



Drought intensity and post-drought precipitation determine vegetation recovery in a desert steppe in Inner Mongolia, China

Xiangyun Li^{a,b,d}, Zhaobin Song^{a,b,d}, Ya Hu^{a,d}, Jingjuan Qiao^{a,b,d}, Yuheng Chen^e, Shaokun Wang^{a,c,d}, Ping Yue^{a,c,d}, Min Chen^{a,c,d}, Yuguang Ke^f, Chong Xu^f, Qiang Yu^g, Xiaoan Zuo^{a,c,d,*}

^a Urat Desert-grassland Research Station, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Science, Lanzhou 730000, China

^b University of Chinese Academy of Sciences, Beijing 100049, China

^c Naiman Desertification Research Station, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Science, Lanzhou 730000, China

^d Key Laboratory of Stress Physiology and Ecology in Cold and Arid Region, Gansu Province, Lanzhou 730000, China

^e Ecology and Biodiversity Group, Department of Biology, Utrecht University, Padualaan 8, 3584 CH Utrecht, the Netherlands

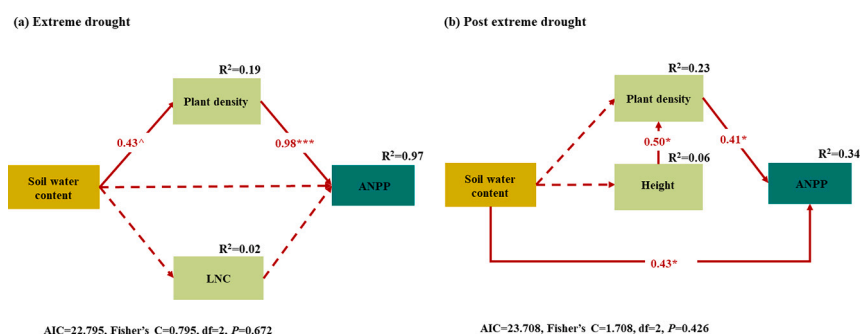
^f Hulunber Grassland Ecosystem National Observation and Research Station, Institute of Agricultural Resources and Regional Planning, Chinese Academy of Agricultural Sciences, 100081 Beijing, China

^g School of Grassland Science, Beijing Forestry University, Beijing 10008, China

HIGHLIGHTS

- Both press and pulse drought led to a sharp decrease in ANPP after four years.
- ANPP under pulse drought could recover fully after four years of post-drought, but not under press drought.
- Community structure recovered within 1 year after the end of the two extreme drought treatments.
- Both plant density and CWM of plant height contributed to the ANPP recovery after pulse drought.

GRAPHICAL ABSTRACT



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ABSTRACT

Extreme drought events are expected to increase in frequency and severity, posing significant threats to ecosystems worldwide. While considerable research has been concentrated on the effects of climate extremes on the stability of grasslands, the process by which grassland productivity may recover after extreme drought events are still not well understood. Here, we conducted a four-year (2019–2022) recovery investigation after four-year's (2015–2018) extreme drought treatments of different intensities (control, press and pulse) to explore the vegetation recovery of desert-grassland ecosystems Inner Mongolia, China. Press drought involved a 66 % reduction in natural precipitation from May to August, while pulse drought reduced it by 100 % during June and July. We found that both press and pulse droughts led to a sharp decrease in aboveground net primary productivity (ANPP) after four years, primarily due to reduced growth, density, and productivity of annual and

* Corresponding author at: Urat Desert-grassland Research Station, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Science, Lanzhou 730000, China.

E-mail address: zuoxa@lzb.ac.cn (X. Zuo).

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perennial plants. However, ANPP under pulse drought could recover fully after four years of stopping of drought treatment, and it could not under press drought. Additionally, community structure (i.e., species richness, plant density, and height) fully recovered within 1 year after the end of the two extreme drought treatments. Both plant density and height contributed to the ANPP recovery after press and pulse droughts. Structural equation modeling (SEM) results further revealed that the reduction in ANPP during the extreme drought was primarily due to a decrease in plant density caused by reduced soil water content. The recovery of ANPP in pulse drought was directly caused by increased soil water content in the post-extreme drought. These results suggest that drought intensity and precipitation determine ANPP recovery in a degraded desert steppe. Our findings are crucial for deepening understanding of the processes and mechanisms of ecosystem recovery after extreme drought, as well as for the successful management and protection of grassland ecosystems.

1. Introduction

Precipitation plays a primary climatic role in determining the functions and services of ecosystems (Knapp et al., 2002; Huxman et al., 2004; Sun et al., 2022). However, the frequency and duration of extreme drought events are projected to increase in the future due to global climate change (Su et al., 2018; Bradford et al., 2020). These more severe (i.e., pulse drought) and prolonged droughts (i.e. press drought) will likely have substantial and long-lasting impacts on ecosystem structure and function (Luo et al., 2020; Zhang et al., 2020; Xu et al., 2021a), leading to limitations in vegetation growth (Kannenberg et al., 2021), with legacy effects on ecosystem productivity (Sun et al., 2022) and the possibility of ecosystem degradation (Reichstein et al., 2013; Xu et al., 2016). Ecosystems following extreme drought events generally become vulnerable and sensitive to other environmental disturbances (Anderegg et al., 2020; Wu et al., 2018). The potential impacts of extreme droughts create significant uncertainty in assessing terrestrial feedbacks to climate change. Therefore, a better understanding of the mechanisms by which ecosystems recover from extreme drought is essential to predict terrestrial ecosystem dynamics after extreme climate disturbances.

Previous researches have demonstrated that ecosystem exhibit some degree of resilience to press drought events, with rapid and complete recovery once the drought subsides (Schwalm et al., 2017; Meng et al., 2019; Jiao et al., 2021). However, pulses droughts may surpass vegetation's physiological thresholds, resulting in a substantial increase in plant mortality and reduced productivity, delaying ecosystem recovery (Yahdjian and Sala, 2006; Hoover et al., 2014; Schnabel et al., 2022). In future climate change scenarios, where the intensity and duration of extreme droughts are projected to increase, more ecosystems are likely to experience multi-year extreme droughts (Ru et al., 2023). Our earlier study results, as presented in Li et al. (2021), provided insights into the dynamics of the drought period. However, the recovery processes and dynamics following these extreme drought events remain relatively unexplored. This study seeks to fill this gap by shedding light on the intricate mechanisms that drive ecosystem recovery.

Community dynamics play a crucial role in regulating grasslands recovery during and after extreme drought (Luo et al., 2020; Sun et al., 2022; Ru et al., 2023). Different plant species exhibit unique behaviors and dynamics during drought, leading to changes in community composition that ultimately affect grasslands recovery after drought (Sun et al., 2022). Recent studies conducted in semi-arid grasslands have shown that community productivity rapidly recovers after extreme droughts and can even exceed pre-drought levels for years afterwards (Sun et al., 2022). This recovery can be attributed to drought-induced increases in annuals and favorable precipitation patterns that promote annual thriving in subsequent years (Sun et al., 2022). However, prolonged droughts can lead to a reduction in the meristem density of perennial species, while providing opportunities for annuals to potentially flourish due to their faster germination, growth rate, and shorter lifespan.

Grassland recovery after drought requires an understanding of the functional traits of dominant species, as these species typically account for the majority of plant biomass (Grime, 1998; Wilcox et al., 2021).

Recent studies have highlighted the importance of species with resource-conserving traits, such as low specific leaf area (SLA) and high leaf dry matter content (LDMC), in buffering the decline in aboveground net primary productivity (ANPP) during drought (Jung et al., 2014; Májeková et al., 2014). Conversely, after drought, higher soil nutrient and moisture availability favors the growth of species with high resource acquisition efficiency (Bharath et al., 2020; Ru et al., 2023), which is crucial for restoring grassland. In grasslands dominated by species with resource-conserving traits, rapid recovery has been observed (Kinugasa et al., 2012; Jiao et al., 2021; Luo et al., 2023b). Despite their importance, the underlying mechanisms of these trait-based species growth strategies remain understudied.

Desert steppe in northern China, comprising 6 % of China's grassland area (Wang et al., 2018), exhibits high sensitivity to drought conditions. Climate change has led to low and irregular precipitation patterns, particularly during the summer months (John et al., 2016). Over the past few decades, the long-term average annual precipitation in the desert steppe region has remained below 200 mm, with a notable shift towards infrequent, large-scale precipitation events occurring at longer intervals (Zhang et al., 2019). While recent studies suggest that rapid recovery is the primary mechanism by which grasslands maintain productivity after extreme drought (Xu et al., 2021a, 2021b; Luo et al., 2023a), the factors that determine the recovery of desert steppes after drought remain poorly understood. Further research is needed to identify these determinants and improve our ability to predict the effects of drought on these grasslands.

In this study, our objective was to evaluate the impact of press and pulse droughts on desert steppe function, and to compare the recovery potential of dry grasslands following these two drought intensities. Our focus was on investigating the association between community composition and community structure (e.g., species richness, community plant density, and community weighted mean (CWM) traits) and soil parameters with ANPP during post-drought events. In a previous study conducted in the wetter, more species-rich grasslands of the Mongolian Plateau, it was found that communities did not fully recover from 2 years of persistent extreme drought until the second year after the drought ended (Xu et al., 2021a, 2021b). However, in our study area, which experiences drier conditions and has lower species richness (Li et al., 2023), we hypothesize that ecosystem recovery from persistent extreme drought may be slowed or inhibited. Specifically, we predict that (1) the productivity of semi-arid steppe may not fully recover after four years of ongoing extreme drought due to long-lasting damage to the grasslands, including reduced biomass production, decreased species abundance, and compromised soil properties (Alon and Sternberg, 2019); (2) productivity recovery depends on distinct functional groups, with potential higher resilience observed in annual herbs due to epigenetic effects, thereby playing a significant role in overall grassland recovery (Sun et al., 2022). Our study will contribute to a better understanding of the mechanisms underlying desert steppe recovery after extreme drought events, which is critical for predicting the long-term impacts of climate change on grasslands.

2. Materials and methods

2.1. Study site

The research was conducted at the Urat Desert-grassland Research Station, situated at latitude 106°58' E, longitude 41°25' N, and an elevation of 1720 m (Fig. 1a) in the western region of Inner Mongolia, China. The mean annual temperature of the site is 5.3 °C, while the average annual precipitation is 145 mm, with approximately 70 % of rainfall concentrated between July and August (Li et al., 2023). The experimental area is characteristically flat, exhibiting a slope gradient of <2 %. The soil primarily comprises brown and grey brown desert soil as per the Chinese soil taxonomy system (Li et al., 2021). The plant community is dominated by various species, including *Stipa glareosa* (perennial); *Allium mongolicum* (perennial); *Allium polyrhizum* (perennial); *Peganum harmala* (perennial); *Salsola pellucida* (annual), and *Bassia dasyphylla* (annual) etc.

2.2. Experimental design

In 2014, a randomized complete block design was employed to establish the experiment (Fig. 1b). The experiment utilized 18 plots of 6 × 6 m² each, which were divided into three treatments, with six replicates (blocks) assigned to each treatment. To mitigate the influence of the experimental infrastructure, each plot was surrounded by a 1-m external buffer and situated at least 2 m away from the closest neighboring plot. The three treatments were randomly assigned to the plots and included: control (CON, receiving ambient precipitation), press

drought (PRE, with a 66 % reduction in rainfall from May to August), and pulse drought (PUL, with a 100 % reduction in rainfall from June to July). The treatments were carried out for four years (2015–2018), and the study concluded in 2019 to assess the recovery of the desert steppe post extreme drought. All plots received ambient precipitation in 2019–2022. Based on the estimated precipitation probability density function calculated from 37 years (1982–2018) of historical precipitation at our study sites, two drought treatments, PRE and PUL, were considered extreme droughts in 2015–2018 (the average precipitation for the four treatment years was about the 5th percentile, Fig. S1a). Climate data was acquired from China Meteorology Administration (<http://data.cma.cn/>).

To impose extreme drought conditions, passive precipitation exclusion shelters were constructed using lightweight scaffolding and transparent polyethylene strips obtained from the Beijing Plastics Research Institute, Beijing, China. The shelters reduced precipitation by 66 % (press) or 100 % (pulse) during the growing season. PRE and PUL exhibited distinct intra-annual rainfall patterns (Fig. 1d). Before imposing the experimental extreme drought treatments, the perimeter of each plot (control, press and pulse droughts) was trenched to a depth of 1 m and covered with a 6 mm thick plastic and metal waterproof sheet to achieve hydrological isolation of the. The 2.5-meter-high roofs of the shelters were deliberately designed to enable near-surface air exchange and prevent unwanted greenhouse effects.

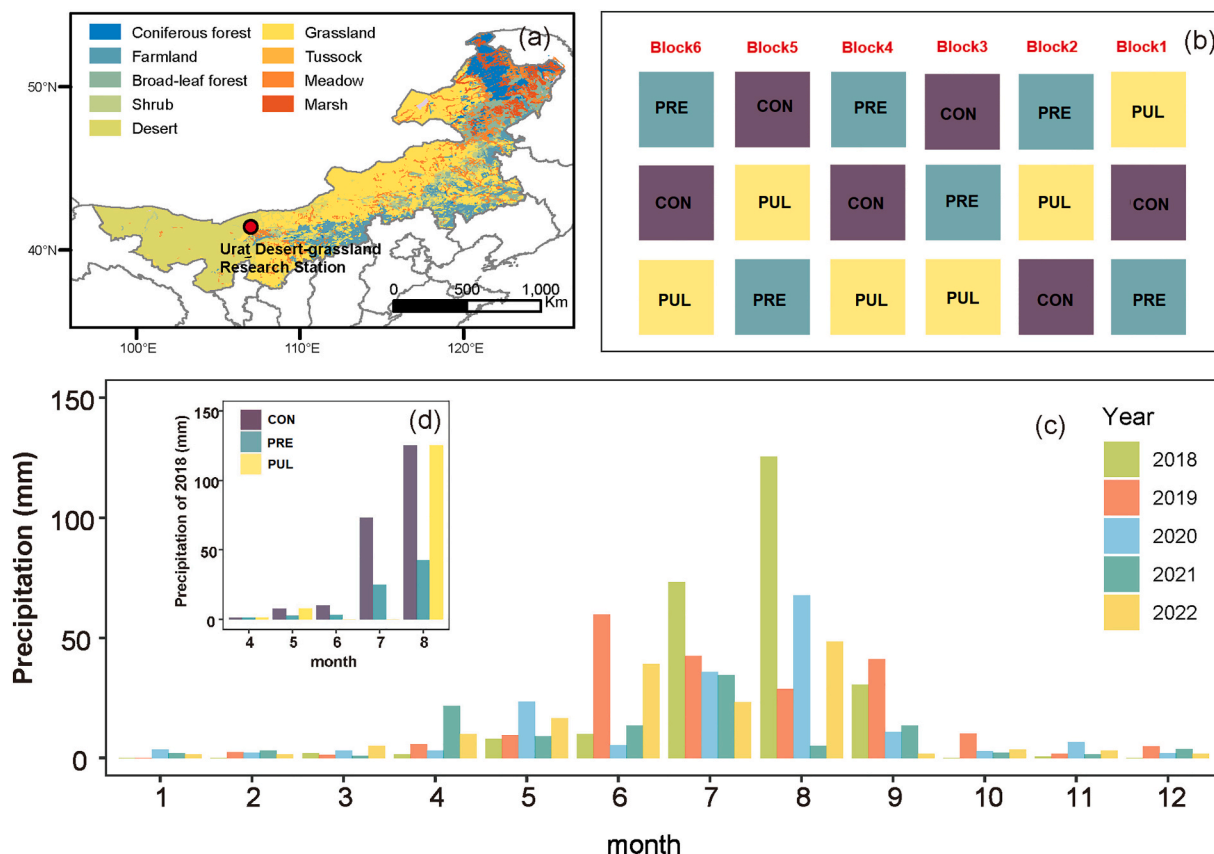


Fig. 1. The location of the Urat desert steppe site is depicted in (a). The experimental design, as shown in the bottom left panel (b), utilized a randomized complete block design with six replications and included three treatments: control, press-drought, and pulse-drought, represented by purple, green, and yellow squares, respectively. In the bottom panel, the monthly precipitation at the study site from 2018 to 2022 (January–December) is illustrated (c), alongside the manipulated precipitation in drought treatments from April to August in 2018 (d). The drought treatments were labeled as CON (control), PRE (press-drought), and PUL (pulse-drought).

2.3. Community composition, community structure and aboveground net primary productivity measurements

In this study, we sampled vegetation from 1×1 m quadrats at the peak of the annual growing season (around mid-August each year), each randomly placed within a plot and subdivided into four 50×50 cm subquadrats. The quadrat locations varied each year to avoid resampling the same area. Within each quadrat, we recorded the height and counted the number of individuals of each species present. Plant density was calculated as the number of all individuals within the quadrat. Besides, we calculated species richness as the total number of plant species present within the quadrat. Plant species were classified into two functional groups, perennials and annuals. ANPP was estimated by harvesting all aboveground biomass at peak growth in mid-August within two diagonal subquadrats of each plot. Biomass was sorted by species and oven-dried at 60°C for 48 h before being weighed to the nearest 0.1 g.

From 2018 to 2022, we quantified the CWM of six plant traits related to growth and resource acquisition. These traits included plant height, leaf thickness (LT), specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen content (LNC), and leaf carbon content (LCC) (Zuo et al., 2022). Data were collected from the most abundant species (cumulative relative biomass up to 90 %) using standard methods (Cornelissen et al., 2003). To calculate the CWM for each trait, which describes the trait values of the dominant species in a community, we weighted each trait by species relative biomass (Valencia et al., 2015). While we omit CWM from the following expressions, we report the names of the single functional traits. Note that we did not measure the LT in 2018.

2.4. Estimation on resistance and recovery

Ecological stability can be characterized by two distinct facets: resistance and recovery (Isbell et al., 2015; Kreyling et al., 2017). Resistance refers to the ability of an ecosystem to maintain its productivity levels during an extreme event, while recovery describes the extent to which it can return to its pre-event state afterwards. In this study, we utilized resistance and recovery to evaluate the impact of extreme drought events on ecosystem productivity. We adopted the definitions outlined in previous research (Isbell et al., 2015; Ingrisch and Bahn, 2018; Kreyling et al., 2017), and calculated the resistance of the ecosystem in the fourth year of the extreme drought treatment (2018) using the following formula:

$$\text{Resistance} = \frac{T_{2018}}{C_{2018}}$$

Additionally, we calculated the recovery of the ecosystem in each year following the extreme drought treatment using the formula:

$$\text{Recovery} = \frac{T_y}{C_y}$$

Here, T and C represent the ANPP or ANPP of different plant functional groups in the extreme drought and control plots, respectively. The years from 2019 to 2022 following the extreme drought treatment were represented by the variable “y”. The recovery index value of 1 indicates complete recovery, whereas values less than or >1 indicate incomplete recovery or overcompensation, respectively.

2.5. Soil parameters

From 2018 to 2022, we collected soil samples in August of each year from three randomly selected points in each plot using soil drills with a diameter of 3 cm. Soil cores were collected at depths of 0–20 cm and uniformly mixed after removing roots, humus, and pebbles, etc. The mixed soil samples were then divided into two parts (Guo et al., 2022). The first part of fresh soil was used to determine soil water content. The

second part was air-dried, passed through a 2 mm sieve, and used to measure soil pH and electrical conductivity in a 1:5 soil-water supernatant mixed probe (Multiline F/SET-3, Germany). Another dry soil sample was taken and ground to determine soil carbon and nitrogen contents using an elemental analyzer (Costech ECS 4010 Italy).

2.6. Statistical analyses

To compare the ANPP and each plant functional group (i.e., perennials versus annuals) in response to extreme drought and control conditions, mixed-effects ANOVA models were constructed using the *lme* function from the *nlme* R package. Each model comprised of “treatment” and “year” as fixed effects, while “block” was considered as a random effect. A separate mixed-effects ANOVA was implemented for each year when the interaction between treatment and year was statistically significant. In this case, “treatment” was considered as the fixed effect, and “block” as a random effect. Similar mixed models were applied to assess community structure (i.e., species richness, plant density, and CWM traits), soil parameters (i.e., soil water content, soil carbon content, soil nitrogen content, soil pH, and soil electrical conductivity) and resistance and recovery between the two drought treatments and functional groups.

Furthermore, the dependence of ecosystem recovery on the recovery of perennials and annuals was evaluated using a linear regression analysis. Similar regression analyses were employed to investigate the relationship between post extreme drought ANPP and community structure and soil parameters after drought. The plant community data was subjected to an unconstrained ordination analysis using nonmetric multidimensional scaling (NMDS) with the Bray-Curtis dissimilarity metric based on the relative biomass. To test the statistical significance, we employed permutational multivariate analysis of variance (PERMANOVA) with 999 permutations using the *vegan* R package.

Based on the above analysis, we found that ANPP under pulse drought recovered to the control level in the post-extreme drought period. Therefore, finally we employed piecewise SEMs to explore the mechanisms underlying the decline of ANPP in extreme drought stage (Fig. 7a, $n = 18$) and the recovery of ANPP under pulse drought in the post-extreme drought period (Fig. 7b, $n = 24$). Fisher's C statistic and AIC were used to determine the best-fit SEM, and “piecewise SEM” package in R was utilized for the analysis. All statistical analyses were performed using R version 4.2.0 software.

3. Results

3.1. Precipitation and soil properties

Over the period of 2015–2022, annual precipitation levels were measured at 144.6 mm, 136 mm, 122.2 mm, 251 mm, 207 mm, 165.5 mm, 110.2 mm, and 154.7 mm (Figs. 1c and S1b). Among these years, 2018 stood out as the year with the highest recorded precipitation levels, whereas 2021 experienced the lowest levels of precipitation. Specifically, during the growing season of 2018 (April to August), precipitation levels were monitored in three distinct treatment groups: press drought, pulse drought, and control, with recorded levels of 74 mm, 135 mm, and 218 mm, respectively (see Fig. 1d). In contrast, during the growing seasons of 2019–2022 (April–August), precipitation levels were recorded at 145.9 mm, 134.9 mm, 83.7 mm, and 137.1 mm, respectively. Our previous studies have demonstrated that the correlation between ANPP and precipitation was primarily observed during the early growing season (Li et al., 2021). Notably, the precipitation levels recorded during the growing seasons of 2019, 2020, and 2022 were more similar to those of the pulse drought treatments observed in 2018, while the precipitation levels observed in 2021 were more similar to those of the press drought treatments observed in 2018.

Our results indicate that press drought had a significant impact on the mean soil water content in the fourth year (2018) of the drought

treatment, while pulse drought did not exhibit any significant differences in soil water content compared to the control treatment (Table S2). However, during the post-extreme drought stage, the soil water content, soil pH, soil electrical conductivity, and very fine sand content under the two drought treatments were not significantly different from the control (Table S2). In the first year (2019) of the post drought stage, the soil carbon and nitrogen contents, as well as the clay silt content, of the press drought were significantly lower compared to the pulse drought (Table S2). Additionally, in the second year (2020) of the post drought stage, both coarse and fine sand contents under the pulse drought treatment were significantly lower than those in the control (Table S2).

3.2. Dynamics in ANPP

During the four-year drought treatment period from 2015 to 2018, the impact of the drought on plant growth was substantial (Fig. S2). Specifically, in the final year of the drought treatment (2018), both the

press and pulse drought treatments demonstrated notable reductions in ANPP when compared to the control. The press drought treatment resulted in a 69 % reduction in ANPP, while the pulse drought treatment exhibited a 60 % reduction (Fig. 2). Furthermore, these drought treatments also led to decreased ANPP of perennials, with the press drought causing a 68 % reduction and the pulse drought resulting in a 59 % reduction (Fig. 2). Besides, no annuals were observed in drought treatment plots. There was no significant difference between the two drought treatments, press and pulse droughts (see Table S2). It is important to note that ANPP is primarily derived from the productivity of perennials (Fig. 2). Furthermore, the severity of drought effects varied significantly by treatment year (Fig. 2; Table S1). During the three years following the extreme drought (2019–2021), the ANPP, annual ANPP, perennial ANPP, and A/P ratio in both drought plots showed recovery to levels close to those of the control plot (Fig. 2, Table S2). However, in the fourth year after the drought (2022), the ANPP and perennial ANPP in the press drought plot were significantly lower than those in the control and pulse drought plots. Specifically, ANPP was 55 % and 43 % lower in

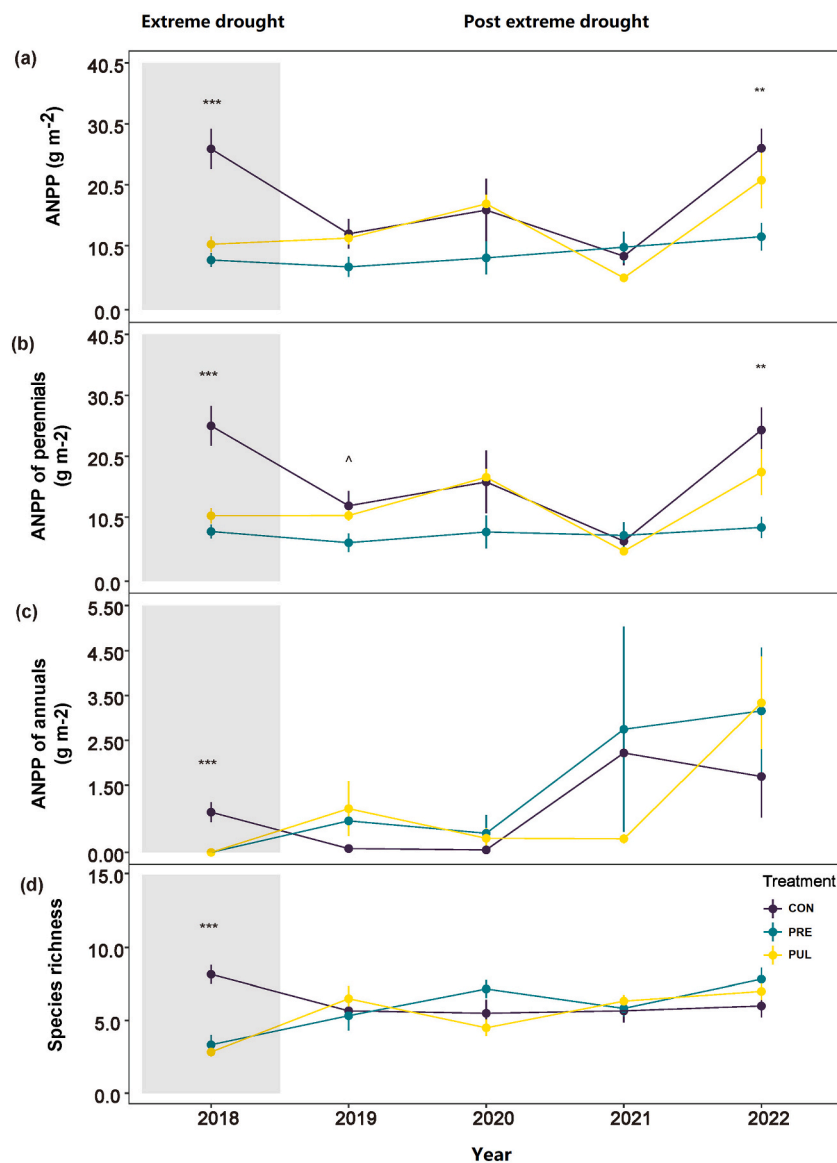


Fig. 2. Effects of press- and pulse-drought on aboveground net primary productivity (ANPP) (total (a), perennials (b), and annuals (c)) and ratio of annuals and perennials ANPP (A/P ratio) (d) during extreme drought and post extreme drought stage. CON, control; PRE, press drought and PUL, pulse drought. Significance level: *** $p < 0.001$, and ** $p < 0.01$. When the effects of extreme drought differ significantly within a year, significant symbols are placed above that year. See Table S1 for ANOVA results.

press drought plots than in control and pulse drought plots, respectively, while perennial ANPP was 64 % and 51 % lower, respectively.

3.3. Recovery dynamics after extreme drought

Considering the sensitivity of plant growth to drought, an analysis was conducted to investigate the resistance and resilience of above-ground net primary productivity (ANPP) under two drought treatments. The results indicated that there was no significant difference in ANPP resistance between the two drought treatments in 2018 (Fig. 3). However, during the post extreme drought period from 2019 to 2022, the two treatments showed different ANPP recovery patterns (Fig. 3; Table S2). Specifically, the recovery of ANPP under pulse drought was higher compared to that under press drought, with a difference of 12 %, 13 %, and 15 % in 2019, 2020, and 2022, respectively. In 2021, no significant difference was observed in ANPP recovery under the two drought treatments. It was also found that the recovery of perennials and annuals contributed significantly, accounting for 68 % of the ANPP recovery (Fig. S3).

3.4. Treatment effects on community composition, community structure

The plant community composition under different treatments was significantly different in extreme drought and post extreme drought (Fig. 4). Treatment and year had marginally significant interaction effects on community composition during post drought (Fig. 4).

Our findings reveal that the fourth year of drought (2018) had significant impacts on species richness, community plant density, and plant height (Fig. 5; Table S2). However, during the post extreme drought period (2019–2022), both species richness and community plant density in the two drought treatments were able to quickly recover to the control level. In terms of leaf thickness (LT), due to the lack of data in 2018, it remains uncertain whether extreme drought had a significant effect.

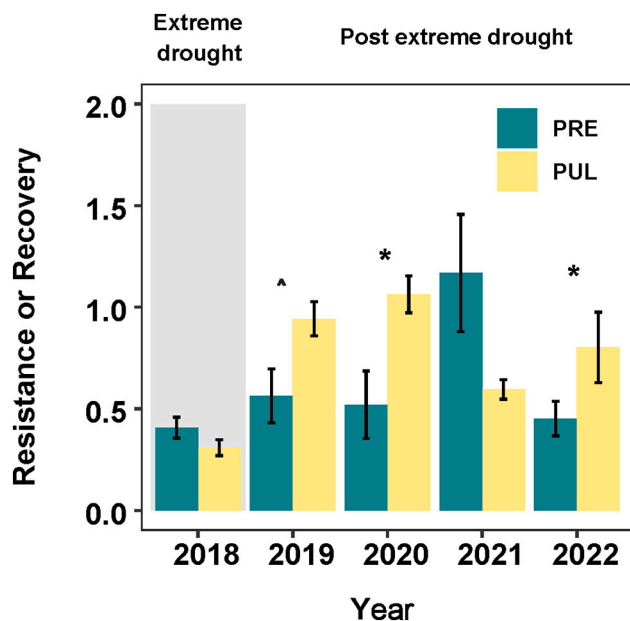


Fig. 3. Extreme drought resistance and recovery of under extreme drought and post extreme drought stage. Ecosystem resistance and recovery were calculated at whole community level based on ANPP. All values are expressed as mean \pm standard error. PRE, press drought and PUL, pulse drought. Significance level: * $p < 0.05$ and ^ $p < 0.1$. When the effects of extreme drought differ significantly within a year, significant symbols are placed above that year. Statistical differences in resistance and recovery were tested with ANOVA with post hoc Duncan tests.

Nonetheless, we can affirm that during the recovery period (2019–2022), LT did not differ significantly between the drought treatments and the control. Additionally, in the press drought plot, both specific leaf area (SLA) and leaf carbon content (LCC) in 2019 were significantly lower than those in the control and pulse drought (Fig. 5; Table S2). Plant height in the 2020 press drought was also significantly lower than that in the control and pulse drought. Moreover, in the press drought of 2022, leaf nitrogen content (LNC) was significantly lower compared to the control and pulse drought (Fig. 5; Table S2). Lastly, the leaf dry matter content (LDMC) in the pulse drought of 2022 was significantly lower than that in the press drought (Fig. 5; Table S2). However, it is important to note that the changes in SLA, LCC, LNC, and LDMC were minor after the drought period, and significant differences observed in a given year may be random and/or less correlated.

3.5. Controlling factors for ANPP response after extreme drought

During the 4-year recovery period 2019–2022, we observed a significant impact of the treatment on the relationship between ANPP and both community structure and soil properties (Table S3). Specifically, we observed a linear increase in ANPP following the press drought and control treatments, which exhibited a positive correlation with species richness (CON: $p < 0.05$, CHR: $p < 0.05$; Fig. 6a). However, the linear increase relationship was not significant under pulse drought. Post-drought ANPP displayed a significant linear increase relationship with community plant density and plant height, which was independent of the drought treatment. This observation indicates that the drought treatment did not have any carryover effect on the relationship between post-drought ANPP and community plant density and plant height (Fig. 6b–c). Moreover, the significant linear reduction of Post-drought ANPP with LDMC and LCC only occurred under the control treatment, and both press and pulse droughts treatments had legacy effects on the relationship between post-drought ANPP and LDMC and LCC (Fig. 6d–e). Upon further analysis of the relationship between post-drought ANPP and soil factors, we observed a significant linear increase in post-drought ANPP with soil water content only in the pulse drought treatment plots, whereas the control and press drought treatments did not exhibit this relationship (Fig. S4).

We employed SEMs to explore the possible causal pathways influencing ANPP in extreme drought and post extreme drought periods (Fig. 7). According to the analysis, soil water content had an indirect positive impact on ANPP through community plant density during extreme drought (Fig. 7a). Besides, soil water content had a direct positive effect on ANPP of pulse drought during post-extreme drought periods (Fig. 7b).

4. Discussion

Our findings indicate that the ANPP in the studied semi-arid grasslands showed a sharp decrease under both press and pulse droughts. While exhibiting rapid and robust recovery from pulse drought with abundant precipitation, recovery was hampered after press drought. Our data suggest that community structure is important in regulating the productivity of desert steppe during the post-drought phase. In general, our study contributes to a deeper understanding of the complex relationships between drought characteristics, community composition and structure, soil properties, and ANPP in semi-arid ecosystems.

In line with our preceding investigations focused on drought period, our current study reaffirmed the deleterious implications of extreme drought events on ANPP (Li et al., 2021). Notably, we observed a significant reduction in ANPP, primarily attributed to decreased annual and perennial plant production (Fig. 2b, c), indicating a physiological response mechanism that reduced growth (Smith et al., 2009). In addition, we focused on recovery processes and dynamics after extreme drought events. Numerous studies have reported the rapid recovery of net primary productivity in various grassland ecosystems (Gilgen and

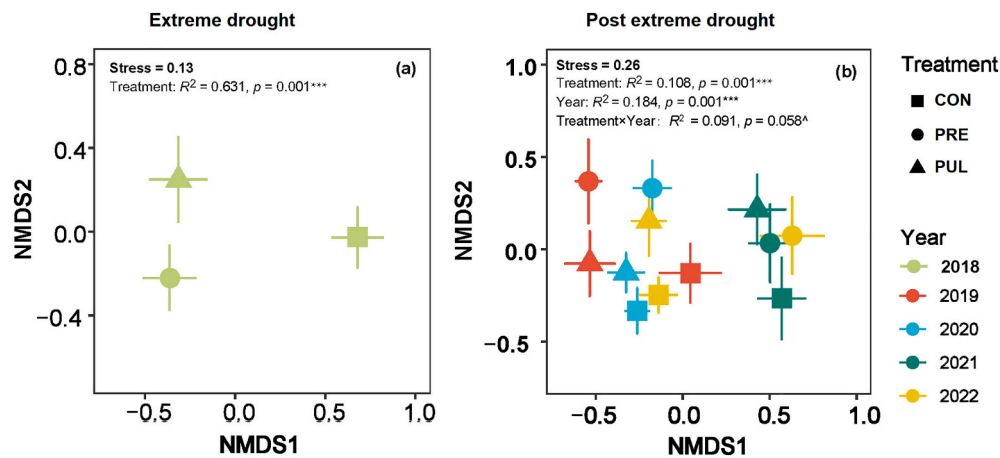


Fig. 4. The nonmetric multidimensional scaling biplots illustrating the alterations in plant community composition during the extreme drought period (a) and post-extreme drought stage (b). Significance level: $***p < 0.001$ and $^{\wedge}p < 0.1$.

Buchmann, 2009; Hoover et al., 2014; Wilcox et al., 2020). However, the negative legacy effects of extreme drought on plant growth (Gao et al., 2018), especially in dry grassland ecosystems (Wu et al., 2018), could result in slow recovery of net primary productivity (Sala et al., 2012; Hoover et al., 2021). In our study, we found that ANPP under press drought conditions failed to recover to control levels even in the fourth year after the drought. This could be attributed to the press drought surpassing the extreme response threshold that hindered community recover in such an extreme environment (Smith, 2011; Kardol et al., 2012). Compensation dynamics following drought were especially critical when individual deaths or species disappearances occur. The cumulative effect of the four-year press drought and the drought in 2021 may have increased mortality of the dominant perennial plants, overshadowing the productivity increase of annuals after the press drought. This means that total ANPP cannot recover to control levels after press drought.

Our investigation revealed a noteworthy disparity in the recovery of ANPP between pulse drought and press drought treatments (Fig. 2). The variation in recovery patterns observed between pulse drought and press drought may be closely tied to root-soil dynamics (Slette et al., 2023). The roots promote ANPP recovery by taking water and nutrients from the soil. In our previous research, we found that pulse drought in the last year of the 4-year extreme drought experiment (2018) prompted plants to develop more root systems than press drought (Li et al., 2021). In addition, recent research has proved that drought-induced reductions in root production may persist for years after a drought, with root production returning to environmental levels only when precipitation is above average (Slette et al., 2023). Thus, in our study, the roots that suffered from press drought were most likely not recovered during the recovery phase, which limited the plants' ability to utilize potential soil water sources, thereby constraining nutrient availability and ANPP recovery (Bayala and Prieto, 2020).

During the post-extreme drought stage, despite observing significant differences in community composition between the control and the two types of extreme drought treatments, we did not find substantial differences in community structure among the treatments (Figs. 4 and 5). The significant differences in community composition observed between the control and the extreme drought treatments can be attributed to the varying responses of individual species to drought conditions (Alon and Sternberg, 2019). Some species exhibited higher tolerance or resilience, maintaining their biomass or recovering more effectively, while others declined or even faced local extinctions due to drought sensitivity (Alon and Sternberg, 2019). In the fourth year of extreme drought, the community structure (including species richness, plant density, and plant functional traits) of different treatments had significant effects, but there was no significant difference in community structure during the post-

extreme drought phase. This aspect indicates the ability of community structure to rapidly balance between control and treatment. On the other hand, compensation dynamics and functional redundancy existed within the community. These compensatory mechanisms, where the decline or loss of certain species is compensated by increased abundance of other species, help maintain similar levels of species richness and overall community structure across the different treatments (MacArthur, 1955; Lawton, 1994; Ghilarov, 2000). In summary, the observed patterns indicate that certain species' responses to drought drive changes in community composition, but functional redundancy and compensation within the community contribute to the maintenance of community structure in terms of species richness, plant density, and functional traits.

Our SEM analysis showed that ANPP was reduced during extreme drought phases due to decreased plant density caused by reduced soil water content, which was consistent with findings from other grassland studies (Hoover et al., 2014; Zuo et al., 2022). As semi-arid grasslands are water-limited ecosystem (Li et al., 2021), it is unsurprising that plant growth is affected by soil water content. During the post-extreme drought phase, an increase in soil water content directly led to the recovery of ANPP in pulse drought (Fig. 7). These findings emphasized the crucial role of drought intensity and precipitation in regulating community productivity and mediating ANPP recovery after drought in desert steppes. Furthermore, an essential factor contributing to the recovery of ANPP after pulse drought was the presence of a well-balanced community structure, characterized by high plant height and large plant density. Our SEM revealed a positive relationship between plant height and plant density, which aligns with the tolerance hypothesis (Semchenko et al., 2018). According to this hypothesis, taller plants tend to possess better competitive tolerance, while reduced competition from neighboring plants supports higher plant density within the community. In a well-structured community, where plant height was positively correlated with density, these taller individuals can maintain their stature and continue to capture vital resources during recovery. This competitive advantage enabled them to allocate resources towards growth and productivity, promoting ANPP recovery. Hence, reasonable community structure promoted ANPP recovery under pulse drought.

Nevertheless, it was worth considering that a more frequent measurement of soil water content throughout the period would yield more meaningful insights into its temporal dynamics and its role in vegetation responses. Future research should study stress impact indicators such as consecutive days below the wilting point, to further elucidate the relationship between soil water content and the recovery of ecosystems after drought events (Reynaert et al., 2021). In addition, while our SEM was limited in its scope, it tentatively explored the importance of post-drought environmental conditions for the recovery of semi-arid

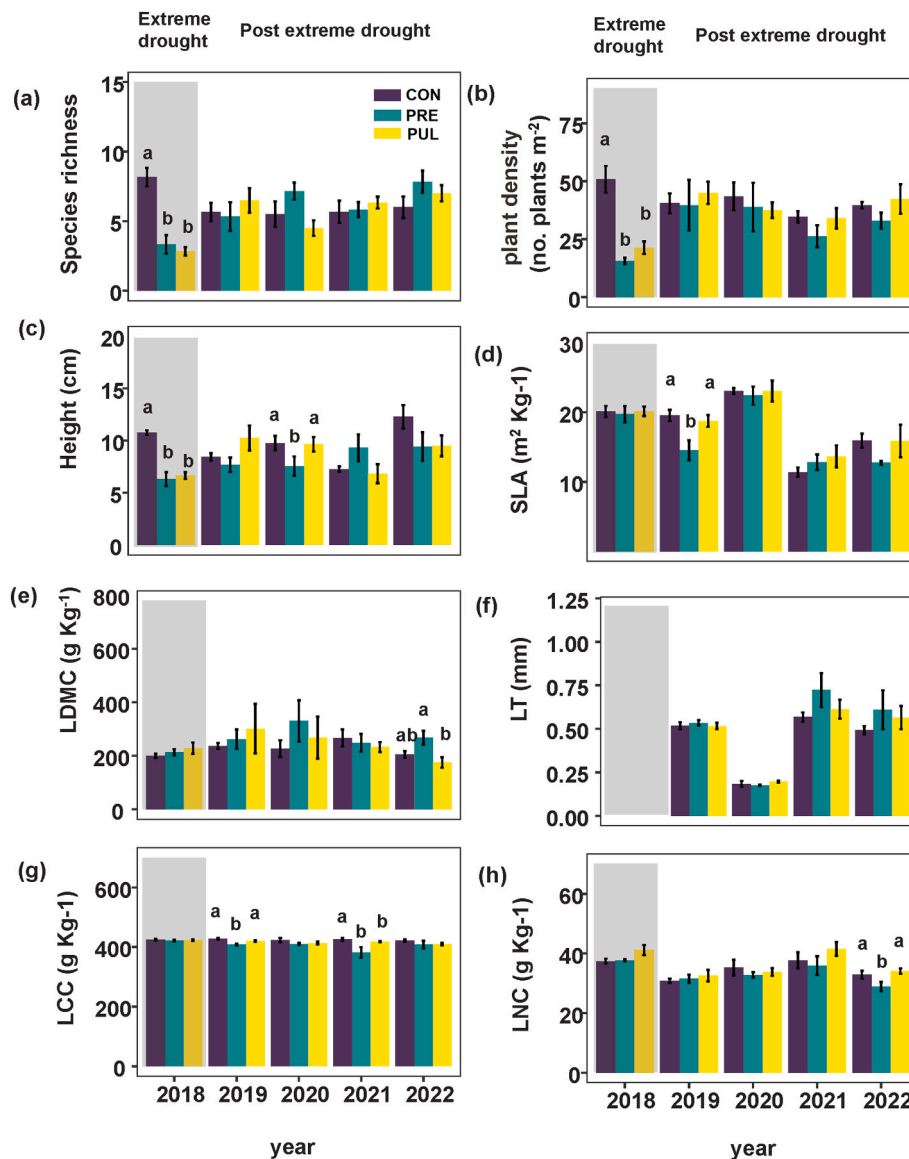


Fig. 5. Effects of extreme drought on metrics of community structure (i.e., species richness, density, and community-weighted traits) during extreme drought and post extreme drought stage. All values are expressed as mean \pm standard error. Different lowercase letters indicate significant differences among the treatments under the same year. SLA, specific leaf area (m² Kg⁻¹); LDMC, leaf dry matter content (g Kg⁻¹); LT, leaf thickness (mm); LCC, leaf carbon content (g Kg⁻¹); LNC, leaf nitrogen content (g Kg⁻¹). CON, control; PRE, press drought and PUL, pulse drought. Significance level: $P < 0.05$.

grasslands from extreme drought.

5. Conclusions

In conclusion, this study investigated the recovery of desert-grassland ecosystems from press and pulse droughts treatments and provided insights into the mechanisms of recovery. Both intensities of droughts caused a decline in ANPP as well as a reduction in the productivity of both annual and perennial plants. This decline can be attributed to the decrease in soil moisture during the extreme drought period, which caused a subsequent decrease in plant density. The reduced plant density ultimately led to a decline in productivity. The grassland productivity exhibited equal resistance to press and pulse droughts. Moreover, following a period of pulse drought, moderate precipitation promotes the increase of soil water content, which can facilitate the recovery of grassland productivity. In response to the press drought, it is noteworthy that ANPP remained persistently lower even after a 4-year recovery period. This observation underscores the idea

that when a certain threshold is surpassed, this ecosystem encounters considerable challenges in its recovery process (at least in some aspects, such as productivity). Overall, these findings highlight the importance of understanding the complex relationships between drought intensities, community composition, and ANPP in semi-arid ecosystems. We contribute to the growing body of evidence on the impact of press and pulse droughts on grasslands and provide insights into the factors that regulate ecosystem productivity following extreme drought events.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.167449>.

CRediT authorship contribution statement

Xiaoan Zuo and Qiang Yu designed this experiment. Zhaobin Song, Ya Hu, Jingjuan Qiao, and Yuheng Chen contributed significantly to analysis and manuscript preparation. Xiangyun Li performed the data analyses and wrote the manuscript. Shaokun Wang, Ping Yue, Min Chen, Yuguang Ke, and Chong Xu

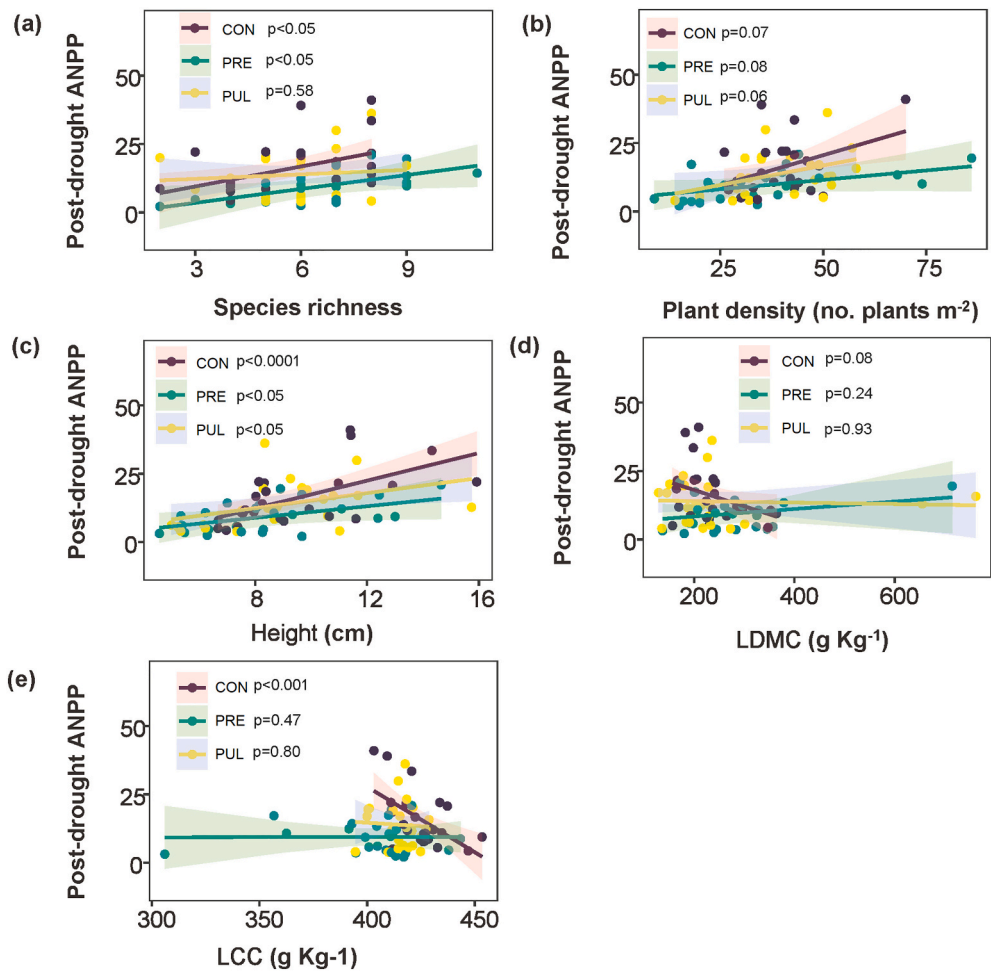


Fig. 6. Relationships of post-drought ANPP with species richness (a), plant density (b), community-weighted height (c), community-weighted LDMC (d), community-weighted LCC (e). Each data point of species richness, plant density, height, LDMC, and LCC represents value in each plot under the stage of post extreme drought in 2019–2022. The shadow indicates the 95 % confidence interval. LDMC, leaf dry matter content (g Kg^{-1}); LCC, leaf carbon content (g Kg^{-1}); CON, control; PRE, press drought and PUL, pulse drought.

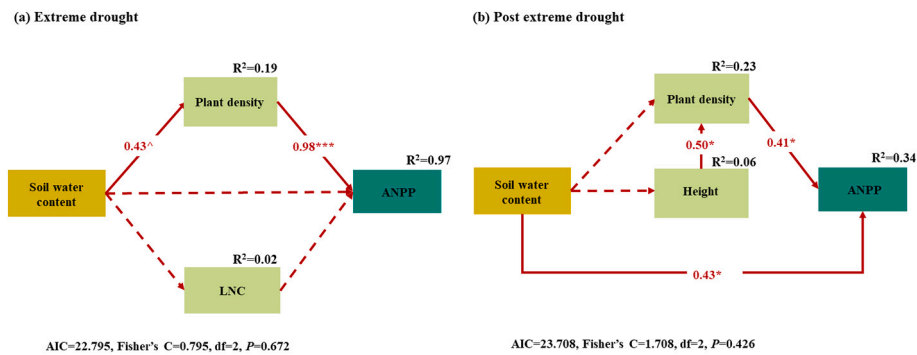


Fig. 7. The best-fit SEM showing ANPP to soil water content and several indices of community structure (e.g., plant density and community-weighted traits) for extreme drought (a, $n = 18$) and post extreme drought (b, $n = 24$). LNC, leaf nitrogen content (g Kg^{-1}). Solid and dash arrows indicate significance and nonsignificant pathways, respectively (significance level: *** $p < 0.001$, * $p < 0.05$ and $\wedge p < 0.1$). Standardized path coefficients are assigned numerical values along the arrows, which signify the effect size of the relationship between variables in the model. The proportion of variance explained (R^2) is shown next to the response variables in each model.

contributed significantly to the revision of the manuscript.
Xiaoan Zuo helped perform the analysis with constructive discussions.

Declaration of competing interest
The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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