





IS PHYLOGENETIC AND FUNCTIONAL TRAIT DIVERSITY A DRIVER OR CONSEQUENCE OF GRASSLAND COMMUNITY ASSEMBLY?**Shifts in plant functional composition following long-term drought in grasslands**

Robert J. Griffin-Nolan¹  | Dana M. Blumenthal² | Scott L. Collins³ |
 Timothy E. Farkas³ | Ava M. Hoffman¹  | Kevin E. Mueller⁴ | Troy W. Ocheltree⁵ |
 Melinda D. Smith¹  | Kenneth D. Whitney³  | Alan K. Knapp¹

¹Graduate Degree Program in Ecology and Department of Biology, Colorado State University, Fort Collins, Colorado

²Rangeland Resources and System Research Unit, USDA Agricultural Research Service, Fort Collins, Colorado

³Department of Biology, University of New Mexico, Albuquerque, NM, USA

⁴Department of Biological, Geological, and Environmental Sciences, Cleveland State University, Cleveland, Ohio

⁵Department of Forest and Rangeland Stewardship, Colorado State University, Fort Collins, Colorado

Correspondence

Robert J. Griffin-Nolan
 Email: rgriffi2@colostate.edu

Funding information

NSF Macrosystems Biology Program, Grant/Award Number: DEB-1137378, 1137363 and 1137342

Handling Editor: Holly Jones

Abstract

1. Plant traits can provide unique insights into plant performance at the community scale. Functional composition, defined by both functional diversity and community-weighted trait means (CWMs), can affect the stability of above-ground net primary production (ANPP) in response to climate extremes. Further complexity arises, however, when functional composition itself responds to environmental change. The duration of climate extremes, such as drought, is expected to increase with rising global temperatures; thus, understanding the impacts of long-term drought on functional composition and the corresponding effect that has on ecosystem function could improve predictions of ecosystem sensitivity to climate change.
2. We experimentally reduced growing season precipitation by 66% across six temperate grasslands for 4 years and measured changes in three indices of functional diversity (functional dispersion, richness and evenness), community-weighted trait means and phylogenetic diversity (PD). Specific leaf area (SLA), leaf nitrogen content (LNC) and (at most sites) leaf turgor loss point (π_{TLP}) were measured for species cumulatively representing ~90% plant cover at each site.
3. Long-term drought led to increased community functional dispersion in three sites, with negligible effects on the remaining sites. Species re-ordering following the mortality/senescence of dominant species was the main driver of increased functional dispersion. The response of functional diversity was not consistently matched by changes in phylogenetic diversity. Community-level drought strategies (assessed as CWMs) largely shifted from drought tolerance to drought avoidance and/or escape strategies, as evidenced by higher community-weighted π_{TLP} , SLA and LNC. Lastly, ecosystem drought sensitivity (i.e. relative reduction in ANPP in drought plots) was positively correlated with community-weighted SLA and negatively correlated with functional diversity.
4. *Synthesis*. Increased functional diversity following long-term drought may stabilize ecosystem functioning in response to future drought. However, shifts in community-scale drought strategies may increase ecosystem drought sensitivity, depending on the nature and timing of drought. Thus, our results highlight the importance

of considering both functional diversity and abundance-weighted traits means of plant communities as their collective effect may either stabilize or enhance ecosystem sensitivity to drought.

KEYWORDS

ANPP, climate change, community-weighted traits, drought, functional diversity, plant functional traits

1 | INTRODUCTION

Ecosystem function is largely determined by the functional attributes of resident plant species. Plant traits are useful for understanding how resources are acquired by plants (Reich, 2014; Wright et al., 2004) and consequently transferred to or stored in various ecosystem pools, such as plant biomass or soil organic matter (Lavorel & Garnier, 2002). Plant community functional composition, defined by community-weighted trait means (CWMs) and functional diversity (i.e. the distribution of traits within a community), responds to environmental change and can affect ecosystem processes, such as above-ground net primary production (ANPP), nutrient cycling and decomposition (Díaz & Cabido, 2001). A trait-based response-and-effect framework has been proposed (Suding et al., 2008) whereby certain plant traits indicate how species will shift in abundance in response to environmental change (e.g. conservative leaf water economic traits improve species tolerance to drought and warming; Anderegg et al., 2016; Soudzilovskaia et al., 2013), whereas other traits (or the same traits) are linked to specific ecosystem functions (e.g. leaf nitrogen content [LNC] is correlated with variability in ANPP; Garnier et al., 2004; Reich, 2012). The importance of climate in governing functional composition is well supported by community scale surveys of plant traits on broad spatial and temporal scales (Newbold, Butchart, Şekercioğlu, Purves, & Scharlemann, 2012; Reich & Oleksyn, 2004; Šimová et al., 2018; Wiczyński et al., 2019; Wright et al., 2005). Few studies, however, have assessed the response of both functional diversity and CWMs to climate extremes, which are rare by definition (Smith, 2011), and the corresponding effect on ecosystem functioning across space and time.

Rising global temperatures increase rates of evapotranspiration and thus the intensity and duration of climate extremes, such as drought (Trenberth, 2011), with immediate and long-lasting negative impacts on Earth's vegetation (Breshears et al., 2005). The magnitude of vegetation responses to drought varies among ecosystems with xeric ecosystems generally being more sensitive than mesic ones (Huxman et al., 2004; Knapp et al., 2015). Ecosystem resistance and resilience to drought have been linked to species diversity, and functional diversity in particular (Díaz & Cabido, 2001; Isbell et al., 2015; Tilman & Downing, 1994; Tilman et al., 1997). Plant communities with high functional diversity are buffered against declines in ecosystem functions, such as ANPP, due to functional insurance (Anderegg et al., 2018; De La Riva et al., 2017; Grime, 1998; Pérez-Ramos et al., 2017). In other words, a greater diversity of species (and

traits) increases the odds of one or more species surviving a drought and compensating for drought-induced senescence or mortality of other species. Beyond diversity, the mean composition of traits (as measured by CWMs) can confer ecosystem resistance and resilience to drought, especially if species with traits linked to drought survival (McDowell et al., 2008) and/or drought avoidance/escape strategies (Kooyers, 2015; Noy-Meir, 1973) are in high abundance.

Increasing complexity arises, however, when functional composition itself is altered by drought. An extreme climate event can act as an environmental filter allowing only certain species (and trait values) to persist, potentially leading to trait convergence and/or decreased functional and genetic diversity (Díaz, Cabido, Zak, Martínez Carretero, & Aranibar, 1999; Grime, 2006; Whitney et al., 2019); however, an array of biotic interactions influencing competition, coexistence and niche differentiation can act simultaneously to structure communities in an opposite manner (Cadotte & Tucker, 2017; Kraft et al., 2015). Thus, given uncertain and counteracting roles of environmental filtering and niche differentiation, the net effects of drought on community functional composition are currently unpredictable. Indeed, the impact of drought, and aridity more broadly, on functional diversity is highly variable with positive (Cantarel, Bloor, & Soussana, 2013), negative (Qi et al., 2015) and neutral (Copeland et al., 2016; Hallett, Stein, & Suding, 2017) responses observed. These inconsistencies are likely due to differences in the selection of traits and functional diversity indices, the extremity of drought, and/or the spatial/temporal context in which aridity is being examined. Thus, coordinated, long-term and multi-site experiments are needed to assess the impact of extreme drought on functional composition and ecosystem function.

The 'Extreme Drought in Grasslands Experiment' (EDGE) was established in 2012 to assess the drought sensitivity of ANPP in six North American grasslands, ranging from desert grassland to tall-grass prairie (Figure 1; Table 1). Grasslands are ideal ecosystems for assessing drought sensitivity as ANPP in these systems is highly responsive to precipitation variability (Hsu, Powell, & Adler, 2012; Knapp & Smith, 2001) and their short stature allows for easy installation of experimental drought infrastructure (Yahdjian & Sala, 2002). We surveyed plant traits of the most common species at each EDGE site (cumulatively representing ~90% plant cover) and tracked changes in three indices of functional diversity (e.g. functional dispersion, richness and evenness) and abundance-weighted traits in response to a 4-year experimental drought. Our trait survey included leaf turgor loss point (π_{TLP}), specific leaf area (SLA) and LNC.

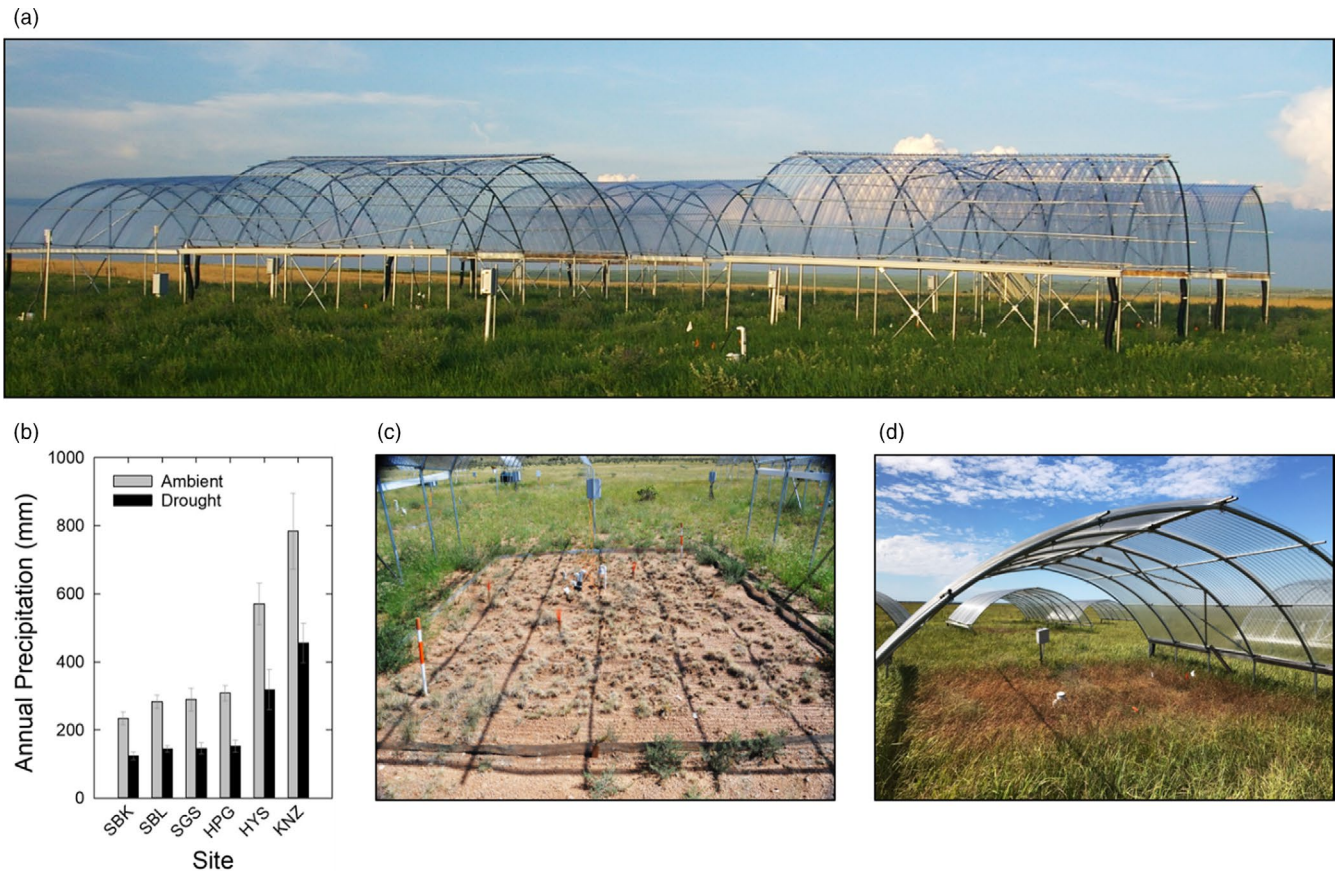


FIGURE 1 (a) Large rainfall exclusion shelters were established in six North American grassland sites as part of the Extreme Drought in Grasslands Experiment (EDGE; <http://edge.biology.colostate.edu/>). (b) These shelters passively remove 66% of incoming precipitation during the growing season leading to a ~40% reduction in annual precipitation for 4 years (error bars represent SE of mean precipitation during the 4 years). Drought treatments had negative effects on above-ground net primary production in all sites ranging from the Sevilleta desert grassland (SBK) in New Mexico (c, photo credit: Scott Collins) to the Konza tallgrass prairie (KNZ) in eastern Kansas (d, photo credit: Alan Knapp). See Table 1 for site abbreviations [Colour figure can be viewed at wileyonlinelibrary.com]

Leaf economic traits such as SLA and LNC have been associated with plant ecological strategies (e.g. fast vs. slow resource economies and drought tolerance vs. avoidance; Frenette-Dussault, Shipley, Léger, Meziane, & Hingrat, 2012; Reich, 2014) and are descriptive of ANPP dynamics (Garnier et al., 2004; Reich, 2012; Suding et al., 2008). Hydraulic traits such as π_{TLP} are informative of leaf-level drought tolerance and are expected to be predictive of plant responses to aridity (Bartlett, Scoffoni, & Sack, 2012; Griffin-Nolan, Bushey, et al. 2018; Reich, 2014). Additionally, we measured plot-level phylogenetic diversity to assess whether functional and phylogenetic diversity are coupled in their response to drought (i.e. whether decreased functional diversity is driven by decreased genetic dissimilarity).

Drought resistance is multidimensional (i.e. a variety of traits can bestow or hinder drought resistance via a variety of mechanisms), thus, there are several plausible shifts in trait diversity and weighted-means in response to drought. Here, we test the hypothesis that high functional diversity and a high abundance of conservative leaf economic traits confer greater resistance of ANPP to drought, and ask how drought influences functional composition over time. A strong role of environmental filtering should be reflected in reduced

functional diversity and altered community-weighted trait means, with the direction of the mean trait shift dependent on the role of various traits in shaping drought resistance within and across ecosystems.

2 | MATERIALS AND METHODS

2.1 | Site descriptions

The impact of long-term drought on community functional diversity and abundance-weighted traits was assessed in six native grassland sites spanning a 620 mm gradient in mean annual precipitation (MAP) and a 5.5°C gradient in mean annual temperature (Table 1; Knapp et al., 2015). These six sites encompass the four major grassland types of North America including desert grassland, shortgrass prairie, mixed grass prairie and tallgrass prairie. Experimental plots were established in upland pastures that had not been grazed for over 10 years, apart from the two mixed grass prairie sites (HPG and HYS) which were last grazed 3 years prior to this study. The tallgrass prairie site (KNZ) is burned annually

TABLE 1 Characteristics of six grassland sites included in the ‘Extreme Drought in Grasslands Experiment’ (EDGE). Five-year averages of Shannon’s diversity index and species richness are shown for ambient plots at each site. Mean annual precipitation (MAP) and temperature (MAT) were taken from Griffin-Nolan, Carroll, et al. (2018)

Site ^a	Grassland type	MAP (mm)	MAT (°C)	Shannon Diversity	Species Richness
Sevilleta Black Grama (SBK)	Desert	244	13.4	2.04	10
Sevilleta Blue Grama (SBL)	Shortgrass	257	13.4	3.39	12
Shortgrass Steppe (SGS)	Shortgrass	366	9.5	5.79	17
High Plains Grassland (HPG)	Mixed-Grass	415	7.9	8.25	23
Hays Agricultural Research Center (HYS)	Mixed-Grass	581	12.3	7.52	23
Konza Prairie (KNZ)	Tallgrass	864	13.0	6.14	16

^aSites include a desert grassland [Sevilleta National Wildlife Refuge, dominated by black grama, *Bouteloua eriopoda* (C_4)—SBK] and a southern Shortgrass Steppe [Sevilleta National Wildlife Refuge, dominated by blue grama (*Bouteloua gracilis* (C_4))—SBL], both in New Mexico; a northern Shortgrass Steppe [Central Plains Experimental Range, dominated by *B. gracilis*—SGS] in Colorado; a northern mixed-grass prairie [High Plains Grassland Research Center, co-dominated by *Pascopyron smithii* (C_3) and *B. gracilis*—HPG] in Wyoming; as well as a southern mixed-grass prairie [Hays Agricultural Research Center, co-dominated by *P. smithii*, *Bouteloua curtipendula* (C_4) and *Sporobolus asper* (C_4)—HYS] and a tallgrass prairie [Konza Prairie Biological Station, dominated by *Andropogon gerardii* (C_4) and *Sorghastrum nutans* (C_4)—KNZ], both in Kansas.

following regional management regimes (Knapp, Briggs, Hartnett, & Collins, 1998), whereas other sites are unburned. Soil textures vary across sites from sandy to clay-loam (Burke et al., 1991, 1989; Kieft et al., 1998).

2.2 | Experimental drought treatments

Drought was experimentally imposed at each site for 4 years using large rainfall exclusion shelters (Figure 1a; Yahdjian & Sala, 2002). At each site, twenty 36-m² plots were established across a topographically uniform area and hydrologically isolated from the surrounding soil matrix using aluminium flashing and 6-mil plastic barriers installed to a depth of at least 20 cm. Plots were split into 4 subplots, each 2.5 × 2.5 m with a 0.5 m buffer on each side. Two of these subplots were designated for destructive measurements of plant biomass, one was designated for non-destructive surveys of species composition, and the final subplot was left for research on decomposition and microbial communities (Fernandes et al., 2018; Ochoa-Hueso et al., 2018).

Drought was imposed in ten plots per site by installing large shelters (10 × 10 m²) which passively blocked 66% of incoming rainfall during each growing season—this is roughly equivalent to a 40% reduction in annual precipitation given that 60%–75% of MAP falls during the growing season in these ecosystems (April–September for SGS, HPG, HYS and KNZ; April–October for SBK and SBL). Rainfall exclusion shelters utilize transparent polyethylene panels arrayed at a density to reduce each rainfall event by 66%, thereby maintaining the natural precipitation pattern of each site (Knapp et al., 2017). The remaining ten plots per site were trenched and hydrologically isolated yet received ambient rainfall (i.e. no shelters were present). Treatment infrastructure was installed in the spring of 2012, yet drought treatments did not begin until April 2013 at the New Mexico sites (SBK and SBL) and 2014 at the northern sites (SGS, HPG, HYS and KNZ).

Rain gauges were established in a subset of control and treatment plots. Rainfall exclusion shelters reduced annual precipitation by ~40% relative to ambient amount across all six sites (Figure 1b), a relative reduction comparable to the extreme drought that affected this region in 2012 (the 4th largest drought in the past century; Knapp et al., 2015). However, the experimental drought imposed here lasted 4 years rather than one.

2.3 | Species composition

Species composition was assessed at each site during spring and fall of each year starting one year before treatments were imposed. Absolute aerial cover of each species was estimated visually within four quadrats (1 m²) placed within the subplot designated for non-destructive measurements. For each plot and species, absolute cover was converted to average percent relative cover with the higher cover value in each year (spring or fall) used in the final analysis (Koerner & Collins, 2014). At the end of each growing season in the four northern sites, all above-ground biomass was harvested in three quadrats (0.1 m²) which were placed randomly in one of two subplots designated for destructive measurements (altering between years). Biomass was sorted to remove the previous year’s growth, dried for 48 hr at 60°C and weighed to estimate total ANPP. At the two Sevilleta sites (SBK and SBL), above-ground biomass was estimated in spring and fall using a non-destructive allometric approach (Muldavin et al., 2008) for each species occurring in each of the species composition subplots.

2.4 | Plant traits

Traits of the most abundant plant species per site were measured in an area adjacent to experimental plots to avoid destructive measurements within plots. Thus, all traits were measured under ambient rainfall conditions. Plant traits were measured at different times of

the growing season to capture peak growth and hydrated soil moisture conditions. For SBK and SBL, traits were measured at the beginning of the 2017 monsoon season (early August) to ensure fully emerged green leaves were sampled. For SGS and HPG, all traits were measured in late May and early June of 2015 to capture the high abundance of C_3 species at these sites. For HYS and KNZ, traits were measured in mid-July 2015, during peak biomass.

Ten individuals were selected along a transect the length of the experimental infrastructure and two recently emerged, fully expanded leaves were clipped at the base of the petiole and placed in plastic bags containing a moist paper towel. Leaves ($n = 20$ per species) were rehydrated in the lab, scanned and leaf area was estimated using IMAGEJ software (<https://imagej.nih.gov/ij/>). Each leaf was then oven-dried for 48 hr at 60°C and weighed. Specific leaf area (SLA) was calculated as leaf area/leaf dry mass (m^2/kg). Dried leaf samples were then ground to a fine powder for tissue nutrient analyses. LNC was estimated on a mass basis using a LECO Tru-Spec CN analyser (Leco Corp.).

Leaf turgor loss point (π_{TLP}) was estimated for each species using a vapour pressure osmometer (Bartlett, Scoffoni, Ardy, et al., 2012; Griffin-Nolan, Blumenthal, et al., 2019). Briefly, a single tiller (for graminoids) or whole individual (for forbs and shrubs) was unearthed to include root tissue and placed in a reservoir of water. Whole plant samples ($n = 6/\text{species}$) were relocated to the lab and covered in a dark plastic bag for ~12 hr to allow for complete leaf rehydration. Leaf tissue was then sampled from 5–8 leaves/species using a biopsy punch. The leaf sample was wrapped in tin foil and submerged in liquid nitrogen for 60 s to rupture cell walls. Each disc was then punctured ~15 times using forceps to ensure cell lysis, and quickly placed in a vapour pressure osmometer chamber within 30 s of freezing (VAPRO 5520, Wescor). Samples were left in the closed chamber for ~10 min to allow equilibration. Measurements were then made every two minutes until osmolarity reached equilibrium (<5 mmol/kg change in osmolarity between measurements). Osmolarity was then converted to leaf osmotic potential at full turgor (π_o) ($\pi_o = \text{osmolarity} \times -2.3958/1000$) and further converted to π_{TLP} using a linear model developed specifically for herbaceous species (Griffin-Nolan, Ocheltree, et al., 2019): $\pi_{TLP} = 0.80\pi_o - 0.845$.

Estimates of functional diversity are highly sensitive to missing trait data (Pakeman, 2014). Our survey of plant traits failed to capture species that increased in abundance in other years or due to treatment effects. Thus, we filled in missing trait data using a variety of sources including published manuscripts or contributed datasets. Sampling year differed depending on data sources, but sampling methodologies followed the same or similar standardized protocols (Bartlett, Scoffoni, Ardy, et al., 2012; Griffin-Nolan, Ocheltree, et al., 2019; Perez-Harguindeguy et al., 2016) and traits were often measured during the same season and from plots adjacent to or nearby the EDGE plots (see Appendix S1 in supporting information for more details). Data for π_{TLP} were lacking for desert species common in the Sevilleta grassland (SBK and SBL), thus our analyses at these sites was constrained to SLA and LNC. For the northern sites (SGS, HPG,

HYS and KNZ), sufficient π_{TLP} data were available and were included in all analyses.

The final trait dataset included trait values for species cumulatively representing an average of 90% plant cover in each plot. Observations with less than 75% relative cover represented by trait data were removed from all analyses (21 of 600 plot-year combinations were removed; final range: 75%–100% plant cover/plot). For this core set of 579 observations, the number of species used to estimate indices of functional composition ranged from 11 to 37, with a mean of 28 species. Covariation between traits was tested across sites using log-transformed data ('cor' function in base R). A significant correlation was observed between LNC and π_{TLP} ($r = .292$), but not between SLA and π_{TLP} ($r = .014$) or SLA and LNC ($r = -.117$).

2.5 | Functional composition

Functional diversity is described by several indices, each of which describe different aspects of trait distributions within a community (Mason, De Bello, Mouillot, Pavoine, & Dray, 2013). Given uncertainty as to which index is most sensitive to drought and/or informative of ecosystem responses to drought (Botta-Dukát, 2005; Carmona, Bello, Mason, & Lepš, 2016; Laliberté & Legendre, 2010; Mason et al., 2013; Mason, MacGillivray, Steel, & Wilson, 2003; Petchey & Gaston, 2002; Villéger, Mason, & Mouillot, 2008), we calculated three separate indices of functional diversity using the *dbFD* function in the 'FD' R-package (Laliberté & Legendre, 2010; Laliberté, Legendre, Shipley, & Laliberté, 2014). Using a flexible distance-based framework and principle components analyses, the *dbFD* function estimates functional richness (FRic; the total volume of x -dimensional functional space occupied by the community), functional evenness (FEve; the regularity of spacing between species within multivariate trait space) and functional dispersion (FDis; the multivariate equivalent of mean absolute deviation in trait space) (Laliberté & Legendre, 2010; Villéger et al., 2008). FDis describes the spread of species within multivariate space and is calculated as the mean-weighted distance of a species to the community-weighted centroid of multivariate trait space. To control for any bias caused by the lack of π_{TLP} data for two sites (SBK and SBL), we also calculated FRic, FEve and FDis using just two traits (SLA and LNC) across sites (i.e. two-dimensional diversity). Multivariate functional diversity indices can potentially mask community assembly processes occurring on a single trait axis (Spasojevic & Suding, 2012); thus, FRic, FEve and FDis were also estimated separately for each of the three traits surveyed in this study.

Species richness is well correlated with both FRic and FDis and can have a strong effect on the estimations of these parameters, especially in communities with low species richness (Mason et al., 2013). To control for this effect, we compared our estimates of FRic and FDis to those estimated from randomly generated null communities and calculated standardized effect sizes (SES) for each plot:

$$\text{SES} = \frac{\text{observed FDis} - \text{mean of expected FDis}}{\text{standard deviation of expected FDis}}$$

where the mean and standard deviation of expected FDis (or FRic) were calculated from 999 randomly generated null community matrices using a 'name-swap' and 'independent-swap' algorithm for FDis and FRic, respectively (R code modified from Swenson, 2014). These null model algorithms randomize the trait data matrix while maintaining species richness and occupancy within each plot. The 'name-swap' method also maintains relative abundance within each plot, thus providing insight into processes structuring plant communities (Spasojevic & Suding, 2012). Observed FEve is independent of species richness and thus was not compared to null communities (Mason et al., 2013).

We also calculated community-weighted means (CWMs) for each trait (weighted by species relative abundance), which further characterizes the functional composition of the community. Each index of functional diversity and CWMs was measured for each plot-year combination using the fixed trait dataset (i.e. traits collected in 2015/2017 plus contributed data) and % cover data from each year. Thus, the responses of CWMs and functional diversity to drought represent species turnover and interspecific trait differences. Intraspecific trait variability and trait plasticity were not assessed in this study, but these typically contribute substantially less to total trait variation than interspecific trait variability, even when sampling across broad spatial scales and strong environmental gradients (Siefert et al., 2015).

2.6 | Phylogenetic diversity

We quantified phylogenetic distinctiveness at the plot level using Faith's phylogenetic diversity (PD) index (Faith, 1992). A mixture of nine protein coding and non-coding gene sequences were acquired from NCBI GenBank for each species. Following sequence alignment and trimming, maximum likelihood trees were constructed using RAxML (1000 bootstrap iterations, with *Physcomitrella patens* as tree outgroup) (version 8.2.10) (Stamakis, 2014). Following tree construction, PD was calculated using the PICANTE package in R (Kembel et al., 2010). To control for the effect of species richness, the standardized effect size (SES) of PD (PD_{ses}) was calculated using the 'independent swap' null model in the PICANTE package.

2.7 | Data analysis

We tested for interactive effects of treatment, year and site on functional/phylogenetic composition using repeated measures mixed effects models ('lme4' package; Bates, Mächler, Bolker, & Walker, 2014). Site, treatment and year were included as fixed effects and plot was included as a random effect. Trait data were log-transformed when necessary to meet assumptions of normality. Separate models were run for multivariate and single trait functional richness and dispersion (FDis_{ses} and FRic_{ses}), FEve, phylogenetic diversity (PD_{ses}), as well as each CWM (i.e. SLA, LNC

and π_{TLP}). Pairwise comparisons were made between drought and control plots within each year and for each site (Tukey-adjusted p -values are presented). With the exception of xeric sites (e.g. Sevilleta), ambient temporal changes in species composition are often greater than treatment effects in global change experiments (Langley et al., 2018); therefore, functional and phylogenetic responses to drought are presented here as either log response ratios ($\ln(\text{drought}/\text{control})$) for FEve and CWMs or treatment differences (i.e. drought–control) for PD_{ses} , FDis_{ses} and FRic_{ses} . Calculating log response ratios of SES values was not appropriate as SES is often negative. Negative log response ratios are shown for community-weighted π_{TLP} as this trait is measured in negative pressure units (MPa). All analyses were repeated for two-dimensional diversity indices (i.e. those including just SLA and LNC).

The sensitivity of ANPP to drought was calculated as the % reduction in ANPP in drought plots for each site and for each year as follows:

$$\text{Drought sensitivity} = \text{abs} \left(100 \times \frac{\text{ANPP}_{\text{drought}} - \text{ANPP}_{\text{control}}}{\text{ANPP}_{\text{control}}} \right)$$

where ANPP is the mean value across all plots of that treatment in a given year. Drought sensitivity is presented as an absolute value (*abs*) such that large positive values indicate greater sensitivity (i.e. greater relative reduction in ANPP). Correlations between annual drought sensitivity ($n = 24$; six sites and 4 years) and either current-year (cy) or previous-year (py) functional/phylogenetic composition indices (e.g. PD_{ses} , CWMs for each trait, as well as single trait and multivariate FDis_{ses} , FRic_{ses} and FEve) were investigated using the *cor* function in base R, with p -values compared to a Benjamin–Hochberg corrected significance level of $\alpha = .0047$ for 32 comparisons. Variables that were significantly correlated with drought sensitivity at this level were included as fixed effects in separate general linear mixed effects models with site included as a random effect. To avoid pseudo-replication, mixed effects models were then compared to null models (using AIC) where null models included only the random effect of site. Both marginal and conditional R^2 values (Nakagawa & Schielzeth, 2013) were calculated for each mixed effect model using the 'rsquared' function in the 'piecewiseSEM' package (Lefcheck, 2016). All analyses were run using R version 3.5.2.

3 | RESULTS

The experimental drought treatments significantly altered community functional and phylogenetic composition with significant three-way interactions in mixed effects models for each diversity index, except FRic_{ses} , and each abundance-weighted trait (treatment \times site \times year; Table 2). The six grassland sites varied extensively in the magnitude and directionality of their response to drought, variation that was associated with diversity index, trait identity and

TABLE 2 ANOVA table for mixed effects models for the standardized effect size (SES) of multivariate functional diversity, community-weighted trait means and SES of phylogenetic diversity

Effect	SES of functional and phylogenetic diversity				Community-weighted trait means		
	FDIs	FRic	FEve	PD	SLA	LNC	π_{TLP}
Trt	3.68	0.0001	3.64	0.075	27.32***	6.99**	0.002
Site	15.31***	0.19	12.91***	51.22***	339.74***	615.62***	286.13***
Year	11.02***	3.26*	1.44	11.18***	33.44***	58.06***	122.19***
Trt × Site	2.43*	2.11	0.51	1.72	3.48**	0.26	6.30***
Trt × Year	11.98***	0.47	1.52	3.51**	15.02***	28.29***	2.34
Site × Year	30.34***	2.53***	3.07***	8.66***	26.72***	32.70***	62.54***
Trt × Site × Year	7.21***	0.89	2.17**	1.76*	9.13***	7.12***	3.52***

Note: F-values are shown for fixed effects and all interactions. Statistical significance is represented by asterisks: * $p < .05$, ** $p < .01$, *** $p < .001$. Abbreviations: FDIs, functional dispersion; FEve, functional evenness; FRic, functional richness; LNC, leaf nitrogen content; PD, phylogenetic diversity; SLA, specific leaf area; π_{TLP} , leaf turgor loss point.

drought duration. The most responsive functional diversity index across sites was functional dispersion (FDIs_{ses}), with significant drought responses observed in all but two sites.

Four years of experimental drought led to significantly higher multivariate FDIs_{ses} in half of the sites (SBK, SGS and HYS) with only a slight decline in FDIs_{ses} observed at SBL in year 3 of the drought (Figure 2a). There were no observable treatment effects on FDIs_{ses} at the wettest site (KNZ) or at the coolest site (HPG). Single trait FDIs_{ses} did not consistently mirror multivariate FDIs_{ses}, especially at the three driest sites (Figure 2b–d). For instance the increase in FDIs_{ses} at SBK was largely driven by increased functional dispersion of LNC (Figure 2c), as FDIs_{ses} of SLA did not differ significantly between drought and control plots. For SBL, multivariate FDIs_{ses} masked the opposing responses of single trait FDIs_{ses}. In the first two years of drought, opposite responses of FDIs_{ses} of SLA and LNC canceled each other out, leading to no change in multivariate FDIs_{ses}. It was not until year 3 that FDIs_{ses} of both SLA and LNC declined at SBL leading to a significant response in multivariate FDIs_{ses}. For SGS, FDIs_{ses} of SLA increased in drought plots relative to control plots and remained significantly higher for the remainder of the experiment (Figure 2b); however, this relative increase in FDIs_{ses} of SLA was not captured in multivariate measures of FDIs_{ses} due to a lack of response of FDIs_{ses} of LNC and π_{TLP} until the final years of drought (Figure 2c,d). On the contrary, single trait FDIs_{ses} largely mirrored multivariate FDIs_{ses} for the three wettest sites, with positive responses of FDIs_{ses} for each trait at HYS and no significant responses observed at HPG and KNZ (Figure 2). Other indices of functional diversity (i.e. FRic_{ses} and FEve) were moderately affected by drought treatments depending on site, with treatment effects not consistent across years (see Appendix S2, Figures S1 and S2). Estimates of functional diversity in two-dimensional trait space (i.e. excluding π_{TLP} from estimates of FDIs_{ses}, FRic_{ses} and FEve across sites) did not differ drastically from estimates in three-dimensional trait space (Appendix S2 and Figure S3).

Experimental drought led to a significant shift in community-weighted trait means across sites, largely away from conservative

resource-use strategies (Figure 3). Community-weighted specific leaf area (SLA_{cw}) initially decreased in response to drought for two sites (SBK and SBL); however, long-term drought eventually led to significant increases in SLA_{cw} at all six sites relative to ambient plots (Figure 3a). The positive effect of drought on SLA_{cw} was not persistent in its significance or magnitude through the fourth year of the experiment for all the sites. Community-weighted LNC (LNC_{cw}) was unchanged until the final years of drought, at which point elevated LNC_{cw} was observed for all sites but KNZ (Figure 3b). Lastly, drought effects on community-weighted leaf turgor loss point (π_{TLP-cw}) were variable among sites with a significant decline in π_{TLP-cw} (i.e. more negative) at HPG, a significant increase in π_{TLP-cw} at SGS, a moderately significant increase at HYS ($p = .06$), and no change observed at KNZ (Figure 3c).

Phylogenetic diversity (PD_{ses}) was most sensitive to drought at the two driest sites, SBK and SBL, with variable effects observed at the wettest site, KNZ (Figure 4). Drought led to increased PD_{ses} at SBK in year 3 and decreased PD_{ses} at SBL in year 4 (Figure 4). At KNZ, PD_{ses} alternated between drought-induced declines in PD_{ses} and no difference between control and drought plots; however, PD_{ses} of drought plots was significantly lower than control plots by the fourth year of drought. PD_{ses} did not respond to drought treatments at SGS, HPG or HYS.

Across all 32 linear models run, the only significant predictors of ANPP sensitivity (following a Benjamin-Hochberg correction for multiple comparisons) were (a) SLA_{cw} of the previous year, (b) FEve of SLA of the current year and (c) multivariate FEve of the current year (Table S2). These predictors were included as fixed effects in separate mixed effects models each with site as a random effect. Following null model comparison (see methods), we observed a statistically significant positive relationship between drought sensitivity and previous year SLA_{cw} (Figure 5a). In other words, grassland communities with low SLA_{cw} in a given year experienced less drought-induced declines in ANPP the following year. Significant negative correlations were observed between current year FEve (both multivariate and FEve of SLA) and drought

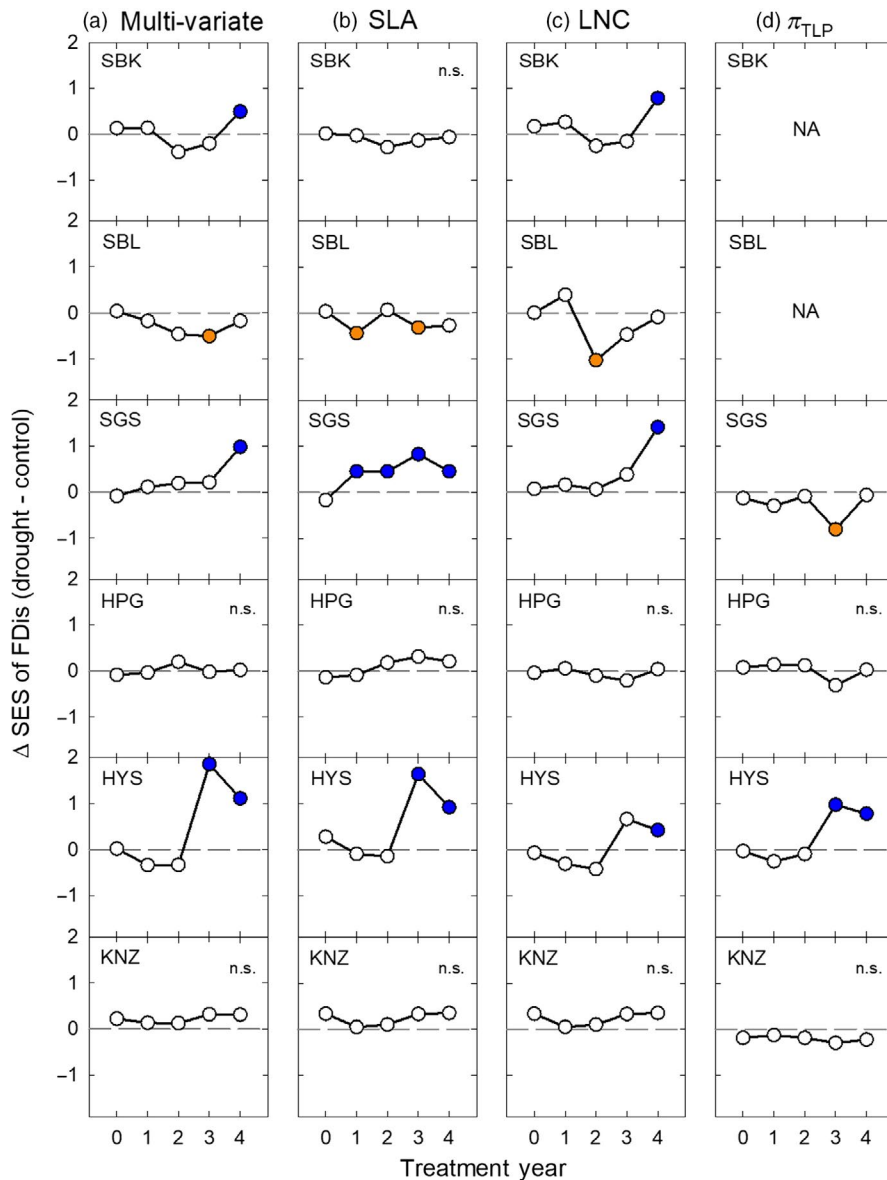


FIGURE 2 The effect of 4 years of drought on the standardized effect size (SES) of functional dispersion (FDIs) estimated in multivariate trait space (a) as well as for each trait individually (b–d). Drought effects are shown as the difference in SES of FDIs between drought and control plots for each year, including the pre-treatment year. Years with statistically significant treatment effects ($p < .05$) are represented by filled in symbols with the colour representing a positive (●) or negative (●) effect of drought. Open circles represent a lack of significant difference between control and drought plots, with 'n.s.' denoting a lack of significance across all years. Note that multivariate FDIs of SBK and SBL are calculated using only two traits (SLA and LNC) while all three traits are included in the calculation of multivariate FDIs for every other site. *Site abbreviations*: HPG, High plains grassland; HYS, Hays agricultural research station; KNZ, Konza tallgrass prairie; SBK, Sevilleta black grama; SBL, Sevilleta blue grama; SGS, Shortgrass steppe [Colour figure can be viewed at wileyonlinelibrary.com]

sensitivity; however, null model comparisons rejected the model with multivariate FEve and accepted the model with FEve of SLA (Figure 5b; Table S2).

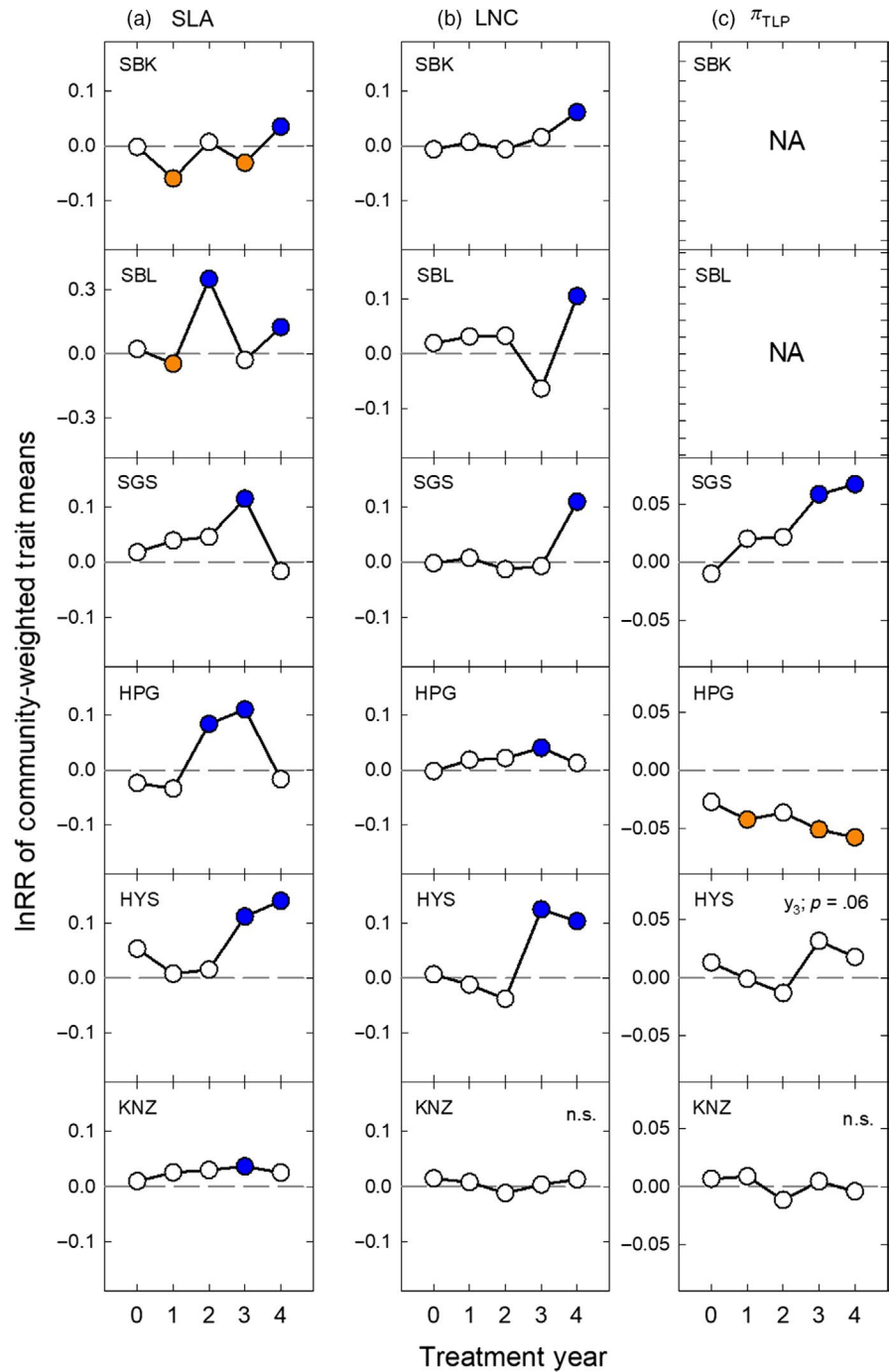
4 | DISCUSSION

4.1 | Functional diversity

We assessed the impact of long-term drought on functional diversity of six North American grassland communities (Table 1). Removal of ~40% of annual rainfall for 4 years negatively impacted ANPP (Figures 1 and 5). In contrast, we observed positive effects of drought on functional dispersion (as compared to null communities; $FDIs_{SES}$) in half of the grasslands surveyed here, with a negative response observed in only one site (Figure 2). While several indices of functional diversity were measured in this study, $FDIs_{SES}$ was the most responsive to drought (Figure 2 and Table 2). Increased functional

diversity following drought has previously been attributed to mechanisms of niche differentiation and species coexistence (Grime, 2006), whereas declines in diversity are attributed to drought acting as an environmental filter (Diaz, Cabido, & Casanoves, 1998; Díaz et al., 1999; Whitney et al., 2019). In grasslands, several indices of functional diversity respond strongly to interannual variability in precipitation (Gherardi & Sala, 2015). Dry years often lead to low functional diversity as the dominant drought-tolerant grasses persist, whereas rare species exhibit drought avoidance (e.g. increased water-use efficiency and slower growth) or escape strategies (e.g. early flowering) (Gherardi & Sala, 2015; Kooyers, 2015). Wet years, however, can lead to high diversity due to negative legacies of dry years acting on dominant grasses and the fast growth rate of 'drought avoiders' which take advantage of large rain events that penetrate deeper soil profiles (Gherardi & Sala, 2015). While traits linked to drought tolerance may allow a species to persist during transient dry periods, long-term intense droughts can lead to mortality of

FIGURE 3 Log response ratios (lnRR) for community-weighted trait means (CWM) in response to the drought treatment (lnRR = ln(drought/control). Focal traits include (a) specific leaf area (SLA), (b) leaf nitrogen content (LNC) and (c) leaf turgor loss point (π_{TLP}). Years with statistically significant treatment effects ($p < .05$) are represented by filled in symbols with the colour representing a positive (●) or negative (○) effect of drought. Open circles represent a lack of significant difference between control and drought plots, with 'n.s.' denoting a lack of significance across all years. Symbol colour also reflects conservative (○) versus acquisitive (●) resource-use strategies at the community-scale as high values of SLA, LNC and π_{TLP} all reflect acquisitive strategies. Note that HYS experienced a moderately significant increase in π_{TLP} ($p = .06$) in year 3 of drought. Axis scaling is not consistent across all panels. Negative lnRR is shown for π_{TLP} such that positive values indicate less negative leaf water potential. *Site abbreviations:* HPG, High plains grassland; HYS, Hays agricultural research station; KNZ, Konza tallgrass prairie; SBK, Sevilleta black grama; SBL, Sevilleta blue grama; SGS, Shortgrass steppe [Colour figure can be viewed at wileyonlinelibrary.com]



species exhibiting such strategies (McDowell et al., 2008). Here, the variable effects of drought on FDi_{ses} can be explained by (a) mortality/senescence and reordering of dominant drought-tolerant species (Smith, Knapp, & Collins, 2009) and (b) increases in the relative abundance of rare or subordinate drought escaping (or avoiding) species (Frenette-Dussault et al., 2012; Kooyers, 2015). Species are considered dominant here if they have high abundance relative to other species in the community and have proportionate effects on ecosystem function (Avolio et al., 2019).

The increase in FDi_{ses} in the final year of drought within the desert grassland site (SBK) corresponded with >95% mortality of the dominant grass species, *Bouteloua eriopoda*. This species

generally contributes ~80% of total plant cover in ambient plots. The removal of the competitive influence of this dominant species allowed a suite of species characterized by a wider range of trait values to colonize this desert community. Indeed, overall trait space occupied by the community (i.e. $Fric_{ses}$) significantly increased in the final year of drought (Figure S1). Mortality of *B. eriopoda* led to a community composed entirely of ephemeral species, deep-rooted shrubs and fast-growing forbs (i.e. drought avoiders/escapers). It is worth noting that phylogenetic diversity (PD_{ses}) increased in the year prior to increased FDi_{ses} and $Fric_{ses}$ (Figure 4), which suggests phylogenetic and functional diversity are coupled at this site.

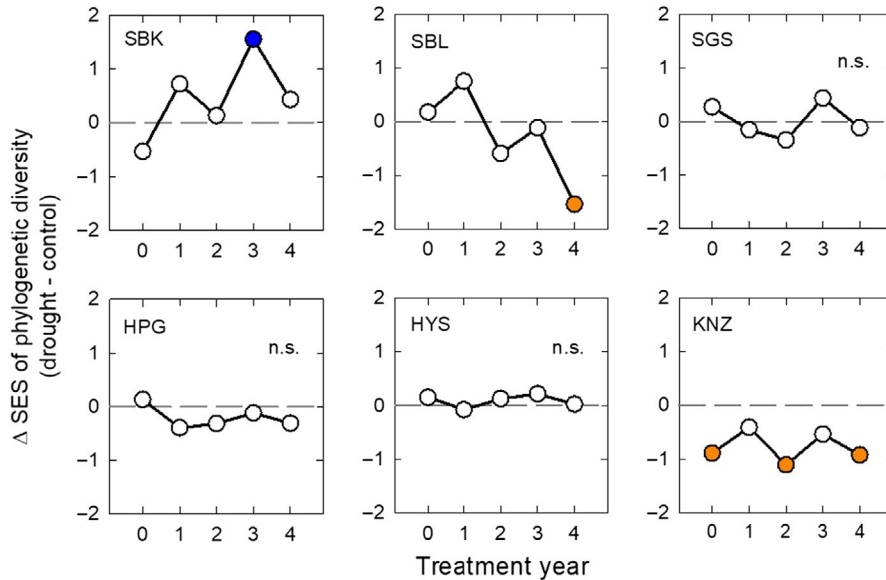


FIGURE 4 Drought effects on standardized effect size (SES) of phylogenetic diversity (PD). The effect of drought (i.e. drought–control) was calculated for the pre-treatment year and each year of the drought treatment. Years with statistically significant treatment effects ($p < .05$) are represented by filled in symbols with the colour representing a positive (●) or negative (●) effect of drought. Open circles represent a lack of significant difference between control and drought plots, with 'n.s.' denoting a lack of significance across all years. Site abbreviations: HPG, High plains grassland; HYS, Hays agricultural research station; KNZ, Konza tallgrass prairie; SBK, Sevilleta black grama; SBL, Sevilleta blue grama; SGS, Shortgrass steppe [Colour figure can be viewed at wileyonlinelibrary.com]

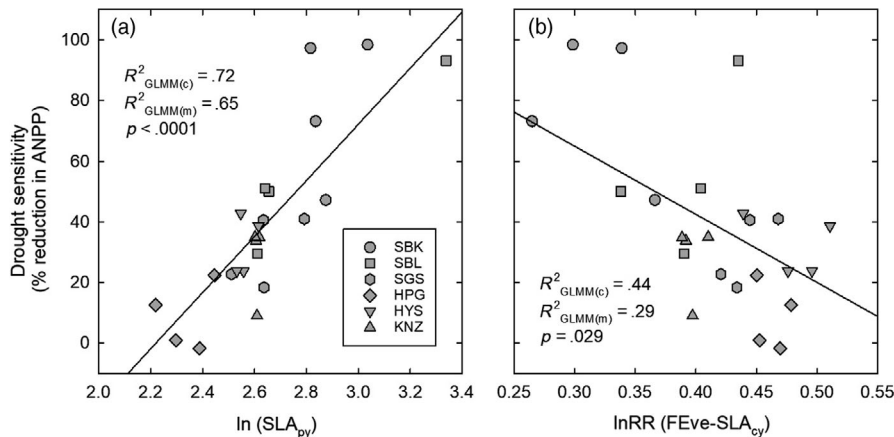


FIGURE 5 Drought sensitivity is (a) positively correlated with community-weighted (log-transformed) specific leaf area of the previous year (SLA_{py}) and (b) negatively correlated with current year functional evenness of specific leaf area ($FEve-SLA_{cy}$). Drought sensitivity was calculated as the absolute value of percent change in above-ground net primary production (ANPP) in drought plots relative to control plots in a given year. The plotted regression lines are from the output of two general linear mixed effect models (GLMM) including site as a random effect and the fixed effect of either SLA_{py} (a; $Sensitivity = 92.55 \times SLA_{py} - 205.44$) or $FEve-SLA_{cy}$ (b; $Sensitivity = -224.8 \times FEve-SLA_{cy} + 132.42$). Both the marginal (m) and conditional (c) R^2 values for the GLMM are shown. Site abbreviations: HPG, High plains grassland; HYS, Hays agricultural research station; KNZ, Konza tallgrass prairie; SBK, Sevilleta black grama; SBL, Sevilleta blue grama; SGS, Shortgrass steppe

The southern shortgrass prairie site in New Mexico (SBL) was the only site to experience decreased FD_{ses} in response to drought (Figure 2). This is surprising considering SBK and SBL are within several kilometres of one another (both within the Sevilleta National Wildlife Refuge) and experience a similar mean climate. This region is characterized by a sharp ecotone, however, resulting in different plant communities at SBK and SBL such that SBL is co-dominated

by *B. eriopoda* and *Bouteloua gracilis*, a closely related C_4 grass. *B. gracilis* is characterized by greater leaf-level drought tolerance than *B. eriopoda* ($\pi_{TLp} = -1.59$ and -1.86 MPa for *B. eriopoda* and *B. gracilis* respectively) which allows it to persist during drought. While *B. eriopoda* and *B. gracilis* both experienced drought-induced mortality (Baur et al. in prep), the greater persistence of *B. gracilis* led to stability in community structure with only moderate declines in FD_{ses}

in the third year of drought. Transient declines in FDis_{ses} may represent environmental filtering acting on subordinate species with traits much different from those of the dominant grasses. Indeed, decreased FDis_{ses} at SBL was accompanied by increased functional evenness (FEve) (Figure S2) and decreased PD_{ses} (Figure 4). Thus, the functional changes observed in this community were driven by both genetically and functionally similar species.

At the northern shortgrass prairie site (SGS), the response of FDis_{ses} to drought was likely due to re-ordering of dominant species. The early season plant community at SGS is dominated by C_3 grasses and forbs, whereas *B. gracilis* represents ~90% of total plant cover in mid- to late summer (Oesterheld, Loreti, Semmartin, & Sala, 2001). The nature of our drought treatments (i.e. removal of summer rainfall) favoured the subordinate C_3 plant community at this site. We observed a shift in species dominance from *B. gracilis* to *Vulpia octoflora*, an early season C_3 grass, beginning in year 2 of drought (Baur et al. in prep). The initial co-dominance of *B. gracilis* and *V. octoflora* increased FDis_{ses} of SLA (Figure 2b) as these two dominant species exhibit divergent leaf carbon allocation strategies (SLA = 12.5 and 19.2 kg/m^2 for *B. gracilis* and *V. octoflora* respectively). This emphasizes the importance of investigating single trait diversity indices (Spasojevic & Suding, 2012) as this community functional change was masked by multivariate measures of FDis_{ses} (Figure 2a). The eventual mortality of *B. gracilis* in the fourth year of drought led to significantly higher multivariate FDis_{ses} (Figure 2) as this late season niche was filled by species with a diversity of leaf carbon and nitrogen economies (LNC and SLA). Indeed, drought led to a 55% increase in Shannon's diversity index at SGS (Baur et al. in prep).

Functional diversity of the northern mixed grass prairie (HPG) was unresponsive to drought (Figure 2). This site has the lowest mean annual temperature of the six sites (Table 1) and is largely dominated by C_3 species which exhibit springtime phenology largely determined by the availability of snowmelt (Knapp et al., 2015). Thus, the nature of our drought treatment (i.e. removal of summer rainfall) had no effect on functional or phylogenetic diversity at this site (Figures 2 and 4). On the contrary, we observed increased FDis_{ses} at the southern mixed grass prairie (HYS) in response to experimental drought (Figure 2a). Again, drought treatments led to increased cover of dominant C_3 grasses and decreased cover of C_4 grasses (Baur et al. in prep). Here, increased multivariate FDis_{ses} was largely mirrored by single trait FDis_{ses} (Figure 2b–d). The three co-dominant grass species at this site (*Pascopyrum smithii* [C_3], *Bouteloua curtipendula* [C_4] and *Sporobolus asper* [C_4]) are characterized by remarkably similar π_{TLP} (ranging from -2.32 to -2.30 MPa). This similarity minimizes FDis_{ses} of π_{TLP} as the weighted distance to the community-weighted trait centroid is minimized (see calculation of FDis in Laliberté & Legendre, 2010). Indeed, HYS has the lowest FDis of π_{TLP} relative to other sites (5-year ambient average: SGS = 0.67; HPG = 0.93; HYS = 0.36; KNZ = 0.37). In the final years of drought, plots previously inhabited by dominant C_4 grasses were invaded by *Bromus japonicus*, a C_3 grass with higher π_{TLP} ($\pi_{\text{TLP}} = -1.6$), as well as perennial forbs, a functional type previously shown to have higher π_{TLP} compared to grasses (Griffin-Nolan, Blumenthal, et al., 2019). Increased

abundance of the dominant C_3 grass, *P. smithii*, maintained the community-weighted trait centroid near the original mean (-2.3 MPa), whereas the invasion of subordinate C_3 species led to increased dissimilarity in π_{TLP} (Laliberté & Legendre, 2010). Additionally, *P. smithii* is characterized by low SLA relative to other species at this site (SLA = 5.73 kg/m^2 for *P. smithii* vs. the $\text{SLA}_{\text{cw}} = 12.3 \text{ kg/m}^2$). Thus, increased abundance of *P. smithii* contributed to the spike in FDis_{ses} of SLA in year 3 of the drought (Figure 2b).

No change in community composition was observed at the tall-grass prairie site (KNZ) and consequently we observed no change in FDis (Figure 2). Drought did cause variable negative effects on PD_{ses} at KNZ (Figure 4); however, the response was not consistent and thus warrants further investigation. It is worth noting that the drought response of PD_{ses} did not match FDis_{ses} responses in either SGS, HYS or KNZ (Figure 4). It is therefore important to measure both functional and phylogenetic diversity as closely related species may differ in their functional attributes (Forrestel et al., 2017; Liu & Osborne, 2015).

4.2 | Community-weighted traits

Functional composition of plant communities is described by both the diversity of traits as well as community-weighted trait means (CWMs), with the latter also having important consequences for ecosystem function (Garnier et al., 2004; Vile, Shipley, & Garnier, 2006). We therefore assessed the impact of experimental drought on community-weighted trait means of several plant traits linked to leaf carbon, nitrogen and water economy. Leaf economic traits, such as SLA and LNC, describe a species strategy of resource allocation/use along a continuum of conservative to acquisitive (Reich, 2014). Empirically and theoretically, conservative species with low SLA and/or LNC are more likely to persist during times of resource-limitation, such as drought (Ackerly, 2004; Reich, 2014; Wright, Reich, & Westoby, 2001), and community-weighted SLA tends to decline in response to drought due to trait plasticity (Wellstein et al., 2017). Alternatively, high SLA and LNC have been linked to strategies of drought escape or avoidance (Frenette-Dussault et al., 2012; Kooyers, 2015). Here, we observed increased SLA_{cw} and LNC_{cw} with long-term drought in all six sites (Figure 3a), suggesting a shift away from species with conservative resource-use strategies (i.e. drought tolerance) and towards a community with greater prevalence of drought avoidance and escape strategies. We likely overestimate these trait values given that we do not account for trait plasticity and the ability of species to adjust carbon and nutrient allocation during stressful conditions (Wellstein et al., 2017); however, our results do indicate species re-ordering towards a plant community with inherently higher SLA and LNC following long-term drought. This is likely due to the observed increase in relative abundance of early-season annual species (i.e. drought escapers) and shrubs (i.e. drought avoiders), species that are characterized by high SLA and LNC, across most sites (Baur et al., in prep). Forbs and shrubs tend to access deeper sources of soil water than grasses (Nippert & Knapp, 2007), a characteristic that has allowed them to persist during historical droughts

(i.e. drought escape; Weaver, 1958) and may have allowed them to persist during our experimental drought. This further supports the conclusion of a community shift towards drought escape strategies and emphasizes the importance of measuring rooting depth, and root traits more broadly, which are infrequently measured in community-scale surveys of plant traits (Bardgett, Mommer, & Vries, 2014; Griffin-Nolan, Bushey, et al., 2018).

While leaf economic traits, such as SLA and LNC, are useful for defining syndromes of plant form and function at both the individual (Díaz et al., 2016) and community-scale (Bruehlheide et al., 2018), they are often unreliable indices of plant drought tolerance (e.g. leaf economic traits might not be correlated with drought tolerance within some communities, even if correlations exist at larger scales) (Brodrigg, 2017; Griffin-Nolan, Bushey, et al., 2018; Rosado, Dias, & Mattos, 2013). We estimated community-weighted π_{TLP} , or the leaf water potential at which cell turgor is lost, which is considered a strong index of plant drought tolerance (Bartlett, Scoffoni, & Sack, 2012). Theory and experimental evidence suggests that dry conditions favour species with lower π_{TLP} (Bartlett, Scoffoni, & Sack, 2012; Zhu et al., 2018). While this may be true of individual species distributions ranging from grasslands to forests (Griffin-Nolan, Ocheltree, et al., 2019; Zhu et al., 2018), this has not been tested at the community scale or within a single community responding to long-term drought. Here, we show that community-scale π_{TLP} responds variably to drought with negative (HPG), positive (SGS and HYS) and neutral effects (KNZ) (Figure 3c). While species can adjust π_{TLP} through osmotic adjustment and/or changes to membrane characteristics (Meinzer, Woodruff, Marias, McCulloh, & Sevanto, 2014), this trait plasticity rarely affects how species rank in terms of leaf-level drought tolerance (Bartlett et al., 2014). Thus, these results suggest that community-scale, leaf-level drought tolerance decreased (i.e. higher π_{TLP}) in response to drought in half of the sites in which π_{TLP} was measured. The opposing effects of drought on community π_{TLP} for SGS and HPG is striking (Figure 3c), especially considering these sites are ~50 km apart and have similar species composition. Increased grass dominance at HPG (Berger-Parker dominance index; Baur et al. in prep) resulted in decreased π_{TLP} (i.e. greater drought tolerance), whereas at SGS, the community shifted towards a greater abundance of drought avoiders/escapers. Forbs and shrubs in these grasslands tend to have higher π_{TLP} compared to both C_3 and C_4 grasses (Griffin-Nolan, Blumenthal, et al., 2019), which explains this increase in community-weighted π_{TLP} . Notably, the plant community at HPG is devoid of a true shrub species, which could further explain the unique effects of drought on the abundance-weighted π_{TLP} of this grassland.

4.3 | Drought sensitivity of ANPP

Biodiversity, and functional diversity more specifically, is well recognized as an important driver of ecosystem resistance to extreme climate events (Anderegg et al., 2018; De La Riva et al., 2017; Pérez-Ramos et al., 2017). We tested this hypothesis

across six grasslands by investigating relationships between several functional diversity indices and the sensitivity of ANPP to drought (i.e. drought sensitivity). We observed a significant negative correlation between functional evenness of SLA and drought sensitivity, providing some support for this hypothesis (Figure 5b) while also emphasizing the importance of measuring single trait functional diversity indices (Spasojevic & Suding, 2012). The significant negative correlation between FEve of SLA_{cy} and drought sensitivity suggests that communities with evenly distributed leaf economic traits are less sensitive to drought. While other indices of functional diversity were weakly correlated with drought sensitivity (Table S2), all correlations were negative implying greater drought sensitivity in plots/sites with lower community functional diversity.

The strongest predictor of drought sensitivity was community-weighted SLA of the previous year (Table S2). The significant positive relationship observed in this study (Figure 5a) suggests that plant communities with a greater abundance of species with high SLA (i.e. resource acquisitive strategies) are more likely to experience greater relative reductions in ANPP during drought in the following year. Furthermore, SLA_{cw} increased in response to long-term drought across sites (Figure 3), which may result in greater sensitivity of these communities to future drought, depending on the timing and nature of drought. The lack of a relationship between π_{TLP} and drought sensitivity was surprising given that π_{TLP} is widely considered an important metric of leaf level drought tolerance (Bartlett, Scoffoni, & Sack, 2012). While π_{TLP} is descriptive of individual plant strategies for coping with drought, it may not scale up to ecosystem level processes such as ANPP. We recognize that the lack of π_{TLP} data from the two most sensitive sites (SBK and SBL) limits our ability to accurately test the relationship between community-weighted π_{TLP} and drought sensitivity of ANPP. Our results clearly demonstrate, however, that leaf economic traits such as SLA are informative of ANPP dynamics during drought (Garnier et al., 2004; Reich, 2012).

It is important to note that this analysis equates space for time with regards to functional composition and drought sensitivity. The drivers of the temporal patterns in functional composition observed here (i.e. species re-ordering) are likely not the same drivers of spatial patterns in functional composition and may have separate consequences for ecosystem drought sensitivity. Nonetheless, these alterations to functional composition will likely impact drought legacy effects (i.e. lagged effects of drought on ecosystem function following the return of average precipitation conditions). This is especially likely for these six grasslands given that they exhibit strong legacy effects even after short-term drought (Griffin-Nolan, Carroll, et al., 2018).

5 | CONCLUSIONS

Grasslands provide a wealth of ecosystem services, such as carbon storage, forage production and soil stabilization (Knapp et al., 1998;

Schlesinger & Bernhardt, 2013). The sensitivity of these services to extreme climate events is driven in part by the functional composition of plant communities (De La Riva et al., 2017; Naeem & Wright, 2003; Pérez-Ramos et al., 2017; Tilman, Wedin, & Knops, 1996). Functional composition responds variably to drought (Cantarel et al., 2013; Copeland et al., 2016; Qi et al., 2015), with long-term droughts largely understudied at broad spatial scales.

We imposed a 4-year experimental drought which significantly altered community functional composition of six North American grasslands, with potential consequences for ecosystem function. Long-term drought led to increased community functional dispersion in three sites and a shift in community-level drought strategies (assessed as abundance-weighted traits) from drought tolerance to drought avoidance and escape strategies. Species re-ordering following dominant species mortality/senescence was the main driver of these shifts in functional composition. Drought sensitivity of ANPP (i.e. relative reduction in ANPP) was linked to both functional diversity and community-weighted trait means. Specifically, drought sensitivity was negatively correlated with community evenness of SLA and positively correlated with community-weighted SLA of the previous year.

These findings highlight the value of long-term climate change experiments as many of the changes in functional composition were not observed until the final years of drought. Additionally, our results emphasize the importance of measuring both functional diversity and community-weighted plant traits. Increased functional diversity following long-term drought may stabilize ecosystem functioning in response to future drought. However, a shift from community-level drought tolerance towards drought avoidance may increase ecosystem drought sensitivity, depending on the timing and nature of future droughts. The collective response and effect of both functional diversity and trait means may either stabilize or enhance ecosystem responses to climate extremes.

ACKNOWLEDGEMENTS

We thank the scientists and technicians at the Konza Prairie, Shortgrass Steppe and Sevilleta LTER sites as well as those at the USDA High Plains research facility for collecting, managing and sharing data. Primary support for this project came from the NSF Macrosystems Biology Program (DEB-1137378, 1137363 and 1137342) with additional research support from grants from the NSF to Colorado State University, Kansas State University and the University of New Mexico for long-term ecological research. We also thank Victoria Klimkowski, Julie Kray, Julie Bushey, Nathan Gehres, John Dietrich, Lauren Baur, Madeline Shields, Melissa Johnston, Andrew Felton and Nate Lemoine for help with data collection, processing, and/or analysis.

AUTHORS' CONTRIBUTIONS

R.J.G.-N., S.L.C., M.D.S. and A.K.K. conceived the experiment. R.J.G.-N., D.M.B., T.E.F., A.M.F., K.E.M., T.W.O. and K.D.W.

collected and/or contributed data. R.J.G.-N. analysed the data and wrote the manuscript. All authors provided comments on the final manuscript.

DATA AVAILABILITY STATEMENT

Trait data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.k4v262p> (Griffin-Nolan, Blumenthal, et al., 2019). See also data associated with the EDGE project following publication of other manuscripts utilizing the same data (<http://edge.biology.colostate.edu/>).

ORCID

Robert J. Griffin-Nolan  <https://orcid.org/0000-0002-9411-3588>

Ava M. Hoffman  <https://orcid.org/0000-0002-1833-4397>

Melinda D. Smith  <https://orcid.org/0000-0003-4920-6985>

Kenneth D. Whitney  <https://orcid.org/0000-0002-2523-5469>

REFERENCES

- Ackerly, D. (2004). Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. *Ecological Monographs*, 74(1), 25–44. <https://doi.org/10.1890/03-4022>
- Anderegg, W. R. L., Klein, T., Bartlett, M., Sack, L., Pellegrini, A. F. A., Choat, B., & Jansen, S. (2016). Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. *PNAS*, 113(18), 5024–5029. <https://doi.org/10.1073/pnas.1525678113>
- Anderegg, W. R. L., Konings, A. G., Trugman, A. T., Yu, K., Bowling, D. R., Gabbitas, R., ... Zenes, N. (2018). Hydraulic diversity of forests regulates ecosystem resilience during drought. *Nature*, 561(7724), 538–541. <https://doi.org/10.1038/s41586-018-0539-7>
- Avolio, M. L., Forrester, E. J., Chang, C. C., La Pierre, K. J., Burghardt, K. T., & Smith, M. D. (2019). Demystifying dominant species. *New Phytologist*, 223, 1106–1126. <https://doi.org/10.1111/nph.15789>
- Bardgett, R. D., Mommer, L., & De Vries, F. T. (2014). Going underground: Root traits as drivers of ecosystem processes. *Trends in Ecology & Evolution*, 29(12), 692–699. <https://doi.org/10.1016/j.tree.2014.10.006>
- Bartlett, M. K., Scoffoni, C., Ardy, R., Zhang, Y., Sun, S., Cao, K., & Sack, L. (2012). Rapid determination of comparative drought tolerance traits: Using an osmometer to predict turgor loss point. *Methods in Ecology and Evolution*, 3(5), 880–888. <https://doi.org/10.1111/j.2041-210X.2012.00230.x>
- Bartlett, M. K., Scoffoni, C., & Sack, L. (2012). The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: A global meta-analysis. *Ecology Letters*, 15(5), 393–405. <https://doi.org/10.1111/j.1461-0248.2012.01751.x>
- Bartlett, M. K., Zhang, Y., Kreidler, N., Sun, S., Ardy, R., Cao, K., & Sack, L. (2014). Global analysis of plasticity in turgor loss point, a key drought tolerance trait. *Ecology Letters*, 17(12), 1580–1590. <https://doi.org/10.1111/ele.12374>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *arXiv preprint arXiv:1406.5823*.
- Botta-Dukát, Z. (2005). Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science*, 16(5), 533–540. <https://doi.org/10.1111/j.1654-1103.2005.tb02393.x>

- Breshears, D. D., Cobb, N. S., Rich, P. M., Price, K. P., Allen, C. D., Balice, R. G., ... Meyer, C. W. (2005). Regional vegetation die-off in response to global-change-type drought. *PNAS*, *102*(42), 15144–15148. <https://doi.org/10.1073/pnas.0505734102>
- Brodribb, T. J. (2017). Progressing from 'functional' to mechanistic traits. *New Phytologist*, *215*(1), 9–11. <https://doi.org/10.1111/nph.14620>
- Bruelheide, H., Dengler, J., Purschke, O., Lenoir, J., Jiménez-Alfaro, B., Hennekens, S. M., ... Jandt, U. (2018). Global trait–environment relationships of plant communities. *Nature Ecology & Evolution*, *2*(12), 1906–1917. <https://doi.org/10.1038/s41559-018-0699-8>
- Burke, I. C., Kittel, T. G. F., Lauenroth, W. K., Snook, P., Yonker, C. M., & Parton, W. J. (1991). Regional analysis of the central Great Plains. *BioScience*, *41*(10), 685–692. <https://doi.org/10.2307/1311763>
- Burke, I. C., Yonker, C. M., Parton, W. J., Cole, C. V., Schimel, D. S., & Flach, K. (1989). Texture, climate, and cultivation effects on soil organic matter content in US grassland soils. *Soil Science Society of America Journal*, *53*(3), 800–805. <https://doi.org/10.2136/sssaj1989.03615995005300030029x>
- Cadotte, M. W., & Tucker, C. M. (2017). Should environmental filtering be abandoned? *Trends in Ecology and Evolution*, *32*(6), 429–437. <https://doi.org/10.1016/j.tree.2017.03.004>
- Cantarel, A. A. M., Bloor, J. M. G., & Soussana, J. F. (2013). Four years of simulated climate change reduces above-ground productivity and alters functional diversity in a grassland ecosystem. *Journal of Vegetation Science*, *24*(1), 113–126. <https://doi.org/10.1111/j.1654-1103.2012.01452.x>
- Carmona, C. P., de Bello, F., Mason, N. W. H., & Lepš, J. (2016). Traits without borders: Integrating functional diversity across scales. *Trends in Ecology & Evolution*, *31*(5), 382–394. <https://doi.org/10.1016/j.tree.2016.02.003>
- Copeland, S. M., Harrison, S. P., Latimer, A. M., Damschen, E. I., Eskelinen, A. M., Fernandez-Goñi, B., ... Thorne, J. H. (2016). Ecological effects of extreme drought on Californian herbaceous plant communities. *Ecological Monographs*, *86*(3), 295–311. <https://doi.org/10.1002/ecm.1218>
- De La Riva, E. G., Lloret, F., Pérez-Ramos, I. M., Marañón, T., Saura-Mas, S., Díaz-Delgado, R., & Villar, R. (2017). The importance of functional diversity in the stability of Mediterranean shrubland communities after the impact of extreme climatic events. *Journal of Plant Ecology*, *10*(2), 281–293.
- Díaz, S., & Cabido, M. (2001). Vive la difference: Plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, *16*(11), 646–655. [https://doi.org/10.1016/s0169-5347\(01\)02283-2](https://doi.org/10.1016/s0169-5347(01)02283-2)
- Díaz, S., Cabido, M., & Casanoves, F. (1998). Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science*, *9*(1), 113–122. <https://doi.org/10.2307/3237229>
- Díaz, S., Cabido, M., Zak, M., Martínez Carretero, E., & Aranibar, J. (1999). Plant functional traits, ecosystem structure and land-use history along a climatic gradient in central-western Argentina. *Journal of Vegetation Science*, *10*(5), 651–660. <https://doi.org/10.2307/3237080>
- Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., ... Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, *529*(7585), 167–171. <https://doi.org/10.1038/nature16489>
- Faith, D. P. (1992). Conservation evaluation and phylogenetic diversity. *Biological Conservation*, *61*(1), 1–10. [https://doi.org/10.1016/0006-3207\(92\)91201-3](https://doi.org/10.1016/0006-3207(92)91201-3)
- Fernandes, V. M., Machado de Lima, N. M., Roush, D., Rudgers, J., Collins, S. L., & Garcia-Pichel, F. (2018). Exposure to predicted precipitation patterns decreases population size and alters community structure of cyanobacteria in biological soil crusts from the Chihuahuan Desert. *Environmental Microbiology*, *20*(1), 259–269. <https://doi.org/10.1111/1462-2920.13983>
- Forrestel, E. J., Donoghue, M. J., Edwards, E. J., Jetz, W., du Toit, J. C., & Smith, M. D. (2017). Different clades and traits yield similar grassland functional responses. *PNAS*, *114*(4), 705–710. <https://doi.org/10.1073/pnas.1612909114>
- Frenette-Dussault, C., Shipley, B., Léger, J. F., Meziane, D., & Hingrat, Y. (2012). Functional structure of an arid steppe plant community reveals similarities with Grime's C-S-R theory. *Journal of Vegetation Science*, *23*(2), 208–222. <https://doi.org/10.1111/j.1654-1103.2011.01350.x>
- Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., ... Toussaint, J.-P. (2004). Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, *85*(9), 2630–2637. <https://doi.org/10.1890/03-0799>
- Gherardi, L. A., & Sala, O. E. (2015). Enhanced interannual precipitation variability increases plant functional diversity that in turn ameliorates negative impact on productivity. *Ecology Letters*, *18*(12), 1293–1300. <https://doi.org/10.1111/ele.12523>
- Griffin-Nolan, R. J., Blumenthal, D. M., Collins, S. L., Farkas, T. E., Hoffman, A. M., Mueller, K. E., ... Knapp, A. K. (2019). Data from: Shifts in plant functional composition following long-term drought in grasslands. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.k4v262p>
- Griffin-Nolan, R. J., Bushey, J. A., Carroll, C. J. W., Challis, A., Chieppa, J., Garbowski, M., ... Knapp, A. K. (2018). Trait selection and community weighting are key to understanding ecosystem responses to changing precipitation regimes. *Functional Ecology*, *32*(7), 1746–1756. <https://doi.org/10.1111/1365-2435.13135>
- Griffin-Nolan, R., Carroll, C. J. W., Denton, E. M., Johnston, M. K., Collins, S. L., Smith, M. D., & Knapp, A. K. (2018). Legacy effects of a regional drought on aboveground net primary production in six central US grasslands. *Plant Ecology*, *219*(5), 505–515. <https://doi.org/10.1007/s11258-018-0813-7>
- Griffin-Nolan, R., Ocheltree, T. W., Mueller, K. E., Blumenthal, D. M., Kray, J. A., & Knapp, A. K. (2019). Extending the osmometer method for assessing drought tolerance in herbaceous species. *Oecologia*, *189*(2), 353–363. <https://doi.org/10.1007/s00442-019-04336-w>
- Grime, J. P. (1998). Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. *Journal of Ecology*, *86*(6), 902–910. <https://doi.org/10.1046/j.1365-2745.1998.00306.x>
- Grime, J. P. (2006). Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. *Journal of Vegetation Science*, *17*(2), 255–260. <https://doi.org/10.1111/j.1654-1103.2006.tb02444.x>
- Hallett, L. M., Stein, C., & Suding, K. N. (2017). Functional diversity increases ecological stability in a grazed grassland. *Oecologia*, *183*(3), 831–840. <https://doi.org/10.1007/s00442-016-3802-3>
- Hsu, J. S., Powell, J., & Adler, P. B. (2012). Sensitivity of mean annual primary production to precipitation. *Global Change Biology*, *18*(7), 2246–2255. <https://doi.org/10.1111/j.1365-2486.2012.02687.x>
- Huxman, T. E., Smith, M. D., Fay, P. A., Knapp, A. K., Shaw, M. R., Loik, M. E., ... Williams, D. G. (2004). Convergence across biomes to a common rain-use efficiency. *Nature*, *429*(6992), 651–654. <https://doi.org/10.1038/nature02561>
- Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., Eisenhauer, N. (2015). Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature*, *526*(7574), 574–577.
- Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., ... Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, *26*(11), 1463–1464. <https://doi.org/10.1093/bioinformatics/btq166>
- Kieft, T. L., White, C. S., Loftin, S. R., Aguilar, R., Craig, J. A., & Skaar, D. A. (1998). Temporal dynamics in soil carbon and nitrogen resources at a grassland–shrubland ecotone. *Ecology*, *79*(2), 671–683. [https://doi.org/10.1890/0012-9658\(1998\)079\[0671:tdisca\]2.0.co;2](https://doi.org/10.1890/0012-9658(1998)079[0671:tdisca]2.0.co;2)
- Knapp, A. K., Avolio, M. L., Beier, C., Carroll, C. J. W., Collins, S. L., Dukes, J. S., ... Smith, M. D. (2017). Pushing precipitation to the extremes

- in distributed experiments: Recommendations for simulating wet and dry years. *Global Change Biology*, 23(5), 1774–1782. <https://doi.org/10.1111/gcb.13504>
- Knapp, A. K., Briggs, J. M., Hartnett, D. C., & Collins, S. L. (1998). *Grassland dynamics: Long-Term ecological research in Tallgrass Prairie. Long-term ecological research network series* (Vol. 1). New York, NY: Oxford University Press.
- Knapp, A., Carroll, C. J. W., Denton, E. M., La Pierre, K. J., Collins, S. L., & Smith, M. D. (2015). Differential sensitivity to regional-scale drought in six central US grasslands. *Oecologia*, 177(4), 949–957. <https://doi.org/10.1007/s00442-015-3233-6>
- Knapp, A. K., & Smith, M. D. (2001). Variation among biomes in temporal dynamics of aboveground primary production. *Science*, 291(5503), 481–484. <https://doi.org/10.1126/science.291.5503.481>
- 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. <https://doi.org/10.1890/13-0526.1>
- Kooyers, N. J. (2015). The evolution of drought escape and avoidance in natural herbaceous populations. *Plant Science*, 234, 155–162. <https://doi.org/10.1016/j.plantsci.2015.02.012>
- Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, 29(5), 592–599. <https://doi.org/10.1111/1365-2435.12345>
- Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91(1), 299–305. <https://doi.org/10.1890/08-2244.1>
- Laliberté, E., Legendre, P., Shipley, B., & Laliberté, M. E. (2014). Package 'FD'. Measuring functional diversity from multiple traits, and other tools for functional ecology.
- Langley, J. A., Chapman, S. K., La Pierre, K. J., Avolio, M., Bowman, W. D., Johnson, D. S., ... Tilman, D. (2018). Ambient changes exceed treatment effects on plant species abundance in global change experiments. *Global Change Biology*, 24(12), 5668–5679. <https://doi.org/10.1111/gcb.14442>
- Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology*, 16, 545–556. <https://doi.org/10.1046/j.1365-2435.2002.00664.x>
- Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, 7(5), 573–579. <https://doi.org/10.1111/2041-210x.12512>
- Liu, H., & Osborne, C. P. (2015). Water relations traits of C_4 grasses depend on phylogenetic lineage, photosynthetic pathway, and habitat water availability. *Journal of Experimental Botany*, 66(3), 761–773. <https://doi.org/10.1093/jxb/eru430>
- Mason, N. W. H., De Bello, F., Mouillot, D., Pavoine, S., & Dray, S. (2013). A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. *Journal of Vegetation Science*, 24(5), 794–806. <https://doi.org/10.1111/jvs.12013>
- Mason, N. W. H., MacGillivray, K., Steel, J. B., & Wilson, J. B. (2003). An index of functional diversity. *Journal of Vegetation Science*, 14(4), 571–578. <https://doi.org/10.1111/j.1654-1103.2003.tb02184.x>
- McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., ... Yezzer, 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>
- Meinzer, F. C., Woodruff, D. R., Marias, D. E., Mcculloh, K. A., & Sevanto, S. (2014). Dynamics of leaf water relations components in co-occurring iso- and anisohydric conifer species. *Plant Cell and Environment*, 37(11), 2577–2586. <https://doi.org/10.1111/pce.12327>
- Muldavin, E. H., Moore, D. I., Collins, S. L., Wetherill, K. R., & Lightfoot, D. C. (2008). Aboveground net primary production dynamics in a northern Chihuahuan Desert ecosystem. *Oecologia*, 155, 123–132.
- Naeem, S., & Wright, J. P. (2003). Disentangling biodiversity effects on ecosystem functioning: Deriving solutions to a seemingly in-surmoundable problem. *Ecology Letters*, 6(6), 567–579. <https://doi.org/10.1046/j.1461-0248.2003.00471.x>
- Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4(2), 133–142. <https://doi.org/10.1111/j.2041-210x.2012.00261.x>
- Newbold, T., Butchart, S. H. M., Şekerciöğlu, Ç. H., Purves, D. W., & Scharlemann, J. P. W. (2012). Mapping functional traits: Comparing abundance and presence-absence estimates at large spatial scales. *PLoS ONE*, 7(8), e44019. <https://doi.org/10.1371/journal.pone.0044019>
- Nippert, J. B., & Knapp, A. K. (2007). Soil water partitioning contributes to species coexistence in tallgrass prairie. *Oikos*, 116(6), 1017–1029. <https://doi.org/10.1111/j.0030-1299.2007.15630.x>
- Noy-Meir, I. (1973). Desert ecosystems: Environment and producers. *Annual Review of Ecology and Systematics*, 4(1), 25–51. <https://doi.org/10.1146/annurev.es.04.110173.000325>
- Ochoa-Hueso, R., Collins, S. L., Delgado-Baquerizo, M., Hamonts, K., Pockman, W. T., Sinsabaugh, R. L., ... Power, S. A. (2018). Drought consistently alters the composition of soil fungal and bacterial communities in grasslands from two continents. *Global Change Biology*, 24(7), 2818–2827. <https://doi.org/10.1111/gcb.14113>
- Oesterheld, M., Loreti, J., Semmartin, M., & Sala, O. E. (2001). Inter-annual variation in primary production of a semi-arid grassland related to previous-year production. *Journal of Vegetation Science*, 12(1), 137–142. <https://doi.org/10.2307/3236681>
- Pakeman, R. J. (2014). Functional trait metrics are sensitive to the completeness of the species' trait data? *Methods in Ecology and Evolution*, 5(1), 9–15. <https://doi.org/10.1111/2041-210X.12136>
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., ... Cornelissen, J. H. C. (2016). Corrigendum to: New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, 64(8), 715. https://doi.org/10.1071/BT12225_CO
- Pérez-Ramos, I. M., Díaz-Delgado, R., de la Riva, E. G., Villar, R., Lloret, F., & Marañón, T. (2017). Climate variability and community stability in Mediterranean shrublands: The role of functional diversity and soil environment. *Journal of Ecology*, 105(5), 1335–1346. <https://doi.org/10.1111/1365-2745.12747>
- Petchey, O. L., & Gaston, K. J. (2002). Functional diversity (FD), species richness and community composition. *Ecology Letters*, 5(3), 402–411. <https://doi.org/10.1046/j.1461-0248.2002.00339.x>
- Qi, W., Zhou, X., Ma, M., Knops, J. M. H., Li, W., & Du, G. (2015). Elevation, moisture and shade drive the functional and phylogenetic meadow communities' assembly in the northeastern Tibetan Plateau. *Community Ecology*, 16(1), 66–75. <https://doi.org/10.1556/168.2015.16.1.8>
- Reich, P. (2012). Key canopy traits drive forest productivity. *Proceedings of the Royal Society B: Biological Sciences*, 279(1736), 2128–2134. <https://doi.org/10.1098/rspb.2011.2270>
- Reich, P. (2014). The world-wide “fast-slow” plant economics spectrum: A traits manifesto. *Journal of Ecology*, 102(2), 275–301. <https://doi.org/10.1111/1365-2745.12211>
- Reich, P., & Oleksyn, J. (2004). Global patterns of plant leaf N and P in relation to temperature and latitude. *PNAS*, 101(30), 11001–11006. <https://doi.org/10.1073/pnas.0403588101>
- Rosado, B. H. P., Dias, A. T. C., & de Mattos, E. A. (2013). Going back to basics: Importance of ecophysiology when choosing functional traits for studying communities and ecosystems. *Natureza & Conservação*, 11(1), 15–22. <https://doi.org/10.4322/natcon.2013.002>

- Schlesinger, W. H., & Bernhardt, E. S. (2013). *Biogeochemistry: An analysis of global change*. Cambridge, MA: Academic press.
- Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., ... Wardle, D. A. (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, 18(12), 1406–1419. <https://doi.org/10.1111/ele.12508>
- Šimová, I., Violle, C., Svenning, J.-C., Kattge, J., Engemann, K., Sandel, B., ... Enquist, B. J. (2018). Spatial patterns and climate relationships of major plant traits in the New World differ between woody and herbaceous species. *Journal of Biogeography*, 45(4), 895–916. <https://doi.org/10.1111/jbi.13171>
- Smith, M. D. (2011). The ecological role of climate extremes: Current understanding and future prospects. *Journal of Ecology*, 99(3), 651–655. <https://doi.org/10.1111/j.1365-2745.2011.01833.x>
- Smith, M. D., Knapp, A. K., & Collins, S. L. (2009). A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. *Ecology*, 90(12), 3279–3289. <https://doi.org/10.1890/08-1815.1>
- Soudzilovskaia, N. A., Elumeeva, T. G., Onipchenko, V. G., Shidakov, I. I., Salpagarova, F. S., Khubiev, A. B., ... Cornelissen, J. H. C. (2013). Functional traits predict relationship between plant abundance dynamic and long-term climate warming. *PNAS*, 110(45), 18180–18184. <https://doi.org/10.1073/pnas.1310700110>
- Spasojevic, M. J., & Suding, K. N. (2012). Inferring community assembly mechanisms from functional diversity patterns: The importance of multiple assembly processes. *Journal of Ecology*, 100(3), 652–661. <https://doi.org/10.1111/j.1365-2745.2011.01945.x>
- Stamakis, A. (2014). RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, 30, 1312–1313. <https://doi.org/10.1093/bioinformatics/btu033>
- Suding, K. N., Lavorel, S., Chapin, F. S., Cornelissen, J. H. C., Díaz, S., Garnier, E., ... Navas, M.-L. (2008). Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. *Global Change Biology*, 14(5), 1125–1140. <https://doi.org/10.1111/j.1365-2486.2008.01557.x>
- Swenson, N. G. (2014). *Functional and phylogenetic ecology in R*. New York, NY: Springer.
- Tilman, D., & Downing, J. A. (1994). Biodiversity and stability in grasslands. *Nature*, 367(6461), 363–365. <https://doi.org/10.1038/367363a0>
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., & Siemann, E. (1997). The influence of functional diversity and composition on ecosystem processes. *Science*, 277(5330), 1300–1302. <https://doi.org/10.1126/science.277.5330.1300>
- Tilman, D., Wedin, D., & Knops, J. (1996). Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, 379(6567), 718–720. <https://doi.org/10.1038/379718a0>
- Trenberth, K. E. (2011). Changes in precipitation with climate change. *Climate Research*, 47(1–2), 123–138. <https://doi.org/10.3354/cr00953>
- Vile, D., Shipley, B., & Garnier, E. (2006). Ecosystem productivity can be predicted from potential relative growth rate and species abundance. *Ecology Letters*, 9(9), 1061–1067. <https://doi.org/10.1111/j.1461-0248.2006.00958.x>
- Villéger, S., Mason, N. W., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89(8), 2290–2301. <https://doi.org/10.1890/07-1206.1>
- Weaver, J. E. (1958). Classification of root systems of forbs of grassland and a consideration of their significance. *Ecology*, 39(3), 393–401. <https://doi.org/10.2307/1931749>
- Wellstein, C., Poschlod, P., Gohlke, A., Chelli, S., Campetella, G., Rosbakh, S., ... Beierkuhnlein, C. (2017). Effects of extreme drought on specific leaf area of grassland species: A meta-analysis of experimental studies in temperate and sub-Mediterranean systems. *Global Change Biology*, 23(6), 2473–2481. <https://doi.org/10.1111/gcb.13662>
- Whitney, K. D., Mudge, J., Natvig, D. O., Sundararajan, A., Pockman, W. T., Bell, J., ... Rudgers, J. A. (2019). Experimental drought reduces genetic diversity in the grassland foundation species *Bouteloua eriopoda*. *Oecologia*, 189(4), 1107–1120. <https://doi.org/10.1007/s00442-019-04371-7>
- Wieczynski, D. J., Boyle, B., Buzzard, V., Duran, S. M., Henderson, A. N., Hulshof, C. M., ... Savage, V. M. (2019). Climate shapes and shifts functional biodiversity in forests worldwide. *PNAS*, 116(2), 587–592. <https://doi.org/10.1073/pnas.1813723116>
- Wright, I. J., Reich, P. B., Cornelissen, J. H. C., Falster, D. S., Hikosaka, K., Lamont, B. B., Lee, W., Oleksyn, J., Osada, N., Poorter, H., Villar, R., Warton, D. I., & Westoby, M. (2005). Assessing the generality of leaf trait of global relationships. *New Phytologist*, 166(2), 485–496. <https://doi.org/10.1111/j.1469-8137.2005.01349.x>
- Wright, I. J., Reich, P. B., & Westoby, M. (2001). Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. *Functional Ecology*, 15(4), 423–434. <https://doi.org/10.1046/j.0269-8463.2001.00542.x>
- Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., ... Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, 428(6985), 821–827.
- Yahdjian, L., & Sala, O. E. (2002). A rainout shelter design for intercepting different amounts of rainfall. *Oecologia*, 133(2), 95–101. <https://doi.org/10.1007/s00442-002-1024-3>
- Zhu, S.-D., Chen, Y.-J., Ye, Q., He, P.-C., Liu, H., Li, R.-H., ... Cao, K.-F. (2018). Leaf turgor loss point is correlated with drought tolerance and leaf carbon economics traits. *Tree Physiology*, 38(5), 658–663. <https://doi.org/10.1093/treephys/tpy013>

SUPPORTING INFORMATION

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

How to cite this article: Griffin-Nolan RJ, Blumenthal DM, Collins SL, et al. Shifts in plant functional composition following long-term drought in grasslands. *J Ecol*. 2019;107: 2133–2148. <https://doi.org/10.1111/1365-2745.13252>