

LETTER

Extreme Drought Increases the Temporal Variability of Grassland Productivity by Suppressing Dominant Grasses

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ABSTRACT

Extreme droughts are intensifying, yet their impact on temporal variability of grassland functioning and its drivers remains poorly understood. We imposed a 6-year extreme drought in two semiarid grasslands to explore how drought influences the temporal variability of ANPP and identify potential stabilising mechanisms. Drought decreased ANPP while increasing its temporal variability across grasslands. In the absence of drought, ANPP variability was strongly driven by the dominant plant species (i.e., mass-ratio effects), as captured by community-weighted traits and species stability. However, drought decreased the dominance of perennial grasses, providing opportunities for subordinate species to alter the stability of productivity through compensatory dynamics. Specifically, under drought, species asynchrony emerged as a more important correlate of ANPP variability than community-weighted traits or species stability. Our findings suggest that in grasslands, prolonged, extreme droughts may decrease the relative contribution of mass-ratio effects versus compensatory dynamics to productivity stability by reducing the influence of dominant species.

1 | Introduction

The temporal variability of ecosystem productivity—defined as fluctuations in aboveground net primary productivity

(ANPP) over time—is critical for maintaining ecosystem functions and services (Tilman et al. 1998). Ecological theory presents two distinct mechanisms that explain ANPP variability in response to climate disruptions. One mechanism, grounded

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in biodiversity-ecosystem functioning (BEF) theory, posits that diversity reduces variability primarily through compensatory dynamics, where declines in abundance of some species are balanced by increases in others (Bai et al. 2004; Loreau et al. 2001). Alternatively, the mass-ratio hypothesis suggests that variability is primarily driven by the dynamics of dominant species (Avolio et al. 2019; Smith et al. 2020), with variability closely tied to the variability and functional traits of these key species (Luo, Muraina, et al. 2023; Luo, Shi, et al. 2023). While both theories consider species dominance, BEF emphasises species diversity and compensatory dynamics, whereas the mass-ratio hypothesis focuses on the traits of dominant species. The distinction between these mechanisms—compensatory dynamics versus mass-ratio effects—has important implications for managing ecosystems, ensuring food security and enhancing resilience, particularly in ecosystems with highly variable climates (Grman et al. 2010; Isbell et al. 2015).

Chronic water shortages and long-term extreme droughts are expected to become more common in grasslands in the coming decades due to global climate change (Bradford et al. 2020). These climate extremes are expected to increase ANPP variability (Hautier et al. 2015; He et al. 2022); thus, it is increasingly important to understand the ecological mechanisms that stabilise ANPP variability under drought. In ecosystems with strong dominance by one or few species, such as many grasslands, ANPP variability is often more closely tied to mass-ratio effects (i.e., the stability and functional traits of dominant species) than to compensatory dynamics (i.e., species richness and temporal asynchrony in species abundances) (Sasaki and Lauenroth 2011). However, it remains unclear whether ANPP during drought periods would be more stable (i.e., decreased ANPP variability) with higher species diversity and asynchrony (BEF theory) or with larger contributions from the traits of dominant species (mass-ratio hypothesis).

Grasslands cover more than 40% of Earth's ice-free land surface, and their productivity is predominantly water-limited, making it particularly important to understand how they respond to intensified droughts (Luo, Muraina, et al. 2023; Maurer et al. 2020; Yu et al. 2025). Many studies have demonstrated that drought can reduce ANPP and alter community diversity, composition and species turnover, but these effects vary across grassland types (Knapp et al. 2020; Smith et al. 2024). Such divergent patterns of drought-induced compositional shifts in grassland communities may alter the mechanisms underpinning the variability of ANPP, underscoring the need to improve understanding of stabilising mechanisms—specifically those that alleviate ANPP variability—under drought conditions.

We used a 6-year extreme drought experiment in Chihuahuan Desert and Great Plains grasslands to evaluate potential biotic drivers of temporal variability in ANPP (Collins et al. 2020; Figure S1). Specifically, we investigated the relative importance of five mechanisms of ANPP variability, classified into diversity mechanisms that support BEF theory: species asynchrony, species richness and functional diversity; and mass-ratio theory mechanisms: species stability and six

community-weighted mean (CWM) functional traits. We tested the hypotheses that (i) drought reduces ANPP while increasing its temporal variability by altering the drivers of ANPP variability, and (ii) drought weakens the influence of mass-ratio effects—driven by dominant species' traits and stability—on ANPP variability, making diversity mechanisms (e.g., species richness, functional diversity and species asynchrony) a more important driver of temporal variability in ANPP.

2 | Materials and Methods

2.1 | Site Description

This research occurred in the Sevilleta National Wildlife Refuge (SNWR) in central New Mexico, USA (34°20'20" N, 106°43'30" E), home to the Sevilleta Long-Term Ecological Research program (SEV-LTER). The two grasslands were located ~5-km apart and shared similar climate and soil conditions but differed in their dominant species (Brown and Collins 2023). The Chihuahuan Desert grassland is dominated by the stoloniferous *C₄* grass *Bouteloua eriopoda*, while the Great Plains grassland is dominated by the *C₄* bunchgrass *B. gracilis* (Loydi and Collins 2021; Figure S2). Livestock grazing has been excluded since 1973 following a century of rangeland use. Mean annual precipitation is 234 mm, with ~50% falling during the summer monsoon (June–September), and the remaining including a mixture of snow and rain throughout winter and spring (Brown and Collins 2023). This precipitation pattern creates distinct spring and fall growing seasons, with herbaceous plants—mostly perennials—dying back or going dormant between these seasons (Collins and Xia 2015).

2.2 | Experimental Design

Our drought experiment was established in a relatively homogeneous area of plant species composition at each site (Figure S1), as part of the Extreme Drought in Grasslands Experiment (EDGE, Song et al. 2024; Yu et al. 2025). We compared an extreme drought treatment against ambient rainfall (control plots)—with 10 replicates per treatment per site (Loydi and Collins 2021). The experiment began in spring 2012 (pre-treatment year), and we tracked ANPP from 2013 to 2018. Drought treatments were implemented with rainout shelters that intercepted 66% of growing season precipitation (April–September). Rainout shelters were 2.5 m tall, allowing air exchange near the surface and minimising the effects of microclimate, causing minimal change (~0.4°C) to mean growing season air temperature (mean ± SE: shelter 22.84°C ± 0.86°C; control 22.42°C ± 0.86°C). Each plot included an external buffer to minimise edge effects associated with the infrastructure, and the experimental plots (3 m × 4 m) under shelters were hydrologically isolated from the surrounding soil matrix by aluminium flashing to a depth of 15 cm (Rudgers et al. 2023). Control plots had no overhead infrastructure and were spatially paired with drought plots into blocks to account for site spatial heterogeneity (Loydi and Collins 2021).

2.3 | Precipitation Treatment Effectiveness

Ambient growing season precipitation varied at both sites over the 6-year period with all years bracketing the long-term mean (approx. 50th percentile of historic amounts; Figure S1c). The drought treatment reduced precipitation close to the 5th percentile in each experimental year in both grasslands (Figure S1c). Accordingly, the drought treatment simulated a 1-in-20-year drought during the study period, reducing growing season precipitation amount without altering precipitation event number or frequency (Figure S1c).

2.4 | Data Collection

In 2012, four permanent 1 m² quadrats were established in each plot. Plant community composition was surveyed in the four quadrats in May when cool season annuals were abundant and in September or October during peak biomass of perennials and warm season annuals. The aerial coverage (to the nearest 0.1%) and height of each living plant species was recorded in each plot annually from 2013 to 2018. The biomass of each species was calculated using the best climate-invariant allometric model, which included species cover and height measurements (Rudgers et al. 2018, 2019). For each species, we used the highest annual biomass value (either spring or fall) for analyses. This non-destructive approach allowed us to sample species composition and ANPP in the same permanent quadrats in each site over time.

We measured six plant traits associated with grassland responses to drought: specific leaf area (SLA; leaf area per dry mass, cm² g⁻¹), leaf dry matter content (LDMC; leaf dry mass per fresh mass, g g⁻¹), stem dry matter content (SDMC, stem dry mass per fresh mass; g g⁻¹), stem tissue density (SD, stem dry mass per volume; g cm⁻³), root dry matter content (RDMC, root dry mass per fresh mass; g g⁻¹) and root tissue density (RD, root dry mass per volume; g cm⁻³). We measured traits of plants collected between 2017 and 2021 from ambient plots to minimise destructive sampling. The final trait dataset included mean trait values for 75 species cumulatively representing, on average, 90% plant cover in each plot at each site.

2.5 | Mechanisms of ANPP Variability—Metrics

We aimed to determine the relative importance of five mechanisms underpinning ANPP variability, as well as how the relative importance shifts under extreme drought. The mechanisms were binned into two groups: diversity effects (BEF theory and compensatory dynamics), represented by species asynchrony, species richness and functional diversity, and mass-ratio effects, represented by species stability and the six CWM traits.

We calculated the variability of ANPP for each quadrat as the standard deviation (σ) of ANPP over 6 years (2013–2018), where σ is given by:

$$\sigma = \sqrt{\frac{1}{n} \sum_{i=1}^n (x_i - \bar{x})^2}$$

In this equation, x_i represents the ANPP for year i , $\bar{x}$ is the temporal mean of ANPP across the 6 years, and $n = 6$ is the number of years. To estimate species stability, we first calculated the temporal stability of individual species in each quadrat as the ratio of the inter-annual mean of community biomass to its standard deviation over the six drought years. Species stability was then determined as the abundance-weighted mean of temporal stability across all species within the quadrat.

We quantified CWM traits as $CWM = \sum_{i=1}^S p_i x_i$, where p_i is the relative abundance of species i in the community of the experiment, x_i is the trait value of species i from outside the experiments and S is the species number in the plant community per quadrat in the last treatment year. Additionally, we determined community functional diversity as functional dispersion (i.e., the multivariate equivalent of mean absolute deviation in trait space using all species) in each quadrat in the last treatment year using the *FD* package.

During each sampling period, species richness was recorded as the number of different species in each quadrat in the last treatment year. We calculated species asynchrony in each quadrat as log variance ratio multiplied by -1 (Lepš et al. 2018):

$$\text{Species asynchrony} = -\log \left(\frac{\text{var} \left(\sum_{i=1}^S x_i \right)}{\sum_{i=1}^S \text{var}(x_i)} \right)$$

In this equation, x_i is the vector of aboveground biomass of species i in a quadrat with S species over six years.

2.6 | Statistical Analyses

All statistical analyses were performed using *R* version 4.1.2. We used generalised linear mixed-effects models from the *glmmTMB* package to test the drought effects on the temporal mean and variability of ANPP, as well as species stability, species asynchrony, species richness, functional dispersion and CWM trait values, both at the site level and across the two sites (hypothesis i). For the site-level model, treatment and site were fixed factors, with block and quadrat as random factors. In the across-site model, treatment was the fixed factor, and site, block and quadrat were random factors.

We used piecewise structural equation models (SEMs) to understand the relative impacts of mechanisms on ANPP variability across both sites under ambient versus drought conditions (hypothesis ii). The a priori SEMs were informed by existing literature and incorporated hypothesised direct and indirect causal mechanisms (Figure S3). We constructed separate SEMs for the control and drought treatments across both grasslands. Given multiple candidate variables for CWM traits—two each for leaf, stem, and root traits—we initially included one or two traits from each organ in the models. Similarly, for plant diversity, we initially incorporated one candidate variable (either species richness or functional dispersion) in each model. The final model for each treatment was selected based on the highest explained variation in ANPP variability and a non-significant Chi-square

test ($p > 0.05$) for model fit. Relationships between dependent and independent variables were modelled using linear mixed models with the *lmer* function in the *lme4* package, and the *psem* function in the *piecewiseSEM* package was used for model analysis. In these models, site, block and quadrat were used as random factors. The overall fit of each SEM was evaluated using Shipley's test of d-separation (Fisher's C statistic, $p > 0.05$ for a good fit) (<https://github.com/jslefcche/piecewiseSEM>).

3 | Results

3.1 | ANPP Variability and Its Drivers

Extreme drought reduced mean ANPP by 74% in the Chihuahuan Desert grassland but by only 36% in the Great Plains grassland (Table S1, Figure 1a). Across both sites, drought reduced the temporal mean of ANPP by 59% but the effect on temporal variability also differed by site (Table S1, Figure 1). Drought reduced ANPP variability by 13% in the Chihuahuan Desert grassland but increased it by 49% in the Great Plains grassland (Table S1, Figure 1b).

Experimental drought altered CWMs of several functional traits in Chihuahuan Desert and Great Plains grasslands (Table S1, Figure 2a,b). Specifically, CWMs of SLA, LDMC, SD, RDMC and RD decreased in response to drought in both grasslands (all $p < 0.05$; Figure 2). In contrast, CWMs of SDMC decreased in the Chihuahuan Desert grassland ($p < 0.001$) but were unaffected by drought in the Great Plains grassland (Table S1, Figure 2c).

Under ambient precipitation, species richness was 80% greater in the Chihuahuan Desert grassland compared to the Great Plains grassland (9 vs. 5 per m^2 ; Figure 2g). Experimental drought did not alter species richness in the Chihuahuan Desert grassland but increased species richness in the Great Plains grassland (Table S1, Figure 2g). Functional dispersion increased with drought in both grasslands (Table S1, Figure 2h). In contrast,

drought reduced species stability by ~68% in both grasslands (Table S1, Figure 2j). Drought had no effect on species asynchrony in either grassland (Table S1, Figure 2i).

3.2 | Relative Importance of Mechanisms Underpinning ANPP Variability

The SEMs revealed clear differences in the mechanisms underlying ANPP variability in drought versus ambient conditions. Under ambient conditions (control plots), ANPP variability was negatively correlated with both species stability and species asynchrony, with species stability playing a more than 50% stronger role in reducing ANPP variability than asynchrony (path [i.e., standardised coefficient] = -0.55 for stability vs. -0.35 for asynchrony; Figure 3a). However, extreme drought reversed the relative importance of species stability and asynchrony to ANPP variability. Specifically, under extreme drought, species asynchrony had a more than 100% stronger negative effect on ANPP variability than species stability (path = -0.28 for stability vs. -0.58 for asynchrony), although both contributed significantly to reducing ANPP variability (Figure 3b). Neither species richness nor functional dispersion had significant direct or indirect effects on ANPP variability under either ambient (Figure 3a) or drought conditions (Figure 3b).

The potential influence of CWM traits on ANPP variability was stronger under ambient than drought conditions, although greater variability in ANPP tracked higher SLA or higher LDMC under both drought and ambient conditions (Figure 3). Under ambient conditions, CWMs of both SLA and LDMC negatively influenced ANPP variability indirectly through a positive association with species stability (SLA: path = $0.28 \times (-0.55) = -0.15$; LDMC = $0.80 \times (-0.55) = -0.44$; Figure 3a), whereas CWMs of SLA positively impacted ANPP variability indirectly via decreasing species asynchrony (path = $(-0.30) \times (-0.35) = 0.09$; Figure 3a). Consequently, the total effects of CWM traits on ANPP variability were negative, with a combined path coefficient of -0.50 (path = $(-0$

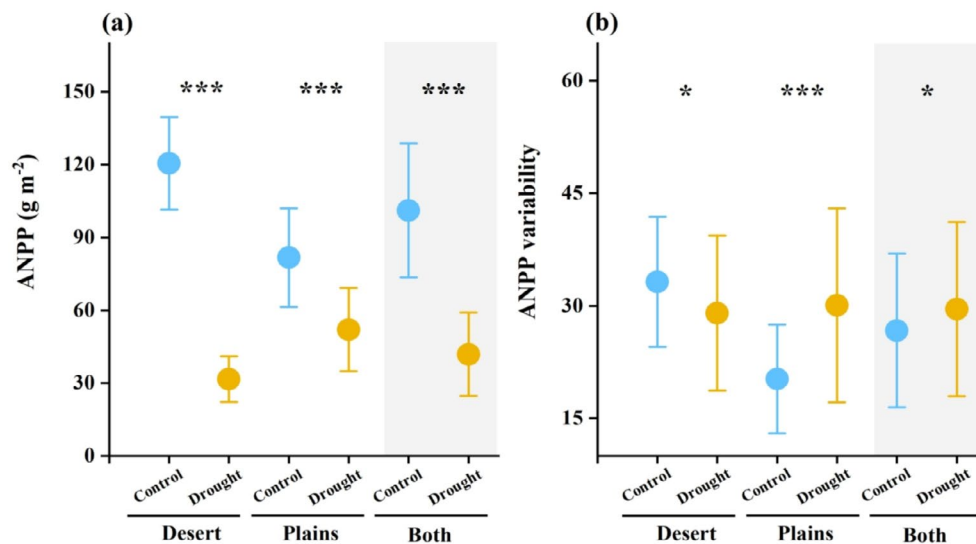


FIGURE 1 | Effects of experimental drought on temporal means and variability of aboveground net primary productivity (ANPP) in Chihuahuan Desert and Great Plains grasslands. Asterisks represent * $p < 0.05$ and *** $p < 0.001$. Error bars indicate standard deviation.

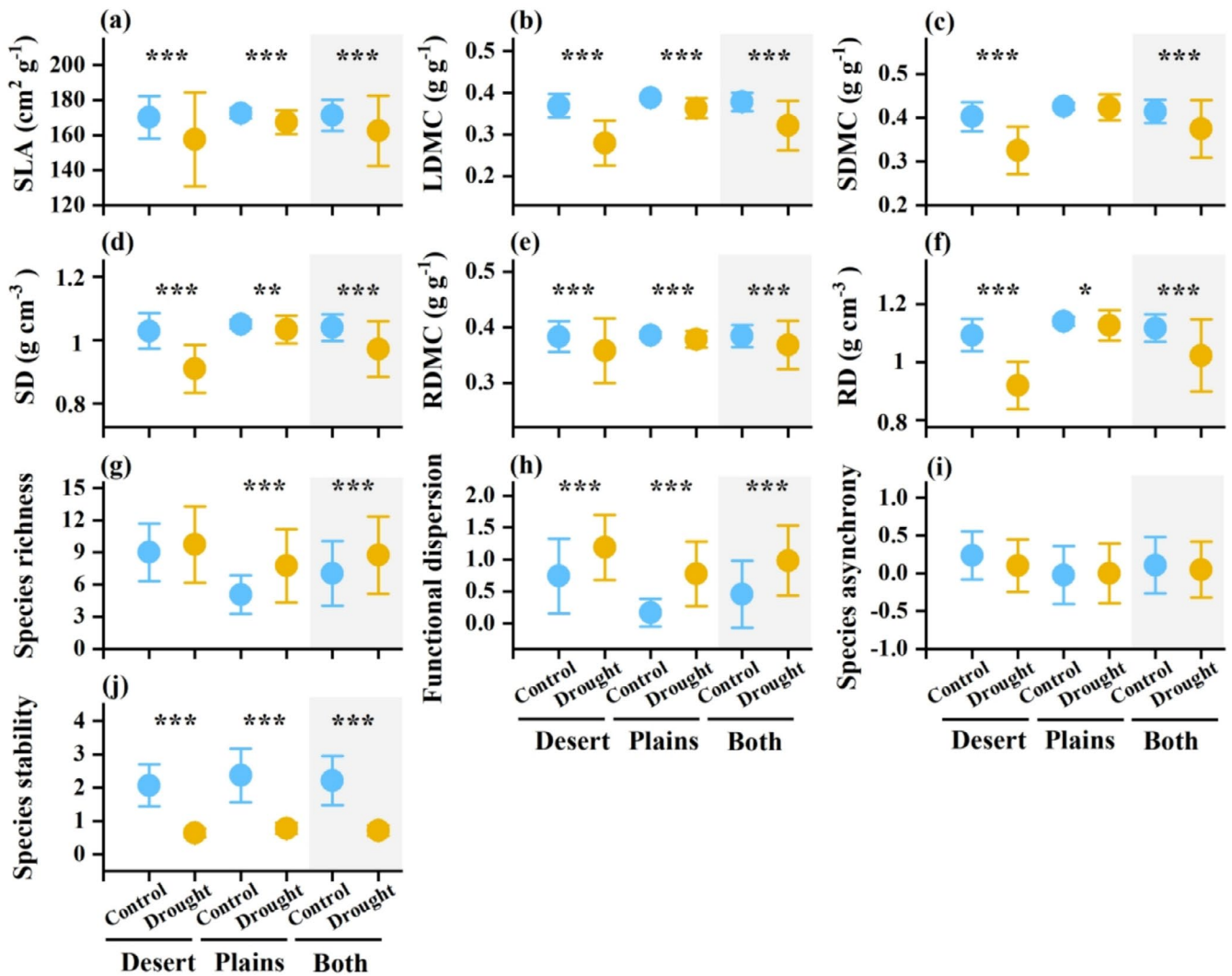


FIGURE 2 | Effects of experimental drought on (a–f) community-weighted means (CWMs) of specific leaf area (SLA), leaf dry matter content (LDMC), stem dry matter content (SDMC), stem tissue density (SD), root dry matter content (RDMC), root tissue density (RD), (g) species richness, (h) functional dispersion, (i) species asynchrony and (j) species stability in Chihuahuan Desert and Great Plains grasslands. Asterisks represent * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$. Error bars indicate standard deviation.

.44) + (−0.15) + 0.09; Figure 3a). Similarly, under extreme drought, CWMs of SLA and SDMC were also associated with lower ANPP variability through their positive effects on species stability (SLA: path = $0.37 \times (-0.28) = -0.10$; SDMC: path = $0.29 \times (-0.28) = -0.08$; Figure 3b). However, the total effect of CWM traits on ANPP variability was less negative under drought, with a combined path coefficient of −0.18 (path = (−0.10) + (−0.08); Figure 3b).

4 | Discussion

Extreme drought had a larger negative effect on ANPP in the Chihuahuan Desert grassland than in the Great Plains grassland, and had contrasting effects on ANPP variability—reducing it in the Chihuahuan Desert but increasing it in the Great Plains (Figure 1). The declines in average ANPP at both grasslands are consistent with previous findings (Knapp and Smith 2001; Luo et al. 2021). Despite similar climatic conditions at both sites, experimental drought had contrasting impacts on ANPP and its

temporal variability. This suggests that factors beyond climate, such as plant functional traits and species composition, play key roles in modulating drought impacts across these common ecosystems (Muraina et al. 2021; Song et al. 2024).

Our results indicate that the mass-ratio hypothesis (and species dominance) plays a greater role than biodiversity or compensatory dynamics in reducing ANPP variability in both grasslands, at least under ambient conditions. Specifically, CWM trait values and species stability, both of which are heavily weighted by the influence of dominant species, significantly reduced ANPP variability under ambient rainfall conditions (Figure 3 and Figure S4). This finding is unsurprising, as each grassland in our study is strongly dominated by a single species that contributes a substantial portion of productivity, akin to other dryland ecosystems (Rudgers et al. 2018; Figure S2). This result also suggests that ANPP variability in these ecosystems under environmental fluctuations is closely tied to the sensitivity of the dominant species (Hallett et al. 2014; Smith et al. 2020). ANPP variability also declined with species asynchrony under

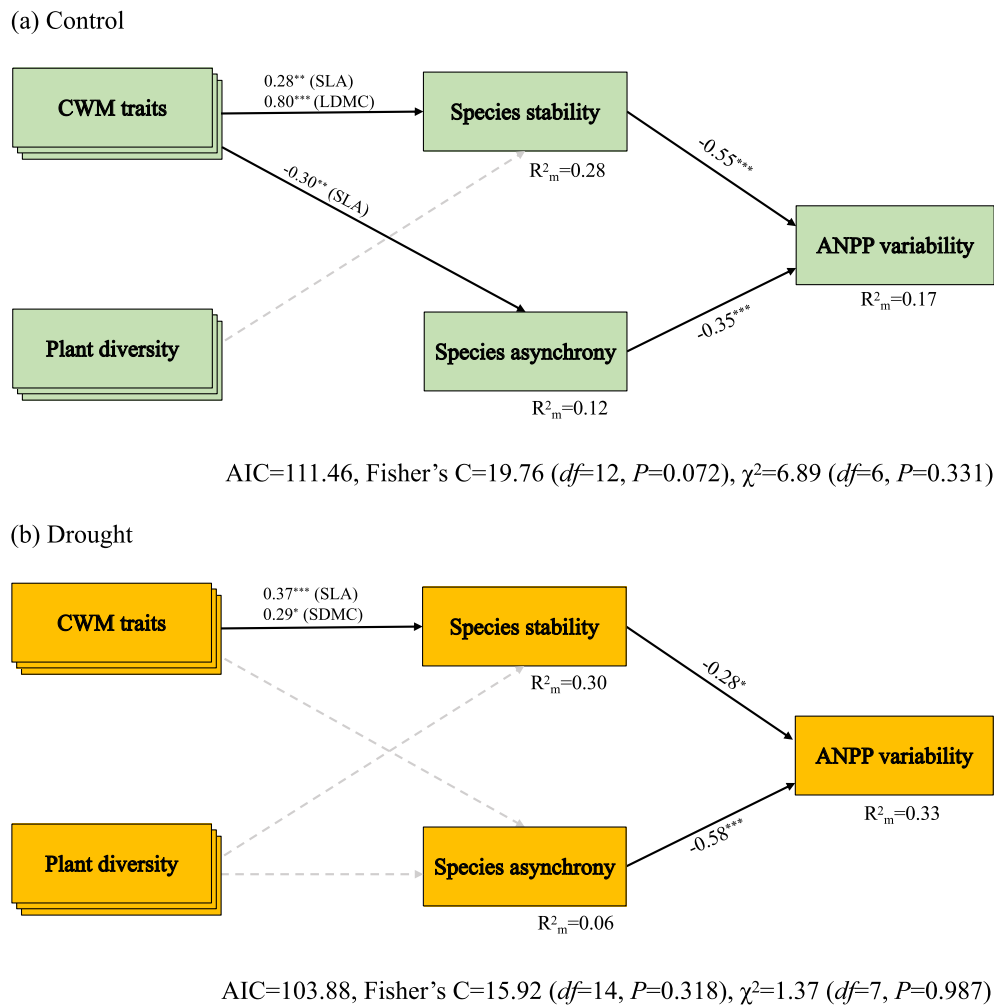


FIGURE 3 | Piecewise structural equation models (SEMs) showing the direct and indirect effects of community-weighted mean (CWM) traits (i.e., specific leaf area [SLA], leaf dry matter content [LDMC] and stem dry matter content [SDMC]), plant diversity (i.e., species richness and functional dispersion), species asynchrony and species stability on the temporal variability of aboveground net primary productivity (ANPP) in Chihuahuan Desert and Great Plains grasslands under (a) control (ambient) conditions or (b) extreme drought conditions. The model was fitted using non-standardised values first, and the overall fitting statistics correspond to these values. Solid black arrows show significant effects and dashed grey arrows show non-significant effects. Numbers next to the solid arrows represent the standardised path coefficients. Asterisks represent * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$.

ambient precipitation in each grassland; however, species asynchrony was less important than species stability in explaining ANPP variability (Figure 3). These results suggest that mass-ratio effects predominantly govern ANPP and its variability in these semiarid ecosystems (Avolio et al. 2019; Smith et al. 2020). However, it is important to note that the dominance of a single species in these ecosystems likely contributes a substantial portion of both overall productivity and variability. Consequently, the strong correlation between ANPP variability and the mass-ratio effect may reflect this dominance, even if the relationship is not directly causal.

Under drought conditions, species asynchrony appeared to play a more important role than dominant species in stabilising ANPP (Figure 3 and Figure S4). This shift from mass-ratio to diversity-driven mechanisms of stability occurred because long-term extreme drought suppressed the dominant grasses (i.e., species stability and CWM traits; Figure S2), creating opportunities for subordinate species to limit ANPP variability through interspecific compensatory dynamics. The relative suppression

of dominant grasses under drought highlights a critical drought-induced shift in the mechanisms driving variability of grassland productivity. When dominant species are less prevalent, subordinate species, despite their lower productivity, can play more significant roles in the variability of ANPP, by contributing biomass and functions that collectively buffer grasslands against environmental fluctuations (Arnillas and Cadotte 2019). Similarly, a 6-year experiment in a drier, hotter grassland in southern New Mexico found that increased precipitation variability favoured rare plant species, which peaked under extreme wet conditions, partly offsetting declines in ANPP from precipitation manipulations (Gherardi and Sala 2015a, 2015b). Thus, a general pattern may occur in which the degree of drought interacts non-additively with climate variability to change the mechanisms that stabilise ANPP. We propose that the predicted drier and more variable climate of future grasslands (Maurer et al. 2020; Rudgers et al. 2018) enhances biodiversity's role in ecosystem stability through species asynchrony. Our findings underscore the enhanced role of diversity—most notably species asynchrony—in stabilising essential grassland functions

and services under extreme drought. This insight is particularly relevant for semiarid grasslands, where water limitation is common and likely to become more severe in the future (Bradford et al. 2020).

Neither species richness nor functional diversity were directly or indirectly related to ANPP variability during drought, as supported by our SEM results. This finding aligns with other global change experiments which found that a weaker diversity–stability relationship in fertilised grasslands was not caused by species loss after eutrophication. These results suggest that, despite the potential for diversity to stabilise ecosystems through compensatory and other mechanisms, it is not the primary driver of ANPP variability in these grasslands under extreme conditions. Instead, species-level temporal dynamics (i.e., asynchrony) appeared to be more critical to grassland variability than overall species diversity. This finding highlights that plant diversity in dryland grasslands primarily consists of subordinate species that contribute relatively little to variability in ANPP (Hautier et al. 2014; Muraina et al. 2021).

SEM results imply that grassland communities with high SLA combined with high LDMC (under ambient conditions) or SDMC (under drought) tend to be more stable in their productivity (Figure 3). Functionally, high SLA supports rapid resource acquisition and efficient photosynthesis which, during intermittent drought or ambient conditions, facilitates rapid growth when water is available (Lepš et al. 2018; Levine et al. 2025). In contrast, high LDMC or SDMC—reflecting thicker cell walls and denser tissues—enhances resistance to water loss and cellular stress during prolonged drought (Luo, Shi, et al. 2023; Levine et al. 2025). These results suggest that functional traits such as SLA, LDMC and SDMC play a key role in sustaining grassland productivity by mitigating fluctuations in ANPP across different soil moisture regimes.

In conclusion, our study investigated the mechanisms through which long-term extreme drought influences the temporal variability of ANPP in both Chihuahuan Desert and Great Plains grasslands. Under ambient conditions, the variability of ANPP was primarily driven by mass-ratio effects, such as community-level traits and species stability. However, under a future drier climate, results from the drought treatment predict an increasing relative importance of diversity mechanisms, primarily through species asynchrony. This drought-induced shift in the mechanisms determining ANPP stability underscores the importance of biodiversity effects, including compensatory dynamics of diverse species, in buffering grasslands against the adverse effects of climate change. These results suggest that extreme drought amplifies the role of compensatory dynamics over mass-ratio effects in determining grassland productivity, emphasising the need to consider the interplay of different mechanisms under multiple climatic conditions when assessing grassland responses to climate change.

Author Contributions

A.K.K., M.D.S. and S.L.C. designed the experiment. W.L., N.T. and N.I.I. conceived of the analyses. S.L.C. performed the experiments. W.L., N.I.I. and T.O.M. wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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Data Availability Statement

The datasets and R scripts generated in this study are available in the Zenodo repository (<https://doi.org/10.5281/zenodo.15036719>), which were derived from Baur et al. (2024, <https://doi.org/10.6073/pasta/8d28fa9c31095c4c15836cbd3467f0d1>) and Farkas et al. (2021, <https://doi.org/10.6073/pasta/5b3a6d80a1c6d3121a2196cb40838849>).

Peer Review

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Supporting Information

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