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Responses of a semiarid grassland to recurrent drought are linked to community functional composition

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Abstract

Recurrent droughts are an inevitable consequence of climate change, yet how grasslands respond to such events is unclear. We conducted a 6-year rainfall manipulation experiment in a semiarid grassland that consisted of an initial 2-year drought (2015–2016), followed by a recovery period (2017–2018) and, finally, a second 2-year drought (2019–2020). In each year, we estimated aboveground net primary productivity (ANPP), species richness, community-weighted mean (CWM) plant traits, and several indices of functional diversity. The initial drought led to reduced ANPP, which was primarily driven by limited growth of forbs in the first year and grasses in the second year. Total ANPP completely recovered as the rapid recovery of grass productivity compensated for the slow recovery of forb productivity. The subsequent drought led to a greater reduction in total ANPP than the initial drought due to the greater decline of both grass and forb productivity. The structural equation models revealed that soil moisture influenced ANPP responses directly during the initial drought, and indirectly during the subsequent drought by lowering functional diversity, which resulted in reduced total ANPP. Additionally, ANPP was positively influenced by CWM plant height and leaf nitrogen during the recovery period and recurrent drought, respectively. Overall, the greater impact of the second drought on ecosystem function than

the initial drought, as well as the underlying differential mechanism, underscores the need for an understanding of how increased drought frequency may alter semiarid grassland functioning.

INTRODUCTION

Extreme droughts are expected to occur more frequently in certain regions over the next century (Spinoni et al., 2014). The economic, social, and environmental losses associated with drought are of increasing concern across the globe. Understanding the negative effects of extreme drought is especially important in grassland ecosystems, given that grasslands are particularly vulnerable to alterations in water availability (Maurer et al., 2020). Over the last few decades, there has been an increase in the number of manipulative experiments assessing grassland responses to extreme drought around the world (e.g., Jung et al., 2014; Luo et al., 2021). Yet these drought effects on grasslands are usually measured in response to a single, intense drought event, whereas climate change is expected to increase not only the severity but the frequency of droughts (Spinoni et al., 2014).

Legacies from past climate anomalies can precondition grassland ecosystems and influence their response trajectory to subsequent events (Müller & Bahn, 2022). Thus, ecosystem responses to recurrent drought may not be predictable from studies of single drought events (Korell et al., 2020; Slette et al., 2022). Although the relevance of drought legacies on ecosystem structure and function has been increasingly acknowledged in recent years, only a few case studies have examined the consequences of recurrent droughts on primary production, community composition, and plant traits (Anderegg et al., 2020). Results from these recurrent drought studies vary and depend on plant species composition, community structure, and type of ecosystem. For example, some studies found increased drought tolerance following the adaptation of ecosystem functioning to previous drought (i.e., ecological memory; Walter et al., 2013). In contrast, Slette et al. (2022) demonstrated that repeated droughts decreased belowground productivity more than twice as much as a single drought in a mesic grassland. Hence, the understanding of how drought legacies modulate ecosystem responses to subsequent droughts is still incomplete, and the potential impacts of recurrent droughts on ecosystem functioning, ranging from increased acclimation to increased sensitivity, remain unresolved.

The effects of recurrent drought on aboveground net primary productivity (ANPP) might deviate from the impact of single droughts due to the legacy effects of initial drought on plant community composition and ecosystem functioning (Backhaus et al., 2014). For example, initial drought can reduce species diversity, potentially exacerbating ecosystem responses to subsequent drought, as the ANPP of species-rich communities tends to be more resistant to climate extremes than that of species-poor communities (Loreau et al., 2021). Additionally, species-rich communities are more likely to include particular species with a strong influence on ecosystem functioning (i.e., the selection effect; Loreau et al., 2021). Community and ecosystem responses to subsequent drought may also be influenced by shifts in functional trait composition during the initial drought (Müller & Bahn, 2022). Some studies have investigated the role of functional diversity (i.e., the range and distribution of traits within a community) in buffering the effects of extreme drought on grassland ecosystem function (Díaz et al., 2007; Griffin-Nolan et al., 2019). High taxonomic and functional diversity can decrease the impact of climate extremes on ANPP because (1) functionally distinct species promote the overall resource-use efficiency of the community, and/or (2) multiple species with similar functions or traits can compensate for each other if one suffers mortality during drought (Loreau et al., 2021).

Further, the functional traits of dominant species are another potential driver of grassland responses to drought, because these dominant species make up the largest proportion of the community (Grime, 1998). This dominance effect can be estimated using community-weighted mean (CWM) traits (i.e., the average trait value weighted by the relative abundance of each species), which is a community-aggregated metric representative of the traits of the most abundant species within a community (Díaz et al., 2007). Shifts in CWM traits following drought are well documented in grassland ecosystems (Griffin-Nolan et al., 2019). These adaptations usually involve an increase in the dominance of drought-adapted species and increased variation in plant traits at the community level (Jung et al., 2014). Such a shift in functional composition can mediate plant community responses to recurrent

drought. For example, drought can increase the relative abundance of species with resource-conservative traits (e.g., low specific leaf area [SLA] and high leaf dry matter content [LDMC]), which may buffer against declines in ANPP (Jung et al., 2014; Majekova et al., 2014). Similarly, drought can increase the abundance of species with drought-tolerant hydraulic traits to buffer the productivity dynamics during subsequent droughts (Trugman et al., 2021). Overall, whether ecosystems are more or less vulnerable to a recurrent extreme drought depends on plant community composition and its response to initial drought (Anderegg et al., 2020; Ogle et al., 2015); however, we currently lack a thorough understanding of the role that community composition may play in ecosystem responses to recurrent drought in semiarid grassland ecosystems that are highly sensitive to changes in soil moisture availability.

We conducted a three-stage extreme drought experiment in a semiarid grassland in northern China that consisted of an initial drought in 2015 and 2016 followed by a 2-year recovery period (2017–2018), and a subsequent drought in 2019 and 2020. We used structural equation modeling (SEM) to investigate how multiple dimensions of community composition (i.e., species richness, CWM traits, and functional diversity) influenced the response of ANPP to repeated drought events. We tested the hypothesis that recurrent drought would have a similar influence on ecosystem function (i.e., ANPP) as a single drought. This hypothesis is based on expected shifts in community composition following the initial drought. Specifically, we expected that the initial drought would reduce species and functional diversity and lead to a shift in community-weighted trait values toward more conservative traits. Given that the drought sensitivity of ANPP increases with reduced species and functional diversity, but decreases with an increased abundance of species with conservative traits, these two predicted alterations to community composition are likely to have counteracting effects on ecosystem responses to subsequent drought. Therefore, we predict that the effect of subsequent drought on ecosystem function should depend on the relative influence of community-weighted traits vs. species and functional diversity on drought sensitivity and the relative responses of each of these metrics of community composition to drought treatments.

MATERIALS AND METHODS

Study sites

We conducted our drought experiment at the Erguna Forest-Steppe Ecotone Research Station, a semiarid grassland in northeastern Inner Mongolia, China (50°10′46″ N, 119°22′56″ E) (Appendix S1: Figure S1). The experimental field was an intact, native grassland that had not been grazed by large ungulates for several years. The region is characterized by a temperate mid-continental climate, with a mean annual precipitation of 362 mm and mean annual temperature of $-2.4°C$, and deep Kastanozem soils. The dominant plant species in the grassland were the C_3 perennial grass, *Leymus chinensis*, and the C_3 perennial forb, *Pulsatilla turczaninovii*.

Experimental design

We conducted a recurrent drought experiment, consisting of two treatments: a control (ambient precipitation) and a drought (Appendix S1: Figure S1). The drought plots received the following three treatments: (1) an initial extreme drought treatment over 2 years (66% reduction in ambient growing season precipitation in 2015 and 2016), (2) a recovery treatment in the next 2 years (ambient rainfall in 2017 and 2018), and (3) a subsequent extreme drought treatment (66% reduction in growing season precipitation in 2019 and 2020).

To manipulate precipitation in drought plots, we used passive precipitation exclusion shelters constructed with light scaffolding and covered by strips of transparent polyethylene (Beijing Plastics Research Institute, Beijing, China) to reduce each precipitation event by ∼66% during the growing season (Appendix S1: Figure S1). This is the equivalent of an ∼50% reduction in annual precipitation because 60%–75% of annual precipitation falls during the growing season. This rainfall reduction treatment simulates a once-in-40-year event and meets the criteria that define an extreme drought event (Appendix S1: Figure S1). Twelve 6×6 m plots ($n = 6$ control; $n = 6$ drought) were arrayed in a block design ($n = 6$ blocks) with at least a 5-m distance between blocks (Appendix S1: Figure S1). All plots within a block (including the control) were located at least 2 m apart. We established a 5×5 m sampling plot in the center of each control plot and a 4×4 m sampling plot in the center of each drought plot. The control and drought plots included a 0.5 and 1-m buffer perimeter, respectively, to minimize edge effects. Prior to imposing experimental drought, we trenched the perimeter of each plot (both control and drought) to a depth of 1 m and lined the trench with 6-mm-thick plastic and metal flashing to hydrologically isolate the soil. The roofs of these shelters were 2.5 m high at the highest point, allowing for near-surface air exchange while avoiding unwanted greenhouse effects. The rainout shelters permitted more than 90% penetration of photosynthetically active radiation.

Measurements

In each year, we sampled from a 1×1 m quadrat, which was randomly established in each plot and split into four 50×50 cm subquadrats. The locations of quadrats in each treatment year were different to prevent resampling of the same quadrat for each year. We estimated ANPP by harvesting all aboveground biomass at its peak in mid-August of each year within two diagonal subquadrats in each plot. We sorted biomass by species before oven drying at $60°C$ for 48 h and weighing to the nearest 0.1 g. We measured the species richness of each subplot as the total number of plant species recorded within the 1 m² quadrat in which ANPP was measured.

Plant traits of the most abundant species were not measured in the drought-treatment plots to avoid destructive measurements and to determine trait composition under more common ambient conditions. All plant traits were estimated from 2015 to 2018 in each of the six control plots, following similar studies (Griffin-Nolan et al., 2019; Sandel et al., 2010). For each species, we averaged trait values across plots and years. Here, we focused on six key functional traits: plant height, SLA, LDMC, leaf carbon concentration (LCC), leaf nitrogen concentration (LNC) and leaf phosphorus concentration (LPC). The measurement approach of each trait is provided in Appendix S1. Additionally, we sampled soils every 2 weeks during the growing season (May–August) of 2015–2020 in each sampling plot to determine soil water content (calculated as the percentage of weight loss from fresh to dry soil).

Data analysis

We compared precipitation totals for the control and drought treatments with the estimated probability density functions (pdfs) of long-term growing season precipitation for this site. We analyzed plant community data using unconstrained ordination analysis of nonmetric multidimensional scaling (NMDS; Bray–Curtis dissimilarity) based on relative biomass data to assess community divergence between treatments across the 2 years of each experimental stage (i.e., initial extreme drought, recovery period, and subsequent extreme drought). The statistical significance of this difference was tested using permutational multivariate analysis of variance (PERMANOVA, permutations = 999) using the *vegan* R package.

We quantified the CWM of each plant trait as well as several metrics of community functional diversity (Díaz et al., 2007). CWM was calculated as: $CWM = \sum_{i=1}^{S} p_i x_i$, where p_i is the relative abundance (percentage biomass) of species i, x_i is the trait value of species i, and S is the species number in the plant community per plot.

We calculated four separate indices of functional diversity based on dissimilarity across all plant traits (Laliberté & Legendre, 2010). Specifically, we used a flexible distance-based framework and principal component analyses to estimate functional richness (FRic; the total volume of x-dimensional functional space occupied by the community), functional evenness (FEve; the regularity of spacing between species within multivariate trait space), functional divergence (FDiv; the divergence in the distribution of abundance in the trait volume) and functional dispersion (FDis; the multivariate equivalent of mean absolute deviation in trait space) (Laliberté & Legendre, 2010). Additional details on these four indices are provided in Appendix S1. We measured each index of CWM traits and functional diversity for each plot-year combination using the average species trait collected in the control plots during 2015–2018. Thus, the variation in CWM traits and functional diversity in response to drought represents species turnover and interspecific trait differences. Intraspecific trait variability and trait plasticity were not assessed, but these typically contributed substantially less to total trait variation than interspecific trait variability (Garnier et al., 2001). We calculated CWM traits and functional diversity using the *FD* package in R.

To test for significant differences in total ANPP and that of each functional type (i.e., grass vs. forb) in drought versus control plots, we constructed mixed-effects ANOVA models using the *lme* function from the *nlme* R package. Across the 2 years of each experimental stage (i.e., initial extreme drought, recovery period, and subsequent extreme drought), each ANOVA model included "drought treatment" and "year" as fixed effects and "block" as a random effect. When the interactive effects of drought treatment and year were significant, the mixed-effects ANOVA was separately applied within each year with "drought treatment" as a fixed effect and "block" as a random effect. Similar mixed models were run to test for significant differences in mean soil moisture and community composition (i.e., species richness, CWM traits, and functional diversity). To identify which species contributed to ANPP during drought, we estimated the effect of drought on each species by calculating the difference in biomass between drought and control plots.

Piecewise SEM, which allows the assessment of hypothesized causal relationships between variables, was used to examine the causal pathways (i.e., changing aspects of community composition) through which extreme drought affected total ANPP in each of the three experimental stages. Using knowledge from the literature and hypothesized causal relationships between variables (Appendix S1: Table S1), we developed an a priori piecewise SEM (Appendix S1: Figure S2). Given that we had

multiple candidate variables for CWM traits and functional diversity, we included one CWM trait and one functional diversity index in each initial model to obtain multiple possible models (Luo et al., 2021). We then selected the model with the highest explained variation of ANPP as the best-fitting model. The modified models were developed by removing direct and indirect pathways with low path coefficients, when the initial model did not produce an adequate fit. We included "block" and "year" as random factors in each piecewise SEM and fitted the component models of the piecewise SEM as linear models. We reported the standardized coefficient for each path from each component model. We evaluated the overall fit of the piecewise SEM using Shipley's test of d-separation, Fisher's C statistic (if $p > 0.05$, then no paths are missing and the model is a good fit), and AIC in the R package *piecewiseSEM*.

RESULTS

Precipitation and soil moisture

Growing season precipitation was close to the 50th percentile of historic amounts throughout the experiment (2015–2020) (Appendix S1: Figure S1 and Table S2). Furthermore, ambient growing season precipitation during the initial drought period (2015 and 2016) was similar to precipitation during the subsequent drought period (2019 and 2020) (Appendix S1: Figure S1 and Table S2). Both the initial and subsequent drought treatments reduced precipitation close to the 2.5th percentile of historical precipitation probability distribution functions based on long-term records of growing season precipitation (Appendix S1: Figure S1). Drought treatments significantly reduced average soil water content, corresponding to a 35% relative reduction in soil water content during both the initial and recurrent drought stages (Appendix S1: Figure S3). The soil water content in the treatment plots was still significantly lower compared with the control plots during the 2016–2017 growing seasons following the initial drought, indicative of a drought legacy during the recovery stage (Appendix S1: Figure S3).

Net primary productivity

Total ANPP in control plots did not vary significantly between the two drought periods (i.e., 2015–2016 vs. 2019–2020; Appendix S1: Table S2). The initial drought significantly decreased total ANPP by 37% and 31% in 2015 and 2016, respectively (Figure 1; Appendix S1: Table S3). The magnitude of drought effects on total ANPP did not differ significantly by treatment year (Figure 1; Appendix S1: Table S3). The initial drought reduced grass and forb ANPP by 24% and 48%, respectively in 2015, and by 43% and 22%, respectively in 2016 (Figure 1; Appendix S1: Table S3). Accordingly, the relative contribution of grass biomass to total ANPP (represented as the ratio of grass to forb productivity) increased in 2015 but decreased in 2016 (Figure 1).

Following the 2-year initial drought, the total ANPP and grass ANPP in the drought plots recovered to near the levels of the control plots in both recovery years, whereas forb ANPP was marginally lower in the treatment plots compared with the control plots (Figure 1; Appendix S1: Table S3). Accordingly, the relative contribution of grass biomass to total ANPP increased in both years (Figure 1). The drought had a negative legacy effect on the biomass of the dominant forb, *P. turczaninovii* during both recovery years (Appendix S1: Figures S4 and S5). The high resilience of total ANPP was driven by the strong recovery of the dominant grass, *L. chinensis* (Appendix S1: Figures S4 and S5), which compensated for the reduced growth of forbs, such as *P. turczaninovii* and *Artemisia frigida* (Appendix S1: Figures S4 and S5).

In the first year of the subsequent drought (2019–2020), total, forb and grass ANPP were lower in the treatment plots relative to the control plots (Figure 1; Appendix S1: Table S3). The response was greater in magnitude in the second year for total ANPP as well as both grass and forb ANPP separately (Figure 1; Appendix S1: Table S3). The relative contribution of grass biomass to total ANPP increased dramatically, especially in 2020 (Figure 1). The greater responses of total ANPP to subsequent drought in the second year corresponded with large reductions in ANPP of the dominant forb (e.g., *P. turczaninovii* biomass was zero in the treatment plots during the second drought) and dominant grass (e.g., *L. chinensis* biomass significantly declined from 74.28 to 32.71 g m^{-2}) (Appendix S1: Figure S5).

Species and functional diversity

Plant community composition was altered substantially by both the initial and subsequent droughts, with greater changes in community composition during the second drought (Figure 2).

We observed that the initial drought period marginally reduced total species richness in the first year and increased the richness of forbs in the second year (Appendix S1: Tables S3 and S4). During the recovery period, we observed a lower richness of grass species in treatment than in control plots in both years (Appendix S1: Tables S3 and S4). Finally, the subsequent drought reduced total species richness by 45% and forb
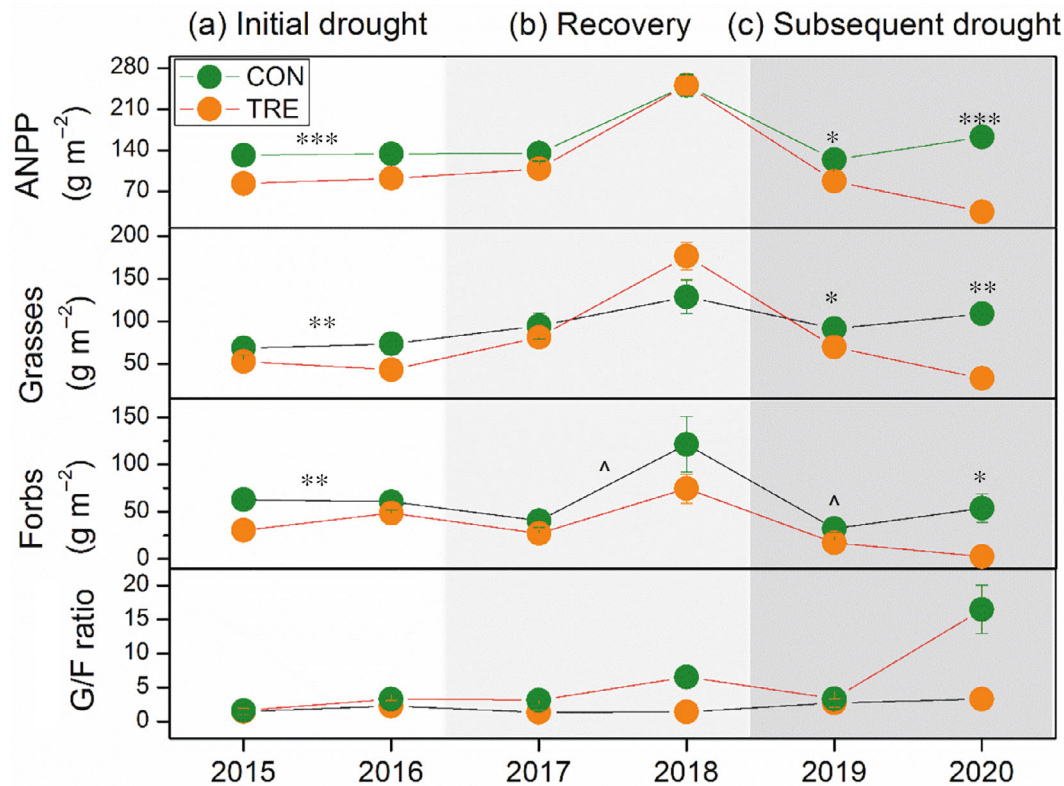
FIGURE 1 Effects of drought on aboveground net primary productivity (ANPP) (total, grass, and forbs) and ratio of grass and forb ANPP (G/F ratio) during initial drought (a), recovery stage (b), and subsequent drought (c). CON, control; TRE, treatment. ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$ and ^$p < 0.1$. When the drought effects were different between years, a symbol was separately placed above each year; when the responses were consistent between years, a symbol was only placed in the middle of the 2 years. See Appendix S1: Table S3 for ANOVA results.

richness by 60% in 2020 but not in 2019. However, subsequent drought had no impact on grass species richness in either year (Appendix S1: Tables S3 and S4).

The initial drought marginally reduced $FEve_T$ (subscript T, total) in both treatment years but did not alter $FRic_T$ or $FDiv_T$ in either treatment year (Appendix S1: Tables S3 and S4). The first year of the initial drought led to a significant increase (12%) in $FDis_T$, but this was not the case in the second year (Appendix S1: Tables S3 and S4). During the recovery years, we observed lower $FDis_T$ in the treatment plots compared with the control plots, but no differences in $FRic_T$, $FDiv_T$, or $FEve_T$ were observed (Appendix S1: Tables S3 and S4). The subsequent drought had no effect on $FRic_T$ and $FDiv_T$ but led to reduced $FEve_T$ and $FDis_T$ in both treatment years (Appendix S1: Tables S3 and S4).

Plant traits

We did not detect any significant effect of the initial drought on any of the community-weighted traits measured here (Appendix S1: Tables S3 and S4). During the recovery period, CWMs of plant height$_T$, LDMC$_T$, and LCC$_T$ were significantly higher in treatment plots than in control plots, whereas SLA$_T$ and LPC$_T$ in treatment plots were similar to those in control plots in either recovery year (Appendix S1: Tables S3 and S4). LNC$_T$ was significantly higher in treatment plots than in control plots in the first recovery year, but did not differ in the second recovery year (Appendix S1: Tables S3 and S4). Subsequent drought significantly increased plant height$_T$, LDMC$_T$, and LCC$_T$, but significantly reduced SLA$_T$ and LPC$_T$ in both treatment years (Appendix S1: Tables S3 and S4).

Drivers of productivity responses to drought

Linear regression models showed that ANPP was significantly correlated with plant height$_t$ during the initial drought stage and significantly correlated with FRic during the recovery stage. ANPP was significantly correlated with species richness, FRic, FDis, and most CWM traits (plant height, SLA, LDMC, LCC, and LPC) during the subsequent drought stage (Appendix S1: Table S5).

Using SEMs, we assessed the potential multivariate causal pathways through which drought impacted total
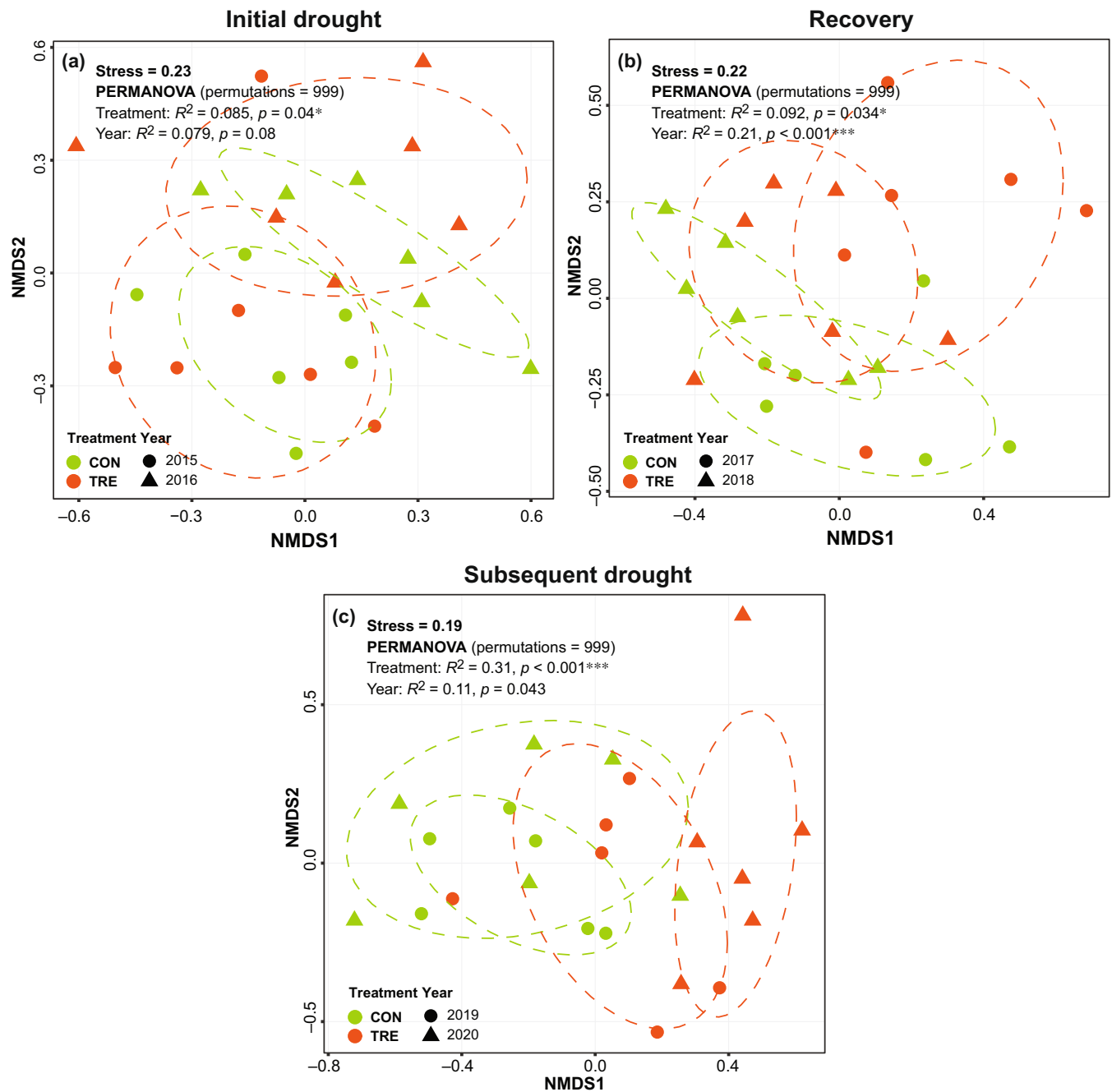
FIGURE 2 Biplots of nonmetric multidimensional scaling showing the changes in plant community composition in response to initial drought (a), recovery stage (b) and subsequent drought (c). CON, control; TRE, treatment. The dashed circle represents the 60% confidence ellipses for each treatment in each year.

ANPP at each of the three stages of the experiment (Figure 3). We observed a direct positive effect of soil moisture on total ANPP during the initial drought and recovery stages, but not during the subsequent drought stage (Figure 3). Soil moisture had an indirect positive effect on total ANPP via $FRic_T$ and $FDis_T$ during the recovery and subsequent drought, respectively, but not during the initial drought stage (Figure 3). Moreover, the positive effects of soil moisture on species richness did not affect total ANPP during the subsequent drought

stage (Figure 3). Total ANPP was also positively influenced by plant $height_T$ during recovery and LNC_T during the recurrent drought (Figure 3).

DISCUSSION

In this study, we assessed the impact of a repeated extreme drought on the functioning of native semiarid grassland. We aimed to identify the mechanisms and
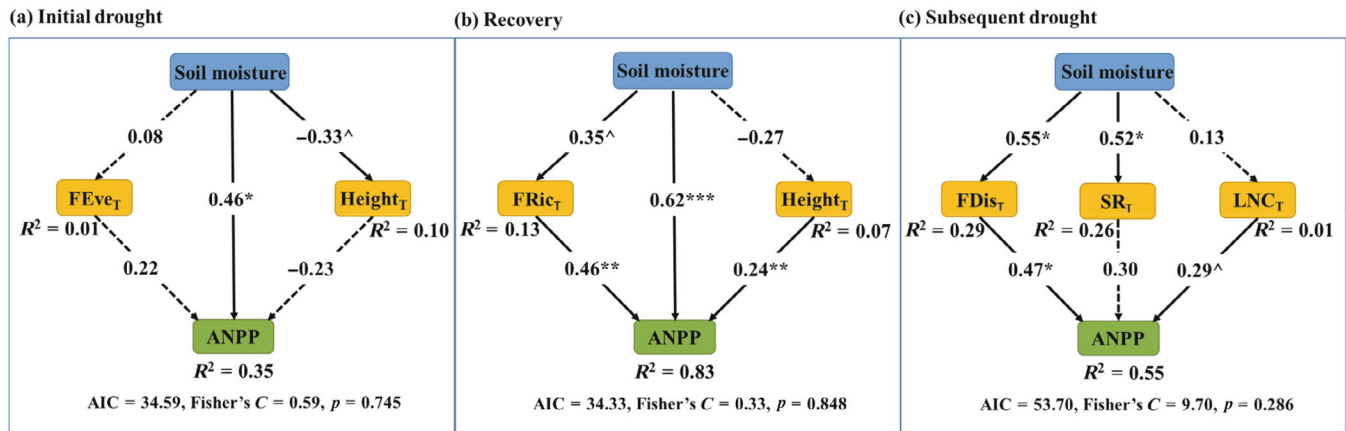
FIGURE 3 Best-fit structural equation model relating aboveground net primary productivity (ANPP) to soil moisture and several indices of community composition (e.g., community-weighted traits, species richness, and functional diversity) for initial drought (a), recovery (b), and subsequent drought (c). FDis, functional dispersion; FEve, functional evenness; FRic, functional richness; LNC, leaf nitrogen concentration; SR, species richness. Solid and dash arrows indicate significance ($^p < 0.1$; $*p < 0.05$, $**p < 0.01$, and $***p < 0.001$) and nonsignificant pathways, respectively. Numbers along the arrows are standardized path coefficients indicating the effect size of the relationship. The proportion of variance explained (R^2) appears alongside response variables in the model. A positive path coefficient emerging from the soil moisture box indicates a negative effect of drought.

pathways by which soil moisture influences ANPP dynamics during repeated drought events through several indices of community composition (e.g., species richness, CWM traits, and functional diversity). Overall, we found that ANPP was highly resilient to the initial drought, returning to pre-drought levels in a single year. This was driven by dominant grass species compensating for continued loss of growth in forb ANPP during recovery years. The complete recovery of ANPP following this drought was linked to plant height and functional richness of traits. Importantly, the magnitude of the ANPP response to the subsequent drought was greater than the initial drought. Causal path analysis revealed the underlying community-based mechanisms for such differential responses to drought. Specifically, soil moisture influenced ANPP responses directly during the initial drought, but indirectly during the subsequent drought by altering functional trait diversity and trait values of dominant species. Inconsistent with our hypothesis, SEM analysis revealed a stronger negative influence of drought on species and functional diversity than CWM traits, which led to greater sensitivity to the subsequent drought.

Our results showed that the initial extreme drought caused similar reductions in total ANPP in the first and second years, however, this was driven by differential sensitivities of forb and grass biomass in each year (Figure 1; Appendix S1: Table S3). Indeed, grass ANPP did decline more in the second year of drought compared with the first year (Figure 1; Appendix S1: Table S3). The loss of ANPP and associated shifts in community composition following the initial extreme drought did not

preclude rapid recovery in ecosystem function (Figure 1). We observed complete recovery in total ANPP after the initial drought, which was primarily driven by grass productivity, especially the dominant grass *L. chinensis*, which was more productive in treatment plots (94.58 g m^{-2}) compared with control plots (72.34 g m^{-2}), compensating for the low recovery of forbs such as *P. turczaninovii* and *A. frigida* (Appendix S1: Figures S4 and S5). The recovery following the extreme drought immediately increased soil moisture in the shallower soil layers, possibly driving greater resilience to the extreme drought that was observed for grasses compared with forbs in our study. Post-drought functional compensatory dynamics are particularly important when drought results in individual mortality or loss of species (Appendix S1: Figure S4). When mortality occurs, compensation may be manifest as reduced density (abundance) or loss of drought-intolerant plant species along with an increased abundance of those species that persist through drought or rapidly recover and expand after drought. This shift in abundance (i.e., density or mortality compensation) may be a primary mechanism of ecosystem resilience to drought (Nippert & Knapp, 2007). High resilience to extreme drought, as well as functional compensation after extreme drought, has also been observed in a South African savanna (Wilcox et al., 2020) and North American tallgrass prairie (Hoover et al., 2014), suggesting that this characteristic may be generalized across the grassland biome. Despite the complete recovery of ANPP, species composition did not completely recover to the initial state during the 2 years

following extreme drought (Figure 2). These results suggest longer recovery times for semiarid grasslands in the future, which could influence the impact of recurrent extreme droughts on these ecosystems.

Indeed, our results showed that the subsequent extreme drought imposed greater negative effects on total ANPP than that of the initial extreme drought (Figure 1). This was driven by the higher reduction in ANPP in the responses to recurrent vs. initial extreme drought for most individual species including grasses and forbs. For example, the biomass of the dominant species (*L. chinensis*) declined by 19% in the initial drought and 53% in the subsequent drought (Appendix S1: Figure S5). In contrast with the initial extreme drought, the recurrent extreme drought had a cumulative effect on ANPP (i.e., the negative effects were greater in the second year than the first year) (Figure 1; Appendix S1: Table S3). Similarly, Gherardi and Sala (2015) demonstrated a cumulative response of ecosystem functioning to a recurrent 1-year drought event in a desert grassland. These results suggest that ecosystem responses to repeated droughts may differ from those of single droughts, with repeated droughts having potentially greater negative consequences (Anderegg et al., 2020).

One potential concern is that the greater response that we observed during our second drought treatment could result from conditions that were more extreme during the second drought period. However, both mean annual and growing season precipitation were similar across all 6 years of our drought experiment (Appendix S1: Table S2). Moreover, in another drought experiment that also reduced precipitation by 66% that was located adjacent to our repeated drought experiment, the decline in ANPP during our second drought was much greater than in the first 2 years of the adjacent drought experiment (Appendix S1: Table S6). Therefore, we are confident that the decline in ANPP during our second drought treatment represents a legacy effect of the first drought rather than a response to differences in climate conditions between droughts.

Increased drought sensitivity following recurrent drought coincided with reduced species richness (Appendix S1: Tables S3 and S4), which supports previous work suggesting that biodiversity is related to ecosystem functioning (Alon & Sternberg, 2019). Interestingly, we did not observe any decline in species richness during the initial drought. There are myriad mechanisms by which drought may reduce ANPP beyond the loss of species (Kreyling et al., 2017), although productivity loss is likely to be larger when drought is severe or frequent enough to cause species loss. Here, increased ANPP sensitivity following recurrent drought coincided with shifting community trait means (Appendix S1: Tables S3 and S4), which supports previous work suggesting that plant traits drive ecosystem responses to drought (Luo et al., 2021).

Piecewise SEMs revealed that drought-induced reductions in soil water availability directly decreased ANPP at the initial drought stage (Figure 3), which is consistent with many other studies in grasslands (Hoover et al., 2014; Luo et al., 2021). Semiarid grasslands are water-limited ecosystems (Luo et al., 2021), so it is not surprising that soil moisture directly influenced plant growth. However, SEM analysis revealed that ANPP reductions during subsequent drought were associated with drought-induced reductions in the functional dispersion of traits (Figure 3). In other words, drought led to a shift in community composition such that species were more functionally similar, leading to reduced productivity. This supports previous work suggesting that ANPP sensitivity to drought is linked to functional diversity in grasslands (Griffin-Nolan et al., 2019).

Functional trait means significantly influenced total ANPP during the subsequent, but not initial, drought periods according to SEMs (Figure 3). The greater reduction in ANPP during the subsequent drought coincided with shifts in several other functional traits (e.g., plant height and SLA; Appendix S1: Tables S3 and S4). Indeed, we observed positive associations between ANPP and plant traits when weighted by relative biomass contribution (Figure 3). SEM analysis revealed that ANPP was positively associated with community LNC_T during the subsequent drought (Figure 3). Resource-acquisitive species and/or drought avoiders with annual life cycles are often associated with high LNC_T (Kooyers, 2015), thus the abundance of these species may increase with drought and further influence ANPP (Griffin-Nolan et al., 2019; Luo et al., 2021). Note that several other community traits (e.g., SLA_T and $LDMC_T$) also showed positive or negative relationships with ANPP in bivariate regressions (Appendix S1: Table S5) but were eliminated from the final SEMs because they tended to be closely associated with LNC_T. The dependence of ANPP on CWM traits is a quantitative translation of the mass ratio hypothesis (Grime, 1998), whereby ANPP is likely to be influenced more by the functional traits of the most abundant species and is relatively insensitive to changes in the abundance/presence of rare and subordinate species in a community. The greater influence of plant traits on ANPP in the recurrent drought compared with the initial drought highlights the diverse mechanisms by which plant communities respond to different frequencies of drought.

In conclusion, we observed decreased productivity with differential reductions in the growth of grasses and forbs following an initial drought, which was primarily

driven by declines in soil moisture. The complete recovery of ANPP following this drought was linked to plant height and functional richness. Additionally, grasses compensated for the lack of recovery in forb biomass, a response similar to that observed in other grassland ecosystems. ANPP responses to the recurrent drought were greater in magnitude and drought-induced reductions in functional dispersion emerged as another mechanism of ANPP drought sensitivity. Overall, the larger impacts of subsequent drought on ecosystem functions than the initial drought as well as the underlying differential pathways indicate that increased drought frequency with climate change may fundamentally alter semiarid grasslands in ways we could not predict from single drought studies.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
Data (Luo et al., 2022) are available in Figshare at https://doi.org/10.6084/m9.figshare.21298833.v1.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.