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RESEARCH PAPER

Environmental factors covary with plant diversity–productivity relationships among Chinese grassland sites

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ABSTRACT

Aim Our objective was to document the general relationship between plant species richness (SR) and above-ground net primary productivity (ANPP) at different spatial scales and the environmental influence on this relationship.

Location Temperate and alpine grasslands of China.

Methods We investigated SR and ANPP at 321 field sites (1355 plots) across the widely distributed temperate and alpine grasslands of China. Ordinary least squares (OLS) regressions were used to test SR–ANPP relationships among site means. Plot-level data of SR and ANPP were analysed with general linear models (GLMs) and the correlation between SR and ANPP was decomposed into covariance components to test the influence of climatic variables, region, vegetation type and remaining variation among sites on SR, ANPP and their relationship.

Results We found positive linear relationships between SR and ANPP among sites in both the alpine and temperate grassland regions and in different grassland vegetation types of these biomes. Environmental gradients such as growing-season precipitation affected both SR and ANPP in parallel. However, after removing the among-site environmental variation, residual SR and ANPP were no longer correlated at the pooled within-site level.

Main conclusions The positive SR–ANPP relationship across large-scale environmental gradients among sites was most likely the result of climatic variables influencing SR and ANPP in parallel. Our results suggest that in China's natural grasslands there is no direct relationship between SR and ANPP, presumably because the pool of available species for local community assembly is large, in contrast to experiments where species pools are artificially reduced.

Keywords

Above-ground NPP, alpine grassland, among-site variation, China, field study, plant diversity–productivity relationship, species richness, temperate grassland, within-site variation.

INTRODUCTION

The general pattern and the mechanisms for relationships between biodiversity and ecosystem functioning are fundamental issues in ecology (Schulze & Mooney, 1993; Lawton, 1994). Among several key questions studied, the relationship between plant species richness (SR) and above-ground net primary productivity (ANPP) has been particularly hotly debated (Waide *et al.*, 1999; Schmid, 2002; Grace *et al.*, 2007).

Many observational studies on the SR–ANPP relationship have been conducted in grassland ecosystems (see review in Waide *et al.*, 1999; Mittelbach *et al.*, 2001; Gillman & Wright, 2006), probably due to the easy measurement of productivity in these regularly mown or grazed ecosystems. The SR–ANPP

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relationship can be positive, negative, unimodal, U-shaped or no relationship (Guo & Berry, 1998; Schläpfer & Schmid, 1999; Mittelbach *et al.*, 2001; Gillman & Wright, 2006; Bai *et al.*, 2007; Zobel & Pärtel, 2008). A meta-analysis of the published relationships by Mittelbach *et al.* (2001) indicated that unimodal shapes predominate at local to landscape scales, while positive linear shapes are common at large spatial scales. However, a reassessment of the same dataset and other studies found that the positive SR–ANPP relationship is dominant from the regional to the global scale, whereas an unimodal relationship occurs only rarely in the studies of small spatial extent (Gillman & Wright, 2006).

A number of studies have discussed possible factors influencing the SR–ANPP relationship, e.g. disturbance by fire or grazing (Rusch & Oesterheld, 1997; Kirkman *et al.*, 2001), evolutionary history (Harrison & Grace, 2007; Pärtel *et al.*, 2007) or spatial scale (Moore & Keddy, 1989; Chase & Leibold, 2002; Aarssen, 2004; Ni *et al.*, 2007). However, none of these studies decomposed the SR–ANPP relationship into covariance components due to environmental factors such as climate and vegetation type as we do in the present paper. These environmental factors may affect both productivity and diversity in natural ecosystems at the same time (Hooper *et al.*, 2005; Lamb, 2008). Thus, it has been suggested that a positive SR–ANPP relationship could arise from the covariance of species richness and productivity across environmental gradients (Loreau, 2000; Adler & Levine, 2007; Bai *et al.*, 2007). Recent studies (Kahmen *et al.*, 2005; Adler & Levine, 2007; Grace *et al.*, 2007; Lamb, 2008) used statistical methods to show that when the influence of environmental factors on the SR–ANPP relationship is removed, the residual relationship can be weak or even undetectable.

As in other disciplines, progress in ecology has resulted from the accumulation of specific patterns, and through the synthesis of accumulated results into general patterns and underlying mechanisms (Pickett *et al.*, 1994; Knapp *et al.*, 2004), with the ultimate goal of identifying general principles to improve predictive capability. A key step in this process is to test patterns found in one study in another to generate broader understanding. Recently, Ma & Fang (2006), Bai *et al.* (2007) and Ni *et al.* (2007) addressed the SR–ANPP relationships in eastern Eurasian steppes. Ma & Fang (2006) and Bai *et al.* (2007) observed a positive linear relationship across all organizational levels and spatial scales examined in grasslands of northern China, while Ni *et al.* (2007) found that the relationship was mostly unimodal from landscape to regional scales in south-eastern Mongolia. These differences highlight the importance of assessing the SR–ANPP relationships extensively across a broader range of grassland environments.

When the SR–ANPP relationship in grassland is examined, it is essential to consider the different origins and community characteristics of specific regions. Temperate grasslands in western and central Europe are associated with human activities, and their origin and maintenance are mostly linked to regular management such as mowing or grazing by domestic livestock. These grasslands are therefore considered semi-natural (Pott, 1995; Poschlod & WallisDeVries, 2002; Kahmen *et al.*, 2005). Eastern Eurasian steppes, however, are considered primary grasslands that represent climax vegetation as a result of aridity (Chinese Academy of Sciences Integrative Expedition Team to Inner Mongolia and Ningxia, 1985; Bredenkamp *et al.*, 2002). North American prairies are very similar to Eurasian steppes, in that they are considered temperate grasslands, probably also representing climax vegetation (Walter, 1979). The Chinese grasslands are distributed in three regions: temperate grassland in the Inner Mongolia Plateau, mountain grassland in the Xinjiang mountain areas and alpine grassland on the Tibetan Plateau (Wu, 1980). Unlike Inner Mongolian grassland, which belongs to the eastern Eurasian steppes and occurs in arid regions, alpine grassland of the Tibetan Plateau occurs at high altitudes, where the limiting abiotic factor that restricts growth of trees is low temperature rather than aridity. Xinjiang mountain grassland can be seen as a transition between the arid and high-altitude grasslands. Differences in the dominant environmental factor limiting plant growth in the different regions and differences in regional species pools may lead to different SR–ANPP relationships among these regions.

The objectives of the present study were to answer the following questions. (1) What is the general pattern of SR–ANPP relationships across Chinese grassland biomes when the study region is expanded to include alpine grassland of the Tibetan Plateau? (2) Does the relationship change with spatial scale? (3) Can the relationship be explained by variation in climatic factors or among vegetation types? (4) Does the relationship among sites differ from the relationship within sites?

METHODS

Study area

We set up a north-east–south-west grassland transect (referred to in short as 'Transect') across the temperate and alpine regions in China (Fig. 1). The Transect was approximately 4000 km long and covered latitudes from 29.3 to 49.6° N and longitudes from 80.8 to 120.5° E. Mean growing-season temperature (GST, from April to August) along the Transect ranged from 1.5 to 18.2°C, mean growing-season precipitation (GSP) ranged from 85 to 475 mm and elevation ranged from 575 to 5168 m (Table 1). The climate of the two regions is seasonal with marked annual variation in both temperature and precipitation. The temperate region is characterized by dry, continental climate and the alpine region by dry, continental and cold climate (Table 1).

Natural vegetation types along the Transect include temperate meadow steppe (dominated by *Stipa baicalensis* and *Leymus chinensis*), typical steppe (dominated by *Stipa grandis* and *Stipa krylovii*), and desert steppe (dominated by *Stipa klemenzii* and *Stipa breviflora*) in Inner Mongolia and alpine steppe (dominated by cold-xerophytic, short, dense tussock grasses such as *Stipa purpurea* and *Festuca ovina*) and alpine meadows (dominated by perennial tussock grasses such as *Kobresia pygmaea* and *Kobresia tibetica*, usually mixed with alpine forbs, including *Polygonum viviparum* and species of *Gentiana* and *Pedicularis*)

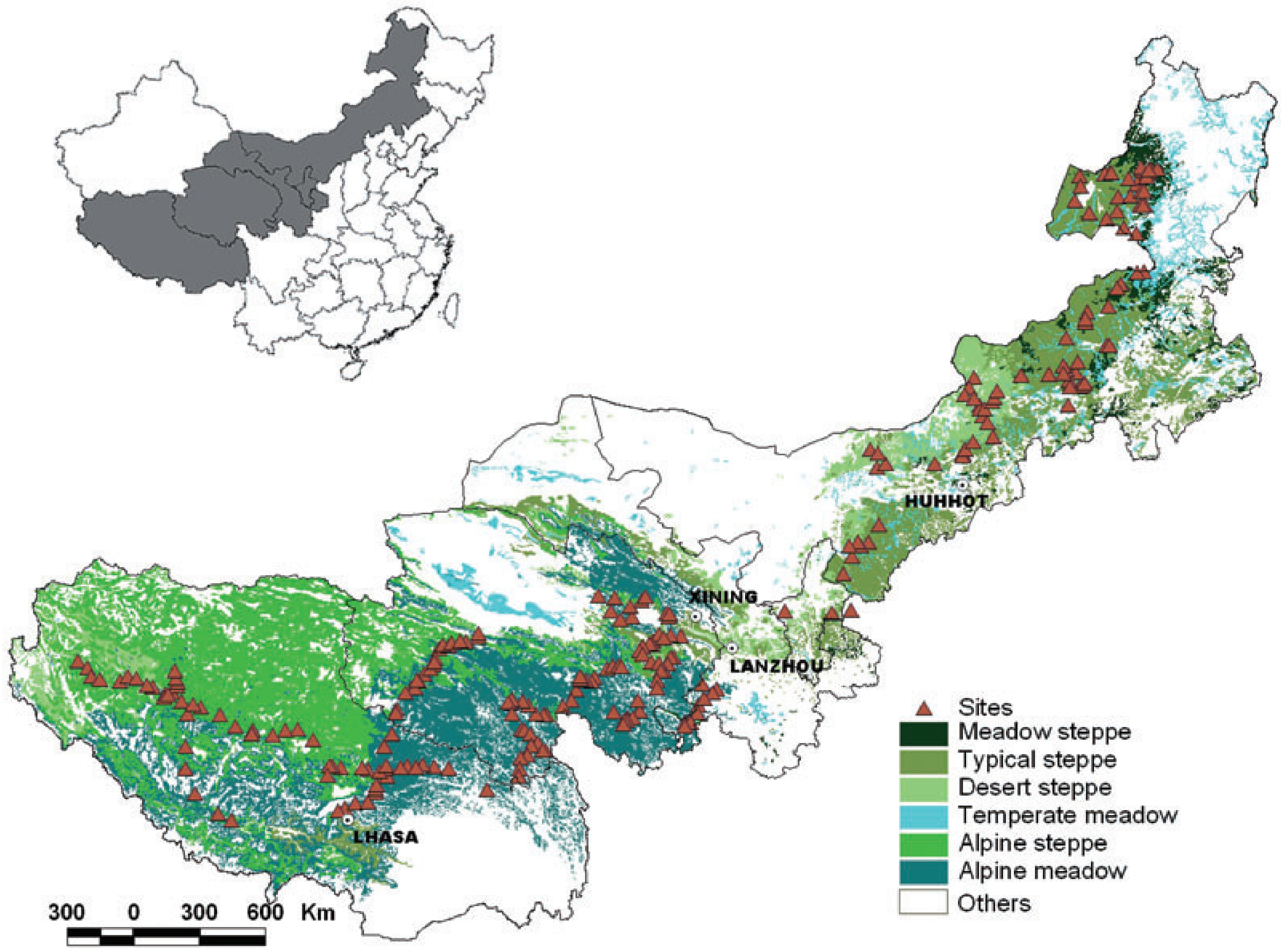

Figure 1 Sampling sites and vegetation map of the study regions, based on the 'Vegetation Map of China' (Hou, 1982).

in the Tibetan Plateau (Chinese Academy of Sciences Integrative Expedition Team to Inner Mongolia and Ningxia, 1985; Zhang *et al.*, 1988).

Data collection

Over the period of the four summers (late July to early August) of 2002, 2003, 2004 and 2006, we visited in total 321 field sites across the Transect (Fig. 1). At each site, a 10 × 10 m quadrat was randomly located. Within each quadrat, three (along the diagonal line of the quadrat) or five (at each corner and the centre of the quadrat) 1 × 1 m plots were surveyed for field sites visited in 2006 or 2002–04, respectively. We recorded the geographical coordinates, elevation, climate data and vegetation type for each site. The climate data included GST (from April to August) and GSP and were compiled from the 1950–2000 temperature/precipitation records of a global climate database (Hijmans *et al.*, 2005).

We listed all vascular plant species and their cover for each of the 1355 plots and then harvested all above-ground biomass to ground level. This above-ground biomass in late July/early August approximates the ANPP in temperate, Northern Hemisphere grasslands (Sala *et al.*, 2000). The harvested above-ground biomass was pre-dried at the field sites using a portable oven and dried to constant weight at 65°C after return to the laboratory at Peking University, Beijing.

Data analysis

The relationship between SR and ANPP of the 1355 plots was partitioned into among-site ($n = 321$) and within-site levels. The within-site relationship was pooled over sites because there were insufficient numbers of plots per site to reliably calculate a separate relationship for every individual site. Separate among-site relationships were fitted for the two regions (temperate and alpine grassland) and the five different vegetation types (for temperate grassland region: meadow steppe, typical steppe and desert steppe; for alpine grassland region: alpine meadow and alpine steppe).

We first conducted ordinary least-squares (OLS) regression using site means ($n = 321$) to see whether there was a significant linear or quadratic SR–ANPP relationship among sites for the overall data and for the two regions and five vegetation types separately. If significant quadratic effects occurred, we used the

Table 1 Geographic, climatic (GST and GSP) and vegetation (vegetation cover, species richness, above-ground net primary productivity) characteristics of the two study regions and five vegetation types.

	No. of sites	Altitude (m)	Longitude (°E)	Latitude (°N)	GST (°C), mean (range)	GSP (mm), mean (range)	Cover (%) mean (range)	SR, mean (range)	ANPP (g m^{-2} $year^{-1}$), mean (range)
Overall	321	575–5168	80.8–120.5	29.3–49.6	9.2 (1.5–18.2)	260 (85–475)	51 (8–100)	13 (2–35)	97.8 (9.8–368.1)
Temperate grassland	132	575–1814	105.2–120.5	37.3–49.6	14.0 (11.2–18.2)	250 (110–327)	37 (9–90)	15 (4–35)	102.9 (13.0–305.7)
Alpine grassland	189	2925–5168	80.8–102.9	29.3–37.4	5.8 (1.5–11.0)	267 (85–475)	61 (8–100)	12 (2–35)	94.3 (9.8–368.1)
Vegetation types									
Meadow steppe	52	618–1204	117.8–120.5	44.6–49.6	12.5 (11.2–13.6)	306 (277–327)	48 (25–90)	20 (10–35)	114.1 (31.7–305.7)
Typical steppe	51	575–1670	106.9–119.7	37.3–49.5	14.0 (12.6–18.2)	242 (174–295)	35 (12–70)	12 (4–25)	112.8 (17.0–247.0)
Desert steppe	29	944–1814	105.2–113.2	37.3–43.9	16.5 (14.7–17.6)	163 (110–219)	22 (9–34)	10 (4–23)	65.3 (13.0–175.1)
Alpine steppe	96	2925–5168	80.8–101.2	29.8–37.3	5.7 (1.8–11.0)	207 (85–401)	42 (8–89)	8 (2–20)	56.3 (9.8–188.0)
Alpine meadow	93	2996–5105	85.3–102.9	29.3–37.4	6.0 (1.5–9.6)	330 (140–475)	80 (15–100)	17 (5–35)	133.5 (15.8–368.1)

GST, mean growing-season temperature; GSP, mean growing-season precipitation; Cover, vegetation cover; SR, species richness, ANPP, above-ground net primary productivity.

test of Mitchell-Olds & Shaw (1987) to determine whether the SR–ANPP relationship reached a maximum (unimodal) or minimum (U-shaped) within the range of ANPP.

Statistical models with several explanatory terms were fitted to the individual plot data ($n = 1355$). We eliminated variation due to different sampling years by first entering 'year' as a categorical covariate with four levels (three degrees of freedom) into the statistical models (Schmid *et al.*, 2002). To examine the effects of climatic variation, differences between regions, variation among vegetation types and residual environmental variation among sites on SR, ANPP and their relationship, we conducted three analyses. First, we used a general linear model (GLM) to test the influence of environmental factors on SR and ANPP separately. In the second analysis, we performed residual regression to examine the SR–ANPP relationship when the effects of environmental factors varying among sites were removed one after another until only the pooled within-site variation among plots remained. We began this analysis by partialling out climatic variables: residuals of SR and ANPP were obtained from regression models with year and climatic variables as explanatory terms. This procedure was repeated, and the effects of further partialling out region, vegetation and residual variation among sites were thus examined.

In the third analysis, we directly quantified the effects of different explanatory variables on the covariation between SR and ANPP using a decomposition of sums of products of the two dependent variables as described in Kempthorne (1969, Table 4 therein; see also He *et al.*, 2009). This is the analysis of covariance in the original sense of the word and should not be confused with an analysis of variance adjusted for a covariate. The contribution of each term was calculated as the percentage of sum of products explained (Falconer & Mackay, 1996; He *et al.*, 2008). Because site was nested within year, climatic variables, region and vegetation type, the significance of climatic variables, region, vegetation type and year were tested against the remaining among-site (instead of the residual among-plot) variation as the error term. All statistical analyses were calculated with the software product R (R Development Core Team, 2004).

RESULTS

SR and ANPP

There was considerable variation in both SR and ANPP. Across the 321 field sites, SR ranged from 2 to 35 species per plot, with an average of 13 species per plot, and ANPP ranged from 9.8 to 368.1 g m^{-2} $year^{-1}$, with an average of 97.8 g m^{-2} $year^{-1}$ (Table 1). Mean SR and ANPP were slightly higher in temperate (15 species m^{-2}, 102.9 g m^{-2} $year^{-1}$) than in alpine grasslands (12 species m^{-2}, 94.3 g m^{-2} $year^{-1}$). There was more than twofold variation in SR and ANPP among the five vegetation types, with SR ranging from 8 (alpine steppe) to 20 (meadow steppe), and ANPP ranging from 56.3 g m^{-2} $year^{-1}$ in alpine steppe to 133.5 g m^{-2} $year^{-1}$ in alpine meadow.

Table 2 Summary of regression analyses of plant species richness as a function of above-ground net primary productivity (fitted as linear and quadratic term) using site means for the overall data set and for two regions and five vegetation types.

		Linear model		Quadratic model			
Level of organization	No. of sites	Adjusted R^2	P	Adjusted R^2	P	Significance of quadratic term	Patterns (Figure)
Overall	321	0.41	< 0.001	0.42	< 0.001	0.008	PQ (Fig. 2a)
Biomes							
Alpine grassland	189	0.56	< 0.001	0.57	< 0.001	0.014	PQ (Fig. 2b)
Temperate grassland	132	0.18	< 0.001	0.18	< 0.001	0.298	PL (Fig. 2c)
Vegetation type							
Alpine meadow	93	0.45	< 0.001	0.45	< 0.001	0.222	PL (Fig. 2d)
Alpine steppe	96	0.24	< 0.001	0.33	< 0.001	< 0.001	UN (Fig. 2e)
Meadow steppe	52	0.14	0.003	0.15	0.007	0.259	PL (Fig. 2f)
Typical steppe	51	0.20	0.001	0.20	0.002	0.254	PL (Fig. 2g)
Desert steppe	29	0.07	0.084	0.14	0.051	0.085	NS (Fig. 2h)

P, significance level; PL, positive linear relationship; PQ, positive quadratic relationship; UN, unimodal relationship according to test of Mitchell-Olds & Shaw (1987); NS, non-significant relationship.

The SR–ANPP relationship at different spatial scales

Plant SR was significantly related to ANPP in both regions and four of the five vegetation types (analyses of site means shown in Table 2 and Fig. 2). The overall data set and both temperate and alpine grasslands exhibited a positive linear SR–ANPP relationship (Fig. 2b,c). This was also the case for three vegetation types, i.e. alpine meadow, meadow steppe, and typical steppe (Fig. 2d,f,g). Three of the eight curves also had a significant quadratic term (Fig. 2a,b,e), indicating a decelerating increase of SR with increasing ANPP, but in only one case was the maximum SR achieved within the observed range of ANPP. This single case of a significantly hump-shaped relationship was obtained for the alpine steppe vegetation type (Fig. 2e).

Influence of environmental variables on SR and ANPP

When tested with the GLM (analysis of plot data), strong effects of climatic variables were found, with GSP alone explaining 43.7% of the total variance in SR and 36.2% in ANPP (Table 3). This was also visible in univariate OLS regressions using site means (Fig. 3). Specifically, at the level of the whole study region, both SR and ANPP positively increased with GSP (SR: $r^2 = 0.49$, $P < 0.01$; ANPP: $r^2 = 0.35$, $P < 0.01$; Fig. 3a,b), whereas the overall effect of GST was weaker (SR: $r^2 = 0.022$, $P = 0.007$; ANPP: $r^2 = 0.008$, $P = 0.116$) because both SR and ANPP responded in opposite directions between temperate and alpine grasslands (Fig. 3c,d), suggesting that a warmer temperature at the lower temperate sites might have caused drought stress. Returning to the GLM analysis, year of observation, region and vegetation type had relatively weak effects on SR and ANPP (explaining 11.4% of the total variance in SR and 2.8% in ANPP). However, remaining variation among sites explained 34% of the total variance in SR and 47% in ANPP (Table 3).

Table 3 Summary of general linear models for the effects of environmental variables on plant species richness (SR) and above-ground net primary productivity (ANPP).

Term	d.f.	MS	F	P	%SS	Error term
SR						
Year	3	1120.0	16.2	< 0.001	5.3	Site
GSP	1	27660.1	400.4	< 0.001	43.7	Site
GST	1	2611.2	37.8	< 0.001	4.1	Site
Region	1	1525.0	22.1	< 0.001	2.4	Site
Vegetation	3	770.6	11.2	< 0.001	3.7	Site
Site	311	69.1	16.6	< 0.001	34.0	Residual
Residuals	1034	4.2			6.8	
ANPP						
Year	3	37071.1	3.4	0.018	1.5	Site
GSP	1	2619923.1	240.0	< 0.001	36.2	Site
GST	1	212734.5	19.5	< 0.001	2.9	Site
Region	1	1745.1	0.2	0.69	0.0	Site
Vegetation	3	30646.9	2.8	0.04	1.3	Site
Site	311	10916.6	13.9	< 0.001	46.9	Residual
Residuals	1034	786.5			11.2	

Explanatory terms used included year of observation (Year), climatic variables (GSP, growing-season precipitation; GST, growing-season temperature), region, vegetation type (Vegetation), and remaining variation among sites (Site). Explanatory terms are listed in the order of their entry into the models. d.f., degree of freedom; MS, mean squares; *F*, variance ratio; *P*, significance level; %SS, percentage of total sum of squares explained.

SR–ANPP relationships before and after removing the effects of environmental variation among sites

When entered into a GLM before other explanatory terms, ANPP explained 38.5% of the total variance in SR (Appendix S1, Fig. 4a). To test the influence of environmental variation among

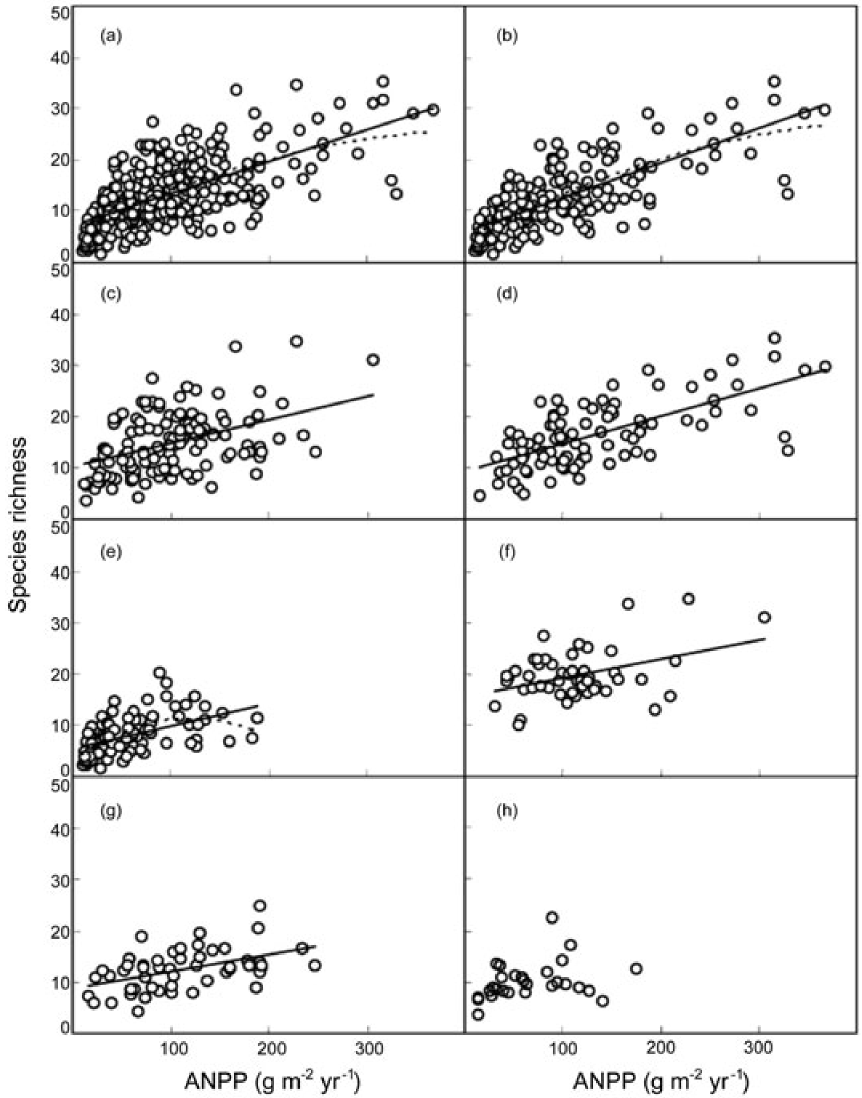

Figure 2 Relationships between species richness (SR) and above-ground net primary productivity (ANPP) for all sites and for the two regions and five vegetation types separately. Each data point corresponds to a pair of site means of SR and ANPP (see also Table 2). (a) All data together, (b) alpine grasslands, (c) temperate grasslands, (d) alpine meadow, (e) alpine steppe, (f) meadow steppe, (g) typical steppe, (h) desert steppe. The linear (solid) and quadratic (dashed) regressions are shown where significant ($P < 0.05$).

sites on the residual relationship between SR and ANPP, we fitted the environmental variables to both and plotted the residuals of SR and ANPP against each other. The residual relationship between SR and ANPP was decreased when environmental variation among sites related to climate, region and vegetation type was explained by the fitting process and removed from the residuals: $r^2 = 0.10$ after fitting of year and climatic variables ($P < 0.01$, Fig. 4b); $r^2 = 0.11$ after fitting of year, climatic variables and region ($P < 0.01$, Fig. 4c); $r^2 = 0.13$ after fitting of year, climatic variables, region and vegetation type ($P < 0.01$, Fig. 4d). When all among-site variation was partialled out (fitting of year, climatic variables, region, vegetation type and site), there was no longer a significant relationship between the residuals of ANPP and SR ($r^2 = 0.0004$, $P = 0.46$, Fig. 4e). This final graph, representing the pooled relationship among plots within sites, suggests that SR and ANPP are uncorrelated in the absence of climatic and other among-site variation, which had affected SR and ANPP in parallel.

Partitioning the covariance between SR and ANPP

When the covariance between SR and ANPP was partitioned into components due to environmental variables (Table 4), GSP accounted for 64% and GST for an additional 5.6% of the total covariance, indicating that parallel effects of climate on both SR and ANPP were largely responsible for their positive relationship across sites. Both region and vegetation type had a slightly but significantly negative effect on the covariance between SR and ANPP. However, the remaining environmental variation among sites again had a positive influence and accounted for 28% of the total covariance, indicating further parallel effects of environmental variation across sites (e.g. soil type or disturbance regime) on both SR and ANPP. The residual covariance, reflecting the pooled within-site covariance as mentioned in the previous section, was insignificant – despite its large residual degree of freedom (1033) – only accounting for a minute fraction of 0.3% of the total covariance.

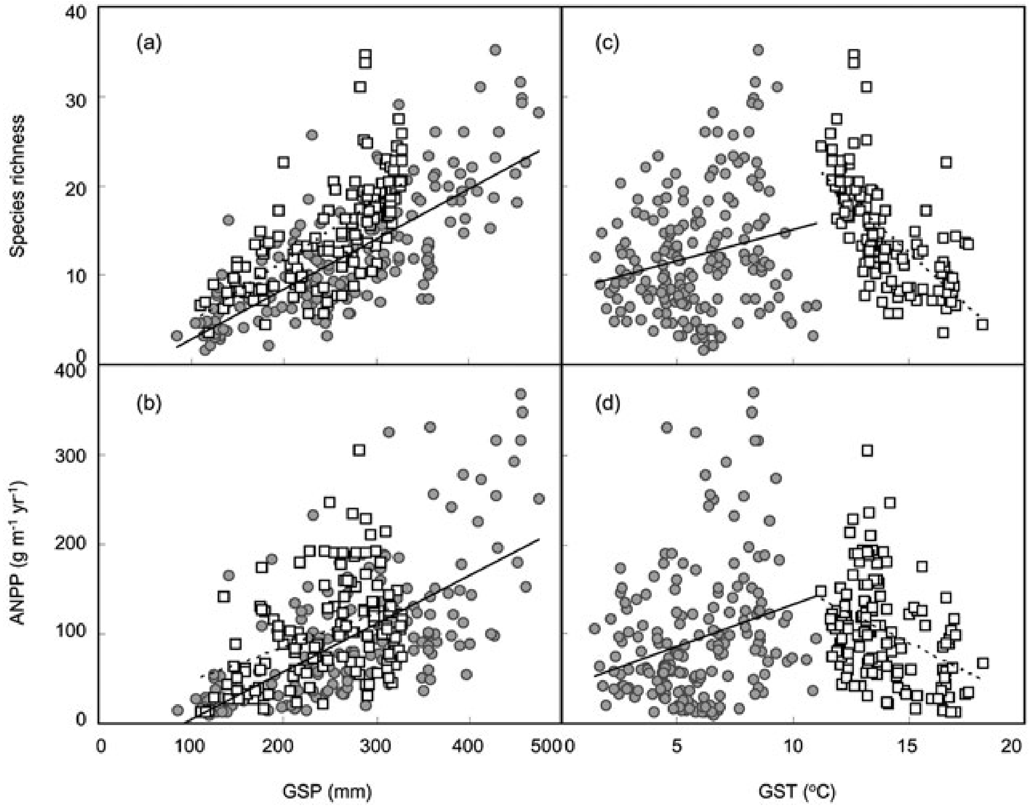

Figure 3 Species richness (SR) and above-ground net primary productivity (ANPP) in relation to mean growing-season precipitation (GSP, from April to August) (a,b) and growing-season temperature (GST) (c,d). Solid circles represent alpine grasslands and squares represent temperate grasslands. Each data point corresponds to a pair of site means of SR and ANPP. Regression lines are shown for alpine grasslands (solid line) and temperate grasslands (dashed line).

Table 4 Decomposition of covariance between plant species richness and above-ground net primary productivity (ANPP) using sums of products for the effects of year of observation, climatic variables (GSP, GST), region, vegetation type and remaining variation among sites.

Term	d.f.	Mean SP	*P*	%SP	Error term
Environmental variation between sites					
Year	3	4324.0	< 0.001	3.1	Site
GSP	1	269197.7	< 0.001	64.0	Site
GST	1	23568.8	< 0.001	5.6	Site
Region	1	−1631.3	0.039	−0.4	Site
Vegetation	3	−1184.4	0.027	−0.8	Site
Site	311	381.3	< 0.001	28.2	Residual
Residual covariance within sites					
Residual	1033	1.2	0.46	0.3	

Terms used: year of observation (Year), climatic variables (GSP, growing-season precipitation; GST, growing-season temperature), region, vegetation type (Vegetation), and remaining variation among sites (Site). d.f., degree of freedom; Mean SP, mean sums of products; *P*, significance level; %SP, percentage of total sum of products explained. The significance of the residual mean sum of products term (i.e. the residual covariance) was assessed by fitting the residuals of species richness and ANPP against each other and correcting the residual degree of freedom for the number of fitted parameters.

DISCUSSION

Positive SR–ANPP relationships among grassland sites in China

To the best of our knowledge, the SR–ANPP relationship across temperate and alpine plant communities has not been previously explored in a single large-scale comparative field study. Our study, using field-measured above-ground productivity and plant species richness over a large geographical range from temperate and alpine regions, indicated that positive SR–ANPP relationships among sites were the rule in the two regions and in three of five vegetation types. A positive SR–ANPP relationship was also observed in a recent study from temperate grassland of Inner Mongolia (Bai *et al.*, 2007). Although a few studies have been carried out in alpine plant communities (Callaway *et al.*, 2002; Grytnes & Birks, 2003), clear positive relationships between SR and ANPP have not been reported previously for this biome. The growth and survival of plant species in alpine regions are constrained by abiotic factors (mainly low temperature and low nutrient availability) due to high altitude (Shaver & Jonasson, 1999). Under stressful environmental conditions, high species richness may be particularly important to maintain productivity (Callaway *et al.*, 2002).

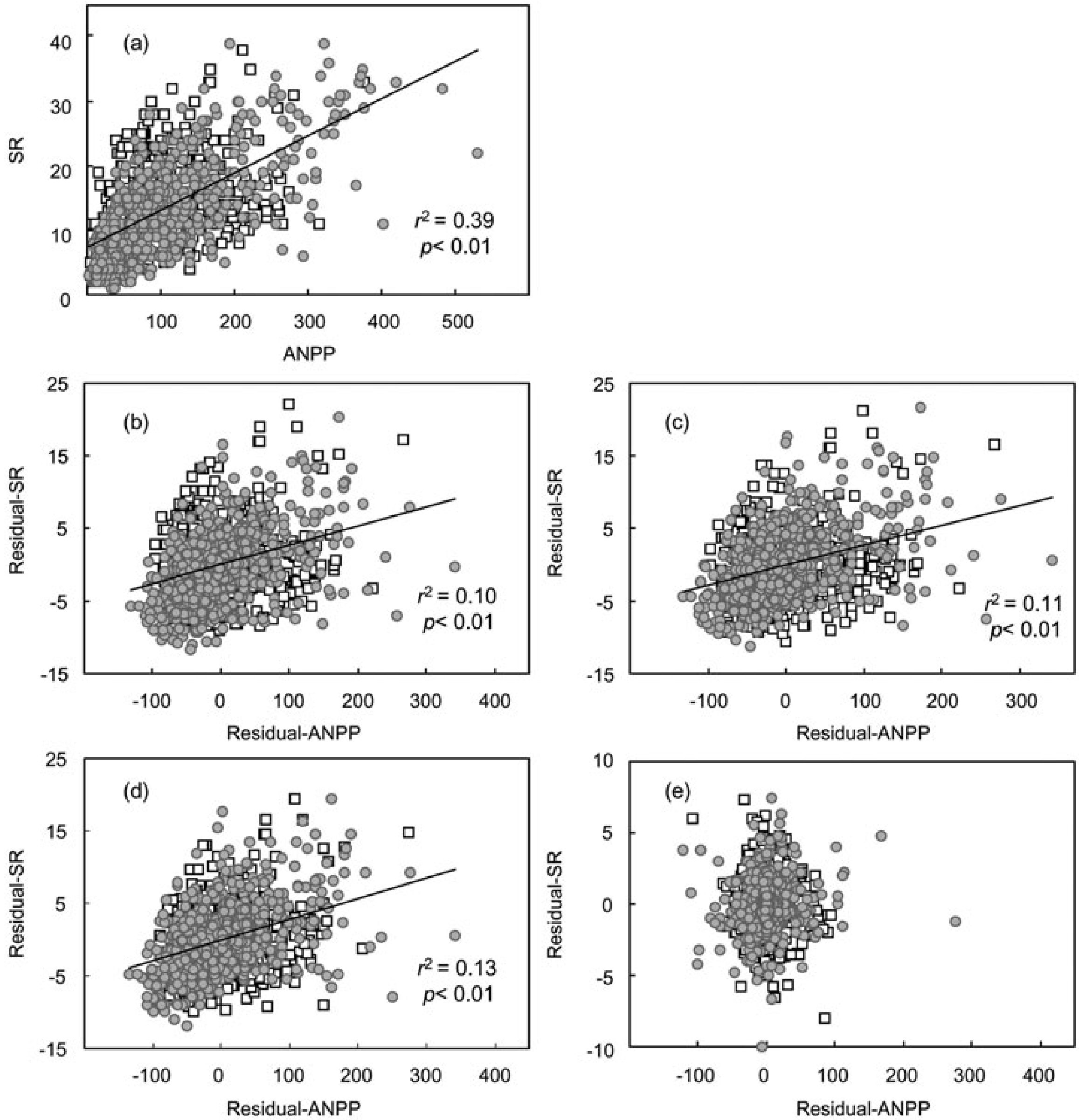

Figure 4 Relationships between species richness (SR) and above-ground net primary productivity (ANPP) for all 1355 plots. Among-site variation was included or removed by fitting environmental variables prior to drawing the scatter plots. Solid circles represent alpine grasslands and squares represent temperate grasslands. (a) All among-site variation included; (b) effects of year of observation and climatic variables (growing-season temperature (GST) and growing-season precipitation (GSP)) removed; (c) effects of year, climatic variables and region removed; (d) effects of year, climatic variables, region and vegetation type removed; (e) effects of year, climatic variables, region, vegetation type and remaining among-site variation removed. The linear regression lines are shown for significant relationships ($P < 0.05$).

Although the relationship between species richness and productivity has been studied in a large number of plant communities and over a large geographic range, no particular shape of relationship has obtained a clear majority (Waide *et al.*, 1999; Mittelbach *et al.*, 2001), and no consensus about the major driving forces of such a relationship has been reached (Gillman & Wright, 2006). Early reports that species richness should reach a maximum at intermediate levels of site fertility, which could be explained by at least nine different potential mechanisms (Rosenzweig & Abramsky, 1993), are no longer supported by a majority of studies (Mittelbach *et al.*, 2001). The shape of the relationship may differ depending on the spatial scale considered (Gross *et al.*, 2000; Chase & Leibold, 2002; Chalcraft *et al.*, 2004). Positive SR–ANPP relationships are typically found in large regional- or global-scale analyses (Mittelbach *et al.*, 2001; Chase & Leibold, 2002). These authors assumed that unimodal curves might be more typical at a local scale, yet in the present study the among-site relationships were positive whereas no relationship was found within sites. Thus, our study supports the general trend observed in an increasing number of large-scale observational studies (Mittelbach *et al.*, 2001). It has also been suggested that a unimodal relationship may result from an accumulation of consecutive linear relationships (Guo & Berry, 1998), but again this was not the case in our study since the positive linear relationship was observed even at the largest scale of two Chinese grassland regions.

Environmental factors explain positive SR–ANPP relationships

At the regional scale, species richness and productivity of vegetation are primarily driven by environmental variables such as climate, soil fertility and level of disturbance (Baer *et al.*, 2003; Kahmen *et al.*, 2005; Bai *et al.*, 2007; Kreft & Jetz, 2007). As shown in our analysis, climatic factors accounted for a large proportion of variation in both SR and ANPP, with GSP having a strong and GST a weaker positive effect on the two dependent variables. The latter was due to a difference in the direction of temperature effects between temperate (negative) and alpine regions (positive) (see Fig. 3c,d). Higher productivity is generally associated with high water availability in grassland biomes (Sala *et al.*, 1988; Jobbágy *et al.*, 2002). However, temperature effects may have positive direct effects on plant growth, in particular at high elevations where low temperatures can be limiting to plant developmental processes (Shi *et al.*, 2008), and negative indirect effects, e.g. via increased drought stress (Barber *et al.*, 2000), which might have occurred in the temperate regions of our study.

Thus, because climatic and other environmental differences among sites caused a positive covariation between SR and ANPP in our study (see Table 4), environmental variables were probably the key driver in shaping the positive SR–ANPP relationships among sites. Several theoretical and observational studies recently reported such influences of environmental conditions (Loreau, 2000; Dimitrakopoulos & Schmid, 2004; Adler & Levine, 2007; Bai *et al.*, 2007; Lamb, 2008). For instance, Loreau (2000) suggested that a positive SR–ANPP relationship might be generated when the responses of biodiversity and productivity to environmental factors are both positive. However, when biodiversity and productivity are affected in opposite directions by an environmental factor such as soil fertility, negative or hump-shaped patterns may result (Schmid, 2002; see, e.g., Kahmen *et al.*, 2005).

An alternative cause of variation in diversity–productivity relationships may be differences in evolutionary history among grassland vegetation types (Harrison & Grace, 2007; Pärtel *et al.*, 2007). Pärtel *et al.* (1996, 2007) hypothesized that local species richness and productivity could be related to the size of the species pool determined by evolutionary history (speciation or migration events) in different regions. In this case, different species richness along productivity gradients may just reflect the size of pools in a particular geographic region. For example, dispersal limitation of large-seeded plant species (small seed pool) (Pärtel & Zobel, 2007) or non-resource environmental factors (e.g. soil pH or salinity) may only limit the number of species (Grace, 2001; Pärtel *et al.*, 2007) but not productivity. We cannot exclude the possibility that such effects of evolutionary history were also contributing to the positive SR–ANPP relationship in our study, in particular the positive contribution of the remaining variation among sites which was not explained by climatic variables (see Table 4). However, it is also conceivable that this remaining among-site variation was due to differences in soil fertility or disturbance regime among sites, which may have affected SR and ANPP in the same direction, thus contributing to their positive relationship.

Positive SR–ANPP relationships disappear if environmental variation among sites is removed

The positive correlation between plant species richness and productivity decreased when the effects of climate, region and vegetation were removed, and the residual correlation between SR and ANPP disappeared completely when the remaining variation among sites was also removed (see Fig. 4e). That is, there was no indication for a relationship between SR and ANPP at the pooled within-site level. Within-site environmental heterogeneity between plots such as variation in soil fertility or disturbance regime, potentially causing a positive relationship between SR and ANPP within sites, may be negligible compared with environmental variation among sites and at larger spatial scales (Aarssen, 2004). Furthermore, in contrast to experiments (where the experimenter manipulates it), there may be no drivers causing persistent variations in species richness at the within-site scale, unless extremely strong dispersal limitation were to prevent a mixing of species available in the local pool (Pärtel & Zobel, 2007). Thus, if species richness generally reaches a relatively constant level determined by local environmental conditions, no SR–ANPP relationship would be expected. It appears that SR and ANPP may independently fluctuate at the local community scale due to random events such as plant growth, reproduction, dispersal and mortality events, or herbivory, trampling and other disturbance events.

CONCLUSION

Our results show that SR and ANPP are positively related to each other across temperate and alpine grasslands in China. However, this positive SR–ANPP relationship is driven by environmental factors which vary among sites. The potential effects of environmental conditions on the SR–ANPP relationship at a large spatial scale may mask direct effects of ANPP on SR potentially operating at a smaller scale.

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SUPPORTING INFORMATION

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Appendix S1 Summary of general linear models for species richness.

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BIOSKETCH

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