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ARTICLE

Grassland sensitivity to drought is related to functional composition across East Asia and North America

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Abstract

Plant traits can be helpful for understanding grassland ecosystem responses to climate extremes, such as severe drought. However, intercontinental comparisons of how drought affects plant functional traits and ecosystem functioning are rare. The Extreme Drought in Grasslands experiment (EDGE) was established across the major grassland types in East Asia and North America (six sites on each continent) to measure variability in grassland ecosystem sensitivity to extreme, prolonged drought. At all sites, we quantified community-weighted mean functional composition and functional diversity of two leaf economic traits, specific leaf area and leaf nitrogen content, in response to drought. We found that experimental drought significantly increased community-weighted means of specific leaf area and leaf nitrogen content at all North American sites and at the wetter East Asian sites, but drought decreased community-weighted means of these traits at moderate to dry East Asian sites. Drought significantly decreased functional richness but increased functional evenness and dispersion at most East Asian and North American sites. Ecosystem drought sensitivity (percentage reduction in

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aboveground net primary productivity) positively correlated with community-weighted means of specific leaf area and leaf nitrogen content and negatively correlated with functional diversity (i.e., richness) on an intercontinental scale, but results differed within regions. These findings highlight both broad generalities but also unique responses to drought of community-weighted trait means as well as their functional diversity across grassland ecosystems.

KEYWORDS
community-weighted traits, drought sensitivity, functional dispersion, functional evenness, functional richness, plant functional traits

INTRODUCTION

Anthropogenic warming is predicted to alter precipitation patterns and increase the frequency and severity of drought globally, and evidence suggests that these predicted changes in precipitation are already occurring (Williams et al., 2020). Extreme and prolonged droughts have the potential to severely disrupt ecosystem structure and function worldwide (Sankaran & Staver, 2019). Grasslands, which provide many ecosystem functions and services (e.g., water conservation, biodiversity, climate regulation, and forage for livestock), are particularly sensitive to precipitation variability (Maurer et al., 2020). Therefore, understanding grassland responses to altered precipitation regimes will inform predictions of how these ecosystems will function under future climate regimes (Koerner & Collins, 2014; Smith et al., 2022).

The ecological impacts of drought are most often assessed from single site-level studies of natural drought (Ignacio et al., 2022) or, less often, across multiple sites spanning a regional precipitation gradient (Batbaatar et al., 2021; Cherwin & Knapp, 2012; Knapp et al., 2015). However, the sensitivity of grasslands to extreme drought is expected to differ between sites, regions, and continents, given their differences in evolutionary history, community structure, precipitation regimes, temperature variability, and soil properties (Smith et al., 2022). Two contrasting hypotheses exist for how and why grassland ecosystems may respond differently to extreme drought (Muraina, 2020). One suggests that mesic and hydric grasslands should be less sensitive to drought than xeric grasslands, given that precipitation is less of a limiting resource in those ecosystems (Cherwin & Knapp, 2012), while the other hypothesis suggests that xeric grasslands should be less sensitive to drought, given that the constituent species are adapted to dry conditions and have relevant traits related to stress tolerance (Grime et al., 2008). To disentangle some of this complexity and test large-scale hypotheses, a unified multiregional drought experiment is needed.

Multiregional drought studies can provide a unique perspective to coordinate response measurements, assess ecosystem sensitivity across different grassland types, and compare divergent mechanisms of drought sensitivity across regions (Christian et al., 2021; Smith et al., 2022). For example, drought experiments in North American grasslands suggest that sensitivity of aboveground net primary productivity (ANPP) to drought is driven in part by the functional evenness of specific leaf area (Griffin-Nolan et al., 2019), whereby communities with evenly distributed leaf economic traits are less sensitive to drought. A similar study found that drought sensitivity in East Asian grasslands was linked to community-weighted mean seed-coat thickness (Luo et al., 2022). Thus, there is need for coordinated measurements to unravel the mechanisms of drought sensitivity along broad, multiregional precipitation gradients.

Plant functional traits can both respond to environmental change and influence ecosystem functioning during drought (Bruelheide et al., 2018). Because traits are agnostic regarding species identity, they can serve as a common currency across ecosystems that differ in species composition. Ecosystems with a high abundance and diversity of species with drought survival traits can exhibit low sensitivity to drought (Anderegg et al., 2018). Thus, plant traits are an important tool for understanding the driving mechanisms of drought sensitivity (Reich, 2014).

Studies are increasingly exploring community-weighted means of plant traits (i.e., the aggregated community trait mean weighted by species relative abundances) and functional diversity (i.e., the variation in functional trait values among species in a community) to unravel how traits may determine grassland drought sensitivity (He et al., 2019). Plant functional traits can provide insight into the strength and characteristics of plant interactions under drought stress. For instance, grasses and forbs are often highly competitive in low drought stress conditions, and competition can promote growth of species with similar trait values and, thus, increase the relative

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community-weighted means of that trait. As conditions become more stressful, competition intensity may be reduced and facilitation may increase (Maestre et al., 2009) regardless of traits or magnitude of competitive responses. Resource partitioning or facilitation may promote growth of species with dissimilar trait values and, thus, increase the relative effect of functional diversity (Bongers et al., 2021).

Leaf economic traits, such as specific leaf area (leaf area/dry mass) and leaf nitrogen content, may be particularly informative of community-level drought sensitivity (Kramp et al., 2022) as plants with resource-conservative strategies (e.g., low specific leaf area and low leaf nitrogen content) are often less sensitive to drought (Ocheltree et al., 2016). Additionally, plant communities with high functional diversity are buffered against declines in ecosystem functions during drought (Griffin-Nolan et al., 2019). However, how conservative leaf economic traits and functional diversity determine the sensitivity pattern of grasslands across multiple continents experiencing similar multiyear droughts is relatively unknown. Thus, studies across regions are needed to assess how community functional composition and its corresponding effects on ecosystem function will respond under a future of extreme, prolonged droughts.

We conducted a coordinated 4-year extreme drought experiment at six grassland sites along precipitation gradients in both East Asia and in North America. We assessed the impacts of the multiyear extreme drought on community-weighted means and functional diversity of two leaf economic traits (specific leaf area and leaf nitrogen content) and their corresponding links with drought sensitivity (percentage reduction in ANPP). We hypothesized that (1) extreme drought would act as an environmental filter causing a shift in community-weighted means of leaf economic traits and lower functional diversity, (2) drought sensitivity would be positively correlated with leaf economic traits but negatively correlated with functional diversity, and (3) mechanisms of drought sensitivity would be consistent across both regions.

MATERIALS AND METHODS

Study sites

We established a 4-year drought experiment (i.e., the Extreme Drought in Grasslands experiment [EDGE]) in six North American grasslands and six East Asian grasslands (Figure 1). Experimental sites were established in 2012 in North America and in 2014 in East Asia. The six North American sites span a large precipitation gradient (244–864 mm) and encompass the four major grassland types in the central United States: desert grassland, shortgrass prairie, mixed grass prairie, and tallgrass prairie. In East Asia, we selected six sites along a moderate precipitation gradient (175–363 mm) capturing the three major grassland types in northern China: desert steppe, typical steppe, and meadow steppe. Soil texture varies among sites, ranging from sandy to clay loams. See Appendix S1: Table S1 and Figure S1 for more site information.

Experimental drought treatments

Treatments began in 2013 at Sevilleta National Wildlife Refuge, dominated by black grama (SBK), and Sevilleta National Wildlife Refuge, dominated by blue grama (SBL), in 2014 in all other North American sites, and 2015 in East Asia. We established twenty 6 × 6-m plots per site (10 drought, 10 control) in North America and twelve 6 × 6-m plots per site (six drought, six control) in East Asia. At each site, all plots were randomly arranged on a topographically uniform area using a randomized complete block design. Plots were located at least 2 m from each other and were hydrologically isolated by trenching the perimeter to a depth of 1 m and installing 6-mm-thick plastic barriers to prevent lateral water flow. We used rainout shelters to impose drought by reducing each precipitation event by 66% for the entire growing season for 4 years across the 12 sites, while the control plots received all ambient rainfall throughout the year. The rainout shelter roofs were built with transparent polyethylene panels covering 66% of the surface and were supported by a scaffolding/cold frame greenhouse structure. To allow for air flow below the panels and minimize any potential greenhouse effect, shelter roofs were 2 m above the ground at their lowest point. This rainout shelter design has been used in a wide range of ecosystems globally due to its low cost and minimal impact on microclimate (Knapp et al., 2015).

Sampling and measurements

We established a permanent 2 × 2-m quadrat under each shelter and within each unsheltered control plot in the pretreatment year at each site. Absolute aerial cover of each species was estimated visually within four quadrats (1 m^2) placed within the subplot designated for nondestructive measurements. Species composition was assessed at each site for four treatment years. For each plot and species, absolute cover was converted to average percentage relative cover in each year, and this value was used in all analyses (Koerner & Collins, 2014). At the end of each growing season, we estimated ANPP

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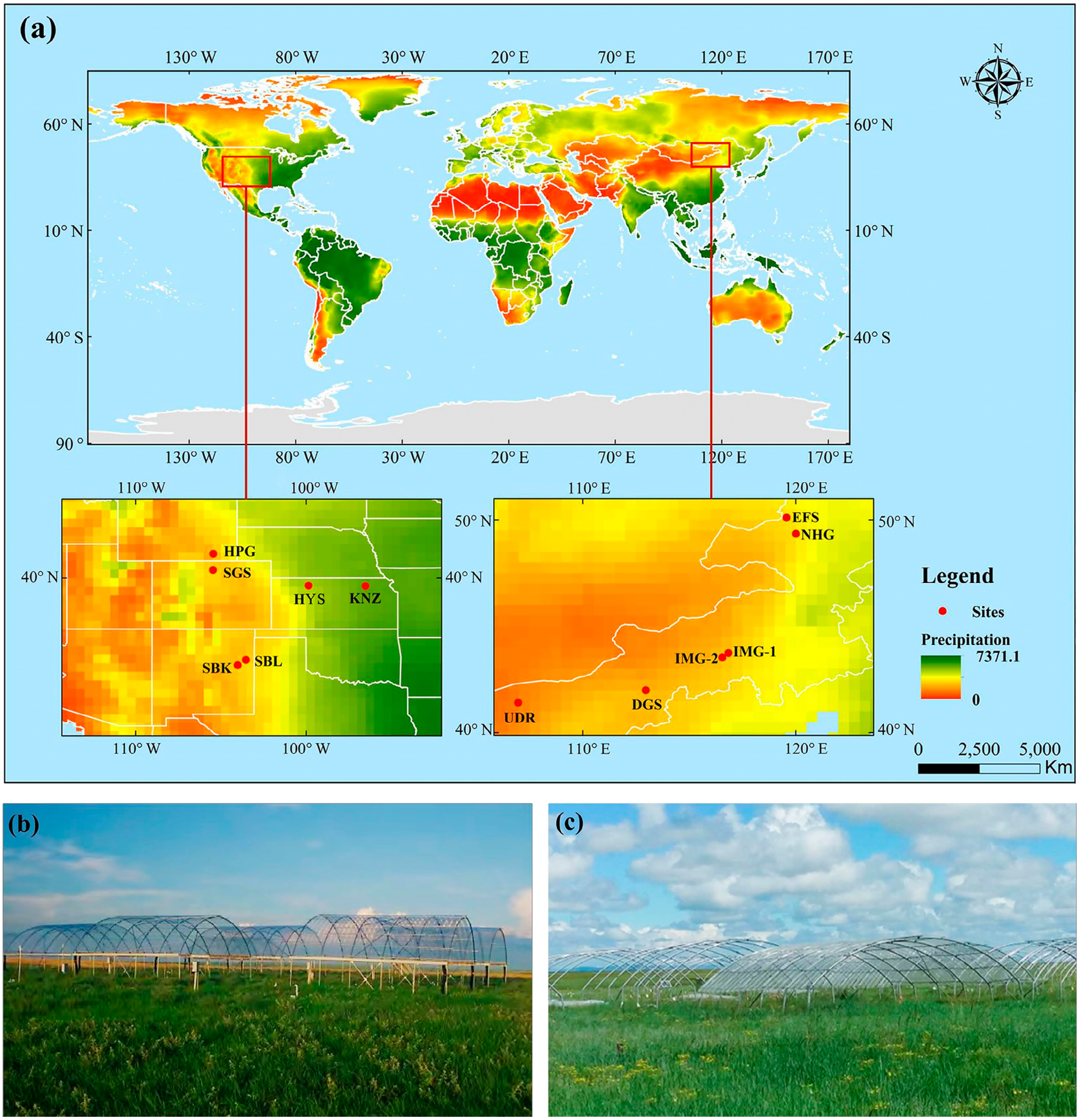

FIGURE 1 (a) Map of study site locations in grasslands of East Asia and North America. Rainout shelters of study site in (b) North America (photo credit: Alan K. Knapp) and (c) East Asia (photo credit: Lin Song). EFS, Erguna Forest-Steppe Ecotone Research Station; HPG, High Plains Grassland Research Center; HYS, Hays Agricultural Research Center; IMG-1 and IMG-2, Inner Mongolia Grassland Ecosystem Research Station; KNZ, Konza Prairie Biological Station; NHG, National Hulunber Grassland Ecosystem Observation and Research Station; SBK, Sevilleta National Wildlife Refuge, dominated by black grama; SBL, Sevilleta National Wildlife Refuge, dominated by blue grama; SGS, Central Plains Experimental Range; UDR, Urat Desert-Grassland Research Station.

by harvesting all aboveground biomass from two 0.5 × 0.5-m quadrats in each plot designated for destructive measurements at all sites in East Asia. All aboveground biomass was harvested in three quadrats ($0.1\ m^2$) in each plot designated for destructive measurements at the four northern sites (Konza Prairie Biological Station [KNZ], Hays Agricultural Research Center [HYS], High Plains Grassland Research Center [HPG], and Central Plains Experimental Range [SGS]) in North America. We sorted plant biomass by species

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at the East Asia sites and by the two or three most dominant grasses, other grasses, forbs, and woody plants at the four northern North American sites and dried the samples at 65°C for 48 h before weighing. For the two southern sites in North America (SBL and SBK), aboveground biomass was estimated using a nondestructive allometric approach for each species occurring in each of the species composition subplots (details in Rudgers et al., 2019).

We measured the plant traits of the most abundant species under ambient conditions per site in an area adjacent to the experimental plots. To avoid destructive sampling, traits from ambient conditions were used in this analysis. Measuring traits in ambient conditions can reflect the potential for how each species will respond to experimental drought, as has been done in similar studies (Griffin-Nolan et al., 2019; Sandel et al., 2010), although we recognize traits may shift intraspecifically in response to drought. Briefly, we collected the youngest, fully expanded leaf on 10 individuals of each species per plot in North American sites in 2015 and 2017 and on three individuals of each species per plot in East Asian sites from 2017 to 2020. Leaves were scanned at 300 dpi, and leaf area was measured for each of the collected leaves per individual using ImageJ software (https://imagej.nih.gov/ij/). Furthermore, we calculated specific leaf area (area per dry mass, in square meters per kilogram) using the same leaves after oven-drying the leaves at 65°C for 48 h. We measured leaf nitrogen content (in milligrams per gram) of leaves collected in East Asian sites with a 2400II CHN elemental analyzer (Perkin-Elmer, Waltham, MA, USA), while a LECO Tru-Spec CN analyzer (Leco Corp.) was used for the leaves from North American sites. In North America, traits were measured in 2015 at the northern sites and 2017 at southern sites. In East Asia, the species mean traits from ambient plots across years (2017 to 2020) were used in the final analysis. The final trait data set included trait values for species cumulatively representing an average of 90% plant cover in each plot. Plots with less than 75% relative cover represented by trait data were removed from all analyses (24 of 768 plot-year combinations were removed; final range: 75%–100% plant cover/plot). Additionally, mean annual temperature, mean annual precipitation (MAP), and potential evapotranspiration were obtained, and aridity was defined as precipitation/potential evapotranspiration for each site.

Data analysis

After determining the average trait value of each species, we calculated community-weighted mean trait values for specific leaf area and leaf nitrogen content. That is, trait values for each species were weighted by their relative abundance in each plot at the 12 sites over the 4-year experimental period. Furthermore, we calculated three separate indices of functional diversity using the "dbFD" function in the FD R package (Bongers et al., 2021). Using a flexible distance-based framework and principal component analysis, the "dbFD" function estimates functional richness (the total volume of x-dimensional functional space occupied by the community), functional evenness (the regularity of spacing between species within multivariate trait space), and functional dispersion (the mean distance of species trait values to the mean trait value of all species) (Laliberte & Legendre, 2010). Each index of functional diversity (i.e., functional richness, evenness, and dispersion) was also estimated for each trait individually as well as in two-trait bivariate space in this study. Intraspecific plant trait variability and plant trait plasticity were not assessed. Thus, responses of community-weighted means of traits and functional diversity to drought resulted from species turnover and interspecific plant trait differences.

We tested for the interactive effects of treatment and site on community-weighted means of specific leaf area and leaf nitrogen content and functional richness, evenness, and dispersion for the community in East Asia and North America (six sites in each continent) using repeated measures mixed-effects models with drought treatment and site as fixed factors and block nested in year as a random factor (i.e., to reduce the effect of year-to-year rainfall variability) in the lme4 R package. Similar mixed model analysis of variance with drought treatment as a fixed factor and block nested in year as a random factor was separately applied for each site to assess the impacts of drought on the community-weighted means of specific leaf area and leaf nitrogen content and measures of functional diversity.

Drought sensitivity was calculated as the percentage reduction in ANPP in drought plots for each site and for each year (Equation 1):

$$\text{Drought sensitivity} = \text{abs}\left(100 \times \frac{\text{ANPP}_{\text{drought}} - \text{ANPP}_{\text{control}}}{\text{ANPP}_{\text{control}}}\right), \tag{1}$$

where ANPP is the mean value across all plots of that treatment in a given year. To determine trait-drought sensitivity relationships, we used mixed linear models to relate community-weighted means of specific leaf area and leaf nitrogen content and functional richness, evenness, and dispersion to drought sensitivity with year as a random effect across all experimental sites. Analogous models were used to relate drought sensitivity and community functional composition (i.e., the variation in drought plots compared to control plots) with MAP and aridity.

The original data were log-transformed when it was necessary to meet normality and homogeneity of variance criteria. All statistical analyses were performed in R statistical programming (R version 4.2.0; R Core Team, 2022).

RESULTS

Effects of experimental drought on community-weighted mean traits

There was a significant treatment × site interaction for community-weighted means of specific leaf area in both East Asia and North America (Appendix S1: Table S2), indicating that the responses of community-weighted means of specific leaf area to extreme drought differed among experimental sites within each region. Experimental drought had a more noticeable impact on community-weighted means of specific leaf area when averaged across years in East Asia and North America. In East Asia, drought significantly increased community-weighted means of specific leaf area at National Hulunber Grassland Ecosystem Observation and Research Station (NHG) and decreased it at Inner Mongolia Grassland Ecosystem Research Station 2 (IMG-2) and Urat Desert-Grassland Research Station (UDR), while no change was observed at Erguna Forest-Steppe Ecotone Research Station (EFS), Inner Mongolia Grassland Ecosystem Research Station 1 (IMG-1), or Damaoqi Grassland Station (DGS) (Figure 2; Appendix S1: Table S3). Drought increased community-weighted means of specific leaf area at all North American sites except SBK, where specific leaf area was unaffected by drought (Figure 2; Appendix S1: Table S3).

There was a significant treatment × site interaction for community-weighted means of leaf nitrogen content in East Asia (Appendix S1: Table S2), but the interaction was not significant for community-weighted means of leaf nitrogen content in North America. Drought significantly increased community-weighted means of leaf nitrogen content at all but two sites (KNZ and SBL) in North America (Figure 2; Appendix S1: Table S3). Drought increased community-weighted means of leaf nitrogen content at NHG and decreased it at UDR, but no change was observed at the other four sites in East Asia (Figure 2; Appendix S1: Table S3).

Effects of experimental drought on functional diversity

There were significant treatment × site interactions for multivariate functional diversity indices (i.e., functional richness, evenness, and dispersion) in North America, but not in East Asia (Appendix S1: Table S2). Functional diversity response to experimental drought varied among sites in East Asia and North America (Figure 2). Multivariate functional richness significantly decreased in drought plots at EFS, but no change was observed at the other five sites in East Asia (Figure 2; Appendix S1: Table S3). In North America, drought increased multivariate functional richness at SBL and decreased multivariate functional richness at KNZ and SGS, but no change was observed at the other three sites (Figure 2; Appendix S1: Table S3). Multivariate functional evenness significantly increased in drought plots at all but two sites (EFS and IMG-1) in East Asia (Figure 2; Appendix S1: Table S3). Drought led to a significant increase in multivariate functional evenness at KNZ and SGS, but no change was observed at the other four sites in North America (Figure 2; Appendix S1: Table S3). Multivariate functional dispersion significantly increased in drought plots at NHG and DGS, but no change was observed at the other four sites in East Asia (Figure 2; Appendix S1: Table S3). Drought led to a significant increase in multivariate functional dispersion at KNZ, HYS, and SGS, but no change was observed at the other three sites in North America (Figure 2; Appendix S1: Table S3).

Drought effects on the functional diversity of specific leaf area were variable among sites in East Asia and in North America (Appendix S1: Table S2). The functional richness of specific leaf area significantly decreased in drought plots at DGS, but no change was observed at the other five sites in East Asia (Appendix S1: Table S3). In North America, drought increased the functional richness of specific leaf area at SBL and decreased the functional richness of specific leaf area at KNZ, HPG, SGS, and SBK, but no change was observed at HYS (Figure 2; Appendix S1: Table S3). The functional evenness of specific leaf area significantly increased in drought plots at DGS, but no change was observed at the other five sites in East Asia (Appendix S1: Table S3). Drought effects led to a significant decline in the functional evenness of specific leaf area at KNZ, but no change was observed at the other five sites in North America (Figure 2; Appendix S1: Table S3). The functional dispersion of specific leaf area significantly increased in drought plots at DGS, but no change was observed at the other five sites in East Asia (Figure 2; Appendix S1: Table S3). Drought effects led to a significant increase in the functional dispersion of specific leaf area at HYS and SGS, but no change was observed at the other four sites in North America (Figure 2; Appendix S1: Table S3).

Drought effects on the functional diversity of leaf nitrogen content were variable among sites in East Asia

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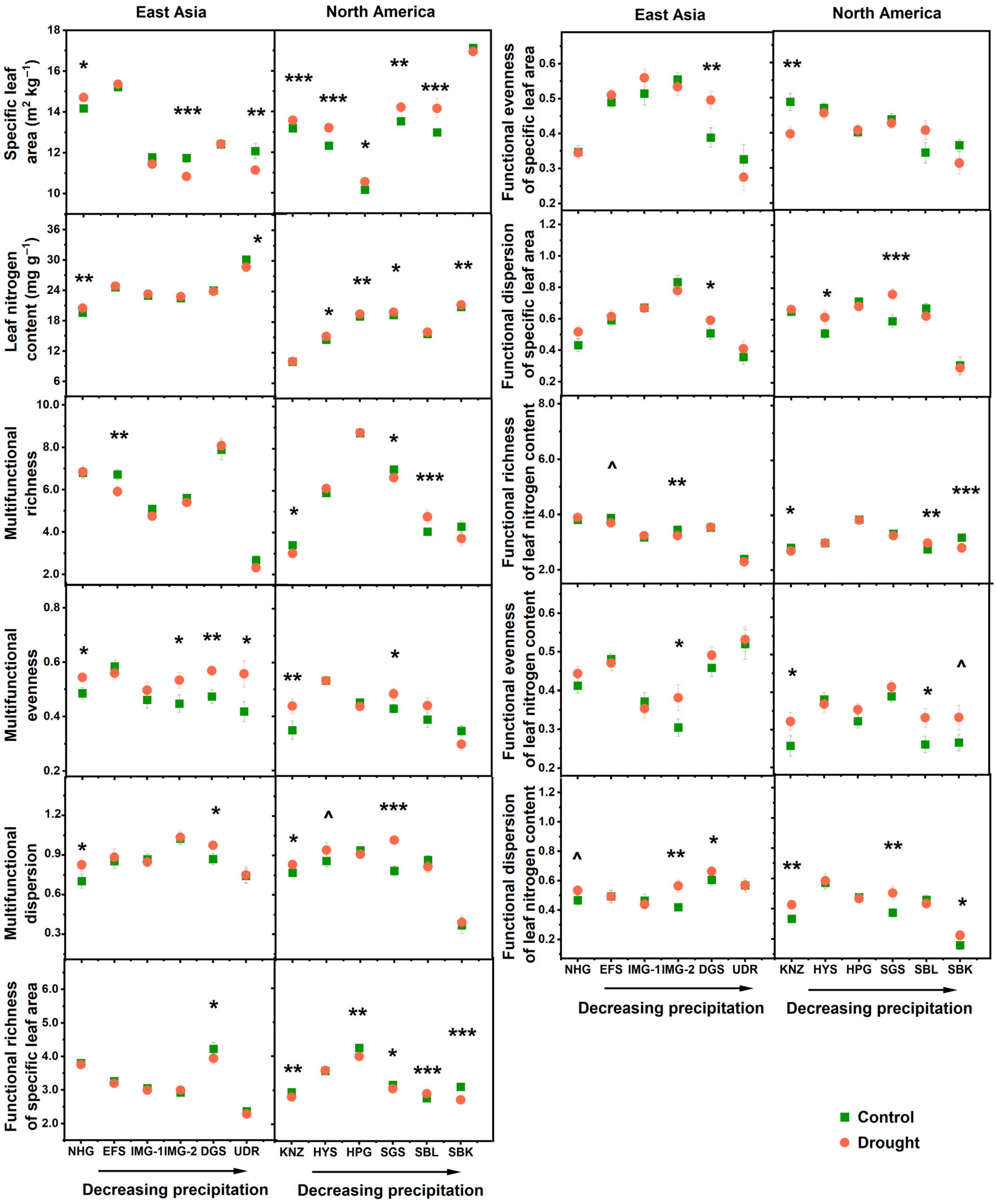
and in North America. The functional richness of leaf nitrogen content significantly decreased in drought plots at EFS and IMG-2, but no change was observed at the other four sites in East Asia (Appendix S1: Table S3). In North America, drought significantly decreased the functional richness of leaf nitrogen content at KNZ and SBK



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and increased the functional richness of leaf nitrogen content at SBL, but no change was observed at the other three sites (Figure 2; Appendix S1: Table S3). The functional evenness of leaf nitrogen content significantly increased in drought plots at IMG-2, while no change was observed at the other five sites in East Asia (Figure 2; Appendix S1: Table S3). Drought effects led to a significant increase in the functional evenness of leaf nitrogen content at KNZ, SBL, and SBK, but no change was observed at the other three sites in North America (Figure 2; Appendix S1: Table S3). The functional dispersion of leaf nitrogen content significantly increased in drought plots at NHG, IMG-2, and DGS, but no change was observed at the other three sites in East Asia (Figure 2; Appendix S1: Table S3). Drought effects led to a significant increase in the functional dispersion of leaf nitrogen content at KNZ, SGS, and SBK, but no change was observed at the other three sites in North America (Appendix S1: Table S3).

Relationships between drought sensitivity and functional composition

On a multiregional scale, the community-weighted means of specific leaf area and leaf nitrogen content were positively correlated with drought sensitivity (i.e., percentage reduction in ANPP; Figure 3a; Appendix S1: Table S4). The multivariate functional richness and functional richness of specific leaf area were negatively correlated with drought sensitivity across the 12 sites (Figure 3b; Appendix S1: Table S4). There were no significant relationships between other measures of functional diversity and drought sensitivity across the 12 sites in East Asia and North America.

On a regional scale, the community-weighted means of leaf nitrogen content, but not specific leaf area, were positively correlated with drought sensitivity across the six East Asian sites (Figure 3a; Appendix S1: Table S4). There were no other significant relationships between functional diversity and drought sensitivity across all sites in East Asia. In contrast, the community-weighted means of specific leaf area were positively correlated with drought sensitivity across the six sites in North America, but the community-weighted means of leaf nitrogen content were not significantly correlated with drought sensitivity across the six sites in North America (Figure 3a; Appendix S1: Table S4). All functional diversity indices except the functional richness of leaf nitrogen content were negatively correlated with drought sensitivity across the six sites in North America (Figure 3b; Appendix S1: Table S4).

The community-weighted mean of specific leaf area was negatively correlated with aridity across the six sites in North America, while no relationship was detected between the community-weighted means of traits and MAP or aridity on a multiregional or regional scale (Appendix S1: Figures S2 and S3). Functional richness and evenness were generally negatively correlated with MAP and aridity, while no relationship was observed between functional dispersion and MAP and aridity on a multiregional or regional scale. Drought sensitivity was negatively correlated with MAP and aridity across the six sites in North America and on a multiregional scale (Appendix S1: Figures S2 and S3).

DISCUSSION

Responses of community-weighted mean of traits to experimental drought

We assessed the impact of a 4-year experimental drought on the community-weighted means and diversity of two plant functional traits, specific leaf area and leaf nitrogen content, in 12 grassland communities across East Asia and North America. We found that plant functional composition responded strongly to extreme drought, even though droughts are historically common in these ecosystems, and they have experienced considerable interannual variability in rainfall. Specifically, our study showed that community-weighted means of specific leaf area and leaf nitrogen content responded inconsistently to experimental drought across regions. Experimental drought significantly increased community-weighted means of specific leaf area or leaf nitrogen content in most grasslands of North America, but drought effects

FIGURE 2 Experimental drought effects on plant community-weighted means for specific leaf area and leaf nitrogen content and plant functional diversity estimated in multivariate trait space as well as separately for each trait in grasslands of East Asia and North America. Values are shown as mean ± SE. Statistical significance is represented by $^{\wedge}0.1 \geq p > 0.05$, $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$. See Appendix S1: Table S3 for exact *p*-values and ANOVA results. EFS, Erguna Forest-Steppe Ecotone Research Station; HPG, High Plains Grassland Research Center; HYS, Hays Agricultural Research Center; IMG-1 and IMG-2, Inner Mongolia Grassland Ecosystem Research Station; KNZ, Konza Prairie Biological Station; NHG, National Hulunber Grassland Ecosystem Observation and Research Station; SBK, Sevilleta National Wildlife Refuge, dominated by black grama; SBL, Sevilleta National Wildlife Refuge, dominated by blue grama; SGS, Central Plains Experimental Range; UDR, Urat Desert-Grassland Research Station.

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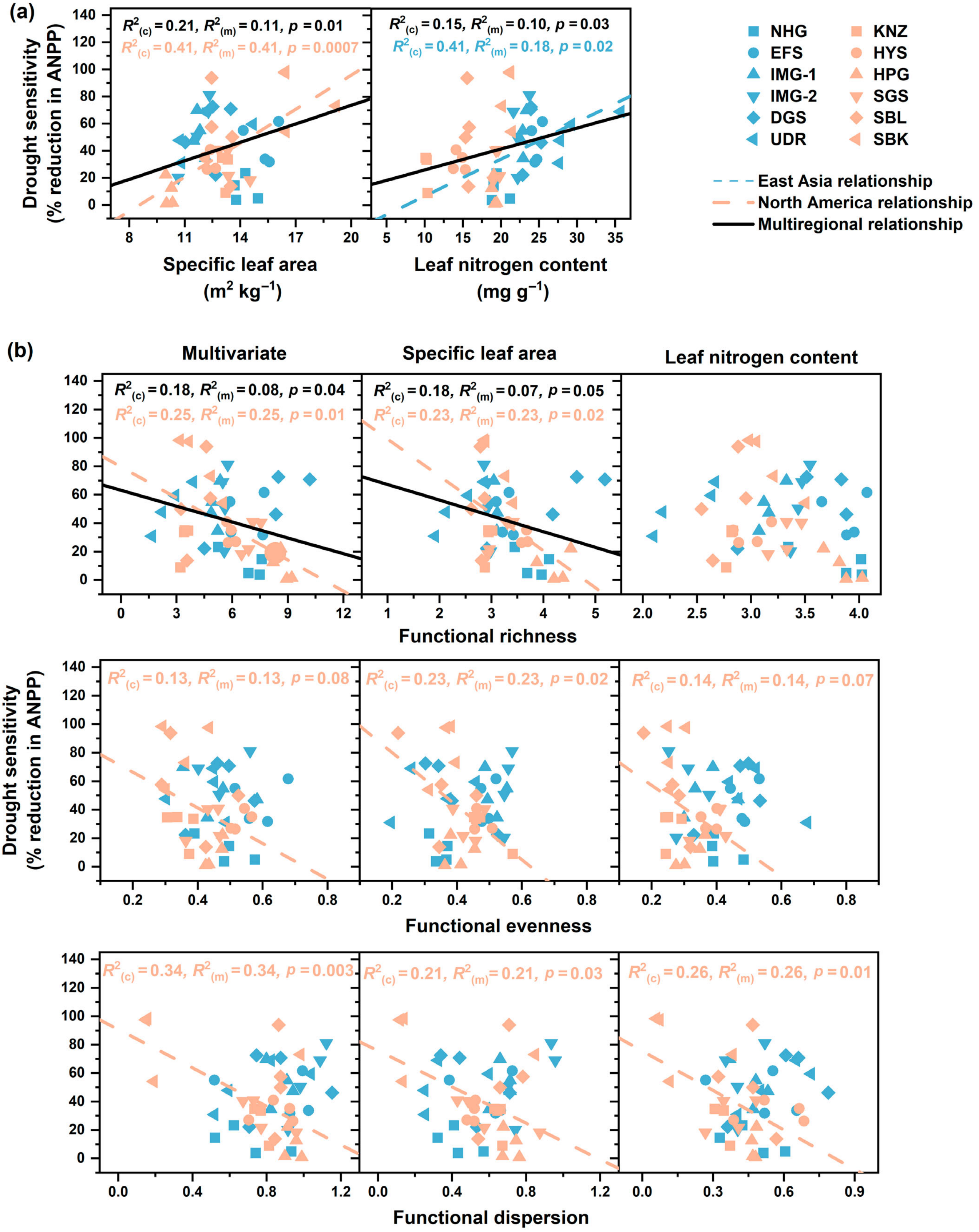

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on community-weighted means of traits varied among sites in East Asia, with a significant increase in wetter sites (NHG) and a significant decrease in moderate and drier sites (IMG-2 and UDR; Figure 2). These results may be the result of differences in resource-use strategies exhibited by plants under experimental drought in East Asia and North America. Specific leaf area and leaf nitrogen content both describe a species' resource-use strategy along a spectrum from conservative (low values) to acquisitive (high values) (Reich, 2014; Sandel et al., 2010). The increasing community-weighted means of specific leaf area or leaf nitrogen content with long-term drought at all sites in North America and at the wetter site (NHG) in East Asia (Figure 2) suggest a shift away from a community with conservative resource-use strategies (i.e., drought tolerance) to a community with greater prevalence of drought avoidance and escape strategies (Kooyers, 2015; Kramp et al., 2022). However, plant species adopted a conservative strategy with low specific leaf area and leaf nitrogen content at two of the East Asian sites (IMG-2 and UDR; Figure 2), which might make them more likely to persist in response to prolonged drought (Chen et al., 2013). More broadly, these responses were of greater magnitude at the drier sites along the aridity gradient (Appendix S1: Figures S2 and S3), consistent with previous studies (e.g., Knapp et al., 2015). In addition, the variable effect of drought on the community-weighted means of traits across sites in East Asia may be the result of different drought response mechanisms across sites. Biotic factors (e.g., competition) are likely more important for determining community composition at wetter sites (i.e., NHG), while abiotic factors (e.g., water availability) are more important at moderate and drier sites (i.e., IMG-2 and UDR). Regardless of the mechanism, our results suggest that community trait responses to drought are predominantly site- and region-specific. Overall, our hypothesis that drought acts as a common environmental filter leading to trait convergence toward drought tolerance was not supported by the data for most sites as functional diversity increased and drought avoidance traits became more prevalent at many sites.

Responses of functional diversity to experimental drought

In our study, we found that functional richness, evenness, and dispersion responded consistently to experimental drought in the grasslands of East Asia and North America, with a few exceptions. For those sites where functional diversity responded significantly to drought, functional richness declined, and both functional evenness and dispersion increased (Figure 2). The decline in functional richness suggests available resources are not being utilized efficiently (Mason et al., 2005). However, the increase in functional evenness and dispersion can maximize trait dissimilarity in multiple dimensions and possibly minimize competition and/or increase complementarity and allow for successful recruitment under drought (Anderegg et al., 2018). Increased functional dispersion and evenness may reflect the mortality of dominant species that previously dominated a uniform trait space (Whitney et al., 2019). Furthermore, single-trait functional evenness did not consistently mirror multivariate functional evenness. For example, the increase in multivariate functional evenness at KNZ under drought was primarily driven by an increased functional evenness of leaf nitrogen content, even though the functional evenness of specific leaf area decreased (Figure 2), underscoring the importance of investigating single-trait diversity indices (Spasojevic & Suding, 2012) as this community functional change was masked by multivariate measures of functional evenness.

Effects of community composition on ecosystem sensitivity of ANPP

We examined whether community-weighted means of traits and measures of functional diversity influenced the drought sensitivity of ANPP across and within the two studied regions. Across both regions, we found significant positive relationships between the drought sensitivity and community-weighted means of specific leaf area and leaf nitrogen content and significant negative relationships between drought sensitivity and multivariate functional richness and the functional richness of specific leaf area

FIGURE 3 Relationship between drought sensitivity and (a) community-weighted means for specific leaf area and leaf nitrogen content and (b) functional diversity estimated in multivariate trait space as well as separately for each trait in grasslands of East Asia and North America. The marginal (m) and conditional (c) R^2 values of the models are shown in the panels. EFS, Erguna Forest-Steppe Ecotone Research Station; HPG, High Plains Grassland Research Center; HYS, Hays Agricultural Research Center; IMG-1 and IMG-2, Inner Mongolia Grassland Ecosystem Research Station; KNZ, Konza Prairie Biological Station; NHG, National Hulunber Grassland Ecosystem Observation and Research Station; SBK, Sevilleta National Wildlife Refuge, dominated by black grama; SBL, Sevilleta National Wildlife Refuge, dominated by blue grama; SGS, Central Plains Experimental Range; UDR, Urat Desert-Grassland Research Station.

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(Figure 3). These results indicate that drought sensitivity is related to changes in community composition across regions. A positive relationship between the community-weighted means of specific leaf area and leaf nitrogen content and drought sensitivity suggests that communities or sites with low drought sensitivity were dominated by species characterized by conservative traits (i.e., low specific leaf area and low leaf nitrogen content). This mechanism is consistent with mass-ratio theory (Chiang et al., 2016; Smith et al., 2020) and extends previous results from US grasslands to East Asian grasslands (Griffin-Nolan et al., 2019). Moreover, a negative relationship of functional richness with drought sensitivity indicates that plant communities and sites with higher functional richness were buffered against declines in ecosystem productivity. Therefore, the community-weighted means of traits and functional richness of grasslands are likely to be useful predictors for how communities will respond to future changes in precipitation (Cleland et al., 2013).

In North American grasslands, we found a positive relationship between the drought sensitivity and community-weighted means of specific leaf area and negative relationships between drought sensitivity and functional diversity indices (i.e., functional richness, evenness, and dispersion) (Figure 3). These results suggest that decreased community-weighted means of specific leaf area could decrease drought sensitivity in North America. Indeed, an analysis conducted in the same region found that functional traits associated with water conservation strategies (i.e., low specific leaf area and high leaf dry mass per fresh mass) buffered species' relative abundance against dry years in a semiarid shortgrass prairie of North America (Wilcox et al., 2021). Moreover, the negative relationships between functional diversity indices and drought sensitivity indicate that the combination of functionally different species in some communities buffered them against high drought sensitivity through resource partitioning, facilitation, and/or biotic feedbacks (Turnbull et al., 2016).

We also observed a positive relationship between the drought sensitivity and community-weighted means of leaf nitrogen content across six sites in East Asia (Figure 3a); these results suggest that decreased community-weighted means of leaf nitrogen content could decrease drought sensitivity in East Asia. Cross-continental studies often reveal different mechanisms driving patterns of species richness in grasslands (Smith et al., 2022), which makes the patterns here that are consistent across continents even more striking. Nevertheless, it is likely that factors other than community composition (e.g., precipitation and temperature) co-determine patterns of drought sensitivity on a regional scale (Sasaki et al., 2023).

CONCLUSION

Ecosystem responses to climatic extremes are partially driven by community functional composition. Understanding the drought sensitivity of plant community traits may improve predictions of ecosystem responses to climate change. Our study found that experimental drought effects on community functional composition (i.e., community-weighted means of traits and functional diversity) and plant traits (i.e., specific leaf area and leaf nitrogen content) will impact ANPP and responses to a changing climate. Importantly, our results demonstrate that leaf economic traits (i.e., specific leaf area and leaf nitrogen content) and functional diversity are informative of drought sensitivity across regions. Although the predictive value of leaf economic traits under ambient conditions varies on a regional scale, increased functional diversity and decreased community-weighted means of conservative traits (e.g., specific leaf area) following long-term drought may stabilize ecosystem functioning in response to future drought on a multiregional scale.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Song, 2023) are available in Figshare at https://doi.org/10.6084/m9.figshare.22790636.

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