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COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Climate variability decreases species richness and community stability in a temperate grassland

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Abstract

Climate change involves modifications in both the mean and the variability of temperature and precipitation. According to global warming projections, both the magnitude and the frequency of extreme weather events are increasing, thereby increasing climate variability. The previous studies have reported that climate warming tends to decrease biodiversity and the temporal stability of community primary productivity (i.e., community stability), but the effects of the variability of temperature and precipitation on biodiversity, community stability, and their relationship have not been clearly explored. We used a long-term (from 1982 to 2014) field data set from a temperate grassland in northern China to explore the effects of the variability of mean temperature and total precipitation on species richness, community stability, and their relationship. Results showed that species richness promoted community stability through increases in asynchronous dynamics across species (i.e., species asynchrony). Both species richness and species asynchrony were positively associated with the residuals of community stability after controlling for its dependence on the variability of mean temperature and total precipitation. Furthermore, the variability of mean temperature reduced species richness, while the variability of total precipitation decreased species asynchrony and community stability. Overall, the present study revealed that species richness and species asynchrony promoted community stability, but increased climate variability may erode these positive effects and thereby threaten community stability.

Keywords Biodiversity · Climate extremes · Inter-annual variability · Ecosystem function · Resilience

Introduction

Human activities, such as burning of fossil fuels, have significantly contributed to climate warming (IPCC 2013; Seneviratne et al. 2016). Global warming, however, increased not only the magnitude but also the probability of occurrence of climate extremes and unusual weather, i.e., climate variability (Min et al. 2011; Orlowsky and Seneviratne 2012; Putnam and Broecker 2017). For example, our planet has recently experienced more frequent and intense snowstorms, rainfall events, floods, heatwaves, droughts, and wildfires (Fischer and Knutti 2016; Wehner et al. 2017; Zhou et al. 2017). Moreover, the coupling of climate warming and drought can also lead to additional warming at a regional scale due to decreases in evapotranspiration (Berg et al. 2014; Diro and Sushama 2017), thereby increasing the variability of mean temperature and total precipitation (Berg et al. 2014). Recent climate models have also projected that, in addition to climate warming, the amplitude of inter-annual temperature oscillations will increase (Diro

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and Sushama 2017; Hawkins et al. 2014), meaning that high inter-annual climate variability will be superimposed on an unprecedented level of global warming in the coming decades. Because anomalies in average global temperature are much smaller than the expected changes in regional temperatures over most land areas (Orlowsky and Seneviratne 2012), the alterations in temperature and precipitation variability at regional and seasonal scales may be stronger than responses at global and annual scales (Donat et al. 2016).

Current increases in the magnitude of global climate changes are altering ecosystem functioning, causing biodiversity loss (Thomas et al. 2004; Walker et al. 2006) and species composition changes (Walker et al. 2006; Ma et al. 2017), increasing ecosystem vulnerability (Lesk et al. 2016), and threatening ecosystem production (Kennedy et al. 2003; Ma et al. 2017; Wagg et al. 2017). For example, climate warming significantly reduced species richness in a Tibetan grassland (Klein et al. 2004) and the aboveground net primary productivity (ANPP) of tallgrass prairie monoliths in Reno, Nevada, USA (Arnone et al. 2011). The decrease in the annual precipitation also caused species richness loss (Kennedy et al. 2003; Wilby and Shachak 2004) and ecosystem production reduction in the Kruger National Park, South Africa (Kennedy et al. 2003) and in a tallgrass prairie in northeastern Kansas, USA (Hoover et al. 2014).

Although it is important to explore the effects of changes in the mean value of climate variables (e.g., mean temperature and total precipitation) on ecosystem functioning, changes in climate variability may have stronger effects (Craine et al. 2012; Knapp et al. 2017; Reyer et al. 2013; Wilcox et al. 2017). For example, Knapp et al. (2002) found that increasing precipitation variability, while maintaining a constant precipitation amount by decreasing watering frequency, increased species richness but reduced community ANPP in a native grassland ecosystem in northeast Kansas, USA. Vasseur et al. (2014) reported that temperature variability increased the risk of species extinction more than warming. Moreover, climate variability may tend to reduce community stability (defined as the inverse of inter-annual variability that measures the variation of community productivity over time). Although the total rainfall amount was not altered, increases in precipitation variability decreased community primary productivity (Gherardi and Sala 2015a) and tended to damage plant community stability in New Mexico, USA (Gherardi and Sala 2015b). Temperature variability weakened the diversity effects in aquatic microcosms (Petchey et al. 2002). The variabilities of temperature and precipitation often naturally covary. For instance, either extreme drought or intense snowstorm (i.e., precipitation variability) may largely change temperature, thereby increasing temperature variability. However, the lack of long-term data currently limits our understanding the response of natural communities to variability in both mean temperature and total precipitation (Knapp et al. 2017; Solow 2017). In particular, an important but unresolved question is how climate variability affects biodiversity, community stability, and their relationship.

Climate variability and biodiversity may not be fully independent, and both affect ecosystem functioning (Isbell et al. 2015b). In fact, a few previous studies have carefully separated the effects of climate variability and biodiversity on ecosystem functioning. Testing the effect of biodiversity on the residuals of community stability after controlling the effects of mean temperature and total precipitation variabilities, or employing structural equation modeling, are ways to explore the effect of climate variability on community stability through realistic species changes (Grace et al. 2015; Zhang et al. 2016).

Here, we used long-term data on monthly species richness (number of plant species m^{-2}) and the ANPP over the growing season of 1982–2014 to analyze the responses of a temperate grassland ecosystem in northern China to the long-term inter-annual variability in mean temperature and total precipitation. We hypothesized that (1) climate variability decreases biodiversity in the temperate grassland and (2) climate variability may reduce community stability due to species richness loss.

Methods

Study site

This study was performed near the Inner Mongolia Grassland Ecosystem Research Station (116°14′E, 43°13′N), which is located in a temperate grassland in the Xilin River basin, Inner Mongolia, China. The C_3 perennial rhizome grass *Leymus chinensis* and the C_3 perennial bunchgrass *Stipa grandis* were dominant at the study site. The soil is classified as Haplic Calcisol and Calcic-Orthic Aridisol, according to FAO (Food and Agriculture Organization of the United Nations) and USA soil classification system, respectively. The long-term (1982–2014) mean annual temperature was 0.97 °C, with mean monthly temperatures ranging from -21.4 °C in January to 19.7 °C in July, and mean annual precipitation was 345.2 mm with approximately four-fifths falling from May to September. In this region, the grassland often turns green in late April and yellow in early September (Zhang et al. 2018). In 1979, two 25-ha relative flat areas were fenced to exclude large grazing animals (Bai et al. 2004). In each area, an east–west transect of 200×100 m^2 was equally divided into five replicates (40×100 m^2 each) (Fig. S1).

Field sampling

The ANPP of the community was estimated from aboveground plant biomass, which is an acceptable approximation for ANPP in this region, because aboveground plant tissues die during winter (Zhang et al. 2018). Due to changes in species composition throughout the growing season, plant aboveground biomass was measured on the 15th of every month throughout the growing season (i.e., from May to September) by clipping green parts of all vascular plants above the soil surface within a 1×1 m^2 plot within each block, over 1982–2014 (Fig. S1). All clipping plant materials were sorted into species, oven-dried at 65 °C for 48 h to a constant weight, and then weighed. Species richness was recorded in the same plot in which aboveground biomass was measured. As 10 plots were sampled each month (i.e., 5 plots per site × 2 sites = 10 plots), 50 plots were sampled each year (i.e., 10 plots per month × 5 months per year = 50 plots). Hence, species richness and community ANPP were estimated for 1650 plots (i.e., 50 plots per year × 33 years = 1650 plots).

Community stability

Community temporal stability was defined as μ/σ (Lehman and Tilman 2000), where μ and σ are the inter-annual mean and standard deviation of community ANPP for every month of the growing season over the 33 years, respectively. Community stability was natural logarithm transformed for homogeneity to meet the normality assumption required for further analyses. A larger community stability value indicates a smaller inter-annual variability of community production (Lehman and Tilman 2000; Zhang et al. 2016).

Species asynchrony

Species asynchrony, which is the asynchronous dynamics across species to environmental fluctuations and/or disturbances, was quantified as $1 - \frac{\sigma_{b_T}^2}{\left(\sum_{i=1}^{N} \sigma_{b_i}\right)^2}$ (Loreau and de Mazancourt 2008), where $\sigma_{b_T}^2$ is the inter-annual variance of community ANPP and σ_{b_i} is the inter-annual standard deviation of ANPP of species i in a community with N species for every month of the growing season over the 33 years. Coexistent species tend to asynchronously respond to environmental fluctuations (Bai et al. 2004). Species asynchrony varies from zero, which indicates perfectly synchronized species fluctuations, to one, which indicates perfectly desynchronized species fluctuations.

Climate data

Anomalies in mean temperature and total precipitation were determined based on 1961–1990 averages. Similar to community stability, the inter-annual coefficients of variation (*CV*) were calculated as $\sigma/\mu \times 100$, where μ and σ were the inter-annual temporal mean and standard deviation of mean temperature or total precipitation for May (i.e., from 16th April to 15th May), June (i.e., from 16th May to 15th June), July (i.e., from 16th June to 15th July), August (i.e., from 16th July to 15th August), and September (i.e., from 16th August to 15th September) across 1982–2014. For homogeneity, the *CV* of mean temperature and total precipitation were logarithm transformed for further analyses.

Statistical analysis

Repeated-measures analysis of variance (ANOVA) was used to test changes in either species richness or community ANPP differences between growing seasons. One-way ANOVAs were performed to explore the difference of species asynchrony and community stability among months within growing season. Residuals (Zhang et al. 2016) from the regressions of community stabilities on the *CV* of mean temperature or total precipitation were used to test for independent effects of diversity and asynchrony on community stability after accounting for climate variability.

Structural equation modeling (SEM) was employed to estimate the direct and indirect effects of climate variability on community stability through species richness and species asynchrony across the 33-year period. Data (sample size: 5 replicates per month per site × 5 months per site × 2 sites = 50) were fitted to the model using the maximum-likelihood estimation method. Adequacy of the model was determined using a Chi-squared test, the root-square-mean errors of approximation (RMSEA), and Akaike Information Criterion (AIC) values. Adequate model fits were indicated by a nonsignificant chi-squared test test ($P > 0.05$), low RMSEA (< 0.08), and low AIC. A nonsignificant chi-squared test test ($\chi^2 = 0.066$, $P = 0.797$), RMSEA = 0.000, and AIC = 28.066 was reported for the final model.

AMOS™ 22.0 (Amos Development Co., Greene, Maine, USA) was used for the SEM analysis, and the SPSS® software package (SPSS 18.0 for windows, SPSS Inc., Chicago, IL, USA) was employed for all other tests.

Results

Climate change and its variability (*CV*)

Air mean temperature increased through time (Fig. 1a), while total precipitation did not show any temporal trends

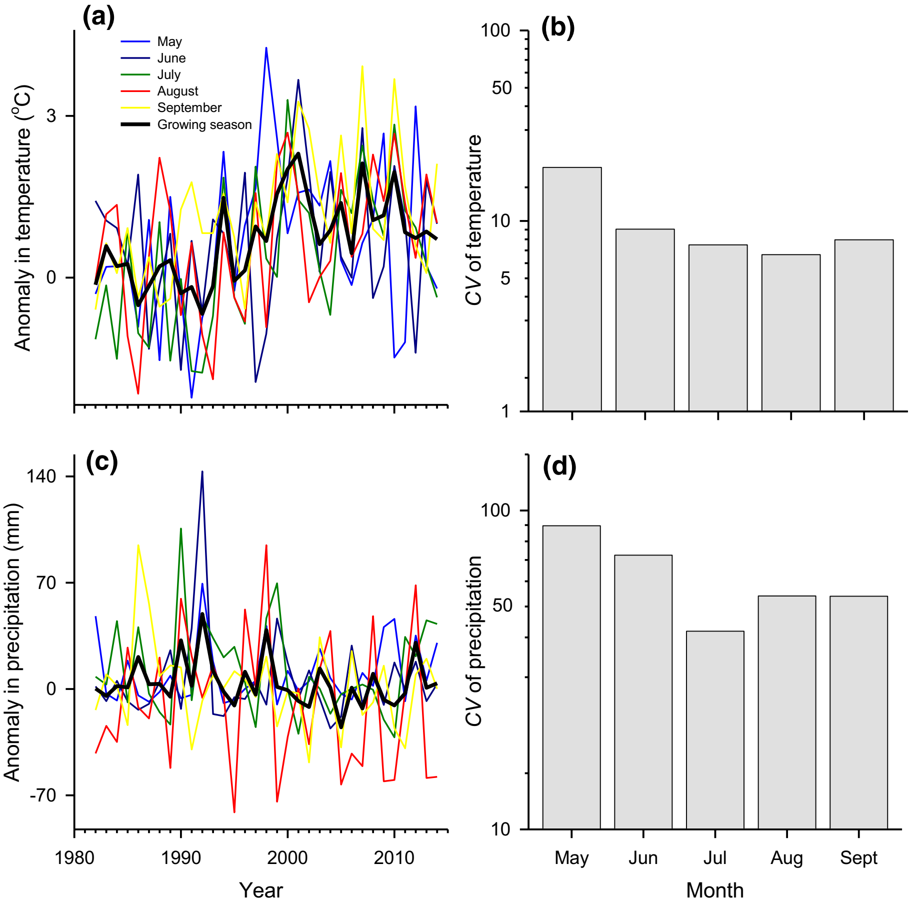

Fig. 1 Anomalies in mean monthly **a** temperature and **c** precipitation over 33 years (1982–2014) relative to the 1961–1990 average. The coefficients of variation (*CV*) of mean **b** temperature and **d** precipitation over 33 years (1982–2014) over the growing season. Note that the *CV* is expressed as a percentage (%) and is defined as the ratio of the standard deviation to the mean. Colors correspond to months during the growing season (i.e., from May to September); black correspond to the mean temperature and precipitation over the growing season. Color version of this figure is available online

(Fig. 1c). The *CV* of mean temperature (Fig. 1b) and total precipitation (Fig. 1d) was relatively high in May (i.e., in spring).

Community diversity, ANPP, and stability

Species richness (Fig. 2a) and community ANPP (Fig. 2b) peaked in August during the 1982–2014 period. The average rate of species richness loss was 0.8, 2.0, 2.4, 3.0, and 2.6 species m^{-2} $decade^{-1}$ in May, June, July, August, and September, respectively (Fig. 2a; all $P<0.05$). Community mean ANPP increased through time (i.e., from 1982 to 2014) in May (Fig. 2b; $F_{1,32}=8.4$, $P=0.0069$; $R^2=0.21$) and in September ($F_{1,32}=5.2$, $P=0.0303$; $R^2=0.14$).

Species asynchrony (Fig. 2c) and community stability (Fig. 2d) peaked in July. Community stability in August (i.e., period of peak species richness and ANPP) was significantly positively associated with species richness (Fig. 3a; $F_{1,9}=11.0$, $P=0.0107$; $R^2=0.58$) and species asynchrony (Fig. 3b; $F_{1,9}=21.8$, $P=0.0016$; $R^2=0.73$), and species richness was significantly positively associated with species asynchrony (Fig. 3c; $F_{1,9}=12.1$, $P=0.0083$; $R^2=0.60$). Moreover, species richness and species asynchrony throughout the growing season were significantly positively related to community stability (Fig. 3; All $P<0.0001$). These positive relationships during the peak biomass period and throughout the entire growing season illustrate that plant diversity may promote community stability via increasing species asynchrony in this temperate grassland.

Effects of climate variability on the diversity–stability relationship

Community stability was significantly negatively associated with the *CV* of mean temperature (Fig. 4a; $F_{1,49}=63.9$, $P<0.0001$; $R^2=0.57$) and total precipitation (Fig. 4b; $F_{1,49}=68.7$, $P<0.0001$; $R^2=0.59$). Moreover, species richness was positively related to the residuals of community stability after controlling for the effect of the *CV* of mean temperature (Fig. 4c; $F_{1,49}=16.2$, $P=0.0002$; $R^2=0.25$) and total precipitation (Fig. 4e; $F_{1,49}=29.1$, $P<0.0001$; $R^2=0.38$). Species asynchrony was also positively related to the residuals of community stability after controlling for the effect of the *CV* of mean temperature (Fig. 4d; $F_{1,49}=15.2$, $P=0.0003$; $R^2=0.24$) and total precipitation (Fig. 4f; $F_{1,49}=14.0$, $P=0.0005$; $R^2=0.23$).

Results of the SEM revealed that the *CV* of mean temperature had direct negative effects on species richness

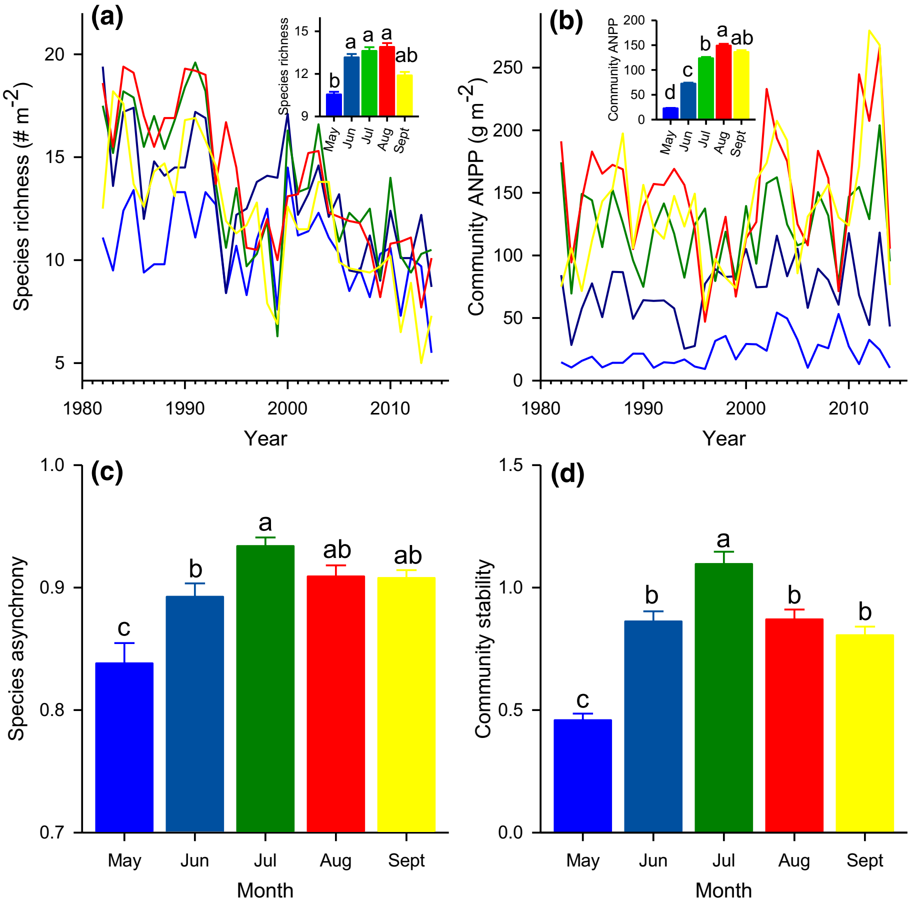

Fig. 2 **a** Species richness (number of plant species m^{-2}) and **b** community aboveground net primary productivity (ANPP) throughout the growing season from 1982 to 2014. Each line was the averages across 10 plots (i.e., 5 plots per site × 2 sites = 10 plots). **c** Species asynchrony and **d** community stability across 1982–2014. Bars with the same letter were not significantly different in Duncan's multiple range tests ($P > 0.05$). Error bars indicate 1 + SE. Different colors correspond to months during the growing season (i.e., from May to September). Color version of this figure is available online

(Fig. 5; standardized effect size: –0.45, $P < 0.001$), species asynchrony (standardized effect size −0.06, $P = 0.663$), and community stability (standardized effect size −0.15, $P = 0.226$). The *CV* of total precipitation directly significantly reduced species asynchrony (standardized effect size −0.43, $P = 0.002$) and community stability (standardized effect size −0.34, $P = 0.007$). Species richness promoted species asynchrony (standardized effect size 0.52; $P < 0.001$). Both species richness (standardized effect size 0.26; $P = 0.006$) and species asynchrony (standardized effect size 0.31; $P = 0.009$) were positively related to community stability. Thus, the SEM showed that species richness could promote community stability both directly and indirectly via an increase in species asynchrony, whereas climate variability might impair community stability both directly and indirectly.

Discussion

Consistent with our hypothesis, this 33-year field experiment provided substantial evidence that climate variability might cause significant declines in species richness and community stability. Moreover, with the diversity effect on community stability due to species asynchrony, climate variability can increase the vulnerability of community production both directly and indirectly via decreased species richness and species asynchrony.

We also found that community aboveground primary productivity increased throughout the 33-year period, at both the beginning (i.e., May) and end (i.e., September) of the growing season. The changes in primary production reported in this study are consistent with the positive relationships between global warming and the advance of phenological events like spring leaf unfolding (Peñuelas et al. 2009; Wang et al. 2017), and between the extended length of the growing season and the delay of autumn leaf drop (Liu et al. 2016; Wang et al. 2017), which have been observed in recent decades.

Consistent with the previous studies on peak primary production (Hector et al. 2010; Gross et al. 2014; Tilman et al. 2014), species richness and species asynchrony significantly enhanced community stability, and species richness was significantly positively associated with species asynchrony. Moreover, we found that species richness was positively associated with species asynchrony and community stability in the other months within the growing season as well as throughout the growing season. Species composition,

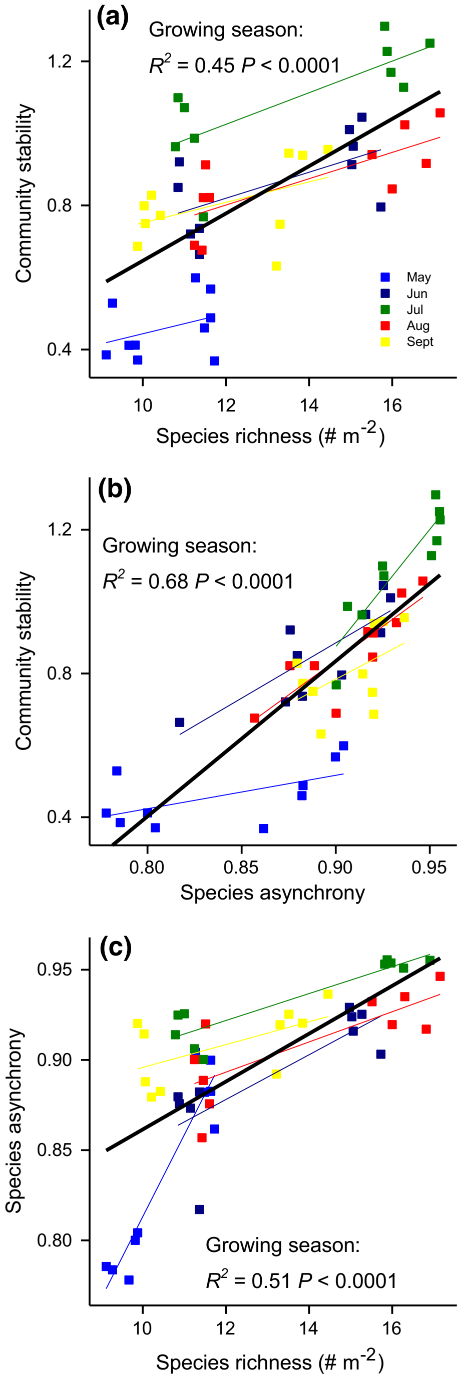

Fig. 3 Community stability as a function of **a** species richness and **b** species asynchrony. **c** Species asynchrony as a function of species richness. Each point represents the value from one plot across 1982–2014 and different colors correspond to months during the growing season (i.e., from May to September). Black regression indicates the relationship throughout the growing season ($n = 50$). Color version of this figure is available online

plant phenological characteristics, and environmental factors might contribute to asynchronous responses of species throughout the growing season (de Mazancourt et al. 2013; Loreau and de Mazancourt 2013; Zhang et al. 2018). In the grassland examined here, the C_3 grass *Agropyron cristatum* and the forbs *Potentilla acaulis* with yellow flowers and *Pulsatilla turczaninovii* with white flowers contributed to community ANPP in May; the C_3 forb *Carex korshinskyi* and the C_3 grasses *A. cristatum*, *Koeleria cristata*, and *Poa subfastigiate* contributed to more than half of the community ANPP in June; the C_3 perennial rhizome grass *L. chinensis*, the C_3 grasses *A. cristatum* and *S. grandis*, and the colorful forbs *Iris tenuifolia*, *Thalictrum petaloideum*, and *Allium tenuissimum* started to flower in July; *L. chinensis*, the C_3 grasses *S. grandis* and *Achnatherum sibiricum*, the C_4 grass *Cleistogenes squarrosa*, some forbs like *Saussurea japonica* and *Allium condensatum*, and most annuals, such as *Salsola collina*, *Axyria amaranthoides*, *Chenopodium aristatum*, and *Artemisia sieversiana*, bloomed in August; most species died in September. These seasonal changes in species richness and composition suggest that, in natural communities, the diversity-dependent community stability is positively associated with asynchronous dynamics between species throughout the growing season. These positive relationships support the results of the previous studies (Bai et al. 2004; Cardinale et al. 2012; Tilman et al. 2014), showing that restoring and protecting biodiversity can provide sustainable ecosystem functioning.

Moreover, we found that climate variability negatively affected species richness, species asynchrony, and community stability. It has been reported that changes in climate variability may affect species distribution (Barga et al. 2017; Kelly and Goulden 2008; Reyer et al. 2013), thereby reducing local species richness. Particularly, we found that the variability of mean temperature directly decreased species richness, while the variability of total precipitation directly damaged species asynchrony and community stability (Fig. 5). According to the significant changes in climate variability, plant reproduction may be reduced due to severe physical environment restriction and high mortality due to physiological failure, e.g., failure in seedling establishment, that decrease species richness (Reyer et al. 2013). For example, Andrus et al. (2018) found that the deficit of soil moisture, which was directly affected by increased climate variability, was negatively associated with species recruitment. Concomitantly, plant community might display considerable reduction in production, thus increasing the inter-annual variability of community dynamics. As water is often limited in arid and semi-arid grasslands (Bai et al. 2004; Sala et al. 2012), precipitation variability may directly influence the asynchronous responses of species, on which root distribution may play an important role. The previous studies have showed that increases in precipitation variability decreased the biomass of grasses with shallow roots but enhanced tree productivity due to the deep distribution of their roots (Gherardi

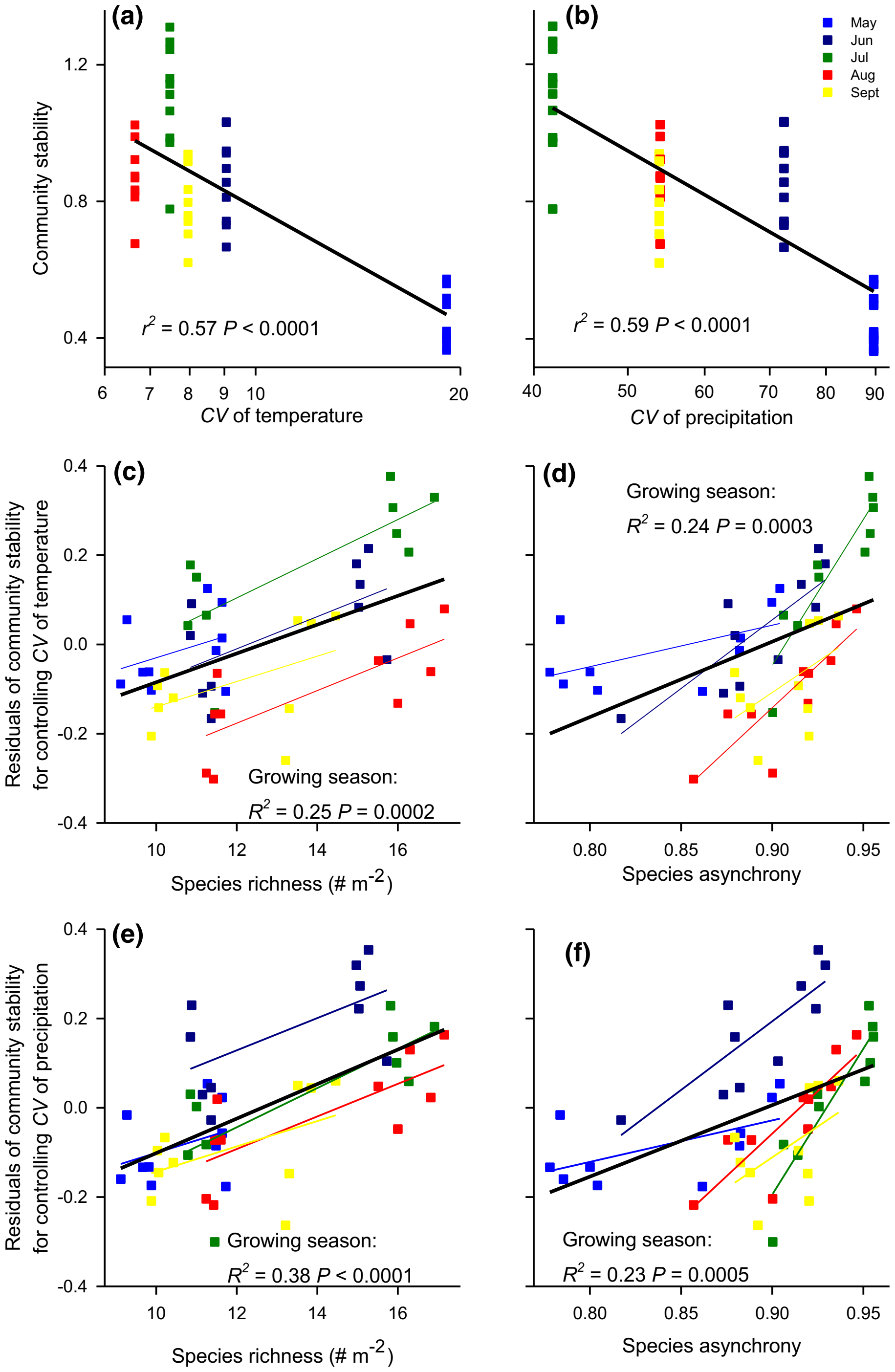

Fig. 4 Relationship between community stability and the coefficients of variation (*CV*) of **a** mean temperature [stability = − 1.1 × $\log_{10}$(*CV* of temperature) + 1.9] and **b** total precipitation [stability = − 1.6 × $\log_{10}$(*CV* of precipitation) + 3.6]. The relationship between residuals of community stability [from **a**] and **c** species richness and **d** species asynchrony, after controlling for the effect of the *CV* of temperature. Relationship between residuals of community stability [from **b**] and **e** species richness and **f** species asynchrony, after controlling for the effect of the *CV* of precipitation. Each point represents the value from one plot across 1982–2014. Black regression indicates the relationship throughout the growing season (n = 50). Different colors correspond to months during the growing season (i.e., from May to September). Color version of this figure is available online

and Sala 2015b), thereby leading to decreased community stability (Gherardi and Sala 2015a). Based on the strong inter-annual precipitation fluctuations in our ecosystem, perennial grasses (e.g., *S. grandis* and *A. cristatum*) may have competitive advantages over forbs and annuals in dry environmental conditions (Bai et al. 2004), because their generally deeper root systems allow them exclusive access to deep soil water resources, which are expected to increase in wet years (Zhang et al. 2015). In relatively wet years, annuals (e.g., *C. glaucum* and *S. collina*) were favored and over shoot (Zhang et al. 2015), as their high growth rate provides them advantage during months with above mean precipitation (i.e., under increased precipitation variability), increasing the inter-annual variability of community production (i.e., reducing community stability). Therefore, increases in mean temperature and total precipitation variabilities might have negative impacts on biodiversity and community stability.

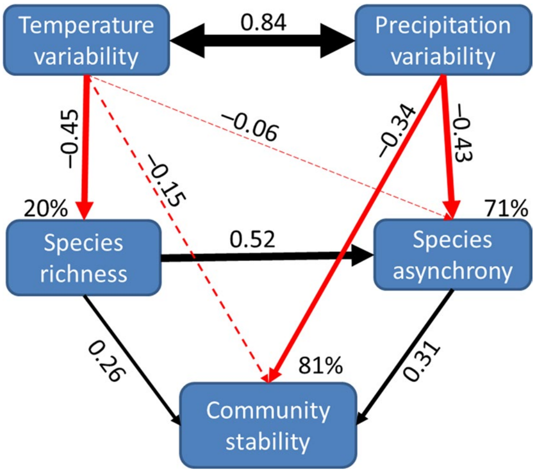

Fig. 5 Structural equation model examining the effects of climate variability on species richness, species asynchrony, and community stability over 33 years ($n=50$, 5 replicates/plots per month per site × 5 months × 2 sites). Numbers adjacent to arrows are standardized path coefficients, and width of the arrows indicates the strength of the relationship. Dashed and solid arrows indicate $P>0.05$ and $P<0.01$, respectively. Black and red arrows indicate positive and negative relationship, respectively. Percentages close to endogenous variables indicate the variance explained by the model (R^2). Color version of this figure is available online

Notably, this study showed that, even under climate variability, community stability could benefit from greater biodiversity, which is consistent with the recent report synthesizing global biodiversity and ecosystem functioning experiments that incorporated a random assortment of plant species (Isbell et al. 2015a). We also found that species richness can still promote community stability after removing the negative effects of climate variability. By separating the effects of climate variability and species richness on community stability, we found that species richness and species asynchrony were positively related to the residuals of community stability after controlling for the effect of climate variability. Thus, biodiversity and their asynchronous responses might provide insurance effects against climate variability in natural communities to some extent (Martin and Watson 2016).

Conclusions

Our study showed that climate variability impaired community stability by decreasing species richness and species asynchrony, suggesting that increasing climate variability has negative impacts on ecosystem functioning. More important, irrespective of climate variability, both species richness and species asynchrony enhanced community stability in the temperate grassland examined here. Thus, urgent actions are needed to prevent further climate warming, thereby decreasing climate variability (Ricke and Caldeira 2014), and to maintain biodiversity to ensure the sustainable provision of ecosystem services as well as regional and global food security.

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Author contribution statement YZ, ML, and XH conceived and designed the experiments. YZ, NH, YB, and JW performed the experiments and collected the data. YZ analyzed the data. YZ, ML, and NH wrote the manuscript; other authors provided editorial advice.

Compliance with ethical standards

Conflict of Interest The authors declare that they have no conflict of interest.

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