

Full Length Research Paper

Relationship between plant diversity and spatial stability of aboveground net primary productivity (ANPP) across different grassland ecosystems

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Theory predicts that greater biodiversity is expected to enhance stability of ecosystem. In field experiment, we created some diversity-level assemblages by removing functional groups across two grassland ecosystems and evaluated the responses of spatial stability of aboveground net primary productivity (ANPP) to varying functional trait diversity. The results revealed that higher diversity promoted greater spatial stability in the semi-shrub grassland ecosystem except SGB, whereas the similar pattern in diversity-stability relationship had been scarcely found in the typical steppe ecosystem. Additionally, we found that factors-influencing spatial stability varied across different grassland types. In the typical steppe ecosystem, spatial stability was only accounted for by positive sampling effect induced by high dispersal rate of rhizomatous grass. By contrast, in the semi-shrub grassland ecosystem, diversity level together with positive sampling effect commonly contributed to spatial stability, moreover, effect of particular trait overshadowed that of diversity. We also found that the positive diversity-stability relationship did not exist when compared with two grassland types. Research provides new insights into understanding the relationship between biodiversity and ecosystem functioning in varying environments. This relationship is not consistent across different ecosystems and is often system-dependent. Critical trait of species is particularly an important determinant for ecosystem functioning.

Key words: Biodiversity experiment, spatial variability, functional trait diversity, ecosystem type.

INTRODUCTION

There is little doubt that the ecosystem is confronted with enormous challenges accompanying declining biodiversity.

The long-standing problem has been captivating more and more ecologists to explore the influence of biodiversity on the ecosystem function (MacArthur, 1955; Hooper and Vitousek, 1997; Isbell et al., 2009), but the conclusions remain controversial. As early as the 1950s, ecologists advanced that complex and diverse communities could avoid destructive oscillations in populations (MacArthur, 1955; Elton, 1958). Subsequently, considerable studies have suggested that communities that have more species numbers are more stable (Loreau et al., 2001; Balvanera et al., 2006; Isbell et al., 2009). Meanwhile, some ecologists have showed that functional trait diversity is more directly responsible for stability than species richness (Huston, 1997; Tilman et al., 1997; Weigelt et al., 2008). However, other studies have con-

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Abbreviations: ANPP, Aboveground net primary productivity; SSS, semi-shrub only; SFL, semi-shrub + forbs + legume; SGB, semi-shrub + rhizomatous grass + bunchgrass; NATS, an untrimmed natural community containing semi-shrub + rhizomatous grass + bunchgrass; FLB, forbs + legume + bunchgrass; NATR, non-trimmed natural community containing forbs + legume + bunchgrass + rhizomatous grass; RRR, only rhizomatous grass.

cluded that diversity has either negative or negligible effect on the community stability (Hooper and Vitousek, 1997; Huston et al., 2000; Pfisterer and Schmid, 2002; Tilman et al., 2006). Infact, some early ecologists have stated that lower species richness could buffer the community dynamics (Pimm and Lawton, 1978). The uncertain relationship between diversity and ecosystem functioning is probably attributed to variation in ecosystems and community composition. In contrast to the wealth of studies on the influence of biodiversity on temporal stability, field tests of spatial stability are surprisingly few and demand substantial undertakings. Spatial stability refers to the similarity of community properties among replicate quadrats for a particular community. All the relevant researches completely focus on the idea that higher diversity positively impacts on the spatial reliability in microbial ecosystems (Naeem and Li, 1997; McGrady-Steed et al., 1997; Morin and McGrady-Steed, 2004) and in complex terrestrial ecosystems (Weigelt et al., 2008).

Biological diversity has been studied extensively for many decades. However, there is not still an accepted standard. Species richness as a traditional community-level descriptor is the first, intuitionist but poor way (Ricotta, 2005b). Shannon entropy and Simpson diversity are afterwards proposed in connection with the information on species richness, as well as species evenness (Ricotta, 2002). Functional group richness is also a relative simple expressive form. In the early nineties, Vane-Wright et al. (1991) advanced a measure of species taxonomic distinctiveness with the purpose of biological conservation. A species distance matrix was presented and this functional diversity embodied the taxonomic discrepancies for inter-species. Since then, functional diversity has been considered as a key feature to understand the link between ecosystem processes (ecosystem function and ecosystem reliability) and biodiversity (Diaz and Cabido, 2001). Nevertheless, all the diversity measures fail to combine the trait discrepancy and the abundance of each species in assemblage. A quantifying functional trait diversity measurement (Rao's quadratic Q) resolves the problem better (Rao, 1982; Ricotta, 2005a, b). Rao's quadratic Q as a continuous diversity measure takes into account the biological information on the functional distance on one hand and the relative abundances of species on the other.

Most relevant biodiversity experiments have been based on a gradient of plant species richness created by manually sowing the seeds of different species, with little attention paid to completely natural ecosystems (Roscher et al., 2004). However, the naturally assembled systems are strongly different from artificially created ones (Grime, 1998; Bai et al., 2004). With these considerations, we manipulated the diversity by removing different functional groups in different natural grassland ecosystems. Our aim is to evaluate the response of spatial stability of aboveground net primary productivity (ANPP) to functional

trait diversity in some varying ecosystems. Specifically, we tried to find whether the relationship between plant diversity and spatial stability was consistent in different component ecosystems.

MATERIALS AND METHODS

Study site

The study was carried out at the National Key Grassland Experiment Station, which is situated in the southern end of Hunshandak Sandy Land and belongs to the typical agro-pastoral ecotone in Hebei Province in northern China (41°46'N, 115°40'E, 1380 m above sea level). The region is characterized by a typical semi-arid monsoon climate. Mean annual air temperature is 1°C. Mean annual precipitation ranges from 350 to 450 mm and averages 80% in July - September. The annual potential evaporation is 1700 – 2300 mm (Huang et al., 2007). Prior to the beginning of the study, enclosure regime has been applied since 1990s. Therefore, there is visually heterogenous grassland landscape inside and outside the enclosure. The plant community types are the typical steppe ecosystem within the enclosure, in contrast to the degraded semi-shrub grassland ecosystem within the enclosure. The field study was operated inside and outside the enclosure, several kilometres apart from each other, where typical steppe ecosystem is dominated by the rhizomatous grass *Leymus chinensis* (Trin.) Tzvel. and semi-shrub: *Artemisia frigida* (Willd.) L. The study was conducted during May and October in 2008 and 2009.

Experimental design and treatment

The experiment was arranged in completely randomized blocks with three replications. Each block consisted of four constructed diversity-level communities in the semi-shrub grassland ecosystem and three constructed diversity-level communities in the typical steppe ecosystem, respectively. Four types of manipulated communities in each block for semi-shrub grassland ecosystem comprised of four different functional group mixtures: i) SSS, only semi-shrub; ii) SFL, semi-shrub + forbs + legume; iii) SGB, semi-shrub + rhizomatous grass + bunchgrass and iv) NATS, an untrimmed natural community of all the above mentioned functional groups. Additionally, in each block for typical steppe ecosystem, three types of manipulated communities comprised three different functional group mixtures: i) FLB, forbs + legume + bunchgrass ; ii) NATR, non-trimmed natural community containing forbs + legume + bunchgrass + rhizomatous grass and iii) RRR, only rhizomatous grass. The entire experiment was constructed 6 blocks, summing up 21 different diversity-level communities for two ecosystems in all. Each constructed diversity-level community in two grassland types was 2.5 × 3 m in size. These diversity-level communities were separated by buffer zones of about 0.5 m wide. Once a week from early May to early October in both experimental years, all the plants of non-target plant functional groups in two research sites were mechanically cut to the ground level to maintain the desired functional group composition.

Diversity measure and data collection

Rao's quadratic entropy is calculated thus:

$$Q = \sum_{i=1}^s \sum_{j=1}^s d_{ij} p_i p_j$$

Table 1. The list of functional attributes expressed at species level.

Species characteristics	Data type		Scale
Morphological traits Growth form			
(1) Caspitosa	binary		(0) non caespitosa; (1) caespitosa
(2) Rosulata	binary		(0) non rosulata; (1) rosulata
(3) Scaposa	binary		(0) non scaposa; (1) scaposa
(4) Reptantia	binary		(0) non reptantia; (1) reptantia
Clonal growth			
(5) Capacity to lateral spread by vegetative growth	ordinal	3 categories	(0) no lateral spread; (1) over short distances (short stolons rhizoms, commonly <5cm); (3) over longer distances (creeping stems, above- and below-ground stolons).
Above-ground species performance			
(6) Height of vegetative plant	ordinal	5 categories	(1) up to 10 cm; (2) up to 20 cm; (3) up to 30 cm; (4) up to 40 cm; (5) >40 cm
(7) Height of flowering plant	ordinal	5 categories	(0) non flowing plant; (1) up to 20 cm; (2) up to 50 cm; (3) up to 90 cm; (4) >90 cm
Below-ground species performance			
(8) Depth of the root system	ordinal	7 categories	(1) <5 cm; (2) <10 cm; (3) <20 cm; (4) <40 cm; (5) <60 cm; (6) <100 cm; (7) >100 cm
(9) Type of the root system	ordinal	3 categories	(1) Long-living primary root system; (2) secondary fibrous roots in addition to the primary root system; (3) short-living primary root system, extensive secondary root system
Longevity			
(10) Life cycle	ordinal	3 categories	(1) Annual; (2) biennial; (3) perennial
(11) Seasonality of foliage	ordinal	3 categories	(0) summer green; (1) partly evergreen; (2) evergreen
Phenological traits			
(12) Start of flowering period	ordinal	5 categories	(1) before May; (2) May; (3) June; (4) July; (5) August
(13) Duration of flowering period	ordinal	4 categories	(1) 1 month; (2) 2 months; (3) 3 months; (4) more than 3 months
(14) Start of seeding period	ordinal	3 categories	(1) July; (2) August; (3) October
(15) Duration of seeding period	ordinal	4 categories	(1) 1 month; (2) 2 months; (3) 3 months; (4) more than 3 months
(16) Mean seed kiloweight	ordinal	5 categories	(1) <0.5 g; (2) <1 g; (3) <1.5 g; (4) <2 g; (5) >2 g
Physiological traits			
(17) Legume (nitrogen fixation)	binary		(0) non legume; (1) legume.

where S is the total number of species in the community, P_i, P_j are the relative abundances of the i th and j th species. d_{ij} shows the functional trait discrepancy between stochastic two species. Q expresses the sum of trait diversity dissimilarity for all the species in any diversity-level community and d_{ij} is expressed as follows:

$$d_{ij} = \sum_{t=1}^T (x_{it} - x_{jt})^2$$

In order to calculate d_{ij} , A functional trait matrix is constructed and consists of functionally relevant traits ($t = 1, \dots, T$) for the different species ($s = 1, \dots, i, \dots, j, \dots, S$) (Weigelt et al., 2008):

$$X = (x_1, \dots, x_t) = \begin{bmatrix} x_{11} & \dots & x_{1T} \\ \vdots & \ddots & \vdots \\ x_{S1} & \dots & x_{ST} \end{bmatrix}$$

To construct the functional trait matrix, 17 selected attributes at species level were monitored in every created diversity-level community of 2.5 x 3 m every 10 days from early May to early October 2009. These ecological traits mainly reflected spatial and temporal complementarities of species (Table 1). Fourteen of these attributes have been defined as the functional groups in previous literatures (Roscher et al., 2004). All the chosen attributes were mapped to a scalar and forced to have a single value along different

Table 2. One-way ANOVA of functional trait diversity, coefficient of variance (CV) of aboveground net primary productivity (ANPP) and ANPP among twelve subplots within experimental communities across two grassland ecosystems. Functional trait diversity is based on diversity of selected 17 attributes (see Method).

Source	Typical steppe ecosystem			Semi-shrub ecosystem		
	Functional trait diversity	CV	ANPP	Functional trait diversity	CV	ANPP
Sum of Squares	170.547	0.042	257.625	326.318	0.082	12870.226
df	2	2	3	3	3	2
Mean Square	85.274	0.021	85.875	108.773	0.027	6435.113
F	13.856	1.113	3.452	26.593	13.783	82.024
Significance	0.000	0.388	0.036	0.000	0.002	0.000

F = Frequency; df = degree of freedom.

trait dimensions. However, 17 attributes were assigned the disparate weighting value because of different measurement scales and standards. Consequently, all the traits were square-root transformed and simultaneously standardized to mean zero and unit variance to eliminate skewed distribution of trait. All the data were analyzed in SPSS 16.0. The spatial stability is determined by the coefficient of variation (CV):

$$CV = \delta / \mu$$

Where δ is the standard deviation of ANPP and μ is the mean of ANPP (Lehman and Tilman, 2000).

From 15 to 20 August 2009, aboveground plant parts were harvested. In each constructed community for individual grassland type, four subplots of 0.5 × 0.5 m were randomly chosen and harvested separately. Two stochastic samples were sorted into species and then cut to ground level. The remainders were directly cut at the soil surface. All the plant samples were dried for 48 h at 80°C and weighed for dry mass.

RESULTS

Semi-shrub ecosystem

There were some evidences that functional trait diversity could increase spatial stability in semi-shrub ecosystem with the exception of SGB. There were remarkable differences in functional trait diversity and spatial stability for four diversity-level communities (Table 2). The considerable increase in functional trait diversity ranged from SSS to NATS (Figure 1a), with concurrently increase in stability from SSS to NATS except SGB (Figure 1b). By multiple comparisons, SSS was significantly lower than other three communities in functional trait diversity ($P = 0.000$ for all). SSS achieved the lowest stability and significantly overran SFL ($P = 0.011$), SGB ($P = 0.000$) and NATS ($P = 0.003$). Although functional trait diversity of SGB was significantly smaller than NATS

($P = 0.004$), SGB resulted in stronger spatial stability than NATS ($P = 0.037$). Furthermore, ANPP of SGB was significantly higher than SSS ($P = 0.025$), SFL ($P = 0.010$) and NATS ($P = 0.021$) (Table 2 and Figure 1c).

Typical steppe ecosystem

We found weak evidence that biodiversity enhanced spatial stability of ANPP in typical steppe ecosystem. Increasing functional trait diversity did not reduce spatial variation of ANPP among experimental communities (from RRR to FLB) (Figures 2a and b). The three diversity-level communities showed considerable differences in functional trait diversity but not in stability (Table 2). By multiple comparisons, we found that functional trait diversity of FLB was significantly greater than NATR ($P = 0.000$) and RRR ($P = 0.000$), whereas the discrepancies in spatial stability among three constructed communities were not significant. Additionally, despite the fact that functional trait diversity of RRR was lower four times than that of FLB (Figure 2a), the spatial stability of RRR nearly equaled to FLB (Figure 2b). These results showed that functional trait diversity did not significantly influence spatial stability. In addition, ANPP of RRR was also greater than FLB and NATR ($P = 0.000$ for both) (Table 2 and Figure 2c).

The spatial stability of ANPP in two types of grassland ecosystems

We tested the relationship between functional trait diversity and spatial variability of ANPP as well across two grassland ecosystems, and was similarly found that functional trait diversity rarely impacted on spatial stability.

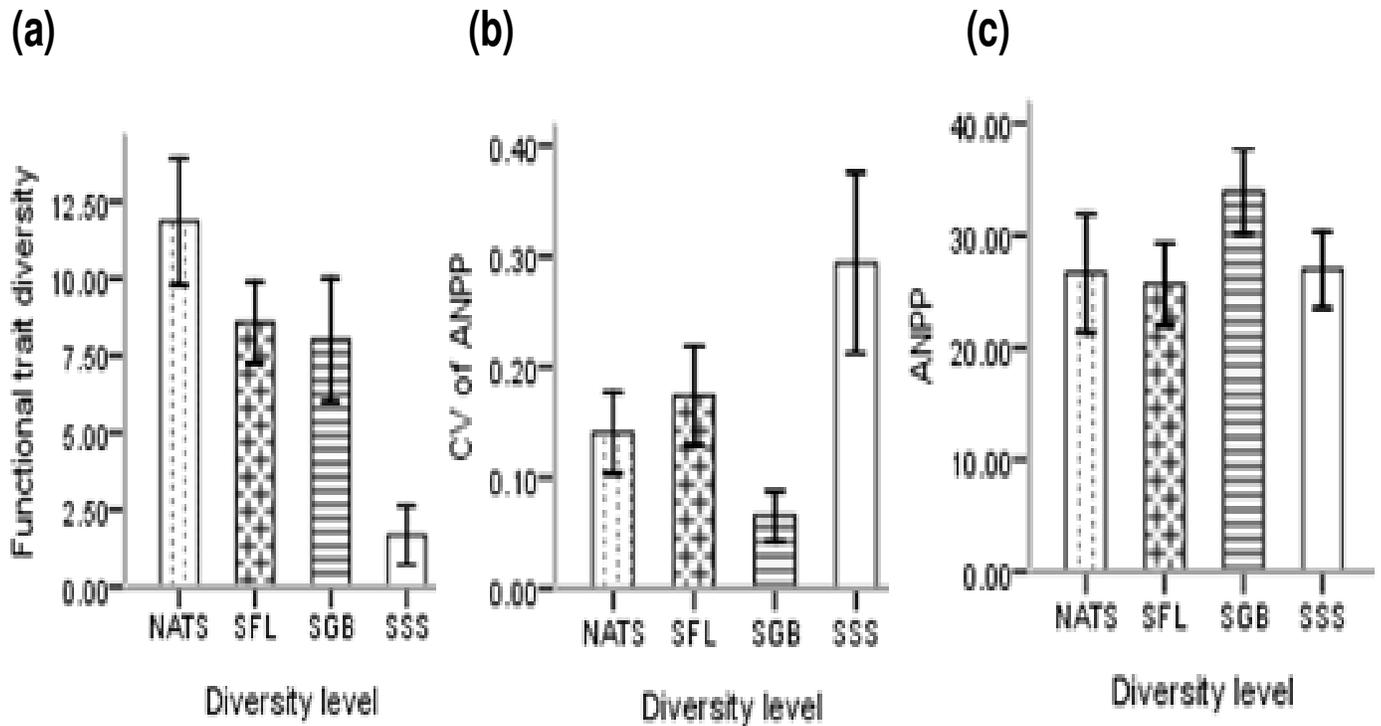


Figure 1. The changes of functional trait diversity, coefficient of variance (CV) of aboveground net primary productivity (ANPP) and ANPP in a semi-shrub ecosystem. Error bars indicate ± 2 SE.

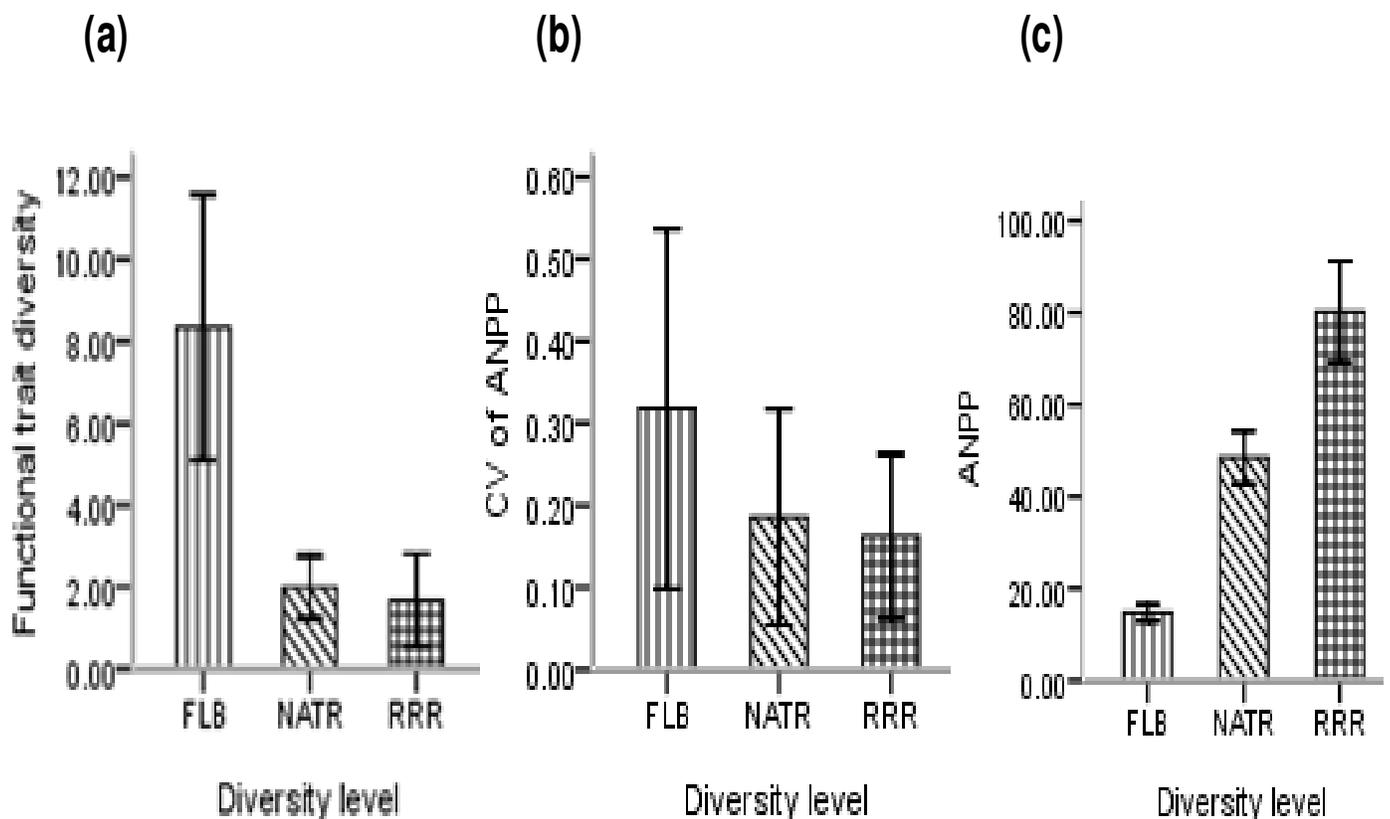


Figure 2. The changes of functional trait diversity, CV of ANPP and ANPP in a typical steppe ecosystem. Error bars indicate ± 2 SE.

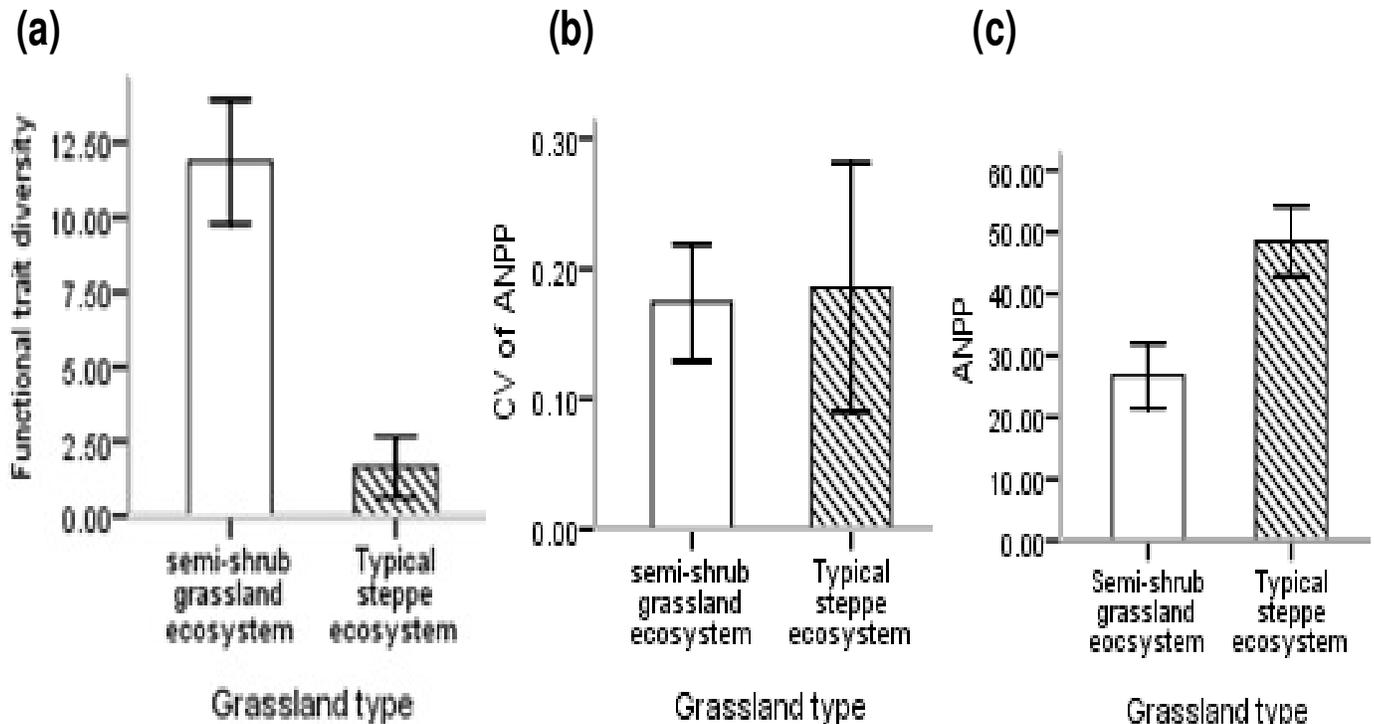


Figure 3. The changes of functional trait diversity, CV of ANPP and ANPP in two grassland ecosystems. Error bars indicate ± 2 SE.

Although functional trait diversity was significantly larger for semi-shrub ecosystem than for typical steppe ecosystem ($t = -8.906$, $P = 0.000$) (Figure 3a), two grassland ecosystems were almost equal in spatial stability ($t = 0.219$, $P = 0.837$) (Figure 3b). Moreover, we also found that ANPP of typical steppe ecosystem was obviously greater than that of semi-shrub ecosystem ($t = -5.631$, $P = 0.000$) (Figure 3c).

DISCUSSION

The communities gained higher spatial stability with increasing functional trait diversity in semi-shrub ecosystem except SGB. This case supports the most prevailing biodiversity idea that higher diversity promotes community temporal stability (Bai et al., 2004) and spatial stability (Weigelt et al., 2008). Meanwhile, it presents some experimental evidence for “insurance” hypothesis, which states that increasing biodiversity insures ecosystem against an increase in the biomass variance (Loreau et al., 2003; Richard et al., 2007).

However, it was difficult to find that higher functional trait diversity was related to higher stability in typical steppe ecosystem. Surprisingly, increasing functional trait diversity greatly reduced spatial reliability of ANPP. This conflicts with the usual conception that greater biodiversity provides the basis for more stable community. Although substantial studies have indicated that higher diversity is closely associated with ecosystem stability, diversity is

not directly responsible for ecosystem functioning as such (Huston, 1997; McCann, 2000). Some researches operated in perennial grassland have suggested that diversity effects on ecosystem properties were mainly attributed to traits of involved species, but not diversity itself (Wardle et al., 1999).

As observed in the study, SGB achieved the greatest stability in semi-shrub ecosystem (Figure 1b) and RRR gained the highest stability in typical steppe ecosystem (Figure 2b). It should be noted that the communities of SGB and RRR are both dominated by rhizomatous grass. Moreover, we also found the stability of typical steppe ecosystem which was dominated by rhizomatous grass was almost equal to semi-shrub ecosystem, albeit the former had significantly lower functional trait diversity than the latter (Figures 3a and b). Therefore, it is assumed that the community-stabilizing factor is to a greater extent determined by rhizomatous grass.

Rhizomatous grass was found to form the powerful competition matrix of tillers in the upper soil layers and it was conjectured that this property could better stabilize the community. Our result is consistent with some statements that the positive effect of rhizomatous grass on spatial stability has been attributed to a continuous matrix of tillers (Hodge, 2004; Weigelt et al., 2008). Therefore, SGB and RRR achieved the greatest stabilities that were caused by rhizomatous grass trait rather than by diversity. The results emphasize that effect of particular trait has played more important role in stabilizing communities than diversity. Diaz and Cabido

(2001) have reported that species traits rather than diversity, strongly determine ecosystem functioning. Other ecologists have also proposed that trait discrepancies within communities have strongly controlled ecosystem-level dynamics (Ernest and Brown, 2001; Rees et al., 2001).

Additionally, the high dispersal rates of the rhizomatous grass lead to competitive exclusion of other functionally redundant species and therefore produce positive sampling effect. Aftermath of positive sampling effect would result in the fall of diversity, but synchronously augment mean productivity (Aarssen, 1997). The present study has also provided some evidence for positive sampling effect. For instance, the communities dominated by rhizomatous grass tended to exhibit lower diversity and higher productivity. Lehman and Tilman (2000) have indicated that stability-increasing approaches involve either increase in mean productivity or decrease in the variance in productivity, or both. Moreover, Tilman et al. (2006) have demonstrated that community stability is positively influenced by productivity. Therefore, productivity-enhancing regulators are bound to lead to the increase in stability.

Conclusion

In conclusion, the experiment shows that functional trait diversity has a significantly positive effect on spatial stability of ANPP except SGB in the semi-shrub grassland ecosystem. However, spatial stability of ANPP in the typical steppe ecosystem seems unaffected by functional trait diversity. This indicates that the relationship between plant diversity and spatial stability varies with the component of ecosystem. We further find that the effects of crucial functional traits, such as high dispersal rate of rhizomatous grass, have overwhelmed those of diversity on spatial stability of ANPP. Research will trigger new awareness and consideration of prevalent biodiversity hypothesis that greater biodiversity is expected to enhance ecosystem stability. The relationship between plant diversity and spatial stability is often ecosystem-specific.

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