Seasonal climate change drives the community intra-annual stability of a temperate grassland by altering species asynchrony in Inner Mongolia, China

Ze Zhang[1], Tiejun Bao[1], Yann Hautier[2], Jie Yang[1], Zhongling Liu[1], and hua qing[1]

[1]Inner Mongolia University
[2]Utrecht University Department of Biology

April 22, 2022

Abstract

Understanding the factors that regulate the functioning of our ecosystems in response to environmental changes can help to maintain the stable provisioning of ecosystem services to mankind. This is especially relevant given the increased variability of environmental conditions due to human activities. In particular, maintaining a stable production and plant biomass during the growing season (intra-annual stability) despite pervasive and directional changes in temperature and precipitation through time can help to secure food supply to wild animals, livestock, and humans. Here, we conducted a 29-year field observational study in a temperate grassland to explore how the intra-annual stability of primary productivity is influenced by biotic and abiotic variables through time. In particular, we analyzed the relationship of community biomass intra-annual stability with plant diversity and seasonal distribution patterns of temperature and precipitation. We found that lower accumulated precipitation between June and September during the 29-year investigated contributed to lower intra-annual community stability because of a decrease in compensatory mechanisms among species (species asynchrony). Additionally, higher precipitation in July contributed to higher intra-annual stability because higher species richness with higher precipitation led to higher average intra-annual stability of all species in the community (species stability). In contrast, we found no evidence that temperature influenced community intra-annual stability. Our results indicates that ongoing reduced seasonal precipitation leading to reduced intra-annual stability in the temperate grassland, which has important theoretical significance for us to take active measures to deal with climate change.

Seasonal climate change drives the community intra-annual stability of a temperate grassland by altering species asynchrony in Inner Mongolia, China Ze Zhang[1,2,3], Tiejun Bao[1,2,3], Yann Hautier[4], Jie Yang[1,2,3], Zhongling Liu[1,2,3], Hua Qing[1,2,3*]

[1]School of Ecology and Environment, Inner Mongolia University, Hohhot, China [2]Inner Mongolia University, Ministry of Education Key Laboratory of Ecology and Resource Use of the Mongolian Plateau, Hohhot, China

[3]Inner Mongolia University, Inner Mongolia Key Laboratory of Grassland Ecology, School of Ecology and Environment, Hohhot, China

[4]Ecology and Biodiversity Group, Department of Biology, Utrecht University, Padualaan 8, 3584 CH Utrecht, Netherlands

*Corresponding Author: Hua Qing, E-mail:*qinghua_ 515@126.com*

Abstract:

Understanding the factors that regulate the functioning of our ecosystems in response to environmental changes can help to maintain the stable provisioning of ecosystem services to mankind. This is especially

relevant given the increased variability of environmental conditions due to human activities. In particular, maintaining a stable production and plant biomass during the growing season (intra-annual stability) despite pervasive and directional changes in temperature and precipitation through time can help to secure food supply to wild animals, livestock, and humans. Here, we conducted a 29-year field observational study in a temperate grassland to explore how the intra-annual stability of primary productivity is influenced by biotic and abiotic variables through time. In particular, we analyzed the relationship of community biomass intra-annual stability with plant diversity and seasonal distribution patterns of temperature and precipitation. We found that lower accumulated precipitation between June and September during the 29-year investigated contributed to lower intra-annual community stability because of a decrease in compensatory mechanisms among species (species asynchrony). Additionally, higher precipitation in July contributed to higher intra-annual stability because higher species richness with higher precipitation led to higher average intra-annual stability of all species in the community (species stability). In contrast, we found no evidence that temperature influenced community intra-annual stability. Our results indicates that ongoing reduced seasonal precipitation leading to reduced intra-annual stability in the temperate grassland, which has important theoretical significance for us to take active measures to deal with climate change.

KEYWORDS: long-term observation, seasonal temperature and precipitation, species richness, plant functional group intra-annual stability, dominant species intra-annual stability

INTRODUCTION

Stability is one of the most fundamental and studied properties of an ecosystem (Hautier et al., 2014; Xu et al., 2015; Ma et al., 2017). In particular, the stability of ecosystem primary productivity through time gives us information about the ability of an ecosystem to provide reliable biomass despite environmental fluctuations (Pimm, 1984; Jiang et al., 2009; Craven et al., 2018). Grasslands are one of the most widely distributed ecosystems worldwide (Häyhä et al., 2014), providing not only key habitat for biodiversity but also other important ecosystem functions and services to humanity (Toombs et al. 2010; Isbell et al. 2009). Understanding the processes that influence the stability of grasslands' productivity is a pressing issue in ecology, especially given its vulnerability to anthropogenic and climatic changes (Ives and Carpenter, 2007).

Profound climate changes such as global warming and changes in precipitation patterns (Min et al., 2011; Orlowsky et al., 2012; IPCC, 2013; Putnam et al., 2017) are affecting the diversity and functioning of grassland ecosystems (Kardol et al., 2010). These changes in temperature and precipitation might be notably stronger at the seasonal rather than annual scale (Donat et al., 2016; Zhang et al., 2018), suggesting that the seasonal distribution patterns of temperature and precipitation may be the main driver of grassland stability. However, previous studies have primarily focused on the stability of primary productivity measured at one time during the growing season (usually at peak biomass production) each year over multiple years (inter-annual stability). Hence, whether the seasonal distribution patterns of temperature and precipitation affect the stability of productivity during the growing season (intra-annual stability) remains unknown. This is important given that intra-annual stability governs secure food supply to wild animals, livestock, and humans.

Previous studies in grasslands have shown that decreased precipitation in the early growing season results in a decline in aboveground net primary productivity (ANPP) by delaying plant phenology and limiting leaf expansion as well as reducing tillering, root range and microbial biomass carbon (De et al., 2012; Craine et al., 2012; Robinson et al., 2013; Yang et al., 2016; Chen et al., 2020). Additionally, different plant functional groups may respond differently to seasonal variability of temperature and precipitation based on differences in their physiology and life history (Huenneke et al., 2002; Munson et al., 2014; Mulhouse et al., 2017). For example, change in timing of maximum precipitation from summer to spring slightly favored C_3 plants over C_4 due to differences in C_3 and C_4 plant phenology in Colorado shortgrass prairie (Epstein et al., 1999). Algorithmic analysis based on seasonal water availability showed that the relative biomass of C_3/C_4 grasses is determined by the allocation of effective water and temperature between C_3grasses and C_4 grasses during the growing season (Winslow et al., 2003). Decreased precipitation in the early growing season mainly results in decreased ANPP of grass, whereas decreased precipitation in the late growing season primarily results in decreased ANPP of perennial forbs (Zhang et al., 2020). A study of semi-arid grassland in Inner Mongolia, China found that heavy rainfall in the late growing season reduced below-ground productivity and total biomass, while heavy rainfall in the middle of the growing season increased CO_2 exchanges (Li et al., 2019). These changes in productivity through time may translate into lower stability of productivity in response to climate change. However, to our knowledge, our study is the first to investigate whether the seasonal variability of precipitation and temperature affects grassland ecosystem community intra-annual stability (Grime et al., 2008).

Previous studies suggests that climate change affects community stability through multiple mechanisms (Ma et al., 2017; Huang et al., 2020). First, a higher number of plant species usually results in a higher stability of biomass production (Tilman et al. 2006, Hector et al. 2010). Thus, a reduction in plant diversity in response to climate change may result in the reduction of stability (Campbell et al., 2011; Hautier et al., 2014; Zhang et al., 2018). Second, community stability may be driven primarily by the stability of dominant species and/or functional groups, especially when dominant species and/or functional groups account for a considerable proportion of community biomass (Hillebrand et al., 2008; Huang et al., 2020; Ma et al., 2021). Third, asynchronous dynamics among species may contribute largely to stabilizing community properties against environmental changes (Loreau and de Mazancourt 2013; Valencia et al. 2020). Species asynchrony usually increases with increasing species richness (Hector et al. 2010, Hautier et al. 2014). As a result, changes in temperature and precipitation may affect community stability by changing asynchronous dynamics among species which directly or indirectly are induced via changes in species richness (Hallett et al., 2014; Sasaki et al., 2019, Hautier et al. 2020). To summarize, seasonal variations of temperature and precipitation may affect community stability by changing species richness (Klein et al., 2004; Wilby et al., 2004; Arnone et al., 2011), dominant species stability (Xu et al., 2015), functional group stability (Huang et al., 2020) and/or species asynchrony (Zhang et al., 2018; Zhou et al., 2019).

Here, we collected long-term monthly data on community ANPP, community composition, species richness and climate of a temperate grassland from 1981–2011 in northern China. The temperate grassland is distributed extensively throughout the arid-semiarid regions of Eurasia. Long-term monitoring can reveal the long-term dynamic of plant communities in response to climate change, and the relationship between community stability with long-term climate change (Bai et al., 2004; Li et al., 2015; Zhou et al., 2019). We related community intra-annual stability of ANPP with changes in seasonal distribution patterns of temperature and precipitation as well as with plant diversity and community composition. Specifically, we explored the following questions: (1) Does the seasonal distribution of temperature and precipitation affect the intra-annual stability of community productivity? (2) Which mechanisms determine community intra-annual stability in response to seasonal change in temperature and precipitation, species richness, species asynchrony, dominant species stability or the stability of any specific functional group?

MATERIALS AND METHODS

2.1 Study site

The investigation was conducted at Inner Mongolia Grassland Ecosystem Research Station (IMGERS, 116.8°E, 43.5°N, 1179 m a.s.l.), which is located in a temperate grassland in the Inner Mongolia, China (Fig. S1). The study site has a temperate continental climate. The long-term (1981-2011) mean annual temperature (MAT) is 0.78, the mean monthly minimum temperature is -21.3 in January, and the mean monthly maximum temperature is 19.3 in July. The annual precipitation (AP) is 330.1 mm, of which 85% falls in the growing season (from May to September) (Fig. S2a, 2b). Over the period 1981–2011, MAT showed an increasing trend with a rate of 0.06 $year^{-1}$, while AP fluctuated between 166.1 and 507 mm (Fig. S2a). The meteorological data were collected from the IMGERS weather station, located approximately 9 km from the study area. The study site is dominated by two perennial rhizome grasses,*Agropyron cristatum* and *Leymus chinensis* , and two perennial bunchgrass species, *Stipa grandis* and *Achnatherum sibiricum* , which were the most widely distributed species and accounted for 62.9% of the above-ground biomass. According to Chinese classification, the soil type is chestnut soil, with an average bulk density of 1.29 g cm^{-3} and a pH of 7.68 (Yuan et al., 2005).

2.2 Sample site design

The study site consists of a relatively flat and even area of 600 m by 300 m, fenced since 1979 to prevent grazing by large animals (Li et al., 2015). In 1981, the area was separated into ten replicate blocks (60 m x 300 m each). Community aboveground biomass was surveyed in the middle of every month throughout the growing season (from May to September) each year by clipping all plants within a 1 m x 1 m quadrat that was randomly located within each block, over 1981–2011. After harvesting, all living vascular plants were sorted into species, and oven-dried at 65 to a constant weight. Species richness was calculated as the total number of species present in ten blocks in a year. All species were classified into five plant functional groups primarily on the basis of life forms (Bai et al., 2004): perennial rhizome grass (PR), perennial bunchgrasses (PB), perennial forbs (PF), shrubs and semi-shrubs (SS), and annuals and biennials (AB). Functional group biomass was determined as the biomass sum of all the species in each functional group. Then, the proportion of aboveground biomass of each functional group to the community total aboveground biomass was calculated and used for the analysis of biomass complementarity among different functional groups (Bai et al., 2004). Data on productivity and diversity were collected monthly between May and September over a period of 29 years from 1981 to 2011, excluding the missing data from the years 1995–1996 (Ma et al., 2010).

2.3 Climate data

Plant phenology and aboveground community biomass in the study region have been found to be affected by growing season (May-September) and winter precipitation (January-April) as well as fluctuations in temperature and precipitation during the growing season (Bai et al., 2004; Li et al., 2015; Li et al., 2019; Zhang et al., 2020). So, the meteorological data for the present study were divided into the following meteorological variables. Hence, we used 60 meteorological variables: (1) monthly mean temperature ($\mathrm{T}_{\mathrm{month}}$) and monthly precipitation ($\mathrm{P}_{\mathrm{month}}$) for January to September (i.e., 9 + 9 variables), (2) mean temperature and precipitation for all possible two- to nine-month periods between January and September ($\mathrm{T}_{\text{month-month}}$, $\mathrm{P}_{\text{month-month}}$) (21 + 21 variables).

2.4 Statistical analysis

Community intra-annual biomass stability was calculated annually as μ/σ (Ma et al., 2017), where μ is the intra-annual (from May to September) temporal mean community biomass, and σ is its standard deviation. The dominant species (*Leymus chinensis* , *Agropyron cristatum* ,*Achnatherum sibiricum* and *Stipa grandis*) and functional group biomass stability were calculated annually using the same method. A higher value of community stability means a lower intra-annual variability of community biomass (Lehman et al., 2000).

Species asynchrony, which refers to the asynchronous response of species to environmental fluctuations (Loreau et al., 2008), was calculated as:

$$\varphi_x = 1 - \sigma^2 / \left(\sum_{l=1}^{T} \sigma_l \right)$$

where φ_x is intra-annual species synchrony,σ^2 and σ_l are the variance of intra-annual community biomass, and the standard deviation of biomass of species$l$ in a plot with T species. Intra-annual species asynchrony ranges between 0 and 1, higher values correspond to higher asynchronous dynamics between species within the community is, and vice versa.

Simple linear regression was used to analyze the inter-annual variation of mean temperature and accumulated precipitation for different distribution patterns, community biomass, relative biomass of functional group/dominant species, community species richness, species richness of functional group, and intra-annual biomass stability of community/dominant species/functional group, with the slope representing the rate of change. Stepwise regression and correlation analysis were used to analyze the relationships between different distribution patterns of mean temperature and accumulated precipitation with community biomass intra-annual stability, relative biomass intra-annual stability of functional groups, and relative biomass/biomass intra-annual stability of dominant species. Simple regression is used to analyze relationships between community biomass, functional groups biomass intra-annual stability, species richness, dominant species biomass intra-annual stability, species asynchrony and community biomass intra-annual stability.

To address mechanisms determining community stability in response to different seasonal change patterns in temperature and precipitation, structural equation modeling (SEM) was employed to estimate how climatic factors (mean temperature and accumulated precipitation in each combination month) and biological factors (community biomass, species richness, species asynchrony, functional groups intra-annual stability and dominant species intra-annual stability) contribute to the intra-annual stability of community biomass. Simple linear regression was used to check bivariate relationships between all the variables and filter the variables available to ensure that the linear model was appropriate (Table S1). By testing for covariance, we found that none of the climatic and biological factors showed significant covariance, so all the variables were put into SEM for analysis (Table S2). Based on regression weight estimation, the initial model was simplified and non-significant path and state variables were eliminated, and the final model contained only statistically significant paths that could not be rejected (Table S3). Accuracy of the model was confirmed using a Chi-squared test, the Akaike Information Criterion (AIC) and the root-mean-square errors of approximation (RMSEA). The model has a good fit when Chi-squared test $\chi^2 \geq 0$, $P > 0.05$, and RMSEA [?] 0.05. Structural equation model analysis was performed by AMOS 22.0, and the SPSS 19.0 software package was employed for all other tests.

RESULTS

3.1 Change in mean temperature and accumulated precipitation

During the period 1981-2011, the mean monthly temperature generally increased, especially in June (T_6), July (T_7) and September (T_9) (Fig. 1). Affected by the monthly mean temperature, the mean temperature of different distribution patterns also increased with time. This was particularly the case for the periods January-June ($T_{1\text{-}6}$), January-July ($T_{1\text{-}7}$), May-September ($T_{5\text{-}9}$) and June-September ($T_{6\text{-}9}$) (Fig. 1). In contrast, monthly accumulated precipitation did not show any trend though time, but fluctuated between years. The accumulated precipitation from January to September ($P_{1\text{-}9}$), June to September ($P_{6\text{-}9}$) showed a decreasing trend from 1981 to 2011 (Fig. 1).

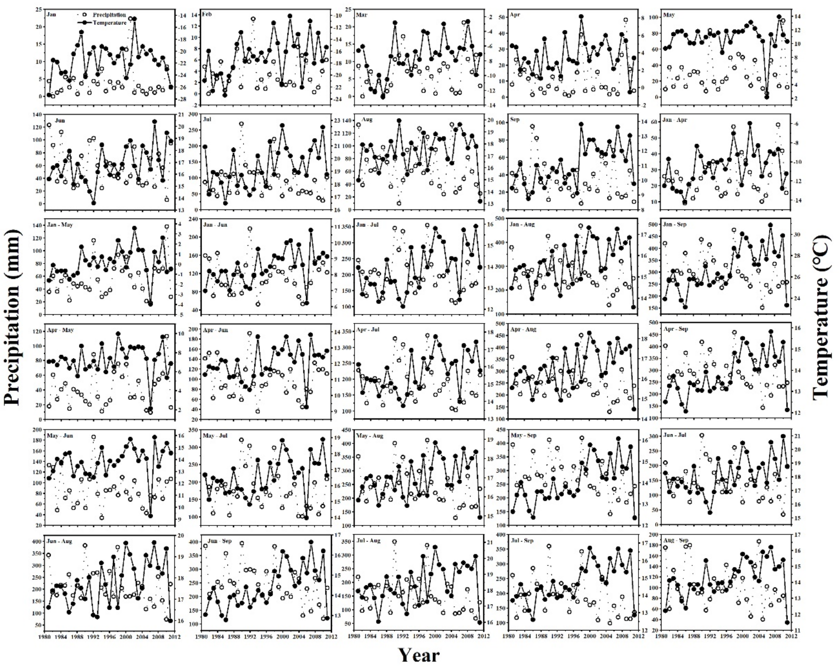

Fig. 1 Mean temperature and precipitation for each month and each two-nine month period between January and September, for the study area in 1981-2011.

3.2 Inter-annual variation of community biomass, functional groups and dominant species relative biomass and their relationship with climatic factors

The mean community biomass was 198.68 g m^{-2} with a range between 124.61 and 310.10 g m^{-2}, and showed no significant trend through time (Fig. 2).

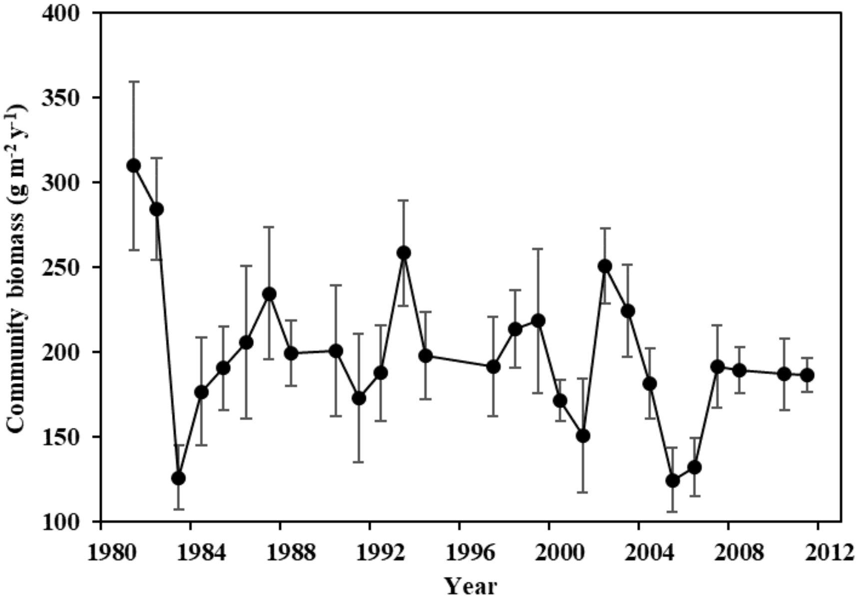

Fig. 2 Mean growing season community biomass at the study site between 1981 and 2011 (n = 10, with standard deviation)

The relative biomass of functional group PF decreased from 1981 to 2011 (Fig. 3c, $P = 0.015$; $R^2 = 0.20$). The relative biomass of the other functional groups fluctuated inter-annually, but did not show any trend through time (Fig. 3a-b, d-e). The relative biomass of the dominant species also fluctuated during the observation period, but there was no significant trend through time (Fig. 3f).

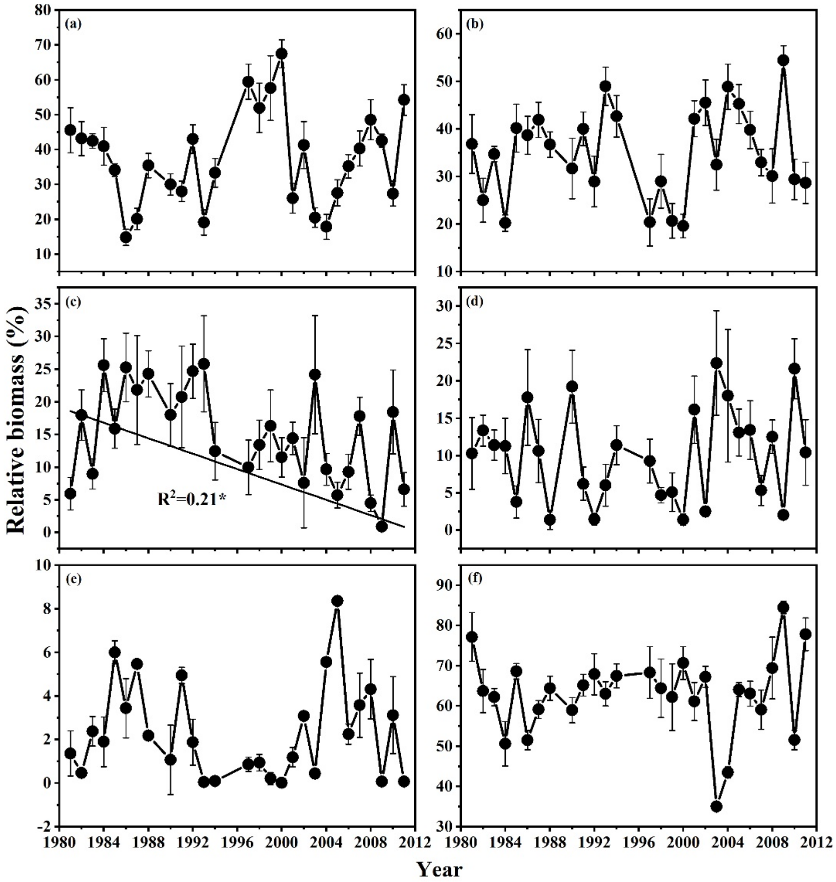

Fig. 3 Mean relative growing season biomass of the functional groups - (a) perennial rhizome grasses, (b) perennial bunchgrasses,(c) perennial forbs, (d) shrubs and semi-shrubs, (e) annuals and biennials - and (f) the dominant species at the study site between 1981 and 2011 (n = 10, with standard deviation). Asterisks indicate significant changes in relative biomass (*P¡0.05).

Having analyzed all possible mean temperature and accumulative precipitation distribution patterns, we found that the community biomass was positively correlated with P_{1-9} and P_{5-9}, but negatively correlated with T_{4-8} and T_8 (Table 1). The relative biomass of functional group PR was negatively correlated with P_9, but positively correlated with P_{1-6}, P_{4-6} and T_7. The relative biomass of functional group PB was negatively correlated with $P_{1-6}$and P_{5-6} in the early growing season. The relative biomass of PF was positively correlated with P_{6-9}, but negatively correlated with T_{6-8}. P_9 had positive and negative relationships with the relative biomass of functional group SS and dominant species, respectively. In addition, the relative biomass of dominant species was negatively correlated with P_{8-9} (Table 1).

Table 1 Climate factors retained in the stepwise regression of community biomass, functional groups relative biomass, species richness, community intra-annual stability, functional groups biomass intra-annual stability

	Biomass/ relative biomass	Biomass/ relative biomass	Biomass/ relative biomass		Species richness	Species richness	Species richness		Biomass intra-annual stability	Biomass intra-annual stability	Biomass intra-annual stability
	Factors	R	P		Factors	R	P		Factors	Factors	R

	Biomass/ relative biomass	Biomass/ relative biomass	Biomass/ relative biomass		Species richness	Species richness	Species richness		Biomass intra-annual stability	Biomass intra-annual stability	Biomass intra-annual stability	B i a s
Community	$P_{1\text{-}9}$	0.446	0.017		P_7	0.493	0.008		*Nsf*	*Nsf*	*Nsf*	*N*
	$P_{5\text{-}9}$	0.489	0.008		$P_{5\text{-}9}$	0.528	0.004					
	$T_{4\text{-}8}$	-0.417	0.027		$T_{6\text{-}8}$	-0.482	0.011					
	T_8	-0.460	0.014		T_8	-0.522	0.006					
PR	P_9	-0.504	0.006		T_7	0.405	0.040		*Nsf*	*Nsf*		
	$P_{1\text{-}6}$	0.416	0.028									
	$P_{4\text{-}6}$	0.456	0.015									
	T_7	0.418	0.033									
PB	$P_{1\text{-}6}$	-0.427	0.023		$P_{7\text{-}9}$	0.373	0.049		P_8	P_8	0.383	0
	$P_{5\text{-}6}$	-0.485	0.009						$P_{4\text{-}7}$	$P_{4\text{-}7}$	-0.394	0
									$P_{8\text{-}9}$	$P_{8\text{-}9}$	0.426	0
									T_8	T_8	-0.404	0
									$T_{5\text{-}9}$	$T_{5\text{-}9}$	-0.394	0
PF	$P_{6\text{-}9}$	0.401	0.035		P_7	0.459	0.014		P_7	P_7	0.478	0
	$T_{6\text{-}8}$	-0.472	0.015		$P_{1\text{-}9}$	0.461	0.013		$P_{6\text{-}9}$	$P_{6\text{-}9}$	0.504	0
					$P_{6\text{-}9}$	0.517	0.005		$P_{7\text{-}9}$		0.488	0
					T_8	-0.517	0.007					
					$T_{6\text{-}8}$	-0.446	0.022					
SS	P_9	0.432	0.022		*Nsf*				*Nsf*	*Nsf*		
AB	*Nsf*	*Nsf*	*Nsf*		P_5	0.430	0.022		$P_{1\text{-}7}$	$P_{1\text{-}7}$	0.409	0
					P_7	0.430	0.022		$P_{4\text{-}7}$	$P_{4\text{-}7}$	0.412	0
									$P_{5\text{-}7}$	$P_{5\text{-}7}$	0.446	0
									$P_{6\text{-}7}$	$P_{6\text{-}7}$	0.440	0
Dominant species	P_9	-0.499	0.017		*Nsf*	*Nsf*	*Nsf*	*Nsf*	*Nsf*	*Nsf*		
	$P_{8\text{-}9}$	-0.394	0.038									

Note: The table only shows the climate factors with significant relationship, and the blank element is meaningless.

Abbreviations: no significant factors (*Nsf*), perennial rhizome grass (PR), perennial bunchgrasses (PB), perennial forbs (PF), shrubs and semi-shrubs (SS), and annuals and biennials (AB), accumulated precipitation in March (P_3), accumulated precipitation in April (P_4), accumulated precipitation in May (P_5), accumulated precipitation in July (P_7), accumulated precipitation in September (P_9), accumulated precipitation from January to June ($P_{1\text{-}6}$), accumulated precipitation from January to September ($P_{1\text{-}9}$), accumulated precipitation from April to June ($P_{4\text{-}6}$), accumulated precipitation from May to June ($P_{5\text{-}6}$), accumulated precipitation from May to July ($P_{5\text{-}7}$), accumulated precipitation from May to September ($P_{5\text{-}9}$), accumulated precipitation from July to September ($P_{7\text{-}9}$), accumulated precipitation from August to September ($P_{8\text{-}9}$), mean temperature in March (T_3), mean temperature in July (T_7), mean temperature in August (T_8), mean temperature from April to August ($T_{4\text{-}8}$), mean temperature from May to September ($T_{5\text{-}9}$), mean temperature from June to August ($T_{6\text{-}8}$), mean temperature from August to September ($T_{8\text{-}9}$).

3.3 Species richness of communities and functional groups and their relationship with climate factors

Community species richness ranged from 18 to 44 (mean 34), and declined through time (Fig. 4a; $P = 0.001$; $R^2 = 0.34$). The average rate of loss of species richness was 4.5 species $m^{-2}decade^{-1}$ during the period of 1981–2011. Similar to community species richness, species richness of functional group PF decreased during the observation period (Fig. 4d; $P = 0.003$; $R^2 = 0.29$). In contrast, we found no trend of species richness of functional groups PR, PB, SS, and AB through time (Fig. 4b-c, e-f). The average loss rate of species richness of functional group PF was 3.7 species $m^{-2}decade^{-1}$, community species richness was largely related to the species richness of functional group PF (Fig. S3).

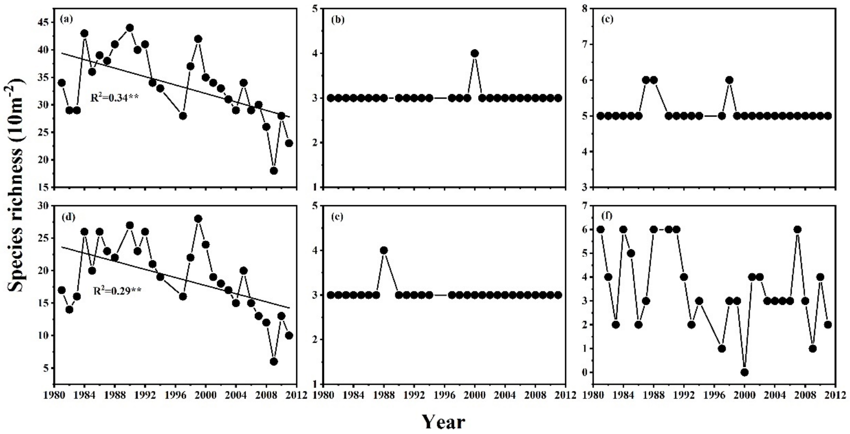

Fig. 4 Changes in species richness of (**a**) community, (**b**) PR, (**c**) PB, (**d**) PF, (**e**) SS, and (**f**) AB from 1981-2011. Asterisks indicate significant changes in species richness (*P¡0.05, **$P < 0.01$). Abbreviations: perennial rhizome grass (PR), perennial bunchgrasses (PB), perennial forbs (PF), shrubs and semi-shrubs (SS), and annuals and biennials (AB).

The dynamics of species richness were also related to climate factors (Table 1). The species richness of the community and functional group PF were positively correlated with P_7 and $P_{6\text{-}9}$, and negatively correlated with T_6 and $T_{6\text{-}7}$, respectively. In addition, a positive correlation was also observed between $P_{1\text{-}9}$ and species richness of functional group PF. The species richness of functional groups PR and PB were positively correlated with T_7 and $P_{7\text{-}9}$, respectively. Additionally, P_5 and P_7 were positively correlated with species richness of functional group AB. The species richness of functional group SS was not related to any of the climate factors investigated.

3.4 Intra-annual community biomass stability and its relationship with climatic and biotic factors

Intra-annual community stability of biomass (Fig. 5a; $P = 0.009$, $R^2 = 0.23$) and intra-annual species asynchrony (Fig. 5h; $P = 0.000$, $R^2 = 0.51$) tended to increase during the period 1981–2011. In contrast, intra-annual biomass stability of the functional group PF trended to decrease (Fig. 5d; $P = 0.001$; $R^2 = 0.35$) during the 29-year observation period. Intra-annual biomass stability of dominant species and functional groups PR, PB, SS and AB showed no obvious change (Fig. 5b-c, e-g).

Intra-annual biomass stability of functional group PB was positively correlated with P_8 and $P_{8\text{-}9}$, but negatively correlated with $P_{4\text{-}7}$, T_8 and $T_{5\text{-}9}$. Intra-annual biomass stability of functional group PF was positively correlated with P_7, $P_{6\text{-}9}$ and $P_{7\text{-}9}$. Intra-annual biomass stability of functional group AB was positively correlated with precipitation in the growing season, including $P_{1\text{-}7}$, $P_{4\text{-}7}$, $P_{5\text{-}7}$ and $P_{6\text{-}7}$. In contrast, we didn't find correlation between climate factors and intra-annual stability of community biomass, functional groups biomass of PR and SS, and dominant species biomass (Table 1).

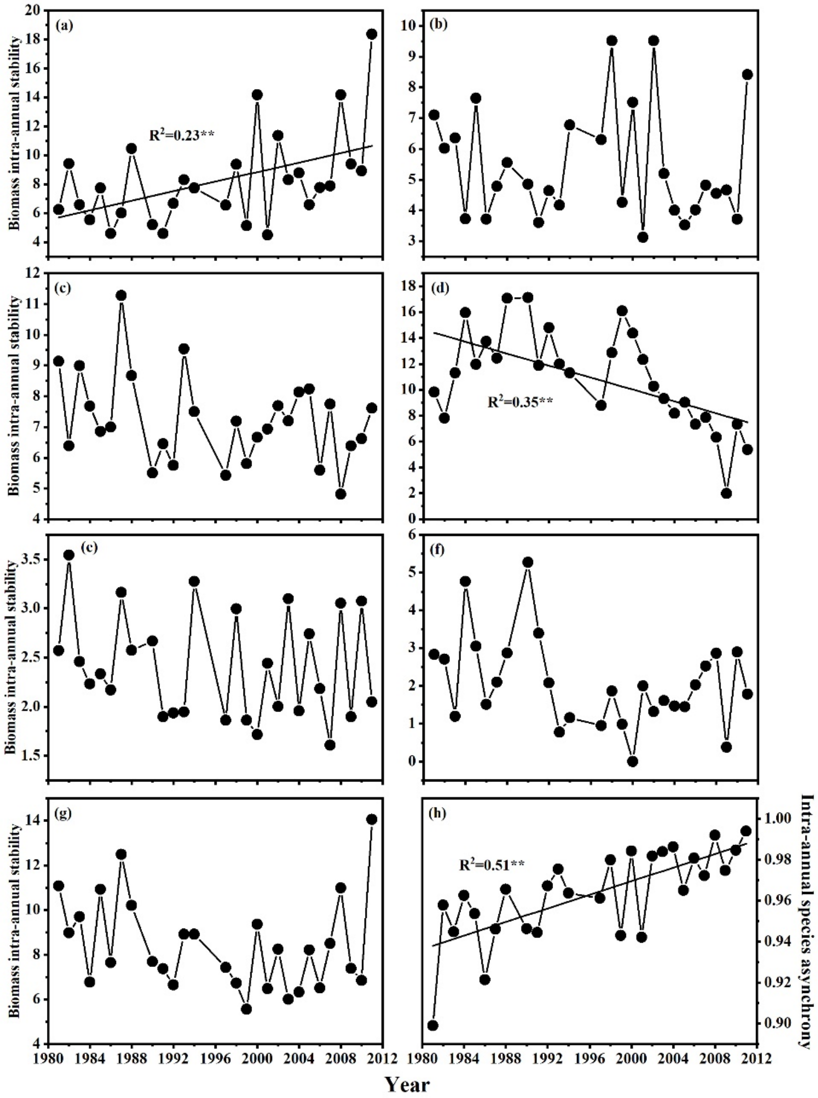

Fig. 5 Changes in intra-annual biomass stability of (**a**) community, (**b**) PR, (**c**) PB, (**d**)PF, (**e**) SS, (**f**) AB, (**g**) dominant species and (**h**) intra-annual species asynchrony from 1981–2011.

Asterisks indicates significant changes in biomass stability (*P < 0.05, **P < 0.01).

Abbreviations: perennial rhizome grass (PR), perennial bunchgrasses (PB), perennial forbs (PF), shrubs and semi-shrubs (SS), and annuals and biennials (AB).

Linear regressions showed that intra-annual community biomass stability was positively correlated with biomass stability of functional group PR ($R^2 = 0.29$, $P = 0.004$), dominant species stability ($R^2 = 0.28$, $P = 0.004$), and species asynchrony ($R^2 = 0.48$, $P < 0.001$; Fig. 6a, h and i), while it was negatively correlated with intra-annual biomass stability of functional group PF ($R^2 = -0.19$, $P = 0.024$; Fig. 6c). In addition, no significant relationships between community intra-annual biomass stability and intra-annual biomass stability of functional groups PB, SS and AB, species richness and community biomass were found (Fig. 6b, d-g).

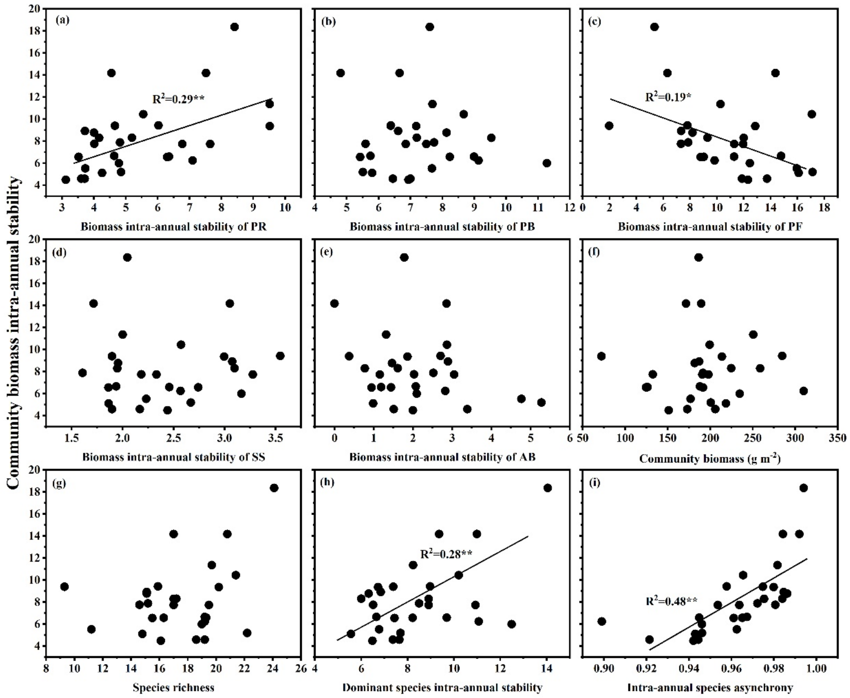

Fig. 6 The community biomass intra-annual temporal stability in relation to (a) biomass intra-annual stability of PR, (b) biomass intra-annual stability of PB, (c) biomass intra-annual stability of PF, (d) biomass intra-annual stability of SS, (e) biomass intra-annual stability of AB, (f) community biomass, (g) species richness, (h) dominant species intra-annual stability, and (i) intra-annual species asynchrony. Asterisks indicates significant changes in biomass stability (*$P < 0.05$, **$P < 0.01$). Abbreviations: perennial rhizome grass (PR), perennial bunchgrasses (PB), perennial forbs (PF), shrubs and semi-shrubs (SS), and annuals and biennials (AB).

3.5 Effects of climatic and biotic factors on the intra-annual stability of community biomass

Consistent with simple regression results, SEM revealed that intra-annual species asynchrony, functional group PR biomass intra-annual stability and dominant species intra-annual biomass stability contributed to community intra-annual biomass stability (Fig. 7). Decreased accumulated amount of precipitation between June and September ($P_{6\text{-}9}$) resulted in lower community intra-annual biomass stability by reducing species asynchrony. Consistent with the results of simple regressions (Table 1), precipitation in July (P_7) increased species richness. Intra-annual biomass stability of functional group PF, which was negatively correlated with community stability in simple regression model, was removed from SEM.

Hosted file

`image7.emf` available at https://authorea.com/users/478060/articles/566399-seasonal-climate-change-drives-the-community-intra-annual-stability-of-a-temperate-grassland-by-altering-species-asynchrony-in-inner-mongolia-china

Fig. 7 The structural equation model with the effects of meteorological and vegetation variables on the intra-annual stability of community biomass. The red arrow represents a negative pathway, the blue arrows show positive pathways, and the grey dashed arrows indicate nonsignificant pathways. Arrow width is proportional to the strength of the relationship. 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. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$; $\chi^2 = 17.05$, $P = 0.383$; root-mean-square error of approximation (RMSEA) = 0.05, $P = 0.453$; Akaike information criteria (AIC) =141.045.

DISCUSSION

Climate change, including increased temperature and variability in precipitation as well as changed distribution patterns of temperature or precipitation, have had an important impact on community composition and species dynamics of the Inner Mongolia temperate grassland over the past several decades (Ma et al., 2010; Zhang et al., 2020), which may affect the stability of community biomass. In our study, based on 29 years of field observation data, we found that the functional group perennial rhizome grass biomass intra-annual stability, dominant species intra-annual biomass stability and intra-annual species asynchrony contributed to stabilize community intra-annual biomass. In addition, decreased accumulated precipitation from June to September ($P_{6\text{-}9}$) decreased community intra-annual stability by reducing intra-annual species asynchrony.

Our findings are consistent with previous studies that have reported that temperate grasslands in Inner Mongolia have experienced warming and drying over the past few decades (Ma et al., 2010; Li et al., 2015). Notably, we found that seasonal temperature and precipitation changes were more pronounced than inter-annual changes. However, we found no relationships between seasonal warming and community biomass intra-annual stability, which is consistent with results of climate control experiments on temperate grassland and alpine meadow (Ma et al., 2017; Yang et al., 2017). In contrast, we found evidence that decreased seasonal precipitation affects the stability of community biomass. This is consistent with previous studies showing that seasonal precipitation affects the community structure and productivity of grassland ecosystem (Bai et al., 2004; Guo et al., 2012; Robinson et al., 2013; Chen et al., 2020; Zhang et al., 2020). Consistent with previous reports, our results indicate that seasonal precipitation reduced community stability by reducing species asynchrony (Xu et al., 2015; Ma et al., 2017).

Several field observations and theoretical models have suggested that community stability may increase with increasing species richness (Jiang et al., 2009; Gross et al., 2014; Mougi et al., 2012). Our results are consistent with the positive diversity-stability relationship often reported in experimental studies. In the present study, although linear regression did not show a relationship between species richness and community intra-annual stability (Fig. 6g), SEM showed that species richness indirectly contributed to community intra-annual stability through a positive relationship between dominant species stability (Fig. 7). None of the diversity-dependent stabilizing mechanisms, including overyielding (Fig. S4a), diversity-dependent species asynchrony (Fig. S4b) and the portfolio effect (Fig. S4c), operated. In experiments manipulating species diversity, overyielding (i.e., positive diversity-productivity relationships) often contributes to stabilize community biomass through time (Cardinale et al., 2006; Gross et al., 2014). But productivity does not necessarily increase with diversity in natural communities, especially in long-term observations like ours (Adler et al., 2011; Grace et al., 2007). SEM results showed that precipitation in July (P_7) could promote community species richness, which is consistent with previous studies (Adler and Levine 2007; Cleland et al., 2013). Increased precipitation benefits shallow-rooted species that are disadvantaged in dry soils, thereby promoting species richness, especially in July when plant growth was strongest (Yang et al., 2011a). The species richness of functional groups PB, PF and AB was also positively correlated with precipitation in July (Table 1). In addition, seasonal warming (T_8 and $T_{6\text{-}8}$) negatively affected the species richness of community and functional group PF (Table 1). We found a decreasing trend in community species richness during the 30-year fenced period (Fig. 4a), which may be attributed to the moderate disturbance hypothesis (i.e., under fenced conditions, competition between species for resources increased, and rare species richness decreased, leading to a decrease in community species richness) (Herrero and Oesterheld 2018; Wang et al., 2020a). In addition, the seasonal decrease in precipitation may be another reason for the decrease of community species richness (Fig. 1) (Robertson et al., 2010; Adler and Levine 2007).

Ecosystems are largely controlled by the characteristics of the dominant species, i.e., the mass ratio hypothesis (Grime, 1998), which may even constrain the effect of species diversity on biomass stability (Polley et al., 2007). Many experimental studies have shown that when dominant species regulate community stability, the diversity-stability relationship is weak or insignificant (Grime 1998; Grman et al., 2010; Wang et al., 2020b). In our study, we found support that dominant species stability largely contributes to community intra-annual stability (Sasaki et al., 2011; Wilsey et al., 2014; Xu et al., 2015). It is noteworthy that seasonal climate warming and precipitation changes did not affect the dominant species stability (Table 1). In our study area, the dominant species, two perennial rhizome grasses, *Leymus chinensis* and *Agropyron cristatum* , and two perennial bunchgrass,*Stipa grandis* and *Achnatherum sibiricum* , account for 62.9% of community above-ground biomass. Compared with the functional groups SS and AB with lower relative abundance, the dominant species had greater biomass stability (Fig. 5). These species are relatively insensitive to environmental changes, which may be related to their ability to obtain nutrients through a well-developed root system, and they have higher plant height and larger specific leaf area, which allows them to get more light (Yang et al., 2011b; Zhang et al., 2020). Although functional group PR and functional group PB plants have greater access to resources, their seasonality in resource use is also evident (Table 1). The relative biomass of functional group PR was positively correlated with cumulative precipitation through June, while the opposite was true for functional group PB. This may be related to their life history, with functional group PR tending to emerge earlier, having a larger leaf area and better access to water in the early part of the growing season (Yang et al., 2011b; Zhang et al., 2018; Zhang et al., 2020).

Species asynchrony is a common feature of ecological communities (Gonzalez et al., 2009; Bluthgen et al., 2016), and could be dependent on asynchronous species responses to environmental fluctuations (Ives et al., 2007; Loreau et al., 2008). The biomass of each species changes through time, but the total biomass of the community is retained due to the increase in biomass of some species compensating for the decrease in biomass of other species (Ma et al., 2010; Douda et al., 2018). In our study, the community biomass did not significantly vary over the 29 years investigated (Fig. 2), and species asynchrony determined the community biomass stability to a great extent (Fig. 7). SEM analysis showed that precipitation from June to September ($P_{6\text{-}9}$) weakened species asynchrony (Fig. 7), which is different from previous studies (Xu et al., 2015; Ma et al., 2017; Chi et al., 2019). This may be related to the grassland's seasonal water use strategy. Water is the main limiting factor of productivity in arid and semi-arid grassland (Sala et al. 2012; Yiruhan et al., 2014), it creates intense competition among species for water sources (Yang et al., 2011b). The non-dominant and rare species in this study area are mainly perennial hybrid grasses and biennial plants, which mainly take advantage of precipitation in the late growing season (July to September) (Table 1) (Bai et al., 2004; Li et al., 2015; Zhang et al., 2020). Adequate moisture may reduce competition among species for water sources, with both deep-rooted and shallow-rooted species preferring to utilize shallow soil water, especially in the late growing season, when moisture promotes the productivity of flowering forbs and shallow-rooted annuals, such as,*Iris tenuifolia* , *Thalictrum petaloideum* , *Allium tenuissimum* , *Chenopodium aristatum* , and *Artemisia sieversiana* (Loreau and de Mazancourt 2013; Zhang et al., 2020). When there is more water in the growing season from June to September, competition for water between species decreases and plants tend to grow in sync, resulting in a decrease in asynchrony between species (Zhang et al., 2018; Wang et al., 2020b), as shown by our SEM results (Fig. 7). In addition, there was a decreasing trend in accumulated precipitation from June to September ($P_{6\text{-}9}$) during the observation period 1981-2011 (Fig. 1), which may have contributed to the negative relationship between the precipitation pattern and species asynchrony. Seasonal distribution of precipitation may directly provide new evidence for precipitation and asynchronous dynamics.

An important finding of our study is that functional group biomass stability is also one of the important contributors to community intra-annual stability. In simple linear regression, functional group PR biomass stability was significantly positively correlated with community stability (Fig. 6a), while functional group PF biomass stability was significantly negatively correlated with community stability (Fig. 6c). However, in SEM, the negative effect of PF was excluded and only the positive effect of PR was retained (Fig. 7). This may be due to the fact that PR had the highest biomass in the community (34.5%), while PF only accounted for 14.9% of the community biomass. In addition, there were two PR species among the four dominant species. PR was the dominant functional group in this study area, which stabilized community productivity to a large extent. In contrast, functional group PF was mainly composed of secondary dominant or rare species, which contributed relatively little to the stability of community biomass, so it could not be considered as one of the main factors affecting the stability of community biomass.

Based on a long-term study spanning 29 years of observation, our study provides new empirical evidence for ongoing reduced seasonal precipitation leading to reduced biomass intra-annual stability in the temperate grassland in North China, which has important theoretical significance for us to take active measures to deal with climate change.

ACKNOWLEDGEMENTS

This study was financially supported by the Major Science and Technology Projects of Inner Mongolia Autonomous Region (2020ZD0009, 2019ZD002), the Applied Technology Research and Development Projects of Inner Mongolia Autonomous Region (2019GG015), and the Natural Science Foundation of Inner Mongolia Autonomous Region (2019BS03008).

AUTHORS CONTRIBUTIONS

Ze Zhang: Conceptualization (lead); Formal analysis (lead); Methodology (equal); Writing – original draft (lead); Writing – review & editing (equal). **Tiejun Bao:** Conceptualization (equal); Investigation (equal); Resources (lead). **Yann Hautier:**Conceptualization (equal); Methodology (lead); Writing – review & editing (equal). **Jie yang:** Funding acquisition (lead); Resources (equal); Supervision (lead). **Zhongling Liu:**Investigation (lead); Resources (equal); Supervision (equal).**Hua Qing:** Conceptualization (equal); Data curation (lead); Formal analysis (equal); Methodology (equal); Writing - review & editing (lead).

COMPETING INTERESTS

The authors declare no competing interests.

DATA AVAILAVILITY STATEMENT

Data available from the Dryad Digital Repository: Dryad, Dataset, https://doi.org/10.5061/dryad.hmgqnk9k9

REFERENCES

Adler, P. B. and Levine, J. M. (2007). Contrasting relationships between precipitation and species richness in space and time. *Oikos* ,*116* , 221–232.

Adler, P. B. (2011). Productivity is a poor predictor of plant species richness. *Science* , *333* , 1750–1753.

Arnone III, J. A. et al. (2011). Arnone III, J. A., Jasoni, R. L., Lucchesi, A. J., Larsen, J. D., Leger, E. A., Sherry, R. A., … & Verburg, P. S. (2011). A climatically extreme year has large impacts on C4 species in tallgrass prairie ecosystems but only minor effects on species richness and other plant functional groups. *Journal of Ecology* , 99(3), 678-688.

Bai, Y., Han, X., Wu, J., Chen, Z., & Li, L. (2004). Ecosystem stability and compensatory effects in the Inner Mongolia grassland.*Nature* , *431* (7005), 181-184.

Blüthgen, N., Simons, N. K., Jung, K., Prati, D., Renner, S. C., Boch, S., … & Gossner, M. M. (2016). Land use imperils plant and animal community stability through changes in asynchrony rather than diversity.*Nature Communications* , *7* (1), 1-7.

Campbell, V., Murphy, G., & Romanuk, T. N. (2011). Experimental design and the outcome and interpretation of diversity–stability relations.*Oikos* , *120* (3), 399-408.

Cardinale, B. J., Srivastava, D. S., Emmett Duffy, J., Wright, J. P., Downing, A. L., Sankaran, M., & Jouseau, C. (2006). Effects of biodiversity on the functioning of trophic groups and ecosystems.*Nature* , *443* (7114), 989-992.

Chen, H., Zhao, X., Lin, Q., Li, G., & Kong, W. (2020). Spring watering interactively improves aboveground net primary productivity and soil microbial biomass in a semi-arid grassland of China. *Catena* ,*189* , 104478.

Chi, Y., Xu, Z., Zhou, L., Yang, Q., Zheng, S., & Li, S. P. (2019). Differential roles of species richness versus species asynchrony in regulating community stability along a precipitation gradient.*Ecology and evolution* , *9* (24), 14244-14252.

Cleland, E. E., Collins, S. L., Dickson, T. L., Farrer, E. C., Gross, K. L., Gherardi, L. A., … & Suding, K. N. (2013). Sensitivity of grassland plant community composition to spatial vs. temporal variation in precipitation. *Ecology* , *94* (8), 1687-1696.

Craine, J. M., Nippert, J. B., Elmore, A. J., Skibbe, A. M., Hutchinson, S. L., & Brunsell, N. A. (2012). Timing of climate variability and grassland productivity. *Proceedings of the National Academy of Sciences* , *109* (9), 3401-3405.

Craven, D., Eisenhauer, N., Pearse, W. D., Hautier, Y., Isbell, F., Roscher, C., … & Manning, P. (2018). Multiple facets of biodiversity drive the diversity–stability relationship. *Nature ecology & evolution* , *2* (10), 1579-1587.

De Micco, V., & Aronne, G. (2012). Morpho-anatomical traits for plant adaptation to drought. In *Plant responses to drought stress* (pp. 37-61). Springer, Berlin, Heidelberg.

Donat, M. G., Lowry, A. L., Alexander, L. V., O'Gorman, P. A., & Maher, N. (2016). More extreme precipitation in the world's dry and wet regions. *Nature Climate Change* , *6* (5), 508-513.

Douda, J., Doudová, J., Hulík, J., Havrdová, A., & Boublík, K. (2018). Reduced competition enhances community temporal stability under conditions of increasing environmental stress. *Ecology* ,*99* (10), 2207-2216.

Epstein, H. E. 1999. Response of the shortgrass steppe to changes in rainfall seasonality. *Ecosystems* , *2* : 139-50.

Gonzalez, A., & Loreau, M. (2009). The causes and consequences of compensatory dynamics in ecological communities. Annu. Rev. Ecol. Evol. Syst., 40, 393-414.

Grace, J. B. 2007. Does species diversity limit productivity in natural grassland communities? *Ecology. Letters* , *10* , 680–689.

Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* . *86* (6), 902-910.

Grime, J. P., Fridley, J. D., Askew, A. P., Thompson, K., Hodgson, J. G., & Bennett, C. R. (2008). Long-term resistance to simulated climate change in an infertile grassland. *Proceedings of the National Academy of Sciences* , *105* (29), 10028-10032.

Grman, E., Lau, J. A., Schoolmaster Jr, D. R., & Gross, K. L. (2010). Mechanisms contributing to stability in ecosystem function depend on the environmental context. *Ecology letters* , *13* (11), 1400-1410.

Gross, K., Cardinale, B. J., Fox, J. W., Gonzalez, A., Loreau, M., Wayne Polley, H., … & van Ruijven, J. (2014). Species richness and the temporal stability of biomass production: a new analysis of recent biodiversity experiments. *The American Naturalis* t, *183* (1), 1-12.

Hallett, L. M., Hsu, J. S., Cleland, E. E., Collins, S. L., Dickson, T. L., Farrer, E. C., … & Suding, K. N. (2014). Biotic mechanisms of community stability shift along a precipitation gradient.*Ecology* , *95* (6), 1693-1700.

Hautier, Y., Seabloom, E. W., Borer, E. T., Adler, P. B., Harpole, W. S., Hillebrand, H., … & Hector, A. (2014). Eutrophication weakens stabilizing effects of diversity in natural grasslands. *Nature* ,*508* (7497), 521-525.

Hautier, Y., Zhang, P., Loreau, M., Wilcox, K. R., Seabloom, E. W., Borer, E. T., … & Wang, S. (2020). General destabilizing effects of eutrophication on grassland productivity at multiple spatial scales.*Nature communications* , *11* (1), 1-9.

Häyhä, T., & Franzese, P. P. (2014). Ecosystem services assessment: A review under an ecological-economic and systems perspective.*Ecological Modelling* , *289* , 124-132.

Herrero-Jauregui, C., & Oesterheld, M. (2018). Effects of grazing intensity on plant richness and diversity: A meta-analysis.*Oikos* , *127* (6), 757-766.

Hillebrand, H., Bennett, D. M., & Cadotte, M. W. (2008). Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology* , *89* (6), 1510-1520.

Hoover, D. L., Knapp, A. K., & Smith, M. D. (2014). Resistance and resilience of a grassland ecosystem to climate extremes. *Ecology* ,*95* (9), 2646-2656.

Huang, M., Liu, X., & Zhou, S. (2020). Asynchrony among species and functional groups and temporal stability under perturbations: Patterns and consequences. *Journal of Ecology* , *108* (5), 2038-2046.

Huenneke, L. F., Anderson, J. P., Remmenga, M., & Schlesinger, W. H. (2002). Desertification alters patterns of aboveground net primary production in Chihuahuan ecosystems. *Global Change Biology* ,*8* (3), 247-264.

IPCC, 2013. Climate Change 2013: the Physical Science Basis. (Contribution of Working Group I to the Fifth Assessment. Report of the Intergovernmental Panel on Climate Change). Cambridge University Press, Cambridge, pp. 1535.

Isbell, F. I., Polley, H. W., & Wilsey, B. J. (2009). Biodiversity, productivity and the temporal stability of productivity: patterns and processes. *Ecology letters* , *12* (5), 443-451.

Ives, A. R., and Carpenter, S. R. 2007. Stability and diversity of ecosystems. *Science* . *317* (5834), 58-62.

Jiang, L., Wan, S., & Li, L. (2009). Species diversity and productivity: why do results of diversity-manipulation experiments differ from natural patterns? *Journal of Ecology* , 603-608.

Kardol, P., Campany, C. E., Souza, L., Norby, R. J., Weltzin, J. F., & Classen, A. T. (2010). Climate change effects on plant biomass alter dominance patterns and community evenness in an experimental old-field ecosystem. *Global Change Biology* , *16* (10), 2676-2687.

Klein, J. A., Harte, J., & Zhao, X. Q. (2004). Experimental warming causes large and rapid species loss, dampened by simulated grazing, on the Tibetan Plateau. *Ecology Letters* , *7* (12), 1170-1179.

Lehman, C. L., & Tilman, D. (2000). Biodiversity, stability, and productivity in competitive communities. *The American Naturalist* ,*156* (5), 534-552.

Li, L., Zheng, Z., Biederman, J. A., Xu, C., Xu, Z., Che, R., … & Hao, Y. (2019). Ecological responses to heavy rainfall depend on seasonal timing and multi-year recurrence. *New Phytologist* ,*223* (2), 647-660.

Li, Z., Ma, W., Liang, C., Liu, Z., Wang, W., & Wang, L. (2015). Long-term vegetation dynamics driven by climatic variations in the Inner Mongolia grassland: findings from 30-year monitoring. *Landscape Ecology* , *30* (9), 1701-1711.

Loreau, M., & de Mazancourt, C. (2008). Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. *The American Naturalist* , *172* (2), E48-E66.

Loreau, M., & De Mazancourt, C. (2013). Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. *Ecology letters* ,*16* , 106-115.

Ma, W., Liu, Z., Wang, Z., Wang, W., Liang, C., Tang, Y., ... & Fang, J. (2010). Climate change alters interannual variation of grassland aboveground productivity: evidence from a 22-year measurement series in the Inner Mongolian grassland. *Journal of plant research* ,*123* (4), 509-517.

Ma, Z., Liu, H., Mi, Z., Zhang, Z., Wang, Y., Xu, W., ... & He, J. S. (2017). Climate warming reduces the temporal stability of plant community biomass production. *Nature Communications* , *8* (1), 1-7.

Ma, Z., Zeng, Y., Wu, J., Zhou, Q., & Hou, F. (2022). Plant litter influences the temporal stability of plant community biomass in an alpine meadow by altering the stability and asynchrony of plant functional groups. *Functional Ecology* , *36* (1), 148-158.

Min, S. K., Zhang, X., Zwiers, F. W., & Hegerl, G. C. (2011). Human contribution to more-intense precipitation extremes. *Nature* ,*470* (7334), 378-381.

Mougi, A., and Kondoh, M. (2012). Diversity of interaction types and ecological community stability.*Science* , *337* (6092), 349-351.

Mulhouse, J. M., Hallett, L. M., & Collins, S. L. (2017). The influence of seasonal precipitation and grass competition on 20 years of forb dynamics in northern Chihuahuan Desert grassland. *Journal of Vegetation Science* , *28* (2), 250-259.

M Munson, S. M., Belnap, J., Webb, R. H., Hubbdrd, J. A., Reiser, M. H., & Gallo, K. (2014, January). Climate change and plant community composition in national parks of the Southwestern US: Forecasting regional, long-term effects to meet management needs. In *The George Wright Forum* (Vol. 31, No. 2, pp. 137-148). George Wright Society.

Orlowsky, B., & Seneviratne, S. I. (2012). Global changes in extreme events: regional and seasonal dimension. *Climatic Change* ,*110* (3), 669-696.

Pimm, S. L. (1984). The complexity and stability of ecosystems.*Nature* , *307* (5949), 321-326.

Putnam, A. E., & Broecker, W. S. (2017). Human-induced changes in the distribution of rainfall. *Science Advances* , *3* (5), e1600871.

Robertson, T. R., Zak, J. C., & Tissue, D. T. (2010). Precipitation magnitude and timing differentially affect species richness and plant density in the sotol grassland of the Chihuahuan Desert.*Oecologia* , *162* (1), 185-197.

Robinson, T. M., La Pierre, K. J., Vadeboncoeur, M. A., Byrne, K. M., Thomey, M. L., & Colby, S. E. (2013). Seasonal, not annual precipitation drives community productivity across ecosystems.*Oikos* , *122* (5), 727-738.

Sala, O. E., Gherardi, L. A., Reichmann, L., Jobbagy, E., & Peters, D. (2012). Legacies of precipitation fluctuations on primary production: theory and data synthesis. *Philosophical Transactions of the Royal Society B: Biological Sciences* , *367* (1606), 3135-3144.

Sasaki, T., & Lauenroth, W. K. (2011). Dominant species, rather than diversity, regulates temporal stability of plant communities.*Oecologia* , *166* (3), 761-768.

Sasaki, T., Lu, X., Hirota, M., & Bai, Y. (2019). Species asynchrony and response diversity determine multifunctional stability of natural grasslands. *Journal of Ecology* , *107* (4), 1862-1875.

Shiyomi, M., Akiyama, T., Wang, S., Yamamura, Y., & Hori, Y. (2014). Long-term prediction of grassland production for five temporal patterns of precipitation during the growing season of plants based on a system model in Xilingol, Inner Mongolia, China. *Ecological modelling* ,*291* , 183-192.

Valencia, E., de Bello, F., Galland, T., Adler, P. B., Lepš, J., Anna, E., … & Götzenberger, L. (2020). Synchrony matters more than species richness in plant community stability at a global scale.*Proceedings of the National Academy of Sciences* , *117* (39), 24345-24351.

Wang, X., Li, F. Y., Tang, K., Wang, Y., Suri, G., Bai, Z., & Baoyin, T. (2020a). Land use alters relationships of grassland productivity with plant and arthropod diversity in Inner Mongolian grassland.*Ecological Applications* , *30* (3), e02052.

Wang, Y., Niu, X., Zhao, L., Liang, C., Miao, B., Zhang, Q., … & Ma, W. (2020b). Biotic stability mechanisms in Inner Mongolian grassland.*Proceedings of the Royal Society B* , *287* (1928), 20200675.

Wayne Polley, H. et al. 2007. Dominant species constrain effects of species diversity on temporal variability in biomass production of tallgrass prairie. – Oikos. 116(12), 2044-2052.

Wayne Polley, H., Wilsey, B. J., & Derner, J. D. (2007). Dominant species constrain effects of species diversity on temporal variability in biomass production of tallgrass prairie. *Oikos* ,*116* (12), 2044-2052.

Wilsey, B. J., Daneshgar, P. P., Hofmockel, K., & Polley, H. W. (2014). Invaded grassland communities have altered stability-maintenance mechanisms but equal stability compared to native communities.*Ecology Letters* , *17* (1), 92-100.

Winslow, J. C., Hunt Jr, E. R., & Piper, S. C. (2003). The influence of seasonal water availability on global C_3 versus C_4 grassland biomass and its implications for climate change research. *Ecological modelling* , *163* (1-2), 153-173.

Xu, Z., Ren, H., Li, M. H., van Ruijven, J., Han, X., Wan, S., … & Jiang, L. (2015). Environmental changes drive the temporal stability of semi-arid natural grasslands through altering species asynchrony.*Journal of Ecology* , *103* (5), 1308-1316.

Yang, H., Li, Y., Wu, M., Zhang, Z. H. E., Li, L., & Wan, S. (2011a). Plant community responses to nitrogen addition and increased precipitation: the importance of water availability and species traits.*Global Change Biology* , *17* (9), 2936-2944.

Yang, H., Auerswald, K., Bai, Y., & Han, X. (2011). Complementarity in water sources among dominant species in typical steppe ecosystems of Inner Mongolia, China. *Plant and Soil* , *340* (1), 303-313.

Yang, Z., Jiang, L., Su, F., Zhang, Q., Xia, J., & Wan, S. (2016). Nighttime warming enhances drought resistance of plant communities in a temperate steppe. *Scientific Reports* , *6* (1), 1-9.

Yang, Z., Zhang, Q., Su, F., Zhang, C., Pu, Z., Xia, J., … & Jiang, L. (2017). Daytime warming lowers community temporal stability by reducing the abundance of dominant, stable species. *Global Change Biology* , *23* (1), 154-163.

Yuan, Z. Y., Li, L. H., Han, X. G., Huang, J. H., Jiang, G. M., & Wan, S. Q. (2005). Soil characteristics and nitrogen resorption in*Stipa krylovii* native to northern China. *Plant and Soil* ,*273* (1), 257-268.

Zhang, J., Miao, Y., Zhang, T., Wei, Y., Qiao, X., Miao, R., … & Yang, Z. (2020). Drought timing and primary productivity in a semiarid grassland. *Land Degradation & Development* , *31* (15), 2185-2195.

Zhang, Y., Feng, J., Isbell, F., Lu, X., & Han, X. (2015). Productivity depends more on the rate than the frequency of N addition in a temperate grassland. *Scientific Reports* , *5* (1), 1-12.

Zhang, Y., Loreau, M., He, N., Wang, J., Pan, Q., Bai, Y., & Han, X. (2018). Climate variability decreases species richness and community stability in a temperate grassland. *Oecologia* , *188* (1), 183-192.

Zhou, B., Li, S., Li, F., Dong, S., Ma, F., Zhu, S., … & Stufkens, P. (2019). Plant functional groups asynchrony keep the community biomass stability along with the climate change-a 20-year experimental observation of alpine meadow in eastern Qinghai-Tibet Plateau.*Agriculture, Ecosystems & Environment* , *282* , 49-57.