

LETTER

Diversity-dependent stability under mowing and nutrient addition: evidence from a 7-year grassland experiment

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Abstract

Anthropogenic perturbations may affect biodiversity and ecological stability as well as their relationships. However, diversity–stability patterns and associated mechanisms under human disturbances have rarely been explored. We conducted a 7-year field experiment examining the effects of mowing and nutrient addition on the diversity and temporal stability of herbaceous plant communities in a temperate steppe in northern China. Mowing increased population and community stability, whereas nutrient addition had the opposite effects. Stability exhibited positive relationships with species richness at population, functional group and community levels. Treatments did not alter these positive diversity–stability relationships, which were associated with the stabilising effect of species richness on component populations, species asynchrony and portfolio effects. Despite the difficulty of pinpointing causal mechanisms of diversity–stability patterns observed in nature, our results suggest that diversity may still be a useful predictor of the stability of ecosystems confronted with anthropogenic disturbances.

Keywords

Community stability, covariance effect, diversity, ecosystem stability, mowing, nitrogen deposition, nutrient addition, population stability, species richness, species synchrony, statistical averaging, temperate steppe.

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INTRODUCTION

The relationship between biodiversity and ecological stability is a long-standing issue in ecology (MacArthur 1955; Elton 1958) and has gained renewed interest among ecologists in recent years, driven by concerns that widespread biodiversity loss may affect the ability of ecosystems to provide reliable products and services for humanity (Hooper *et al.* 2005). Evidence is accumulating that higher diversity can promote community-level stability and that different mechanisms contribute to the stabilising effect of species richness. Theoretical models (Tilman 1999; Lehman & Tilman 2000) suggest that increasing diversity can enhance community stability through mechanisms such as statistical averaging (also known as the portfolio effect), the covariance effect and overyielding. Experimental studies (e.g. Romanuk *et al.* 2006; Jiang *et al.* 2009) have also found that, under certain circumstances, increasing species richness can make the dynamics of individual populations more stable, which can in turn contribute to increased stability at the community level. However, other studies (e.g. Tilman *et al.* 2006; van Ruijven & Berendse 2007) have yielded the opposite pattern that population stability declines with increasing species richness. This discrepancy among different studies adds to the ongoing diversity–stability debate (McCann 2000), inviting more empirical studies that are essential for resolving the debate (McNaughton 1977).

Although mounting evidence indicates that diversity can be a major driver of ecological stability (Ives & Carpenter 2007; Jiang & Pu 2009; Campbell *et al.* 2011), how environmental changes resulted from

human activities affect diversity–stability relationships remains poorly understood (Romanuk *et al.* 2006, 2010; Grman *et al.* 2010), posing serious challenges for predicting community dynamics under global change scenarios. For instance, global nutrient enrichment has markedly altered the composition and diversity of many natural communities (e.g. Stevens *et al.* 2004; Yang *et al.* 2011), potentially leading to changes in ecosystem functioning and stability. Nutrient deposition may also directly influence population and community stability (Rosenzweig 1971). In addition to nutrient enrichment, biomass harvesting is also common in natural and managed ecosystems across the world. For instance, annual hay harvesting is a widely used practice in grasslands. Elucidating the effects of biomass harvesting, nutrient enrichment, and their possible interactions on diversity, stability and the diversity–stability relationship will help conserve biodiversity, function and stability of ecosystems under global change scenarios.

As part of a comprehensive research project (Global Change Multifactor Experiment in Duolun, Inner Mongolia, China) in a temperate steppe in northern China, this study was conducted to evaluate the effects of nutrient addition and mowing on grassland diversity, stability, and their relationships using a 7-year (2005–2011) vegetation data. The temperate steppe represents the typical vegetation of the world's largest grassland biome across the Eurasian continent, and has experienced intensifying anthropogenic (e.g. land use change, climate change and nutrient deposition) disturbances (Niu *et al.* 2010; Yang *et al.* 2011). Nutrient enrichment often stimulates biomass accumulation and primary productivity of plant communities (Elser *et al.*

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2007), leading to increased canopy coverage and reduced light availability under the canopy (Hautier *et al.* 2009). This can in turn lead to declines in species richness (e.g. Clark & Tilman 2008; Hautier *et al.* 2009; Yang *et al.* 2011). By contrast, mowing may increase species richness by improving canopy radiation and facilitating seedling recruitment and plant growth (Collins *et al.* 1998). However, response patterns of diversity, stability and diversity–stability relationships and the associated mechanisms under the combined influence of both nutrient addition and mowing have yet to be investigated. Our study hence aimed to test the following hypotheses: (1) mowing will increase and nutrient addition will decrease species richness; (2) stability will increase (decrease) as richness increases (decreases) in response to mowing (nutrient addition) and (3) under mowing and nutrient addition, community stability will still be positively related to species diversity.

MATERIALS AND METHODS

Study site and experimental design

Our study site is located at a semiarid steppe (42°02' N, 116°17' E, 1324 m a. s. l.) in the Inner Mongolia Autonomous Region of China, which has a monsoon climate. Long-term (1953–2010) mean annual precipitation is approximately 378 mm with 90% fallen from May to October. Mean annual temperature is 2.1 °C, and average monthly temperature ranges from –17.5 °C in January to 18.9 °C in July. According to the FAO and Chinese classification, the soil is of Haplic Calcisols and chestnut type, respectively. The vegetation is classified as a temperate steppe in which perennial herbs, such as *Stipa krylovii*, *Agropyron cristatum* and *Cleistogenes squarrosa*, are dominant.

A 199 × 265 m experimental site with fairly uniform vegetation was established in 2005 (Niu *et al.* 2010). Within this experimental area, eight 92 × 60 m plots were laid out in two columns and four rows with a 5 m-wide buffer zone between the plots. Mowing treatments (control, mowing) were randomly assigned to plots, yielding four control and four mowing plots. Each 92 × 60 m plot was divided into four 44 × 28 m subplots, resulting in a total of 32 subplots. Each of the four subplots within one plot was randomly assigned to one of the four nutrient treatments, including the control (C; no nutrient addition), nitrogen addition (N; 10 g N m⁻² year⁻¹, treated with urea in 2005 and NH₃NO₄ in 2006–2011), phosphorus addition (P; 5 g P₂O₅ m⁻² year⁻¹, treated with calcium superphosphate), and addition of both N and P (NP). These nutrient levels are within the range of airborne nutrient deposition observed in Northern China (He *et al.* 2007). Nutrient was added once a year in the middle of July from 2005 to 2011 (see Niu *et al.* (2010) for detailed information). Mowing was conducted annually in August at the height of 10 cm above the soil surface to mimic hay harvesting. The harvested plant materials were removed immediately after mowing.

Vegetation sampling

Plant cover was measured annually in the permanent quadrats from 2005 to 2011. Two permanent quadrats (1 × 1 m) were established at two opposite positions of each subplot in June 2005. During the measurement, a 1 × 1 m frame with 100 equally distributed grids, spaced 10 cm apart, was placed above the canopy in each quadrat. The per cent cover of each species was visually point estimated in all grids,

and summed across grids to obtain species cover in each quadrat. Per cent coverage was summed across species to obtain the cover at the functional group (see below) and community levels. Community coverage thus can exceed 100% owing to the canopy overlap of different plant species. Species richness was recorded as the number of plant species found in each quadrat. Following common practice (e.g. Yang *et al.* 2011), we classified the recorded plants into three functional groups: grasses (GR), legumes (LE) and non-leguminous forbs (NF).

Data analyses

Compositional stability was estimated by calculating the community change rate (species loss, gain and turnover rate) and temporal stability of community species richness in each quadrat. To evaluate treatment effects on the community change rate, we calculated the species gain rate (G_p ; the rate at which previously absent species appear in the community), species loss rate (L_p ; the rate at which species disappear from the community) and species turnover rate (T_p ; the sum of gain and loss rate) (Anderson 2007; Xu *et al.* 2010). The three variables are expressed as: $G_p = 100 \times G / (S_1 + S_2) (1/2)$; $L_p = 100 \times L / (S_1 + S_2) (1/2)$; $T_p = 100 \times (G + L) / (S_1 + S_2)$, where G is the number of previously absent species and L is the number of species that disappeared from the community; S_1 and S_2 are species richness within the measured quadrat (1 × 1 m) in 2005 and 2011, respectively. In addition to compositional stability, we estimated functional stability (Báez & Collins 2008), calculated as the temporal variation of coverage at each ecological organisation (population, functional group and community) level.

The ratio of the temporal standard deviation of species richness/vegetation cover to its mean value during the seven consecutive years (i.e. the coefficient of variation) was used as a measure of temporal stability (Tilman *et al.* 2006). Greater coefficients of variation (CVs) in species richness and vegetation coverage suggest lower temporal stability. There were no significant temporal trends in vegetation coverage or species richness from 2005 to 2011, hence detrending was not necessary. Temporal CVs were calculated for the coverage of individual species, functional groups and plant communities in each quadrat over 7 years. To explore potential mechanisms for the observed diversity–stability relationships, we partitioned the temporal variance in total community coverage into summed variances of all (N) species and summed covariance between these species over time (Lehman & Tilman 2000). This was done by constructing an N × N variance/covariance matrix for each quadrat; the sum of all the diagonal elements equals to the summed variances and the sum of the off-diagonal elements corresponds to the summed covariance. Community-wide species synchrony in vegetation coverage (ϕ_c) was calculated as $\phi_c = \sigma_{ct}^2 / (\sum_{i=1}^S \sigma_{ci}^2)$ (Loreau & de Mazancourt 2008), where σ_{ct} is the variance in community coverage and σ_{ci} is the standard deviation in the coverage of species i in a S-species community.

A split-plot repeated measures ANOVA was used to examine treatment effects on species richness, with mowing, N and P addition, and their interactions as fixed-effects terms and design variables as random-effects terms. Given that the mowing treatments were applied to the main plots and nutrient addition treatments were applied to the subplots, we tested mowing effect against the plot mean square error and nutrient addition effects and their interactions with mowing against the subplot mean square error. When there was a significant time (year) × treatment interaction term, three-way ANOVA with a

split-plot design was performed to determine the effects of mowing, nitrogen (N) addition, phosphorus (P) and their interactions on species richness in each year. Species richness was log-transformed to meet the normality assumption of ANOVA.

A split-plot analysis of covariance (ANCOVA) was used to assess treatment effects on temporal variability, in which mowing (M), nitrogen (N) addition and phosphorus (P) addition were the categorical variables, whereas species richness was the continuous variable. A significant interactive effect between treatments and species richness would suggest that treatments altered the diversity–stability relationship. Student–Newman–Keuls (SNK-q) tests were conducted to discern the difference in temporal variability among the three functional groups. All the analyses were performed with log-transformed data.

To explore the potential mechanisms associated with the observed diversity–stability relationships, we performed a series of regression models. First, we fitted Taylor's power function $\sigma^2 = c\mu^\alpha$ to the entire data set, where σ^2 is the variance in species vegetation coverage, c is a constant, μ is the average species vegetation coverage and α is the scaling coefficient (Taylor 1961). The value of α influences the strength of statistical averaging (the portfolio effect), with $\alpha > 1$ suggesting that diversity enhances community stability (Tilman 1999). Second, we plotted community variability against species synchrony; a significant increase of community variability with species synchrony would suggest that species asynchrony (covariance effect) contributes to stability (Isbell *et al.* 2009). The relationship between plot covariance and species richness has often been used to test the covariance effect. However, Loreau & de Mazancourt (2008) suggested that the plot covariance may not be directly compared across communities with different species richness. Therefore, we regressed temporal variability in vegetation coverage on species synchrony to test the covariance effect. Third, we evaluated the overyielding effect by examining the relationship between community coverage and species richness (Tilman *et al.* 2006). Finally, Pearson correlation coefficient between community variability and population variability was calculated to assess whether diversity affected community-level stability via its effect on component populations. All the analyses were performed in sas V. 8.1 (SAS Institute Inc., Cary, NC, USA).

RESULTS

Species richness of community and functional groups

Nitrogen addition reduced community species richness by 17.5% (Fig. 1; split-plot ANOVA: $F_{1, 18} = 22.4$, $P < 0.05$) whereas mowing

slightly, but insignificantly elevated it by 6.8% ($F_{1, 6} = 2.6$, $P > 0.05$) over the 7 years of the experiment. The effects of both N and P addition on community species richness varied between years (both $P < 0.05$ for N/P addition \times time in the split-plot ANOVA). P addition suppressed community species richness by 13.0, 16.7 and 16.0% from 2009 to 2011, respectively, but had no effect on it in the first 4 years of the experiment. N addition reduced community species richness by 11.5, 23.4, 11.6, 26.9, 28.9 and 31.9% from 2006 to 2011, respectively, but did not affect it in the first year of the experiment. No other significant interactive effects on community species richness were detected (all $P > 0.05$).

Mowing and P addition interactively influenced GR species richness ($F_{1, 18} = 5.5$, $P < 0.05$). Mowing promoted species richness of GR by 20.3% under ambient P conditions, but reduced it by 2.4% in the P addition plots. Phosphorus addition suppressed GR species richness by 7.7% with mowing, but enhanced it by 13.7% without mowing across the 7 years (Fig. 1). The effect of N addition on LE species richness also varied with P addition ($F_{1,18} = 7.4$, $P < 0.05$). In addition, N addition reduced NF species richness by 22.9% ($F_{1,18} = 18.4$, $P < 0.01$) and the effects of both mowing and N addition on NF species richness varied with year (both $P < 0.05$). Mowing marginally increased NF species richness by 16.4% in the second year but had no impact in the other 6 years. Nitrogen addition did not affect NF species richness in the first year (2005), but significantly suppressed it by 14.1, 31.1, 12.5, 37.9, 37.1 and 41.3% in the last 6 years (2006–2011), respectively. The effect of P addition on LE species richness also showed interannual variations ($F_{6,145} = 4.7$, $P < 0.01$). Phosphorus addition significantly decreased LE species richness by 37.3 and 36.0% in 2010 and 2011, respectively, but did not affect it in the first 5 years (2005–2009). No other interactive effects on the species richness of functional groups were observed (all $P > 0.05$).

Effects of species richness and treatments on compositional and functional stability

Split-plot ANCOVA showed that the CVs of community species richness and plant cover at both the functional group and community levels was negatively correlated with community species richness (Table 1). Mowing did not affect the CV of community species richness whereas N and P addition increased it by 13.3 and 6.0% (Table 1; Fig. 2a), respectively. Mowing decreased community change rate, but nutrient addition had the opposite effect (Fig. 2b). The CVs

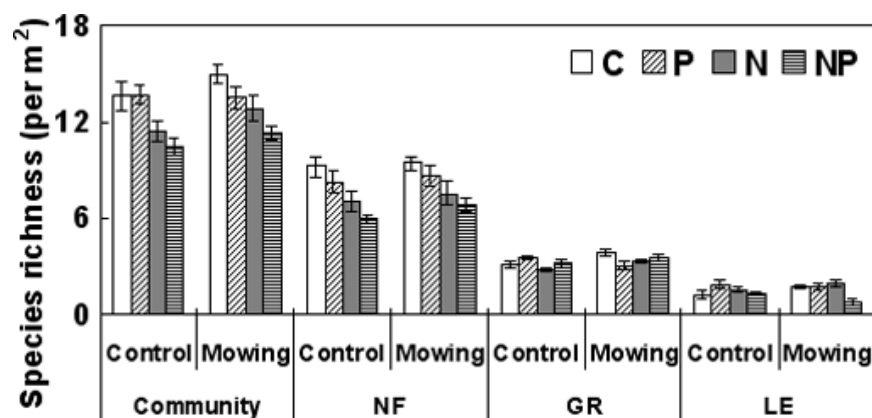


Figure 1 Species richness (\pm SE) of the community and functional groups under the mowing and control treatments, averaged from 2005 to 2011. GR, grass; NF, non-leguminous forbs; LE, legumes; C, control; P, phosphorus addition; N, nitrogen addition, NP, phosphorus addition plus nitrogen addition.

Table 1 Results of the split-plot ANCOVA (without the treatment \times species richness interaction term) for the effects of species richness (SP), mowing (M), nitrogen addition (N), phosphorus addition (P), and their interactions on the CV of community species richness (CSP), and CVs of community (CO), NF, grass (GR), legumes (LE) coverage. DF and DDF are the abbreviations of the degree of freedom and denominator degree of freedom, respectively

	d.f.	d.d.f.	CSP		CO		NF		GR		LE	
			<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
SP	1	32	2.0	0.172	4.4	0.043	4.2	0.048	22	<.001	6.6	0.015
M	1	6	5.4	0.060	10.4	0.018	8.8	0.025	0.5	0.514	0.3	0.638
N	1	18	50	<.001	43.0	<.001	23	<.001	0.9	0.354	2.4	0.139
P	1	18	15	0.001	1.0	0.328	3.3	0.087	0.0	0.952	14	0.002
M \times N	1	18	1.9	0.182	0.2	0.632	0.2	0.648	1.5	0.234	0.3	0.577
M \times P	1	18	1.2	0.288	1.2	0.280	0.0	0.896	0.0	0.841	5.8	0.027
N \times P	1	18	0.9	0.360	2.5	0.133	0.5	0.481	4.1	0.057	0.6	0.441
M \times N \times P	1	18	6.1	0.024	0.2	0.632	0.0	0.878	0.7	0.426	0.4	0.542

of community and NF coverage were lowered by 5.6 and 14.6%, respectively, under mowing. However, N addition markedly increased the CV of community and NF coverage by 13.9 and 30.9%,

respectively. Phosphorus addition also increased the CV of LE coverage by 34.9% (Table 1; Fig. 2c). Significant interactive effects of mowing and P addition on the CV of LE coverage were observed (Table 1). No other two- or three-way interactions of mowing, N and P addition were found on the CV of functional group coverage (Table 1). The CVs of vegetation coverage changed with plant functional groups (PFGs; $F_{2, 189} = 14.6$, $P < 0.01$), with functional groups with higher vegetation cover having lower CV (Fig. 2c).

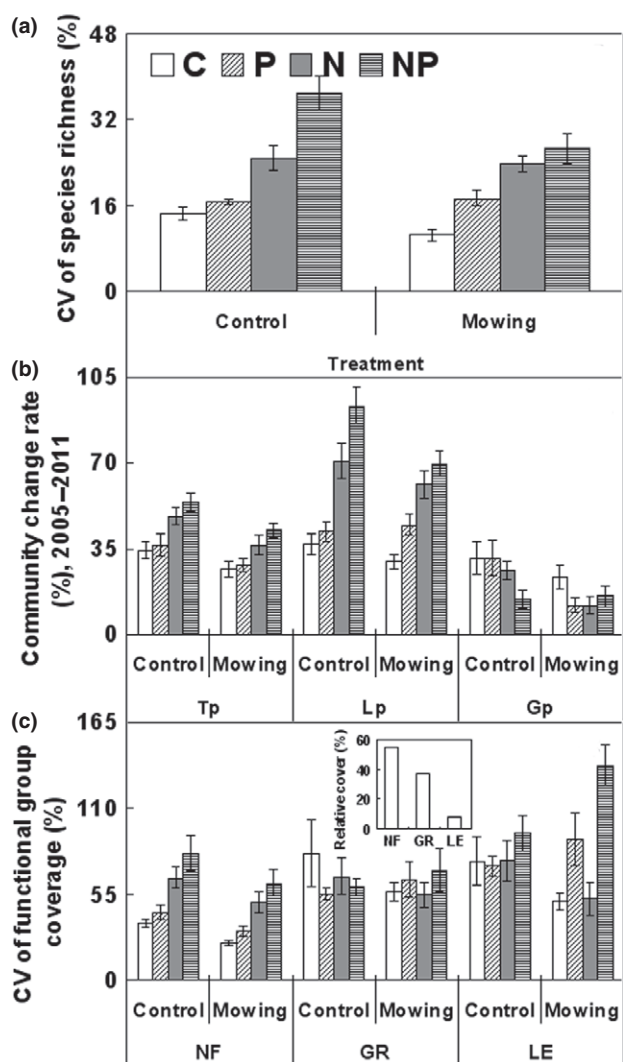


Figure 2 Temporal coefficients of variation (CV) of species richness, vegetation coverage at different organisational levels, and species change rates under eight treatment combinations of mowing (M), nitrogen (N) and phosphorus (P) addition. (a) CV of community species richness; (b) Species turnover rate (T_p), loss rate (L_p) and gain rate (G_p); (c) CVs of PFGs coverage and relative coverage-based values of PFGs in the descending order. See Fig. 1 for treatment abbreviations.

Diversity–stability relationships and possible mechanisms

The CVs of vegetation variables all exhibited negative relationships with the species richness of communities or respective functional groups (Fig. 3a–f). Significant interactive effects between P addition and species richness on both species turnover rate (T_p ; $P < 0.05$) and the CV of population coverage ($P < 0.05$; Table S1) indicated that P addition altered the diversity–stability relationships (Fig. 3b,d). On the other hand, mowing and nutrient addition did not alter the relationships between the CVs of vegetation coverage and species richness.

Temporal variance scaled with its community coverage with $\alpha = 1.73$, supporting the role of statistical averaging in stabilising community coverage under higher diversity. However, α attained different values in the ambient ($\alpha = 0.78$) and N addition ($\alpha = 1.32$) plots, respectively (Fig. 4a). Also consistent with the statistical averaging effect, summed variances decreased with community species richness (Fig. 4b); it, however, increased as community coverage increased (Fig. 4c). In accordance with the role of species asynchrony in promoting stability, the CV of community coverage was positively correlated with species synchrony (Fig. 4d). Community coverage decreased with species richness, which did not support the overyielding effect (Fig. 4e). In addition, the CV of community coverage showed positive dependence upon the CV of population coverage ($F_{1, 62} = 40.2$, $P < 0.01$; Fig. 4f), indicative of the influence of population-level variability on community-level variability.

DISCUSSION

Treatment effects on species richness

Mowing tended to increase community species richness in our experiment, a result consistent with previous studies in grasslands (e.g. Collins *et al.* 1998; Huhta *et al.* 2001). The reduced species richness under nutrient amendment in our experiment has also been reported in other grasslands (e.g. Stevens *et al.* 2004; Clark & Tilman 2008;

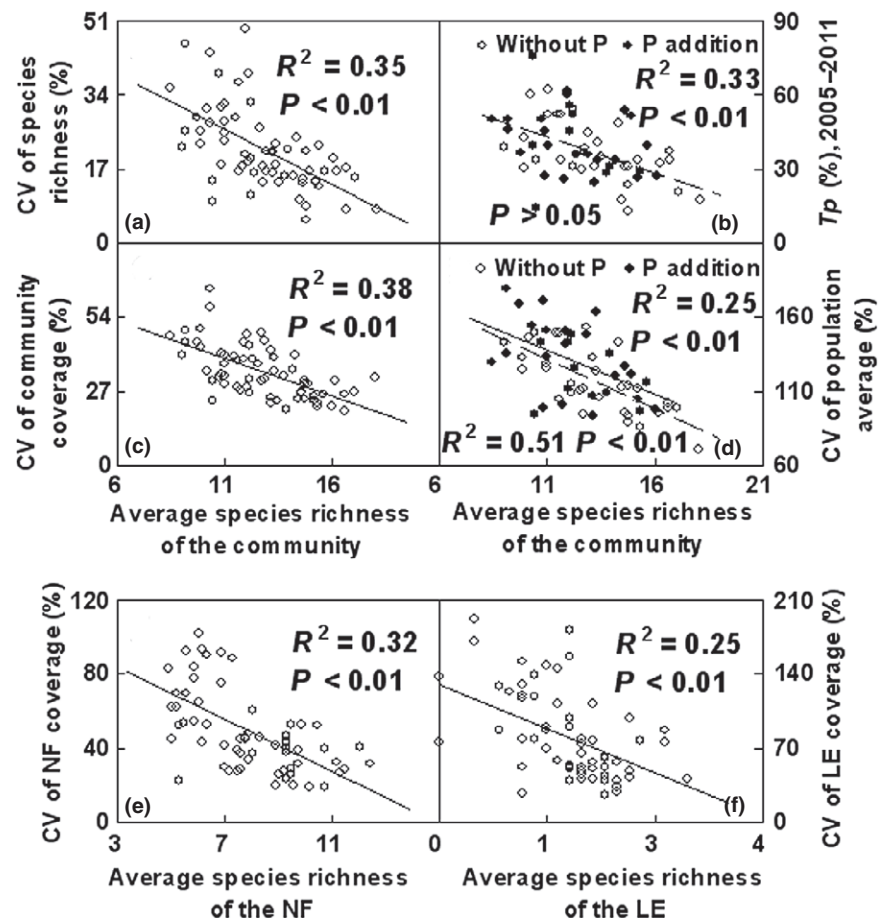


Figure 3 Dependence of the coefficients of variation (CV) of community species richness (a) and species turnover rate (b) on average species richness of the community; CV of the community- (c) and population-level (d) coverage vs. average species richness of the community; relationships between the CV of NF (e), legumes (f) coverage and their species richness, respectively. Black symbols and solid lines correspond to the diversity–stability relation under P addition. Open symbols and dashed lines correspond to the diversity–stability relation without P addition.

Yang *et al.* 2011) and other terrestrial ecosystems (Suding *et al.* 2005; Hillebrand *et al.* 2007). The contrasting effects of mowing and nutrient addition on community species richness are also in line with the results of a recent meta-analysis that herbivory (simulated by mowing in our experiment) tends to increase species richness and fertilisation tends to reduce richness in terrestrial ecosystems (Hillebrand *et al.* 2007). The mechanisms underlying these effects are the subject of much recent research (e.g. Suding *et al.* 2005; Harpole & Tilman 2007; Hillebrand *et al.* 2007; Hautier *et al.* 2009). For example, Harpole & Tilman (2007) found that soil nutrient addition reduced species diversity in a California grassland via reducing the number of limiting soil nutrients. On the other hand, Hautier *et al.* (2009) reported a greenhouse experiment in which increased competition for light was responsible for grassland species loss after nutrient addition. Regardless of the underlying mechanisms, our results suggest that grazing and mowing, as the traditional grassland management practice, can be a useful tool for mitigating species loss under global nutrient enrichment.

Treatment effects on compositional and functional stability

Compositional stability, measured as community change rate, is an important component of community stability. It has been suggested that resource availability could affect the temporal pattern of community change rate (Anderson 2007), an idea borne out in our experiment. Likewise, in an area adjacent to our experimental site, Xu

et al. (2010) found that an old-field grassland with higher nutrient content exhibited higher community change rate compared with an infertile steppe. It has also been hypothesised that community change rate should decline with increasing species richness, as the rate of species gain tends to decline and the rate of species loss does not change significantly over time during community development (Anderson 2007). Consistent with this, we found a negative relationship between species richness and the coefficient of variation of community species richness. Also consistent with this idea, compositional stability was enhanced by mowing that increased richness, but weakened by nutrient enrichment that reduced richness in our experiment.

In concert with changes in compositional stability, the functional stability of vegetation coverage was significantly altered by our experimental treatments. Nutrient enrichment resulted in a decrease in coverage stability, which is consistent with the general prediction of nutrient enrichment destabilising population and community dynamics (Rosenzweig 1971). It should be noted that even though many empirical studies supported this prediction, exceptions are not uncommon (Roy & Chattopadhyay 2007). For example, Grman *et al.* (2010) reported that N addition did not alter stability in a disturbance and fertilisation experiment in an old-field grassland. They suggested that the maintenance of stability in the N-fertilised communities could have been accounted for by increased compensatory dynamics between species and enhanced stability of the dominant species, which did not occur in our experiment.

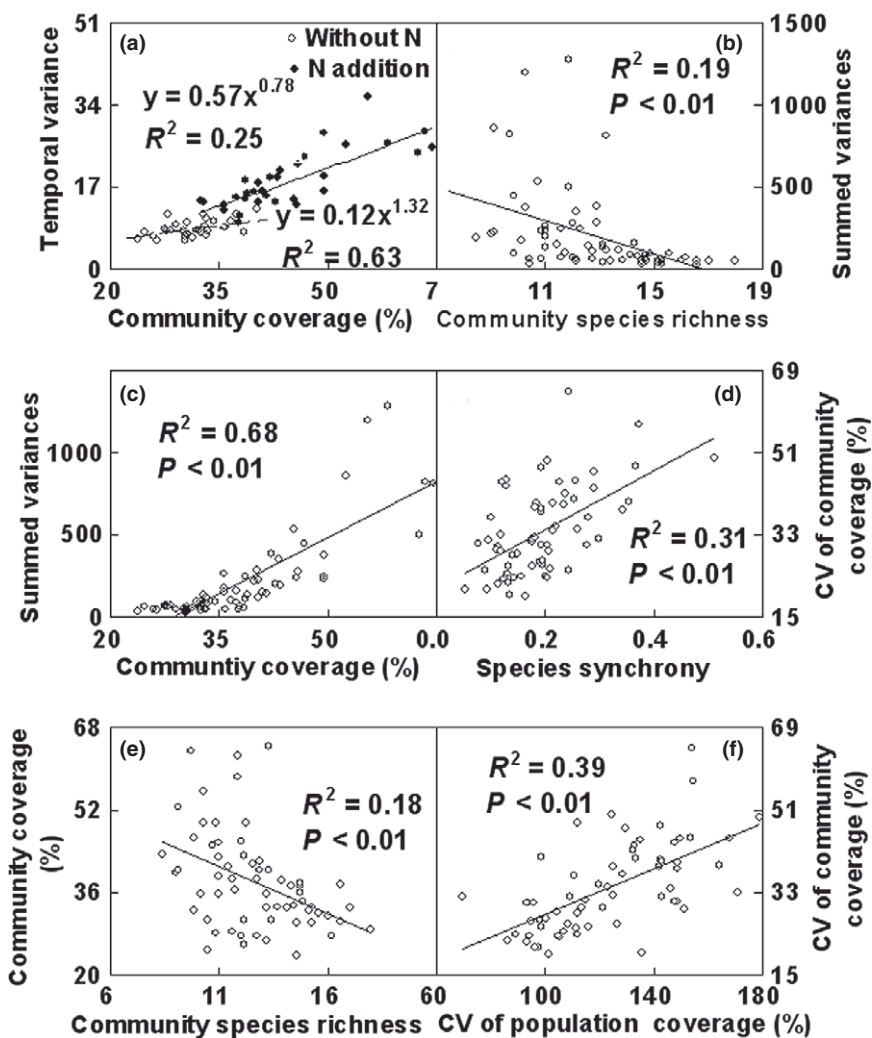


Figure 4 Relationships between temporal variance (a), summed variances (c) and community coverage; dependences of summed variances (b) and the CV of community coverage (d) on average community species richness and species synchrony, respectively; the relationships between community coverage and community species richness (e) and between the CV of community coverage and the CV of mean population coverage (f).

Positive diversity–stability relationships and underlying mechanisms

The positive diversity–stability relationships at the community and functional group levels observed in this study are in agreement with the results of many theoretical (e.g. Tilman 1999; Lehman & Tilman 2000) and empirical studies (e.g. van Ruijven & Berendse 2007; Proulx *et al.* 2010; reviewed in Jiang & Pu 2009). By contrast, we found a positive relationship between population stability and species richness. This result is at odds with the predictions of several theoretical models (e.g. Lehman & Tilman 2000) and results of many experiments based on artificially constructed communities (e.g. Tilman *et al.* 2006), but agree with the results from a number of empirical studies of natural communities (e.g. Valone & Hoffman 2003; Romanuk *et al.* 2006). The exact causes of this disparity are unknown, but may be related to the fact that most natural communities contain multiple trophic levels, whereas artificially constructed communities often comprise only one trophic level (Jiang & Pu 2009). Moreover, diversity may not necessarily be the major driver of stability in natural communities where positive relationships between the two could possibly arise from their similar responses to changes in other environmental variables. For example, Valone & Hoffman (2003) found that population size and temporal stability of most species were both greater in more diverse annual plant communities that they

surveyed in Arizona, USA, and suggested that it may have been caused by environmental productivity overriding diversity effect on stability.

Most importantly, our results suggest that mowing and nutrient amendment, to a large extent, did not alter the positive diversity–stability relationships. Several factors may have contributed to this general pattern. First, as stated above, this pattern could be at least partly explained by both diversity and stability varying in a similar fashion along environmental gradients. In our experiment, both diversity and stability increased in response to mowing, and both decreased in response to nutrient amendment. Likewise, variation in ambient environmental conditions (i.e. ‘hidden treatment’ as defined by Huston 1997) at our experimental site, which presumably drove the natural variation in species diversity among our plots, may have had similar effects on stability. Second, in our experiment NF dominated in both species richness and vegetation cover, and exhibited greater stability than other functional groups. These suggest that diversity–stability relationships for this functional group would strongly influence diversity–stability relationships at the whole community level. As NF showed similar responses in diversity and stability to our experimental treatments, they contributed importantly to the observed positive diversity–stability patterns at the community level. Third, the frequently reported stabilising effect of species diversity on community properties (Jiang & Pu 2009) may also contribute to the positive

diversity–stability relationships observed in our experiment. Indeed, our analyses showed that several stabilising mechanisms, including the portfolio effect, population asynchrony and the positive effects of species diversity on population-level stability, operated in our experiment. We discuss these mechanisms in the following paragraphs.

First, the portfolio effect may have played a role in causing greater stability in more diverse communities. The portfolio effect requires that the temporal variance in community coverage scales with mean community coverage such that the slope of this scaling relationship, α , is > 1 . The fact that $\alpha = 1.73$ in our system supports the role of the portfolio effect in stabilising communities at higher levels of diversity. The negative dependence of summed variances upon species richness is also consistent with the portfolio effect (Tilman *et al.* 2006). One thus expects population stability to decline with increasing species richness, according to theoretical predictions (Tilman 1999). On the contrary, greater population stability was observed for more diverse communities in our experiment. The strength of the portfolio effect is known to be greatest when all constituent species are evenly distributed, and to decline with decreasing evenness (Cottingham *et al.* 2001). However, the condition of high evenness is unlikely to be met for many natural communities, including our study communities (Fig. S1). The portfolio effect is thus less likely to result in reduced population-level stability in nature (Valdivia & Molis 2009), which is probably the reason for the apparent paradox between the positive diversity–stability relationship at the population level and the large α value in our system.

Second, species asynchronous population dynamics, resulting from different responses of species to environmental changes and/or biotic interactions (e.g. competition), may also promote stability in diverse communities. Species asynchrony contributes to community stability because functional redundancy allows high abundance organisms to compensate for low abundance ones that perform similar functions, ensuring communities to attain relatively constant levels of functions despite possibly substantial population fluctuations. This is thought to have stronger effects in more diverse communities containing more species with different responses to environmental fluctuations (Yachi & Loreau 1999). The positive relationship between species synchrony and temporal variability of vegetation cover found in our experiment supports this insurance effect of species diversity.

Third, overyielding, the increase in community biomass with increasing species richness, may also have the potential to lead to positive diversity–community stability relationships (Tilman 1999). We were unable to explicitly examine the overyielding effect, which requires comparing multi-species treatments to species monoculture treatments, owing to the absence of monoculture plots in our experiment. However, the decline of community coverage with increasing species richness clearly indicates that the overyielding effect did not operate in our system.

Finally, increasing diversity can also stabilise communities if it leads to an increase in the stability of populations of component species (Petchey *et al.* 2002; Romanuk *et al.* 2006). The positive relationship between population stability and species diversity and the positive relationship between community and population stability in our study provided support for this idea. Together, the portfolio effect, population asynchrony, and the greater stability of component populations may have contributed to the greater stability in more diverse plant communities.

The elevated species extinction rate due to anthropogenic activities has attracted considerable attention from ecologists, triggering much research on the impacts of species losses on ecosystem functions and stability (Hooper *et al.* 2005). Numerous studies have demonstrated that increasing diversity can lead to greater biomass in various ecosystems (summarised in Cardinale *et al.* 2006, 2011). Despite the difficulty of pinpointing the exact mechanisms underlying diversity–stability patterns observed in nature, our work demonstrates that natural grassland communities with higher species diversity tend to exhibit greater temporal stability. Moreover, the positive diversity–stability relationships were robust to environmental changes resulted from human activities. If our results can be extrapolated to other natural communities, the conservation of diversity will be important for stabilising community structure and ecosystem functioning under intensified anthropogenic disturbances, and for providing more reliable goods and services for humankind in the changing environment.

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AUTHORSHIP

SW and LL designed the research; HY, LJ, AL and SW analysed the data and wrote the paper; HY and MW conducted field measurements.

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