

## LETTER

# Linking stoichiometric homeostasis with ecosystem structure, functioning and stability

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### Abstract

Ecosystem structure, functioning and stability have been a focus of ecological and environmental sciences during the past two decades. The mechanisms underlying their relationship, however, are not well understood. Based on comprehensive studies in Inner Mongolia grassland, here we show that species-level stoichiometric homeostasis was consistently positively correlated with dominance and stability on both 2-year and 27-year temporal scales and across a 1200-km spatial transect. At the community level, stoichiometric homeostasis was also positively correlated with ecosystem function and stability in most cases. Thus, homeostatic species tend to have high and stable biomass; and ecosystems dominated by more homeostatic species have higher productivity and greater stability. By modulating organism responses to key environmental drivers, stoichiometric homeostasis appears to be a major mechanism responsible for the structure, functioning and stability of grassland ecosystems.

### Keywords

Biodiversity, ecological stoichiometry, ecosystem services, species traits.

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## INTRODUCTION

The ecosystems upon which humans rely have been altered in unprecedented ways by human population expansion and industrialization. As a result, biodiversity is decreasing (Chapin *et al.* 2000), species invasions are expanding (Cohen & Carlton 1998) and major biogeochemical cycles are changing (Falkowski *et al.* 2000; Elser *et al.* 2009). These forces put ecosystems under considerable stress, making it critical to understand the mechanisms that underpin ecosystem structure, functioning and stability (McCann 2000; Loreau *et al.* 2001; Ives & Carpenter 2007). Many studies have shown that greater ecological diversity leads to greater ecosystem production and stability (Tilman & Downing 1994; Tilman *et al.* 1996, 2006; Naeem & Li 1997; Bai *et al.* 2004; Ptacnik *et al.* 2008) but the topic

remains controversial (Wu & Loucks 1995; Chapin *et al.* 1997; McCann 2000; Loreau *et al.* 2001; Ives & Carpenter 2007). The diversity of species traits present, especially in nutrient use strategies, is likely to play a fundamental role in modulating the relationship between biodiversity and ecosystem structure, functioning and stability (Chapin *et al.* 1997; Knops *et al.* 2002) because these traits link organismal functioning to ecological dominance and to key environmental factors such as biogeochemical nutrient supplies.

Stoichiometric homeostasis is the ability of an organism to maintain a given elemental composition despite variation in the elemental composition of its environment or diet (Sternner & Elser 2002) and reflects the net outcome of many underlying physiological and biochemical adjustments as organisms respond to their surroundings (Hessen *et al.*

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2004). Indeed, stoichiometric homoeostasis is a foundational concept of ecological stoichiometry as applied to trophic interactions (Sternner & Elser 2002). While early studies have emphasized strong physiological variation in elemental composition in photoautotrophs ('weak' stoichiometric homoeostasis), especially algae and cyanobacteria (Rhee 1978), only a few studies have actually quantified the degree of stoichiometric homoeostasis in terrestrial vascular plants (Güsewell 2004; Elser *et al.* 2010). To our knowledge, no studies have examined the relationship between stoichiometric homoeostasis and key aspects of ecological performance, such as species dominance, ecosystem function and stability.

Our exploration of these patterns took place in the Inner Mongolia grassland of China, part of the largest contiguous grassland in the world. First, we examined the strength of stoichiometric homoeostasis ( $H$ ; Sternner & Elser 2002) by measuring the nitrogen (N) and phosphorus (P) contents and N:P ratio in the aboveground biomass (generally foliage) of 12 vascular plants that were grown across a broad range of soil N and P contents and N:P ratios in a 2-year field N and P addition experiment (see Material and methods). Then we took three approaches to test the relationship of stoichiometric homoeostasis with species dominance, ecosystem functioning and stability. These involved a 2-year field N and P addition experiment, a long-term (27 years) observational data set of grassland excluded from sheep grazing and a 1200-km spatial transect. Our primary objective was to determine if stoichiometric homoeostasis could predict the observed patterns of primary productivity and stability at both the species and ecosystem levels and across a broad range of spatial and temporal scales.

## MATERIAL AND METHODS

### Study sites and field sampling

Data used in the paper comes from three sources: a 2-year field N and P addition experiment, a 27-year field monitoring program and 1200-km spatial transect.

The field N and P addition experiments were conducted in a *Leymus chinensis* grassland that had been fenced since 1999 to prevent grazing by large animals. The N addition experiment had seven treatments with six replicates for each treatment, including Control, 0, 0.4, 0.8, 1.6, 2.8, 4.0 mol N m<sup>-2</sup> (added as urea). Each plot, except for Control, also received 0.05 mol P m<sup>-2</sup> (as KH<sub>2</sub>PO<sub>4</sub>) to ensure that N was the only limiting nutrient (Tilman 1986, 1987; Bai *et al.* 2010). The P addition experiment also had seven treatments with six replicates, including Control, 0, 0.05, 0.1, 0.2, 0.3, 0.4 mol P m<sup>-2</sup> (as KH<sub>2</sub>PO<sub>4</sub>). The effect of K was controlled by adding appropriate levels of KCl so that all received similar levels of K. For the P addition experiment, each plot, except for Control, also received 0.2 mol N m<sup>-2</sup> (urea) to ensure that P was the only limiting nutrient. We note that both the N and P addition rates are below saturation levels in this 2-year study. The fertilizer was thoroughly mixed with sand and then applied to the plot surfaces in May 2006 and 2007. The aboveground biomass was sampled by clipping all plants at ground level within a 1 m × 1 m quadrat on 20 July 2006 and 2007. All living vascular plants were sorted to species, oven-dried at 60 °C and weighed. Fifty mature and healthy leaves of 12 species were selected (Table 1), ground and mixed evenly for analysis. Soil was randomly sampled with three replicates at the depth of 0–10 cm within quadrats also on 20 July 2006 and 2007, and the three replicates were mixed as one sample.

**Table 1**  $H$  values and associated  $R^2$  of the 12 species in the field experiments calculated by using  $y = cx^{1/H}$  to describe the relationship between tissue N content, P content or N:P ratio of plants ( $y$ ) and soil ( $x$ ) (all  $P < 0.0001$ ,  $n = 42$ )

Species	2006								2007							
	$H_N$	$R^2$	$H_{N:P(+N)}$	$R^2$	$H_P$	$R^2$	$H_{N:P(+P)}$	$R^2$	$H_N$	$R^2$	$H_{N:P(+N)}$	$R^2$	$H_P$	$R^2$	$H_{N:P(+P)}$	$R^2$
<i>Leymus chinensis</i>	7.16	0.93	8.88	0.88	5.41	0.83	7.17	0.54	7.61	0.84	9.45	0.73	4.96	0.64	5.91	0.65
<i>Stipa grandis</i>	5.40	0.79	6.93	0.64	4.20	0.90	4.04	0.80	6.23	0.78	6.98	0.81	3.68	0.73	5.25	0.60
<i>Agropyron cristatum</i>	5.45	0.82	6.40	0.71	3.46	0.93	3.71	0.76	6.08	0.84	6.90	0.60	3.37	0.88	4.06	0.84
<i>Cleistogenes squarrosa</i>	6.13	0.62	6.64	0.58	4.20	0.83	4.40	0.59	6.04	0.84	8.03	0.51	2.98	0.84	4.44	0.62
<i>Achnatherum sibiricum</i>	5.74	0.71	6.56	0.70	4.99	0.65	5.27	0.63	5.36	0.78	5.87	0.50	4.36	0.91	4.52	0.58
<i>Koeleria cristata</i>	5.48	0.82	6.48	0.68	4.09	0.88	3.67	0.77	5.12	0.83	6.11	0.54	3.99	0.89	3.73	0.91
<i>Poa sphondylodes</i>	4.61	0.86	5.46	0.62	3.03	0.89	3.28	0.72	4.85	0.79	5.99	0.75	2.94	0.86	3.80	0.76
<i>Carex korsbinskyi</i>	5.03	0.78	6.50	0.53	3.00	0.70	3.89	0.54	4.67	0.95	5.27	0.91	2.79	0.69	3.04	0.63
<i>Allium ramosum</i>	3.92	0.93	4.26	0.83	3.65	0.92	3.77	0.79	4.37	0.90	4.99	0.65	3.55	0.79	3.93	0.76
<i>Allium tenuissimum</i>	4.56	0.85	4.57	0.72	4.02	0.90	3.53	0.69	4.11	0.95	5.39	0.64	3.66	0.90	3.97	0.72
<i>Axyris amarantoides</i>	4.18	0.88	4.74	0.70	2.83	0.94	2.62	0.81	3.92	0.93	4.51	0.63	2.60	0.94	3.00	0.83
<i>Chenopodium glaucum</i>	3.60	0.93	4.54	0.57	2.76	0.92	2.89	0.72	3.53	0.92	4.23	0.56	2.71	0.88	2.90	0.75

The long-term experimental data were obtained by monitoring the personnel of the Inner Mongolia Grassland Ecosystem Research Station of a *L. chinensis* grassland that was fenced in 1979. The aboveground biomass was sampled during 28–30 August of each year using methods previously described by Chen & Wang (2000) and Bai *et al.* (2004). We used the data from 1980 to 2007 (except 1986, for which data were lost).

The large spatial scale data were obtained from a 1200-km east–west transect in Inner Mongolia, China completed in July 2004. Mean annual precipitation across the transect ranged from 120 to 450 mm, and mean annual temperature ranged from 0.5 to 7.1 °C. Fifty-three sampling locations, 20–25 km apart, were GPS-referenced with latitude, longitude and elevation. Plant samples within a 1 m × 1 m quadrat at each location were sorted into species, air-dried and oven-dried at 70 °C before being weighed. Three vegetation types were encompassed by the transect: meadow steppe, typical steppe and desert steppe.

### Laboratory analysis

N concentrations (% of dry mass) of the leaves were analysed using the micro-Kjeldahl method (Bremner 1996). P contents (%) of the leaves were measured by the ammonium molybdate method after persulfate oxidation (Kuo 1996), standardized against known reference materials.

For soil inorganic N measurement, dried and pre-weighed soil samples were first extracted using 2 mol L<sup>-1</sup> KCl. The concentrations of inorganic N (NH<sub>4</sub><sup>+</sup>-N and NO<sub>3</sub><sup>-</sup>-N) in the filtrates were determined using a flow injection autoanalyser (FIAstar 5000 Analyser; Foss Tecator, Hillerød, Denmark). The concentrations of soil inorganic N were calculated based on dry soil weight. To measure available P, air-dried and pre-weighed soil was extracted using 0.5 mol L<sup>-1</sup> NaHCO<sub>3</sub> and P concentration in the extract was determined by the ammonium molybdate method. Soil water content was determined gravimetrically by oven-drying subsamples at 105 °C for 24 h.

### Calculation of homeostatic regulation coefficients

The homeostatic regulation ability of each plant species was estimated by calculating the homeostatic regulation coefficient ( $H$ ) according to the following equation (Sterner & Elser 2002):

$$y = cx^{1/H},$$

where  $y$  is the N or P content (% dry mass) or N:P ratio of plants,  $x$  is the inorganic N or available P content or N:P ratio in the soil and  $c$  is a constant.

Community  $H$  is the overall mean of  $H$  across all species ( $n$ ) weighted by each species' relative (fractional) contribution to overall biomass. That is:

$$\begin{aligned} \text{Community } H &= (\text{relative biomass}_1 \times H_1) \\ &+ (\text{relative biomass}_2 \times H_2) \\ &+ \dots + (\text{relative biomass}_n \times H_n). \end{aligned}$$

According to the theory of stoichiometric homeostasis, community  $H$  can also be calculated using the community N concentrations or P content or N:P ratio vs. soil inorganic N or P or N:P ratio. As very similar results were obtained using the two methods, we used the weighted mean of species'  $H$  to calculate the community  $H$ .

### Data analysis and statistics

To estimate the strength of plant homeostasis for a given measure of plant nutrient content, we used regression analysis to fit the data to the homeostatic model equation  $y = cx^{1/H}$ . Linear regression was then used to assess the relationship between  $H$  and species dominance and stability. Total least square linear regression model was used to estimate the association between community  $H$  and community production and stability. All statistical analyses were performed using SAS (version 9.0; SAS Inst., Cary, NC, USA).

Species dominance was expressed by relative biomass, i.e. each species' aboveground biomass as a fraction of the total community biomass. Species stability was calculated as the ratio of its biomass mean to its standard deviation in the context of interest (Tilman *et al.* 2006). Community production was the total biomass of all living species within a quadrat, while community  $H$  was estimated from data for the 12 species' relative biomass and  $H$  values. The biomass of the 12 species that we included in this study was 95% of the total biomass in the field N and P addition experiment and was 80% in the long-term experiment. In the large-scale transect, three species (*Achnatherum sibiricum*, *Koeleria cristata* and *Axyris amarantoides*) were very infrequently observed in the communities. Hence, only nine species (54% of the total biomass) were included in the large-scale transect analysis, and five quadrats in which the nine species contributed < 10% to the total biomass were precluded.

Community stability was calculated as the ratio of community aboveground biomass mean to standard deviation. We examined stability in three contexts. First, stability was assessed as relative response to N and P addition in the field nutrient enrichment experiment. Second, stability was assessed as intraannual variation within five plots in long-term experiment. Finally, we characterized spatial stability by considering mean biomass relative to variability for eight quadrats within each 200 km section of the spatial transect.

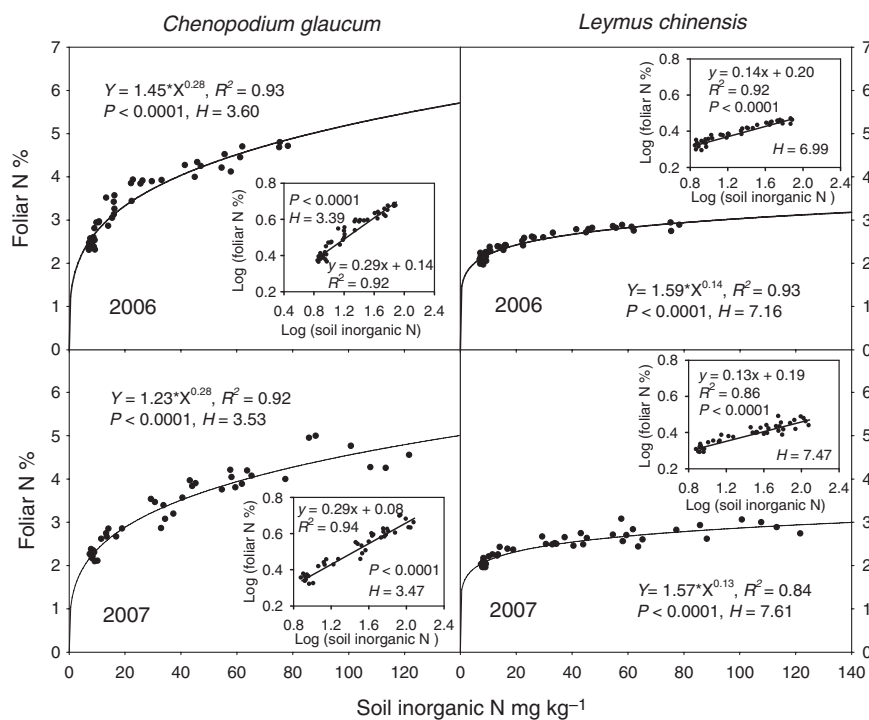
## RESULTS

In the N and P addition experiment, associations of plant N and P contents and N:P ratio with soil nutrient contents and N:P ratio could be rigorously described by the stoichiometric homoeostasis model (Sternier & Elser 2002):  $y = cx^{1/H}$  (Table 1, all  $P < 0.0001$ ). In this formulation, species with strong stoichiometric regulation of elemental composition have high values of  $H$ . Exemplary data for strong N homoeostasis in *L. chinensis*, a dominant rhizomatous plant, and weak N homoeostasis in *Chenopodium glaucum*, an annual species, from the field N addition experiment are given in Fig. 1. Almost identical results were obtained by fitting the homoeostasis model and by analysing its linearized form using log-transformed data (inset). On average, the homoeostasis model explained  $77 \pm 13\%$  (mean  $\pm$  SD,  $n = 96$ ; Table 1) of the variation in plant elemental composition for the 12 plant species. There was no difference between  $H$  for 2006 vs. 2007 (paired  $t$ -test;  $P = 0.74$ ).

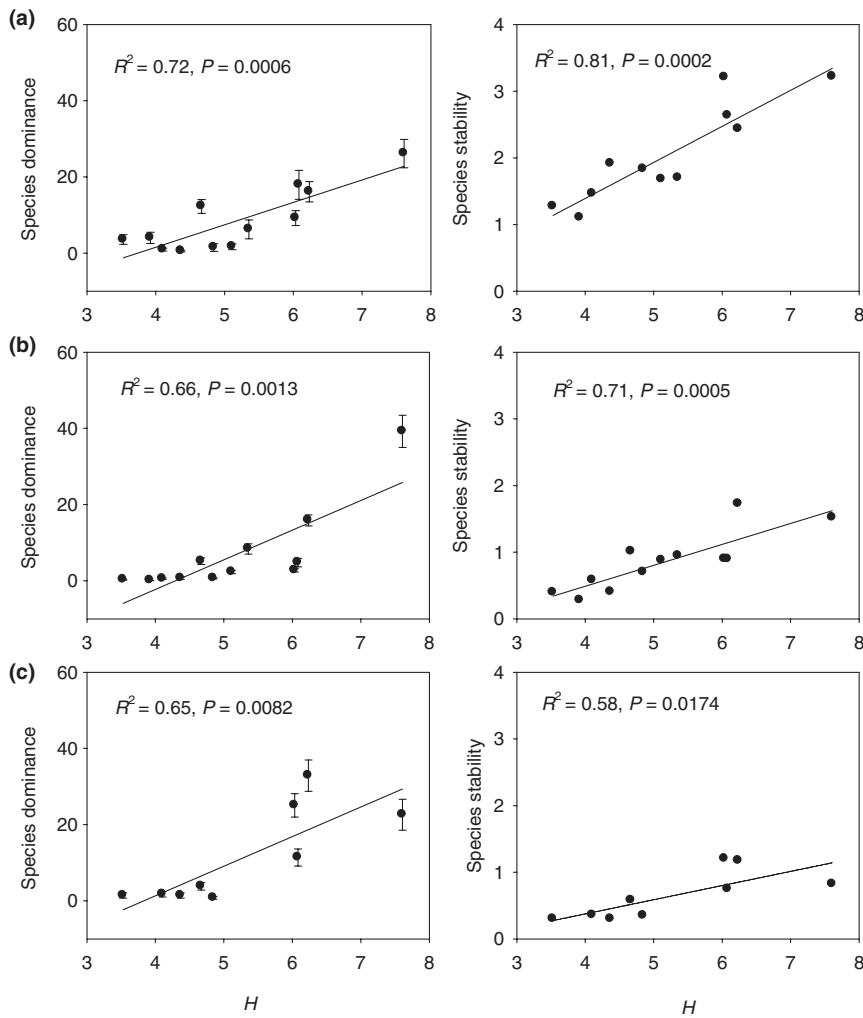
Using these foliar  $H$  values, we analysed the relationship between  $H$  and species dominance (expressed as percentage of aboveground biomass) for these 12 species in natural grassland in short term (i.e. the Control treatment in the 2-year fertilization experiment), long term and large spatial scale contexts. In the short-term experiment,  $H$  for N ( $H_N$ ) was significantly and positively correlated with species dominance (2007 data; Fig. 2a,  $r^2 = 0.72$ ,  $P = 0.0006$ ,  $n = 12$ ). Similar relationships were observed for  $H_N$  in 2006 as well as for  $H$  for N:P in N addition experiment

( $H_{N:P(+N)}$ ), and  $H$  for N:P in P addition experiment ( $H_{N:P(+P)}$ ) in 2006 and 2007 (Table 2) and thus we focused on data for  $H_N$  in further analyses ( $H$  hereafter). However, the associations were not significant for  $H$  for P ( $H_P$ ) in the P addition experiment ( $P = 0.12$  and  $0.15$  in 2006 and 2007, respectively). More importantly, species-specific  $H$  values obtained from the short-term N and P addition experiment were significantly and positively correlated with species dominance in both the long term and the spatial transect studies (Fig. 2b,c; Table 2) with the exception of 2007  $H_P$  ( $P = 0.24$ ) and 2006  $H_{N:P(+P)}$  ( $P = 0.12$ ) in the large spatial transect. Higher  $H$  was also significantly associated with higher species stability (defined as its mean biomass divided by its standard deviation; Tilman *et al.* 2006) in each of the three data sets with the exception of  $H_P$  ( $P = 0.12$  and  $0.53$  in 2006 and 2007 respectively) and 2006  $H_{N:P(+P)}$  in the spatial transect ( $P = 0.23$ ; Table 2). Overall,  $H_N$  was much more tightly associated with species dominance and biomass stability than  $H_P$  (higher  $r^2$  and lower  $P$ ; Table 2), furthermore,  $H_{N:P(+N)}$  and  $H_{N:P(+P)}$  were more rigorously correlated (higher  $r^2$ ) with species dominance and stability than  $H_N$  and  $H_P$  respectively.

At the species level,  $H$  was positively correlated with the dominance and stability of a given species. Next we asked: what are the relationships between  $H$  and production and stability at the community level? To evaluate these relationships, we calculated dominance-weighted  $H$  values (community  $H'$ , see Material and methods) for our grassland study sites and compared those to measures of aboveground



**Figure 1** Two examples showing the relationship between foliar N content (per cent of leaf dry mass) and soil inorganic N content (NH<sub>4</sub><sup>+</sup>-N + NO<sub>3</sub><sup>-</sup>-N) for two focal species in the field N addition experiment. Coefficients fitting the data to the equation for stoichiometric homoeostasis are given along with an estimate of  $H$ . The insets showed the linearized analysis using log-transformed data according to Sternier & Elser (2002).



**Figure 2** Relationships between  $H$  and species dominance and stability. Error bars represent standard errors of the mean.  $H$  represents the  $H_N$  value obtained for each species from the 2007 field N addition experiment (values of  $H$  for P and N:P are given in Table 2). Species dominance was expressed by its relative biomass in the natural community (i.e. Control plots for a). Species stability was expressed by mean/standard deviation. (a) Field N addition experiment. One outlier value of species stability was dropped (see the result in Table 2 with full data). (b) The 27-year monitoring study. (c) The 1200-km transect. See Material and methods for more information about data analysis.

biomass and its overall stability (Fig. 3; Table 3). Here, again we found a significantly positive relationship between community  $H$  and community production in the short-term and the long-term experiments (Fig. 3a,b). Furthermore, community stability was positively correlated with community  $H$  in both the short-term and long-term data sets with the exception of  $H_{N:P(+P)}$  and  $H_P$  in long term for both years and for  $H_{N:P(+N)}$  in 2007 (Fig. 3a,b; Table 3). However, we only found a significant relationship between community  $H$  and community production and stability in meadow grassland across the large-scale transect (Fig. 3c); no significant relationships were found in typical steppe and desert steppe.

## DISCUSSION

In this study, we estimated  $H$  of 12 species in a 2-year field N and P addition experiment and found positive relationships between  $H$  and species dominance. Using these  $H$  values, we subsequently confirmed these general patterns on

a 27-year temporal scale and a 1200-km spatial scale (with some exceptions for  $H_P$ , which will be discussed later). Overall, these positive associations indicate that species with higher foliar  $H$  are more dominant than those with lower  $H$ , supporting the view that stoichiometric homeostasis is an important mechanism underpinning community structure.  $H$  was also positively associated with species stability in each of the three data sets. Thus,  $H$  predicted species stability not only in relation to short-term variation in nutrient supply (Fig. 2a) but also in the context of long-term temporal dynamics (i.e. changes due to precipitation or temperature, Fig. 2b) and large-scale spatial variability (Fig. 2c).

However, we only found positive relationships between  $H_P$  and species dominance and stability in the long-term experiment, whereas no relationships in the field P addition experiment and large scale experiment were found. This suggests that N controls ecosystem structure more tightly than P in these study sites, consistent with prior conclusions that primary production in Inner Mongolia grassland is primarily limited by N (Bai *et al.* 2010). However, the



**Table 2** Results of regression analyses of the relationship between  $H$  and species dominance and species stability

Species factors	Experiments	$H$	2006				2007			
			Slope	Intercept	$R^2$	$P$	Slope	Intercept	$R^2$	$P$
Species dominance	Short term	$H_N$	7.27	-28.80	0.65	0.0015	6.12	-23.20	0.72	0.0006
		$H_{N:P(+N)}$	5.66	-25.64	0.70	0.0007	4.33	-18.29	0.60	0.0032
		$H_P$	5.05	-10.87	0.22	0.1223	5.24	-9.83	0.20	0.1465
		$H_{N:P(+P)}$	5.01	-11.80	0.44	0.0181	6.29	-17.11	0.45	0.0170
	Long term	$H_N$	8.43	-36.32	0.57	0.0045	7.78	-33.40	0.66	0.0013
		$H_{N:P(+N)}$	7.00	-35.24	0.70	0.0007	5.75	-28.61	0.59	0.0033
		$H_P$	9.46	-29.25	0.51	0.0092	11.44	-32.96	0.54	0.0067
		$H_{N:P(+P)}$	8.22	-26.31	0.78	< 0.0001	10.19	-34.51	0.67	0.0011
	Large scale	$H_N$	4.54	-17.08	0.55	0.0215	4.2	-16.1	0.65	0.0082
		$H_{N:P(+N)}$	3.36	-14.16	0.55	0.0227	3.17	-14.1	0.60	0.0137
		$H_P$	5.63	-15.02	0.47	0.0409	4.27	-8.49	0.19	0.2369
		$H_{N:P(+P)}$	2.97	-6.22	0.31	0.1202	5.55	-16.91	0.63	0.0107
Species stability	Short term	$H_N$	1.24	-3.58	0.47	0.0133	0.47	-0.22	0.38	0.0337
		$H_{N:P(+N)}$	1.06	-3.60	0.61	0.0027	0.36	0.00	0.36	0.0384*
		$H_P$	0.88	-0.71	0.40	0.0282	0.85	-0.83	0.43	0.0199
		$H_{N:P(+P)}$	0.83	-0.69	0.71	0.0006	0.80	-1.13	0.61	0.0029
	Long term	$H_N$	0.33	-0.86	0.60	0.0031	0.31	-0.77	0.71	0.0005
		$H_{N:P(+N)}$	0.28	-0.85	0.76	0.0002	0.22	-0.49	0.57	0.0044
		$H_P$	0.33	-0.40	0.41	0.0257	0.35	-0.36	0.33	0.0499
		$H_{N:P(+P)}$	0.24	-0.13	0.46	0.0161	0.38	-0.71	0.63	0.0020
	Large scale	$H_N$	0.24	-0.60	0.55	0.0217	0.21	-0.47	0.58	0.0174
		$H_{N:P(+N)}$	0.17	-0.40	0.50	0.0320	0.16	-0.39	0.55	0.0224
		$H_P$	0.25	-0.27	0.31	0.1206	0.13	-0.22	0.06	0.5354
		$H_{N:P(+P)}$	0.13	-0.12	0.20	0.2305	0.24	-0.35	0.41	0.0624

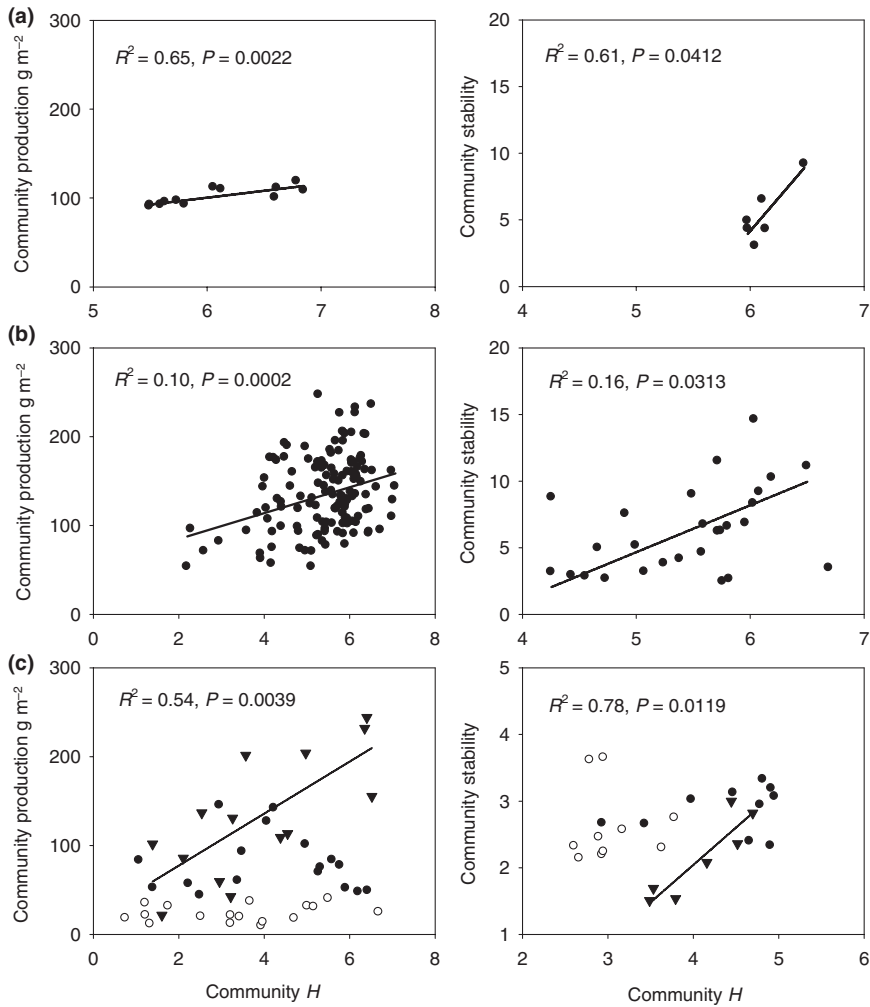
\*The result was  $R^2 = 0.87$ ,  $P < 0.0001$  after removing a single outlier value.

positive relationship between  $H_P$  and species dominance and stability in long-term experiment indicates that P can also become an important factor over more extended time scales, consistent with the view that many ecosystems appear to be co-limited by N and P (Elser *et al.* 2007). It is also interesting to note that  $H_{N:P}$  was as strongly related with species dominance and stability as corresponding  $H_N$  and  $H_P$ , further suggesting that the integrated management of both N and P in plants is important in influencing ecosystem processes (Sterner & Elser 2002).

Many studies have shown that dominant plant species strongly influence ecosystem properties and control the major part of the resources (Hooper *et al.* 2005). This suggests that dominant plant species became homoeostatic, possibly because they control the major part of the resources, whereas sub-dominant species and minor species have to live on what is left over. Since that left-over resource pool will be a much more variable environment, these species appear to be less homoeostatic. However, we undermined this possibility by an independent sand culture experiment. Three representative species, i.e. *L. chinensis*, *Cleistogenes squarrosa* and *C. glaucum*, were mono-cultured with varying N and P concentrations. We obtained consistent

$H$  rankings for the three species and similar  $H$  values (Yu, Elser, He, Wu, Chen, Zhang & Han, unpublished data) with field fertilization experiment, which clearly indicates that species interactions had no significant effect on  $H$ , at least for the three species we investigated.

Indeed, our experimental results suggest that the higher and more stable biomass production of dominant perennial grass species is associated with their husbanding of key limiting nutrients as indexed by  $H$ . Previous studies have proposed a variety of parameters as predictive of species dominance and biomass stability in grasslands, such as water use efficiency (Dawson *et al.* 2002; Chen *et al.* 2007), nutrient use efficiency (Yuan *et al.* 2005) and productivity strategy (Whittaker 1965). However, these parameters change considerably when the environment fluctuates (Field *et al.* 1983) and some of them are qualitative in nature and rely on subjective inferences, while  $H$  can be directly quantified, providing a more objective, 'higher order' index of a plant species' overall nutritional strategy that integrates multiple aspects of plant response to local environmental conditions. Thus,  $H$  may yield more powerful insight into community structure and species stability in terrestrial ecosystems.



**Figure 3** Relationships between community *H* and community production and stability. (a) Two-year field N addition experiment. (b) The 27-year monitoring study. (c) The 1200-km transect, there were three vegetation types: meadow grassland (triangles), typical steppe grassland (black dots) and desert grassland (open dots), however, significant relationships only found in meadow grassland. For community production, each point presents the total biomass of all the species within a quadrat in the natural community (i.e. Control plots in a). See Material and methods for details on data collection and analysis.

**Table 3** Results of regression analyses of the relationship between community *H* and community production and stability

Community factors	Experiments	<i>H</i>	2006				2007			
			Slope	Intercept	<i>R</i> <sup>2</sup>	<i>P</i>	Slope	Intercept	<i>R</i> <sup>2</sup>	<i>P</i>
Community production	Short term	<i>H<sub>N</sub></i>	17.66	2.56	0.90	0.0002	15.55	7.02	0.65	0.0022
		<i>H<sub>N:P(+N)</sub></i>	13.28	12.47	0.89	0.0003	11.68	17.61	0.53	0.0098
		<i>H<sub>P</sub></i>	24.59	2.15	0.91	0.0001	27.54	-1.85	0.63	0.0025
		<i>H<sub>N:P(+P)</sub></i>	16.27	27.86	0.71	0.0010	22.46	0.13	0.62	0.0031
	Long term	<i>H<sub>N</sub></i>	14.51	61.39	0.08	0.0011	14.93	53.40	0.10	0.0002
		<i>H<sub>N:P(+N)</sub></i>	11.55	63.12	0.08	0.0023	10.51	66.69	0.09	0.0018
		<i>H<sub>P</sub></i>	20.44	56.49	0.10	0.0007	18.87	69.79	0.08	0.0023
		<i>H<sub>N:P(+P)</sub></i>	11.94	80.57	0.07	0.0018	17.74	60.75	0.08	0.0008
Community stability	Short term	<i>H<sub>N</sub></i>	12.54	-65.68	0.76	0.0289	10.36	-58.12	0.61	0.0412
		<i>H<sub>N:P(+N)</sub></i>	12.25	-79.23	0.81	0.0191	6.78	-41.65	0.80	0.0271
		<i>H<sub>P</sub></i>	11.46	-39.14	0.72	0.0379	6.04	-20.83	0.60	0.0742
		<i>H<sub>N:P(+P)</sub></i>	7.24	-21.05	0.66	0.0628	6.93	-20.90	0.52	0.1475
	Long term	<i>H<sub>N</sub></i>	2.22	-3.16	0.16	0.0521	1.83	-2.74	0.16	0.0313
		<i>H<sub>N:P(+N)</sub></i>	5.28	-26.24	0.61	0.0003	1.56	-2.65	0.16	0.0637
		<i>H<sub>P</sub></i>	2.73	-2.55	0.14	0.0638	2.82	-2.89	0.15	0.0524
		<i>H<sub>N:P(+P)</sub></i>	1.31	0.67	0.11	0.1127	2.67	-3.58	0.15	0.0768

Community production and stability was positively correlated with community  $H$  both in the short-term and the long-term experiments. However, the strength of the relationship between community production and stability and community  $H$  declined substantially from short-term to long-term studies. This suggests that linking short-term species  $H$  with long-term community production and stability requires consideration of more environmental factors, particularly rainfall and temperature (Bai *et al.* 2004). No significant relationships were found in typical steppe and desert steppe across the large-scale transect (a significant relationship was only found in meadow grassland). This may reflect the fact that community structure and environmental factors differed considerably across the spatial transect as suggested by previous studies (Cheng *et al.* 2009). More importantly, grazing was not excluded at sites along the transect. It is likely that grazing was heavier in the desert grassland and typical grassland sites relative to the meadow grassland sites we sampled, which could be seen clearly from the biomass data (Fig. 3c). Thus, both direct and indirect grazer impacts may have altered species responses to resource supply regimes modulated by  $H$ . Nevertheless, these results suggest that aggregated community stoichiometric homoeostasis can predict ecosystem functioning and stability at the local scale in grasslands.

Many biotic and abiotic factors can affect  $H$  of vascular plants, ecosystem structure, functioning and stability, and thus their relationships. These include soil properties, grazing, year-to-year variation of precipitation and temperature, plant development stages, organs (aboveground vs. belowground, Yu *et al.*, unpublished data), elements (Karimi & Folt 2006), light intensity (Güsewell 2004) and growth rates (Elrifi & Turpin 1985; Egli 1991; Shafik *et al.* 1997; Ågren 2008; Persson *et al.* 2010). We found that variation of growth rate was negatively related with  $H$  (Yu *et al.*, unpublished data), suggesting that the ability of a species to control growth rate variation may be another mechanism responsible for ecosystem properties. However, we found no difference between the results of 2006 and 2007 although the precipitation changed dramatically (304 and 240 mm respectively). In addition, we note the concordance of the patterns from long-term and large-scale studies and similar findings for the field experiment. Furthermore,  $H$  values of three species estimated in a monoculture experiment were very similar to those obtained from field experiment (Yu *et al.*, unpublished data), suggesting that  $H$  was not strongly influenced by possible difficulties arising from differences in N and P actually available in soil vs. our analytical estimates of soil N and P. The consistency of these results suggests that, although diverse factors may affect ecosystem properties,  $H$  could be a dominant factor associated with ecosystem structure, functioning and stability. Further

research should address the mechanisms that underpin these associations.

The pattern of species dominance and  $H$  reported here is a result of long-term interactions between biotic community and its physical environment and interactions among species themselves. Thus, although the pattern seems robust for mature natural steppe ecosystems, it may be altered by human disturbances. For example, in a 4-year N addition experiment adjacent to our site, the biomass of low  $H$  species increased after N addition while the biomass of high  $H$  species decreased in the mature community (Bai *et al.* 2010). However, after 4 years N addition the biomass of high  $H$  species is still higher than that of low  $H$  species, and the dominance of high  $H$  species has continued to increase in the degraded community (Bai *et al.* 2010). This suggests that, for disturbed sites, low  $H$  species can increase their relative biomass quickly for a period of time, but the pattern of species dominance and  $H$  will be restored gradually after disturbances are removed. The effect of disturbances on the species dominance– $H$  relationship needs to be further examined.

Biodiversity affects ecosystem function and stability through compensatory mechanisms (Tilman & Downing 1994; Tilman *et al.* 1996, 2006; Naeem & Li 1997; Bai *et al.* 2004). However, the strength of biodiversity – ecosystem function and stability relationships can vary considerably (Wu & Loucks 1995; Chapin *et al.* 1997; McCann 2000; Loreau *et al.* 2001; Ives & Carpenter 2007) because there are many biological factors that influence biomass productivity and stability. Our data suggest that stoichiometric homoeostasis is a key species trait linked to ecosystem functioning and stability. In this study, the species with high foliar  $H$  are perennial grasses with high root:shoot ratios (Bai *et al.* 2004). This suggests that the resource scavenging and storage functions of roots allow these species to buffer the metabolism and production of aboveground biomass against environmental variation, promoting community stability. This is consistent with the fact that ecosystem stability has been observed to be positively dependent on root mass (Tilman *et al.* 2006). While additional research is needed to establish the underlying mechanisms by which  $H$  is related to important aspects of ecological dynamics, the predictive ability of  $H$  likely reflects the fact that many intrinsic properties of individual species, including their physiological adjustments to abiotic environmental factors, are embodied in it. Thus, the strength of stoichiometric homoeostasis is not only a key concept for understanding the nature of trophic interactions at the plant–herbivore interface in food webs (Sterner & Elser 2002), it also appears to be a powerful indicator of species dominance and stability and of ecosystem structure, function and stability. Our results also imply that, in seeking to conserve key ecosystem services, we should not only pay attention to



overall biodiversity but also to those 'keystone' species having strong stoichiometric homeostasis, as they are especially important in maintaining high production and ecological resistance to disturbances.

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