

Species asynchrony stabilises productivity under extreme drought across Northern China grasslands

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Abstract

1. Biodiversity can stabilise productivity through different mechanisms, such as asynchronous species responses to environmental variability and species stability. Global changes, like intensified drought, could negatively affect species richness, species asynchrony and species stability, but it is unclear how changes in these mechanisms will affect the stability of above-ground primary productivity (ANPP) across ecosystems.
2. We studied the effects of a 4-year extreme drought on ANPP stability and the underlying mechanisms (species richness, species asynchrony and species stability) across six grasslands in Northern China. We also assessed the relative importance of these mechanisms in determining ANPP stability under extreme drought.
3. We found that extreme drought decreased ANPP stability, species richness, species asynchrony and species stability across the six grasslands. However, structural equation modelling revealed that species asynchrony, not species richness or species stability, was the most important mechanism promoting stability of ANPP, regardless of drought across the six grasslands.
4. *Synthesis.* Our results suggest that species asynchrony, not species richness and species stability, consistently buffers ecosystem stability against extreme drought across and within grasslands spanning a broad precipitation gradient. Thus, species asynchrony may be a more general mechanism for promoting stability of ANPP in grasslands in the face of intensified drought.

KEYWORDS

above-ground productivity, biodiversity, coordinated experiments, ecosystem function and structure, Eurasia steppe, global change ecology, grassland communities, terrestrial ecosystem

1 | INTRODUCTION

The temporal stability of ecosystems is important for sustaining ecosystem functioning and services (Oliver, Heard, et al., 2015). As global change intensifies its impacts on ecosystems, understanding mechanisms underlying ecosystem stability has emerged as a pressing issue (Ma et al., 2017). Several mechanisms could contribute to the maintenance of temporal ecosystem stability (measured as the ratio of temporal mean of ANPP to its temporal standard deviation; Tilman, 1999). First, ecosystems with high species richness (i.e. number of species) tend to have high stability because a greater number of species increases the potential and magnitude of asynchronous dynamics among species (Hautier et al., 2014; Zhang et al., 2018). When communities are comprised of a small number of species, reduction in the stability of dominant species in response to any environmental fluctuations could erode stability (Xu et al., 2015). Second, species asynchrony—dissimilar responses among species to environmental variability—can increase temporal ecosystem stability through shifts in relative abundances of species with different ecological niches (Hector et al., 2010; Loreau & de Mazancourt, 2013; Wilcox et al., 2017; Xu et al., 2015) such that an increase in the abundance of some species compensates for decline in others as a result of environmental changes (Hautier et al., 2014). Third, theoretical and empirical studies also suggest that high species stability (stability of individual species averaged across all species in a community) results in high temporal ecosystem stability (Hautier et al., 2020; Wang & Loreau, 2014, 2016; Yang et al., 2012; Zhang, Feng, et al., 2019). However, the relative contribution of species richness, species asynchrony and species stability to temporal ecosystem stability remains unclear.

Naturally high climatic variability is a key determinant of grassland structure and function globally (Huxman et al., 2004; Knapp et al., 2008; Knapp & Smith, 2001; Weltzin et al., 2003). However, forecast climate-change-induced increases in this variability have the potential to negatively impact ecological processes in grassland ecosystems (Godfree et al., 2011; Hautier et al., 2015; Kerr, 2007a, 2007b; Lepetz et al., 2009; Vogel et al., 2012) and trigger biodiversity loss (Oliver, Isaac, et al., 2015; Wagg et al., 2017). Ongoing loss of species, shifts in species abundances (species re-ordering; Smith et al., 2009) and alteration of species asynchrony in response to extreme climate events could weaken or erode stability (Cardinale et al., 2012; Hautier et al., 2014; Ives & Carpenter, 2007). Thus, there has been renewed interest, at global, regional and local scales, in understanding how ecosystem stability could be impacted by extreme climatic events. For example, a recent global-scale study revealed eutrophication decreased ecosystem stability via an increase in temporal variation of productivity along with reduction in species asynchrony (Hautier et al., 2014). Zhang et al. (2018) also reported that, in Northern China, 33 years of variability of mean temperature decreased species richness, species asynchrony and ecosystem stability while variability of total precipitation reduced species asynchrony and temporal ecosystem stability. Likewise, in an alpine grassland, climate warming reduced the temporal stability of ANPP via reduced

species asynchrony (Ma et al., 2017), whereas a reduction in species stability due to nitrogen enrichment led to reduction in temporal stability of ANPP in a temperate steppe (Zhang, Feng, et al., 2019). These findings emphasise that altered climate conditions may disrupt stability of ecosystems through the erosion of species richness, weakened species asynchrony and reduced species stability (Grman et al., 2010; Hautier et al., 2014; Zhang, Feng, et al., 2019; Zhang et al., 2018). Increasing precipitation variability and multi-year extreme drought have been predicted for many ecosystems globally (IPCC, 2013); however, the response of ecosystem stability to this climate change remains unresolved (Smith et al., 2017). Thus, it is important to study how extreme drought may impact temporal stability of ANPP by affecting species richness, species asynchrony and species stability.

Grassland ecosystems are naturally complex with different biotic (e.g. species assemblage) and abiotic (e.g. soil, precipitation, temperature) components and processes; and their responses to environmental perturbations may greatly differ among communities and sites (Grimm et al., 2013; Heisler-White et al., 2009; Knapp et al., 2016). Previous studies showed that drought effects on temporal stability of ANPP, species asynchrony and species richness varied among ecosystems, with negative effects in some systems (Wagg et al., 2017; Zhang, Quan, et al., 2019) or no impacts in others (Ma et al., 2017; Zhang, Quan, et al., 2019). These differential responses of temporal stability of ANPP, species asynchrony and species richness increases uncertainty regarding how grassland ecosystems that vary in composition and abiotic factors will be affected by extreme drought. Coordinated drought experiments with identical treatments, encompassing wide geographical scales or regions (Fraser et al., 2013; Knapp et al., 2015, 2016) make it possible to compare responses across different grassland types and to identify mechanisms underlying temporal ecosystem stability (Knapp et al., 2016).

Here we conducted identical experiments across six grasslands in Northern China that imposed extreme growing season drought over a 4-year period. This allowed us to examine the impact of extreme drought on temporal ecosystem stability, species richness, species asynchrony, species stability and their relationships, and whether these relationships differ among grasslands spanning a broad precipitation gradient. We addressed two questions: (a) Does extreme drought affect temporal stability of ANPP and the underlying mechanisms (species richness, species asynchrony and species stability)? (b) Does extreme drought change the relative importance of these mechanisms in determining temporal stability of ANPP?

2 | MATERIALS AND METHODS

2.1 | Study sites

This study was conducted in the context of the Extreme Drought in Grasslands Experiment (EDGE; <http://edge.biology.colostate.edu/>) spanning six grassland sites across Northern China (Table 1). These sites are representatives of the major grassland (steppe) types in Northern China and were distributed along a broad precipitation

TABLE 1 Description of the six EDGE study sites in Northern China

Site name	Site label	Colour code	Latitude	Longitude	Steppe type	Habitat	MAP _a (mm)	MAP _b (mm)
Sher Tara	A	●	49°21'00"N	120°06'00"E	Meadow	Semi-arid	363	297.8
Erguna	B	●	50°10'46"N	119°22'56"E	Meadow	Semi-arid	354	307.8
Xilinhote-Leymus	C	●	43°33'6"N	116°40'20"E	Typical	Semi-arid	323	311.6
Xilinhote-Stipa	D	●	43°32'25"N	116°33'18"E	Typical	Semi-arid	323	311.6
Sheila Muren	E	●	41°47'00"N	111°53'00"E	Desert	Arid	236	233.5
Urat	F	●	41°25'00"N	106°58'00"E	Desert	Arid	175	137.5

Note: Colour codes and site labels correspond with those in Figures 1–6. MAP_a (mm) represents mean annual precipitations from 1972 to 2018 while MAP_b represents mean annual precipitations during the study period (2015–2018) measured adjacent to each site. Sites were grouped into 'habitat' and 'steppe type' following the classification of Kang et al. (2007).

gradient in Inner Mongolia (Table 1). Mean annual precipitation (MAP) ranged from 175 to 363 mm (Table 1; see Figure S1; Luo, Xu, et al., 2018; Luo, Zuo, et al., 2018 for further description of the sites).

2.2 | Experimental design

All six EDGE sites have identical control (ambient) and extreme drought treatments. The experiments were set up in 2014, and the data were collected from 2015 through 2018. Extreme drought was achieved through the installation of rainout shelters designed to intercept 66% of ambient precipitation (Griffin-Nolan et al., 2019; Yahdjian & Sala, 2002) during the growing season (May–August) at all sites. The experiment was a randomised complete block design with six replicates of each treatment at each site. All plots were arranged in blocks, with each treatment randomly allotted within each block, to control for possible differences in environmental and soil gradients. Each plot was 6 × 6 m in size, with at least 2 m spacing between plots. Every plot had a 1-m buffer perimeter that minimised edge effects associated with the rainout shelter. At the onset of each growing season (May–August) of each year, the rainout shelter roofs were installed and then removed at the end of the growing season (see Knapp et al., 2015; Luo, Zuo, et al., 2018 for further details on the rain-out shelter). Each 6 × 6 m plot was hydrologically isolated by installing aluminium flashing to a depth of 1 m around the perimeter to reduce surface and subsurface water flow (Luo et al., 2019). The effects of rainout shelters on the light environment were small, permitting more than 90% penetration of photosynthetically active radiation (Luo et al., 2019).

2.3 | Sampling protocol and metrics

All EDGE sites have unified and standardised data collection protocols for comparing drought effects across the sites. ANPP was annually harvested at peak biomass by clipping all plants at ground level within a single 1 m² quadrat in each replicate 6 m × 6 m plot. All constituent species were identified, their biomass separated and ANPP per species per plot was used to estimate species asynchrony. Species richness was annually recorded as the total number of constituent plant

species within the 1 m² quadrat in which ANPP was measured (Zhang et al., 2018). Average species richness was calculated as the mean species richness over four consecutive growing seasons per 1 m² plot.

Temporal stability of ANPP in each grassland site was calculated at plot level as μ/σ , where μ and σ are the temporal mean and temporal standard deviation of total ANPP in a plot, respectively, over the 4-year period (Hautier et al., 2014). The temporal stability of individual species in each plot was also calculated as μ/σ , where μ and σ are the temporal mean and standard deviation (σ) of ANPP of each species over the 4-year period. Species stability was the average value of the temporal stability of all species within a plot (Zhang, Feng, et al., 2019). Following the metric of Loreau and de Mazancourt (2008) and as described and measured by Hautier et al. (2014), species asynchrony was calculated for each plot as $1 - \varphi_b = 1 - \sigma^2 / (\sum_{i=1}^n \sigma_i)^2$. φ_b is species synchrony, and it was derived from the estimation of σ^2 , the temporal inter-annual variance in community ANPP; and σ_i , the inter-annual standard deviation in ANPP of a particular species i in a plot with n species over the 4 years. Species asynchrony metrics range from 0 (perfect synchronisation or fluctuations of the species in a community) to 1 (perfect asynchrony).

2.4 | Statistical analyses

All analyses were conducted in R (version 3.4.0; R Core Team, 2017). To test both the across site and within-site drought treatment effects on temporal stability of ANPP, average species richness, species asynchrony and species stability, we constructed mixed-effects ANOVA models using the *lme* function from the *nlme* library (Pinheiro et al., 2018). Across site tests included 'site and treatment' fixed effects and 'block' as a random effect (model 1; Table S1). The within-site ANOVA models (model 2; Table S1) differed from across sites models by not including 'site' as a fixed effect.

$$y \sim \text{site} * \text{treatment} + (1|\text{block}) \quad (\text{model 1})$$

$$y \sim \text{treatment} + (1|\text{block}) \quad (\text{model 2})$$

Next, we constructed linear mixed-effects models with the *lme* function to examine the bivariate relationships between temporal stability

of ANPP and its potential underlying mechanisms (average species richness, species asynchrony and species stability). To assess relationships across sites, 'a continuous explanatory variable, x ' and 'site' were considered as fixed and random effects, respectively, and 'y' was the continuous response variable (model 3; Table S1). The within-site models only differed from the across site models in the specification of 'block' as a random effect (model 4; Table S1). Where necessary, the response variables were natural log-transformed to improve normality before the regression analyses.

$$y \sim x + (1|\text{site}) \quad (\text{model 3})$$

$$y \sim x + (1|\text{block}) \quad (\text{model 4})$$

Third, we used ANCOVA to test for homogeneity of slopes for any kind of bivariate relationship that was separately detected ($p < 0.05$) under ambient and drought conditions (Quinn & Keough, 2002; Zhang, Feng, et al., 2019). The across- (model 5) and within-site (model 6) mixed-effects ANCOVA models only differed from the across- (model 3) and within-site (model 4) bivariate regressions in the addition of 'a categorical variable, treatment' as fixed effects.

$$y \sim x * \text{treatment} + (1|\text{site}) \quad (\text{model 5})$$

$$y \sim x * \text{treatment} + (1|\text{block}) \quad (\text{model 6})$$

A significant interaction between 'x' and 'treatment' was interpreted to imply a difference between the slopes of a particular relationship separately obtained from the two treatment conditions (ambient and drought). A non-significant interaction implies that the slopes are similar (Borich, 1972; Huitema, 2011; Quinn & Keough, 2002).

Finally, we conducted structural equation modelling (SEM) analysis to further assess how drought impacts stability of ANPP through the contributions of the three mechanisms (species richness, species stability and species asynchrony) to stability of ANPP. The SEM model was primarily built from previous theoretical and empirical findings (Grace et al., 2016) on how the three drivers could

promote stability of ANPP. The SEM construction and analyses were performed using IBM® SPSS® AMOS 22.0.0 (Build 1384; Amos Development Corporation). The endogenous variables (species richness, species asynchrony, species stability and stability of ANPP) were natural log-transformed to improve normality and homoscedasticity before the SEM analysis. Data were fitted to the model using the maximum likelihood estimation method and the goodness of fit of the model was determined by non-significant Chi-square (χ^2 ; $p > 0.05$; Fan et al., 2016).

3 | RESULTS

3.1 | Effects of extreme drought on temporal stability of ANPP, species richness, species asynchrony and species stability

Extreme drought decreased temporal stability of ANPP by 25% across the six sites (control = 1.22; drought = 0.91; Figure 1a; Table S2). Within sites, extreme drought increased temporal stability of ANPP (Figure 1a; Table S2) for site B (control = 1.04, drought = 1.46), decreased for sites C (control = 1.11, drought = 0.49) and D (control = 0.98, drought = 0.16); and had no effect at other three sites (A, E and F). Extreme drought reduced species richness by an average of 20% across the six sites (control = ~11 species; drought = ~9 species; Figure 1b; Table S2). Extreme drought reduced species richness (Figure 1b; Table S2) for the wettest sites, A (17% loss; control = ~16 species; drought = ~13 species) and B (29% loss; control = ~16 species; drought = 11 species), as well as the driest sites, E (~25% loss; control = ~14 species; drought = 11 species) and F (~35% loss; control = 5 species; drought = 3 species). The sites with intermediate precipitation, C (control = ~9 species; drought = 8 species) and D (control = 6 species; drought = ~7 species), showed no significant effect of extreme drought on species richness. Across the six sites, species asynchrony declined by ~9% under drought (0.76) relative to the control (0.84; Figure 1c;

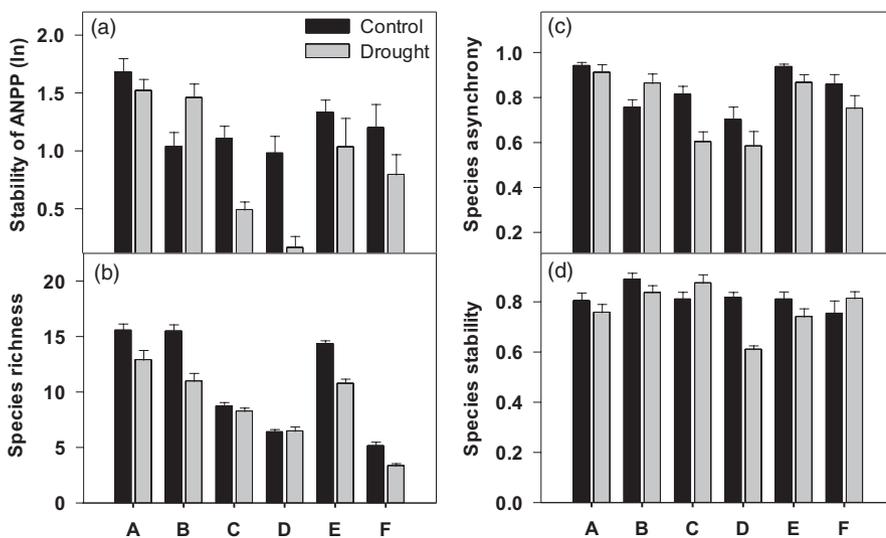


FIGURE 1 Effects of drought on temporal stability of ANPP, species richness, species asynchrony and species stability for six grassland sites in Northern China. See Table 1 for the descriptions of sites A–F. Error bars denote one standard error of mean (± 1 SEM). $n = 6$ per treatment in each site. The mixed-effects ANOVA results are presented in Table S2. Stability of ANPP data were natural log-transformed prior to analysis

Table S2). Drought had no effect on species asynchrony (Figure 1c; Table S2) in four sites (A, D, E and F), but increased (~12%; control = 0.76; drought = 0.86) and reduced (~26%; control = 0.81; drought = 0.60) species asynchrony for sites B and C, respectively. Drought reduced species stability by 5% across the sites (Figure 1d; Table S2), but this change was only significant at site D (Figure 1d; Table S2; control = 0.82; drought = 0.61).

3.2 | Effects of extreme drought on relationships between temporal stability of ANPP, species richness, species asynchrony and species stability

We found that species richness (Figure 2a) and species stability (Figure 2b) were not related to stability of ANPP across the six grasslands (Table S3). Instead, we found strong positive relationships between species asynchrony and temporal stability of ANPP across both ambient (Figure 2c; Table S3; slopes and 95% confidence intervals: 2.47[1.68–3.26]) and drought treatments

(Figure 2c; 2.56[1.87–3.25]). ANCOVA revealed that the slope of the asynchrony–stability relationship across the six sites was not significantly affected by extreme drought (Figure 2c; Table S4). Moreover, we found no significant richness–asynchrony (Figure S1) relationships across the six grasslands (Table S3).

Temporal stability of ANPP was not related to species richness nor species stability in ambient and drought treatments for any site (Table S3). A strong positive relationship between species asynchrony and temporal stability of ANPP was found in the ambient treatments within four sites, but not at sites D and F; as well as in drought treatments at all sites except for site C (Figure 3; Table S3). ANCOVA results (Figure 3; Table S4) showed that drought did not affect the asynchrony–stability relationship in any site. Moreover, we did not find significant richness–asynchrony relationships in either the ambient or drought communities within any site (Table S3).

Our SEM analysis confirmed the strong, direct contribution of species asynchrony to the temporal stability of ANPP (standardised path coefficient = 0.77) compared to species stability (0.20; Figure 4). SEM also revealed that species richness contributed to

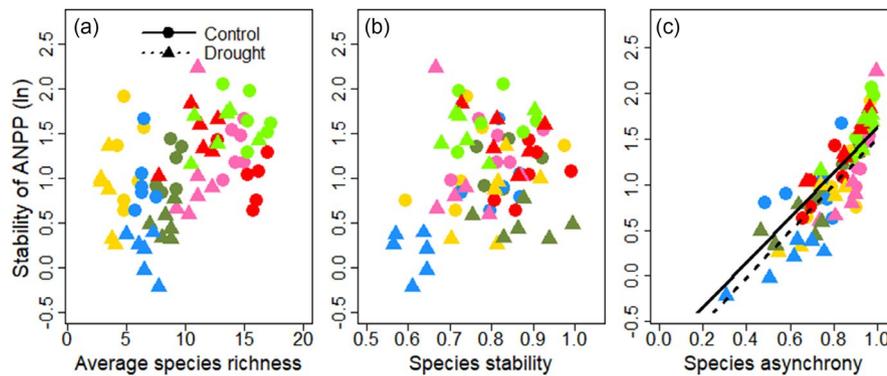


FIGURE 2 Effects of extreme drought on the relationship of temporal stability of ANPP with species richness (a), species stability (b) and species asynchrony (c) across six grasslands in Northern China. Each colour represents a site (see Table 1). $n = 6$ per treatment in each site. Stability of ANPP was natural log-transformed prior to analysis. Results of the regressions and ANCOVA are presented in Tables S3 and S4, respectively

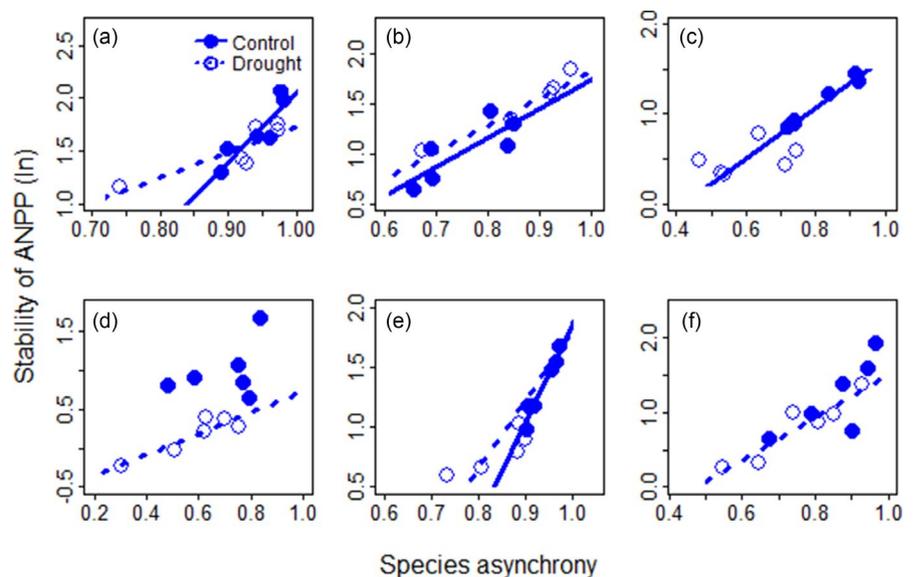


FIGURE 3 Effects of drought on the relationship between temporal stability of ANPP and species asynchrony within six grasslands in Northern China. Panels (a–f) represent sites a–f (see Table 1 for the sites descriptions). Slopes and ANCOVA results are presented in Tables S3 and S4, respectively. Non-significant relationships are not shown (Table S3). $n = 6$ per treatment in each site. Stability of ANPP was natural log-transformed prior to analysis

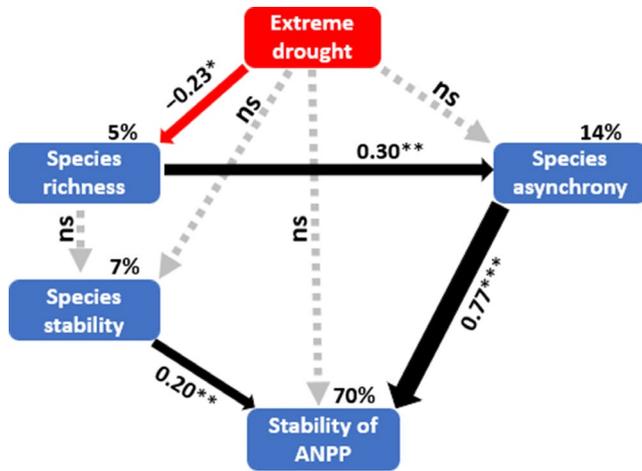


FIGURE 4 Structural equation model showing the paths through which extreme drought impacts temporal stability of ANPP across six grasslands in Northern China ($n = 72$, i.e. 6 observations/treatment/site). All endogenous variables were natural log-transformed to improve normality and homoscedasticity before the SEM analysis. Standardised path coefficients of significant paths ($p < 0.05$) are placed next to paths. Arrow width is proportional to path strength; black and red arrows represent positive and negative effects, respectively; ns and dashed grey arrows represent non-significant paths ($p > 0.05$). Asterisks on path coefficients represent * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$. Percentage value on every dependent variable denotes the proportion of variance (R^2) explained by the model, and goodness of fit for the model was based on $\chi^2 = 3.28$, $df = 2$; $p = 0.19$

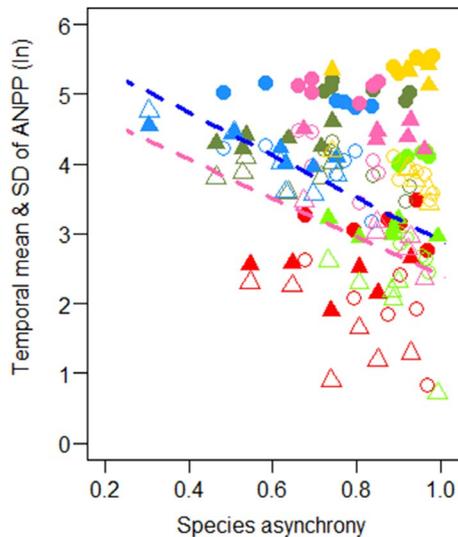


FIGURE 5 Effects of drought on the relationship between species asynchrony and mean and standard deviation of ANPP across six grasslands. Blue dashed lines and open circles denote asynchrony–standard deviation of ANPP relationship in ambient treatments while pink dashed lines and open triangles are for drought treatments. Blue filled circles represent asynchrony–mean ANPP relationships in ambient conditions while the pink filled triangles represent drought treatments. Asynchrony–mean ANPP relationships are not significant and are not shown. $n = 6$ per treatment in each site. Each colour represents each site as shown in Table 1. Response variables were natural log-transformed prior to analysis. Slopes and ANCOVA results are presented in Tables S5 and S6, respectively

stability of ANPP via species asynchrony and not via species stability; and that drought reduced the stability of ANPP by diminishing the contribution of species richness to species asynchrony.

3.3 | Species asynchrony predicts temporal variability of ANPP

Across the sites, species asynchrony was negatively related with the standard deviation (SD) of ANPP in both the ambient (Figure 5; Table S5; slopes and 95% confidence intervals: $-3.04[-4.20$ to $-1.88]$) and drought (Figure 5; Table S5; $-2.75[-3.77$ to $-1.73]$) treatments. ANCOVA showed that the two slopes were not significantly different (Table S6). However, no significant relationship was found between asynchrony and mean of ANPP across the ambient and drought communities (Figure 5; Table S5).

At the site level (Figure 6; Table S5), the relationship between asynchrony and the SD of ANPP was significant for the ambient treatments at sites C (slopes and 95% confidence intervals: $-3.54[-4.99$ to $-2.08]$) and E ($-6.11[-9.57$ to $-2.65]$); and in the drought treatments for sites A ($-2.55[-4.81$ to $-0.28]$), B ($-3.17[-5.55$ to $-0.79]$), D ($-2.65[-4.53$ to $-0.77]$) and E ($-6.33[-12.09$ to $-0.57]$). However, ANCOVA revealed that there was no significant drought effect on the slope of the relationship between asynchrony and SD of ANPP within each site. A significant asynchrony–mean ANPP relationship (Figure 6; Table S5) was found for the ambient treatments for sites A ($2.17[0.28-4.05]$), D ($-0.78[-1.53$ to $-0.03]$) and E ($2.06[0.25$ to $0.89]$), and for drought treatments only for site D ($-1.29[-2.30$ to $-0.29]$).

4 | DISCUSSION

We examined how extreme drought impacts temporal stability of ANPP and evaluated three potential mechanisms that may explain ANPP responses: species richness, species asynchrony and species stability. We expected drought to decrease stability of ANPP and its potential drivers in all the six sites, however with higher decrease in xeric compared to the more mesic sites (Knapp et al., 2015). Contrary to our expectation, we found an unexpected pattern of diverse effects of extreme drought on ANPP stability across the six grasslands. Stability of ANPP either did not change or increased in the moist meadow grasslands (A and B), and declined in the two sites (C and D) with intermediate levels of precipitation. Thus, the two intermediate sites appear to be more sensitive to extreme drought than the moist grasslands. However, the stability of ANPP did not change in the driest grasslands, perhaps because plants in dry sites possess drought tolerance mechanisms (Grime et al., 2000; Tielbörger et al., 2014). Species richness declined with drought in four of six sites, but surprisingly did not decline at the two intermediate sites where temporal stability of ANPP decreased. Similar drought impacts on diversity in grassland ecosystems have been reported from previous drought studies (Kreyling et al., 2017; Tielbörger et al., 2014), and in response to

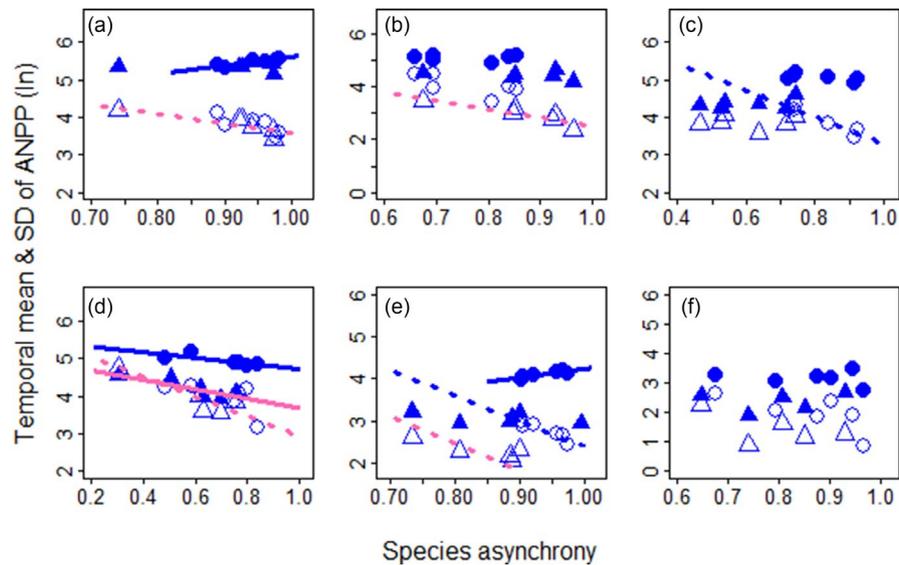


FIGURE 6 Relationships of species asynchrony and mean and standard deviation of ANPP within six grasslands across China. Panels (a–f) represent sites a–f arranged (see Table 1). Each 'blue closed circle' and 'blue open circle' denotes mean ANPP in ambient and drought treatments, respectively ($n = 6$ per treatment in each site). Each 'blue closed triangle' and 'blue opened triangle' denotes temporal standard deviation (SD) of ANPP in the ambient and drought treatments, respectively ($n = 6$ per treatment in each site). Response variables were natural log-transformed prior to analysis. Thick blue and pink lines represent the relationship between mean ANPP in the ambient and drought treatments while the dashed blue and pink lines signify relationships between the SD of ANPP in ambient and drought treatments, respectively. Non-significant relationships (regression lines) are not shown. Slopes and ANCOVA results are presented in Tables S5 and S6, respectively

other global change factors (Ma et al., 2017; Soons et al., 2017). Although it was not clear why species richness was unaffected by drought in the two sites experiencing similar climate but with different dominant species, the results suggest that the response of species richness to drought varies across sites. Extreme drought increased species asynchrony in a moist site (B), and only reduced species asynchrony and species stability in intermediate precipitation sites C and D, respectively. The decline in species asynchrony and species stability appear as the likely causes of the reduction in stability of ANPP in sites C and D, respectively. This thus suggests that different mechanisms determine the response of different grasslands to environmental variability, as previously noted by Hallett et al. (2014). Additionally, most of our results differ from the previously reported weakening effects of climate warming (Ma et al., 2017) and fertilisation (Hautier et al., 2014) on species asynchrony and species stability (Yang et al., 2012; Zhang, Feng, et al., 2019) in natural grasslands. Instead, our results indicate that extreme drought effects on species asynchrony and species stability differ from other global change factors.

We assessed the widely reported role of species richness on temporal stability of ANPP. Contrary to our expectations, we found no significant relationship between temporal stability of ANPP and species richness across and within the six natural semi-arid and arid grasslands under ambient conditions in Northern China. This finding contradicts most previous reports from single-site manipulative experiments (Isbell et al., 2009; Proulx et al., 2010; Tilman et al., 2006), meta-analyses (Craven et al., 2018; Isbell et al., 2015), globally distributed natural grasslands studies

(Hautier et al., 2014, 2020), as well as a 33-year study in Inner Mongolia, China (Zhang et al., 2018). Thus, species richness might not have a direct mechanistic effect on ANPP stability in these grasslands because richness and stability could respond differently to environmental fluctuations (Ma et al., 2010). Moreover, our finding suggests that the strength of stability of ANPP in natural grasslands may not be universally or directly dependent on species richness (Wilcox et al., 2017).

Theoretical developments have demonstrated that the temporal stability of ANPP can be fully decomposed into two key underlying mechanisms: species asynchrony and species stability (Wang & Loreau, 2014, 2016). Thus, we investigated the direct role of species asynchrony and species stability as mechanisms maintaining stability in these natural grasslands under ambient condition (Hautier et al., 2014; Zhang, Feng, et al., 2019). In contrast to the lack of relationship between richness and temporal stability, we found consistent positive asynchrony–stability relationships across and within the six natural grasslands. This is in agreement with empirical (Loreau & de Mazancourt, 2008), single-site (Zhang et al., 2018) and global-scale (Hautier et al., 2014, 2020) studies that reported similar relationships. However, we did not find significant relationships between species stability and ANPP stability, suggesting that species stability does not contribute to ecosystem stability but species asynchrony does, at least in our study sites in Inner Mongolia. Following the positive relationship between stability of ANPP and species asynchrony, we tested for a probable dependency of asynchrony on species richness. We found no species richness–asynchrony relationship, and this further revealed

the disconnect between richness and stability in the six natural grasslands.

We also investigated how extreme drought impacted ANPP stability through species richness, species asynchrony, and species stability in the six natural grasslands. As found in the grasslands under ambient conditions, our bivariate regressions showed species richness did not directly contribute to ANPP stability under extreme drought, both across and within the sites, which is contrary to previous report of the ANPP stability–species richness relationship (Wagg et al., 2017). Even in relatively high diversity site B, species richness declined while species asynchrony and stability of ANPP increased under drought. This suggests that species richness is not directly responsible for stability as found in most of the previous studies (Hautier et al., 2014; Zhang et al., 2018). The bivariate regressions showed species asynchrony positively contributed to stability of ANPP independent of species richness under drought. Additional regression analyses were conducted using data combined from both ambient and drought conditions to determine whether the results from the decomposed data were driven by low sample size. These analyses yielded similar bivariate relationships. Instead, SEM analysis revealed species richness contributions to stability of ANPP were indirect through species asynchrony under drought. This SEM finding thus confirms the existing theoretical (Loreau & de Mazancourt, 2013; Wang & Loreau, 2014, 2016) and empirical (Hautier et al., 2014, 2020; Hector et al., 2010; Wilcox et al., 2017) studies that linked the stabilising role of species richness to asynchrony in response to environmental variability.

Consistent with theoretical predictions (Wang & Loreau, 2014, 2016) and experimental findings (Hautier et al., 2020; Zhang, Feng, et al., 2019), our SEM results further revealed that species stability promoted stability of ANPP under drought, though independent of species richness. More importantly, SEM revealed that drought neither directly nor indirectly reduced stability of ANPP through species stability, rather it reduced stability of ANPP by diminishing the contribution of species richness to asynchrony. Thus, by linking the SEM and ANOVA results, we can conclude that the overall 5% reduction in species stability due to drought was not enough to directly or indirectly trigger a negative impact on stability of ANPP, whereas the 9% reduction in species asynchrony due to 25% reduction in species richness did. However, the contrasting bivariate relationships and SEM results could be attributed to low explanatory power of bivariate regressions compared to SEM in understanding complex interdependent ecological mechanisms (Fan et al., 2016; Grace et al., 2016).

Nevertheless, our consistent finding of positive impact of species asynchrony on stability of ANPP under ambient and drought conditions indicates that extreme drought did not erode asynchrony–stability relationships across or within the six natural grasslands. This finding is similar to how asynchrony positively drives ANPP stability under other global changes, like warming or eutrophication (Hautier et al., 2014, 2020; Ma et al., 2017). Despite that the SEM analysis showed that extreme drought indirectly reduced species asynchrony by reducing species richness, species asynchrony was nearly fourfold more important to stability of

ANPP than species stability. This result, unlike the previously reported prevalence of species stability under nutrient enrichment (Hautier et al., 2020; Zhang, Feng, et al., 2019), indicates that species asynchrony is the main mechanism that stabilises ANPP under extreme drought. Our within-site bivariate relationships between asynchrony and stability of ANPP, and that of other variables in this study, should be treated with caution because their regressions were based on a relatively small sample size (Jenkins & Quintana-Ascencio, 2020).

Given that the stability of productivity is a ratio of the temporal mean to the temporal variation (Hautier et al., 2015; Tilman, 1999), there is the possibility that species asynchrony maintained the stability of ANPP under extreme drought via a decrease in temporal standard deviation of ANPP (Hautier et al., 2014), or increase in the temporal mean of ANPP (Hautier et al., 2015; Hector et al., 2010; Tilman et al., 2006). Here we consistently found a negative relationship of asynchrony with temporal variation of ANPP both across and within sites. Overall, our results suggest that different mechanisms determine the response of different grasslands to extreme drought, but species asynchrony, not species richness or species stability, consistently buffers ecosystem stability against extreme drought across and within grasslands spanning a broad precipitation gradient. Species asynchrony promoted and maintained ecosystem stability by decreasing the temporal variability of ANPP under drought. Thus, species asynchrony may be a more general mechanism for promoting stability of ANPP in grasslands in the face of intensified drought.

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AUTHORS' CONTRIBUTIONS

Q.Y. and M.D.S. conceived the study; T.O.M. analysed the data; T.O.M. and Q.Y. wrote the first draft; C.X., W.L. and X.Z. coordinated data collection, data and field management. All other authors edited and revised the paper.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.djh9w0vzk> (Muraina et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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