Effects of plant diversity on semiarid grassland stability depends on functional group composition and dynamics under N and P addition

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HIGHLIGHTS

- Perennial forb or grass had higher stability than legume or annual and biennial.
- High N and P increased annual and biennial dominance, but decreased its stability.
- Diversity decline negatively affected community stability only in annual grassland.
- Functional group shift was the main driver of perennial grassland stability.

GRAPHICAL ABSTRACT
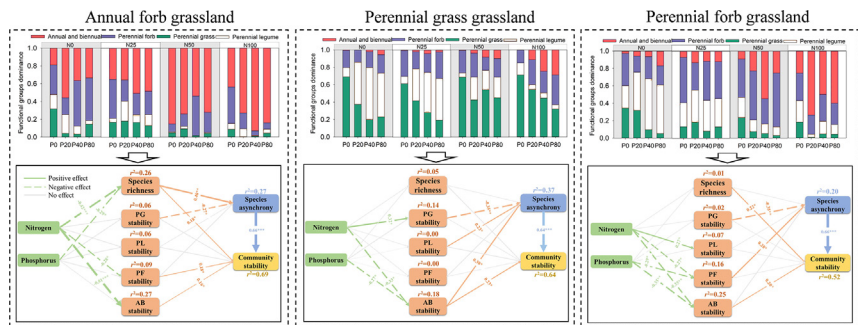
ABSTRACT

Exogenous fertilization could efficiently improve grassland productivity and promote grassland restoration. Increasing fertilization may profoundly affect community stability, whereas the underlying compensatory dynamics among functional groups in regulating grassland stability remain unclear. Three different grasslands, annuals forb (AF) community, perennial grass (PG) community and perennial forb (PF) community, on semiarid Loess Plateau were selected. We designed a 3-year split-plot experiment (main-plot: 0, 25, 50, and 100 kg N ha^{-1} yr^{-1}; subplot: 0, 20, 40 and 80 kg P$_2$O$_5$ ha^{-1} yr^{-1}) to explore how N and P addition affects community stability and its relationship with species richness, species asynchrony and functional group stability. Temporal stability differed largely between functional groups under N and P addition, perennial forbs or grasses had higher stability than perennial legumes or annuals and biennials. Decreased stability of PG and PF communities was primarily due to reduced species asynchrony under N addition alone, while it attributed to increased dominance of perennial legumes after P addition alone. 50 and 100 kg N ha^{-1} yr^{-1} combined with P addition significantly increased dominance of annuals and biennials, but decreased stability of annuals and biennials, which caused significant declines in stability of the three communities. Significant species richness decline induced by N and P addition only occurred in AF community, which suppressed AF community stability through reducing species asynchrony. AF community stability was regulated by additively negative effect of diversity decline and decreased annuals and biennials stability. Whereas, in PG and PF communities, nutrient-induced changes of functional groups stability were the main driver of community stability rather than diversity. Our study highlights the role of functional group composition and dynamics in regulating the effects of diversity on community stability and rational N and P combined addition was essential for conserving stability of different grasslands on semiarid Loess Plateau.

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1. Introduction

Primary production and ecological process of natural grasslands are mainly co-limited by nitrogen (N) and phosphorus (P) (Fay et al., 2015; Harpole et al., 2011). Exogenous nutrient application has become an effective strategy to improve grassland production and promote vegetation restoration, as indicated by grassland studies in Europe (Fay et al., 2015; Lepš, 2014), Australia (Rawnsley et al., 2019), North America (Avolio et al., 2014; Suding et al., 2005) and China (Bai et al., 2010; Yang et al., 2011). However, continued and increased fertilization often caused biodiversity reduction, species composition changes and soil acidification, threatening the stability of ecosystem (Hautier et al., 2014; Zhou et al., 2020). Ecosystem stability provides information about an ecosystem's ability to maintain sustainable functioning and services in response to abiotic and biotic factors changes (Craven et al., 2018; Isbell et al., 2009). Many studies have demonstrated the stabilizing effects of biodiversity on ecosystem stability, and suggested an integrative underlying mechanism for sustaining stability, including species asynchrony and dominant species stability, overyielding effect (known as multispecies communities yield more than expected from their constituent species in monoculture) and portfolio effects (known as the scaling of the temporal variance of a species to its mean productivity) (Grman et al., 2010; Melts et al., 2018).

Various diversity–stability relationships have been detected in different grassland ecosystems (positive relationships: Craven et al., 2018; Huang et al., 2020; negative relationships: Sasaki and Lauenroth, 2011; Yang et al., 2011; no relationships: J.S. Liu et al., 2019; Xu et al., 2015), which argued the historical perspectives of diversity-stability relationship. Despite this controversy, there have been surprisingly few studies explored the underlying mechanism of diversity–stability relationship by considering changes in species or functional groups composition. More importantly, the multiplicity of stability definition further clouded the debates of diversity-stability relationship (Lehman and Tilman, 2000; McCann, 2000). Ecological stability consists of numerous definitions, including temporal variability, resistance to environmental change and rate of recovery from disturbance. In recent years, temporal stability, the reciprocal of temporal coefficient of variation of productivity, has been widely used to evaluate ecological stability (Tilman et al., 2006; Grman et al., 2010; De Mazancourt et al., 2013). This is because temporal stability, as a dimensionless and scale invariant measurement, is readily observable from species and functional group level to community and ecosystem level and especially useful for the quantification of species or functional group stability (Lehman and Tilman, 2000; Bai et al., 2004; Tilman et al., 2006). Here, we shall use temporal stability of productivity in both community and functional group level, which is defined as the ratio of the mean value of annual community or functional group productivity for a time period to its temporal standard deviation over the same interval (Tilman et al., 2006).

The effects of diversity on temporal stability of community productivity are closely associated with temporal species asynchrony (Craven et al., 2018; Huang et al., 2020). Species belong to different functional groups are more asynchronous in response to environment changes, whereas species within a specific functional group are more likely to perform synchrony (Collins et al., 2012; Mackie et al., 2019; Marquard et al., 2009). Meanwhile, different functional groups in a community potentially exhibit different intrinsic stability under environmental fluctuations (Tredennick et al., 2017). Many studies found that perennial, tall and clonal species generally perform more stable than annuals, short and non-clonal species in semiarid area because of low but high fluctuation precipitation (Bai et al., 2004; Huang et al., 2020; Wang et al., 2017). High community-level stability is associated with dominance of species or functional groups with high stability. Dominant species or functional group usually had high stability than subdominant and rare species because of long-term environmental adaptation (Sasaki and Lauenroth, 2011; Smith and Knapp, 2003).

N and P fertilization may influence community stability via multiple facets (Isbell et al., 2009; J.S. Liu et al., 2019). Firstly, N and P addition could cause species loss and biodiversity decline in long-term and thus reduce community stability by decreasing species asynchrony, portfolio effect and overyielding effect (Hautier et al., 2014; Loreau and De Mazancourt, 2013; Marquard et al., 2009). The temporal species variance average out with increasing species richness and rise more slowly compared with mean species productivity because of portfolio effect, which would decrease the temporal variance of community productivity (Tilman et al., 2006; Niu et al., 2018). Overyielding effects occurs when total community productivity increases with diversity and stabilized productivity by increasing mean community productivity relative to temporal variance as diversity increased (Marquard et al., 2009). Species asynchrony helps diversity to reduce the temporal variance of community productivity through species complementarity and overyielding effect (Xu et al., 2015). By contrast, diversity decline induced by N and P addition would increase the temporal variance of community productivity by weakening these effects. Secondly, the reduction of community stability after short-term N and P addition was associated with large shifts in species composition when biodiversity decline is not occurred (Huang et al., 2020; J.S. Liu et al., 2019). This may be due to that dominant species shift from species with high temporal stability of productivity to species with low temporal stability after N and P addition (Mackie et al., 2019; Yang et al., 2011). Thirdly, increased plant height and community productivity may translate into changes in competition strength among species after N and P addition, which impacts species asynchrony (Niu et al., 2018; Xu et al., 2015). Strong competition may benefit some opportunistic species with similar traits and allows them perform more synchronously (Niu et al., 2018; Song et al., 2019). Short species are susceptible to be suppressed by tall species because of light limitation after N and P addition (Collins et al., 2012; DeMalach et al., 2017). Clonal species perform high competitiveness for light and water than non-clonal species because of resource sharing via vegetative growth (Chen et al., 2020; Dickson et al., 2014).

Grassland accounts for nearly 40% of the national land in China. However, about 61% of grassland is experiencing serious degradation due to human activity in the northwest China (Y.Y. Liu et al., 2019). The semiarid Loess Plateau is typical vulnerable ecoregion because of soil erosion, over-grazing and frequent drought (Deng et al., 2014; Zhang, 2005). The "Grain-for-Green" eco-restoration program was proposed since the 1990s to promote revegetation and control soil erosion across the Loess Plateau (Deng et al., 2014; Gang et al., 2018). Up to now, grassland has accounted for about 42.86% of area, which has various grassland types dominated by different species due to different abandoned years and terrain conditions (Gang et al., 2018; Zhang and Dong, 2010). During the early succession, the grassland had unstable biomass production and coverage in response to frequent drought and changeable rainfall. This is because species composition and community structure are highly simple and the dominant species are unstable annual forbs. Thus, the early successional grassland cannot provide stable productivity, soil and water conservation and other functions. As succession extends, more perennial species progressively establishing and become dominant species due to the improvement of soil nutrient and water conditions. The species richness and diversity increased considerably in 6–15 years after abandonment. As a consequence, grassland in later succession stage generally performed high temporal stability of productivity on the Loess Plateau (Chen et al., 2020; Zhang, 2005; Zhang and Dong, 2010).

Grassland production and ecosystem services are widely limited by low soil nutrient availability in the Loess Plateau (Zhang and Dong, 2010). However, reconciliations of productivity improvement and stability conservation among various grasslands are community-specific and rate-dependent when using N and P fertilization. The relative importance of biodiversity decline, species and functional group asynchrony, functional group stability for determining community-level stability in this region under N and P addition remains unclear. Thus, a

three-year N and P addition experiment in three representative grassland communities were conducted on semiarid Loess Plateau, to examined the effects of N and P addition on community stability and its relationship with species richness, species and functional groups asynchrony and functional group stability. The specific aims were to: (1) clarify the effect of different N and P addition on species richness, species asynchrony, functional group asynchrony and stability. (2) assessed the relative importance of diversity and compensatory dynamics of functional groups in maintaining stability of grassland communities after N and P addition. (3) explore the specific underlying mechanism in stabilizing productivity of different grasslands under different N and P addition.

2. Materials and methods

2.1. Study site

The study site is located in the Zhifanggou watershed at Ansai district (36°42′42″–36°46′28″N, 109°13′46″–109°16′03″E, 1010–1431 m altitude), Yan'an City, Shaanxi Province, northwest China (Fig. 1). The region is characterized by semiarid temperate climate with a mean annual temperature of 8.8 °C (min. −6.9 °C in January and max. 22.6 °C in July) and a mean annual precipitation of 528.8 mm (1951–2016), of which about 82.2% falling during growing season (May–September). The zonal soil is mainly Huangmian soil (Calcaric Cambisol, FAO classification), developed on wind deposited loess parent material. The landform and vegetation are representative loess hilly gullied landscape. The common vegetation in this region are mainly xeric herbaceous species including *Bothriochloa ischaemum*, *Artemisia sacrorum*, *Artemisia giraldii*, *Lespedeza davurica* and *Stipa bungeana*.

2.2. Experimental design

Based on succession process, one representative grassland in early successional stage (annual forb-AF community), two representative grasslands in late successional stage (perennial grass (PG) community and perennial forb (PF) community) were selected in 2017. Geographical and vegetation informations of the three grassland communities before N and P additions were shown in Table 1. At each community, a 20 × 30 m area was fenced for grazing exclusion in early May 2017. A split-plot field experiment with N addition in main-plot and P addition in subplot was conducted from 2017 to 2019. Three randomly blocks were established in three communities, respectively. Each block was split into four 4.0 × 4.0 m main-plots and each main-plot split into four 2.0 × 2.0 m subplots. Four N addition rates (0, 25, 50, and 100 kg N ha^{-1} yr^{-1}; coded as N0, N25, N50,

and N100) were applied to four main-plots as calcium ammonium nitrate [5Ca(NO$_3$)$_2$·NH$_4$NO$_3$·10H$_2$O]. Four P addition rates (0, 20, 40 and 80 kg P$_2$O$_5$ ha^{-1} yr^{-1}; coded as P0, P20, P40, and P80) were applied to four subplots randomly as triple superphosphate [Ca (H$_2$PO$_4$)$_2$·H$_2$O]. The N0P0 treatment was regarded as control. Each community included 12 main-plots and 48 subplots. The distribution diagram of N and P addition treatments in the three communities was shown in Fig. 2. N25 treatment was set up to assess the effects of current annual N deposition rate (about 21.76 kg N ha^{-1} yr^{-1}) on Loess Plateau (Liang et al., 2016). N50 and N100 treatments were used to assess the further impacts of N deposition. The N and P fertilization were applied manually to each subplot once a year during natural rain event in early growing season on 4 June 2017, 21 May 2018 and 13 June 2019, respectively. Precipitation and air temperature data was obtained from meteorological station in the Zhifanggou watershed (Fig. 1). Active accumulated temperature was used to evaluate local thermal condition during growing season, which was calculated by the accumulated daily mean air temperature above 10 °C during growing season.

2.3. Plant sampling

Vegetation sampling were carried out in late August from 2017 to 2019. A 1.0 × 1.0 m quadrat was setup to measure abundance, coverage and height of each species in each subplot. The 1.0 × 1.0 m quadrat was quartered into four 0.5 × 0.5 m parts to measure the coverage of each species and whole community. Then two 0.5 × 0.5 m parts were clipped to ground level. To describe compensatory dynamics of functional groups, we classified species into perennial grasses (PG), perennial legumes (PL), perennial forbs (PF) and annuals and biennials (AB). Biomass of different functional groups were oven-dried for 48 h (80 °C). Relative biomass contribution of different functional groups was calculated by the percentage of functional group biomass to community biomass.

2.4. Soil sampling and analysis

In each subplot, three 0–20 cm soil samples were collected and mixed into one composite sample per subplot after vegetation investigation. Soil samples were air-dried and sieved through 0.25-mm mesh for soil total N and P measurement. Soil total N was determined following Kjeldahl digestion (Kjeltec System 2300 Distilling Unit, Foss, Sweden). Soil total P was determined by molybdenum-antimony colorimetric method after wet digestion with sulphuric acid and perchloric acid.
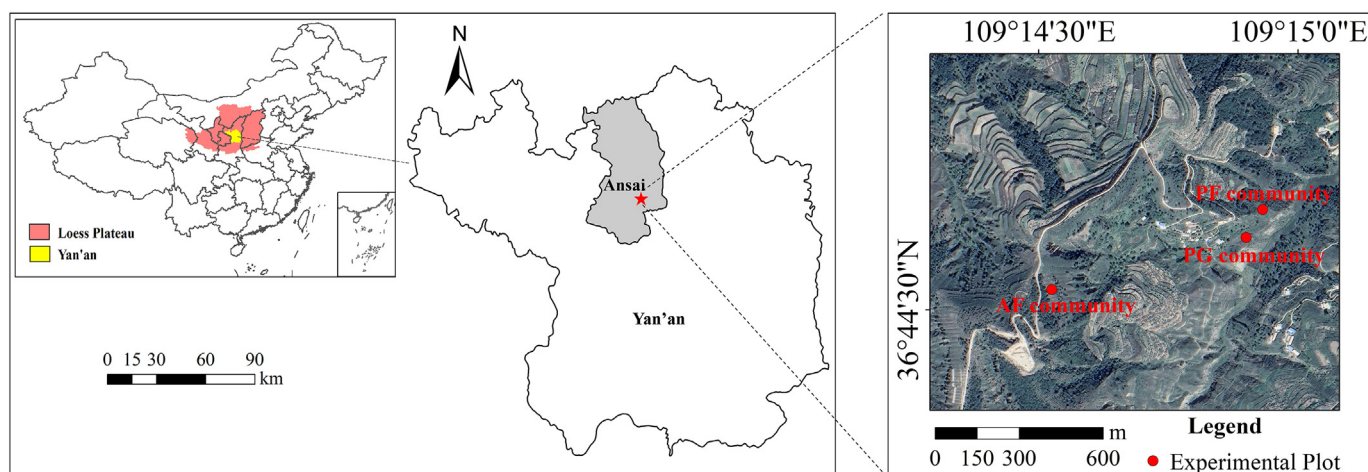

Fig. 1. The location of experimental plot on the Loess Plateau of China.

Table 1
Geographical and vegetation information of the three grassland communities before N and P additions in 2017.

Grassland type	Restoration years (a)	Latitude and longitude	Altitude (m)	Aspects	Slope	Soil total N (TN) and total P (TP) content	Dominant species	Minor species
Annual forb (AF) community	7	109°14′30.68″E 36°44′36.29″N	1272	E	12°	TN: 0.50 g kg^{-1} TP: 0.62 g kg^{-1}	*Setaria viridis* (Linn.) Beauv. *Artemisia capillaris* Thunb.	*Bidens pilosa* Linn. *Geranium wilfordii* Maxim. *Artemisia scoparia* Waldst. & Kit.
Perennial grass (PG) community	20	109°14′53″E 36°44′38″N	1164	E46°S	9°	TN: 0.60 g kg^{-1} TP: 0.58 g kg^{-1}	*Bothriochloa ischcemum* (Linn.) Keng.	*Stipa bungeana* Trin. *Lespedeza davurica* (Laxm.) Schindl. *Artemisia sacrorum* Ledeb.
Perennial forb (PF) community	20	109°14′56″E 36°44′41″N	1153	E46°S	13°	TN: 0.69 g kg^{-1} TP: 0.53 g kg^{-1}	*Artemisia sacrorum* Ledeb. *Artemisia giraldii* Pamp.	*Artemisia capillaris* Thunb. *Artemisia scoparia* Waldst. & Kit. *Lespedeza davurica* (Laxm.) Schindl.

2.5. Statistical analysis

Species richness (*S*) and Simpson's dominance index (*D*) were selected to estimate diversity, *D* was calculated as (Niu et al., 2018):

$$D = 1 - \sum_{i=1}^{S} Pi^2 \tag{1}$$

P_i represents the relative important values (IV) of species *i*, which was calculated as: IV = (relative abundance + relative height + relative coverage) / 3.

Temporal stability in both community and functional groups levels was quantified as μ/σ, where μ is the interannual mean aboveground biomass and σ is the interannual standard deviation during 2017–2019. The calculation formula is essentially the reciprocal of coefficient of variation of biomass (Huang et al., 2020).

Species and functional group asynchrony $(1-\varphi_b)$ were quantified as:

$$1-\varphi_b = 1 - \frac{\sigma_{bT}^2}{\left(\sum_{i=1}^{S}\sigma_{bi}\right)^2} \tag{2}$$
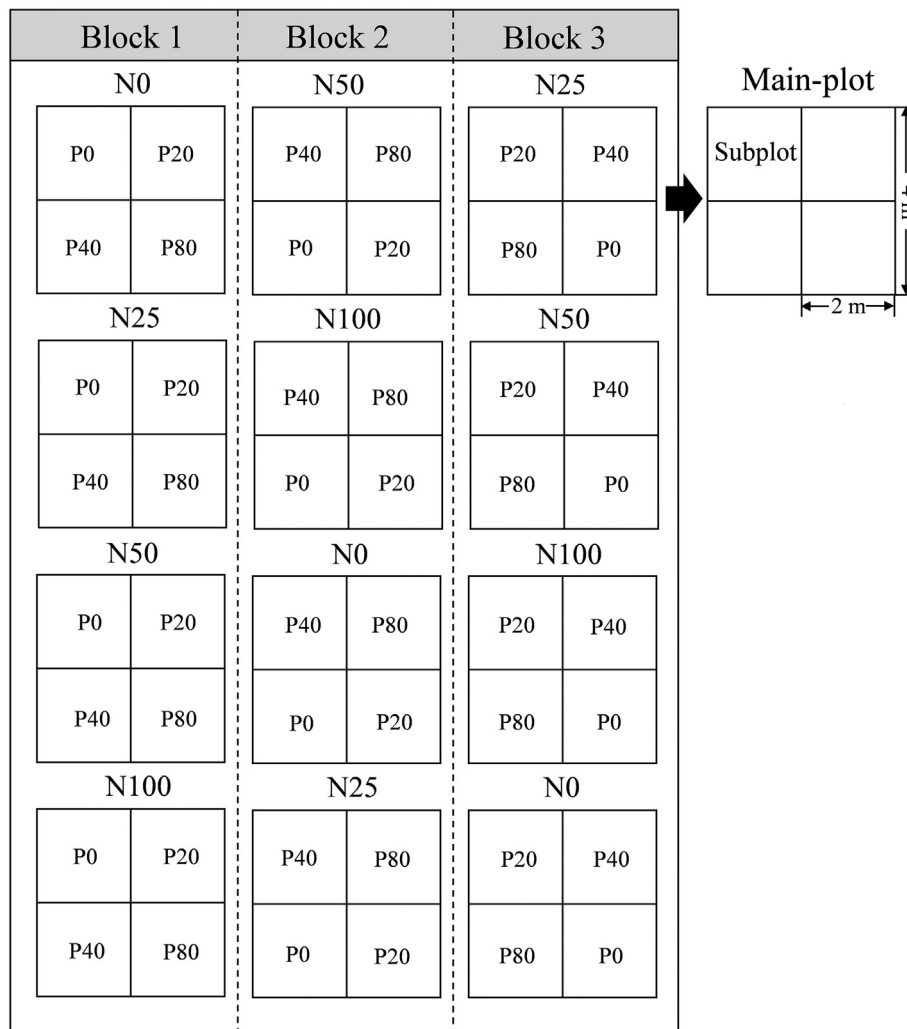

Fig. 2. The distribution diagram of N and P addition treatments in the three communities.

where φ_b is species and functional group synchrony, σ_{bT}^2 is temporal variance of community aboveground biomass over 2017–2019 and σ_{bi} is temporal standard deviation of species and functional group i aboveground biomass over 2017–2019 (Huang et al., 2020).

Statistical analyses were performed with GenStat 18th edition (VSN international Ltd., Rothamsted, UK). The main and interaction effects of N and P addition on community stability, functional group stability, relative aboveground biomass contribution of functional groups, species and functional group asynchrony, aboveground biomass, species richness and Simpson's dominance index (D) were analyzed using split-plot design analysis of variance (ANOVA). Effects for all tests were assessed for significance at $p \leq 0.05$, $p \leq 0.01$ and $p \leq 0.001$. Significant differences ($p \leq 0.05$) between treatments means were identified using the least significant difference (LSD) test. The graphs were created in SigmaPlot 12.5 (Systat Software Inc., San Jose, CA, USA).

Structural equation modelling (SEM) was used to analyze hypothetical paths how N and P addition impacted community stability in the three communities. In the SEM analyses, we assumed that N and P addition potentially altered community stability indirectly through functional groups stability, species richness and species asynchrony. SEM analyses were conducted using AMOS 24.0 (IBM SPSS Inc., Chicago, IL, USA). The goodness of models fit were based on both chi-square (χ^2) test ($0 \leq \chi^2/df \leq 2$ and $0.05 < p \leq 1.00$) and root mean square error of approximation ($0 \leq RMSEA \leq 0.1$ and $0.10 < p \leq 1.00$) (Xu et al., 2015).

The relationship heat map between the relative biomass contribution of different functional groups, Simpson's dominance, species richness, species asynchrony, functional group asynchrony and community stability were run in R 3.5.2 (R Development Core Team) using packages corrplot and car. SPSS 20.0 (IBM SPSS Inc., Chicago, IL, USA) was used to test the least significant difference at $p < 0.05$.

3. Results

3.1. Precipitation and air temperature

Annual precipitations were 485.6 mm and 464.4 mm in 2017 and 2018, respectively, which were obviously lower than mean precipitation of 1951–2016 (528.8 mm). From May to September, growing season precipitations of 2017 and 2018 (2017: 328.8 mm, 2018: 399.8 mm), which account for 67.7% and 86.1% of annual precipitation, were lower than mean of 1951–2016 (434.8 mm). In 2019, the annual precipitation (538.6 mm) and growing season precipitations (424.2 mm) was similar to mean of 1951–2016. The active accumulated temperature in 2019 (2977.6 °C) were obviously higher than that of 2017 (2845.5 °C) and 2018 (2816.8 °C). Monthly mean temperature of March (8.6 °C), July (23.6 °C) and August (21.9 °C) in 2019 were higher than that of 2017 (March: 3.3 °C; July: 22.1 °C; August: 20.0 °C) and 2018 (March: 4.5 °C; July: 21.7 °C; August: 20.2 °C) (Fig. 3).

3.2. Community and functional group stability

For AF community, only N had significant effect on community stability ($p < 0.05$). Community stability decreased significantly after N50 and N100 addition alone as compared to no N and P addition (N0P0) and N25 addition alone ($p < 0.05$). Community stability increased significantly under N25P20 compared to P20 addition alone, while it decreased significantly under N50 and N100 combined with P addition as compared with N25 ($p < 0.05$; Fig. 4). Perennial forb stability was significantly higher than perennial grass and perennial legume stability across all N and P treatments (Fig. S1). N had significant effect on the stability of perennial forb and annual and biennial ($p < 0.05$). Annual and biennials stability decreased significantly under N50 and N100 alone or combined with P addition, while the significant reductions of perennial forb stability occurred at N100 alone or combined with addition compared with N0 and N25 ($p < 0.05$; Fig. 5).

For PG community, N and P had significant effect on community stability. Community stability decreased significantly after N50 and N100 addition alone or P addition alone compared to N0P0 ($p < 0.05$). Community stability showed significant increases after N25P20 and N25P40 addition compared to P20 and P40 addition alone, while it decreased significantly under N100 combined with P addition as compared with N25 ($p < 0.05$; Fig. 4). Perennial grass and perennial forb performed significantly higher stability than annual and biennials
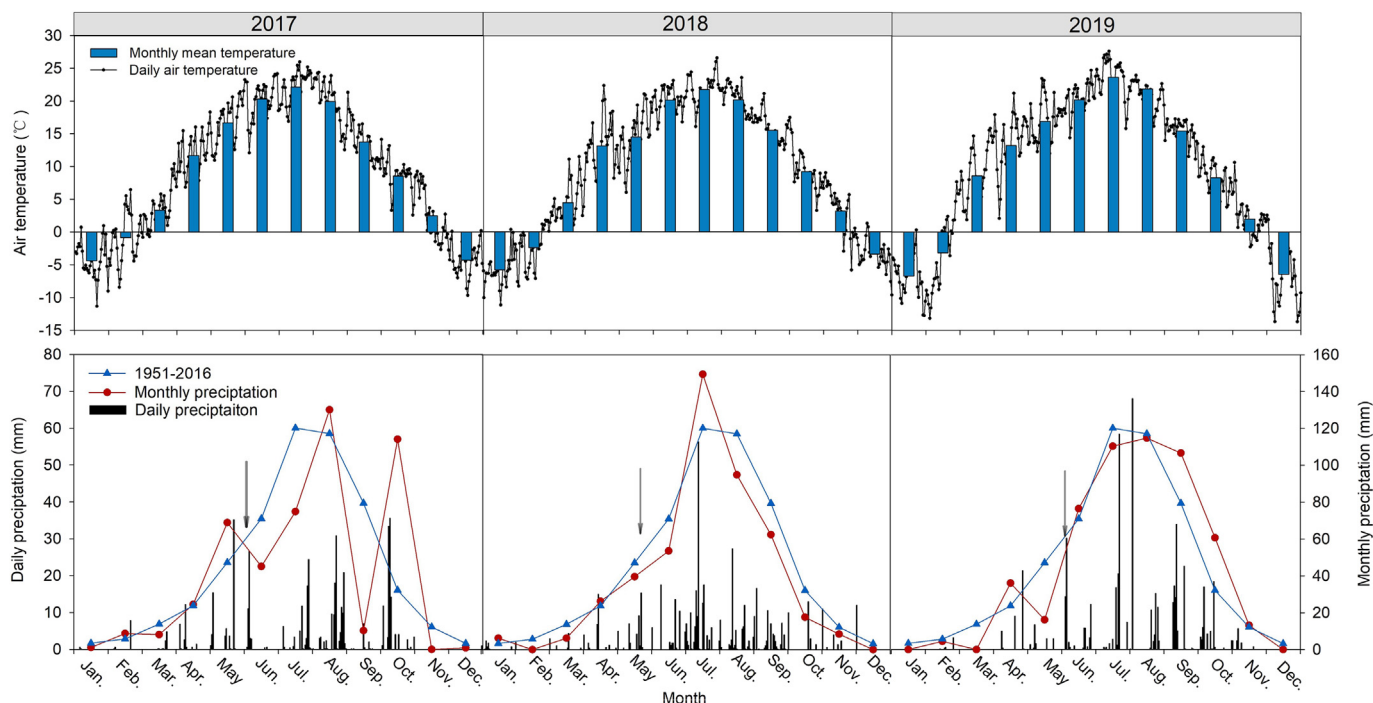

Fig. 3. Daily and monthly precipitation during 2017–2019, and mean monthly precipitation over 66 years (1951–2016). Grey arrows are N and P addition dates.
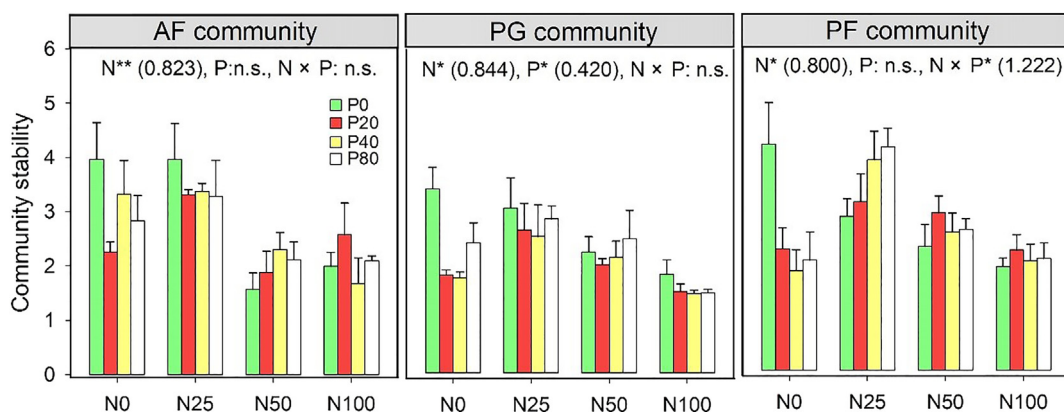
Fig. 4. Temporal stability of the three grassland communities under N and P additions during 2017–2019. AF community: annual forb community; PG community: perennial grass community; PF community: perennial forb community. The data in brackets are LSD values among treatments ($p \leq 0.05$). *, ** and *** indicate statistically significant at $p \leq 0.05$, $p \leq 0.01$, and $p \leq 0.001$, respectively. n.s. indicate no significant differences. Same as following.

and perennial legume across all N and P treatments (Fig. S1). P had significant effect on perennial legume stability. N and P showed significant effect on annual and biennial stability. The stability of perennial legume and annual and biennial showed significant decreases under P addition

alone or N25 combined with P addition as compared with N0P0 or N25 addition alone ($p < 0.05$). Annual and biennials stability decreased significantly after N50 and N100 addition alone compared to N0P0 ($p < 0.05$). Annual and biennial stability after N50 and N100 combined
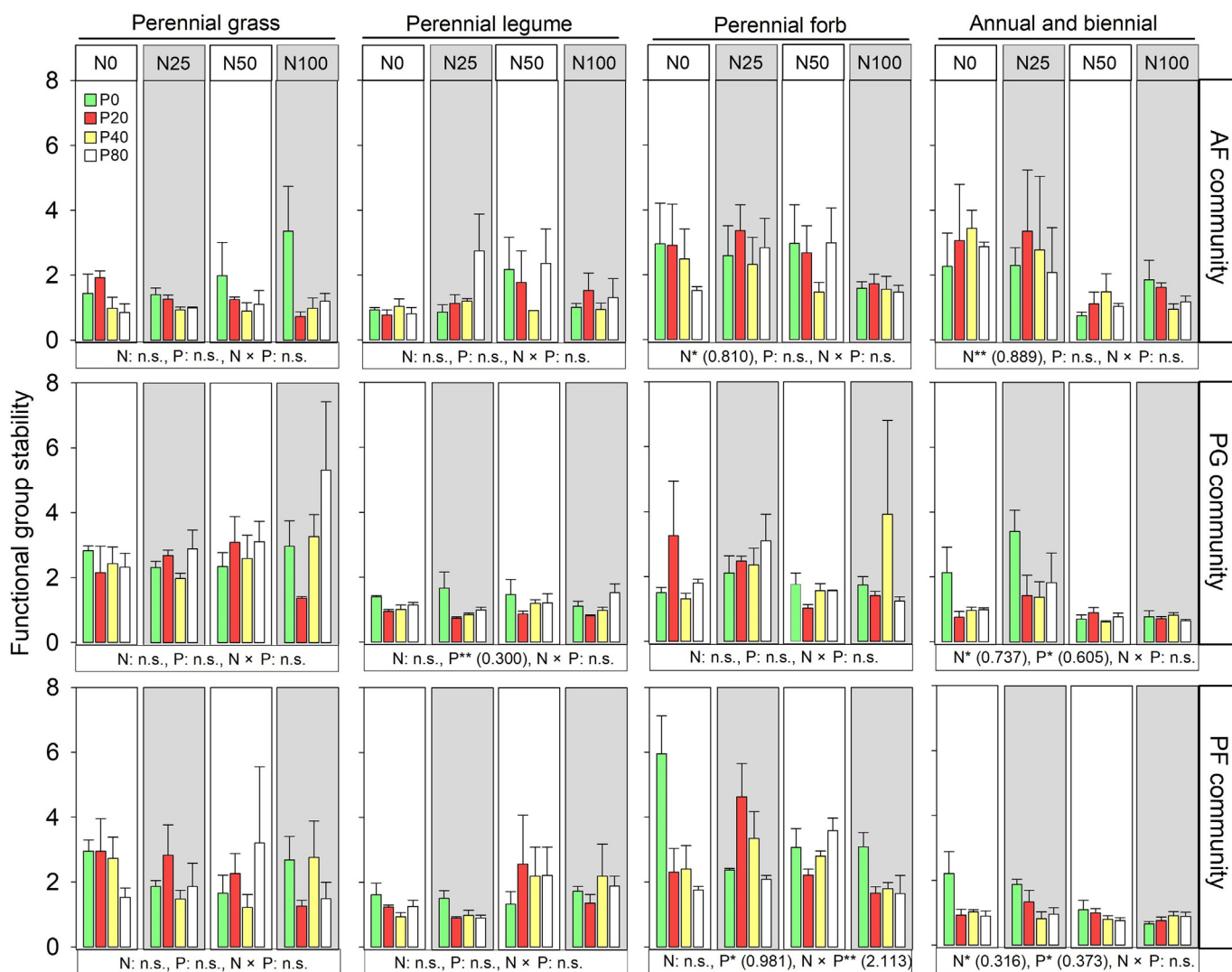

Fig. 5. Temporal stability of four functional groups in the three grassland communities under N and P addition during 2017–2019.
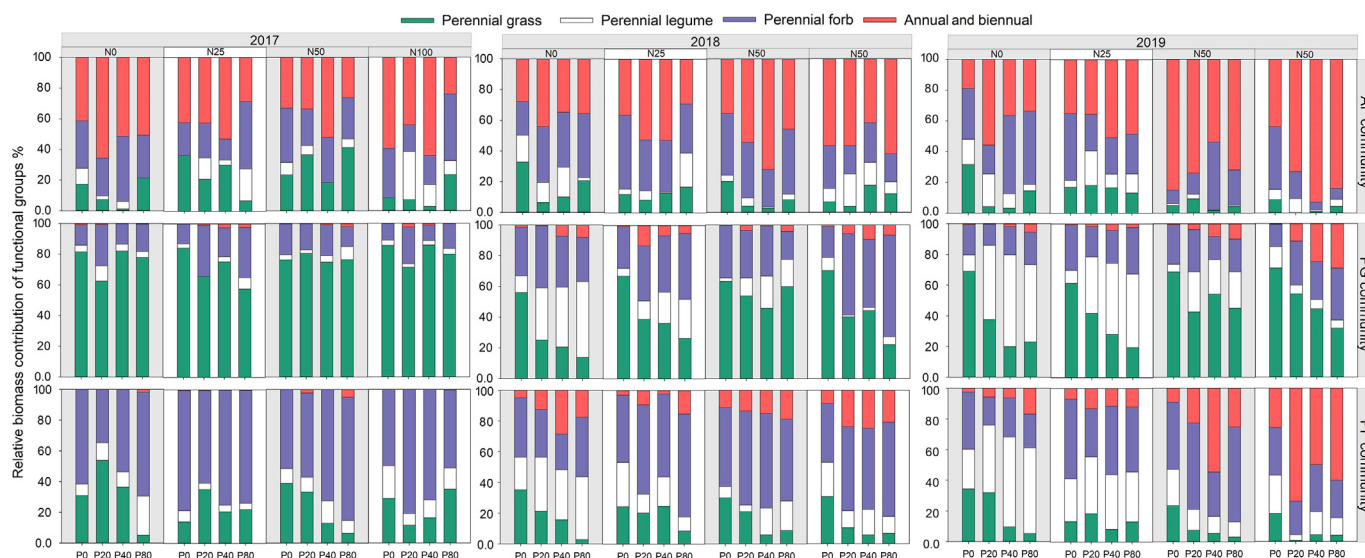
Fig. 6. Relative aboveground biomass contribution of four functional groups in the three grassland communities under N and P addition during 2017–2019.

with P addition showed significant reductions as compared with N25 ($p < 0.05$; Fig. 5).

For PF community, N and N × P interactions had significant effect on community stability. Community stability decreased significantly after N addition alone compared with N0P0. Community stability showed significant increases under N25 combined with P addition compared with P addition alone, while it showed significant declines under N50 and N100 combined with P addition as compared with N25 ($p < 0.05$; Fig. 4). Perennial forb performed significantly higher stability than the other three functional groups across all N and P treatments (Fig. S1). P and N × P interactions showed significant effect on perennial forb stability. N and P showed significant effect on annual and biennial stability. Perennial forb stability decreased significantly after P addition alone or N100 combined with P addition as compared with N0P0 or N100 addition alone ($p < 0.05$). Annual and biennials stability decreased significantly after N50 and N100 addition alone or P addition alone compared with N0P0. Annual and biennials stability after N25 combined with P addition showed significant decreases compared with N0P0 or N25 addition alone ($p < 0.05$; Fig. 5).

3.3. Compensatory dynamics of functional groups

For AF community, N, P and their interaction had no significant effect on relative biomass of different functional groups in 2017. P had significant effect on relative biomass of perennial grass and N showed

significant effect on relative biomass of perennial legume only in 2019. N showed significant effect only on relative biomass of annual and biennials in both 2018 and 2019. Relative biomass of annual and biennials increased significantly under N100 addition alone in 2018, while it increased significantly under N25, N50 and N100 addition alone in 2019 compared with N0P0. The relative biomass of annual and biennial increased significantly under N50 and N100 combined with P addition compared to P addition alone in both 2018 and 2019 (Fig. 6; Table 2).

For PG community, N, P and their interaction had no significant effect on relative biomass of different functional groups in 2017. N and P showed significant effect on relative biomass of perennial grass in both 2018 and 2019. Relative biomass of perennial grass increased significantly under N50 and N100 combined with P addition as compared with P addition alone, but it decreased significantly under P addition alone or N and P combined addition compared to N0P0 or N addition alone in 2018 and 2019. N, P and their interaction showed significant effect on relative biomass of perennial legume in both 2018 and 2019. Relative biomass of perennial legume increased significantly under P addition alone or N25 and N50 combined with P addition compared with N0P0 or N25 and N50 addition alone, while it decreased significantly under N100 combined with P addition as compared with P addition alone in both 2018 and 2019. N and P showed significant effect on relative biomass of annual and biennial only in 2019. Under N50 and N100 combined with P addition, relative biomass of annual and biennial

increased significantly compared with N or P addition alone in 2019 (Fig. 6; Table 2).

For PF community, N, P and their interaction had no significant effect on relative biomass of different functional groups in 2017. P had significant effect on relative biomass of perennial grass in 2018 and 2019. Relative biomass of perennial grass showed significant decreases under P addition alone or N50 and N100 combined with P addition compared with N0P0 or N50 and N100 addition alone in 2018 and 2019. N showed significant effect on relative biomass of perennial legume in 2019. Relative biomass of perennial legume decreased significantly under N50 and N100 combined with P addition compared with P addition alone in 2019. N, P and their interaction showed significant effect on relative biomass of annual and biennial only in 2019. Under N50 and N100 combined with P addition, relative biomass of annual and biennial increased significantly compared with N or P addition alone in 2019 (Fig. 6; Table 2).

3.4. Species and functional group asynchrony

N showed significant effect on species and functional groups asynchrony in AF community. Species and functional groups asynchrony showed significant decreases under N50 and N100 addition alone compared to N0P0 in AF community ($p < 0.05$). Other than N50P20, species asynchrony increased significantly under N and P combined addition as compared with P addition alone in AF community ($p < 0.05$; Fig. 7). N and N × P interactions showed significant effect on species asynchrony, N, P and N × P interactions showed significant effect on functional group asynchrony in PG community. Species and functional group asynchrony of PG community after N100 addition alone showed significant declines compared to N0P0. Functional group asynchrony of PG community decreased significantly under N50P20 and N50P40 as compared with N50 addition alone, while it increased significantly under N100P40 and N100P80 compared with N100 addition alone ($p < 0.05$; Fig. 7). P and N × P interactions showed significant effect on species asynchrony in PF community. Species and functional group asynchrony of PF community decreased significantly under P addition alone compared with N0P0, while it showed significant increases under N and P combined addition compared with N addition alone ($p < 0.05$; Fig. 7).

3.5. Factors influencing community stability

Structural equation model revealed that the direct and indirect effects of N and P addition explained 69% of total variations in AF community stability via species richness, species asynchrony, annual and biennials stability and perennial forb stability. Reduced species richness induced by N and P addition decreased AF community stability directly and indirectly through reducing species asynchrony. Decreased annual and biennials and perennial forb stability induced by N addition reduced AF community stability directly (Fig. 8). N and P addition explained 64% of total variation in PG community stability by influencing the stability of perennial grass and annual and biennial and species asynchrony. Decreased annual and biennial stability induced by N and P addition reduced PG community stability directly and indirectly via decreasing species asynchrony. The increases of perennial grass stability induced by N addition showed indirectly negative effect on PG community stability through reducing species asynchrony (Fig. 8). N and P addition explained 52% total variations in PF community stability by affecting species asynchrony, perennial forb and annual and biennial stability. Decreased annual and biennial stability induced by N and P addition directly caused decreases in PF community stability. Reduced perennial forb stability induced by N and P addition decreased PF community stability indirectly through species asynchrony (Fig. 8).

4. Discussion

Our results demonstrated that the response of aboveground biomass in the three grassland communities to N and P addition showed apparent interannual variation from 2017 to 2019, which indicated the effects of N and P addition were mediated by precipitation and air temperature fluctuation on the Loess Plateau (Fig. S3) (Wang et al., 2017). The response size of community productivity to N and P addition was restricted by low growing season precipitation in 2017, while the effect of N and P addition increased notably with increasing growing season precipitation in 2018. In 2019, the community productivity of the three grasslands showed the strongest response to N and P addition, which was facilitated by the highest accumulated temperature and precipitation during growing season. Many studies confirmed that variation in spring temperature and precipitation had significant effects on
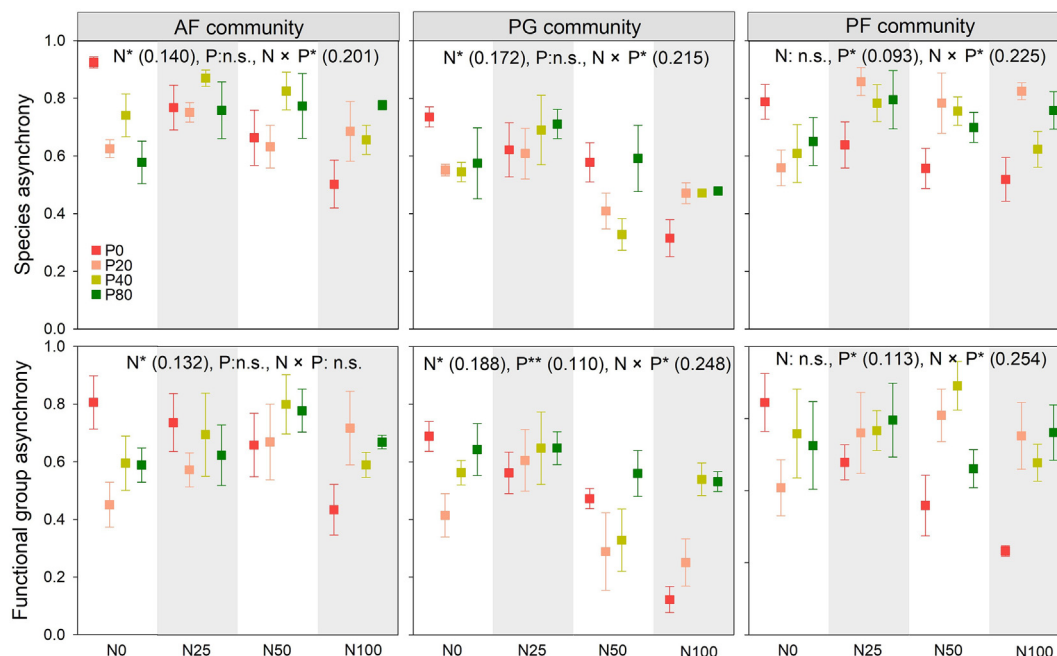
Fig. 7. Species and functional group asynchrony of the three grassland communities under N and P addition during 2017–2019.
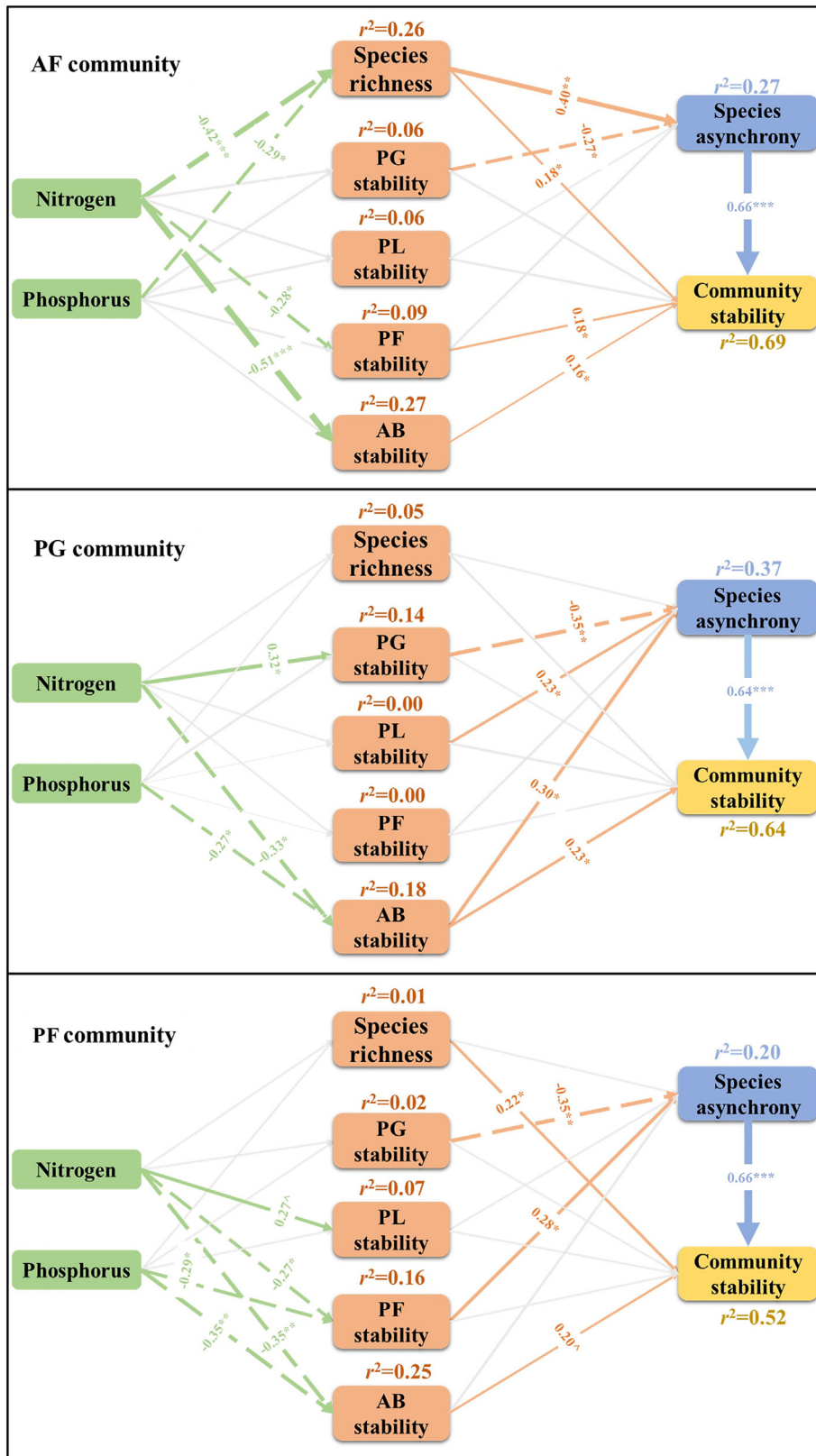
Fig. 8. Structural equation modelling results of the effect of N and P addition, community stability relating functional group (PG: perennial grass; PL: perennial legume; PF: perennial forb; AB: annuals and biennials) stability, species richness and species asynchrony in the three grassland communities. Numbers beside lines are standardized path coefficients. The solid and dotted lines indicate significant positive and negative paths ($\hat{}p \leq 0.1$, $^*p \leq 0.05$, $^{**}p \leq 0.01$, $^{***}p \leq 0.001$). Path width is scaled by the size of standardized path coefficient. The model fitting for AF community: $\chi^2 = 19.91$, $df = 15$, $p = 0.175$; RMSEA $= 0.083$, $p = 0.19$. The model fitting for PG community: $\chi^2 = 26.99$, $df = 15$, $p = 0.105$; RMSEA $= 0.095$, $p = 0.16$. The model fitting for PF community: $\chi^2 = 22.05$, $df = 15$, $p = 0.107$; RMSEA $= 0.100$, $p = 0.18$.

the start date of the vegetation growing season (SOS) in the temperate grasslands of China (Shen et al., 2018; Shen et al., 2019). In 2019, both warmer temperature and more precipitation during March and April led to advancing SOS, which extended growing season and increased biomass accumulation. High responsiveness of productivity in 2019 after N and P addition driven a reduction in temporal stability in all three communities. N and P addition resulted in large shifts in functional groups, and their temporal stability differed largely. The community-specific shifts of functional group had large but variable effects on community stability in different grassland types. We found that large shifts of functional group composition and its stability changes were more important than diversity in regulating semiarid grassland stability under short-term N and P addition (Craven et al., 2018; Liu et al., 2018).

The effects of diversity on community stability were associated with the magnitude of diversity decline and species composition (Isbell et al., 2009; Melts et al., 2018). Species richness declines in AF community were because increased tall and dense annuals and biennials under N50 and N100 combined with P addition produced strong light limitation and thus caused short species loss (Fig. S3) (Avolio et al., 2014; DeMalach et al., 2017). The significant decrease of species richness caused negative effects on AF community stability by reducing species asynchrony (Figs. 8; S3). In contrast to AF community, N and P addition had minimal effects on species richness in PG and PF communities, suggesting that diversity changes were not the main driver affecting community stability in perennials grassland (Fig. S3) (J.S. Liu et al., 2019; Wang et al., 2017). Meanwhile, N and P addition induced overyielding effect may overwhelmed the role of slight diversity changes in regulating perennial grassland stability (Liu et al., 2018; Xu et al., 2015). Whereas this result did not deny the positive effect of diversity in stabilizing natural communities (Hautier et al., 2014). Likewise, some studies in semiarid grasslands have demonstrated that species diversity is not the primary factor influencing community stability, they identified changes functional groups composition and its stability are frequently more important drivers for community stability under N and P addition (Bai et al., 2004; Wang et al., 2017; Yang et al., 2011).

N and P addition induced large shifts in dominance of functional groups in the three communities in 2018 and 2019. The negative relationships between biomass contribution of different functional groups, a potential complementary effect, could support community stability (Fig. S4) (Grman et al., 2010). Different N and P addition modulated compositional dynamics of functional group through intensified competition between N-fixing and non-N-fixing species, tall and short species and annual and perennial species (Avolio et al., 2014; Song et al., 2019; Suding et al., 2005). The significant increased abundance of legumes under P addition alone and N25 combined with P addition suppressed perennial grasses or forbs (Figs. 6; S4) (Avolio et al., 2014). On the one hand, P addition could promote legume growth by facilitating root development. On the other hand, P addition also could improve formation of nodules and the nitrogenase activity of nodule with symbionts to promote biological nitrogen fixation process (Ren et al., 2016). The dominance of tall perennial species, especially tall clonal species, in PG and PF communities increased significantly under N50 combined with P addition due to its superior nutrient and light competitive ability (Suding et al., 2005). This is because tall clonal vegetative branch generates the potential to behave as an interconnected network of ramets and could efficiently take advantage of soil nutrient, water and light resources (Dickson et al., 2014). The increased dominance of high clonal species would rapidly create local colonization and occupy more space in the community and suppressed the growth of short species (Gough et al., 2012). Under N100 combined with P addition, the decreased stability in all three communities was driven by plastic responses of increased annuals and biennials in wet year (Wang et al., 2017). This is because annuals and biennials could best take advantage of higher nutrient availability and growth rapidly, which was facilitated by their functional traits, including acquisitive resource use strategy and tall stature

(Suding et al., 2005; Wang et al., 2017). The increased dominance of annuals and biennials and its abundant seed production would increase the seed bank in the soil, which potentially enhanced annuals and biennials dominance in the coming year (Wang et al., 2017). In addition, the start date of the growing season of annuals and biennials was advanced due to high nutrient availability, which further increased the biomass accumulation (Bai et al., 2010). As a consequence, strong light limitation induced by tall clonal species and annuals and biennials suppressed and exclude species with conservative resource use strategy and short stature (Chen et al., 2020; DeMalach et al., 2017). Perennial legume in PG and PF communities was significantly suppressed under N50 and N100 combined with P addition (Figs. 6; S4), which was due to that the stimulatory effects of P addition on legume were offset by strong light limitation (Ren et al., 2016). In addition, high N addition level could lead to the potential breakdown of symbiotic nitrogen fixation, which would decrease the perennial legume dominance in subsequent years (Regus et al., 2017).

The influences of large functional group shift on community stability were tightly associated with the stability of functional groups (Huang et al., 2020). Different functional groups performed different stabilizing effects on community stability (Fig. 8) (Bai et al., 2004). The stability of functional group was related to functional trait, relative biomass and species numbers within functional groups (Bai et al., 2004; Marquard et al., 2009). Firstly, functional traits largely determine intrinsic stability of functional groups. The high stability of perennial grasses in PG and PF communities was mainly due to that most species within perennial grasses were clonal grasses (i.e. rhizome grasses and bunchgrasses) (Tables S1–S3). Clonal species that spread vegetative growth can effectively integrate and share limiting soil moisture through ramets in relative dry tears, thus performed low temporal variation in the context of changeable precipitation (Bai et al., 2004; Dickson et al., 2014). However, perennial grasses in AF community were primarily non-clonal species and showed low stability, which was susceptible to interannual precipitation variation (Tables S1–S3). These results are comparable to that rhizome grasses and bunchgrasses performed the lowest coefficients of variation (highest stability) among all functional groups in natural Inner Mongolia grassland over 24-year study (Bai et al., 2004). Perennial legumes performed consistently low stability under all N and P addition in PG and PF communities. The changeable soil moisture and temperature during 2017–2019 would affect the activity of soil phosphatase and availability of phosphate fertilization, which further caused large variations in legume under P addition alone (Sardans et al., 2006). Under N50 and N100 combined with P addition, the plastic responses of tall annual and biennial during 2017–2019 would result in different light limitation strength on legumes, and thus short legume performed low stability (Chen et al., 2020). In addition, high N addition level caused potential breakdown of symbiotic nitrogen fixation would also reduce legumes stability (Regus et al., 2017). The low stability of annuals and biennials was attributed to its abundant seed production, acquisitive resource use strategy and shallow root system (Bai et al., 2010; Wang et al., 2017). Annuals and biennials grow rapidly in relative wet years, while they disappeared and retreated to soil seed bank in subsequent dry years (Bai et al., 2010; Wang et al., 2017). Secondly, the stability of dominant functional group which had high relative biomass contribution was considered as a significant contributor to community stability (Sasaki and Lauenroth, 2011; Smith and Knapp, 2003). The negative effect of annuals and biennials on PG and PF community stability under N0 or N25 addition was not significant because of its low biomass contribution. However, annuals and biennials became dominant species and resulted in significantly negative effect on community stability under N50 and N100 combined with P addition (Fig. 6). Increased dominance of perennial legume caused significant decreases in the stability of PG and PF communities (Figs. 4; 6). Thirdly, functional groups with more species were generally highly stabilized (Huang et al., 2020; Marquard et al., 2009). Annuals and biennials in AF community which contained more species performed relative higher

stability than that in PG and PF communities (Fig. S1; Tables S1–S3). Perennial forbs in all three communities performed consistent relatively higher stability, which was associated with its highest species number (Fig. S1; Tables S1–S3). These indicated that species within functional groups were not completely redundant with respect to community stability.

Shifts in functional groups and its stability changes also affect community stability via influencing species and functional group asynchrony (De Mazancourt et al., 2013; Liu et al., 2018). Species asynchrony promotes community stability when species sustains functional complementary interactions and response divergent under N and P addition (Loreau and De Mazancourt, 2013; Tredennick et al., 2017). N or P addition alone caused decreases in species and functional groups asynchrony, in turn, reduced stability in PG and PF communities. This was because N or P addition alone only relieved perennial grasses or perennial legumes from nutrient limitation and allow them to respond more strongly and synchronously (Fig. 6) (Collins et al., 2012; Wang et al., 2017). This supported the fact that the similar response of species belonging to a specific functional group caused reduction in species and functional group asynchrony (Tredennick et al., 2017). However, the improved species or functional group asynchrony under N100 combined with P addition may be possibly attributed to all functional groups free of N and P limitation simultaneously, allowing them response more asynchrony (Yang et al., 2011). In addition, the growing season of perennial species runs from early May to late September on Loess Plateau, whereas annuals and biennials usually germinate in early July following rainy season under N100 combined with P addition which could promote species asynchrony (Bai et al., 2004; Wang et al., 2017). However, the positive effects of increased species asynchrony were outweighed by the negative effects of decreased annuals and biennials stability under N100 combined with P addition, leading to reductions in community stability (Bai et al., 2010; Wang et al., 2017).

In summary, there were clear differences in the main factors governing community temporal stability for different grassland types under short-term N and P addition on Loess Plateau. The decreased community stability in annual forb grassland was due to additive negative effect of diversity decline and changes in annuals and biennials and perennial forb stability. However, species diversity is not the primary driver in regulating the stability of two perennial grasslands under N and P addition. Instead, in perennial grass and perennial forb grasslands, N and P addition reduced community stability mainly through influencing the stability of different functional groups, but the underlying regulatory processes were different between the two perennial grasslands (Wang et al., 2017; Liu et al., 2018). Our results highlighted that different functional group composition could modulate the response of community stability to N and P addition. Therefore, we suggest that grassland types should be considered to accurately evaluate the ability of ecosystems to provide and maintain long-term functions during grassland restoration when using N and P fertilizers (Bai et al., 2010; Liu et al., 2018). For restoring the vast areas of farming-withdraw grasslands in Loess Plateau, it is highly necessary to employ targeted N and P combination for various grassland communities based on functional group composition to simultaneously sustain high productivity and high stability.

Our study revealed the specific underlying mechanism in stabilizing productivity of different semi-arid grasslands under short-term N and P addition. The N and P effects on semi-arid grassland productivity and species composition are strongly contingent on variation in precipitation and temperature, suggesting the grassland stability will vary with future climate change with the extension of fertilization experiment. Meanwhile, the co-variation of soil nutrient and water after N and P fertilization had significant coupling effects on grassland productivity and stability in semiarid area. Therefore, further long-term studies are needed to verify underlying possible mechanism behind coupling changes of various environmental factors in regulating grassland stability when using fertilization to promote grassland restoration on Loess Plateau.

5. Conclusion

N and P addition resulted in large shifts in functional groups and apparent compensatory dynamics in all three communities. Temporal stability differed largely between functional groups under N and P addition, and perennial forbs or grass had higher stability than perennial legumes or annuals. Significant species richness decline under N and P addition only occurred in annuals forb community, which suppressed community stability through reducing species asynchrony. In addition, N addition decreased the stability of annual forb community by reducing perennial forb and annual and biennial stability. Whereas, in the two perennial grasslands, species diversity is not the primary driver of stability under N and P addition. Perennial grass or forb stability indirectly regulated the two perennial grassland stability through influencing species asynchrony. Meanwhile, decreased annual and biennial stability could directly suppressed community stability of the two perennial grasslands under N and P addition. Our study highlights the role of functional group composition and dynamics in regulating the effects of diversity on community stability. Our findings point to the need of targeted N and P combination for various farming-withdrawn grasslands to conserve the function and service stability when applying fertilization to promote grassland restoration in semiarid Loess Plateau.

CRediT authorship contribution statement

Xu B. C. and Chen Z. F. designed the entire experiment. Chen Z. F., Xiong P. F., Zhou J. J. Lai S. B. and Jian C. X. conducted the experiments, and data collection. Xu B. C. supervised the research. Chen Z. F., Xu B. C., Xiong P. F., Xu W. Z., Zhou J. J. and Jian C. X. analyzed the data, wrote and edited the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.149482.

References

Avolio, M.L., Koerner, S.E., La Pierre, K.J., Wilcox, K.R., Wilson, G.W.T., Smith, M.D., 2014. Changes in plant community composition, not diversity, during a decade of nitrogen and phosphorus additions drive above-ground productivity in a tallgrass prairie. J. Ecol. 102, 1649–1660. https://doi.org/10.1111/1365-2745.12312.

Bai, Y.F., Han, X.G., Wu, J.G., Chen, Z.Z., Li, L.H., 2004. Ecosystem stability and compensatory effects in the Inner Mongolia grassland. Nature 431, 181–184. https://doi.org/10.1038/nature02850.

Bai, Y.F., Wu, J.G., Clark, C.M., Naeem, S., Pan, Q.M., Huang, J.H., Zhang, L.X., Han, X.G., 2010. Tradeoffs and thresholds in the effects of nitrogen addition on biodiversity and ecosystem functioning: evidence from Inner Mongolia grasslands. Glob. Chang. Biol. 16, 358–372. https://doi.org/10.1111/j.1365-2486.2009.02142.x.

Chen, Z.F., Xiong, P.X., Zhou, J.J., Yang, Q., Wang, Z., Xu, B.C., 2020. Grassland productivity and diversity changes in responses to N and P addition depend primarily on tall clonal and annual species in semiarid Loess Plateau. Ecol. Eng. 145, 105727. https://doi.org/10.1016/j.ecoleng.2020.105727.

Collins, S.L., Koerner, S.E., Plaut, J.A., Okie, J.G., Brese, D., Calabrese, L.B., Evansen, R.J., Nonaka, E., 2012. Stability of tallgrass prairie during a 19-year increase in growing

season precipitation. Funct. Ecol. 26, 1450–1459. https://doi.org/10.1111/j.1365-2435.2012.01995.x.

Craven, D., Eisenhauer, N., Pearse, W.D., et al., 2018. Multiple facets of biodiversity drive the diversity–stability relationship. Nat. Ecol. Evol. 2, 1579–1587. https://doi.org/10.1038/s41559-018-0647-7.

De Mazancourt, C., Isbell, F., Larocque, A., Berendse, F., De Luca, E., Grace, J.B., Haegeman, B., Wayne Polley, H., Roscher, C., Schmid, B., Tilman, D., Van Ruijven, J., Weigelt, A., Wilsey, B.J., Loreau, M., 2013. Predicting ecosystem stability from community composition and biodiversity. Ecol. Lett. 16, 617–625. https://doi.org/10.1111/ele.12088.

DeMalach, N., Zaady, E., Kadmon, R., 2017. Light asymmetry explains the effect of nutrient enrichment on grassland diversity. Ecol. Lett. 20, 60–69. https://doi.org/10.1111/ele.12706.

Deng, L., Shangguan, Z.P., Sweeney, S., 2014. "Grain for green" driven land use change and carbon sequestration on the Loess Plateau, China. Sci. Rep. 4, 1–8. https://doi.org/10.1038/srep07039.

Dickson, T.L., Mittelbach, G.G., Reynolds, H.L., Gross, K.L., 2014. Height and clonality traits determine plant community responses to fertilization. Ecology 95, 2443–2452. https://doi.org/10.1890/13-1875.1.

Fay, P.A., Prober, S.M., Harpole, W.S., Knops, J.M.H., Bakker, J.D., Borer, E.T., 2015. Grassland productivity limited by multiple nutrients. Nat. Plants 1, 15080. https://doi.org/10.1038/nplants.2015.80.

Gang, C.C., Zhao, W., Zhao, T., Zhang, Y., Gao, X.R., Wen, Z.M., 2018. The impacts of land conversion and management measures on the grassland net primary productivity over the Loess Plateau, Northern China. Sci. Total Environ. 645, 827–836. https://doi.org/10.1016/j.scitotenv.2018.07.161.

Gough, L., Gross, K.L., Cleland, E.E., Clark, C.M., Collins, S.L., Fargione, J.E., Pennings, S.C., Suding, K.N., 2012. Incorporating clonal growth form clarifies the role of plant height in response to nitrogen addition. Oecologia 169, 1053–1062. https://doi.org/10.1007/s00442-012-2264-5.

Grman, E., Lau, J.A., Schoolmaster, D.R., Gross, K.L., 2010. Mechanisms contributing to stability in ecosystem function depend on the environmental context. Ecol. Lett. 13, 1400–1410. https://doi.org/10.1111/j.1461-0248.2010.01533.x.

Harpole, W.S., Ngai, J.T., Cleland, E.E., Seabloom, E.W., Borer, E.T., Bracken, M.E., 2011. Nutrient co-limitation of primary producer communities. Ecol. Lett. 14, 852–862. https://doi.org/10.1111/j.1461-0248.2011.01651.x.

Hautier, Y., Seabloom, E.W., Borer, E.T., et al., 2014. Eutrophication weakens stabilizing effects of diversity in natural grasslands. Nature 508, 521–525. https://doi.org/10.1038/nature13014.

Huang, M.J., Liu, X., Zhou, S.R., 2020. Asynchrony among species and functional groups and temporal stability under perturbations: patterns and consequences. J. Ecol. 108, 2038–2046. https://doi.org/10.1111/1365-2745.13418.

Isbell, F., Polley, H.W., Wilsey, B.J., 2009. Biodiversity, productivity and the temporal stability of productivity: patterns and processes. Ecol. Lett. 12, 443–451. https://doi.org/10.1111/j.1461-0248.2009.01299.x.

Lehman, C.L., Tilman, D., 2000. Biodiversity, stability, and productivity in competitive communities. Am. Nat. 156, 534–552. https://doi.org/10.1086/303402.

Lepš, J., 2014. Scale- and time-dependent effects of fertilization, mowing and dominant removal on a grassland community during a 15-year experiment. J. Appl. Ecol. 51, 978–987. https://doi.org/10.1111/1365-2664.12255.

Liang, T., Tong, Y.A., Xu, W., Wei, Y., Lin, W., Pang, Y., Liu, F., Liu, X.J., 2016. Atmospheric nitrogen deposition in the Loess area of China. Atmos. Pollut. Res. 7, 447–453. https://doi.org/10.1016/j.apr.2015.11.001.

Liu, H.Y., Mi, Z.R., Lin, L., et al., 2018. Shifting plant species composition in response to climate change stabilizes grassland primary production. Proc. Natl. Acad. Sci. U. S. A. 115, 4051–4056. https://doi.org/10.1073/pnas.1700299114.

Liu, J.S., Li, X.F., Ma, Q.H., Zhang, X., Chen, Y., Isbell, F., Wang, D.L., 2019a. Nitrogen addition reduced ecosystem stability regardless of its impacts on plant diversity. J. Ecol. 107, 2427–2435. https://doi.org/10.1111/1365-2745.13187.

Liu, Y.Y., Wang, Q., Zhang, Z.Y., Tong, L.J., Wang, Z.Q., Li, J.L., 2019b. Grassland dynamics in responses to climate variation and human activities in China from 2000 to 2013. Sci. Total Environ. 690, 27–39. https://doi.org/10.1016/j.scitotenv.2019.06.503.

Loreau, M., De Mazancourt, C., 2013. Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. Ecol. Lett. 16, 106–115. https://doi.org/10.1111/ele.12073.

Mackie, K.A., Zeiter, M., Bloor, J.M.G., Stampfli, A., 2019. Plant functional groups mediate drought resistance and recovery in a multisite grassland experiment. J. Ecol. 107, 937–949. https://doi.org/10.1111/1365-2745.13102.

Marquard, E., Weigelt, A., Temperton, V.M., Roscher, C., Schumacher, J., Buchmann, N., Fischer, M., Weisser, W.W., Schmid, B., 2009. Plant species richness and functional composition drive overyielding in a six-year grassland experiment. Ecology 90, 3290–3302. https://doi.org/10.1890/09-0069.1.

McCann, K.S., 2000. The diversity-stability debate. Nature 405, 228–233. https://doi.org/10.1038/35012234.

Melts, I., Lanno, K., Sammul, M., Uchida, K., Heinsoo, K., Kull, T., Laanisto, L., 2018. Fertilising semi-natural grasslands may cause long-term negative effects on both biodiversity and ecosystem stability. J. Appl. Ecol. 55, 1951–1955. https://doi.org/10.1111/1365-2664.13129.

Niu, D., Yuan, X.B., Cease, A.J., Wen, H.Y., Zhang, C.P., Fu, H., Elser, J.J., 2018. The impact of nitrogen enrichment on grassland ecosystem stability depends on nitrogen addition level. Sci. Total Environ. 618, 1529–1538. https://doi.org/10.1016/j.scitotenv.2017.09.318.

Rawnsley, R.P., Smith, A.P., Christie, K.M., Harrison, M.T., Eckard, R.J., 2019. Current and future direction of nitrogen fertilizer use in australian grazing systems. Crop Pasture Sci. 70, 1034–1043. https://doi.org/10.1071/CP18566.

Regus, J.U., Wendlandt, C.E., Bantay, R.M., Gano-Cohen, K.A., Gleason, N.J., Hollowell, A.C., O'Neill, M.R., Shahin, J.L., Sachs, J.L., 2017. Nitrogen deposition decreases the benefits of symbiosis in a native legume. Plant Soil 414, 159–170. https://doi.org/10.1007/s11104-016-3114-8.

Ren, F., Song, W., Chen, L., Mi, Z., Zhang, Z., Zhu, W., Zhou, H.K., Cao, G.M., He, J.S., 2016. Phosphorus does not alleviate the negative effect of nitrogen enrichment on legume performance in an alpine grassland. J. Plant Ecol. 9, 1–9. https://doi.org/10.1093/jpe/rtw089.

Sardans, J., Peñuelas, J., Estiarte, M., 2006. Warming and drought alter soil phosphatase activity and soil P availability in a Mediterranean shrubland. Plant Soil 289, 227–238. https://doi.org/10.1007/s11104-006-9131-2.

Sasaki, T., Lauenroth, W.K., 2011. Dominant species, rather than diversity, regulates temporal stability of plant communities. Oecologia 166, 761–768. https://doi.org/10.1007/s00442-011-1916-1.

Shen, X.J., Liu, B.H., Henderson, M., Wang, L., Wu, Z.F., Wu, H.T., Jiang, M., Lu, X.G., 2018. Asymmetric effects of daytime and nighttime warming on spring phenology in the temperate grasslands of China. Agric. For. Meteorol. 259, 240–249.

Shen, X.J., Liu, B.H., Xue, Z.S., Jiang, M., Lu, X.G., Zhang, Q., 2019. Spatiotemporal variation in vegetation spring phenology and its response to climate change in freshwater marshes of northeast China. Sci. Total Environ. 666, 1169–1177.

Smith, M.D., Knapp, A.K., 2003. Dominant species maintain ecosystem function with non-random species loss. Ecol. Lett. 6, 509–517. https://doi.org/10.1046/j.1461-0248.2003.00454.x.

Song, M.H., Zong, N., Jiang, J., Shi, P.L., Zhang, X.Z., Gao, J.Q., Zhou, H.K., Li, Y.K., Loreau, M., 2019. Nutrient-induced shifts of dominant species reduce ecosystem stability via increase in species synchrony and population variability. Sci. Total Environ. 692, 441–449. https://doi.org/10.1016/j.scitotenv.2019.07.266.

Suding, K.N., Collins, S.L., Gough, L., Clark, C.M., Cleland, E.E., Gross, K.L., Milchunas, D.G., Pennings, S., 2005. Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. Proc. Natl. Acad. Sci. U. S. A. 102, 4387–4392. https://doi.org/10.1073/pnas.0408648102.

Tilman, D., Reich, P.B., Knops, J.M., 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. Nature 441, 629–632. https://doi.org/10.1038/nature04742.

Tredennick, A.T., De Mazancourt, C., Loreau, M., Adler, P.B., 2017. Environmental responses, not species interactions, determine synchrony of dominant species in semi-arid grasslands. Ecology 98, 971–981. https://doi.org/10.1002/ecy.1757.

Wang, J.F., Knops, J.M.H., Brassi Mu, l C.E., 2017. Increased productivity in wet years drives a decline in ecosystem stability with nitrogen additions in arid grasslands. Ecology 98, 1779–1786. https://doi.org/10.1002/ecy.1878.

Xu, Z.W., Ren, H.Y., Li, M.H., Van Ruijven, J., Han, X.G., Wan, S.Q., Li, H., Yu, Q., Jiang, Y., Jiang, L., 2015. Environmental changes drive the temporal stability of semi-arid natural grasslands through altering species asynchrony. J. Ecol. 103, 1308–1316. https://doi.org/10.1111/1365-2745.12441.

Yang, Z., Van Ruijven, J., Du, G.Z., 2011. The effects of long-term fertilization on the temporal stability of alpine meadow communities. Plant Soil 345, 315–324. https://doi.org/10.1007/s11104-011-0784-0.

Zhang, J.T., 2005. Succession analysis of plant communities in abandoned croplands in the eastern Loess Plateau of China. J. Arid Environ. 63, 458–474. https://doi.org/10.1016/j.jaridenv.2005.03.027.

Zhang, J.T., Dong, Y.R., 2010. Factors affecting species diversity of plant communities and the restoration process in the loess area of China. Ecol. Eng. 36, 345–350. https://doi.org/10.1016/j.ecoleng.2009.04.001.

Zhou, M., Yang, Q., Zhang, H.J., Yao, X.D., Zeng, W.J., Wang, W., 2020. Plant community temporal stability in response to nitrogen addition among different degraded grasslands. Sci. Total Environ. 729, 138886. https://doi.org/10.1016/j.scitotenv.2020.138886.