1988. Biodiversity. National Academy Press, Washington, D.C., US.

Wilson, E. O. 1993. Diversity of Life. Harvard University Press, Cambridge, MA, US.

Wu, J. and O. L. Loucks. 1995. From balance-of-nature to hierarchical patch dynamics: A paradigm shift in ecology. Quarterly Review of Biology 70:439-466.

Wu, J. , D. E. Jelinski, M. Luck, and P. T. Tueller. 2000. Multiscale analysis of landscape heterogeneity: Scale variance and pattern metrics. Geographic Information Sciences 6:6-19.

Yachi, S. and M. Loreau. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. Proceedings of the National Academy of Sciences (USA) 96:1463-1468.

Zhang, Q. and D. Zhang. 2006. Resource availability and biodiversity effects on the productivity, temporal variability and resistance of experimental algal communities. Oikos 114:385-396.

Chapter 2

Augustine, D. J. and D. A. Frank. 2001. Effects of migratory grazers on spatial heterogeneity of soil nitrogen properties in a grassland ecosystem. Ecology 82:3149-3162.

Bai, Y., X. Han, J. Wu, Z. Chen, and L. Li. 2004. Ecosystem stability and compensatory effects in the Inner Mongolia grassland. Nature 431:181-184.

Bai, Y., J. Wu, Q. Pan, J. Huang, Q. Wang, F. Li, A. Buyantuyev, and X. Han. 2007. Positive linear relationship between productivity and diversity: Evidence from the Eurasian steppe. Journal of Applied Ecology 44:1023-1034.

Bond, E. M. and J. M. Chase. 2002. Biodiversity and ecosystem functioning at local and regional spatial scales. Pages 467-470.

Burrough, P. A. 1995. Spatial aspects of ecological data. Pages 213-265 *in* R. H. G. Jongman, C. J. F. ter Braak, and O. F. R. Van Tongeren, editors. Data Analysis in Community and Landscape Ecology. Cambridge University Press, Cambridge, UK.

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

Cheng, X., S. An, J. Chen, B. Li, Y. Liu, and S. Liu. 2007. Spatial relationships among species, above-ground biomass, N, and P in degraded grasslands in Ordos Plateau, northwestern China. Journal of Arid Environments 68:652-667.

Clifford, P., S. Richardson, and D. Hémon. 1989. Assessing the significance of the correlation between two spatial processes. Biometrics 45:123-134.

Colwell, R. K. and J. A. Coddington. 1995. Estimating terrestrial biodiversity through extrapolation. Pages 101-119 in D. L. Hawksworth, editor. Biodiversity Measurement and Estimation. Chapman and Hall, London, UK.

David, M. 1977. Geostatistical Ore Reserve Estimation. Elsevier Scientific, New York, US.

Davies, K. F., P. Chesson, S. Harrison, B. D. Inouye, B. A. Melbourne, and K. J. Rice. 2005. Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship. Ecology 86:1602-1610.

De Jager, N. R. and J. Pastor. 2009. Declines in moose population density at Isle Royle National Park, MI, USA and accompanied changes in landscape patterns. Landscape Ecology 24:1389-1403.

Don, A., J. Schumacher, M. Scherer-Lorenzen, T. Scholten, and E. D. Schulze. 2007. Spatial and vertical variation of soil carbon at two grassland sites: Implications for measuring soil carbon stocks. Geoderma 141:272-282.

Fortin, M.-J. and M. R. T. Dale. 2005. Spatial Analysis: A Guide for Ecologists. Cambridge University Press, Cambridge, UK.

Gaston, K. J. 2000. Global patterns in biodiversity. Nature 405:220-207.

Gross, K., K. Pregitzer, and A. J. Burton. 1995. Spatial variation in nitrogen availability in three successional plant communities. Journal of Ecology 83:357-367.

He, Z. B., W. Z. Zhao, and X. L. Chang. 2007. The modifiable areal unit problem of spatial heterogeneity of plant community in the transitional zone between oasis and desert using semivariance analysis. Landscape Ecology 22:95-104.

Hector, A. and R. Hooper. 2002. Darwin and the first ecological experiment. Science 295:639-640.

Hector, A., J. Joshi, M. Scherer-Lorenzen, B. Schmid, E. M. Spehn, L. Wacker, M. Weilenmann, E. Bazeley-White, C. Beierkuhnlein, M. C. Caldeira, P. G. Dimitrakopoulos, J. A. Finn, K. Huss-Danell, A. Jumpponen, P. W. Leadley, M. Loreau, C. P. H. Mulder, C. Nesshoover, C. Palmborg, D. J. Read, A. S. D. Siamantziouras, A. C. Terry, and A. Y. Troumbis. 2007. Biodiversity and ecosystem functioning: Reconciling the results of experimental and observational studies. Functional Ecology 21:998-1002.

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

Holland, J. D., D. G. Bert, and L. Fahrig. 2004. Determining the spatial scale of species' response to habitat. BioScience 54:227-233.

Hooper, D. U., F. S. Chapin III, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setala, A. J. Symstad, J. Vandermeer, and D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecological Monographs 75:3-35.

Hooper, D. U., N. Buchmann, V. Degrange, S. M. Diaz, M. Gessner, P. Grime, and et al. 2002. Species diversity, functional diversity and ecosystem functioning. Pages 195-208 in M. Loreau, S. Naeem, and P. Inchausti, editors. Biodiversity and Ecosystem Functioning. Oxford University Press, Oxford, UK.

Huston, M. A. 1997. Hidden treatments in ecological experiments: Re-evaluating the ecosystem function and biodiversity. Oecologia 110:449-460.

Hutchings, M. J., E. A. John, and D. K. Wijesinghe. 2003. Toward understanding the consequences of soil heterogeneity for plant populations and communities. Ecology 84:2322-2334.

Inner Mongolia-Ningxia Integrative Expert Team of the Chinese Academy of Science. 1985. Vegetation of Inner Mongolia. Science Press, Beijing, China.

Kareiva, P. and U. Wennergren. 1995. Connecting landscape patterns to ecosystem and population processes. Nature 373:299-302.

Kolasa, J. and S. T. A. Pickett, editors. 1991. Ecological Heterogeneity. Springer-Verlag, New York, US.

Legendre, P. and M. J. Fortin. 1989. Spatial pattern and ecological analysis. Vegetatio 80:107-138.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology 73:1943-1967.

Li, H. and J. F. Reynolds. 1995. On definition and quantification of heterogeneity. Oikos 73:280-284.

Loreau, M., S. Naeem, and P. Inchausti, editors. 2002. Biodiversity and Ecosystem Functioning: Synthesis and Perspectives. Oxford University Press, Oxford, UK.

Matheron, G. 1963. Principles of geostatistics. Ecnonomic Geology 58:1246-1266.

McNaughton, S. J. 1977. Diversity and stability of ecological communities: A comment on the role of empiricism in ecology. American Naturalist 111:515-525.

McNaughton, S. J. 1993. Biodiversity and function of grazing systems. Pages 361-383 *in* H. Mooney and E. Schulze, editors. Biodiversity and Ecosystem Function. Springer-Verlag, Berlin, Germany.

Meisel, J. E. and M. G. Turner. 1998. Scale detection in real and artificial landscapes using semivariance analysis. Landscape Ecology 13:347-362.

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

Moran, P. A. P. 1948. The interpretation of statistical maps. Journal of the Royal Statistical Society B 10:243-251.

Naeem, S., D. E. Bunker, A. Hector, M. Loreau, and C. Perrings, editors. 2009. Biodiversity, Ecosystem Functioning, and Human Wellbeing: An Ecological and Economic Perspective. Oxford University Press, New York, US.

Naeem, S. and J. P. Wright. 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. Ecology Letters 6:567-579.

Naeem, S. and S. B. Li. 1997. Biodiversity enhances ecosystem reliability. Nature 390:507-509.

Okin, G. S., N. Mladenov, L. Wang, D. Cassel, K. K. Caylor, S. Ringrose, and S. A. Macko. 2008. Spatial patterns of soil nutrients in two southern African savannas. Journal of Geophysical Research-Biogeosciences 113.

Oline, D. K. and M. C. Grant. 2002. Scaling patterns of biomass and soil properties: An empirical analysis. Landscape Ecology 17:13-26.

Olofsson, J., C. de Mazancourt, and M. J. Crawley. 2008. Spatial heterogeneity and plant species richness at different spatial scales under rabbit grazing. Oecologia 156:825-834.

Reynolds, H. L., B. A. Hungate, and C. M. D'Antonio. 1997. Soil heterogeneity and plant competition in an annual grassland. Ecology 78:2076.

Robertson, G. P., J. R. Crum, and B. G. Ellis. 1993. The spatial variability of soil resources following long-term disturbance. Oecologia 96:451-456.

Robertson, G. P. and K. L. Gross. 1994. Assessing the heterogeneity of belowground resources: Quantifying pattern and scale. Pages 237-253 *in* M. M. Caldwell and R. W. Pearcy, editors. Exploitation of Environmental Heterogeneity by Plants: Ecophysiological Processes Above- and Belowground. Academic Press, San Diego, US.

Robertson, G. P., K. M. Klingensmith, M. J. Klug, E. A. Paul, J. R. Crum, and B. G. Ellis. 1997. Soil resources, microbial activity, and primary production across an agricultural ecosystem. Ecological Applications 7:158-170.

Roscher, C., V. M. Temperton, M. Scherer-Lorenzen, M. Schmitz, J. Schumacher, B. Schmid, N. Buchmann, W. W. Weisser, and E.-D. Schulze. 2005. Overyielding in experimental grassland communities - irrespective of species pool or spatial scale. Ecology Letters 8:419-429.

Rosenzweig, M. L. 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge, UK.

Rossi, R. E., D. J. Mulla, A. G. Journel, and E. H. Franz. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. Ecological Monographs 62:277-314.

Sala, O. E. and A. T. Austin. 2000. Methods of estimating aboveground net primary productivity. Pages 31-43 *in* O. E. Sala, R. B. Jackson, M. H.A., and R. W. Howarth, editors. Methods in Ecosystem Science. Springer, New York, USA.

Schlesinger, W. H., J. A. Raikes, A. E. Hartley, and A. F. Cross. 1996. On the spatial pattern of soil nutrients in desert ecosystems. Ecology 77:364-374.

Spehn, E. M., A. Hector, J. Joshi, M. Scherer-Lorenzen, B. Schmid, E. Bazeley-White, C. Beierkuhnlein, M. C. Caldeira, M. Diemer, P. G. Dimitrakopoulos, J. A. Finn, H. Freitas, P. S. Giller, J. Good, R. Harris, P. Hogberg, K. Huss-Danell, A. Jumpponen, J. Koricheva, P. W. Leadley, M. Loreau, A. Minns, C. P. H. Mulder, G. O'Donovan, S. J. Otway, C. Palmborg, J. S. Pereira, A. B. Pfisterer, A. Prinz, D. J. Read, E.-D. Schulze, A.-S. D. Saiamantziouras, A. C. Terry, A. Y. Troumbis, F. I. Woodward, S. Yachi, and J. H. Lawton. 2005. Ecosystem effects of biodiversity manipulations in European grasslands. Ecological Monographs 75:37-63.

Tilman, D. 1982. Resource Competition and Community Structure. Princeton University Press, Princeton, US.

Tilman, D. 1985. The resource-ratio hypothesis of plant succession. American Naturalist 125:827-852.

Tilman, D. 1999. The ecological consequences of changes in biodiversity: A search for general principles. Ecology 80:1455-1474.

Tilman, D. and J. A. Downing. 1994. Biodiversity and stability in grasslands. Nature 367:363-365.

Tilman, D. and P. Kareiva, editors. 1997. Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions. Princeton University Press, Princeton, US.

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

Turner, M. G., R. H. Gardner, and R. V. O'Neill. 2001. Landscape Ecology in Theory and Practice: Pattern and Process. Springer-Verlag, New York, US.

Turner, S. J., R. V. O'Neill, W. Conley, M. R. Conley, and H. C. Humphries. 1991. Pattern and scale: statistics for landscape ecology. Pages 17-50 *in* M. G. Turner and R. H. Gardner, editors. Quantitative Methods in Landscape Ecology. Springer-Verlag, New York, US.

Waide, R. B., M. R. Willig, C. F. Steiner, G. Mittelbach, L. Gough, S. I. Dodson, G. P. Juday, and R. Parmenter. 1999. The relationship between productivity and species richness. Annual Review of Ecology and Systematics 30:257-300.

Wang, H. Q., C. A. S. Hall, J. D. Cornell, and M. H. P. Hall. 2002. Spatial dependence and the relationship of soil organic carbon and soil moisture in the Luquillo Experimental Forest, Puerto Rico. Landscape Ecology 17:671-684.

Wang, L. X., P. P. Mou, J. H. Huang, and J. Wang. 2007. Spatial heterogeneity of soil nitrogen in a subtropical forest in China. Plant and Soil 295:137-150.

Wu, J. 2004. Effects of changing scale on landscape pattern analysis: Scaling relations. Landscape Ecology 19:125-138.

Wu, J., K. B. Jones, H. Li, and O. L. Loucks, editors. 2006. Scaling and Uncertainty Analysis in Ecology: Methods and Applications. Springer, Dordrecht, The Netherlands.

Wu, J. and O. L. Loucks. 1995. From balance-of-nature to hierarchical patch dynamics: A paradigm shift in ecology. Quarterly Review of Biology 70:439-466.

Wu, J. and R. Hobbs, editors. 2007. Key Topics in Landscape Ecology. Cambridge University Press, Cambridge, UK.

Wu, J. and S. A. Levin. 1994. A spatial patch dynamic modeling approach to pattern and process in an annual grassland. Ecological Monographs 64:447-464.

Xin, X., X. Li, G. Yang, and B. Xu. 2002. Spatial heterogeneity of grassland pattern under grazing and forage condition. Yingyong Shengtai Xuebao 13:449-453.

Zawadzki, J., C. J. Cieszewski, and M. Zasada. 2005a. Semivariogram analysis of Landsat 5 TM textural data for loblolly pine forests. Journal of Forest Science (Prague) 51:47-59.

Zawadzki, J., C. J. Cieszewski, M. Zasada, and R. C. Lowe. 2005b. Applying geostatistics for investigations of forest ecosystems using remote sensing imagery. Silva Fennica 39:599-617.

Zhang, X. Y., Y. Y. Sui, X. D. Zhang, K. Meng, and S. J. Herbert. 2007. Spatial variability of nutrient properties in black soil of northeast China. Pedosphere 17:19-29.

Zhou, Z. Y., O. J. Sun, Z. K. Luo, H. M. Jin, Q. S. Chen, and X. G. Han. 2008. Variation in small-scale spatial heterogeneity of soil properties and vegetation with different land use in semiarid grassland ecosystem. Plant and Soil 310:103-112.

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

Chapter 3

Bai, Y., X. Han, J. Wu, Z. Chen, and L. Li. 2004. Ecosystem stability and compensatory effects in the Inner Mongolia grassland. Nature 431:181-184.

Bai, Y., J. Wu, M. Clark, S. Naeem, Q. Pan, J. Huang, L. Zhang, and X. Han. 2010. Tradeoffs and thresholds in the effects of nitrogen addition on biodiversity and ecosystem functioning: evidence from inner Mongolia Grasslands. Global Change Biology 16:358-372.

Bjørnstad, O. N., A. Iversen, and M. Hansen. 1995. The spatial structure of the gene pool of a viviparous population of Poa alpina - environmental controls and spatial constraints. Nordic Journal of Botany 15:347-354.

Cain, M. L., S. Subler, J. P. Evans, and M.-J. Fortin. 1999. Sampling spatial and temporal variation in soil nitrogen availability. Oecologia 118:397-404.

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

Chen, Z. & S. Wang. 2000. Typical Steppe Ecosystems of China. Science press, Beijing, China.

Chen, S., H. Zhang, L. Wang, Zhanbula and M. Zhao. 2001. Root Systems of Grassland Plants in Northern China. Jilin University Press, Changchun, China.

Clifford, P., S. Richardson, and D. Hémon. 1989. Assessing the significance of the correlation between two spatial processes. Biometrics 45:123-134.

Diaz, S., A. J. Symstad, F. S. Chapin III, D. A. Wardle, and L. F. Huenneke. 2003. Functional diversity revealed by removal experiments. Trends in Ecology and Evolution 18:140-146.

Feng, D., Z. Liang, X. Xu, X. Zhang, and L. Shan. 2008. Spatial heterogeneity of soil nutrients and aboveground biomass in abandoned old-fields of Loess Hilly region in northern Shaanxi, China. Acta Ecologica Sinica 28:13-22.

Gundale, M. J., D. A. Wardle, and M.-C. Nilsson. 2010. Vascular plant removal effects on biological N fixation vary across a boreal forest island gradient. Ecology 91:1704-1714.

Guo, D., P. P. Mou, R. H. Jones, and R. J. Mitchell. 2002. Temporal changes in spatial patterns of soil moisture following disturbance: An experimental approach. Journal of Ecology 90:338-347.

Hooper, D. U. 1998. The role of complementarity and competition in ecosystem responses to variation in plant diversity. Ecology 79:704-719.

Hooper, D. U., F. S. Chapin III, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setala, A. J. Symstad, J. Vandermeer, and D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecological Monographs 75:3-35.

Isaaks, E. H. and R. M. Srivastava. 1989. An Introduction to Applied Geostatistics. Oxford University Press, New York.

Jackson, R. B. and M. M. Caldwell. 1993a. The scale of nutrient heterogeneity around individual plants and its quantification with geostatistics. Ecology 74:612-614.

Jackson, R. B. and M. M. Caldwell. 1993b. Geostatistical patterns of soil heterogeneity around individual plants. Journal of Ecology 81:683-692.

Keitt, T. H., O. N. Bjornstad, P. M. Dixon, and S. Citron-Pousty. 2002. Accounting for spatial pattern when modeling organism-environment interactions. Ecography 25:616-625.

Knorr, M., S. D. Frey, and P. S. Curtis. 2005. Nitrogen additions and litter decomposition: A meta-analysis. Ecology 86:3252-3257.

Legendre, P. 1993. Spatial autocorrelation: Trouble or new paradigm? Ecology 74:1659-1673.

Li, H. and J. F. Reynolds. 1995. On definition and quantification of heterogeneity. Oikos 73:280-284.

McLellan, A. J., R. Law, and A. H. Fitter. 1997. Response of calcareous grassland plant species to diffuse competition: results from a removal experiment. Journal of Ecology 85:479-490.

Moran, P. A. P. 1948. The interpretation of statistical maps. Journal of the Royal Statistical Society B 10:243-251.

Robertson, G. P., M. A. Huston, F. C. Evans, and J. M. Tiedje. 1988. Spatial variability in a successional plant community: patterns of nitrogen availability. Ecology 69:1517-1524.

Robertson, G. P. and K. L. Gross. 1994. Assessing the heterogeneity of belowground resources: Quantifying pattern and scale. Pages 237-253 *in* M. M. Caldwell and R. W. Pearcy, editors. Exploitation of Environmental Heterogeneity by Plants: Ecophysiological Processes Above- and Belowground. Academic Press, San Diego, US.

Rossi, R. E., D. J. Mulla, A. G. Journel, and E. H. Franz. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. Ecological Monographs 62:277-314.

Ryel, R. J., M. M. Caldwell, and J. H. Manwaring. 1996. Temporal dynamics of soil spatial heterogeneity in sage-brush-wheatgrass steppe during a growing season. Plant and Soil 184:299-309.

Saetre, P. 1999. Spatial patterns of ground vegetation, soil microbial biomass and activity in a mixed spruce-birch stand. Ecography 22:183-192.

Schlesinger, W. H., J. A. Raikes, A. E. Hartley, , and A. F. Cross. 1996. On the spatial pattern of soil nutrients in desert ecosystems. Ecology 77:364-374.

Schroeer, A. E., R. L. Hendrick, and T. B. Harrington. 1999. Root, ground cover, and litterfall dynamics within canopy gaps in a slash pine (Pinus elliottii Engelm.) dominated forest. Ecoscience 6:548-555.

Schulze, A. P. and H. A. Mooney. 1993. Ecosystem Function and Biodiversity. Springer, Berlin, Germany.

Seastedt, T. R., J. M. Briggs, and D. J. Gibson. 1991. Controls of nitrogen limitation in trallgrass prairie. Oecologia 87:72-79.

Silver, W. L. and K. A. Vogt. 1993. Fine root dynamics following single and multiple disturbances in a subtropical wet forest ecosystem. Journal of Ecology 81:729-738.

Stratton, D. A. 1994. Genotype-by-environment interactions for fitness of Erigeron annuus show fine-scale selective heterogeneity. Evolution 48:1607-1618.

Wang, H. Q., C. A. S. Hall, J. D. Cornell, and M. H. P. Hall. 2002. Spatial dependence and the relationship of soil organic carbon and soil moisture in the Luquillo Experimental Forest, Puerto Rico. Landscape Ecology 17:671-684.

Wardle, D. A., K. I. Bonner, G. M. Barker, G. W. Yeates, K. S. Nicholson, R. D. Bardgett, R. N. Watson, and A. Ghani. 1999. Plant removals in perennial grassland: vegetation dynamics, decomposers, soil biodiversity, and ecosystem properties. Ecological Monographs 69:535-568.

Wilson, E. O., editor. 1988. Biodiversity. National Academy Press, Washington, D.C., US.

Yuan, Z., L. Li, and X. Han. 2004. Nitrogen use efficiency of competing individuals in a dense stand of an annual herb, *Chenopodium Album*. 28: 294-299.

Chapter 4

Bai, Y., X. Han, J. Wu, Z. Chen, and L. Li. 2004. Ecosystem stability and compensatory effects in the Inner Mongolia Grassland. Nature 431:181-184.

Bai, Y., J. Wu, Q. Pan, J. Huang, Q. Wang, F. Li, A. Buyantuyev, and X. Han. 2007. Positive linear relationship between productivity and diversity: evidence from the Eurasian Steppe. Journal of Applied Ecology 44:1023-1034.

Bai, Y., J. Wu, Q. Xing, Q. Pan, J. Huang, D. Yang, and X. Han. 2008. Primary production and rain use efficiency across a precipitation gradient on the Mongolia plateau. Ecology 89:2140-2153.

Bond, E. M. and J. M. Chase. 2002. Biodiversity and ecosystem functioning at local and regional spatial scales. Ecology Letters 5:467-470.

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

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

Dyer, M. I., C. L. Turner, and T. R. Seastedt. 1991. Mowing and Fertilization Effect on Productivity and Spectral Reflectance in Bromus Inermis Plots. Ecological Applications 1:443-452.

Glenn, S. M., S. L. Collins, and D. J. Gibson. 1992. Disturbances in tallgrass prairie - Local and regional effects on community heterogeneity. Landscape Ecology 7:243-251.

Guo, Q. 2007. The diversity-biomass-productivity relationships in grassland management and restoration. Basic and Applied Ecology 8:199-208.

Harrison, S., H. D. Safford, J. B. Grace, J. H. Viers, and K. F. Davies. 2006. Regional and local species richness in an insular environment: Serpentine plants in California. Ecological Monographs 76:41-56.

Jiang, G., X. Han, and J. Wu. 2006. Restoration and management of the Inner Mongolia Grassland requires a sustainable strategy. AMBIO 35:269-270.

Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, D. C. Hartnett, L. C. Johnson, and E. G. Towne. 1999. The keystone role of bison in north American tallgrass prairie - Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. Bioscience 49:39-50.

Ludwig, J. A. and D. J. Tongway. 1995. Spatial organisation of landscapes and its function in semi-arid woodlands, Australia. Landscape Ecology 10:51-63.

Marriott, C. A., M. Fothergill, B. Jeangros, M. Scotton, and F. Louault. 2004. Long-term impacts of extensification of grassland management on biodiversity and productivity in upland areas. A review. Agronomie 24:447-462.

Mouquet, N. and M. Loreau. 2003. Community patterns in source-sink metacommunities. American Naturalist 162:544-557.

Olofsson, J., C. de Mazancourt, and M. J. Crawley. 2008. Spatial heterogeneity and plant species richness at different spatial scales under rabbit grazing. Oecologia 156:825-834.

Parton, W. J. and P. G. Risser. 1979. Simulated impact of management practices upon the tallgrass prairie.in N. R. French, editor. Perspectives in Grassland Ecology, Ecological Studies, Vol. 32. Springer, New York, US.

Patten, R. S. and J. E. Ellis. 1995. Patterns of species and community distributions related to environmental gradients in an arid tropical ecosystem. Vegetatio 117:69-79.

Pickett, S. T. A., R. S. Ostfeld, M. Shachak, and G. E. Likens, editors. 1997. The Ecological Basis of Conservation: Heterogeneity, Ecosystems, and Biodiversity. Chapman & Hall, New York, US.

Rietkerk, M., P. Ketner, J. Burger, B. Hoorens, and H. Olff. 2000. Multiscale soil and vegetation patchiness along a gradient of herbivore impact in a semi-arid grazing system in West Africa. Plant Ecology 148:207-224.

Tilman, D. and P. Kareiva, editors. 1997. Spatial Ecology: the Role of Space in Population Dynamics and Interspecific Interactions. Princeton University Press, Princeton, US.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385-397.

Wu, J. and O. L. Loucks. 1995. From balance-of-nature to hierarchical patch dynamics: A paradigm shift in ecology. Quarterly Review of Biology 70:439-466.

Wu, J. and R. J. Hobbs, editors. 2007. Key Topics in Landscape Ecology. Cambridge University Press, Cambridge.UK.

Wu, J. and S. A. Levin. 1994. A spatial patch dynamic modeling approach to pattern and process in an annual grassland. Ecological Monographs 64(4):447-464.