

Environmental changes drive the temporal stability of semi-arid natural grasslands through altering species asynchrony

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Summary

1. Stability is an important property of ecological systems, many of which are experiencing increasing levels of anthropogenic environmental changes. However, how these environmental changes influence ecosystem stability remains poorly understood.

2. We conducted an 8-year field experiment in a semi-arid natural grassland to explore the effects of two common environmental changes, precipitation and nitrogen enrichment, on the temporal stability of plant above-ground biomass. A split-plot design, with precipitation as the main plot factor and nitrogen as the subplot factor, was used. Temporal stability was related to potential explanatory abiotic and biotic variables using regressions and structural equation modelling.

3. Increase in growing season precipitation enhanced plant species richness and promoted temporal stability of plant above-ground biomass. Nitrogen fertilization, however, reduced both plant species richness and temporal stability of plant above-ground biomass. Contrary to expectations, species richness was not an important driver of stability. Instead, community temporal stability was mainly driven by water and nitrogen availability that modulated the degree of species asynchrony and, to a lesser extent, by the stability of dominant plant species.

4. *Synthesis.* Our results highlight the importance of limiting resources for regulating community biomass stability and suggest that the projected increase in growing season precipitation may potentially offset negative effects of increased atmospheric nitrogen deposition on species diversity and community stability in semi-arid grasslands.

Key-words: biodiversity, dominant species stability, global change, nitrogen, overyielding, precipitation, species richness, the portfolio effect, water

Introduction

Understanding stability, an important property of ecological systems, and its regulatory mechanisms, has a long history in ecology (e.g. MacArthur 1955; Huffaker 1958; Lewontin 1969). Despite decades of research, however, ecologists still

lack a good understanding of important determinants of ecological stability. This is, in large part, due to the fact that the stability of any ecological system is influenced by a myriad of abiotic and biotic factors, whereas existing research has generally focused on examining the effects of single variables. In particular, the temporal stability (defined as the inverse of temporal variability that measures the variation of ecological properties over time; *sensu* Pimm 1984) of community/ecosystem properties, which has received much recent attention in the context of biodiversity and ecosystem functioning

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research, has been frequently linked to species diversity (here used interchangeably with species richness, the number of species in a sample or community). A large number of theoretical and empirical investigations have found that more diverse communities tend to exhibit greater temporal stability in their functions and dynamics (reviewed by Jiang & Pu 2009; Campbell, Murphy & Romanuk 2011; Gross *et al.* 2014). However, biodiversity–stability relationships have mainly been explored in experimentally assembled communities, where their member species are typically drawn randomly from a regional species pool. This scenario differs from the assembly of natural communities where species composition and diversity are driven by various abiotic factors including nutrient availability and climatic conditions, which could have their own direct effects on stability (Ives & Carpenter 2007; Yang, Ruijven & Du 2011b; Hautier *et al.* 2014). It is thus essential to consider the role of these drivers of stability, in addition to that of species diversity, if we are to fully understand determinants of stability in natural communities that are currently experiencing both diversity loss and other anthropogenic environmental changes.

Precipitation and nitrogen are important factors influencing primary production in many of the world's terrestrial ecosystems (Hooper & Johnson 1999; Vitousek *et al.* 2002; Xia & Wan 2008). The two factors may influence community temporal stability through multiple pathways. First, increased supply in water/nitrogen may relieve plant species from being limited by these resources, making biomass production less influenced by their variation over time (i.e. increased stability). Alternatively, reduction in water or nitrogen limitation could lead to reduced stability if it causes the system to be limited by a different but more variable resource. Secondly, increasing precipitation/nitrogen in systems where they are in short supply would result in increased community biomass, which may serve to promote community stability if biomass variance does not increase as much (Tilman 1999; Cottingham, Brown & Lennon 2001; Hector *et al.* 2010). On the other hand, higher resource (particularly nitrogen) availability could result in increased vulnerability of vegetation to herbivore outbreaks (de Sassi & Tylianakis 2012) or a shift towards faster turnover tissues (Ren *et al.* 2011), leading to lower stability. Differential changes in the size and variability of populations in response to changes in resource availability may also potentially bring about changes in the portfolio effect (also known as statistical averaging, which depicts the phenomenon of the scaling of the variance of a population to its mean often contributing to greater stability of more diverse communities; Doak *et al.* 1998; Tilman, Lehman & Bristow 1998). Thirdly, changes in precipitation/nitrogen may affect how different species respond to environmental fluctuations, which may in turn influence community stability via changing the degree of species asynchrony (Grman *et al.* 2010; Hautier *et al.* 2014). For example, if the reduction in the limitation of one resource allows species to more strongly respond to natural fluctuations in other limiting resources, then it may have the potential to either promote species asynchrony (e.g. when temporal niche differentiation serves to desynchronize

population dynamics among species (Ives, Gross & Klug 1999; Loreau & de Mazancourt 2013), in the presence of large fluctuations of the other limiting resources) or reduce species asynchrony (e.g. when communities consist of species with similar traits as a result of environmental filtering, resulting in synchronized population dynamics in the presence of resource fluctuation (Rocha, Gaedke & Vasseur 2011; Vasseur *et al.* 2014)). Moreover, changes in community biomass in response to precipitation/nitrogen amendment may translate into changes in the strength of competition among species, which could also influence the degree of synchrony of population dynamics (Loreau & de Mazancourt 2013). Fourthly, changes in population stability in response to alterations in precipitation/nitrogen may translate into changes in stability at the community level, especially when communities are dominated by a small number of species (Smith & Knapp 2003; Hillebrand, Bennett & Cadotte 2008; Grman *et al.* 2010; Yang, Ruijven & Du 2011b). Lastly, changes in precipitation/nitrogen may alter community stability indirectly by changing species diversity, through mechanisms such as diversity-dependent species asynchrony (i.e. the increase in species compensatory dynamics with increasing diversity; Lehman & Tilman 2000; Loreau & de Mazancourt 2008; Thibaut & Connolly 2013), overyielding (i.e. the increase in ecosystem functions, such as community biomass, with increasing diversity; Tilman 1999; Cottingham, Brown & Lennon 2001; Hector *et al.* 2010; Thibaut & Connolly 2013) and the portfolio effect (Doak *et al.* 1998; Tilman, Lehman & Bristow 1998; Thibaut & Connolly 2013). As increased precipitation and nitrogen often differ in their effects on species diversity (negative nitrogen enrichment effect: Stevens *et al.* 2004; Suding *et al.* 2005; positive precipitation increase effect: Adler & Levine 2007; Cleland *et al.* 2013), their effects on stability may also differ if species diversity strongly influences stability. Nevertheless, no studies, to our knowledge, have simultaneously manipulated both precipitation and nitrogen to assess their importance for community stability. Such knowledge, however, is essential for accurately predicting dynamics of ecosystems that are limited by these two resources, when experiencing future changes to nitrogen deposition and climate.

The present study explores the determinants of biomass temporal stability in a semi-arid natural grassland in northern China, where water and nitrogen are in limited supply (Niu *et al.* 2008; Yang *et al.* 2011a). The semi-arid grassland accounts for 78% of total grassland area in China and provides important products and services for humans living in this region (Kang *et al.* 2007). Both summer precipitation (Sun & Ding 2010) and atmospheric nitrogen deposition (Liu *et al.* 2011) are projected to increase for this important ecosystem in the coming decades, which may carry potentially important but largely unknown ecological consequences. We assessed the role of water and nitrogen availability, relative to that of commonly considered biotic factors (e.g. species richness, stability of dominant species), for determining temporal stability of community above-ground biomass using an eight-year precipitation and nitrogen addition experiment.

Materials and methods

STUDY SITES AND EXPERIMENTAL DESIGN

The study site (116°17' E and 42°02' N, elevation 1324 m a.s.l.) is located in Duolun County of Inner Mongolia, China. Climate in the region is characterized by a semi-arid continental monsoon precipitation pattern (i.e. dry spring and wet summer). Mean annual air temperature is 2.1°C, with mean monthly temperature ranging from -17.5°C in January to 18.9°C in July. Mean annual precipitation is 379 mm, with 95% falling during the growing season (April–October), whereas annual potential evaporation is 1194 mm (Su & Shen 2013). Soil is chestnut according to the Chinese classification and Calcis-orthic Aridisol in the US Soil Taxonomy classification (Yuan *et al.* 2005). Dominant plant species in the study grassland include one perennial forb, *Artemisia frigida*, and two perennial grasses, *Stipa krylovii* and *Agropyron cristatum*. Root production (Bai *et al.* 2008, 2009), above-ground biomass (Bai *et al.* 2010; Xu *et al.* 2010), as well as ecosystem carbon exchange (Niu *et al.* 2009), are largely limited by water and nitrogen availability in this grassland ecosystem.

In early April 2005, we established seven blocks containing naturally assembled communities using a split-plot experimental design, with precipitation treatments applied to the main plot and nitrogen treatments applied to the subplot. Each block was divided into two main plots with either ambient precipitation or precipitation addition as treatments. From June to August, the plots with precipitation addition were sprinkled with 15 mm of water weekly. A total of 180 mm precipitation was added during each growing season from 2005 to 2012. Increased precipitation of similar magnitude has occurred in some previous years (e.g. 1979) and is expected to occur more frequently in the future (Sun & Ding 2010). The annual ambient precipitation varied from 186.7 mm to 407.7 mm, with an average value of 291.4 mm during our experimental period. Increasing precipitation did not change the magnitude of temporal variation in total precipitation (SD = 82.9 for both control and precipitation addition plots) or soil moisture (SD = 0.49 ± 0.14 for control plots and SD = 0.51 ± 0.13 for precipitation addition plots). Each main plot was divided into two 8 m × 8 m subplots, and each subplot was randomly assigned to one of two fertilization treatments: with or without nitrogen addition. The nitrogen addition subplots received granular urea (10 g nitrogen m⁻² year⁻¹), applied twice (early May and late June) in equal amount from 2005 to 2012. The amount of nitrogen addition is comparable to the estimated mean total nitrogen deposition rate in northern China (about 8.3 g N m⁻² year⁻¹, He *et al.* 2007). This study thus utilized four treatments: control (no nitrogen or precipitation addition), nitrogen addition, precipitation addition and nitrogen plus precipitation addition. Both the subplots and blocks were separated by a 1-m-wide buffer zone.

PLANT COMMUNITY SURVEY AND SOIL MOISTURE AND NITROGEN MEASUREMENT

In May 2005, a permanent quadrat of 1 m × 1 m was established in each subplot. From 2005 to 2012, we recorded each plant species within each quadrat in mid-July. Species were classified into two functional groups, grasses (including sedges) and forbs. In early September from 2007 to 2012, all living tissues within a randomly selected 0.15 m × 2 m strip in each plot outside the permanent quadrat were clipped, sorted to species and oven-dried at 65°C for 48 h to determine peak above-ground biomass.

From 2006 through 2012, two soil cores, 3 cm in diameter and 10 cm in depth, were collected biweekly between May and September from each plot outside the permanent quadrat. The soil cores were weighed, dried at 105°C for 48 h and weighed again to determine soil moisture content, calculated as the percentage of weight loss from fresh to dry soil. In early August from 2007 to 2012, soil samples (10 cm in depth) were collected from five randomly selected locations in each plot outside the permanent quadrat and mixed afterwards to measure soil inorganic nitrogen concentration. Nitrogen concentration was quantified using a flow-injection autoanalyser (FIAstar 5000 Analyzer, Foss Tecator, Denmark), following extraction with solutions of 2 M KCl.

DATA ANALYSIS

We defined species richness in each subplot as the total number of species recorded in its permanent quadrat within a year. Temporal stability of community and functional groups (i.e. grasses and forbs) was calculated as the ratio of mean above-ground biomass, μ , to its standard deviation, σ , over the sampling period (2007–2012). This measure of temporal stability, which is essentially the reciprocal of coefficient of variation of biomass, has been frequently used in previous studies (e.g. Tilman, Reich & Knops 2006; Hautier *et al.* 2014). No detrending was done as there was no significant temporal trend in community above-ground biomass (assessed by regressing biomass against time, as in Tilman, Reich & Knops 2006) in all but one of the 28 experimental plots during the study period (see Table S1 in Supporting Information). To determine the role of dominant species for community stability, we identified the species that had the largest mean relative biomass over time in each replicate, and calculated their temporal stability in the same way. The three most dominant species (*S. krylovii*, *A. frigida* and *A. cristatum*) accounted for a significant proportion (63.6% on average, see Fig. S1 in Supporting Information) of community biomass across the study period. We also calculated Simpson's dominance index as the sum of the species' squared relative above-ground biomass (Smith & Wilson 1996). Summed variances of species biomass over time in each plot were calculated, and their relationships with species richness were determined via regressions to evaluate the role of the portfolio effect for community stability. We did not quantify the strength of the portfolio effect with the commonly used power equation as suggested by Tilman (1999), because high unevenness in species abundance, which applies to our study communities (see Fig. S1), can invalidate this approach (Valdivia & Molis 2009).

We determined the role of species asynchrony as a potential mechanism regulating stability using a community-wide measure that allowed quantitative comparisons among communities with different species numbers (Loreau & de Mazancourt 2008). Species asynchrony ($1 - \phi_x$) is defined as follows:

$$1 - \phi_x = 1 - \sigma^2 / \left(\sum_{i=1}^S \sigma_i \right)^2 \quad \text{eqn 1}$$

where ϕ_x is species synchrony, σ^2 is the temporal variance of community above-ground biomass, and σ_i is the standard deviation in the above-ground biomass of species i in a community with S species.

Repeated-measures ANOVAS with split-plot design were performed to test the effects of precipitation, nitrogen, year and their interactions on soil moisture, soil inorganic nitrogen content, species richness, dominance and community biomass. ANOVAS with split-plot design

were used to determine the effects of precipitation and nitrogen and their interaction on temporal stability of community, grasses and forbs, and species asynchrony. In all the split-plot ANOVAs, precipitation was the main plot factor, nitrogen was the subplot factor, and block was treated as a random effect. One-way ANOVAs with Duncan's multiple range test were used to evaluate the differences among the experimental treatments.

We used structural equation modelling (SEM) to estimate the strength of direct and indirect relationships between soil moisture, inorganic nitrogen, species richness, dominance, community above-ground biomass, species asynchrony, temporal stability of grasses and forbs, dominant species stability and temporal stability of community biomass. The primary advantage of SEM is to evaluate complex causality between variables by translating the hypothesized causal relationships into a pattern of expected statistical relationships in the data (Grace 2006). We checked the bivariate relationships between all variables with simple linear regressions to ensure that linear models were appropriate. We then constructed an *a priori* model (see Fig. S2 in Supporting Information) based on the known effects and potential relationships among the drivers of community stability. In the model, we assumed that precipitation and N addition had the potential to alter community temporal stability directly, as well as indirectly through changing species richness, species asynchrony, and the stability of dominant species and functional groups (see hypotheses in the Introduction). We used the chi-square test (the model has a good fit when $0 \leq \chi^2 \leq 2$ and $0.05 < P \leq 1.00$), Akaike information criteria (AIC; lower AIC indicating a better fit) and the root mean square error of approximation (RMSEA; the model has a good fit when $0 \leq RMSEA \leq 0.05$ and $0.10 < P \leq 1.00$) to evaluate the fit of the model. We simplified the initial model by eliminating non-significant pathways and state variables based on regression weight estimates, before obtaining the final model including only the statistically significant pathways that we failed to reject (see more detailed information of the model estimations in Table S2 in Supporting Information).

Temporal stability data were ln-transformed to meet the assumptions of normality. SEM analyses were performed using AMOS 18.0 (Amos Development Co., Greene, Maine, USA). The remaining statistical analyses were conducted using SPSS 13.0 (SPSS, Inc., Chicago, IL, USA).

Results

SOIL AND PLANT COMMUNITY RESPONSES TO EXPERIMENTAL TREATMENTS

Across the study period from 2005 to 2012, precipitation and nitrogen addition interactively affected both soil inorganic nitrogen content and moisture (Table S3). Nitrogen addition resulted in increased soil inorganic nitrogen content ($F_{1,124} = 47.2$, $P < 0.001$), but its effect was substantially reduced in soils with increased precipitation. Increasing precipitation resulted in a substantial increase in soil moisture ($F_{1,128} = 443.6$, $P < 0.001$); nitrogen addition marginally increased soil moisture ($F_{1,128} = 3.6$, $P = 0.059$), but its effect dissipated in soils with increased precipitation.

Across our study period, plant species richness and dominance showed opposite responses to increased precipitation and nitrogen addition. Specifically, species richness increased with increasing precipitation but decreased with nitrogen addi-

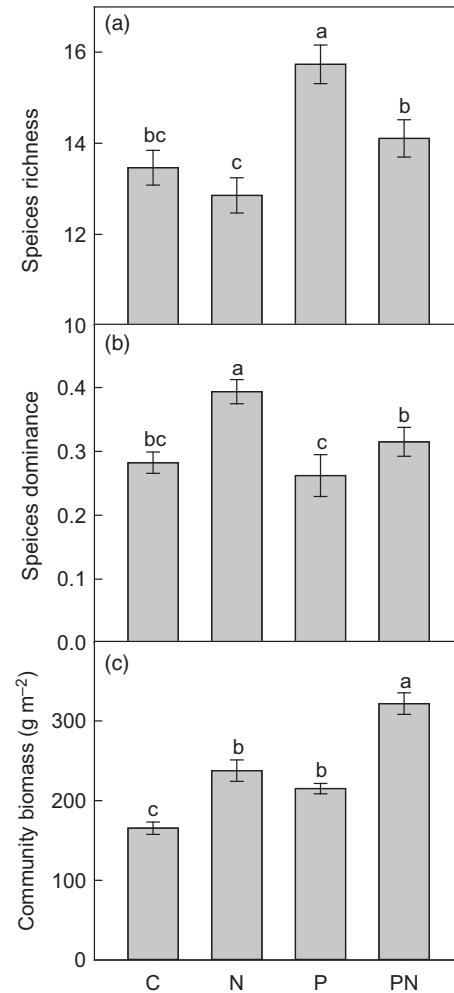


Fig. 1. Effects of nitrogen addition and increased precipitation on (a) species richness, (b) dominance and (c) community above-ground biomass in a semi-arid grassland in North China. C, control; N, nitrogen addition; P, increased precipitation; PN, increased precipitation plus nitrogen addition. Bars indicate means \pm SE. Different letters above bars indicate significant differences according to Duncan's multiple range test ($P < 0.05$).

tion (Fig. 1a, Table S4). Species dominance decreased with increasing precipitation, but increased with nitrogen enrichment (Fig. 1b, Table S4). Community biomass was enhanced both by precipitation addition and by nitrogen enrichment (Fig. 1c, Table S4).

TREATMENT EFFECTS ON TEMPORAL STABILITY AND SPECIES ASYNCHRONY

Community temporal stability significantly increased with increasing precipitation, but decreased with nitrogen enrichment (Fig. 2; Table S4). Precipitation addition significantly increased the stability of grasses, whereas nitrogen addition decreased the stability of forbs (Table S4). Species asynchrony was significantly increased by increased precipitation, but was reduced, though non-significantly, by nitrogen addition (Table S4).

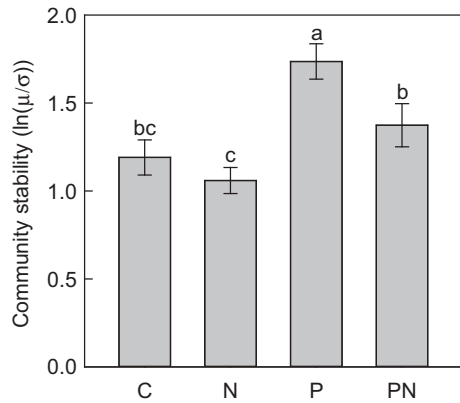


Fig. 2. Effects of nitrogen addition (N) and increased precipitation (P), and their combination (PN), compared to the control (C), on community temporal stability. Bars indicate means \pm SE. Different letters above bars indicate significant differences according to Duncan's multiple range test ($P < 0.05$).

FACTORS INFLUENCING STABILITY

Community temporal stability was significantly negatively correlated with soil inorganic nitrogen (Fig. 3a), but positively correlated with soil moisture (Fig. 3b) and species asynchrony (Fig. 3c). In contrast to many previous findings, we found no significant relationship between species richness and community stability (Fig. 3d). Community stability was also unaffected by species dominance (Fig. 3e) or community

above-ground biomass (Fig. 3f). However, community stability was positively correlated with the stability of both the grass and forb functional groups (Fig. 3g) and was a positive function of dominant species stability (Fig. 3h).

Regression analyses showed that soil moisture was positively correlated with species asynchrony, community biomass and stability of grasses (Fig. S3a–c) and that soil inorganic nitrogen was negatively related to species asynchrony (Fig. S3d), but positively related to species dominance (Fig. S3e). Consistent with the lack of significant diversity–stability relationships, there was no significant relationship between species richness and community biomass (Fig. S3f), species asynchrony (Fig. S3g) and summed variances (Fig. S3h) of species biomass.

Structural equation modelling (SEM) revealed that both soil moisture and inorganic nitrogen affected community temporal stability indirectly, through changing species asynchrony (Fig. 4). Consistent with the results of simple regressions, soil moisture content and inorganic nitrogen had positive and negative effects on species asynchrony, respectively. Also consistent with simple regression results, species richness was not retained as an important state variable in the SEM. On the other hand, the stability of forbs and grasses, which was positively related to community-level stability in simple regression models, was eliminated in the SEM. The stability of dominant species remained a significant, though less important (relative to species asynchrony), variable directly influencing biomass stability in the SEM (Fig. 4).

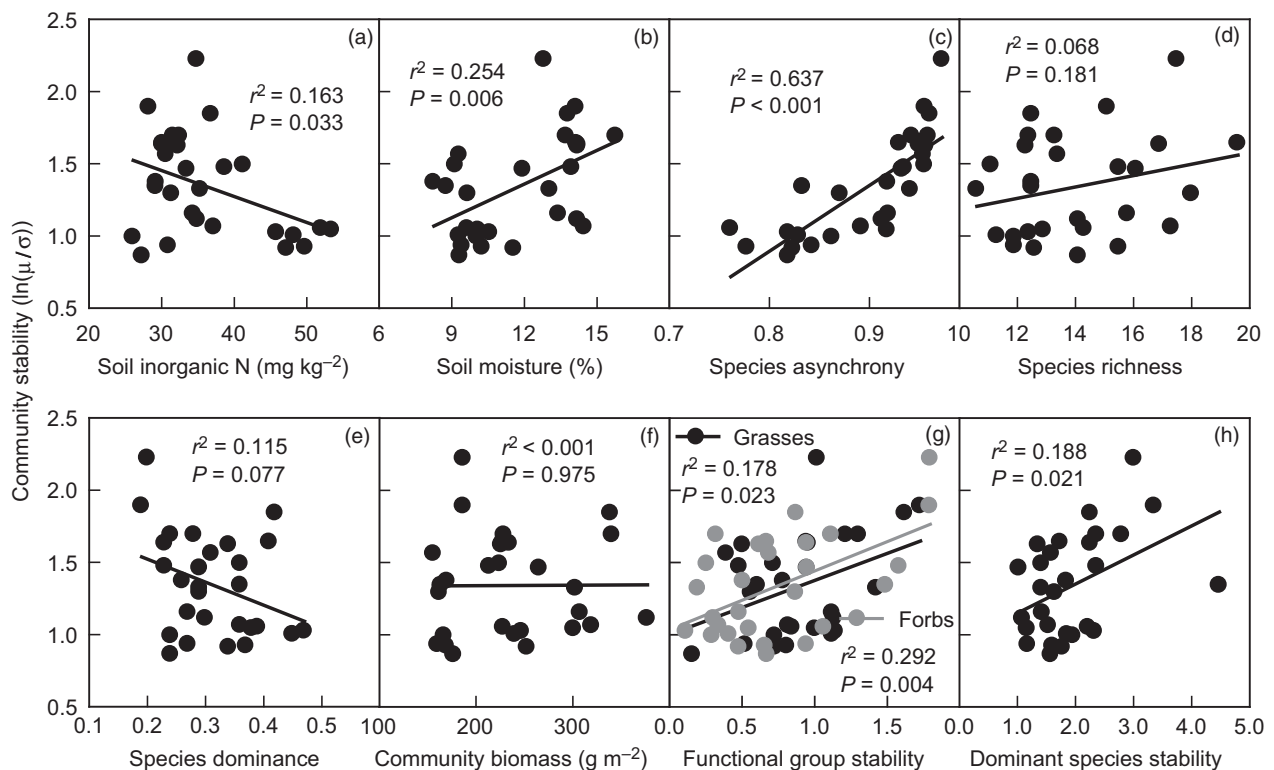


Fig. 3. The natural logarithm of community temporal stability in relation to (a) soil inorganic nitrogen, (b) soil moisture, (c) community-wide species asynchrony, (d) species richness, (e) species dominance, (f) community above-ground biomass, (g) the natural logarithm of temporal stability of grasses and forbs and (h) temporal stability of dominant species.

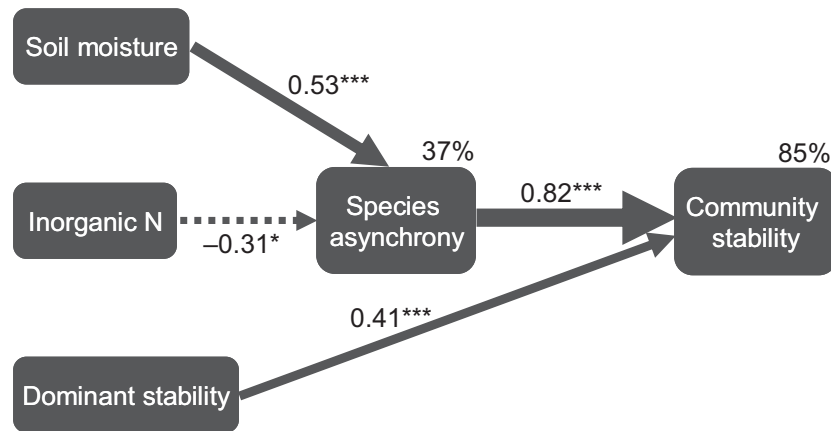


Fig. 4. The result of structural equation modelling relating soil moisture, inorganic nitrogen, dominant species stability and community-wide species asynchrony to community temporal stability. Numbers adjacent to arrows are standardized path coefficients and indicate the effect size of the relationship. The proportion of variance explained (R^2) appears alongside response variables in the model. Arrows indicate positive (solid) and negative (dashed) relationships. Arrow width is proportional to the strength of the relationship. Goodness-of-fit statistics for each model are shown below the model. * $P < 0.05$, *** $P < 0.001$. $\chi^2 = 1.898$, $P = 0.929$, d.f. = 6; RMSEA = 0.000, $P = 0.939$; AIC = 19.980.

Discussion

Our results demonstrate the importance of limiting resources, relative to species diversity, for determining community temporal stability in semi-arid grasslands. Precipitation and nitrogen are two primary factors limiting primary production in this ecosystem (Niu *et al.* 2008; Yang *et al.* 2011a). As expected, increasing availability of these two resources led to increases in plant community biomass. The manipulation of the two resources, however, had different effects on plant richness. Consistent with the generally positive relationship between plant species richness and precipitation in grasslands (Adler & Levine 2007; Cleland *et al.* 2013), precipitation addition resulted in increased species richness. Also consistent with the generally negative effects of nitrogen deposition on plant diversity (Stevens *et al.* 2004; Suding *et al.* 2005), nitrogen addition led to a reduction in plant species richness. Previous work at our study site has shown that nitrogen enrichment modulated plant community structure through intensified competition between high- and low-stature species (Yang *et al.* 2011a) and through increased litter production that suppresses the establishment of new species (Xu *et al.* 2012). Increasing precipitation, on the other hand, promoted richness by favouring shallow-rooted species that were disadvantaged in dry soils (Yang *et al.* 2011a). Similar to their effects on richness, precipitation and nitrogen addition had, respectively, positive and negative effects on the temporal stability of community biomass, which seems to be suggestive of diversity-dependent stability. Our analysis indicated, however, that community temporal stability did not respond to changes in species richness (Fig. 3d). None of the diversity-dependent stabilizing mechanisms, including overyielding (Fig. S3f), diversity-dependent species asynchrony (Fig. S3g) and the portfolio effect (Fig. S3h), operated. Further, SEM revealed that precipitation and nitrogen enrichment influenced stability by increasing and reducing the degree of asynchrony in population fluctuations, respectively, without involving

species diversity. Together, these results suggest that plant diversity is not an important driver of community temporal stability in this semi-arid grassland.

The results of our study contrast with the positive diversity–stability relationships frequently reported in experimental studies (Jiang & Pu 2009; Campbell, Murphy & Romanuk 2011; Gross *et al.* 2014), including those conducted in experimentally created grasslands (e.g. Tilman, Reich & Knops 2006; Isbell, Polley & Wilsey 2009; Hector *et al.* 2010; Wilsey *et al.* 2014). However, it adds to the various diversity–stability relationships found in natural grassland communities (positive relationships: Tilman & Downing 1994; Yang *et al.* 2012; no relationships: Leps 2004; Grman *et al.* 2010; negative relationships: Sasaki & Lauenroth 2011; Yang, Ruijven & Du 2011b). This discrepancy in diversity–stability patterns between experimental and observational studies mirrors the discrepancy in diversity–productivity relationships between the two types of studies. Whereas direct manipulations of species diversity have shown that productivity tends to increase with diversity (Cardinale *et al.* 2006), no consistent diversity–productivity relationships have been found in natural communities (Adler *et al.* 2011). This correspondence is probably not a coincidence, as overyielding (i.e. positive diversity–productivity relationships), which frequently contributes to stability in experimental communities (Gross *et al.* 2014), does not consistently operate in natural communities (i.e. productivity does not necessarily increase with diversity in nature; Mittelbach *et al.* 2001; Grace *et al.* 2007; Adler *et al.* 2011). Such a pattern may simply reflect the fact that other ecological factors are frequently more important drivers of productivity than species richness in natural systems (Grace *et al.* 2007; Adler *et al.* 2011). In our study, for instance, the effects of precipitation and N enrichment on productivity apparently overwhelmed any effect of plant species richness, supporting the general importance of climate (Schoor 2003) and nutrients (Elser *et al.* 2007) in regulating ecosystem productivity.

An alternative and complementary explanation for the discrepancy in diversity–stability patterns between experimental and observational studies is the difference in species dominance patterns between synthetic and natural communities (Jiang, Wan & Li 2009). In synthetically assembled communities, species are typically initiated with equal abundance/biomass. Although uneven abundance among species could quickly develop over the course of the synthetic experiments (e.g. Niklaus *et al.* 2001), the relative short-term nature of these experiments (typically a few years for plant-based experiments) suggests that their results may still be influenced by initial species relative abundance patterns. This contrasts with natural communities in which long-term natural assembly processes often result in highly skewed abundance distributions towards a few dominant species (see Fig. S1 for an example). The high dominance pattern in natural communities would promote the contribution of abundant species to ecosystem processes, diminishing the role of species diversity for ecosystem functioning (Grime 1998). Consistent with this idea, our study identified the stability of dominant species as a significant contributor of community temporal stability. Several other studies have also reported a similar role of dominant species for regulating community stability (Leps 2004; Polley, Wilsey & Tischler 2007; Grman *et al.* 2010; Sasaki & Lauenroth 2011; Yang, Ruijven & Du 2011; Hallett *et al.* 2014; Wilsey *et al.* 2014). Notably, most of these studies have found that increasing diversity did not improve community stability (Leps 2004; Polley, Wilsey & Tischler 2007; Grman *et al.* 2010; Sasaki & Lauenroth 2011; Yang, Ruijven & Du 2011b; and this study), and all these studies are based on observations of natural communities. The high dominance in natural communities may also explain the lack of the portfolio effect in our study, as theory has shown that unevenness in species abundances tends to reduce the strength of the portfolio effect (Doak *et al.* 1998; Tilman, Lehman & Bristow 1998). Future experiments should directly manipulate species dominance, in addition to species diversity, to directly assess its effect on diversity–stability relationships and associated mechanisms (e.g. Isbell, Polley & Wilsey 2009).

The most important finding of our study, which has not been previously reported, is that both precipitation and nitrogen addition affected community temporal stability indirectly through altering species synchrony. Despite some contradictory evidence (e.g. Houlihan *et al.* 2007; Mutshinda, O'Hara & Woiwod 2009), asynchronous population dynamics have been increasingly revealed in a variety of empirical systems (summarized in Gonzalez & Loreau 2009); recent empirical stability studies have also linked them to community temporal stability (Hallett *et al.* 2014; Hautier *et al.* 2014; Wilsey *et al.* 2014). There is little experimental evidence, however, for anthropogenic environmental changes to alter stability through changing species asynchrony. In our study, nitrogen amendment increased soil nitrogen content, resulting in a reduction in asynchrony and, in turn, stability. These results are comparable to those of Hautier *et al.* (2014) that across multiple continents, fertilization destabilized biomass production in diverse natural grasslands due partly to its negative effect on

species asynchrony. Nitrogen addition could relieve plants from nitrogen limitation and allow them to respond more strongly to variation in precipitation (Leps 2004), which is presumably much greater than variation in nitrogen availability. This, coupled with the fact that many species showed similar responses to increased precipitation (see Fig. 1 for the positive effects of precipitation addition on species richness and community biomass, and its negative effect on species dominance), may have caused the reduction in asynchrony. Increasing precipitation, on the other hand, promoted asynchrony in the semi-arid grassland. This pattern may be possibly explained by plants free of water limitation competing more strongly in communities with greater biomass (Yang *et al.* 2011a). The validity of these explanations, of course, needs to be confirmed by future experiments.

Two issues worthy of note are that our analysis of the SEM was based on a relatively small number of samples compared with what is generally required (i.e. 5–10 data points per path in the model) and that the initial model was simplified to eliminate non-significant pathways. As such, our analyses were not testing-specific hypotheses as typical SEMs do and may be considered exploratory in nature. Therefore, our conclusions should be treated with some caution and need to be confirmed by future experiments.

In our study, species diversity is not the main driver of community temporal stability in the semi-arid grassland that we studied. Rather, temporal stability of this important ecosystem is regulated by the availability of dominant limiting resources (precipitation and nitrogen) via changes in species asynchrony and, to a lesser extent, by dominant species stability. It is important to note, however, this result does not necessarily refute the potential role of diversity for stabilizing ecological communities, as revealed by diversity-manipulation studies. Our study was conducted at a single site where variations in species richness were not large (ranging from 10.6 to 19.6 species per m²) and the role of limiting resources and dominant species possibly overwhelmed that of species richness. Studies across larger species diversity gradients, such as those conducted across multiple ecosystems, would be better positioned to detect positive effects of species richness on temporal stability in natural communities (e.g. Hautier *et al.* 2014). Nevertheless, our results have important implications for understanding the dynamics of semi-arid grasslands and other ecosystems similarly limited by precipitation and nitrogen under future global change scenarios. While both growing season precipitation and atmospheric nitrogen deposition are projected to increase for our study region, which would result in increased productivity, the positive effects of precipitation on species diversity and community stability will likely offset the negative effects of nitrogen deposition on species diversity and community stability. Our study also highlights the importance of investigating other drivers of stability, besides species diversity, for a more complete understanding of mechanisms regulating ecological stability. Understanding the multivariate processes controlling ecological stability should be an important goal of future stability research.

Acknowledgements

We thank Zhichao Pu and Jiaqi Tan for their constructive comments on the manuscript, and Yuge Zhang, Jiangping Cai, Ruzhen Wang, Mingming Fu, Peng He, Heyong Liu, Shan Yang, Yongyong Zhang, Pengyu Liu, Xiaobin Li, Wentao Luo, Xue Wang and Haijun Yang for assistance in field experiment. We appreciate the Duolun Restoration Ecology Research Station for permission to access to the study site. This study was financially supported by grants from the National Natural Science Foundation of China (31370009, 41371251, 31300387 and 31361123001), the National Basic Research Program of China (2011CB403204) and the National Science Foundation of USA (DEB-1257858 and DEB-1342754). The authors have no conflict of interest to declare.

Data accessibility

Soil and vegetation data are available from the Dryad Digital Repository (Xu *et al.* 2015).

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Received 9 April 2015; accepted 18 June 2015

Handling Editor: Andrew MacDougall

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Results of the linear regression of community biomass against the sampling year.

Table S2. Results of structural equation modeling of precipitation and nitrogen addition effects on plant community temporal stability through all plausible interaction pathways as illustrated in Figure S3.

Table S3. Mean and range of soil moisture (%) and inorganic nitrogen (mg kg^{-1}) across the sampling years in each treatment.

Table S4. Results (F values) of repeated measures ANOVAs with split-plot design on the effects of treatment time (year), nitrogen addition and increased precipitation, and their interactions on species richness, dominance, and ANOVAs with split-plot design on the effects of nitrogen addition and increased precipitation, and their interactions on community above-ground biomass, the stability of community, grasses and forbs, and community-wide species asynchrony.

Figure S1. The biomass-based ranking of species in the descending order, based on data collected from 2007 to 2012 across all the treatments.

Figure S2. A-priori structural equation model used in this study. Soil moisture, species asynchrony, richness, functional group stability, dominant stability, inorganic nitrogen and community stability were included in this model.

Figure S3. Relationships between soil moisture and (a) species asynchrony, (b) community biomass, (c) stability of grasses; between soil inorganic nitrogen and (d) species asynchrony, (e) species dominance; and between species richness and (f) community biomass, (g) species asynchrony, and (h) summed variance of species biomass.