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Scale-dependent relationships between plant diversity and above-ground biomass in temperate grasslands, south-eastern Mongolia

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Abstract

Relationships between plant diversity (*H* diversity index) and above-ground biomass (as a surrogate of productivity) were analysed using quadrat data and biomass measures from a precipitation gradient in length of ca. 1000 km in temperate grasslands, south-eastern Mongolia. These analyses were performed both at different ecological scales including taxonomic or functional levels, such as species, community and ecosystem, and at different geographic scales, such as local, landscape and region. Results showed that diversity–productivity relationships differ with different observed ecological and geographical scales in the temperate grasslands of south-eastern Mongolia. In detail, at the individual species level, all relationships between plant diversity and above-ground biomass from local scale to landscape and regional scales are positive and non-linear. At the community level, such relationships are mostly unimodal from landscape to regional scales. At the ecosystem level, the relationship is unimodal at regional scale. A general trend of diversity–productivity relationships in this region seems to be from positive non-linear to unimodal patterns if the scales change from low to high ecological levels and from small to large geographical scales. The unimodal pattern is common in this region.

Keywords: Above-ground biomass; Community; Ecological levels; Ecosystem; Geographical scales; Plant functional types; Species; Steppe

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1. Introduction

Relationships between biodiversity and ecosystem functions have received much attention in the past decade (e.g. Baskin, 1994; Risser, 1995; Mawdsley, 1996; Bengtsson, 1998; Hodgson et al., 1998; Lacroix and Abbadie, 1998; Lawton et al., 1998; Tilman, 1999; Bengtsson et al., 2000; Petchey, 2000; Schwartz et al., 2000; Loreau et al., 2001, 2002; Cardinale et al., 2002; Naeem, 2002; Stohlgren et al., 2003; Thebault and Loreau, 2003). More recently, such studies focus on one major question: what is the relationship between plant species diversity or species richness and productivity such as biomass and net primary productivity (e.g. Tilman et al., 1997; Hector et al. 1999; Waide et al., 1999; Yachi and Loreau, 1999; Gross et al. 2000; Scheiner et al., 2000; Mittelbach et al. 2001; Catovsky et al., 2002; Drake, 2003; Smith and Knapp, 2003; Cardinale et al., 2004)?

A great number of studies on plant diversity–productivity relationships at both the local and regional scale have been performed worldwide, resulting in various patterns. Three comprehensive literature surveys have synthesized this information for herbaceous plant communities (Grace, 1999), and for both plants and animals (Waide et al., 1999; Mittelbach et al., 2001). The survey of Waide et al. (1999) showed that approximately 200 relationships for both plants and animals were found in the literature, of which 30% were unimodal, 26% were positive linear, 12% were negative linear and 32% were not significant. A more recent meta-analysis by Mittelbach et al. (2001) further demonstrated that unimodal productivity–diversity relationships occurred most frequently (41–45%) for vascular plants at geographical scales smaller than continents. A positive relationship between productivity and species richness was the next most common pattern, and positive and unimodal relationships co-dominated at the continental scale. For both plants and animals, unimodal curves were also relatively more common in studies that crossed community boundaries compared to studies conducted within a community type, and plant studies that crossed community types tended to span a greater range of productivity compared to studies within community types. However, unimodal curves were especially common (65%) in studies of plant diversity that used plant biomass as a measure of productivity (Mittelbach et al. 2001).

These literature surveys (Grace, 1999; Waide et al., 1999; Mittelbach et al., 2001), as well as experimental and theoretical studies (e.g. Guo and Berry, 1998; Loreau, 2000; Scheiner et al., 2000; Scheiner and Jones, 2002; Symstad et al., 2003), have showed that the relationships between plant species diversity and productivity are strongly scale-dependent. However, these kinds of scale-dependent relationships were derived mostly from meta-data collection from different studies at different scales. Few studies examined the relationships between plant species diversity and productivity at different ecological and/or geographical hierarchies using a single study framework. Furthermore, most experimental studies showed the species richness–ecosystem productivity relationships in relatively small experimental plots. It is uncertain how these relationships scale up to large ecosystems, or to natural gradients of diversity within and across communities (Symstad et al., 2003). On the other hand, most studies were conducted on plant communities in the Europe and North America (Mittelbach et al., 2001), while studies in Asia were rarely reported. Therefore, in this study, along a precipitation gradient in length of ca. 1000 km in temperate grasslands of south-eastern Mongolia, relationships between plant diversity and above-ground biomass (AGB) (as a surrogate of productivity) at different scales are investigated based on field vegetation survey.

The first aim of this study is to test how the relationships between plant diversity and AGB vary with different geographic scales (local to regional) in the temperate grasslands of south-eastern Mongolia. Will the diversity–productivity relationships in Asian steppes agree with the findings from Europe and North America? The second aim is to explore the relationships between plant diversity and AGB in Mongolian grasslands at different ecological levels from species, community to ecosystem.

2. Methods

2.1. Vegetation survey and data collection

The vegetation survey was conducted in the temperate steppes of south-eastern Mongolia along a precipitation gradient from 323 mm in the east to 90 mm in the west in July 1998 (Fig. 1). Eight sites (M1–M8), each measuring $60 \times 60\,m^2$, were chosen based on the land cover types (Table 1). The geographical location of each site was recorded using a Global Position System (GPS, Magellan Company). Three plots (four plots for site M1), each measuring $1 \times 1\,m^2$, were randomly sampled at each of the eight sites, and vegetation type, soil type, plant species numbers, height and coverage were all recorded. The above-ground portion of each plant species was separately clipped in the field, and then dried and weighted in the laboratory. This allowed calculation of the AGB, which was used as a surrogate for vegetation productivity.

From sampling site M1 in the east to M8 in the west of the study area, vegetation changed from typical steppe to desert steppe (Table 1). The first four sites belong to typical steppe, dominated by *Leymus chinense*, *Stipa grandis*, *S. krylovii* and *Cleistogenes squarrosa*. The last four sites belong to desert steppe, dominated by *S. glareosa*, *S. gobica*, *C. squarrosa* and *C. songorica* (Table 1).

Climate data for monthly mean temperature and precipitation were obtained from the CLIMATE database version 2.1 (Wolfgang Cramer, Potsdam, pers. comm.). Two climatic variables, mean annual temperature (MAT) and mean annual precipitation (MAP), were

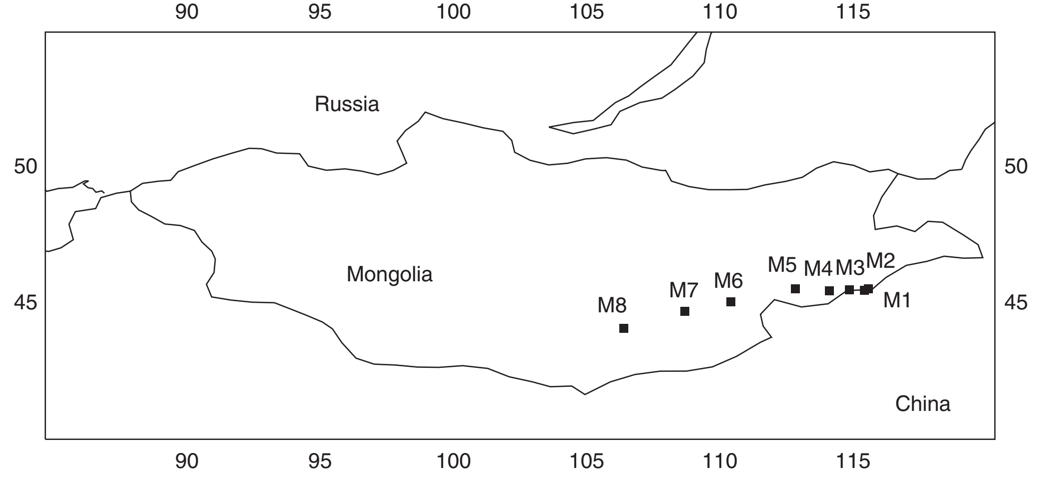

Fig. 1. Study area and locations of sampling sites in temperate grasslands, south-eastern Mongolia.

Table 1
Characteristics of eight sampling sites in south-eastern Mongolia

No.	Site name	Latitude	Longitude	Elevation (m)	Vegetation	Dominants	Soil	Coverage (%)	Mean annual temperature (°C)	Mean annual precipitation (mm)
M1	Bichigt	45°29′51″	115°36′04″	1234	Steppe	*Leymus chinense*, *Stipa grandis*	Chestnut soil	36.8	−1.34	323
M2	Lkhachinvandad	45°27′16″	115°27′12″	1226	Steppe	*Stipa grandis*, *Cleistogenes squarrosa*	Chestnut soil	35.4	−0.47	285
M3	Shilinbogt Mt.	45°28′00″	114°51′54″	1350	Steppe	*Leymus chinense*, *Stipa grandis*	Chestnut soil	37.9	−0.50	273
M4	Dariganga	45°25′25″	114°07′25″	1450	Steppe	*Stipa krylovii*, *Leymus chinense*	Brown soil	40.9	−0.34	252
M5	Ongon	45°30′12″	112°51′29″	1131	Desert steppe	*Cleistogenes squarrosa*, *Carex duriuscula*	Brown soil	34.7	0.53	196
M6	Sainshand	45°01′07″	110°26′08″	960	Desert steppe	*Stipa glareosa*	Brown soil	22.7	2.63	128
M7	Saihandulaan	44°38′53″	108°42′24″	1168	Desert steppe	*Cleistogenes songorica*, *Stipa glareosa*	Brown soil	15.0	2.73	120
M8	Manlai	44°01′20″	106°24′15″	1284	Desert steppe	*Stipa gobica*	Brown soil	22.7	4.09	90

calculated from the above database and used for analysing relationships among plant diversity, productivity and climate.

2.2. Analysis framework

The value of plant diversity was calculated based on the commonly used index of species diversity, 'H' (Spellerberg and Fedor, 2003). First, we calculated the index of individual species diversity as $-p_i \ln(p_i)$, where $p_i = n_i/S$, n_i is the individual number of each plant species i in a plot and S is the total species number in a plot. Then, we summarized the individual species diversity indices as a function of community in each plot. The community species diversity was estimated as follows: $H = -\sum_{i=1}^{n} p_i \ln p_i$. Here, n is the total number of species in a plot. Finally, we averaged the indexes of community species diversity over 3–4 plots of each sampling site, and defined it as an index of ecosystem diversity. Therefore, we defined three kinds of diversity: individual species diversity (in total 288 data points), community diversity (25) and ecosystem diversity (8). Species richness, the number of plant species in a plot, was also used.

Based on the three ecological levels of plant diversity, we further calculated the AGB for individual species, community and ecosystem. The AGB of individual species is the dry matter per area of all individuals in a plot. The community biomass is the summary of dry matter per area of all species in a plot. The ecosystem biomass is the average of AGB of 3–4 plots in a sampling site.

Three geographic scales were recognized. The local scale is within each sampling site from M1 to M8. The landscape scales encompassed the first four sampling sites M1–M4 and the last four sampling sites M5–M8, respectively. The regional scale represented the entire gradient, including all of sampling sites from M1 to M8.

The relationships between plant diversity and productivity were analysed across the three ecological levels (species, community and ecosystem) and linked to the three geographical scales (local, landscape and region). In other words, we analysed the diversity–productivity relationships for each ecological level, at each geographical scale. The relationships between community diversity and AGB at the local scale and between ecosystem diversity and AGB at both local and regional scales were excluded from the analysis due to the small number of sampled points. We took the 'best fit' relationship between plant diversity and biomass in each statistical analysis, i.e. the relationship with the highest R^2 and the lowest p value (SPSS 11.0).

3. Results

Along the eight sampling sites from east to west in the study area, temperature (MAT) increases from -1.34 to $4.09\,^{\circ}\mathrm{C}$ while precipitation (MAP) decreases from 323 to 90 mm (Table 1), which means that sampling sites with more precipitation have lower temperatures, and vice versa. Therefore, typical steppes in the north-eastern part have both higher MAP and lower MAT than desert steppes in the south-western part of the study area.

Site-based plant diversity (H index) has no significant relationship with both MAT and MAP. However, site-based species richness and AGB have significant, positive linear relationships with MAP ($p<0.05$ and 0.01, respectively) and significant, negative linear relationships with MAT ($p<0.05$ and 0.01, respectively). The higher R^2 values and relative lower p values show that MAP ($R^2 = 0.51$–0.84, $p = 0.04$–0.001) is more highly correlated with species richness and AGB than MAT ($R^2 = 0.49$–0.82, $p = 0.05$–0.002), suggesting that precipitation is a major driving factor along the gradient.

3.1. Individual species diversity– AGB relationship

At local scale, individual species diversity has a positive, non-linear (power and exponential) relationship with AGB, although the pattern varies between sites (Fig. 2). Relationships between species diversity and AGB at sites M1–M4 and M7 (Fig. 2a–e) are all significant ($p < 0.01$), while the relationships are not significant in site M5, M6 and M8. At landscape scale, individual species diversity of typical steppes from site M1 to M4 has a significant positive power relationship with AGB (Fig. 2f), while no significant relationship is observed in desert steppes at sites M5–M8. At the regional scale, there is also a significant, positive relationship between individual species diversity and AGB for all sampling sites, but the R^2 is lower than for typical steppes at the landscape scale (Fig. 2g).

3.2. Community diversity– AGB relationship

At the landscape scale, the relationship between community diversity and AGB in typical steppes (M1–M4) is a significant unimodal curve (Fig. 3a), while that in desert steppes (M5–M8) is not significant (Fig. 3b). At the regional scale, the relationship between community diversity and AGB for both typical and desert steppes is also not significant (Fig. 3c).

3.3. Ecosystem diversity and species richness– AGB relationships

At regional scale, the relationship between ecosystem diversity and AGB as well as between the mean species richness of each site and AGB are all not significant (Figs. 3d and e).

4. Discussion

During the past decade, experimental research (e.g. Guo and Berry, 1998; Scheiner and Jones, 2002; Symstad et al., 2003), theoretical investigations (e.g. Loreau, 2000; Scheiner et al., 2000) and literature syntheses (e.g. Grace, 1999; Waide et al., 1999; Mittelbach et al., 2001) have all demonstrated that species diversity–productivity relationships differ depending on the scale examined. However, there are many ways to define scales of study, and sometimes the manner in which a scale is defined leads to different species diversity–productivity patterns. Waide et al. (1999) and Mittelbach et al. (2001) defined two ecological scales: 'within a community type' and 'across community types'. They also defined four geographical scales: local (0–20 km), 'landscape' (20–200 km), 'regional' (200–4000 km) and 'continental to global' (>4000 km). Compared to these worldwide definitions, the ecological levels of species and community used in this study should be included in the 'within a community type', while the ecosystem level belongs to the 'across community types'. The local scale used in the present study is the same as the universally accepted 'local' scale. The landscape scale from site M1 to M4 is the same as but from site M5 to M8 it is larger than the worldwide 'landscape' scale. The regional scale from site M1

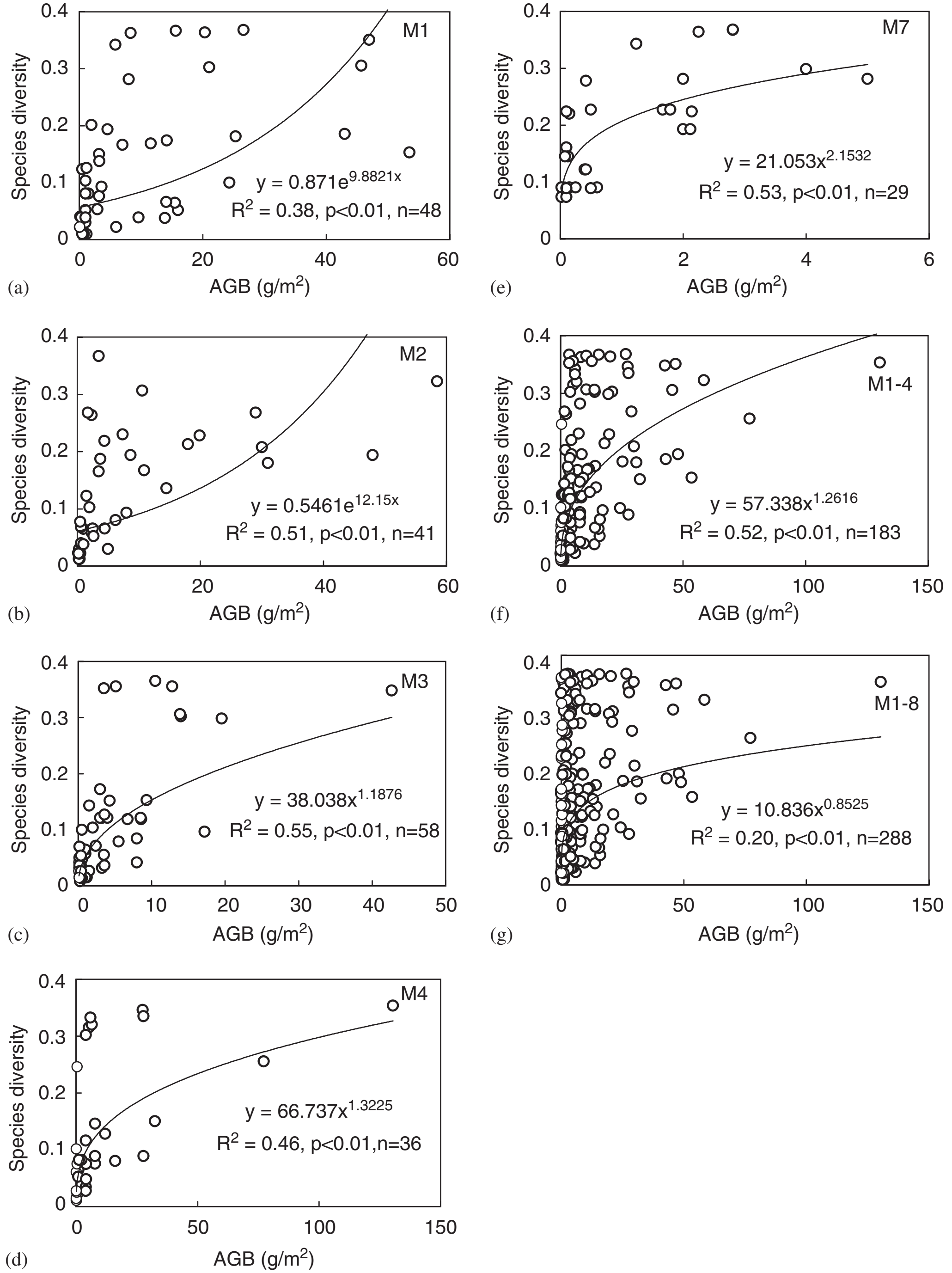

Fig. 2. Relationships between individual species diversity and above-ground biomass (AGB) at the local scale at sites M1 (a), M2 (b), M3 (c), M4 (d) and M7 (e), at landscape scale of steppe grassland from site M1 to M4 (f), and at the regional scale along the whole gradient from site M1 to M8 (g).

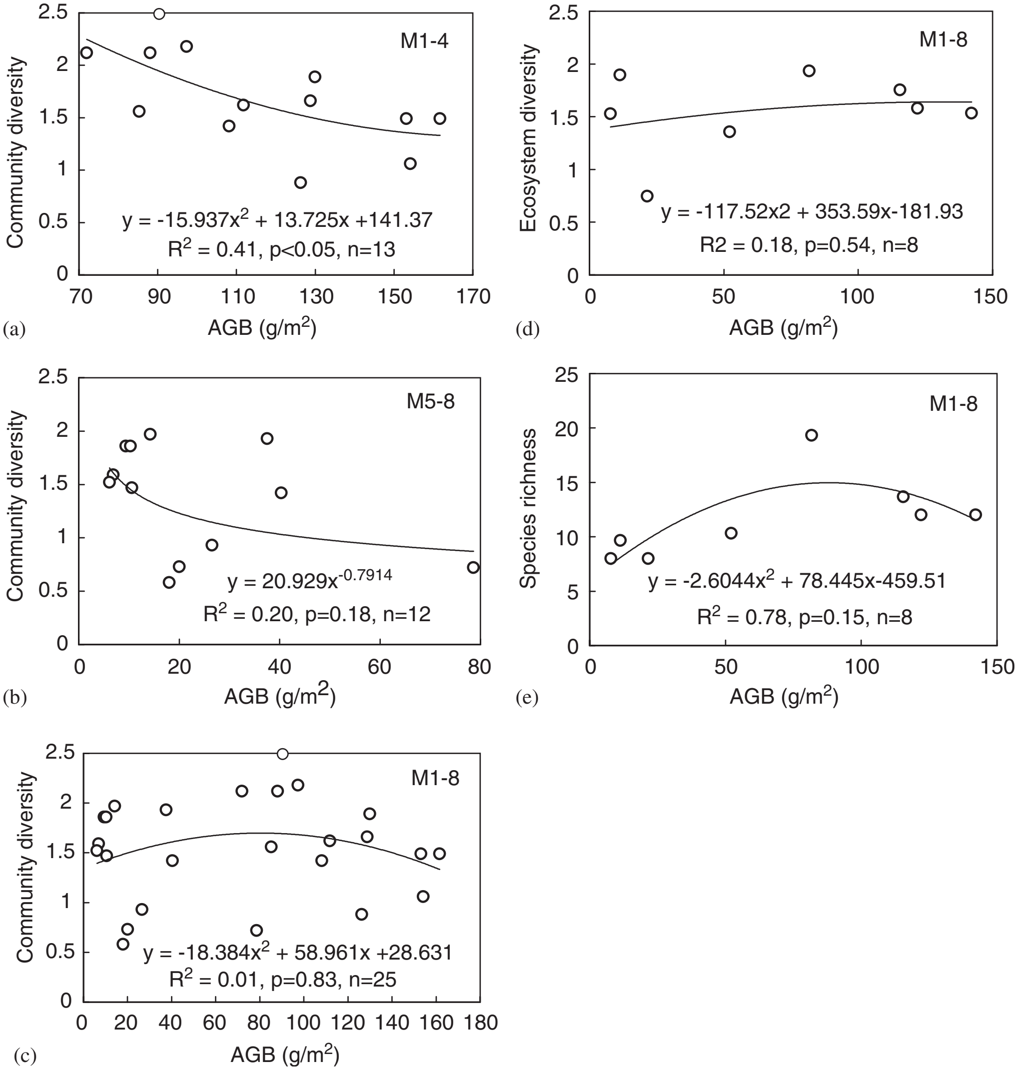

Fig. 3. Left column shows the relationships between community diversity and above-ground biomass (AGB) at the landscape scale of steppe grassland from site M1 to M4 (a), of desert grassland from M5 to M8 (b) and at the regional scale along the whole gradient from M1 to M8 (c). Right column shows the relationships between ecosystem diversity (d) and species richness (e) and above-ground biomass (AGB) at regional scale along the whole gradient from site M1 to M8.

to M8 is within the range of worldwide 'regional' scale, but it is relatively short in only ca. 1000 km.

Using the above scale definition, this current study of Mongolian grasslands confirmed that the relationship between species diversity and productivity is scale-dependent, both geographically and ecologically. In summary, at the individual species level, all relationships between plant diversity and AGB from local scale to landscape and regional scales are positively non-linear (mostly power law and a few exponential patterns, both significant and non-significant; Fig. 2). At the community level, such relationships are mostly unimodal, from the landscape scale (non-linear negative, both significant and non-significant) to the regional scale (unimodal, not significant; Fig. 3). At the ecosystem level, the relationship is unimodal at the regional scale (unimodal, not significant; Fig. 3). Therefore, at different ecological levels and geographic scales, there were different relationships between plant diversity and productivity in south-eastern Mongolian grasslands. Changing scales from the smaller to larger ones could alter the relationship between species richness and productivity (Scheiner et al., 2000; Scheiner and Jones, 2002).

As shown by the synthesis of Mittelbach et al. (2001), the published plant species diversity–productivity relationships were generally unimodal in studies at local and regional geographic scales but became more linearly positive at large continental scales. Furthermore, the plant species diversity–productivity relationships were more commonly unimodal in studies that crossed community types than in studies within a single community type. In the present study, we found that the relationships between plant diversity and AGB are non-linear (positive and negative) and unimodal at local and landscape scales but are unimodal at the regional scale. They are non-linear and unimodal within a community type and tend to be unimodal at the across community types. There is a general trend that the plant diversity–productivity relationships in south-eastern Mongolian grasslands changed from positive non-linear to unimodal patterns as the ecological levels changed from low to high, and as geographical scales changed from small to large. However, the unimodal pattern is common in this study area, except at the species level. Therefore, the relationships between plant diversity and productivity in Mongolian grasslands are basically consistent with the findings from studies in Europe and North America, but there are some exceptions in the present study.

It should be emphasized that the ecological level used in this paper involved not only the within- and across-community types as used by Waide et al. (1999) and Mittelbach et al. (2001), but also different taxonomic and functional levels (species, community and ecosystem). However, the ecological level and geographic scale are partially linked in this study, i.e. the ecological level includes in the geographic scale, and vice versa (e.g. Scheiner and Jones, 2002).

Both experimental and theoretical studies have recently explained plant diversity–productivity patterns (e.g. Tilman et al., 1997; Hector et al., 1999; Tilman, 1999, 2003; Yachi and Loreau, 1999; Loreau, 2000; Loreau et al., 2001, 2002), but ambiguities relating to the scale of application may affect theories proposed to explain productivity–diversity relationships (e.g. Waide et al., 1999; Gross et al., 2000; Mittelbach et al., 2001). The causes of changes in productivity–diversity patterns with scale include the range of productivity, location along a productivity gradient, and heterogeneity of resources and resource supply (Waide et al., 1999). Additional important factors that can determine diversity–productivity patterns include both the type of biodiversity measurement used (e.g. biodiversity index, species richness or species abundance) as well as the kind of productivity measured (e.g. net primary production, AGB, above- and below-ground biomass, or available energy such as rainfall, evapo-transpiration and soil nutrients).

A comprehensive analysis at regional scales was performed along a relatively longer transect (ca. 2100 km) in temperate steppes, from north-eastern China to south-eastern Mongolia (Wang and Ni, unpublished data). It was found that different regional scales could influence the relationships between species diversity (Fisher's alpha index) and productivity (AGB) in this region. One possible cause of these differences is the ecological selection effect. In addition, different surrogates for productivity (AGB or MAP) led to different diversity–productivity patterns (Wang and Ni, unpublished data). On the other hand, the sampling bias or the sampling effect that could affect the diversity–productivity patterns (Waide et al., 1999; Mittelbach et al., 2001; Scheiner and Jones, 2002; Aarssen et al., 2003) should also be considered in an analysis with a limited number of plots.

The diversity–productivity relationships vary not only over space but also over time (Fox, 2003; Symstad et al., 2003; Cardinale et al., 2004; Hooper and Dukes, 2004). Future research with carefully designed experiments that use multivariate approaches across both spatial and temporal scales is encouraged.

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