

# Positive linear relationship between productivity and diversity: evidence from the Eurasian Steppe

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## Summary

1. Understanding the productivity–diversity relationship (PDR) is a key issue in biodiversity–ecosystem functioning research, and has important implications for ecosystem management. Most studies have supported the predominance of a hump-shaped form of PDR in which species richness peaks at an intermediate level of productivity. However, this view has been challenged recently on several grounds.

2. Based on data from 854 field sites across the Inner Mongolia region of the Eurasian Steppe, we tested the form of PDR at different organizational levels (association type, vegetation type and biome) and multiple spatial scales (local, landscape and regional).

3. Our results showed that a positive linear, rather than hump-shaped, form was ubiquitous across all organizational levels and spatial scales examined. On the regional scale, this monotonic PDR pattern corresponded closely with the gradient in mean annual precipitation (MAP) and soil nitrogen. Increasing species dissimilarity with productivity could also contribute to the positive linear form of PDR.

4. Our results also indicated that grazing decreased both primary productivity and species richness but, intriguingly, not the form of PDR.

5. *Synthesis and applications.* This study provides the first direct test of the productivity–diversity relationship for the world’s largest contiguous terrestrial biome – the Eurasian Steppe. The predominance of a positive linear relationship in this region defies the commonly held view that a unimodal form of PDR dominates terrestrial ecosystems, supported mainly by studies in Africa, Europe and North America. It suggests that precipitation has a greater control on the productivity–diversity relationship in the Eurasian Steppe than grasslands elsewhere. Also, the positive linear relationship is surprisingly robust to grazing. Our results provide new insight into the productivity–diversity relationship and have several implications for restoring degraded lands and understanding ecological consequences of climate change in the Eurasian Steppe.

*Key-words:* ecosystem management, Eurasian steppe, grazing land, Inner Mongolia grassland, precipitation gradient, productivity–diversity relationship, spatial scale, species dissimilarity

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## Introduction

The relationship between species diversity and ecosystem productivity has been a central issue in ecology for decades (Rosenzweig 1992; Tilman 1999; Waide *et al.* 1999; Chapin *et al.* 2000; Sala *et al.* 2000; Mittelbach *et al.* 2001; Loreau, Naeem & Inchausti 2002; Hooper

*et al.* 2005). However, several key questions are yet to be answered fully regarding both the form and underlying mechanisms of the productivity–diversity relationship (PDR). For example, does productivity control, or is it controlled by, species diversity? Is there really a general pattern of PDR that exists in different biomes across the world? In particular, is the form of PDR predominantly monotonic or unimodal across different ecosystems and on spatial scales? These are not only fundamental research questions, but also have important implications for biodiversity conservation and ecosystem management.

The dominant view has been that PDR most frequently assumes a hump-shaped or unimodal form in terrestrial ecosystems (Grime 1973; Al-Mufti *et al.* 1977; Huston 1979; Tilman 1982; Rosenzweig 1992; Waide *et al.* 1999; Mittelbach *et al.* 2001). A hump-shaped form means that species diversity increases at low levels of productivity and decreases at high levels of productivity. In the lower range of productivity levels, species diversity increases with productivity because higher resource availability associated with increasing productivity leads to larger populations and lower extinction rates. In the higher range of productivity levels, spatial heterogeneity of limiting resources is reduced, interspecific competition is intensified and as a result species diversity tends to decrease (Grime 1973; Huston 1979; Rosenzweig 1992; Rosenzweig & Abramsky 1993; Tilman & Pacala 1993). However, this widely accepted view has been challenged recently on several grounds (Abrams 1995; Oksanen 1996; Whittaker & Heegaard 2003; Gillman & Wright 2006). Disagreements hinge on both the predominant form of PDR and its underlying causes.

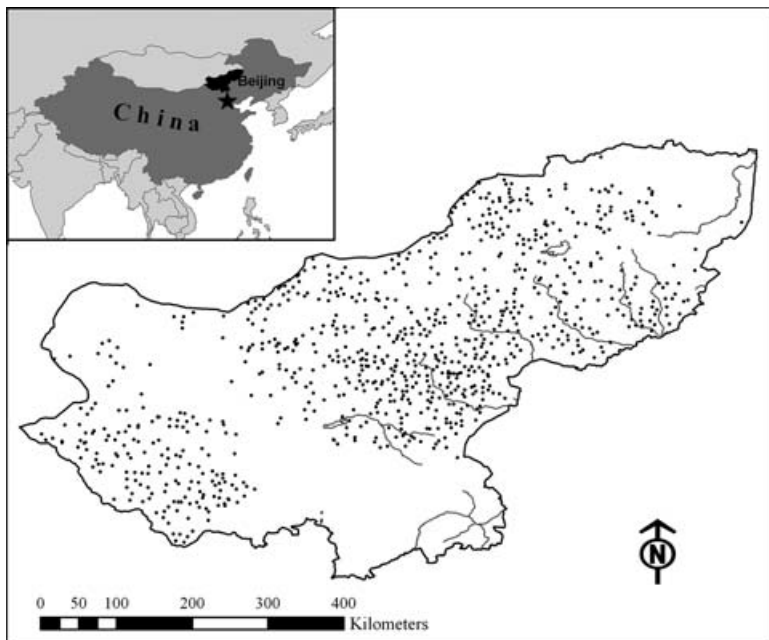
For example, a meta-analysis of 171 published studies by Mittelbach *et al.* (2001) showed that the hump-shaped curve was the dominant form of PDR for plants at local and regional scales. However, Whittaker & Heegaard (2003) pointed out that Mittelbach *et al.*'s (2001) study had several problems associated with spatial scale, surrogates for productivity and statistical methods. To alleviate these problems, Gillman & Wright (2006) re-analysed the pattern of PDR using data in Mittelbach *et al.* (2001) and other studies with a rigorous experimental design. These authors found that the form of PDR was almost always monotonic from regional to global scales, whereas a hump-shaped relationship occurred only rarely on local and landscape scales (Gillman & Wright 2006). Thus, it remains debatable whether a monotonic or hump-shaped form of PDR is dominant in ecosystems.

Accordingly, multiple explanations exist for the various forms of PDR. For example, Grace (1999) suggested that productivity was just one of several factors influencing plant species diversity. Other processes, such as disturbance, spatial heterogeneity and gradients in the species pool, may also be important in controlling species diversity (Grace 1999). Based on theoretical and empirical evidence, Abrams (1995) argued that processes of competition and coexistence

could produce a monotonic form of PDR, but that empirical support is lacking for the hypothesis that high productivity decreases heterogeneity. The unimodal relationship could also be an artefact of sampling schemes as using small plots of fixed size can give rise to the maximum species diversity at intermediate levels of productivity if plants are of varying sizes (Oksanen 1996; Weiher 1999). In a nutshell, studies have shown that PDR may be determined by the interplay of multiple abiotic and biotic factors, including the availability of energy and resources (Currie 1991; Gaston 2000; Fridley 2002; Baer *et al.* 2003; Cornwell & Grubb 2003; Hawkins *et al.* 2003; Evans, Warren & Gaston 2005), species pool (Taylor, Aarssen & Loehle 1990), disturbance (O'Connor 2005), herbivory (Olf & Ritchie 1998; Worm *et al.* 2002), the history of community assembly (Fukami & Morin 2003), spatial heterogeneity (Ritchie & Olf 1999; Mouquet, Moore & Loreau 2002; Anderson, McNaughton & Ritchie 2004) and the scale of analysis (Weiher 1999; Gross *et al.* 2000; Chase & Leibold 2002; Weiher & Howe 2003; Steiner & Leibold 2004; Harrison *et al.* 2006). The relative importance of these factors in determining the form of PDR, however, needs further clarification.

Most of the recent challenges to the prevailing view of PDR were based on either theoretical arguments or meta-analysis of already published studies. While these studies are useful direct tests of the productivity–diversity relationship, using data from a broad spectrum of ecosystems and across a range of scales are much needed. Also, existing studies of PDR for grasslands have been conducted primarily in North America, Europe and Africa (Grace 1999; Gross *et al.* 2000; Mittelbach *et al.* 2001; Anderson, McNaughton & Ritchie 2004; Jennings, Williams & Stromberg 2005; Gillman & Wright 2006), and many have potential problems associated with data acquisition, sample size and surrogates for productivity (i.e. productivity estimated from precipitation, soil nitrogen and potential evapotranspiration rather than field measurements) (Whittaker & Heegaard 2003; Gillman & Wright 2006). Surprisingly, few studies of PDR have ever been reported from the largest grassland region, the Eurasian Steppe.

Here, we examine the form and underlying causes of PDR using multiscaled data collected systematically from 854 field sites in the Inner Mongolia grassland region of China (Fig. 1), which is part of the Eurasian Steppe that extends over 8000 km from north-eastern China, Mongolia, Russia and Ukraine to Hungary (Coupland 1993). The Eurasian steppe is quite different from the prairie of North America in terms of climate, soils and dominant plant functional types, despite taxonomical similarities at the levels of genera and families (Coupland 1992, 1993; US National Research Council 1992). For example, the mean annual precipitation (MAP) of Eurasian grasslands ranges from 150 to 500 mm, whereas MAP of the North American grasslands varies from 300 to about 1000 mm (Coupland



**Fig. 1.** Location map of the study region, the Xilingol Grassland of Inner Mongolia in northern China, and spatial distribution of sampling sites.

1992, 1993). In Eurasian grasslands, the dominant plant functional type (PFT) is perennial  $C_3$  grasses. In North America, however, perennial  $C_4$  grasses predominate in short and tall prairies, and  $C_3$  and  $C_4$  grasses codominate in mixed prairies (Coupland 1992, 1993).

Recognizing the multitude of factors and the effect of spatial scale on PDR, we followed a hierarchical approach to facilitate our analysis and interpretation (O'Neill *et al.* 1986; Wu & Levin 1994; Wu & Loucks 1995). We organized data into a nested hierarchy of three levels: association type, vegetation type and biome. In terms of spatial extent, these three organizational levels correspond to the local, landscape and regional scales, respectively. We intended to address three specific questions: first, how does plant species richness respond to variations in productivity at different organizational levels and across spatial scales in the Eurasian Steppe region? Secondly, how does grazing affect the form of PDR? Thirdly, what are the possible underlying processes responsible for the observed form of PDR, particularly in terms of abiotic factors and changes in species composition along the environmental gradient?

## Materials and methods

### STUDY AREA

Our study was conducted in the Xilingol grassland, located in the middle part of the Inner Mongolia Autonomous Region, China (Fig. 1). The study area runs from  $41.4^\circ$  N to  $46.6^\circ$  N latitude and  $111.1^\circ$  E to  $119.7^\circ$  E longitude, covering an area of 203 000 km<sup>2</sup>.

The Xilingol grassland, where agricultural, residential and forested areas account for less than 10% of the total land area, is representative of the Eurasian steppe in terms of topography, climate, soils, vegetation composition and land use history (Wu & Loucks 1992; Coupland 1993). The topography of the study area consists of gently rolling hills, tablelands and sand dunes, with elevation between about 1000 and 1300 m. The mean annual temperature ranges from  $-2.3$  to  $5.6$  °C with the lowest mean monthly temperatures in January ( $-15.4$  to  $-22.4$  °C) and the highest in July ( $18.2$ – $23.4$  °C). The mean annual precipitation ranges from 104 to 411 mm, with 60–80% occurring in the growing season (May–August) which coincides with the peak temperature. Several soil types are found in this region, including chernozem, chestnut, calcic brown and aeolian soils. Along an East–West precipitation gradient, the study area includes five vegetation types: meadow steppe, typical steppe, sandy land, desert steppe and desert. The Xilingol grassland is composed primarily of  $C_3$  perennial bunchgrasses and perennial rhizome grasses, two dominant functional groups in most plant communities. Perennial forbs are found commonly in meadow steppe and typical steppe communities, while shrubs and semishrubs dominate in sandy land, degraded typical steppe and desert communities (Chinese Academy of Sciences Integrative Expedition Team to Inner Mongolia and Ningxia 1985).

### DATA COLLECTION AND SAMPLING METHODS

Data used in this study were acquired primarily from the Xilingol Grassland Management Station. Our data set is composed of 854 field sites, representing 13 association types that belong to five vegetation types in the study area (Table 1). The sampling sites were distributed fairly evenly across the Xilingol grassland with a 10–15 km spatial interval between sites, and the number of sites for each association was proportional to its area (Fig. 1). Data for each site include geographical coordinates, elevation, soil type, land use type, association type, vegetation type, plant species richness and above-ground biomass production at both species and community levels.

Above-ground biomass was sampled at its peak time in late July and August from 1981 to 1985, which approximated the above-ground net primary productivity (ANPP) in temperate grasslands (Sala & Austin 2000; Bai *et al.* 2004). At each site, ANPP of herbaceous plants was sampled in three  $1 \times 1$  m quadrats, located randomly within a  $100 \times 100$  m area. Above-ground biomass of all vascular plants in each quadrat was harvested at ground level and sorted to species. ANPP for shrubs was sampled using three  $5 \times 5$  m quadrats at the same time. The leaves and current-year twigs of shrubs in each quadrat were collected and separated to species. The average dry mass and the total number of plant species of three quadrats were used to estimate ANPP and species richness for each of the 854 sites.

**Table 1.** Abiotic and biotic characteristics of the 13 association types in the Xilingol grassland

| No. | Association type<br>(named after dominant species)       | Vegetation type | MAP<br>(mm) | MAT<br>(°C) | Soil<br>type                                   | Species richness |       | ANPP (g m <sup>-2</sup> ) |              | Dominant plant<br>functional group             |
|-----|--|-----------------|-------------|-------------|--|------------------|-------|---------------------------|--------------|--|
|     |  |                 |             |             |  | Mean             | Range | Mean                      | Range        |  |
| 1   | <i>Filifolium sibiricum-<br/>Carex pediformis</i>        | Meadow steppe   | 350.2       | 0.0         | Typical chernozem soil<br>Light chernozem soil | 22.25            | 10–36 | 184.85                    | 36.81–334.35 | Perennial forbs                                |
| 2   | <i>Leymus chinensis-<br/>Stipa baicalensis</i>           | Meadow steppe   | 332.7       | 0.5         | Light chernozem soil                           | 21.58            | 8–32  | 128.25                    | 27.02–299.27 | Perennial rhizome and<br>bunch grasses         |
| 3   | <i>Stipa baicalensis</i>                                 | Meadow steppe   | 328.3       | 0.3         | Typical chernozem soil<br>Light chernozem soil | 18.97            | 12–33 | 117.29                    | 42.49–259.08 | Perennial bunch grasses                        |
| 4   | <i>Leymus chinensis</i>                                  | Typical steppe  | 283.5       | 1.0         | Dark chestnut soil                             | 14.04            | 4–29  | 88.61                     | 11.99–324.67 | Perennial rhizome grass                        |
| 5   | <i>Stipa grandis</i>                                     | Typical steppe  | 277.6       | 1.2         | Typical chestnut soil                          | 15.98            | 7–25  | 91.09                     | 16.73–270.18 | Perennial bunch grasses                        |
| 6   | <i>Cleistogenes squarrosa</i>                            | Typical steppe  | 267.8       | 1.4         | Typical chestnut soil<br>Light chestnut soil   | 13.53            | 6–27  | 56.86                     | 17.18–134.33 | Perennial bunch grasses                        |
| 7   | <i>Artemisia frigida</i>                                 | Typical steppe  | 267.2       | 1.8         | Typical chestnut soil<br>Light chestnut soil   | 13.23            | 7–25  | 60.05                     | 9.40–164.58  | Semi-shrubs and<br>perennial bunch grasses     |
| 8   | <i>Caragana microphylla</i>                              | Typical steppe  | 249.1       | 2.5         | Typical chestnut soil<br>Light chestnut soil   | 14.38            | 5–20  | 48.33                     | 11.59–152.71 | Shrubs and perennial<br>bunch grasses          |
| 9   | <i>Artemisia intramongolica-<br/>Psammochloa villosa</i> | Sandy land      | 274.2       | 2.3         | Aeolian soil                                   | 12.45            | 7–23  | 62.82                     | 10.84–201.76 | Semi-shrubs and<br>perennial bunch grasses     |
| 10  | <i>Stipa krylovii</i>                                    | Typical steppe  | 242.0       | 2.3         | Typical chestnut soil<br>Light chestnut soil   | 12.81            | 5–22  | 49.57                     | 6.12–130.27  | Perennial bunch grasses                        |
| 11  | <i>Allium polyrhizum-<br/>Cleistogenes songorica</i>     | Desert steppe   | 180.8       | 4.6         | Typical calcic brown soil                      | 12.22            | 5–17  | 39.89                     | 2.91–85.79   | Perennial forbs and<br>perennial bunch grasses |
| 12  | <i>Stipa klemenzii</i>                                   | Desert steppe   | 169.1       | 3.9         | Typical calcic brown soil                      | 11.00            | 5–19  | 22.06                     | 1.57–64.23   | Perennial bunch grasses<br>and annuals         |
| 13  | <i>Reamuria soongorica-<br/>Salsola passerina</i>        | Desert          | 168.5       | 3.9         | Light calcic brown soil                        | 8.80             | 2–20  | 18.56                     | 5.55–41.88   | Shrub and semishrubs                           |

Long-term meteorological data from 1961 to 2000 were obtained from 48 weather stations within and adjacent to the study area.

#### SCHEME FOR DATA ANALYSIS

In general, levels of nested hierarchies can be related to spatial scales (Wu 1999). In our case, the three organizational levels – association type, vegetation type and biome – correspond to the local, landscape and regional scales (in terms of spatial extent). Relating organizational units to spatial scales helps to reduce the potential confusion caused by using terms such as local or regional scales with arbitrary spatial extents, and facilitates the analysis and interpretation of results by providing a unifying structure (Collins & Glenn 1990; Wu & Levin 1994; Wu & Loucks 1995; Pickett, Wu & Cadenasso 1999).

To address our first question of the form of PDR at different organizational level and corresponding scales, prior to statistical analyses data from different sites were aggregated into three organizational levels: association type (local scale), vegetation type (landscape scale) and biome (regional scale). Specifically, the 854 field sites from the Inner Mongolia grassland biome were classified into 13 association types that belonged to five vegetation types. At the landscape scale, we considered only data from meadow steppe, typical steppe and desert steppe. Data from sandy land and desert, both of which had only one single association type in the region, were excluded from the analysis because they were already used in the analysis at the association level (to avoid repeating the analysis at two levels using the same data set). At the regional scale, the form of PDR is represented in terms of local sites, association types and the vegetation types within the entire biome.

To examine the effects of grazing on PDR, we focused our analysis on the regional scale only, because further grouping data into vegetation and association types for this analysis would result in an insufficient sample size. Our data fell into four land use types representing a gradient of increasing grazing intensity: hayfields (HF), winter-grazing grasslands (WG), year-round-grazing grasslands (YG) and summer-grazing grasslands (SG). Summer grazing is the most intensified land use practice in the Inner Mongolia Grassland because of the highest stocking rate due to the excessively large number of animals in a limited area. We assessed the effects of grazing intensity on ANPP, species richness and forms of PDR. To make the analysis more robust, we used only data from 688 sites of meadow steppe and typical steppe that had all the four land use types and similar land use history.

To explore possible environmental factors responsible for the observed forms of PDR, we examined how ANPP and species richness were related to MAP and MAT (mean annual temperature), respectively, across the region using simple regressions. At the regional

scale, we also assessed how the slope (a) and intercept (b) in the linear regression model (species richness =  $a \times \text{productivity} + b$ ) were related to MAP across different association types. To investigate how the form of PDR may be influenced by differences in species composition ( $\beta$ -diversity) along the environmental gradient, we calculated the dissimilarity index ( $1 - \text{Jaccard's similarity}$ ) for all possible pairs among sites within each association type (Chase & Leibold 2002). To examine further if high average productivity was related to high degree of environmental heterogeneity at the regional scale, we analysed the relationship between the variance in ANPP among sites within each association type and the average ANPP of association types (Chase & Leibold 2002). Similarly, we also analysed the relationship between the variance in MAP within each association type and the average MAP across association types within the region.

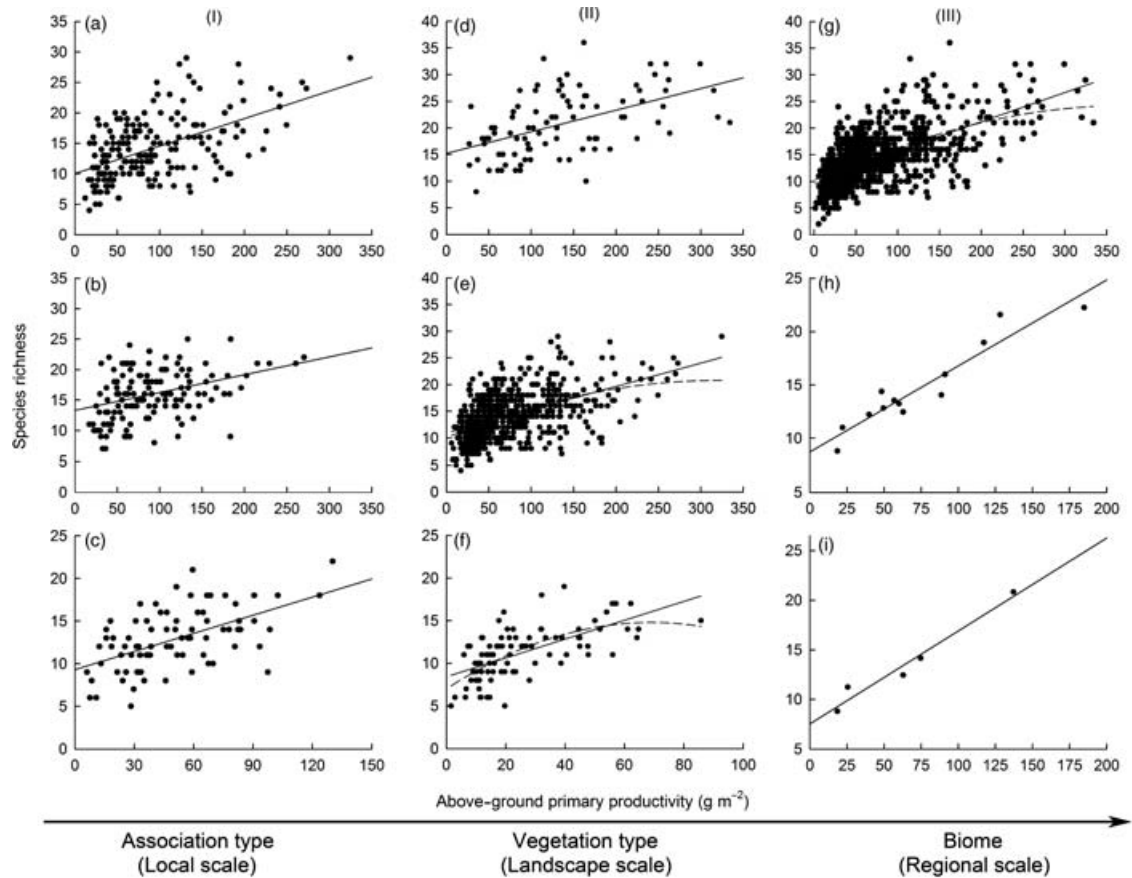
#### STATISTICAL ANALYSIS

Statistical analysis was performed using SAS version 9.1 (SAS Institute Inc. 2004). We used both ordinary least squares (OLS) regression and Poisson regression using generalized linear models (GLM) to examine whether PDR was positive linear or quadratic at each organizational level and corresponding scale as per Mittelbach *et al.* 2001) and Gillman & Wright 2006). For the Poisson GLM, Pearson's  $\chi^2$  was used to correct for over-dispersion and output statistics in cases where species richness data violated the assumption of Poisson errors. In addition, the Mitchell-Olds and Shaw (MOS) test (Mitchell-Olds & Shaw 1987) was used to examine whether a significant quadratic relationship reached the predicted peak within the observed range of ANPP. A given PDR was considered significantly 'positive linear' or 'unimodal' only if the results of both OLS and Poisson GLM regressions were congruent (significant at  $P < 0.05$ ). MAP and MAT for each site were interpolated using a Geographical Information System (GIS)-based multiple regression method developed by Ninyerola *et al.* (Ninyerola, Pons & Roure 2000).

## Results

#### FORM OF PDR AT DIFFERENT ORGANIZATIONAL LEVELS AND SPATIAL SCALES

At the association type level or local spatial scale, 11 of the 13 association types exhibited a statistically significant, positive linear form of PDR (Fig. 2a–c and Table 2), with two of the 11 also showing a significant unimodal relationship (Table 2). The other two association types, i.e. *Filifolium sibiricum* + *Carex pediformis* association and *Caragana microphylla* association, showed no significant relationship (Table 2). At the vegetation type level or landscape scale, we found a



**Fig. 2.** Relationships between productivity and species richness at different organizational levels and spatial scales. (1) At the level of association type or the local scale, three association types are shown as examples: a, *Leymus chinensis* association; b, *Stipa grandis* association; c, *S. krylovii* association. (2) At the level of vegetation type or the landscape scale: d, meadow steppe; e, typical steppe; f, desert steppe. (3) At the level of biome or the regional scale: g, by individual site; h, by association type; i, by vegetation type. The fitted lines represent statistically significant linear (solid line) and quadratic (dashed line) relationships between productivity and species richness.

**Table 2.** Summary of regression analyses of the forms of PDR at different organizational levels and corresponding spatial scales

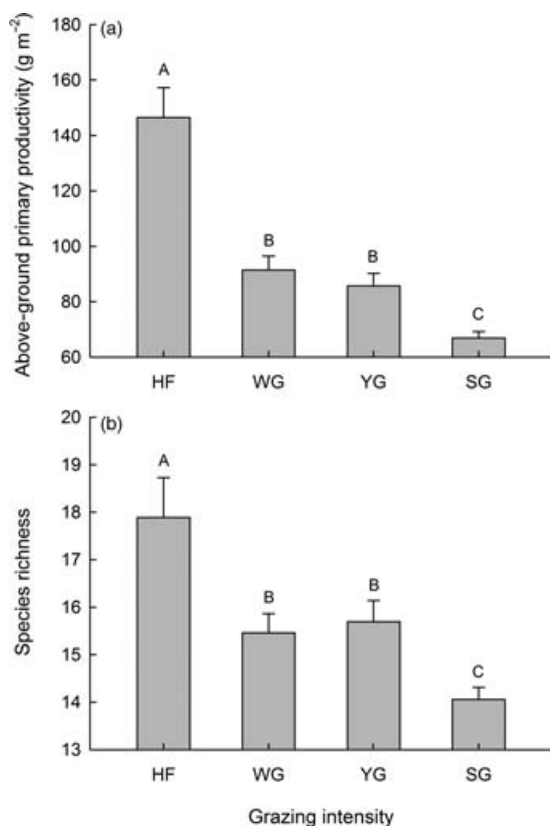
| Organizational level and scale                               | No. of sites | OLS† regression            |                       |                               |                       | MOS* | Poisson GLM‡               |                               | MOS | Pattern summary§ |
|--|--------------|----------------------------|-----------------------|-------------------------------|-----------------------|------|----------------------------|-------------------------------|-----|------------------|
|  |              | <i>P</i> <sub>linear</sub> | <i>R</i> <sup>2</sup> | <i>P</i> <sub>quadratic</sub> | <i>R</i> <sup>2</sup> |      | <i>P</i> <sub>linear</sub> | <i>P</i> <sub>quadratic</sub> |     |                  |
| Association type (local scale)                               |              |                            |                       |                               |                       |      |                            |                               |     |                  |
| <i>Filifolium sibiricum</i> – <i>Carex pediformis</i>        | 20           | 0.1599                     | 0.11                  | 0.1586                        | 0.21                  |      | 0.1522                     | 0.1153                        |     | NS               |
| <i>Leymus chinensis</i> – <i>Stipa baicalensis</i>           | 38           | < 0.0002                   | 0.33                  | 0.8498                        | 0.33                  |      | < 0.0001                   | 0.6180                        |     | PL               |
| <i>Stipa baicalensis</i>                                     | 31           | 0.0008                     | 0.33                  | 0.6484                        | 0.33                  |      | 0.0002                     | 0.8676                        |     | PL               |
| <i>Leymus chinensis</i>                                      | 202          | < 0.0001                   | 0.29                  | 0.8713                        | 0.29                  |      | < 0.0001                   | 0.2662                        |     | PL               |
| <i>Stipa grandis</i>   | 138          | < 0.0001                   | 0.13                  | 0.2420                        | 0.14                  |      | < 0.0001                   | 0.1729                        |     | PL               |
| <i>Cleistogenes squarrosa</i>                                | 62           | < 0.0001                   | 0.33                  | 0.0018                        | 0.44                  | UN   | < 0.0001                   | 0.0002                        | UN  | PL, UN           |
| <i>Artemisia frigida</i>                                     | 92           | < 0.0001                   | 0.21                  | 0.2202                        | 0.23                  |      | < 0.0001                   | 0.1289                        |     | PL               |
| <i>Caragana microphylla</i>                                  | 24           | 0.4605                     | 0.03                  | 0.4371                        | 0.05                  |      | 0.4565                     | 0.4284                        |     | NS               |
| <i>Artemisia intramongolica</i> – <i>Psammochloa villosa</i> | 58           | < 0.0001                   | 0.31                  | 0.8118                        | 0.31                  |      | < 0.0001                   | 0.4747                        |     | PL               |
| <i>Stipa krylovii</i>  | 81           | < 0.0001                   | 0.30                  | 0.6587                        | 0.30                  |      | < 0.0001                   | 0.3562                        |     | PL               |
| <i>Allium polyrhizum</i> – <i>Cleistogenes songorica</i>     | 18           | 0.0005                     | 0.55                  | 0.1717                        | 0.60                  |      | < 0.0001                   | 0.0866                        |     | PL               |
| <i>Stipa klemenzi</i>  | 75           | < 0.0001                   | 0.33                  | 0.0289                        | 0.38                  | UN   | < 0.0001                   | 0.0113                        | UN  | PL, UN           |
| <i>Reamuria songorica</i> – <i>Salsola passerina</i>         | 15           | 0.0368                     | 0.29                  | 0.6707                        | 0.31                  |      | 0.0222                     | 0.8908                        |     | PL               |
| Vegetation type (landscape scale)                            |              |                            |                       |                               |                       |      |                            |                               |     |                  |
| Meadow steppe  | 89           | < 0.0001                   | 0.25                  | 0.0882                        | 0.28                  |      | < 0.0001                   | 0.0378                        |     | PL               |
| Typical steppe   | 599          | < 0.0001                   | 0.25                  | 0.0102                        | 0.26                  | UN   | < 0.0001                   | 0.0003                        | UN  | PL, UN           |
| Desert steppe  | 93           | < 0.0001                   | 0.40                  | 0.0112                        | 0.44                  | UN   | < 0.0001                   | 0.0032                        | UN  | PL, UN           |
| Biome (regional scale)                                       |              |                            |                       |                               |                       |      |                            |                               |     |                  |
| By individual site   | 854          | < 0.0001                   | 0.37                  | 0.0001                        | 0.38                  | UN   | < 0.0001                   | < 0.0001                      | UN  | PL, UN           |
| By association type  | 13           | < 0.0001                   | 0.90                  | 0.4218                        | 0.90                  |      | < 0.0001                   | 0.0400                        |     | PL               |
| By vegetation type   | 5            | 0.0033                     | 0.96                  | 0.4642                        | 0.97                  |      | < 0.0001                   | 0.9525                        |     | PL               |

†OLS = ordinary least squares; ‡GLM = general linear model; §PL = positive linear relationship; UN = unimodal relationship; NS = non-significant relationship. \*MOS = the Mitchell-Olds and Shaw test.

**Table 3.** Effects of grazing on the relationship between productivity and species richness. The abbreviations are the same as in Table 1

| Land use type<br>(grazing intensity) | No. of<br>sites | OLS† regression |       |                 |       | Poisson GLM‡ |              |                 | Pattern<br>summary§ |        |
|--------------------------------------|-----------------|-----------------|-------|-----------------|-------|--------------|--------------|-----------------|---------------------|--------|
|                                      |                 | $P_{linear}$    | $R^2$ | $P_{quadratic}$ | $R^2$ | MOS*         | $P_{linear}$ | $P_{quadratic}$ |                     | MOS    |
| Hay fields                           | 52              | < 0.0001        | 0.41  | 0.7952          | 0.41  |              | < 0.0001     | 0.6701          |                     | PL     |
| Winter-grazed                        | 168             | < 0.0001        | 0.37  | 0.6687          | 0.37  |              | < 0.0001     | 0.1761          |                     | PL     |
| Year-round-grazed                    | 140             | < 0.0001        | 0.30  | 0.0049          | 0.33  | UN           | < 0.0001     | 0.0006          | UN                  | PL, UN |
| Summer-grazed                        | 328             | < 0.0001        | 0.24  | 0.0235          | 0.25  | UN           | < 0.0001     | 0.0031          | UN                  | PL, UN |

†OLS = ordinary least squares. ‡GLM = general linear model; §PL = positive linear relationship; UN = unimodal relationship; NS = non-significant relationship. \*MOS = the Mitchell-Olds and Shaw test.



**Fig. 3.** The effects of the grazing intensity on productivity and species richness (error bars denote standard errors). a, Productivity; b, species richness. Bars with the same letter were not significantly different in Duncan's multiple range tests. HF, hayfields; WG, winter-grazing grasslands; YG, year-round-grazing grasslands; SG, summer-grazing grasslands.

significant positive linear form of PDR in all three major vegetation types (meadow steppe, typical steppe and desert steppe; Fig. 2d–f and Table 2). For the typical steppe and the desert steppe, a unimodal form of PDR was also statistically significant, but the MOS test indicated that there was only one data point beyond the predicted peak value of the quadratic model (Fig. 2e,f), suggesting that the relationship was weak. At the biome level or regional scale a positive linear form of PDR was found across local sites, association types and vegetation types (Fig. 2g–i and Table 2). The regional-scale PDR for local sites also showed a

significant quadratic relationship (Fig. 2g), but again only a few data points fell beyond the predicted peak value in the MOS test.

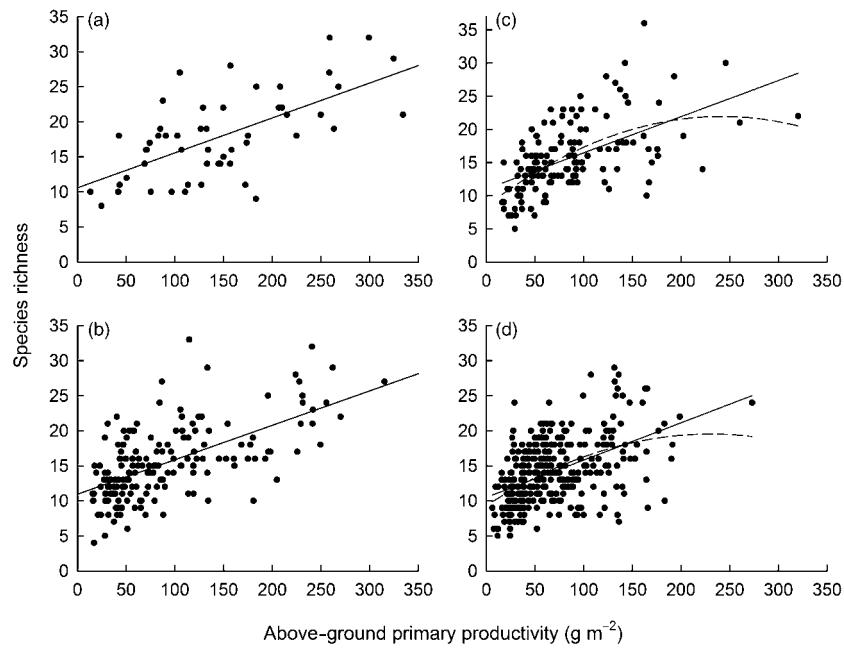
#### EFFECTS OF GRAZING ON THE FORM OF PDR

At the regional scale, both ANPP and species richness decreased significantly with increasing grazing intensity (GLM; for ANPP,  $F = 10.88$ ,  $P < 0.0001$ ; for species richness,  $F = 35.25$ ,  $P < 0.0001$ ; Fig. 3). Among the four land use types, hayfields, which had no grazing, showed the highest average ANPP and species richness. In contrast, summer-grazing grasslands, with the highest grazing intensity, exhibited the lowest average ANPP and species richness (Fig. 3). A positive linear PDR form was found for all four land use types (Fig. 4 and Table 3). Although a unimodal relationship was also statistically significant for both the year-round-grazing and summer-grazing grasslands, only few data points existed beyond the peak value in the MOS test (Fig. 4).

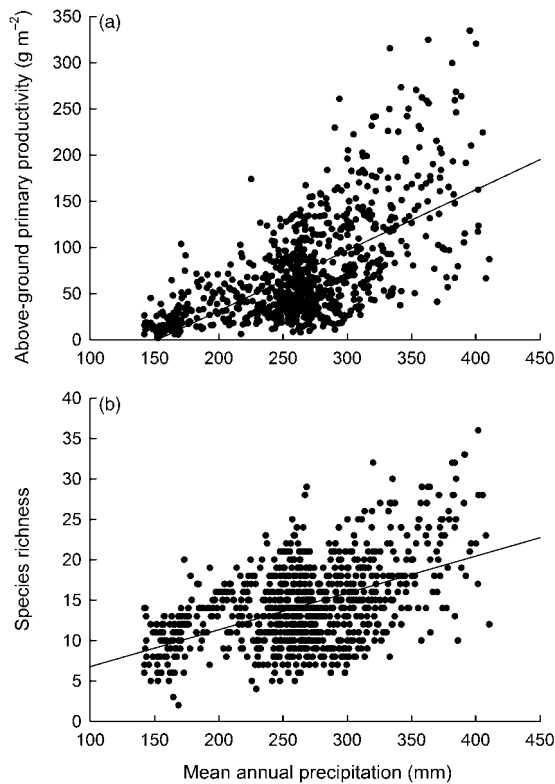
In the linear regression model (species richness =  $a \times$  productivity +  $b$ ), the slopes for HF, WG, YG and SG were 0.050, 0.049, 0.055 and 0.053, respectively. The intercepts for HF, WG, YG and SG were 10.59, 10.98, 11.02 and 10.50, respectively. We further examined if there were quantitative differences among the four land use types in terms of the slope and intercept. Results showed that neither the slope ( $F = 0.19$ ,  $P > 0.05$ ) nor the intercept ( $F = 1.52$ ,  $P > 0.05$ ) differed significantly along the gradient of grazing intensity.

#### EFFECTS OF PRECIPITATION ON ANPP, SPECIES RICHNESS AND PDR

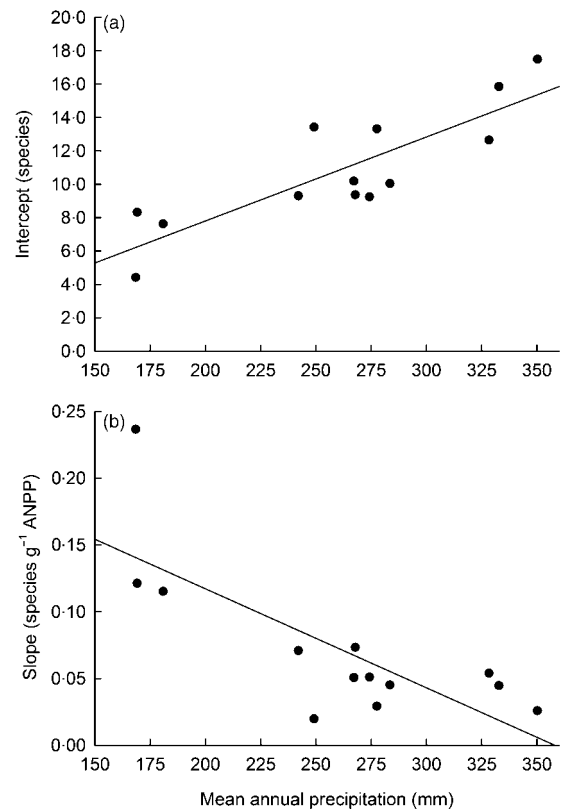
At the regional scale, both ANPP and species richness were correlated linearly with MAP (Fig. 5) as well as with MAT. Results from simple regressions showed that MAP alone explained 41% of the variation in ANPP (ANPP =  $0.654MAP - 99.486$ ;  $n = 854$ ,  $F = 592.03$ ,  $R^2 = 0.41$ ,  $P < 0.0001$ ) and 25% of the variation in species richness (species richness =  $0.046MAP + 2.241$ ;  $n = 854$ ,  $F = 280.62$ ,  $R^2 = 0.25$ ,  $P < 0.0001$ ), while MAT explained only 4% of the variation in



**Fig. 4.** Effects of grazing on the relationship between productivity and species diversity. a, Hayfields; b, winter-grazing grasslands; c, year-round-grazing grasslands; d, summer-grazing grasslands.



**Fig. 5.** Relationship of mean annual precipitation to productivity and species richness. a, Productivity was positively correlated with MAP across all sites; b, species richness was positively correlated with MAP.

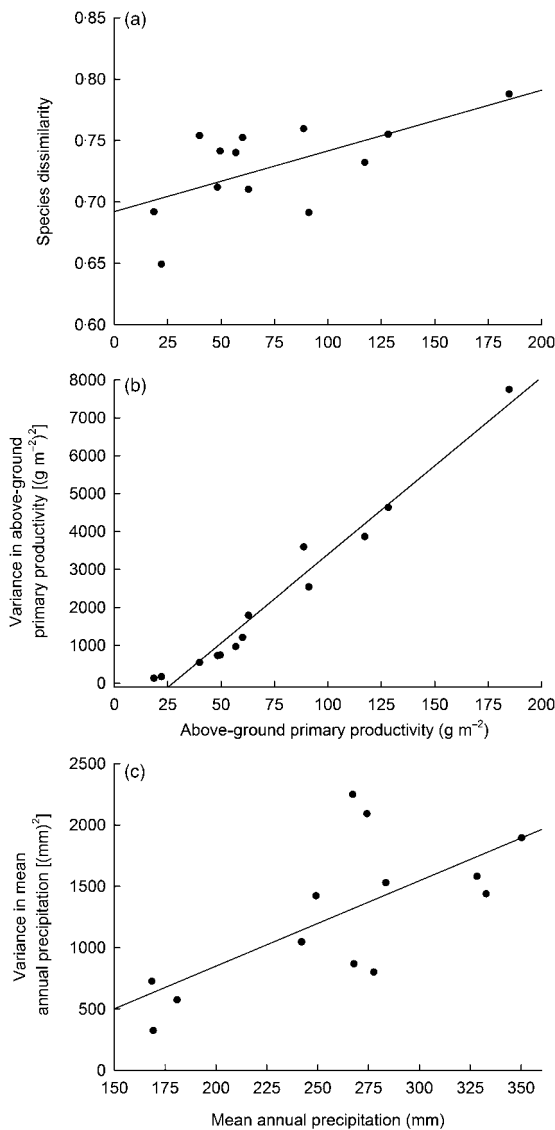


**Fig. 6.** Effects of precipitation on the relationship between productivity and species diversity at regional scale. a, The intercept of the linear regression model (species richness =  $a \times$  productivity + b) was positively correlated with MAP across different association types. b, The slope was negatively correlated with MAP.

species richness ( $F = 39.47$ ,  $R^2 = 0.04$ ,  $P < 0.0001$ ) and 6% of variation in ANPP ( $F = 53.84$ ,  $R^2 = 0.06$ ,  $P < 0.0001$ ). For the linear regression model of PDR, the intercept increased linearly with MAP ( $n = 13$ ,  $F = 27.28$ ,

$R^2 = 0.31$ ,  $P = 0.0003$ ; Fig. 6a), whereas the slope declined linearly with MAP ( $n = 13$ ,  $F = 14.84$ ,  $R^2 = 0.57$ ,  $P = 0.0027$ ; Fig. 6b) across different association types along the precipitation gradient.





**Fig. 7.** Change in species dissimilarity and variability in precipitation and productivity at the regional scale. a, Species dissimilarity–productivity relationship, each point being the average of the dissimilarity estimates among all sites of the same association type; b, productivity variance–productivity relationship; c, precipitation variance–precipitation relationship.

#### EFFECTS OF ENVIRONMENTAL HETEROGENEITY ON SPECIES DISSIMILARITY

Our analysis showed that the dissimilarity in species composition, a measure of  $\beta$ -diversity, increased significantly with productivity across association types in the region ( $n = 13$ ,  $R^2 = 0.43$ ,  $F = 8.25$ ,  $P = 0.0152$ ; Fig. 7a). Species dissimilarity was highest in meadow steppe and lowest in desert. The variance in ANPP among sites within each association type increased with the mean ANPP for each association type ( $n = 13$ ,  $R^2 = 0.97$ ,  $F = 333.03$ ,  $P < 0.0001$ ; Fig. 7b). Similarly, the variance in MAP within each association type was correlated positive with the mean MAP for each association type ( $n = 13$ ,  $R^2 = 0.47$ ,  $F = 9.94$ ,  $P = 0.0092$ ; Fig. 7c).

#### Discussion

This study represents the first comprehensive test of the relationship between productivity and species richness from the Eurasian steppe. Our results have shown that the form of PDR in the Inner Mongolia grassland is predominantly positive linear at multiple organizational levels across local, landscape and regional scales. Although a statistically significant unimodal form was also found in a few cases, this relationship was apparently weak because only a few data points existed beyond the predicted peak value in the MOS test. This means that, within the range of the observed productivity in the Inner Mongolia grassland, a unimodal form of PDR is either a rare situation or an artefact of the statistical analysis. Our general conclusion on the dominance of a positive linear PDR was also corroborated by two recent studies using different and smaller data sets at local to regional scales (Bai *et al.* 2000; Ma & Fang 2006). Lavrenko *et al.* (1993) showed that, along a gradient from the meadow steppe of the Black Sea region to the extremely dry desert steppe of Mongolia, species richness decreased from 33–36 to 7–10 species per m<sup>2</sup>, and ANPP declined from 320–420 to 6–30 g m<sup>-2</sup>. Our re-analysis, after incorporating the most and least productive areas from Lavrenko *et al.* (1993) into our data set, again showed a positive linear PDR across different vegetation types (results not shown here), suggesting that the positive linear relationship may be dominant over the entire Eurasian steppe region.

This finding is in sharp contrast with the commonly held view that a hump-shaped form of PDR is predominant in terrestrial ecosystems of Europe, Africa and North America from local to continental scales (Waide *et al.* 1999; Mittelbach *et al.* 2001; Chalcraft *et al.* 2004; Jennings, Williams & Stromberg 2005). However, our results are congruent with the general conclusion of Gillman & Wright (2006), that a positive, rather than humped-shaped, relationship of PDR predominates terrestrial ecosystems. One may argue that the lack of a unimodal relationship in our analysis may be due to the limited range of productivity. However, our data set covered almost the full range of ANPP in the Eurasian steppe region, which is supported by much less precipitation ( $< 500$  mm year<sup>-1</sup>) than that in North American prairies (up to about 1000 mm year<sup>-1</sup>).

Although our study has demonstrated the unequivocal dominance of a positive linear form of PDR in the Inner Mongolia Grassland, it does not exclude the existence of other forms in this region. Indeed, our results showed that the degree of predominance or exclusiveness of the positive linear form depended on organizational levels and spatial scales. For example, at higher levels of organization (vegetation type and biome) and broader scales (landscape and region), a positive linear form was observed consistently. At the level of association type or local spatial scale, cases in which productivity and diversity showed either no

relationship or a unimodal relationship also existed. At an even finer scale of local plots, no consistent form of PDR was detected (Bai *et al.* unpublished results). Therefore, our results are not inconsistent with the hypothesis that the form of PDR varies with spatial scale and ecological hierarchy (Chase & Leibold 2002).

Ellis & Swift (1988) suggested that many semiarid and arid grassland ecosystems are non-equilibrium grazing systems, which is characterized by stochastic abiotic conditions (e.g. fluctuations in precipitation and perturbations of extended droughts), variable plant growing conditions and density-independent herbivore population patterns. Under these conditions, both above-ground net primary productivity and species richness are controlled primarily by abiotic factors, while interspecific competition and competitive exclusion should not be important regulatory processes of plant communities (Ellis & Swift 1988). This hypothesis seems to be corroborated by our results, that MAP alone explained 41% of the variation in ANPP and 25% of the variation in species richness across the region. At regional scale, we further evaluated how the slope and intercept in the linear regression model of PDR (species richness =  $a \times \text{productivity} + b$ ) were affected by precipitation across different association types. Our study indicated that the intercept increased linearly with MAP, suggesting that, for a given association, the higher local species richness is related to higher MAP. The slope, however, decreased linearly with MAP, which means that the relative importance of precipitation as a controlling variable on PDR also varies between associations. In general, plant associations in the driest sites showed the greatest slopes of PDR, and those in the wettest sites showed the lowest slopes. In the Inner Mongolia grassland region, MAP and total soil N exhibit a linearly increasing trend from desert to meadow steppe (Chinese Academy of Sciences Integrative Expedition Team to Inner Mongolia & Ningxia 1985; Inner Mongolia Soil Census Office & Inner Mongolia Soil and Fertilizer Service 1994). Our previous study also showed that both productivity and species richness were positively correlated to total soil N, which accounted for 44–57% of the variations at regional scale (Bai *et al.* 2000). This is because, in addition to water, both productivity and species richness in arid and semiarid grasslands are limited substantially by nitrogen (Vitousek & Howarth 1991). Thus, MAP and soil N might be the two most important environmental factors controlling productivity, species richness and consequently the regional-scale pattern of PDR in the Inner Mongolia grassland.

Spatial heterogeneity, the manifestation of intertwined patchiness and gradients, underlies many observed ecological patterns at different levels of organization and across a wide range of scales (Levin 1992; Wu & Levin 1994; Wu & Loucks 1995). While the theory of hump-shaped PDR focuses on the patchiness aspect of heterogeneity that tends to increase species diversity, our study suggests that the spatial gradient of environmental

conditions (mainly precipitation) can dictate the pattern of PDR on the Eurasian continent. This does not mean that patchiness is not relevant to our observed pattern of PDR. In fact, our study indicated that species dissimilarity also increased with productivity across the region. Associations with low productivity shared more common species, whereas associations with high productivity shared only a small number of species. Chase & Leibold (2002) proposed that environmental heterogeneity is one of the three possible mechanisms leading to increased species dissimilarity with increasing productivity. Chalcraft *et al.* (2004) also showed that, in the arid and subhumid North American grasslands, increased species dissimilarity among local communities with greater productivity was the key mechanism determining the form of PDR at the regional scale. Our study showed that the variance in ANPP within each association type increased linearly with the average ANPP of association types at the regional scale. We also found a significantly positive relationship between the variance in MAP within each association type and the average MAP of association types across the region. Thus, local community-level patchiness, including both composition and configuration of microhabitats, may increase with productivity along the precipitation gradient.

Much of the Inner Mongolia grassland has been degraded due, primarily, to overgrazing (Jiang, Han & Wu 2006), and we hypothesized originally that the form of PDR might be affected by different land use practices. However, the results of our study showed otherwise, although grazing did decrease both ANPP and species richness. Reduced above-ground biomass and species richness by overgrazing in the Inner Mongolia Grassland had been documented in previous studies (e.g. Li 1988, 1993). Elsewhere, Milchunas *et al.* (1988) indicated that, in North American grasslands with a long history of grazing, plant diversity decreased linearly with increasing grazing intensity as grazing-intolerant rare species were eliminated. Milchunas & Lauenroth (1993) further examined 236 field sites world-wide and found that in most cases grazing negatively affected grassland ANPP.

Drylands occupy more than 50% of the Earth's land surface, and 54% of grasslands have been converted to managed grazing lands (Asner *et al.* 2004). Thus, our results have important implications for understanding the potential effects of climate change and improving the current practices of grassland management in a global context. First, alterations in regional precipitation pattern due to global climate change are likely to affect grassland productivity, species richness and their relationship. These changes may further influence ecosystem resilience in this region (Bai *et al.* 2004). Secondly, as the form of PDR does not seem sensitive to grazing, PDR is apparently a poor indicator of the overgrazing-induced ecosystem degradation that has occurred over vast areas across the Eurasian Steppe region. Instead, a measure of the reduction in species richness or productivity is related more directly to the

actual ecosystem condition. Finally, because species diversity plays an important role in maintaining ecosystem resilience through compensatory interactions (Bai *et al.* 2004), grassland communities in dryer sites are not only species poor and less productive, but also more vulnerable to disturbances and slow to recover. To restore and maintain a high level of biodiversity and ecosystem functioning in this region, it is necessary to reduce the excessively high stocking rate at present to a moderate level in future. We have suggested elsewhere that, to achieve this goal, a landscape-level framework based on sustainability science must be developed to integrate ecological, economic and social dimensions in both research and management policies (Jiang, Han & Wu 2006; Wu 2006).

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