Received: 25 March 2025 | Accepted: 29 July 2025

DOI: 10.1111/1365-2745.70172

RESEARCH ARTICLE

BRITISH ECOLOGICAL SOCIETY Journal of Ecology

Experimental warming drives local grassland plant species loss

Maggie Anderson | **Forest Isbell**

Department of Ecology, Evolution and Behavior, University of Minnesota Twin Cities, St. Paul, Minnesota, USA

Correspondence
Maggie Anderson
Email: maggiea@umn.edu

Funding information
National Science Foundation, Long-Term Ecological Research, Grant/Award Number: DEB-1831944; National Science Foundation, Biodiversity on a Changing Planet, Grant/Award Number: DEB-2224852

Handling Editor: Wentao Luo

Abstract

1. Climate change poses a growing threat to many ecosystems, including grasslands, which are a current priority for conservation due to their vulnerability to interacting threats from human activity.
2. North American grasslands are expected to experience warmer temperatures and more frequent and severe droughts in the coming decades, with potential consequences for native biodiversity.
3. We conducted an experiment at Cedar Creek Ecosystem Science Reserve, Minnesota, USA, to investigate how warming and drought treatments affected grassland plant community structure over 6 years in plots planted with species mixtures.
4. Warming consistently reduced plant species richness with its effects on Shannon diversity (which additionally considers species' relative abundances) and dominance varying across years. These warming-by-year interactions were likely driven by temporal variability in environmental conditions and species-specific responses. Notably, legumes consistently showed positive responses to warming.
5. Drought alone had minimal direct effects on species richness and diversity but reduced variability in diversity responses over time, suggesting greater stability of diversity under drought conditions.
6. *Synthesis*. This study underscores the important role of warming in reducing species richness, altering diversity and reshaping functional group composition in grassland ecosystems. While temporal variability influenced the magnitude of warming effects on diversity, legumes' positive responses highlight the importance of functional group dynamics in potentially buffering against species loss. Long-term experiments that allow consideration of interannual variability are essential for improving predictions of ecosystem responses and informing adaptive management strategies aimed at sustaining biodiversity and ecosystem functioning in grasslands.

KEYWORDS
biodiversity, climate change, determinants of plant community diversity and structure, drought, global change ecology, grassland, plant population and community dynamics, plant–climate interactions, plant–plant interactions, warming

1 | INTRODUCTION

1.1 | Setting and urgency of climate change

Climate change is disrupting biodiversity at local and global scales (Bellard et al., 2012; Sax & Gaines, 2003; Urban et al., 2024). Projections indicate increasing biodiversity loss in the coming decades (Newbold, 2018) driven by increasing temperatures and the frequency of drought and flooding events globally (Masson-Delmotte et al., 2021). Warming and drought are both components of climate change, with the potential to have interactive impacts on plant communities (Hoeppner & Dukes, 2012; Liu et al., 2018; Smith et al., 2024; Wilschut et al., 2022), yet few studies concurrently manipulate both these factors and track community change. If, alone or jointly, these climate changes cause diversity loss, it may reduce the resistance of future ecosystems to extreme climate events (Chapin et al., 2000) and negatively impact ecosystem functioning and services.

1.2 | Impacts of warming and drought on plant communities

Warming and drought both have the potential to drive species loss and changes in plant community structure (i.e. increased dominance, decreased evenness and increased rates of turnover) (Harpole et al., 2016; Klein et al., 2004; Ladouceur et al., 2022; Reich et al., 2004; Vitousek et al., 1997). Warming may favour species with specific functional traits, increasing their dominance and potentially reducing local diversity over time via competitive exclusion (Chao & Jost, 2015; Debouk et al., 2015; Harrison, 2020; Jost, 2006). Mechanistically, the drying effects of warming on soil and increased evapotranspiration (through water loss via stomata) can negatively impact more drought-sensitive species, especially in water-limited environments (Harrison, 2020; Zhang et al., 2012), indicating that warming leads to non-random species loss (Duchicela et al., 2021; Hu et al., 2021; Panetta et al., 2018). However, experimental drought may not always lead to changes in species richness (Batbaatar et al., 2022; Koerner & Collins, 2014) if community composition can respond rapidly to climatic stressors through high turnover—where species are lost but replaced by others—resulting in compositional shifts without altering overall richness (Hillebrand et al., 2018). To fully capture the complex community responses to warming and drought, we must assess other diversity measures beyond evenness and richness such as Shannon's and Simpson's diversity. Shannon's diversity is more sensitive to species richness while still accounting for evenness, while inverse Simpson's diversity is less sensitive to species richness and more heavily influenced by dominant species (Keylock, 2005; Marcon et al., 2014). Despite these insights, most studies have focused on individual stressors, necessitating further exploration of the combined effects of warming and drought on species composition.

Understanding how plant communities respond to the combined effects of warming and drought remains essential for developing effective conservation and management strategies (Csergő et al., 2013; Montalvo et al., 1993). These interactions often lead to significant shifts in species composition and productivity. In some ecosystems, the effects are synergistic, where the combined impact of warming and drought exceeds the sum of their individual effects. For instance, in arid grasslands, the combination of warming and drought weakened community stability and reduced productivity beyond what was expected from each factor alone (Liu et al., 2021). Similarly, in alpine grasslands, research has found that warming-induced drought offset the positive effects of warming on productivity by significantly reducing biomass during periods of severe water scarcity (Schuchardt et al., 2021). Warmer temperatures can also exacerbate drought conditions by increasing soil evaporation and plant transpiration, leading to greater-than-additive impacts on vegetation (Churchill et al., 2022). Conversely, other studies report additive effects where warming and drought operate independently in the same direction. Recent meta-analyses have found that the effects of warming and drought had additive effects on plant biomass (Wilschut et al., 2022) and on plant invasion dynamics (Shi et al., 2025). Responses can also be antagonistic or divergent, depending on species, ecosystems and stressor intensity (Lopez et al., 2022). Another global study found that warming increased the abundance of heat-tolerant species, while responses to changes in precipitation were species-specific (Feeley et al., 2020). Additionally, species richness often increases with additional precipitation but declines under warming (Hou et al., 2013), with elevated temperatures disproportionately affecting drought-sensitive species (McDowell et al., 2008). These responses may vary across life stages and depend on the traits of the dominant species (Alonso-Rodríguez et al., 2022; Yang et al., 2018). For example, dominant grasses often exhibit high specific leaf area (SLA), a trait linked to rapid growth and photosynthetic rates under favourable conditions (Liu et al., 2021); however, high SLA is not always a strong predictor of stability during drought, suggesting it may not confer resistance to water loss (Luo et al., 2023) and may increase susceptibility to heat damage (Valliere et al., 2023). Additionally, many dominant grasses of the Great Plains have C_4 photosynthetic pathways and deep, fibrous root systems, which enhance water-use efficiency and allow access to deeper soil moisture, thereby supporting photosynthesis during heat waves and periods of water stress (Kazemi et al., 2023; Mitchell et al., 2025; Pardo & VanBuren, 2021). In some cases, single climate drivers like warming or drought dominate community responses without interacting to magnify effects (Gruner et al., 2017; Hoover et al., 2014). This variability demonstrated by previous studies underscores the need to disentangle the relative and combined effects of warming and drought, as understanding their interactions over time is essential for predicting plant community responses to climate change.

1.3 | The role of functional groups in warming and drought responses

Functional composition may influence grassland community responses to climate change because different herbaceous plant functional groups, including C_3 grasses, C_4 grasses, non-legume forbs and legumes, exhibit distinct responses to warming and drought (Hoover et al., 2014; Killi et al., 2017; Martin & Norman, 1991; Reynolds-Henne et al., 2010). For instance, C_4 grasses often exhibit greater water use efficiency (An et al., 2005; Edwards & Still, 2008), which enables them to maintain their productivity under warmer conditions (Cowles et al., 2016; Debouk et al., 2015), especially compared to C_3 plants (Hoeppner & Dukes, 2012). Thus, C_4 grasses generally exhibit more drought tolerance than their C_3 counterparts (Nippert & Knapp, 2007; Ward et al., 1999), particularly compared to C_3 legumes and non-legume forbs, which may suffer under drought conditions (Phillips et al., 2018), although the opposite may be true for some legume species (Cowles et al., 2016). However, plant responses to global change can vary as much or more within than among functional groups (Dyer et al., 2001). Species' responses to warming may also be influenced by associated drying effects, making it challenging to disentangle the impacts of warming from those of drought (De Boeck, 2008). Thus, the tendency of plant communities to shift with climate change likely depends on the identities and traits of the plant species present in the community.

1.4 | The critical role of long-term climate experiments

Long-term ecological experiments are crucial for disentangling the complex and often nonlinear effects of climate change on plant community dynamics (Roshani et al., 2022; Zellweger et al., 2020). While short-term studies can detect rapid responses, they often fail to capture the impacts of year-to-year variability (Iler et al., 2013; Olonscheck et al., 2021), especially in systems like the Great Plains, where climate projections forecast increased temperature, frequent drought and variable precipitation patterns (Masson-Delmotte et al., 2021; Schafer et al., 2014). Long-term experiments have already revealed the importance of interannual variation in climate change experiments. For instance, research in drylands has found that warming reduced species richness only in wet years (Chiang et al., 2023; Shi et al., 2015), while warming-induced drought reduced dominant species abundances and community stability during dry years (Liu et al., 2021). Severe climate events, such as simultaneous warming and drought, can challenge even the most resilient species, altering community trajectories (Xu et al., 2014). Importantly, the effects of warming and drought may be amplified in already stressful years—particularly those that are both hot and dry—due to elevated evaporative demand and limited water availability (Churchill et al., 2022; Zhuang et al., 2024). Under such conditions, sensitive species are more likely to experience physiological stress or mortality, while dominant, stress-tolerant species may further increase in abundance (Cowles et al., 2018; Wilschut et al., 2022). These climate-driven differences in background stress may shape how strongly plant communities respond to experimental climate change treatments across years. Moreover, short-term experiments may overrepresent rapid shifts towards stress-tolerant species (Kiebacher et al., 2023; Martin et al., 2019), while underrepresenting long-term community dynamics driven by climate variability, particularly extreme precipitation events, that influence annual plant composition (Pugnaire et al., 2019). This evidence underscores the need for long-term, multifactorial studies that reflect interannual climate variability. In this study, we investigated how plant community structure—encompassing species richness, diversity (Shannon and inverse Simpson), evenness and functional group composition—responds to factorial warming and drought treatments in grasslands. We also explored how treatment effects may be influenced by the temperature and precipitation conditions of each year. Specifically, we hypothesized that (H1) warming will reduce species richness more strongly when combined with drought than when either treatment is applied alone, as the compounded stress of increased temperature and reduced moisture leads to local losses of more sensitive species. Additionally, we predicted that (H2) the effects of these treatments will vary with annual climate conditions: warming and drought will affect plant communities more strongly in warmer and drier years compared to cooler and wetter years. Furthermore, we hypothesized that (H3) warming and drought will interact to decrease evenness, as a few species capable of thriving under warmer and drier conditions become more dominant. Finally, we expected (H4) that heat- and drought-tolerant C_4 grasses will increase in dominance under warming and drought, while herbaceous forbs, which are less resilient to extreme conditions, will decline. We tested these predictions using a fully factorial experimental design over a six-year period, allowing us to evaluate the interactions among warming, drought and year-to-year climate variability.

2 | MATERIALS AND METHODS

2.1 | Study site

Our research was conducted at Cedar Creek Ecosystem Science Reserve (45°24′12″ N, 93°11′22″ W), a mosaic of woodlands, remnant oak savannas and abandoned farm fields. This area, located ~50 km north of St. Paul, MN, is positioned at the ecotone between the Great Plains and the Eastern Hardwood Deciduous Forest. It also features sandy, nutrient-poor Entisols that originated from a glacial outwash plain (Grigal et al., 1976). Cedar Creek experiences a mean annual precipitation of roughly 770 mm (±157 SD), about 64% of which falls during the growing season, summer high temperatures around 27°C (June–August) and winter lows around −14°C (December–February), with measurements based on the period 1963–2022. Cedar Creek is a University of Minnesota biological field station, so, no special fieldwork permits were required to conduct our study.

2.2 | Experimental design

We conducted a six-year experiment (2017–2022), known as Biodiversity and Climate with Drought (BACD), designed to assess the individual and combined effects of warming and drought on grassland plant communities. BACD was nested within the long-term BioDIV experiment, which began in 1994 and has been extensively described in previous studies (Tilman et al., 2001, 2014) (Appendix Box A1). The focus of this study was on 16-species plots originally seeded with equal proportions of species, selected from a pool of 18 species that included two oak species, as well as C_3 and C_4 grasses, legumes and non-leguminous forbs. Notably, at the time of the BACD experiment, there were no surviving oak trees present within the plots studied. Importantly, this study only used data from the 16-species plots of the BACD experiment, due to its focus on community-level responses to warming and drought treatments. At this relatively high level of sown diversity, there is substantial resistance to invasion (Fargione et al., 2003), and thus little impact of weeding and more natural community assembly and disassembly dynamics, allowing for a clearer observation of community-level responses to the warming and drought treatments.

Each 9 × 9 m BACD plot contained four subplots (1.5 × 1.0 m) to which four treatments were randomly assigned: Control, Warming (+Heat), Drought (−Water) and Warming + Drought (+Heat−Water). This fully factorial design allowed us to test the independent and interactive effects of warming and drought on plant community dynamics (nine plots × four subplots per plot = 36 subplots). Warming was applied using 1200 W infrared heaters suspended 1.8 m above the subplots, increasing surface temperatures by approximately 1.5°C (Kimball et al., 2008). The warming treatment was active each year during the growing season from March through November. Drought was implemented using rainout shelters, which excluded 43% of precipitation during the growing season, replicating the intensity of a 1-in-100-year drought for the region (Knapp et al., 2015; Yahdjian & Sala, 2002). The rainout shelters (2.5 × 2.0 m) were constructed with clear plastic slats mounted on a PVC frame, tilted to divert water away from the subplot. All sampling was conducted in the central 1.5 × 1.0 m area of the subplot to avoid edge effects.

2.3 | Efficacy of warming and drought treatments

Previous research employing the same warming infrastructure has demonstrated that high temperature treatments significantly lowered soil moisture and increased vapour pressure deficit and soil temperature (Cowles et al., 2018). Furthermore, warming significantly increased biomass in multi-species communities (Cowles et al., 2016). Treatment effects likely varied in strength depending on local wind conditions (Kimball et al., 2012), time of day (Wall et al., 2011) and seasonality (Cowles et al., 2016). Our rainout shelters, modelled after those originally created by Yahdjian and Sala (Yahdjian & Sala, 2002) to exclude rainfall in the 30%–55% range, have not been found to yield any differences in observed and expected amounts of rainfall reduction, ensuring effective drought implementation. The transparent nature of the rainout shelters ensured minimal differences in photosynthetically active radiation above and below the shelters (<10%), while differences in air temperature above and below the drought shelters were largely inconsequential (Yahdjian & Sala, 2002).

2.4 | Data collection

Beginning in 2017, we harvested biomass annually in a 0.1 × 1.5 m clip strip from each of the 36 BACD subplots. Samples were then sorted by species, dried and weighed. Biomass harvesting took place in early August each year, with the exact clip strip locations varying annually to mitigate potential carryover effects from the previous years' harvests. Soil moisture was also measured monthly in all subplots from May to September using a handheld ProCheck™ meter (Decagon Devices, Pullman, WA, USA) inserted into the top five centimetres of the soil. Soil moisture measurements were taken at five locations in each subplot (northwest, northeast, southwest, southeast and centre) and then averaged for analysis. Here, we only used data from measurements taken in the morning prior to 11:00 AM local time, given that treatment effects on soil moisture can vary throughout the day and night. Annual summaries of soil moisture responses to treatments are found in the Appendix (Figure A1). We also determined annual climate trends using daily maximum and minimum temperature and maximum growing season precipitation data collected from an on-site weather station at Cedar Creek. Growing season temperature and precipitation trends over the six years of the experiment are shown in Figure 1.

2.5 | Calculating community responses

To assess how plant diversity responded to warming and drought treatments in the 16-species plots over time, we utilized the 'vegan' package in R (Oksanen et al., 2007) to compute diversity indices or Hill numbers, where ($q = 0$, 1 and 2) represent different measures of species diversity. We calculated species richness ($q = 0$), the exponential of Shannon's entropy ($q = 1$), hereafter referred to as 'Shannon's diversity' and inverse Simpson's diversity ($q = 2$) at the subplot level (Chao & Jost, 2015). We also quantified evenness based on inverse Simpson's Index, Berger-Parker dominance (proportional biomass of the most abundant species) and the proportional biomass of *Andropogon gerardii* (Big bluestem), the most dominant species in this phase of the experiment. Finally, to better test the effects of treatments on functional group-level responses over time, we calculated the proportional biomass of each functional group: legumes, non-legume forbs, C_3 grasses and C_4 grasses. A complete list of community responses and their definitions can be found in Table 1.

2.6 | Data transformations, standardized precipitation-evapotranspiration index and statistical analyses

To further assess whether warming and drought treatments altered dominant species' identities, we first log-transformed ($\log(x + 1)$) species-level biomass values in the 16-species plots ($N_{\text{plots}} = 9$, $N_{\text{subplots}} = 36$) to illustrate species-level differences more clearly at low levels of biomass (see Figure A2 in the Appendix).

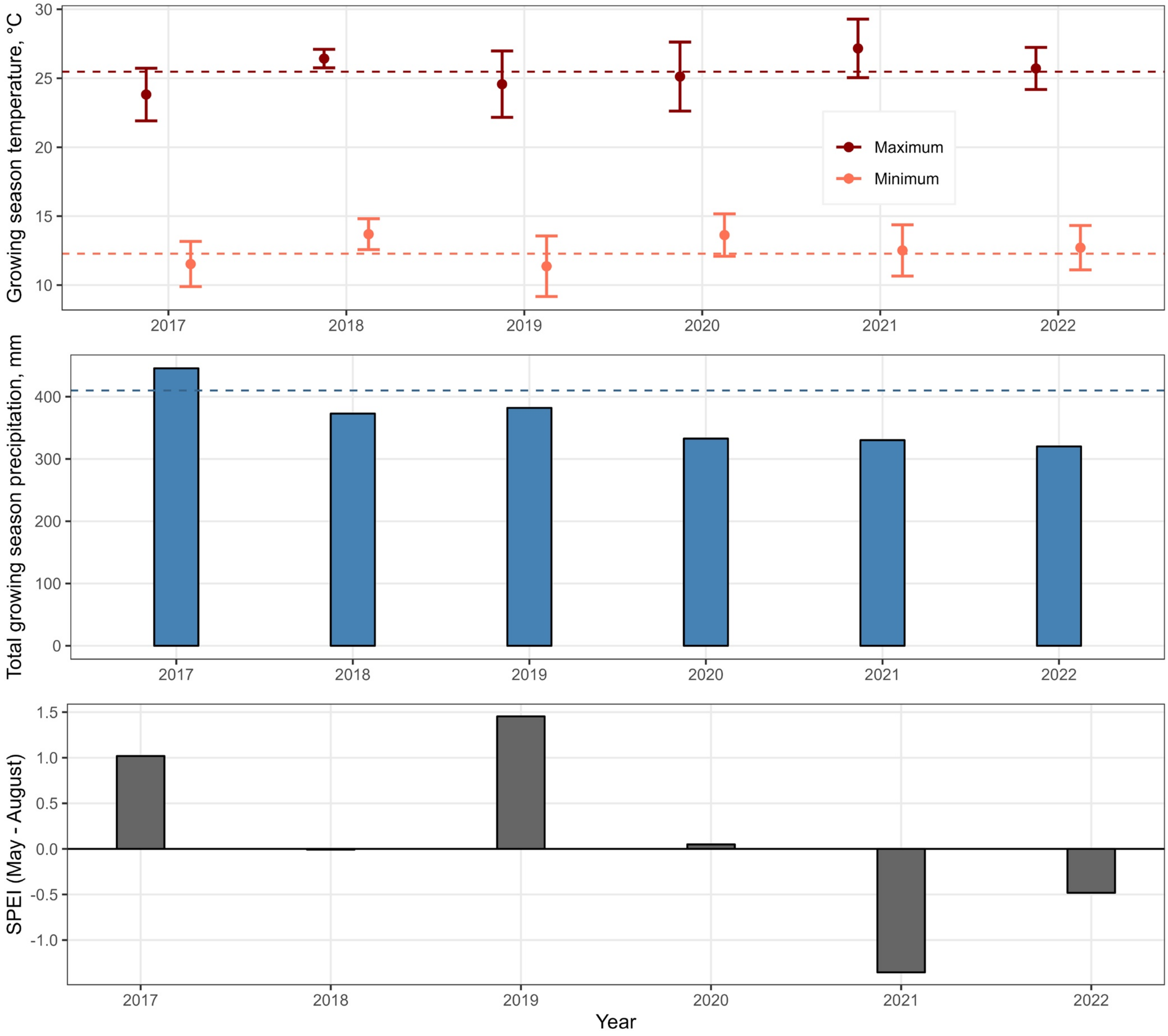


FIGURE 1 Trends in temperature, precipitation and SPEI over 6 years. Annual temperature, precipitation, and four-month Standardized Precipitation Evapotranspiration Index (SPEI-04) trends for all 6 years of the experiment from the growing season months prior to biomass harvest (May–August), showing minimum and maximum growing season temperature (top, red and orange), total (cumulative) growing season precipitation (middle, blue) and SPEI values for each year (bottom, dark grey). Error bars denote ±1 SE from the mean. Dashed lines represent the average minimum and maximum temperatures during the growing season (top) and the cumulative growing season precipitation (middle) over a 50-year period prior to the experiment (1966–2016) at the same location. Graphs summarize daily measurements taken from Cedar Creek Ecosystem Science Reserve.

2.6.1 | Statistical models

To understand how warming and drought treatments affected plant community responses over time, while accounting for repeated measures, we employed linear mixed models using the ‘mmrm’ package in R (Sabanes Bove et al., 2022). Our models incorporated warming treatment, drought treatment and year (as a factor) as interacting fixed effects, with subplots nested within plots as random effects. Year was treated as a factor, given the similarities observed between years one and three and between years two, four and six across most community responses, rather than as linearly or nonlinearly growing or shrinking treatment effects. We then adopted a model selection process (Figure A3) to identify the most parsimonious temporal covariance structure and fixed effect configuration (i.e. testing models where fixed effects were additive, interactive or 3-way interactions were excluded), using Akaike's Information Criterion (AIC) to assess the parsimony of model fits (see Figure A3 in the Appendix for model selection details and Table A3 in the Appendix for delta-AIC values for all models). This method ensures that all potential interactions and main effects are initially considered when the optimal temporal covariance structure is identified. *F*-tests were conducted on the

TABLE 1 Descriptions, distinctions and references for each community-level response employed in this study. Note that our study uses the mass of each species instead of abundances. For more information on the interrelatedness of these responses, see Appendix Box A2.

Response	Description	Distinction from other indices	References
Richness ($q = 0$)	Count of the number of different species present in a community, S.	Does not account for the relative abundances or evenness of the species.	(Chao et al., 2014)
Exponential of Shannon's entropy or Shannon's diversity ($q = 1$)	Effective number of species or Hill numbers ($q = 1$). Defined as $exp(H) = exp(-\Sigma\, pi \times ln(pi))$, where pi is the relative abundance or biomass proportion of individuals belonging to the *ith* species	Accounts for both species richness and evenness in a community, giving weight to species in proportion to their relative abundances.	(Jost, 2006)
Inverse Simpson's diversity ($q = 2$)	The number of equally abundant species required to generate the observed Simpson's index value ($D = \Sigma\, pi^2$). Defined as $1/D = 1/\Sigma\, pi^2$ where pi is the relative abundance or biomass proportion of individuals belonging to the *ith* species and the sum is taken over all species present.	Gives more weight to abundant species than rare species compared to the exponential of Shannon's entropy.	(Chao et al., 2014; Chao & Jost, 2015; Simpson, 1949)
Berger-Parker dominance index	Measure of the proportional abundance of the most abundant species in a community. Defined as $B = N_{max}/N$ where N_{max} is the number of individuals or biomass in the most abundant species and N is the total number of individuals or biomass in the community.	Focuses exclusively on the relative importance of the most dominant species, ignoring information about species richness, evenness and the abundances of other species.	(Berger & Parker, 1970; Ma & Ellison, 2018)
Evenness (inverse Simpson)	Measure of how close the abundances of different species are to being equal in a community. Defined as $E = (1/D)/S$ where $1/D$ is the inverse Simpson diversity index (as defined above) and S is the species richness	It is quantified directly on a 0 to 1 scale, mathematically independent of species richness.	(Jost, 2010; Simpson, 1949; Smith & Bastow Wilson, 1996)
Andropogon gerardii proportional biomass	Measure of the relative abundance or biomass proportion of the single most dominant species in our study	Exclusive focus on a single species, which is historically dominant in the ecosystem. Any differences from Berger-Parker dominance index indicates dominance of a different species in the community.	(Gustafson et al., 2004)

best-fit models for each response variable using the Satterthwaite method, as shown in Table 2. To ensure the validity of the linear mixed-effects models, we tested model assumptions by examining residuals vs. fitted values plots (Appendix Figure A4).

2.6.2 | Coefficient of variation

To better understand the magnitude of year-to-year variability in shaping each response variable over time, we also calculated the coefficient of variation (CV) for all the responses described in our study (Table 1) within subplots across all years of the experiment. We used a linear mixed-effects modelling approach to analyse CV responses to treatments via the lme4 package (Bates et al., 2015), given that there was only one CV value per subplot (i.e. no repeated measures). We used a similar model selection process to that described above to find the model with the most parsimonious fixed effects structure.

2.6.3 | Standardized precipitation-evapotranspiration index

We used the Standardized Precipitation Evapotranspiration Index (SPEI) to contextualize moisture availability and temperature-driven water demand across the study years, as it accounts for both precipitation and potential evapotranspiration (Nwayor & Robeson, 2024; Smith et al., 2024). To calculate SPEI values for our site, we utilized data from SPEIbase (Beguería et al., 2024) (https://digital.csic.es/handle/10261/364137), focusing on the growing season (May to August) for each study year. We then categorized SPEI by extracting quantiles from the normal distribution, defining extremely wet as qnorm(0.1) >1.28 and extremely dry as qnorm(0.9) <−1.28, which are thresholds appropriate for our region (Isbell et al., 2015). Unlike the Standardized Precipitation Index (SPI), SPEI provides a more comprehensive measure of drought conditions (Keyantash & Dracup, 2002), making it particularly valuable for explaining the severity of treatment responses in specific years. For example, extreme drought in 2021 and extremely wet conditions in 2019 likely influenced how plant communities responded to the warming and drought treatments. Although SPEI is useful for interpreting year-to-year variability, it was not included in our statistical models due to its overlap with the year effect, which was included as a fixed effect. Given that SPEI inherently varies by year, and with only six years of data and an imbalanced distribution of wet, dry and normal years, we concluded that including SPEI in these models would risk multicollinearity. Despite this, SPEI is included in Figure 1 to illustrate moisture conditions in specific years and help explain observed treatment effects.

TABLE 2 Output of mixed model for repeated measures (mmrm) showing the effect of warming treatment, drought treatment and experiment year on species richness, Shannon's diversity, inverse Simpson's Index values and evenness (based on inverse Simpson's Index) across four consecutive treatment years while accounting for plot and subplot as random effects. In all models, experiment year is included as both a categorical fixed effect and a categorical random variable while plot and subplot are considered as nested random variables (see methods and Figure A3 in the Appendix for model selection details, Figure A5 for plots of all model coefficients over time and Table A3 for delta-AIC values from model selection). DenDF are based on a Kenward-Roger approximation.

Response	Best-fit model	Covariance structure	Fixed effects	NumDF	DenDF	*F* value	Pr (>*F*)
Richness (*q* = 0)	Fully interactive	CSH	Warming	1	32.21	4.662	0.0384*
			Drought	1	32.21	0.167	0.6856
			Year	5	51.00	15.531	<0.0001***
			Warming:Drought	1	32.21	0.167	0.6856
			Warming:Year	5	51.00	1.413	0.2352
			Drought:Year	5	51.00	0.872	0.5065
			Warming:Drought:Year	5	51.00	1.778	0.1340.
Shannon diversity (*q* = 1)	Fully interactive	CS	Warming	1	32	0.841	0.3660
			Drought	1	32	0.713	0.4048
			Year	5	160	7.5734	<0.0001***
			Warming:Drought	1	32	0.518	0.4768
			Warming:Year	5	160	2.692	0.0230*
			Drought:Year	5	160	0.159	0.9770
			Warming:Drought:Year	5	160	0.575	0.7191
Inverse Simpson diversity (*q* = 2)	Fully interactive	CS	Warming	1	32	0.505	0.4823
			Drought	1	36	0.732	0.3986
			Year	5	180	6.398	<0.0001***
			Warming:Drought	1	36	0.355	0.5554
			Warming:Year	5	180	2.218	0.0550
			Drought:Year	5	180	0.262	0.9332
			Warming:Drought:Year	5	180	0.747	0.5891
Evenness	Fully interactive	CSH	Warming	1	35.85	0.335	0.5661
			Drought	1	35.85	1.129	0.295
			Year	5	64.43	6.678	<0.0001***
			Warming:Drought	1	35.85	0.118	0.7333
			Warming:Year	5	64.43	2.277	0.0571·
			Drought:Year	5	64.43	0.224	0.9506
			Warming:Drought:Year	5	64.43	1.584	0.1772

Note: Significance codes: $p < 0.0001$ = ***, $p < 0.01$ = **, $p < 0.05$ = *, $p < 0.1$ = ".".

3 | RESULTS

3.1 | Effect of warming on species richness and diversity

In support of our first hypothesis (H1), warming significantly reduced species richness across the six-year study (Warming: $F_{1,32.21} = 4.662$, $p = 0.0384$; Figure 2; Table 2). In line with our hypothesis regarding year-to-year variability (H2), we found that warming's effect on diversity varied among years. Specifically, warming significantly reduced Shannon diversity in some years (Warming × year: $F_{5,160} = 2.692$, $p = 0.0230$; Figure 2; Table 2). Warming also marginally significantly reduced inverse Simpson diversity in specific years (Warming × year: $F_{5,180} = 2.218$, $p = 0.0550$; Figure 2; Table 2).

3.2 | Effect of drought on plant communities

Contrary to our hypothesis, drought alone did not have a significant effect on species richness, diversity or evenness, nor did we find any significant interactive effects on the responses we measured when warming and drought treatments were combined. However, drought influenced the coefficient of variation (CV) (Figure 3; Table 3). Specifically, drought significantly decreased the CV of inverse

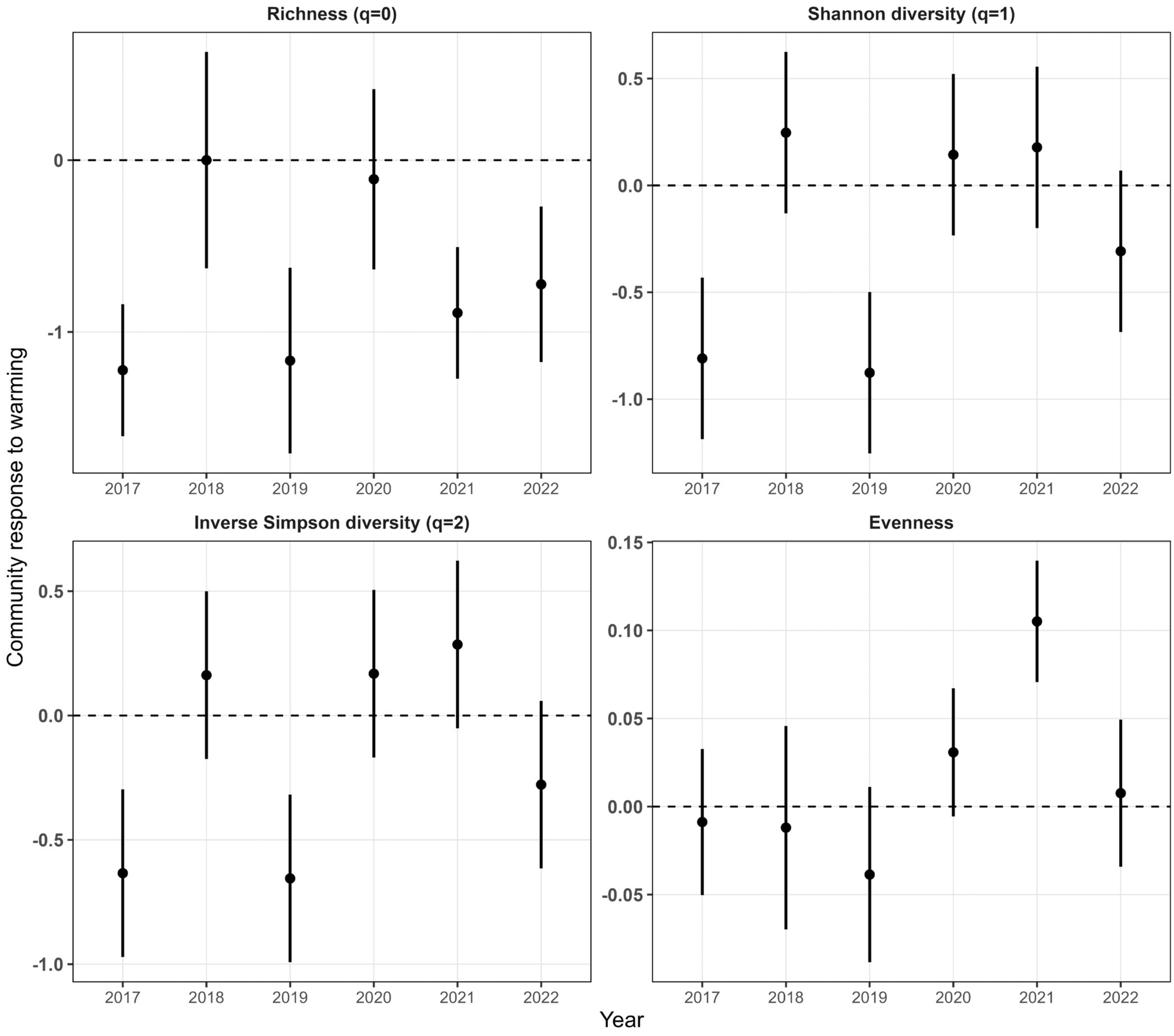


FIGURE 2 Warming effects on plant richness, diversity and evenness responses over 6 years. Effects of experimental warming on four measures of plant community structure across six consecutive treatment years. Responses include richness (top left), Shannon's diversity (top right), inverse Simpson Index diversity value (bottom left) and evenness based on inverse Simpson's Index values (bottom right). All panels show value means for each group ±1 SE. The estimated marginal means and standard errors (SE) are derived from the mixed model repeated measures (MMRM) analysis. Positive values indicate an increase in the response variable due to the treatment, while negative values indicate a decrease. The analysis accounts for the interaction effects of warming, drought and year. See Appendix Figure A5 for all treatment interactions.

FIGURE 3 Difference in coefficient of variation (CV) for community-level and functional group responses to treatment over time. The *y*-axis in all panels measures the difference in CV between treatment and control plots over 6 years, where positive values indicate that the treatment increased variability (higher CV) compared to the control plots and negative values indicate a decrease. (a) Community-level responses: This section shows the CV treatment responses for different community metrics, including species richness, Shannon's diversity, inverse Simpson diversity and evenness. (b) Dominance responses: This section shows the Berger-Parker Index of dominance and the proportional biomass of *Andropogon gerardii*. (c) Functional group biomass proportion responses: This section shows the CV treatment responses for plant functional groups, specifically the proportions of legumes, non-legume forbs, C3 grasses and C4 grasses. Each point represents the mean ± 1 SE, calculated at the subplot level. The CV response is derived from a linear mixed-effects model (lmer) analysis (Bates et al., 2015), which accounts for the interaction effects of warming, drought and experiment year. The detailed statistical results are available in Table 3. The analysis accounts for the interaction effects of warming, drought and experiment year.

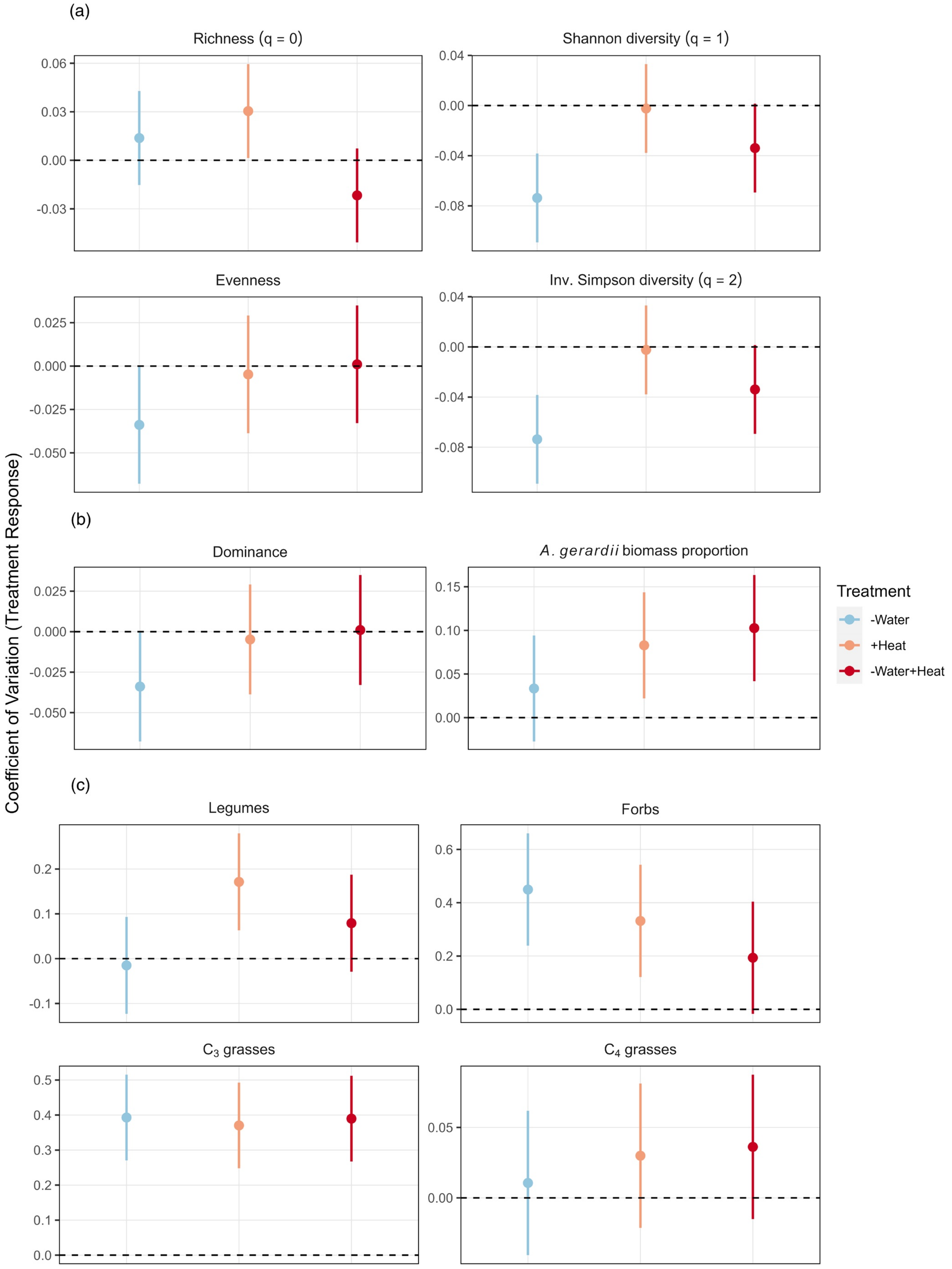

(a)
Richness (q = 0)
0.06
0.03
0.00
-0.03
Shannon diversity (q = 1)
0.04
0.00
-0.04
-0.08
Evenness
0.025
0.000
-0.025
-0.050
Inv. Simpson diversity (q = 2)
0.04
0.00
-0.04
-0.08
Coefficient of Variation (Treatment Response)
(b)
Dominance
0.025
0.000
-0.025
-0.050
A. gerardii biomass proportion
0.15
0.10
0.05
0.00
Treatment
-Water
+Heat
-Water+Heat
(c)
Legumes
0.2
0.1
0.0
-0.1
Forbs
0.6
0.4
0.2
0.0
C_3 grasses
0.5
0.4
0.3
0.2
0.1
0.0
C_4 grasses
0.05
0.00

TABLE 3 Output of linear mixed-effects model (lmer) (Bates et al., 2015) showing the effect of warming treatment and drought treatment on the coefficient of variation (CV) for six community responses: species richness, Shannon's diversity, inverse Simpson's Index values, evenness (based on inverse Simpson's Index), Berger-Parker Index of dominance (proportion of the single most abundant species), *A. gerardii* proportional biomass and the proportional biomass of legumes, non-legume forbs, C_3 grasses and C_4 grasses across four consecutive treatment years while accounting for plot as a random effect. Because CV is taken across all years of the experiment, the models do not incorporate a temporal covariance structure. Instead, model selection was run for an interactive (Warming × Drought) vs. additive (Warming + Drought) fixed effects structure. See Figure A6 in the Appendix for plots of all model coefficients over time. DenDF are based on a Kenward-Roger approximation.

Response	Best-fit model	Fixed effects	NumDF	DenDF	*F* value	Pr (>*F*)
Richness ($q = 0$) CV	Additive	Warming	1	25	0.01	0.907
		Drought	1	25	0.82	0.374
Shannon's diversity ($q = 1$) CV	Additive	Warming	1	25	0.28	0.604
		Drought	1	25	3.55	0.071
Inverse Simpson's diversity ($q = 2$) CV	Additive	Warming	1	25	0.56	0.460
		Drought	1	25	4.47	0.045*
Evenness (Inverse Simpson) CV	Additive	Warming	1	25	1.60	0.218
		Drought	1	25	0.92	0.346
Berger-Parker dominance index CV	Additive	Warming	1	25	0.40	0.534
		Drought	1	25	0.35	0.561
Andropogon gerardii proportional biomass CV	Additive	Warming	1	25	3.26	0.083.
		Drought	1	25	0.40	0.534
Legume biomass proportion CV	Additive	Warming	1	25	3.11	0.090.
		Drought	1	25	0.51	0.483
Forb (non-legume) biomass CV	Additive	Warming	1	25	0.06	0.812
		Drought	1	25	0.98	0.332
C_3 biomass proportion CV	Interactive	Warming	1	24	4.51	0.044*
		Drought	1	24	5.68	0.025*
		Warming:Drought	1	24	4.67	0.041*
C_4 biomass proportion CV	Additive	Warming	1	25	0.61	0.441
		Drought	1	25	0.06	0.814

Note: Significance codes: $p < 0.0001$ = ***, $p < 0.01$ = **, $p < 0.05$ = *, $p < 0.1$ = ".".

Simpson diversity ($F_{1,25} = 4.467$, $p = 0.0447$), indicating that drought decreased variability in diversity.

3.3 | Changes in evenness and dominance under warming

In contrast to our third hypothesis (H3), we did not observe a significant main effect of warming on community evenness (Warming: $F_{1,35.85} = 0.335$, $p = 0.5661$; Figure 2; Table 2). However, a marginally significant increase in evenness was detected under warming during 2021 (Warming × year: $F_{5,64.43} = 2.277$, $p = 0.0571$), which was a dry year in our study (Figure 1). Accordingly, the biomass of *Andropogon gerardii*, a dominant species in our system, was also lowest under warming during this same year (Figure 4). However, in other less-dry years we observed that *A. gerardii* experienced a marginally significant increase in biomass under warming (Warming × Year: $F_{5,180} = 2.115$, $p = 0.0656$; Figure 4; Table 4). In correspondence with *A. gerardii* biomass, dominance (Berger-Parker Index) experienced a marginally significant increase under warming, especially in some years (Warming × year: $F_{5,60.55} = 2.244$, $p = 0.0612$; Figure 4; Table 4).

3.4 | Functional group trends

Support for our fourth hypothesis (H4), was mixed. Although we observed marginally significant increases in the dominance of one C_4 grass species (*A. gerardii*) with warming in specific years (Figure 4; Table 4), this response was not mirrored by other C_4 grasses (Figure 5; Figure A2). We did observe one significant functional group response to warming. Specifically, warming significantly increased the proportional biomass of legumes across all years (Warming: $F_{1,59.01} = 6.485$, $p = 0.0135$; Figure 5; Table 5). This increase in legume dominance suggests that legumes may benefit from warmer conditions, potentially owing to their capacity for nitrogen fixation, which might confer resilience to warming and drought. However, contrary to our hypothesis, neither forbs, C_3 grasses, nor C_4 grasses exhibited significant responses to warming or drought, with biomass proportions of each functional group varying from year-to-year.

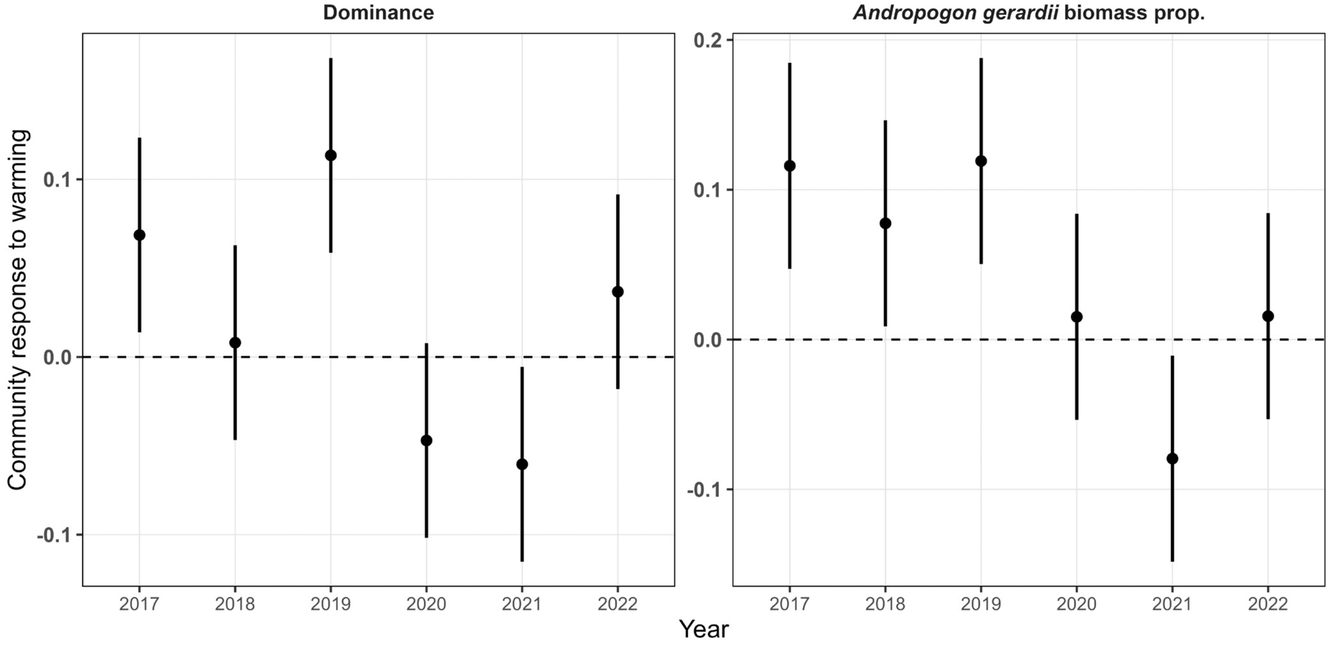


FIGURE 4 Warming effects on dominance and *Andropogon gerardii* responses over 6 years. Effects of experimental warming on two measures of plant community structure across six consecutive treatment years, showing dominance based on a Berger-Parker Index (left) and the proportional biomass of *Andropogon gerardii* (right). All panels show value means for each group ±1 SE. See Figure 2 caption for model interpretation details. See Appendix Figure A6 for all treatment interactions.

TABLE 4 Output of mixed model for repeated measures (mmrm) showing the effect of warming treatment, drought treatment and experiment year on Berger-Parker Index of dominance (proportion of the single most abundant species) and *Andropogon gerardii* proportional biomass across four consecutive treatment years while accounting for plot and subplot as random effects. In all models, experiment year is included as both a categorical fixed effect and a categorical random variable while plot and subplot are considered as nested random variables (see methods and Figure A3 in the Appendix for model selection details and Table A3 for delta-AIC values from model selection. DenDF are based on a Kenward-Roger approximation).

Response	Best-fit model	Covariance structure	Fixed effects	NumDF	DenDF	*F* value	Pr (>*F*)
Dominance	Fully interactive	CSH	Warming	1	36.12	0.362	0.5511
			Drought	1	36.12	1.583	0.2163
			Year	5	60.55	6.519	0.0001**
			Warming:Drought	1	36.12	0.196	0.6608
			Warming:Year	5	60.55	2.244	0.0612
			Drought:Year	5	60.55	0.215	0.9548
			Warming:Drought:Year	5	60.55	0.608	0.6937
Andropogon gerardii biomass proportion	Fully interactive	CS	Warming	1	36	0.956	0.3347
			Drought	1	36	0.768	0.3868
			Year	5	180	8.958	<0.0001***
			Warming:Drought	1	36	0.002	0.9687
			Warming:Year	5	180	2.115	0.0656·
			Drought:Year	5	180	0.857	0.5114
			Warming:Drought:Year	5	180	1.136	0.3428

Note: Significance codes: $p<0.0001$ = ***, $p<0.01$ = **, $p<0.05$ = *, $p<0.1$ = ".".

4 | DISCUSSION

Warming consistently reduced species richness in our study, with additional impacts on diversity and dominance varying by year. Legumes also thrived under warming, likely benefiting from increased nitrogen-fixing activity under higher temperatures (Tang et al., 2024). This response may enhance nutrient cycling and provide a compensatory effect against species losses (Ciavattini et al., 2023;

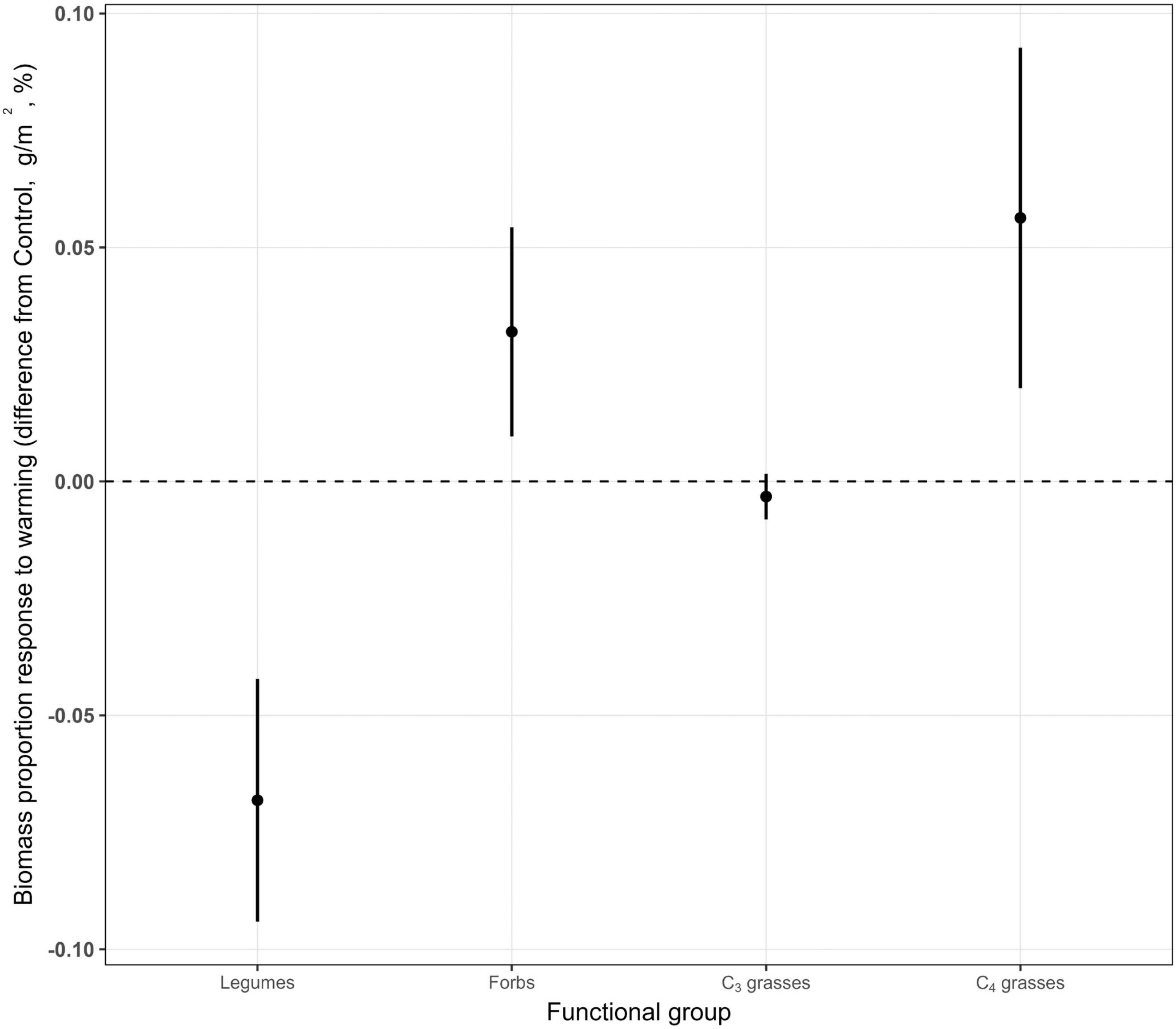


FIGURE 5 Warming effects on plant functional group proportions over 6 years. Effects of warming on proportional biomass of legumes, non-legume forbs, C_3 grasses and C_4 grasses in response to warming treatments across 6 years of the experiment. All panels show value means for each group ±1 SE. See Appendix Figure A7 for all treatment interactions. The estimated marginal means and standard errors (SE) are derived from the mixed model repeated measures (MMRM) analysis. Positive values indicate an increase in the response variable due to the treatment, while negative values indicate a decrease. Note that the standard errors of the coefficients shown here vary between groups in part because they represent the output of four distinct models that tested the effect of the response of each functional group to warming alone. See Table 5 for associated statistics and best-fit models.

Ghahramani et al., 2019). Similarly, dominant grasses such as *Andropogon gerardii* gained a competitive advantage under warmer conditions in some years, potentially monopolizing resources and driving declines in diversity and evenness (Sherry et al., 2008). In contrast, drought alone had little direct effect on richness or diversity metrics, but did significantly reduce the variability (CV) of diversity, suggesting a more stable community response under moisture limitation. This reduced variability may reflect a gradual convergence of the plant community over time, consistent with legacy and acclimation effects reported in other similar systems (Bresta et al., 2018; Chen et al., 2022; Müller & Bahn, 2022). Together, these findings highlight warming and drought as distinct, non-interacting drivers of community structure, with warming exerting more pronounced directional effects on richness, diversity and functional group composition while drought may act to stabilize diversity dynamics over time.

While our results demonstrate consistent declines in richness under warming, the underlying mechanisms behind these declines likely involve both direct physiological stress and altered competitive dynamics. For example, most prairie plant species show optimal germination within a moderate temperature range; temperatures exceeding these thresholds can sharply reduce seedling recruitment

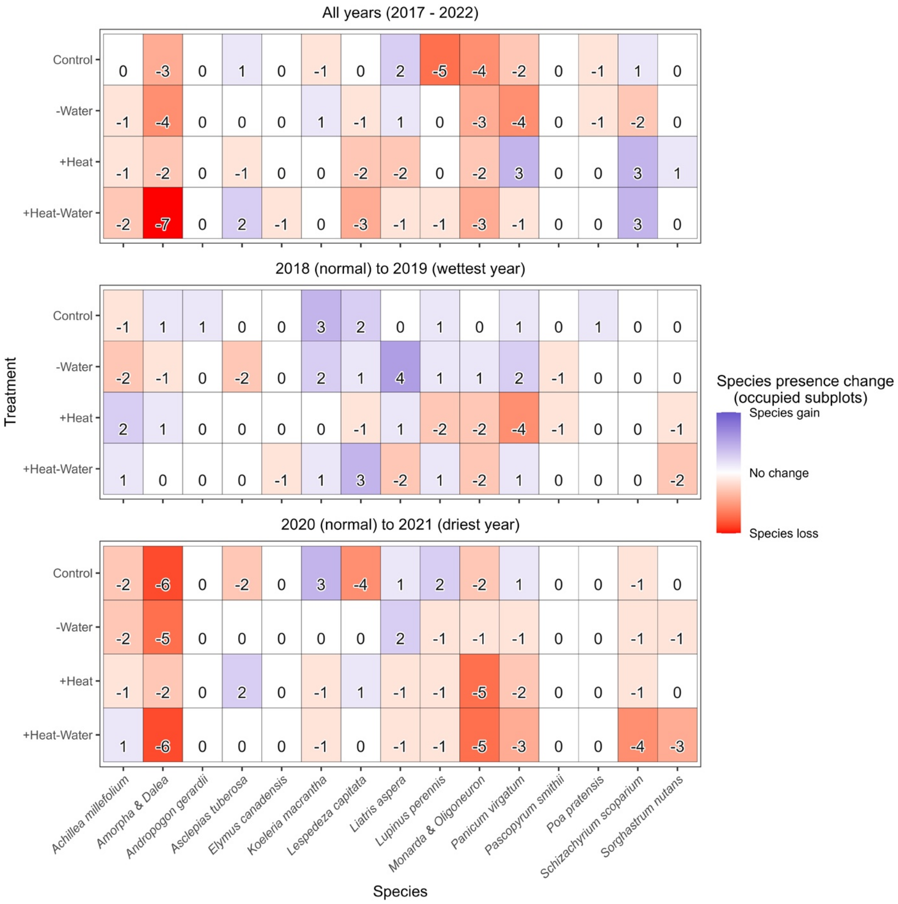
TABLE 5 Output of mixed model for repeated measures (mmrm) showing the effect of warming treatment (Warming), drought treatment (Drought) and experiment year (Year) on the proportional biomass of legumes, non-legume forbs, C_3 grasses and C_4 grasses across four consecutive treatment years while accounting for plot and subplot as random effects. In all models, experiment year is included as both a categorical fixed effect and a categorical random variable while plot and subplot are considered as nested random variables (see methods and Figure A3 in the Appendix for model selection details). DenDF are based on a Kenward-Roger approximation.

Response	Best-fit model	Covariance structure	Fixed effects	NumDF	DenDF	*F* value	Pr (>*F*)
Legume biomass proportion	Fully additive	AD	Warming	1	59.01	6.485	0.0135*
			Drought	1	59.01	0.296	0.5882
			Year	5	33.46	2.001	0.1040
Forb biomass proportion	Fully interactive	AD	Warming	1	65.20	1.753	0.1902
			Drought	1	65.20	0.175	0.6768
			Year	5	68.71	0.911	0.4793
			Warming:Drought	1	65.20	0.172	0.6800
			Warming:Year	5	68.71	1.023	0.4109
			Drought:Year	5	68.71	0.799	0.5544
			Warming:Drought:Year	5	68.71	0.404	0.8445
C_3 biomass proportion	Fully additive	AR1H	Warming	1	51.07	0.314	0.5776
			Drought	1	51.07	3.792	0.570
			Year	5	46.75	7.654	<0.0001***
C_4 biomass proportion	Fully additive	US	Warming	1	33	2.421	0.1293
			Drought	1	33	0.306	0.5837
			Year	5	33	11.697	<0.0001***

Note: Significance codes: $p < 0.0001 =$ ***, $p < 0.01 =$ **, $p < 0.05 =$ *, $p < 0.1 =$ ".".

and establishment success (McGraw et al., 2003; Schellenberg & Biligetu, 2015). Elevated air temperatures can also intensify internal heat stress in leaves—especially when drought limits cooling by transpiration—leading to cellular damage, early senescence and decreased photosynthetic efficiency (Fahad et al., 2017; Hasanuzzaman et al., 2013). These processes may help explain the persistent reductions in species richness we observed in warmed plots across all study years, even in years when moisture was less limiting. Warming also tends to strengthen resource pre-emption by dominant grasses, increasing competitive exclusion of less heat-tolerant subordinate species (De Boeck, 2008; Olsen et al., 2016). Our finding of greater dominance by *A. gerardii* under warming in conjunction with reduced species diversity, particularly in wetter years, aligns well with these expectations. Finally, trait-based differences—such as photosynthetic pathway and nitrogen fixation ability—further shape species' vulnerability, with heat-tolerant C_4 grasses generally maintaining productivity under warming, while many C_3 forbs and shallow-rooted perennials experience sharper declines (Castillioni et al., 2022; Soudzilovskaia et al., 2013; Valliere et al., 2023; Whittington et al., 2013). Together, these interacting processes help explain why warming consistently reduced species richness over time.

Across the six years of our study, external environmental variables likely influenced species abundances, resulting in the annual fluctuations in warming impacts. Here, our results align with previous work finding that environmental variables, such as moisture availability, can modulate the impact of warming from year to year (Chiang et al., 2023; Liu et al., 2018) and that year effects can influence species emergence and establishment (Batbaatar et al., 2022). For example, we observed that tall species like *A. gerardii* were more likely to dominate during wetter years (Figure 4; Table 4), a pattern likely driven by physiological traits such as high water-use efficiency that enable robust growth under warm, moist conditions with high evaporative demand (Osborne & Beerling, 2006; Taylor et al., 2014). These interannual shifts in dominance also help to explain why different diversity indices responded variably to climate treatments. Species richness ($q = 0$), which counts species regardless of abundance, consistently declined under warming—likely reflecting loss of heat-sensitive, subordinate species. In contrast, abundance-weighted metrics such as Shannon ($q = 1$) and inverse Simpson diversity ($q = 2$) varied more across years, shaped by fluctuations in dominant species' biomass. Under drought, evenness remained stable or slightly increased, possibly due to reduced dominance allowing subordinate species to persist. These patterns suggest that drought alters relative abundances without driving species loss and exclusion, which we observed under warming. Consistent with this, we observed that plots under drought treatments experienced minimal species losses over time compared to warmed plots (Figure 6, top panel), supporting the idea that drought drove changes in species' abundances rather than species' extirpations. These findings further underscore the importance of using multiple diversity indices to fully capture ecological responses to climate stress. Furthermore, this shift in dominance (of *A. gerardii*) supports our prediction that warming favours the proliferation of a few heat-tolerant species,



All years (2017 - 2022)

Treatment	Achillea millefolium	Amorpha & Dalea	Andropogon gerardii	Asclepias tuberosa	Elymus canadensis	Koeleria macrantha	Lespedeza capitata	Liatris aspera	Lupinus perennis	Monarda & Oligoneuron	Panicum virgatum	Pascopyrum smithii	Poa pratensis	Schizachyrium scoparium	Sorghastrum nutans
Control	0	-3	0	1	0	-1	0	2	-5	-4	-2	0	-1	1	0
-Water	-1	-4	0	0	0	1	-1	1	0	-3	-4	0	-1	-2	0
+Heat	-1	-2	0	-1	0	0	-2	-2	0	-2	3	0	0	3	1
+Heat-Water	-2	-7	0	2	-1	0	-3	-1	-1	-3	-1	0	0	3	0

2018 (normal) to 2019 (wettest year)

Treatment	Achillea millefolium	Amorpha & Dalea	Andropogon gerardii	Asclepias tuberosa	Elymus canadensis	Koeleria macrantha	Lespedeza capitata	Liatris aspera	Lupinus perennis	Monarda & Oligoneuron	Panicum virgatum	Pascopyrum smithii	Poa pratensis	Schizachyrium scoparium	Sorghastrum nutans
Control	-1	1	1	0	0	3	2	0	1	0	1	0	1	0	0
-Water	-2	-1	0	-2	0	2	1	4	1	1	2	-1	0	0	0
+Heat	2	1	0	0	0	0	-1	1	-2	-2	-4	-1	0	0	-1
+Heat-Water	1	0	0	0	-1	1	3	-2	1	-2	1	0	0	0	-2

2020 (normal) to 2021 (driest year)

Treatment	Achillea millefolium	Amorpha & Dalea	Andropogon gerardii	Asclepias tuberosa	Elymus canadensis	Koeleria macrantha	Lespedeza capitata	Liatris aspera	Lupinus perennis	Monarda & Oligoneuron	Panicum virgatum	Pascopyrum smithii	Poa pratensis	Schizachyrium scoparium	Sorghastrum nutans
Control	-2	-6	0	-2	0	3	-4	1	2	-2	1	0	0	-1	0
-Water	-2	-5	0	0	0	0	0	2	-1	-1	-1	0	0	-1	-1
+Heat	-1	-2	0	2	0	-1	1	-1	-1	-5	-2	0	0	-1	0
+Heat-Water	1	-6	0	0	0	-1	0	-1	-1	-5	-3	0	0	-4	-3

FIGURE 6 Treatment effects on individual species gains and losses. Changes in species presence across subplots in response to warming and drought treatments. The top panel shows species gains and losses between the first and last years of the experiment, while the centre and bottom panels show changes during the wettest and driest years, respectively. Numbers within grid cells represent the net change in the number of subplots occupied by each species under a given treatment over the specific period, with "0" indicating no change. Grid cell colours indicate the direction of change: Blue for gains and red for losses, facilitating visual interpretation of treatment effects.

especially under favourable moisture conditions. This conjecture is supported by the marginally significant increase in evenness detected during 2021, which was a dry year in our study (Figure 1), suggesting that drier conditions may initially allow non-dominant species to persist under warming. Although *A. gerardii* responded positively to warm conditions alone, its marginal decline under warm and dry conditions together may have created new opportunities for other more drought-tolerant species to flourish. In non-dry years, *A. gerardii* may have outcompeted other less-abundant species (Dekirmenjian et al., 2024), further amplifying warming effects. This finding aligns with previous work showing that dominant species can shade or reduce resources for other species, thereby decreasing overall diversity (Eskelinen et al., 2022; Li et al., 2022). These results underscore the importance of temporal variability in shaping warming's effects on plant communities.

Our drought treatment had minimal direct effects on species richness and diversity, with no significant interactions observed between warming and drought across the responses we measured. Interestingly, drought reduced variability (CV) in diversity responses, suggesting greater temporal stability of diversity under drought conditions. This result was unexpected given the known susceptibility of grassland ecosystems to moisture limitation. One possible explanation is that repeated drought events may selectively shift community composition towards species with similar, drought-adapted traits; as less-tolerant species decline in abundance, the remaining community exhibits more uniform responses to drought stress, lowering variability in drought responses over time (Harrison et al., 2018; Müller & Bahn, 2022). Additionally, recurrent drought can induce legacy and acclimation effects, where plants and soil biota become better adapted to drought, leading to enhanced photosynthesis and more stable internal conditions under subsequent drought events (Amoah et al., 2023; Bresta et al., 2018; Chen et al., 2022). Such stability may also reflect site-specific factors such as sandy, well-drained soils at our site, which likely reduced the plant community's sensitivity to drought (Köhl, 1996; Siebielec et al., 2020; Zhou et al., 2014). This soil composition, coupled with the resilience of many grassland species to short-term droughts (Craine et al., 2013; Jung et al., 2020), may additionally help to explain these minimal direct impacts of drought. This interpretation is partially supported by our observation that species loss patterns under drought conditions did not markedly differ from those observed under control conditions (Figure 6, top panel). The absence of strong drought effects in our study differs from other research showing that increased temperatures combined with reduced precipitation often decrease diversity through drought stress by favouring a few drought-tolerant species (Piseddu et al., 2021; Yao et al., 2022), an effect especially prevalent in drier grasslands (Jonas et al., 2015; Yao et al., 2022). Our results highlight the need for ecosystem-specific considerations when predicting climate change effects.

Functional redundancy within the plant community likely played a crucial role in buffering against environmental stressors. Apart from legumes, which thrived under warmer conditions, the absence of distinct responses from other functional groups suggests that species within these groups may have shown asynchronous responses to warming and drought treatments, enabling some to increase in productivity while others declined and thus creating a compensatory dynamic that helped maintain stability (Biggs et al., 2015; Fonseca & Ganade, 2001; Isbell et al., 2015). For example, although we observed marginally significant increases in the dominance of one C_4 grass species (*A. gerardii*) with warming in specific years (Figure 4), this response was not mirrored by other C_4 grasses (Figure 5). Furthermore, the ability of some species to tolerate warming or drought likely helped mitigate large-scale changes in community structure (Hautier et al., 2014; Hector et al., 2010). However, continued species loss under warming could undermine this stability over time. Decreased species richness and diversity leave plant communities more susceptible to extreme climate events such as droughts and heatwaves (Isbell et al., 2015; Tilman et al., 2006). These findings emphasize the importance of preserving functional redundancy to sustain critical ecosystem processes such as nutrient cycling, productivity and carbon sequestration.

Our results highlight the need for adaptive management strategies to maintain grassland biodiversity and ecosystem functionality under climate change. Such strategies should prioritize the introduction of resilient species better suited to thrive in warmer conditions. For example, incorporating historically less-dominant C_4 grasses, such as *Schizachyrium scoparium* (Little bluestem), into seed mixes, along with sourcing seeds from genetically diverse populations, could enhance the adaptive capacity of grassland communities to withstand threats such as disease, invasive species and climate extremes (Dekirmenjian et al., 2024; Lindstrom et al., 2023). Additionally, limiting the dominance of taller warm-season grasses like *A. gerardii* in seed mixes while fostering functional group diversity could help stabilize productivity and mitigate biodiversity loss over the long term.

Future research should focus on disentangling the mechanisms underlying plant community responses to warming and interannual variability. Long-term exclusion experiments targeting dominant species like *A. gerardii* can provide critical insights into competitive interactions and their effects on richness, biomass and light availability (Hernández et al., 2022). Further investigations into how soil properties and hydrology interact with warming and drought could refine site-specific conservation strategies. Mechanistic studies exploring physiological and competitive traits that shape long-term species responses will also be essential for predicting community shifts. Moreover, long-term monitoring that incorporates interannual variability in temperature and precipitation is crucial for improving predictive models of ecosystem responses (Wilcox et al., 2021). Such research will provide actionable insights to guide dynamic management practices, helping to mitigate biodiversity loss and sustain ecosystem functionality in grasslands under climate change.

AUTHOR CONTRIBUTIONS

Forest Isbell contributed to project creation and maintenance; Maggie Anderson analysed the data with substantial input from Forest Isbell; Maggie Anderson wrote the paper with substantial input from Forest Isbell.

ACKNOWLEDGEMENTS

We thank Troy Mielke, Jane Cowles-Ditmer, Carmen Watson, Sydney Hedberg, Nicole Kjerstin and Cedar Creek interns for data collection. We thank Sarah Hobbie, Elizabeth Borer, Daniel Cariveau and Amber Churchill for feedback, discussions and comments on the manuscript. We thank David Tilman and colleagues for conceiving of the original BioDIV experiment in which BACD is nested. We acknowledge support from the University of Minnesota's College of Biological Sciences and the US National Science Foundation's Long-Term Ecological Research program (DEB-1831944) and National Science Foundation, Biodiversity on a Changing Planet (DEB-2224852). Maggie Anderson was supported additionally by the Huempfner Research and Education Fund, the Darby and Geri Nelson Environmental Scholar Award and the Lawrence Research Scholarships through Cedar Creek Ecosystem Science Reserve.

CONFLICT OF INTEREST STATEMENT

The authors declare no competing financial interests.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.70172.

DATA AVAILABILITY STATEMENT

Data is available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.0p2ngf2dh (Anderson & Isbell, 2025).

ORCID

Maggie Anderson https://orcid.org/0000-0001-8188-2399
Forest Isbell https://orcid.org/0000-0001-9689-769X

REFERENCES

Alonso-Rodríguez, A. M., Wood, T. E., Torres-Díaz, J., Cavaleri, M. A., Reed, S. C., & Bachelot, B. (2022). Understory plant communities show resistance to drought, hurricanes, and experimental warming in a wet tropical forest. *Frontiers in Forests and Global Change*, *5*(1), 1–16. https://doi.org/10.3389/ffgc.2022.733967

Amoah, J. N., Adu-Gyamfi, M. O., & Kwarteng, A. O. (2023). Effect of drought acclimation on antioxidant system and polyphenolic content of foxtail millet (*Setaria Italica* L.). *Physiology and Molecular*

Biology of Plants, *29*(10), 1577–1589. https://doi.org/10.1007/s12298-023-01366-w

An, Y., Wan, S., Zhou, X., Subedar, A. A., Wallace, L. L., & Luo, Y. (2005). Plant nitrogen concentration, use efficiency, and contents in a tallgrass prairie ecosystem under experimental warming. *Global Change Biology*, *11*(10), 1733–1744. https://doi.org/10.1111/j.1365-2486.2005.01030.x

Anderson, M., & Isbell, F. (2025). *Data from: Experimental warming drives local grassland plant species loss*. Dryad Digital Repository https://doi.org/10.5061/dryad.0p2ngf2dh

Batbaatar, A., Carlyle, C. N., Bork, E. W., Chang, S. X., & Cahill, J. F., Jr. (2022). Multi-year drought alters plant species composition more than productivity across northern temperate grasslands. *Journal of Ecology*, *110*(1), 197–209. https://doi.org/10.1111/1365-2745.13796

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using Lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Beguería, S., Vicente Serrano, S. M., Reig-Gracia, F., & Latorre Garcés, B. (2024). *SPEIbase v.2.10 [Spei04]: A comprehensive tool for global drought analysis*. Digital.CSIC https://doi.org/10.13039/501100000780

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, *15*(4), 365–377. https://doi.org/10.1111/j.1461-0248.2011.01736.x

Berger, W. H., & Parker, F. L. (1970). Diversity of planktonic foraminifera in deep-sea sediments. *Science*, *168*(3937), 1345–1347. https://doi.org/10.1126/science.168.3937.1345

Biggs, R., Schlüter, M., & Schoon, M. L. (2015). *Principles for building resilience: Sustaining ecosystem Services in Social-Ecological Systems*. Cambridge University Press, M.L. https://doi.org/10.1017/CBO9781316014240

Bresta, P., Nikolopoulos, D., Stavroulaki, V., Vahamidis, P., Economou, G., & Karabourniotis, G. (2018). How does long-term drought acclimation modify structure-function relationships? A quantitative approach to leaf phenotypic plasticity of barley. *Functional Plant Biology*, *45*(12), 1181–1194. https://doi.org/10.1071/FP17283

Castillioni, K., Newman, G. S., Souza, L., & Iler, A. M. (2022). Effects of drought on grassland phenology depend on functional types. *New Phytologist*, *236*(4), 1558–1571. https://doi.org/10.1111/nph.18462

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., & Colwell, R. K. (2014). Rarefaction and extrapolation with hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs*, *84*(1), 46–67. https://doi.org/10.1890/13-0133.1

Chao, A., & Jost, L. (2015). Estimating diversity and entropy profiles via discovery rates of new species. *Methods in Ecology and Evolution*, *6*(8), 873–882.

Chapin, F. S., Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., Hooper, D. U., Lavorel, S., Sala, O. E., Hobbie, S. E., & Mack, M. C. (2000). Consequences of changing biodiversity. *Nature*, *405*(6783), 234–242.

Chen, Y., Vogel, A., Wagg, C., Xu, T., Iturrate-Garcia, M., Scherer-Lorenzen, M., Weigelt, A., Eisenhauer, N., & Schmid, B. (2022). Drought-exposure history increases complementarity between plant species in response to a subsequent drought. *Nature Communications*, *13*(1), 3217. https://doi.org/10.1038/s41467-022-30954-9

Chiang, F., Cook, B. I., & McDermid, S. (2023). Warming overwhelms the efficacy of wet conditions to moderate extreme heat and atmospheric aridity across the Central Plains. *Geophysical Research Letters*, *50*(7), 1–14. https://doi.org/10.1029/2023GL102939

Churchill, A. C., Zhang, H., Fuller, K. J., Amiji, B., Anderson, I. C., Barton, C. V. M., Carrillo, Y., Catunda, K. L. M., Chandregowda, M. H., Igwenagu, C., Jacob, V., Kim, G. W., Macdonald, C. A., Medlyn, B. E., Moore, B. D., Pendall, E., Plett, J. M., Post, A. K., Powell, J. R., … Power, S. A. (2022). Pastures and climate extremes: Impacts of cool season warming and drought on the productivity of key pasture species in a field experiment. *Frontiers in Plant Science*, *13*(836968), 1–16. https://doi.org/10.3389/fpls.2022.836968

Ciavattini, M., Tognetti, P. M., Campana, S., & Yahdjian, L. (2023). Livestock grazing promotes legume abundance under increased nutrient loads: Mechanistic evidence from a temperate grassland. *Applied Vegetation Science*, *26*(4), 1–10. https://doi.org/10.1111/avsc.12751

Cowles, B. B., Liancourt, P., Petraitis, P. S., & Casper, B. B. (2018). Effects of increased temperature on plant communities depend on landscape location and precipitation. *Ecology and Evolution*, *8*(11), 5267–5278. https://doi.org/10.1002/ece3.3995

Cowles, P. D., Wragg, A. J., Wright, J. S., Powers, J. S., & Tilman, D. (2016). Shifting grassland plant community structure drives positive interactive effects of warming and diversity on aboveground net primary productivity. *Global Change Biology*, *22*(2), 741–749. https://doi.org/10.1111/gcb.13111

Craine, J. M., Ocheltree, T. W., Nippert, J. B., Towne, E. G., Skibbe, A. M., Kembel, S. W., & Fargione, J. E. (2013). Global diversity of drought tolerance and grassland climate-change resilience. *Nature Climate Change*, *3*(1), 63–67.

Csergő, A. M., Demeter, L., & Turkington, R. (2013). Declining diversity in abandoned grasslands of the Carpathian Mountains: Do dominant species matter? *PLoS One*, *8*(8), e73533.

De Boeck, H. (2008). Biomass production in experimental grasslands of different species richness during three years of climate warming. *Biogeosciences*, *5*(2), 585–594. https://doi.org/10.5194/bg-5-585-2008

Debouk, H., Bello, F., & Sebastià, M. T. (2015). Functional trait changes, productivity shifts and vegetation stability in mountain grasslands during a short-term warming. *PLoS One*, *10*(10), e0141899.

Dekirmenjian, A., Montano, D., Budny, M. L., & Lemoine, N. P. (2024). Schizachyrium Scoparium (C4) better tolerates drought than *Andropogon Gerardii* (C4) via constant CO_2 supply for photosynthesis during water stress. *AoB Plants*, *16*(2), 1–10.

Duchicela, S. A., Cuesta, F., Tovar, C., Muriel, P., Jaramillo, R., Salazar, E., & Pinto, E. (2021). Microclimatic warming leads to a decrease in species and growth form diversity: Insights from a tropical Alpine grassland. *Frontiers in Ecology and Evolution*, *9*, 673655. https://doi.org/10.3389/fevo.2021.673655

Dyer, A. R., Goldberg, D. E., Turkington, R., & Sayre, C. (2001). Effects of growing conditions and source habitat on plant traits and functional group definition. *British Ecological Society*, *15*(1), 85–95. https://doi.org/10.1046/j.1365-2435.2001.00487.x

Edwards, E. J., & Still, C. J. (2008). Climate, phylogeny and the ecological distribution of C4 grasses. *Ecology Letters*, *11*(3), 266–276.

Eskelinen, A., Harpole, W. S., Jessen, M.-T., Virtanen, R., & Hautier, Y. (2022). Light competition drives herbivore and nutrient effects on plant diversity. *Nature*, *611*(7935), 301–305. https://doi.org/10.1038/s41586-022-05383-9

Fahad, S., Bajwa, A. A., Nazir, U., Anjum, S. A., Farooq, A., Zohaib, A., Sadia, S., Nasim, W., Adkins, S., Saud, S., & Ihsan, M. Z. (2017). Crop production under drought and heat stress: Plant responses and management options. *Frontiers in Plant Science*, *8*(1147), 1–16. https://doi.org/10.3389/fpls.2017.01147

Fargione, J., Brown, C. S., & Tilman, D. (2003). Community assembly and invasion: An experimental test of neutral versus niche processes. *Proceedings of the National Academy of Sciences of the United States of America*, *100*(15), 8916–8920.

Feeley, K. J., Bravo-Avila, C., Fadrique, B., Perez, T. M., & Zuleta, D. (2020). Climate-driven changes in the composition of New World plant communities. *Nature Climate Change*, *10*(10), 965–970. https://doi.org/10.1038/s41558-020-0873-2

Fonseca, C. R., & Ganade, G. (2001). Species functional redundancy, random extinctions and the stability of ecosystems. *Journal of*

Ecology, *89*(1), 118–125. https://doi.org/10.1046/j.1365-2745.2001.00528.x

Ghahramani, A., Howden, S. M., del Prado, A., Thomas, D. T., Moore, A. D., Ji, B., & Ates, S. (2019). Climate change impact, adaptation, and mitigation in temperate grazing systems: A review. *Sustainability*, *11*(24), 24. https://doi.org/10.3390/su11247224

Grigal, D. F., Severson, R. C., & Goltz, G. E. (1976). Evidence of eolian activity in north-central Minnesota 8000 to 5000 Yr ago. *Geological Society of America Bulletin*, *87*(9), 1251–1254.

Gruner, D. S., Bracken, M. E., Berger, S. A., Bracken, M. E. S., Eriksson, B. K., Gamfeldt, L., Matthiessen, B., Moorthi, S., Sommer, U., & Hillebrand, H. (2017). Effects of experimental warming on biodiversity depend on ecosystem type and local species composition. *Oikos*, *126*(1), 8–17.

Gustafson, D. J., Gibson, D. J., & Nickrent, D. L. (2004). Competitive relationships of *Andropogon Gerardii* (big bluestem) from remnant and restored native populations and select cultivated varieties. *Functional Ecology*, *18*(3), 451–457. https://doi.org/10.1111/j.0269-8463.2004.00850.x

Harpole, W. S., Sullivan, L. L., Lind, E. M., Firn, J., Adler, P. B., Borer, E. T., Chase, J., Fay, P. A., Hautier, Y., Hillebrand, H., & MacDougall, A. S. (2016). Addition of multiple limiting resources reduces grassland diversity. *Nature*, *537*(7618), 93–96.

Harrison, S. (2020). Plant community diversity will decline more than increase under climatic warming. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *375*(1794), 1–8. https://doi.org/10.1098/rstb.2019.0106

Harrison, S. P., LaForgia, M. L., & Latimer, A. M. (2018). Climate-driven diversity change in annual grasslands: Drought plus deluge does not equal normal. *Global Change Biology*, *24*(4), 1782–1792. https://doi.org/10.1111/gcb.14018

Hasanuzzaman, M., Nahar, K., Alam, M. M., Roychowdhury, R., & Fujita, M. (2013). Physiological, biochemical, and molecular mechanisms of heat stress tolerance in plants. *International Journal of Molecular Sciences*, *14*(5), 9643–9684. https://doi.org/10.3390/ijms14059643

Hautier, Y., Seabloom, E. W., Borer, E. T., Adler, P. B., Harpole, W. S., Hillebrand, H., Lind, E. M., MacDougall, A. S., Stevens, C. J., Bakker, J. D., Buckley, Y. M., Chu, C., Collins, S. L., Daleo, P., Damschen, E. I., Davies, K. F., Fay, P. A., Firn, J., Gruner, D. S., … Hector, A. (2014). Eutrophication weakens stabilizing effects of diversity in natural grasslands. *Nature*, *508*(7497), 521–525. https://doi.org/10.1038/nature13014

Hector, A., Hautier, Y., Saner, P., Wacker, L., Bagchi, R., Joshi, J., Scherer-Lorenzen, M., Spehn, E. M., Bazeley-White, E., Weilenmann, M., & Caldeira, M. C. (2010). General stabilizing effects of plant diversity on grassland productivity through population asynchrony and overyielding. *Ecology*, *91*(8), 2213–2220. https://doi.org/10.5167/uzh-35301

Hernández, D. L., Antia, A., & McKone, M. J. (2022). The ecosystem impacts of dominant species exclusion in a prairie restoration. *Ecological Applications*, *32*(5), e2592.

Hillebrand, H., Blasius, B., Borer, E. T., Chase, J. M., Downing, J. A., Eriksson, B. K., Filstrup, C. T., Harpole, W. S., Hodapp, D., Larsen, S., Lewandowska, A. M., Seabloom, E. W., van de Waal, D. B., & Ryabov, A. B. (2018). Biodiversity change is uncoupled from species richness trends: Consequences for conservation and monitoring. *Journal of Applied Ecology*, *55*(1), 169–184. https://doi.org/10.1111/1365-2664.12959

Hoeppner, S. S., & Dukes, J. S. (2012). Interactive responses of old-field plant growth and composition to warming and precipitation. *Global Change Biology*, *18*(5), 1754–1768.

Hoover, D. L., Knapp, A. K., & Smith, M. D. (2014). Resistance and resilience of a grassland ecosystem to climate extremes. *Ecology*, *95*(9), 2646–2656.

Hou, Y., Zhou, G., Xu, Z., Liu, T., & Zhang, X. (2013). Interactive effects of warming and increased precipitation on community structure and composition in an annual forb dominated desert steppe. *PLoS One*, *8*(7), e70114. https://doi.org/10.1371/journal.pone.0070114

Hu, X., Zhou, W., Li, X., Niklas, K. J., & Sun, S. (2021). Changes in community composition induced by experimental warming in an Alpine meadow: Beyond plant functional type. *Frontiers in Ecology and Evolution*, *9*, 1–10. https://doi.org/10.3389/fevo.2021.569422

Iler, A. M., Høye, T. T., Inouye, D. W., & Schmidt, N. M. (2013). Long-term trends mask variation in the direction and magnitude of short-term phenological shifts. *American Journal of Botany*, *100*(7), 1398–1406. https://doi.org/10.3732/ajb.1200490

Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., Bezemer, T. M., Bonin, C., Bruelheide, H., De Luca, E., & Ebeling, A. (2015). Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature*, *526*(7574), 574–577.

Jonas, J. L., Buhl, D. A., & Symstad, A. J. (2015). Impacts of weather on long-term patterns of plant richness and diversity vary with location and management. *Ecology*, *96*(9), 2417–2432. https://doi.org/10.1890/14-1989.1

Jost, L. (2006). Entropy and diversity. *Oikos*, *113*(2), 363–375.

Jost, L. (2010). The relation between evenness and diversity. *Diversity*, *2*(2), 207–232. https://doi.org/10.3390/d2020207

Jung, E. Y., Gaviria, J., Sun, S., & Engelbrecht, B. M. (2020). Comparative drought resistance of temperate grassland species: Testing performance trade-offs and the relation to distribution. *Oecologia*, *192*(4), 1023–1036. https://doi.org/10.1007/s00442-020-04625-9

Kazemi, F., Jozay, M., Salahshoor, F., van Etten, E., & Rezaie, S. (2023). Drought stress responses of some prairie landscape C4 grass species for xeric urban applications. *Land*, *12*(6), 6. https://doi.org/10.3390/land12061195

Keyantash, J., & Dracup, J. A. (2002). The quantification of drought: An evaluation of drought indices. *Bulletin of the American Meteorological Society*, *83*(8), 1167–1180. https://doi.org/10.1175/1520-0477-83.8.1167

Keylock, C. J. (2005). Simpson diversity and the Shannon–wiener index as special cases of a generalized entropy. *Oikos*, *109*(1), 203–207. https://doi.org/10.1111/j.0030-1299.2005.13735.x

Kiebacher, T., Meier, M., Kipfer, T., & Roth, T. (2023). Thermophilisation of communities differs between land plant lineages, land use types and elevation. *Scientific Reports*, *13*(1), 11395. https://doi.org/10.1038/s41598-023-38195-6

Killi, D., Bussotti, F., Raschi, A., & Haworth, M. (2017). Adaptation to high temperature mitigates the impact of water deficit during combined heat and drought stress in C3 sunflower and C4 maize varieties with contrasting drought tolerance. *Physiologia Plantarum*, *159*(2), 130–147.

Kimball, B. A., Conley, M. M., & Lewin, K. F. (2012). Performance and energy costs associated with scaling infrared heater arrays for warming field plots from 1 to 100 m. *Theoretical and Applied Climatology*, *108*, 247–265.

Kimball, B. A., Conley, M. M., Wang, S., Lin, X., Luo, C., Morgan, J., & Smith, D. (2008). Infrared heater arrays for warming ecosystem field plots. *Global Change Biology*, *14*(2), 309–320.

Klein, J. A., Harte, J., & Zhao, X. Q. (2004). Experimental warming causes large and rapid species loss, dampened by simulated grazing, on the Tibetan plateau. *Ecology Letters*, *7*(12), 1170–1179.

Knapp, A. K., Hoover, D. L., Wilcox, K. R., Avolio, M. L., Koerner, S. E., La Pierre, K. J., Loik, M. E., Luo, Y., Sala, O. E., & Smith, M. D. (2015). Characterizing differences in precipitation regimes of extreme wet and dry years: Implications for climate change experiments. *Global Change Biology*, *21*(7), 2624–2633.

Koerner, S. E., & Collins, S. L. (2014). Interactive effects of grazing, drought, and fire on grassland plant communities in North America and South Africa. *Ecology*, *95*(1), 98–109.

Köhl, K. (1996). Population-specific traits and their implication for the evolution of a drought-adapted ecotype in *Armeria maritima*. *Botanica Acta*, *109*(3), 206–215. https://doi.org/10.1111/j.1438-8677.1996.tb00565.x

Ladouceur, E., Blowes, S. A., Chase, J. M., Clark, A. T., Garbowski, M., Alberti, J., Arnillas, C. A., Bakker, J. D., Barrio, I. C., Bharath, S., Borer, E. T., Brudvig, L. A., Cadotte, M. W., Chen, Q., Collins, S. L., Dickman, C. R., Donohue, I., Du, G., Ebeling, A., … Harpole, W. S. (2022). Linking changes in species composition and biomass in a globally distributed grassland experiment. *Ecology Letters*, *25*(12), 2699–2712.

Li, J., Charles, L. S., Yang, Z., Du, G., & Fu, S. (2022). Differential mechanisms drive species loss under artificial shade and fertilization in the Alpine meadow of the Tibetan plateau. *Frontiers in Plant Science*, *13*, 832473. https://doi.org/10.3389/fpls.2022.832473

Lindstrom, J., Ahlering, M., & Hamilton, J. (2023). Seed sourcing for climate-resilient grasslands: The role of seed source diversity during early restoration establishment. *Ecology and Evolution*, *13*(11), e10756. https://doi.org/10.1002/ece3.10756

Liu, H., Mi, Z., Lin, L. I., Wang, Y., Zhang, Z., Zhang, F., Wang, H., Liu, L., Zhu, B., Cao, G., & Zhao, X. (2018). Shifting plant species composition in response to climate change stabilizes grassland primary production. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(16), 4051–4056. https://doi.org/10.1073/pnas.1700299114

Liu, Q., Ma, H., Yu, H., Li, Y., Li, L., Qi, M., Wu, W., Zhang, F., Wang, Y., Zhou, G., & Xu, Z. (2021). Climate warming-induced drought constrains vegetation productivity by weakening the temporal stability of the plant community in an arid grassland ecosystem. *Agricultural and Forest Meteorology*, *307*, 108526. https://doi.org/10.1016/j.agrformet.2021.108526

Lopez, B. E., Allen, J. M., Dukes, J. S., Lenoir, J., Vilà, M., Blumenthal, D. M., Beaury, E. M., Fusco, E. J., Laginhas, B. B., Morelli, T. L., & O'Neill, M. W. (2022). Global environmental changes more frequently offset than intensify detrimental effects of biological invasions. *Proceedings of the National Academy of Sciences of the United States of America*, *119*(22), 1–7.

Luo, W., Shi, Y., Wilkins, K., Song, L., te, N., Chen, J., Zhang, H., Yu, Q., Wang, Z., Han, X., & Collins, S. L. (2023). Plant traits modulate grassland stability during drought and post-drought periods. *Functional Ecology*, *37*(10), 2611–2620. https://doi.org/10.1111/1365-2435.14409

Ma, Z., & Ellison, A. M. (2018). A unified concept of dominance applicable at both community and species scales. *Ecosphere*, *9*(11), e02477. https://doi.org/10.1002/ecs2.2477

Marcon, E., Scotti, I., Hérault, B., Rossi, V., & Lang, G. (2014). Generalization of the partitioning of Shannon diversity. *PLoS One*, *9*(3), e90289. https://doi.org/10.1371/journal.pone.0090289

Martin, C. E., Harris, F. S., & Norman, F. J. (1991). Ecophysiological responses of C3 forbs and C4 grasses to drought and rain on a tallgrass prairie in northeastern Kansas. *Botanical Gazette*, *152*(3), 257–262. https://doi.org/10.1086/337887

Martin, V., Devictor, E., Motard, N., Machon, N., & Porcher, E. (2019). Short-term climate-induced change in French plant communities. *Biology Letters*, *15*(7), 1–5. https://doi.org/10.1098/rsbl.2019.0280

Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S. L., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L., Gomis, M. I., & Huang, M. (2021). IPCC 2021: Climate change 2021: The physical science basis. In T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, & B. Zhou (Eds.), *Contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change*. Cambridge University Press.

McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D. G., & Yepez, E. A. (2008). Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist*, *178*(4), 719–739. https://doi.org/10.1111/j.1469-8137.2008.02436.x

McGraw, R. L., Shockley, F. W., & Elam, T. K. (2003). Effects of temperature on germination of 10 native legume species. *Native Plants Journal*, *4*(1), 5–9. https://doi.org/10.3368/npj.4.1.5

Mitchell, D., Schönbeck, L., Shah, S., & Santiago, L. S. (2025). Leaf drought and heat tolerance are integrated across three temperate biome types. *Scientific Reports*, *15*(1), 12201. https://doi.org/10.1038/s41598-025-95623-5

Montalvo, J., Casado, M. A., Levassor, C., & Pineda, F. D. (1993). Species diversity patterns in Mediterranean grasslands. *Journal of Vegetation Science*, *4*(2), 213–222.

Müller, L. M., & Bahn, M. (2022). Drought legacies and ecosystem responses to subsequent drought. *Global Change Biology*, *28*(17), 5086–5103. https://doi.org/10.1111/gcb.16270

Newbold, T. (2018). Future effects of climate and land-use change on terrestrial vertebrate community diversity under different scenarios. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1881), 1–9. https://doi.org/10.1098/rspb.2018.0792

Nippert, J. B., & Knapp, A. K. (2007). Soil water partitioning contributes to species coexistence in tallgrass prairie. *Oikos*, *116*(6), 1017–1029.

Nwayor, I. J., & Robeson, S. M. (2024). Exploring the relationship between SPI and SPEI in a warming world. *Theoretical and Applied Climatology*, *155*(4), 2559–2569. https://doi.org/10.1007/s00704-023-04764-y

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M. H., Oksanen, M. J., & Suggests, M. A. (2007). The vegan package. *Community Ecology Package*, *10*(631–637), 719.

Olonscheck, D., Schurer, A. P., Lücke, L., & Hegerl, G. C. (2021). Large-scale emergence of regional changes in year-to-year temperature variability by the end of the 21st century. *Nature Communications*, *12*, 7237. https://doi.org/10.1038/s41467-021-27515-x

Olsen, S. L., Töpper, J. P., Skarpaas, O., Vandvik, V., & Klanderud, K. (2016). From facilitation to competition: Temperature-driven shift in dominant plant interactions affects population dynamics in seminatural grasslands. *Global Change Biology*, *22*(5), 1915–1926.

Osborne, C. P., & Beerling, D. J. (2006). Nature's green revolution: The remarkable evolutionary rise of C4 plants. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *361*(1465), 173–194. https://doi.org/10.1098/rstb.2005.1737

Panetta, A. M., Stanton, M. L., & Harte, J. (2018). Climate warming drives local extinction: Evidence from observation and experimentation. *Science Advances*, *4*(2), eaaq1819. https://doi.org/10.1126/sciadv.aaq1819

Pardo, J., & VanBuren, R. (2021). Evolutionary innovations driving abiotic stress tolerance in C4 grasses and cereals. *The Plant Cell*, *33*(11), 3391–3401. https://doi.org/10.1093/plcell/koab205

Phillips, B. B., Shaw, R. F., Holland, M. J., Fry, E. L., Bardgett, R. D., Bullock, J. M., & Osborne, J. L. (2018). Drought reduces floral resources for pollinators. *Global Change Biology*, *24*(7), 3226–3235.

Piseddu, F., Bellocchi, G., & Picon-Cochard, C. (2021). Mowing and warming effects on grassland species richness and harvested biomass: Meta-analyses. *Agronomy for Sustainable Development*, *41*(6), 74. https://doi.org/10.1007/s13593-021-00722-y

Pugnaire, F. I., Morillo, J. A., Peñuelas, J., Reich, P. B., Bardgett, R. D., Gaxiola, A., Wardle, D. A., & Van Der Putten, W. H. (2019). Climate change effects on plant-soil feedbacks and consequences for biodiversity and functioning of terrestrial ecosystems. *Science Advances*, *5*(11), 1–11. https://doi.org/10.1126/sciadv.aaz183

Reich, P. B., Tilman, D., Naeem, S., Ellsworth, D. S., Knops, J., Craine, J., Wedin, D., & Trost, J. (2004). Species and functional group diversity independently influence biomass accumulation and its response to CO_2 and N. *Proceedings of the National Academy of Sciences of the United States of America*, *101*(27), 10101–10106.

Reynolds-Henne, C. E., Langenegger, A., Mani, J., Schenk, N., Zumsteg, A., & Feller, U. (2010). Interactions between temperature, drought and stomatal opening in legumes. *Environmental and Experimental Botany*, *68*(1), 37–43.

Roshani, S. H., Kumar, P., Masroor, M., Rahaman, M. H., Rehman, S., Ahmed, R., & Sahana, M. (2022). Forest vulnerability to climate change: A review for future research framework. *Forests*, *13*(6), 917. https://doi.org/10.3390/f13060917

Sabanes Bove, D., Li, L., Dedic, J., Kelkhoff, D., Kunzmann, K., Lang, B. M., Stock, C., Wang, Y., James, D., Sidi, J., & Leibovitz, D. (2022). "mmrm: Mixed models for repeated measures". https://doi.org/10.32614/CRAN.package.mmrm

Sax, D. F., & Gaines, S. D. (2003). Species diversity: From global decreases to local increases. *Trends in Ecology & Evolution*, *18*(11), 561–566. https://doi.org/10.1016/S0169-5347(03)00224-6

Schafer, M., Ojima, D., & Antle, J. M. (2014). "19: Great Plains. Climate change impacts in the United States: The third National Climate Assessment".

Schellenberg, M. P., & Biligetu, B. (2015). The effects of temperature and scarification on seed germination of three *Dalea* species. *Canadian Journal of Plant Science*, *95*(6), 1117–1120. https://doi.org/10.4141/cjps-2015-153

Schuchardt, M. A., Berauer, B. J., Heßberg, A., Wilfahrt, P., & Jentsch, A. (2021). Drought effects on montane grasslands nullify benefits of advanced flowering phenology due to warming. *Ecosphere*, *12*(7), 1–17. https://doi.org/10.5281/zenodo.4772698

Sherry, R. A., Weng, E., Johnson Arnone, J. A., III, Schimel, D. S., Verburg, P. S., Wallace, L. L., & Luo, Y. (2008). Lagged effects of experimental warming and doubled precipitation on annual and seasonal aboveground biomass production in a tallgrass prairie. *Global Change Biology*, *14*(12), 2923–29361. https://doi.org/10.1111/j.1365-2486.2008.01703.x

Shi, X., Liu, Y., & van Kleunen, M. (2025). Additive effects of multiple global change factors on plant invasions are common. *Ecology Letters*, *28*(1), e70057. https://doi.org/10.1111/ele.70057

Shi, Z., Sherry, R., Xu, X., Hararuk, O., Souza, L., Jiang, L., Xia, J., Liang, J., & Luo, Y. (2015). Evidence for long-term shift in plant community composition under decadal experimental warming. *Journal of Ecology*, *103*(5), 1131–1140.

Siebielec, S., Siebielec, G., Klimkowicz-Pawlas, A., Gałązka, A., Grządziel, J., & Stuczyński, T. (2020). Impact of water stress on microbial community and activity in sandy and loamy soils. *Agronomy*, *10*(9), 9. https://doi.org/10.3390/agronomy10091429

Simpson, E. H. (1949). Measurement of diversity. *Nature*, *163*(4148), 688.

Smith, B., & Bastow Wilson, J. (1996). A consumer's guide to evenness indices. *Oikos*, *76*(1), 70–82. https://doi.org/10.2307/3545749

Smith, M. D., Wilkins, K. D., Holdrege, M. C., Wilfahrt, P., Collins, S. L., Knapp, A. K., Sala, O. E., Dukes, J. S., Phillips, R. P., Yahdjian, L., Gherardi, L. A., Ohlert, T., Beier, C., Fraser, L. H., Jentsch, A., Loik, M. E., Maestre, F. T., Power, S. A., Yu, Q., … Zuo, X. (2024). Extreme drought impacts have been underestimated in grasslands and shrublands globally. *Proceedings of the National Academy of Sciences of the United States of America*, *121*(4), e2309881120. https://doi.org/10.1073/pnas.2309881120

Soudzilovskaia, N. A., Elumeeva, T. G., Onipchenko, V. G., Shidakov, I. I., Salpagarova, F. S., Khubiev, A. B., Tekeev, D. K., & Cornelissen, J. H. C. (2013). Functional traits predict relationship between plant abundance dynamic and long-term climate warming. *Proceedings of the National Academy of Sciences*, *110*(45), 18180–18184. https://doi.org/10.1073/pnas.1310700110

Tang, J., Li, W., Wei, T., Huang, R., & Zeng, Z. (2024). Patterns and mechanisms of legume responses to nitrogen enrichment: A global meta-analysis. *Plants*, *13*(22), 3244. https://doi.org/10.3390/plants13223244

Taylor, S. H., Ripley, B. S., Martin, T., De-Wet, L.-A., Woodward, F. I., & Osborne, C. P. (2014). Physiological advantages of C4 grasses in the field: A comparative experiment demonstrating the importance of drought. *Global Change Biology*, *20*(6), 1992–2003.

Tilman, D., Isbell, F., & Cowles, J. M. (2014). Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics*, *45*(1), 471–493. https://doi.org/10.1146/annurev-ecolsys-120213-091917

Tilman, P. B., Reich, J., Knops, D., Wedin, D., Mielke, T., & Lehman, C. (2001). Diversity and productivity in a long-term grassland experiment. *Science*, *294*(5543), 843–845.

Tilman, P. B., Reich, J. M., & Knops, J. M. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, *441*(7093), 629–632. https://doi.org/10.1038/nature04742

Urban, M. C., Swaegers, J., Stoks, R., Snook, R. R., Otto, S. P., Noble, D. W. A., Moiron, M., Hällfors, M. H., Gómez-Llano, M., Fior, S., Cote, J., Charmantier, A., Bestion, E., Berger, D., Baur, J., Alexander, J. M., Saastamoinen, M., Edelsparre, A. H., & Teplitsky, C. (2024). When and how can we predict adaptive responses to climate change? *Evolution Letters*, *8*(1), 172–187. https://doi.org/10.1093/evlett/qrad038

Valliere, J. M., Nelson, K. C., & Martinez, M. C. (2023). Functional traits and drought strategy predict leaf thermal tolerance. *Conservation Physiology*, *11*(1), coad085. https://doi.org/10.1093/conphys/coad085

Vitousek, P. M., Mooney, H. A., Lubchenco, J., & Melillo, J. M. (1997). Human domination of Earth's ecosystems. *Science*, *277*(5325), 494–499.

Wall, G. W., Kimball, B. A., White, J. W., & Ottman, M. J. (2011). Gas exchange and water relations of spring wheat under full-season infrared warming. *Global Change Biology*, *17*(6), 2113–2133. https://doi.org/10.1111/j.1365-2486.2011.02399.x

Ward, J. K., Tissue, D. T., Thomas, R. B., & Strain, B. R. (1999). Comparative responses of model C3 and C4 plants to drought in low and elevated CO_2. *Global Change Biology*, *5*(8), 857–867.

Whittington, H. R., Tilman, D., & Powers, J. S. (2013). Consequences of elevated temperatures on legume biomass and nitrogen cycling in a field warming and biodiversity experiment in a north American prairie. *Functional Plant Biology*, *40*(11), 1147–1158. https://doi.org/10.1071/FP12345

Wilcox, K. R., Blumenthal, D. M., Kray, J. A., Mueller, K. E., Derner, J. D., Ocheltree, T., & Porensky, L. M. (2021). Plant traits related to precipitation sensitivity of species and communities in semiarid shortgrass prairie. *New Phytologist*, *229*(4), 2007–2019.

Wilschut, R. A., De Long, J. R., Geisen, S., Hannula, S. E., Quist, C. W., Snoek, B., Steinauer, K., Wubs, E. J., Yang, Q., & Thakur, M. P. (2022). Combined effects of warming and drought on plant biomass depend on plant woodiness and community type: A meta-analysis. *Proceedings of the Royal Society B: Biological Sciences*, *289*(1984), 20221178. https://doi.org/10.1098/rspb.2022.1178

Xu, Z., Shimizu, H., Ito, S., Yagasaki, Y., Zou, C., Zhou, G., & Zheng, Y. (2014). Effects of elevated CO_2, warming and precipitation change on plant growth, photosynthesis and peroxidation in dominant species from North China grassland. *Planta*, *239*, 421–435.

Yahdjian, L., & Sala, O. E. (2002). A rainout shelter design for Intercepting different amounts of rainfall. *Oecologia*, *133*, 95–101.

Yang, Y., Hopping, K. A., Wang, G., Chen, J., Peng, A., & Klein, J. A. (2018). Permafrost and drought regulate vulnerability of Tibetan plateau grasslands to warming. *Ecosphere*, *9*(5), e02233. https://doi.org/10.1002/ecs2.2233

Yao, Z., Xin, Y., Yang, L., Zhao, L., & Ali, A. (2022). Precipitation and temperature regulate species diversity, plant coverage and aboveground biomass through opposing mechanisms in large-scale grasslands. *Frontiers in Plant Science*, *13*(999636), 1–12. https://doi.org/10.3389/fpls.2022.999636

Zellweger, F., Frenne, P., Lenoir, J., Vangansbeke, P., Verheyen, K., Bernhardt-Römermann, M., Baeten, L., Hédl, R., Berki, I., Brunet, J., & Van Calster, H. (2020). Forest microclimate dynamics drive plant responses to warming. *Science*, *368*(6492), 772–775. https://doi.org/10.1126/science.aba6880

Zhang, H., John, R., Peng, Z., Yuan, J., Chu, C., du, G., & Zhou, S. (2012). The relationship between species richness and evenness in plant communities along a successional gradient: A study from sub-alpine meadows of the Eastern Qinghai-Tibetan Plateau, China. *PLoS One*, *7*(11), e49024. https://doi.org/10.1371/journal.pone.0049024

Zhou, Y., Lambrides, C. J., & Fukai, S. (2014). Drought resistance and soil water extraction of a perennial C4 grass: Contributions of root and rhizome traits. *Functional Plant Biology*, *41*(5), 505–519. https://doi.org/10.1071/FP13249

Zhuang, Y., Fu, R., Lisonbee, J., Sheffield, A. M., Parker, B. A., & Deheza, G. (2024). Anthropogenic warming has ushered in an era of temperature-dominated droughts in the Western United States. *Science Advances*, *10*(45), eadn9389. https://doi.org/10.1126/sciadv.adn9389

SUPPORTING INFORMATION

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

Table A1. Output of linear mixed effects model, which tested whether soil moisture responses (treatment − control) differed significantly from zero (no difference).

Table A2. Model-derived means and standard errors for soil moisture (decimal) responses to treatment by year, corresponding to Figure A1.

Table A3. Delta-AIC values for all models. Model refers to the parameter that was being tested during a given iteration.

Figure A1. Soil moisture response to warming and drought treatments over multiple years.

Figure A2. Species-specific biomass responses to warming and drought over 6 years.

Figure A3. Overview of model selection process and temporal covariance structures.

Figure A4. Residuals vs. fitted value plots for MMRM community response models (Table 2 and Table 4).

Figure A5. Impact of warming and drought on plant richness, diversity, and evenness responses over 6 years.

Figure A6. Impact of warming and drought on dominance over 6 years.

Figure A7. Impact of warming and drought on plant functional group proportions over 6 years.

Box A1. Description of BAC experiment, which existed prior to BACD.

Box A2. Additional information on interrelatedness of richness, diversity (Shannon and Inverse Simpson), evenness, and dominance responses considered in this study.

How to cite this article: Anderson, M., & Isbell, F. (2025). Experimental warming drives local grassland plant species loss. *Journal of Ecology*, *113*, 3418–3437. https://doi.org/10.1111/1365-2745.70172