

# The relationship between species richness and productivity in four typical grasslands of northern China

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**Abstract** The relationship between plant species richness and primary productivity has long been a central topic in biodiversity research. In this paper, we examine the relationship between species richness and productivity in four typical grasslands of Northern China at different spatial scales. At the community scale, a positive correlation was found for six of seven communities. A unimodal pattern was found only for one community (*Stipa glareosa* community), while at a large scale (vegetation type or landscape/region), the relationship was also found significantly positive. Species richness ranged from 4 to 35 species, and community aboveground productivity from 13 to 368 g·m<sup>-2</sup>·a<sup>-1</sup>. The highest species richness and aboveground productivity were found in alpine meadow, followed by meadow steppe, typical steppe and desert steppe.

**Keywords** species richness, productivity, grasslands, scale

## 1 Introduction

The relationship between productivity and species richness and the mechanism driving this relationship have long been a focus for ecologists. Despite a number of experiments and observations that have been conducted, there still remain considerable controversies. This might be due to the great spatial-temporal heterogeneity of energy, resources and other environmental variables, which determined the distribution of species. Thus, unimodal, positively monotonic, negatively monotonic relationships, and non-related patterns have been detected (reviews see Mittelbach et al., 2001; Waide et al., 1999).

Some claim that a unimodal pattern between productivity and species richness was predominant (Guo and Berry, 1998; Gross et al., 2000; Mittelbach et al., 2001; Rosenzweig, 1995), followed by positively monotonic relationships (Mittelbach et al., 2001; Waide et al., 1999). Others argued that the forms of the relationship were scale dependent (Chalcraft et al., 2004; Chase and Leibold, 2002; Chase and Ryberg, 2004; Gross et al., 2000; Guo and Berry, 1998; Mittelbach et al., 2001; Waide et al., 1999). For example, Gross et al. (2000) and Chalcraft et al. (2004) examined the effect of scale on the productivity-species richness relationship and found that unimodal patterns occurred among communities, while negatively monotonic patterns within communities. However, Mittelbach et al. (2001) argued that unimodal patterns existed at a smaller scale, while linear patterns were more frequent at a broader scale.

Recently, the relationship between net primary productivity and species diversity productivity has become a hot topic in China (Shang et al., 2005; Wang et al., 2001; Wu and Zhang, 1997; Yang et al., 2002; Yang et al., 2004). However, relatively few studies have examined the effects of spatial scale on this relationship.

Temperate grasslands in China extend 4500 km from the Northeast China Plain, through the Inner Mongolia Plateau and the Loess Plateau to the Tibet Plateau (Li, 1999). A diverse grassland ecosystem type provides good material for examining the relationship between species richness and productivity on different spatial or ecological scales.

We present an analysis of the relationship between productivity and species richness at different scales in the temperate grassland ecosystems in China. The study was based on wide field measurements collected from 219 sites across the temperate grasslands of the country. The objectives were to examine how the relationship between species richness and productivity vary with ecological scale and explore mechanisms related to the observed patterns.

## 2 Method

### 2.1 Study area

Our study was conducted along the belt from the Hulunber Steppe, Xilin Steppe and Wulanchabu Steppe in the east part of the Inner Mongolia Plateau to the east part of the Tibet Plateau. Along this section, meadow steppe, typical steppe, desert steppe and alpine meadow were distributed from east to west. The area generally had temperate continental climate where mean annual temperature and annual precipitation were  $-2.6$ – $7.9^{\circ}\text{C}$  and 183–499 mm, respectively. More than 50% of the precipitation occurred during summer (Table 1).

### 2.2 Materials and methods

The field works were conducted during the summer time between 2002 and 2004. In total, we investigated 219 sites, representing 19 different community types. Among these sites, 31 were strongly disturbed by grazing.

At each site, a large plot with an area of  $10 \times 10$  m was randomly selected. Five quadrates, each with an area of  $1 \times 1$  m, were selected at the corner and center of each plot for aboveground biomass and species richness measurement. The species in each quadrate were identified and recorded. The green parts of plants in the quadrates were harvested and then oven-dried at  $65^{\circ}\text{C}$  and weighed. Biomass and species richness were calculated by an average of five quadrates for each site.

### 2.3 Data analysis

We examined the relationship between species richness and productivity at different ecological scales by combining different groups of the data (see Gross et al., 2000). We changed the ecological extent from community types, grassland types, to the whole grassland region. The data were aggregated at the scale of sites, community types to grassland types. At the scale of community, we selected seven communities with site replicates over 15.

At the three scales we observed the productivity-species richness patterns:

- 1) among sites within communities;
- 2) among sites within grassland types and within the study region;

3) among communities and grassland types within the study region.

### 2.4 Climate data

The climate data used in this study were calculated from 30-year averaged temperature and precipitation records (1970–1999) at 85 weather stations across the study regions. We calculated mean annual temperature (MAT) and annual precipitation (AP) of the sites based on a linear model by latitude, longitude and altitude as dependent variables.

## 3 Results

### 3.1 Species richness and productivity of different communities and grassland types

Species richness and productivity varied significantly among 19 communities and four grassland types (Table 2). Across all sites, species richness ranged from four in the *Stipa glareosa* community to 35 in the *Polygonum viviparum* community, and aboveground productivity ranged from  $13 \text{ g} \cdot \text{m}^{-2} \cdot \text{a}^{-1}$  in the *Stipa klemenzii* community to  $368 \text{ g} \cdot \text{m}^{-2} \cdot \text{a}^{-1}$  in the *Kobresia bellardii* community. Among the four grassland types, the highest mean productivity ( $264.4 \pm 67.2 \text{ g} \cdot \text{m}^{-2} \cdot \text{a}^{-1}$ ) and species richness (26) occurred in alpine meadows, and the lowest productivity ( $77.2 \pm 36.5 \text{ g} \cdot \text{m}^{-2} \cdot \text{a}^{-1}$ ) and species richness (4) occurred in desert steppes (Table 2).

### 3.2 Relationships between species richness and productivity

#### 3.2.1 Patterns among sites within community types

The relationship between productivity and species richness differed greatly among the seven community types (Fig. 1). We observed a significant unimodal pattern ( $R^2 = 0.64$ ,  $P < 0.001$ ) in the *Stipa glareosa* community (Fig. 1(g)) and a positive linear relationship ( $p < 0.01$ ) in the *Stipa baicalensis* community, the *Stipa grandis* community and the *Filifolium sibiricum* community (Fig. 1(a)–(c)). We did not detect significant relationships between species richness and productivity in the *Stipa klemenzii* community, the *Stipa breviflora*, and the *Stipa krylovii* community ( $p = 0.082$ – $0.454$ ) (Fig. 1(d)–(f)).

**Table 1** Summary of geographic range and environmental characteristics of the four grassland types and all sites

Environment variables	Meadow steppe	Typical steppe	Desert steppe	Alpine meadow	Study area
Mean annual temperature / $^{\circ}\text{C}$	–1.3	1.6	4.1	0.6	1.7
Mean annual temperature range / $^{\circ}\text{C}$	–2.6–1.5	–1.6–7.9	2.4–7.1	–0.8–2.0	–2.6–7.9
Annual precipitation /mm	336	342	274	578	331
Precipitation during summer /mm	246.8	237.5	182.2	282.6	224.8
Annual precipitation range /mm	309–408	225–416	183–329	499–649	183–649
Longitude range /E	117.7–120.5	106.9–119.7	105.2–113.3	101.9–102.9	101.9–120.5
Latitude range /N	44.6–49.6	37.3–49.5	37.28–43.9	33.9–35.1	33.9–49.6
Altitude range /m	618–1 204	557–1 689	944–1 814	2996–3 754	575–3 754

**Table 2** Aboveground net primary production and species richness in different grassland and community types

Vegetation types/communities	No. of sites	Productivity ( $\text{g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$ )			Species richness		
		Mean	SD	Range	Mean	SD	Range
<b>Meadow steppe</b>							
<i>Stipa baicalensis</i>	19	113.9	62.6	31.7–305.7	17.6	4.1	10–30
<i>Filifolium sibiricum</i>	17	90.5	31.3	44.7–167.1	22.5	4.6	12–34
<i>Leymus chinensis</i>	11	117.5	38.6	57.3–193.6	17.4	3.0	11–20
<i>Carex pediformis</i>	6	166.0	57.2	68.3–228.4	22.7	6.5	17–35
Subtotal	53	113.0	52.5	31.7–305.7	19.7	4.9	10–35
<b>Typical steppe</b>							
<i>S. grandis</i>	27	141.2	58.0	22.3–295.3	12.5	4.2	6–25
<i>S. krylovii</i>	43	88.6	57.8	20–247.0	10.8	3.3	5–20
<i>S. bungeana</i>	1	86.3	0.0		14.0	0.0	
<i>Artemisia frigida</i>	4	68.0	59.4	17–142.5	11.8	3.8	7–16
<i>Cleistogenes squarrosa</i>	6	77.0	25.5	37.2–110.1	14.2	3.1	11–19
<i>A. sacrorum</i>	1	220.1	0.0		12.0	0.0	
<i>Scutellaria viscidula</i>	1	59.8	0.0		9.0	0.0	
<i>Lespedeza potaninii</i>	1	122.9	0.0		8.0	0.0	
Subtotal	84	105.3	61.6	17–295.3	11.6	3.7	5–25
<b>Desert steppe</b>							
<i>S. klemenzii</i>	28	63.7	31.1	13–137.8	10.6	3.2	7–23
<i>S. breviflora</i>	25	95.1	34.8	39.7–175.1	11.0	2.1	8–17
<i>S. glareosa</i>	17	73.3	38.3	13.3–141.3	9.0	2.0	4–12
Subtotal	70	77.2	36.5	13–175.1	10.4	2.7	4–23
<b>Alpine meadow</b>							
<i>Elimus nutans</i>	2	258.9	46.6	225.1–291.8	20.0	1.4	19–21
<i>Kobresia bellardii</i>	7	269.7	81.6	153.1–368.1	27.3	5.0	18–32
<i>Brachypodium sylvaticum</i>	1	197.0	0.0		26.0	0.0	
<i>Polygonum viviparum</i>	2	285.4	43.4	254.7–316.1	29.0	8.5	23–35
Subtotal	12	264.4	67.2	153.1–368.1	26.3	5.4	18–35
Total	219	106.9	66.4	13–368.1	14	6.1	4–35
<b>Disturbed by grazing</b>							
<i>Meadow steppe</i>	4	43.7	10.5	31.7–57.3	16.0	4.2	11–20
<i>Typical steppe</i>	26	52.8	33.5	17–142.5	10.9	3.3	5–19
<i>Alpine meadow</i>	1	153.1	0.0		23.0	0.0	
Total of grazed fields	31	54.9	35.9	17–153.1	11.9	4.3	5–23

N, sampling replicates (sites) of community or grassland types; SD, standard deviation.

### 3.2.2 Patterns among sites within grassland types and region and among communities or types within region

When the field data were combined at the scale of grassland types, significantly positive linear patterns were observed in four grasslands ( $p < 0.05$ ) (Fig. 2). In addition, when we pooled all the field data at the regional scale, productivity also increased significantly with increasing species richness (Fig. 3(a)). This monotonically positive pattern was still significant for communities (Fig. 3(b)) or grassland types (Fig. 3(c)) at the regional scale.

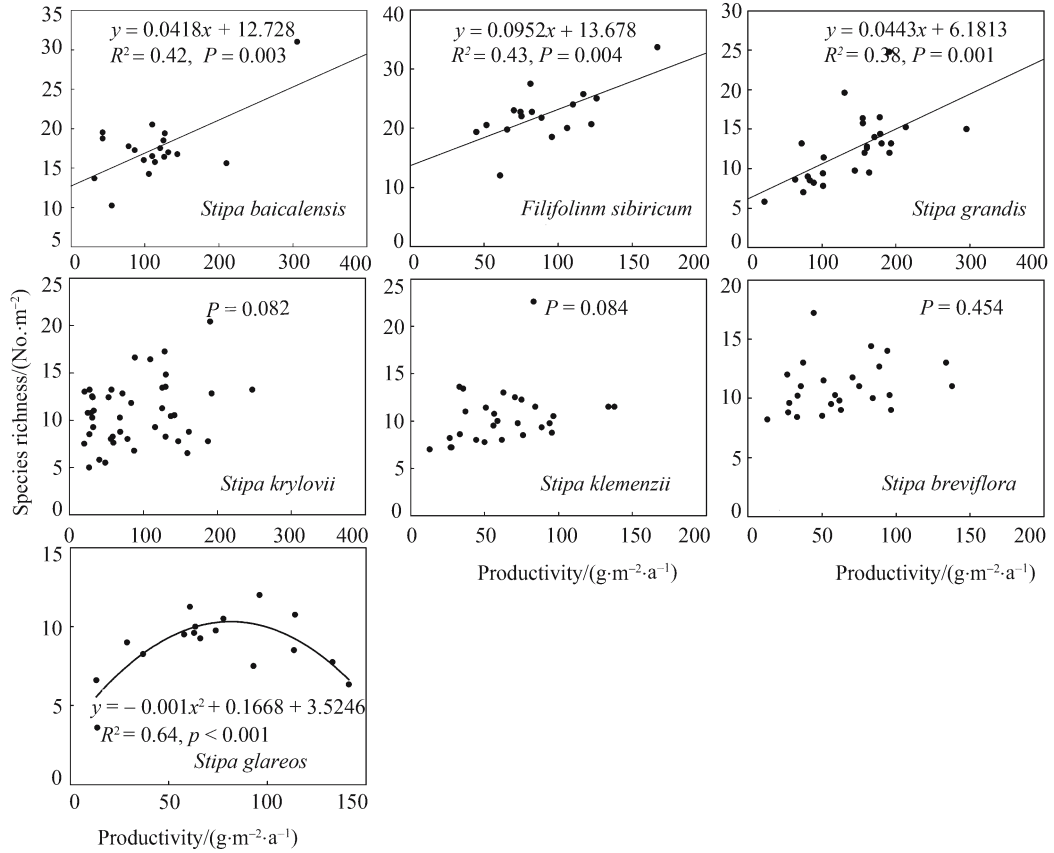
### 3.3 Effect of grazing on the productivity-species richness relationship

Human activity (e.g. grazing) has a strong and long-term influence on processes and functions in grassland ecosystems. As presented in this study, mean aboveground productivity ( $54.9 \text{ g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$ ) for the disturbed communities was less

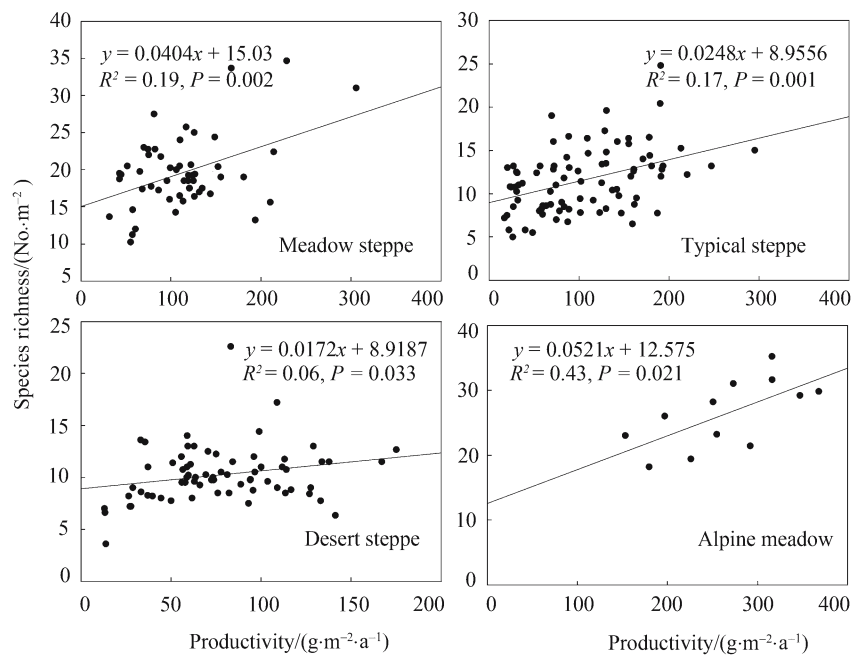
than half of that for undisturbed communities ( $115 \text{ g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$ ). However, we did not detect a decline in the species richness for the disturbed communities (Table 2). Furthermore, we examined the relationships between productivity and species richness among the sites within typical steppes (where most of the disturbed sites were found) and within the region excluding the 31 disturbed-field data. The productivity-species richness pattern was still evidently positive (Fig. 4).

## 4 Discussion

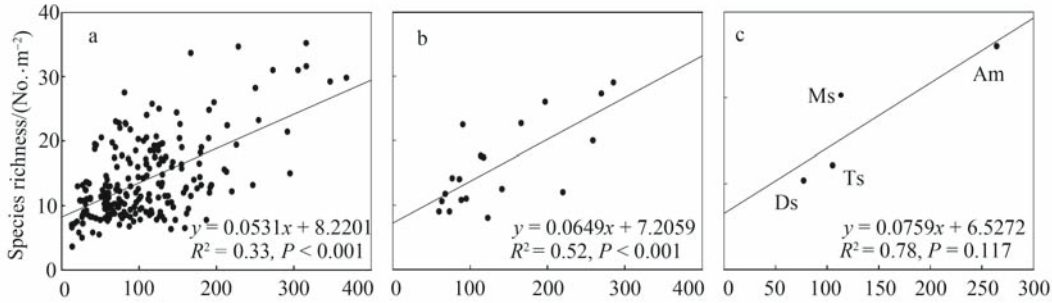
The relationship between productivity and species richness varied by different authors. Spatial extent of the studies has a strong influence on the relationship between productivity and species richness (Chalcraft et al., 2004; Guo and Berry, 1998). In this study, based on field observations and combinations of the data, the relationship between productivity and species



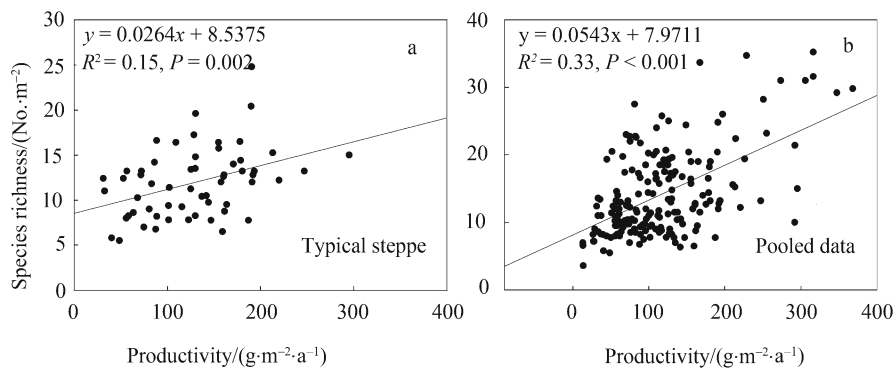
**Fig. 1** Relationships between productivity and species richness for different sites within a community type in the study region (Community types with less than 15 replicates were excluded)



**Fig. 2** Relationships between productivity and species richness for different sites within four grassland types



**Fig. 3** Relationships between productivity and species richness for (a) different sites within the study region ( $n = 219$  sites), (b) different community types within the study region ( $n = 19$  community types), and (c) for different grassland types within the study region ( $n = 4$  grassland types). Ms, Meadow steppe; Ts, Typical steppe; Ds, Desert steppe; Am, Alpine meadow



**Fig. 4** Relationship between productivity and species richness for different sites within typical steppes ( $n = 58$  sites) (a) and study region ( $n = 188$  sites) (b) excluding sites heavily disturbed by grazing

richness was examined at different scales. Although a unimodal pattern was the most commonly documented relationship at various scales, we detected positively linear, unimodal and non-related relationships for temperate grasslands in China. The positive patterns occurred frequently with the extension of the spatial scale, which is consistent with the review of Waide et al. (1999) and Mittelbach et al. (2001).

The dependence of the relationship between species diversity and productivity on spatial scale might be due to other factors. The determinants of species richness and productivity differed across spatial scales (Chase and Leibold, 2002). For example, biotic factors (e.g. competition) may affect the relationship between species richness and productivity primarily at a smaller scale, while abiotic factors (e.g. soil fertility and climate conditions) may drive the patterns at a broader scale. In addition, species composition (Chalcraft et al., 2004) may explain the different forms of productivity-species richness relationships within a community scale.

Several studies predicted that a small productivity range might hide the unimodal relationship between productivity and species richness (Chalcraft et al., 2004; Rosenzweig, 1995; Scheiner et al., 2000). Guo and Berry (1998) assumed that positively or negatively linear relationships, and

non-related patterns at small scales were different parts of the unimodal pattern, i.e. a unimodal relationship was a combination of these linear relationships. Our result did not support their study. It is worthy to note that our data included a large spatial extent and a wide productivity range. For example, the productivity varied approximately 28 multiples from desert steppes to alpine meadows, greater than that observed in the North American grasslands presented by Gross et al. (2000). Thus, it is not necessary that unimodal relationships occurred in wide scales.

Many mechanisms have been proposed to explain the trend linking higher plant productivity to greater species richness. The species-energy hypothesis was the most commonly accepted one, which proposed that species richness in the earth was controlled by fixed energy from photosynthetic processes (i.e. carbohydrate), thus, more species lie in the warmer and wetter environments (Turner and Lennon, 1989; Wright, 1983). Chase and Leibold (2003) presented the following three conditions to possibly link increasing species richness with increasing productivity: first, higher vegetation productivity commonly corresponded to higher spatial heterogeneity, thus promoting richer species; second, species composition varied more frequently in the ecosystems with higher productivity, thus resulting in higher species richness; third, ecosystems with higher productivity can provide a more

stable environment for more species to exist. In the present study, due to the limitation of data availability, it is difficult to evaluate whether these mechanisms can explain our results. More experiments are necessary for future studies.

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