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Functional diversity response to geographic and experimental precipitation gradients varies with plant community type

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Abstract

1. Precipitation is a primary determinant of plant community structure in drylands. However, the empirical evidence and predictions are lacking for how plant functional diversity in desert and steppe communities respond to altered precipitation regimes.
2. We examined how precipitation changes along the natural and experimental gradients affect different components of functional diversity in desert-shrub and steppe-grass communities. We compared the associations of precipitation changes with community-weighted means (CWMs) of six traits, functional divergence (FDvar) of each single-trait and multi-trait functional richness (FRic) and dispersion (FDis) for shrub and grass communities along the natural and experimental gradients. We also disentangle the roles of species turnover and intraspecific variations in affecting the responses of different functional diversity to precipitation changes.
3. We found that in general, the similar responses of functional traits or diversity to both the natural and experimental precipitation gradients were dependent on plant community type. Across both two gradients, precipitation was positively associated with CWM of plant height and negatively associated with the CWM of SLA and leaf thickness in grass community, while positively associated with FDvar of four traits and FDis in shrub communities. Both species turnover and intraspecific variations contributed to the responses of grass community traits to precipitation changes across both two gradients, and to FDvar of traits and FDis in shrub community along the natural gradient. In contrast, species turnover variations contributed to FDvar of traits and FDis in shrub community in experiment.
4. These results suggest that there is better concordance between the effects of naturally and experimentally increased precipitation on functional diversity of

plant communities, but different mechanisms behind the relationship of functional diversity–precipitation between shrub and grass communities. Grass communities can adapt to precipitation changes by average trait differences, while shrub communities persist through FDvar of single-trait and multi-trait dispersion, thus highlighting the important differences in adaptive strategies between shrub and grass communities. Our findings demonstrate that short-term responses of plant communities to manipulative precipitation changes can reflect long-term shifts at spatial scales depending on the specific functional trait and diversity.

KEYWORDS

adaptive strategy, community traits, extreme climate, functional divergence, functional diversity, precipitation changes

1 | INTRODUCTION

Changes in precipitation patterns due to anthropogenic climate change have the pervasive effects on plant community composition and structure in terrestrial ecosystems (Bahn et al., 2014; Cleland et al., 2013; Huxman et al., 2004). Grasslands and deserts, two of the largest terrestrial ecosystems in the world, are primarily water limited, and thus are sensitive to precipitation changes (Huxman et al., 2004; Knapp et al., 2015). Current variation in precipitation across space plays a key role in determining plant communities from desert to grassland (Gao & Reynolds, 2003; Pierce et al., 2019; Zuo et al., 2020). As frequent extreme drought and high precipitation increases with climate change (Bahn et al., 2014; Knapp et al., 2015), the state transitions between desert and grassland caused by species composition shifts might be accelerated by precipitation extremes (Gao & Reynolds, 2003; Pierce et al., 2019; Zuo et al., 2020). Functional diversity defined by the single trait (community-weighted trait means, CWMs) or multiple traits (e.g. functional richness and dispersion) is often used to predict plant community responses to temperature or precipitation changes (Guittar et al., 2016; Kimball et al., 2016). However, it is not clear whether the single- and multi-trait diversity similarly respond to altered precipitation in desert and grassland communities (Eugenio et al., 2011).

Plant functional traits can be used to understand plant community assembly and predict plant community responses to future global change (Kimball et al., 2016; Schellenberger Costa et al., 2017; Xu et al., 2018). Single functional indices have proven to be better predictors of ecosystem productivity (Forrestel et al., 2017), and high functional richness (FRic) or dispersion (FDis) can enhance the resistance of ecosystem function against drought (Valencia et al., 2015). Climate-induced changes in plant community structure can potentially be inferred from the patterns of single traits along a natural gradient (Frenette-Dussault et al., 2013; Guittar et al., 2016; Sandel et al., 2010). Shifts in precipitation patterns can lead to changes in traits and species abundance, thereby shaping plant distributions or compositions along the precipitation gradient (Griffin-Nolan et al., 2018). A linear precipitation–trait relationship along the natural gradient suggests that some traits at the community level (CWM) are the predictors of plant community responses to broad-scale precipitation changes (Le Bagousse-Pinguet et al., 2017; Oyarzabal et al., 2008; Sandel et al., 2010), for example plant height and SLA increased, and leaf dry matter content (LDMC) and leaf N content (LNC) decreased with increasing precipitation across temperate grasslands in South and North America. However, for desert shrub or shrub-dominated communities, the available studies have reported that most shrub traits do not have the linear relationships with natural precipitation gradients (Lang et al., 2018; Moreno et al., 2010), due to the slow-growing and stress-tolerant strategies of shrub species (Valencia et al., 2015). So, the switch from desert shrubland to grassland may be caused by differences in adaptive capacity of shrub and herbaceous plants to precipitation conditions.

Short-term responses of plant functional diversity in grassland communities to precipitation changes may be obtained from experimental studies (Griffin-Nolan et al., 2019; Sandel et al., 2010). Experimental drought can decrease SLA (Wellstein et al., 2017) and FDis (Griffin-Nolan et al., 2019), but increase LNC (Luo et al., 2018), LDMC (Deleglise et al., 2015) and their variations (Luo et al., 2019). Increased precipitation can increase LNC (Sandel et al., 2010), but most traits and FDis have no significant relationships with increased precipitation in grasslands (Kimball et al., 2016; Xu et al., 2018). For desert shrub or shrub-dominated communities, increased precipitation can increase SLA of shrubs (Xin et al., 2018), but most traits are not related to experimental drought (Carvajal et al., 2017; Du et al., 2018). Furthermore, the available studies have documented inconsistent results on plant community trait responses to precipitation in geographic and experimental variations (Luo et al., 2018; Sandel et al., 2010; Zuo et al., 2017), due to different adaption and response of species to rapid precipitation changes. Thus, comparative studies that incorporate large natural and experimental gradients of precipitation are necessary to explicitly assess how altered precipitation affects different plant communities (Knapp et al., 2015; Sandel et al., 2010).

Many studies have reported that precipitation-driven changes in plant community composition and structure are closely associated with plant adaption strategies controlled by diverse traits or trait differentiation (Spasojevic et al., 2014). The responses of community-level traits to precipitation changes are caused by species turnover or intraspecific trait variation (Cleland et al., 2013; Luo et al., 2018; Nguyen et al., 2017; Sandel et al., 2010). The frequency of extreme drought and high precipitation is increasing with effects on plant community structure via species turnover or intraspecific competitions (Knapp et al., 2015; Luo et al., 2018; Nguyen et al., 2017). Increased aridity in drylands world-wide is especially problematic as it causes the replacement of grass by stress-tolerant shrub with specific traits adapted to drought (Schooley et al., 2018; Valencia et al., 2015). On the contrary, high precipitation can support the growth and establishment of herbaceous plants, thus favouring a transition from desert to grassland (Eugenio et al., 2011). To date, however, there are few studies to examine the relative contributions of species turnover and intraspecific trait variations to community-level trait responses to precipitation changes in state transitions between desert and grassland.

Here, we explore how altered precipitation affects multiple components of functional diversity using both a natural and experimental gradient of precipitation in desert-shrub and steppe-grass communities in Inner Mongolia. We utilized the natural gradient of mean annual precipitation (37–380 mm) in Inner Mongolia, where plant communities shift from desert to desert steppe to typical steppe, which provided the ideal study area to examine the effects of global climate change on traits of different communities (Bai et al., 2012). Moreover, two plant communities dominated by either shrub and grass coexisted at a same location in desert steppe, allowing for an experimental comparison of their trait responses to altered precipitation. Using the same natural and experimental gradient, we previously showed that species richness and aboveground biomass responded similar to the two gradients in both plant community types (Zuo et al., 2020). In this paper, we focus on functional diversity, and we ask the following three questions: (a) Do different components of functional diversity respond similar to a natural precipitation gradient across space as they do to an imposed experimental precipitation gradient?; (b) does this response vary with plant community type (shrub vs. grassland)?; and (c) to what extent does interspecific or intraspecific trait variation drive shrub and grass community responses to these precipitation gradients? Specifically, we hypothesized that (a) the responses of different functional diversity in shrub or grass community to precipitation changes could be a mismatch between experimental and natural gradient; (b) functional diversity responses in shrub community to precipitation changes were different from grass community; and (c) the interspecific or intraspecific variation would play different roles in driving the responses of shrub or grass community to precipitation changes.

2 | MATERIALS AND METHODS

2.1 | Study area

We explored the effects of precipitation on plant functional traits in shrub- and grass-dominated communities through an observational study along a natural precipitation gradient and through a short-term manipulative experiment. The field observations occurred along an increasing precipitation gradient from desert to steppe in Inner Mongolia, northern China. The study area ranges from 37 to 354 mm mean annual precipitation, including three vegetation types—desert, desert steppe and typical steppe (Table S1). The mean annual temperature ranges from 0.5 to 3.8℃, and elevation ranges from 944 to 1,700 m (Bai et al., 2012; Mao et al., 2018). Soil types in desert, desert steppe and typical steppe are classified as grey-brown desert soil, brown calcic soil and chestnut soil respectively (Table S1). These soil types belong to the sandy loam texture, and the chestnut soil (sand 62.81%–82.99%, silt and clay 21.69%–38.16%) is the productive, while the grey-brown desert soil (sand 49.65%–88.38%, silt and clay 0.53%–13.15%) and brown calcic soil (sand 68.54%–93.22%, silt and clay 3.14%–39.88%) are relatively barren.

2.2 | Natural precipitation gradient

We selected 32 sites along a natural precipitation gradient across the desert-steppe area (Figure 1), according to the representative plant communities. There were 18 sampling sites in the desert area with precipitation ranging from 37 to 151 mm, which is located at the western part of Inner Mongolia, and dominated by typical shrubs, *Reaumuria soongorica*, *Nitraria tangutorum* and *Zygophllum xanthoxylon*. There were 14 sampling sites in the steppe area with precipitation ranging from 151 to 354 mm, which was located at the mid and eastern part of Inner Mongolia, and dominated by perennial grasses, *Stipa breviflora*, *Stipa glareosa*, *Stipa grandis* and *Leymus chinensis* (Table S1). Three 20 × 30 m plots were randomly chosen at each site. Then, within each plot, we randomly set up one 5 × 5 m subplot for shrub measure and trait sampling and one 1 × 1 m quadrat for the measurement of herbaceous plant composition and biomass. In total, 96 subplots were for leaf trait sampling, 54 subplots for shrub measure and 96 quadrats for herbaceous measure along the natural precipitation gradient.

2.3 | Precipitation manipulative experiment

We also carried out a 2-year experiment in the Urat Desert-Grassland Research Station (106°58′E, 41°25′N) to examine the effects of short-term manipulative precipitation on shrub- and grass-dominated communities (Figure 1). The Urat region located at the transitional zone between desert and steppe in Inner Mongolia has the mean annual precipitation of 151 mm (10 years average), and has the two representative plant communities (Mao et al., 2018),

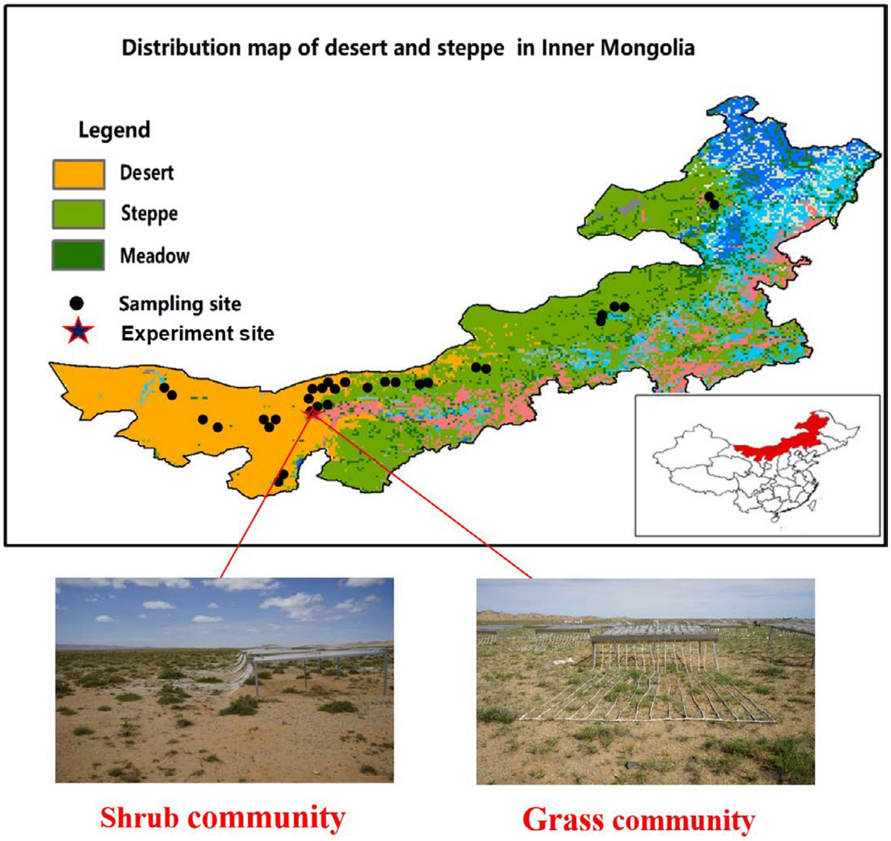

FIGURE 1 Location map of the experiment and felid sampling sites along a natural precipitation gradient across desert and steppe in Inner Mongolia, China. The equipment of rainout shelters with drip irrigation system in shrub and grass community

including shrub community dominated by *Reaumuria soongorica* and grass community dominated by *Stipa glareosa*.

We choose a shrub community and a grass community at a same site with a spacing of 600 m. Within the two plant communities, we separately established the precipitation manipulative experiment in August 2015 by using rainout shelters with drip irrigation systems (Figure 1). The detailed experimental design was described by Zuo et al. (2020). In each community, 18 rainfall shelters (4 × 4 m in size) with different numbers of V-shaped clear polycarbonate plastic strips were established to intercept approximately 20%, 40% and 60% of incoming annual rainfall (Figure 1), according to the distribution and frequency of long-term local precipitation amount and drought events (Huang et al., 2015; Zhang et al., 2019). At the same time, increased precipitation treatments of 20%, 40% and 60% were imposed on plots adjacent to rainout shelters by using the drip irrigation system with small hole pipes connected to the gutters of rainfall shelters (Figure 1). The control plots without rainfall shelters received the natural precipitation of each year. These treatments constituted the experimental precipitation gradient from 60 to 240 mm (Figure S1), which covers the precipitation ranges from desert to desert steppe in Inner Mongolia. In particular, the treatments which receive a 60% reduction or increase are regarded as the extreme drought or high precipitation. In each plant community, the experiment was set up in a randomized block design with six blocks with each of the seven precipitation treatments: control, −60%, −40%, −20%, +20%, +40% and +60%. There was a 4-m wide aisle among blocks and 0.6-m spacing between the area of reduced and increased rainfall. We established a main sampling subplot of 3.5 × 3.5 m for shrub measurements and trait sampling, and a random 1 × 1 m quadrat in each subplot for herbaceous composition and biomass. In total, there were 84 sampling subplots and quadrats established within two plant communities.

2.4 | Vegetation compositions and biomass

We carried out all field measurement and sampling work in August 2017. We recorded species richness within each plot and harvested above-ground biomass (AGB) for each species in each quadrat. We estimated AGB of shrubs in each subplot using the empirical relationships between shrub biomass and crown diameter (Castro & Freitas, 2009; Li et al., 2020). Total shrub biomass in each subplot was estimated by applying the established regression model that best described the relationship between plant height and crown diameter and dry weight for each shrub species. Changes in species richness and AGB among desert and steppe or among different precipitation treatments in the experiment are shown in Figures S2 and S3.

2.5 | Functional trait and diversity

We determined six key functional traits related to the morphological and reproductive characteristics and growth investment (Guittar et al., 2016; Valencia et al., 2015): plant height, SLA, LDMC, leaf thickness (LT), leaf carbon content (LCC) and LNC. These traits were measured for the most abundant species making up 90% of total plant biomass in the natural sites and experimental plots. Ten selected individuals of each shrub or herbaceous species were sampled in each subplot. All functional traits of each species were obtained by using the standard methodologies (Cornelissen et al., 2003). In total, we obtained the trait data of 486 species, in which there were separately 96 and 84 subplots in the natural sites and the experiment.

We quantified the measurement of functional diversity by the CWM, functional divergence (FDvar) of single-trait and multi-trait indices (FRic and FDis) in each subplot. CWM represents the community-level trait value, which is dominated by the trait values of the most abundant species in a community (Valencia et al., 2015). CWM for each of six traits was calculated by multiplying the trait value of each species by its relative biomass in the community. FDvar can reflect the variation in single-trait value weighted by the abundance of each species in plant community (Conti & Díaz, 2013). Functional richness, which measures the volume filled by the community in trait space when considering all traits together, is calculated as the difference between the minimum and maximum functional values in the community (Spasojevic et al., 2014). Functional dispersion, which is a multidimensional index to measure the multi-trait dispersion, reflects the average distance of each species to the centroid of all species in the community trait space weighted by the relative biomass (Griffin-Nolan et al., 2019; Xu et al., 2018). We used log-transformed values of six traits to calculate FRic and FDis in order to avoid scale effects (Casanoves et al., 2011).

2.6 | Statistical analyses

We used the simple linear regression to explore the associations of functional diversity components with precipitation changes along the natural gradient. The linear mixed models with block included as a random effect were used to examine the associations of functional diversity components with precipitation changes in experiment. The grass and shrub communities were analysed separately along the natural gradient or in experiment. For the natural gradient, precipitation amount was mean annual value from 2000 to 2017 from the weather station near to each field site. For the experimental gradient, precipitation amount was calculated as the per cent increases or decreases from the mean annual precipitation from 2015 to 2017 for the site. In addition, by comparing the slope of the linear relationship between functional diversity and precipitation, we can evaluate the sensitivity of plant functional diversity to precipitation changes (Byrne et al., 2017).

To assess how interspecific (species turnover) and intraspecific variation affected the community-level traits, FDvar of single-trait and multi-trait indices determined by precipitation changes, and their relative contributions were calculated by using the following decomposition methods of community-level trait variances (Kichenin et al., 2013; Lang et al., 2018). We performed one-way ANOVA with precipitation amount as a fixed effect for the specific, interspecific and intraspecific average values of functional trait and diversity in shrub and grass communities along the natural site and in the experiment. We separately extracted sum squares for three components ($SS_{interspecific}$, $SS_{specific}$ and $SS_{intraspecific}$) in shrub and grass communities along the natural and experimental gradients (Tables S2 and S3). Total variation in specific averages was regarded as 100%, then we used sum squares of three components to calculate the relative proportions of variability of interspecific and intraspecific variation effects (Kichenin et al., 2013). All statistical analyses were performed using SPSS 23.0 for windows (SPSS, Inc.) and LME4 and SJSTATS packages in R (R version 4.0.0). Functional diversity indices of CWM, FDvar, FRic and FDis were calculated by the FDiversity and R package (Casanoves et al., 2011).

3 | RESULTS

Along the observational gradient, increasing precipitation was positively related to the CWMs of plant height, LCC and LNC, while negatively related to SLA and LT of grass communities ($p < 0.05$, Figure 2). In the experiment, increasing precipitation had the positive associations with the CWM of plant height and LDMC, while had the negative associations with SLA and LNC and weakly negative associations with LT ($p = 0.08$) of grass communities. In contrast, when looking at shrub communities, only LCC was significantly related to precipitation changes along the natural and experimental gradients.

In grass communities, the FDvar of LDMC and LNC decreased with increasing precipitation along the natural gradient, whereas the FDvar of LCC increased with increasing precipitation in the experiment (Figure 3). In shrub communities, the FDvar of SLA, LT, LCC and LNC increased with increasing precipitation along the natural gradient, while the FDvar of plant height, LDMC, LT and LCC increased with increasing precipitation in the experiment.

FRic decreased with increasing precipitation along the natural gradient in grassland sites, and precipitation changes explained 55% of the variance (Figure 4). However, FRic of grassland community was not significantly related to precipitation changes in the experiment, and the similar for FRic of shrub community along the natural and experimental gradients. In contrast to FRic, FDis showed significant relationships in shrub community. FDis increased linearly with increasing precipitation along the natural gradient and in the experiment, explaining 16% and 24% of the variance respectively (Figure 4).

Community-weighted means of plant height, SLA and LT in grass community were more sensitive to altered precipitation along the natural gradient (0.086, −0.03 and −0.001 slope) than in experiment (0.055, −0.02 and −0.0005 slope, Table 1). Similarly, for shrub communities, the CWM of LCC, FDvar of LCC and LT and FDis in shrub community had the relative higher sensitivity to altered precipitation along the natural gradient (0.039, 0.0003, 0.003 and 0.002 slope) than in experiment (0.018, 0.0001, 0.0005 and 0.001 slope). Thus, the responses of these functional traits and diversity in grass and

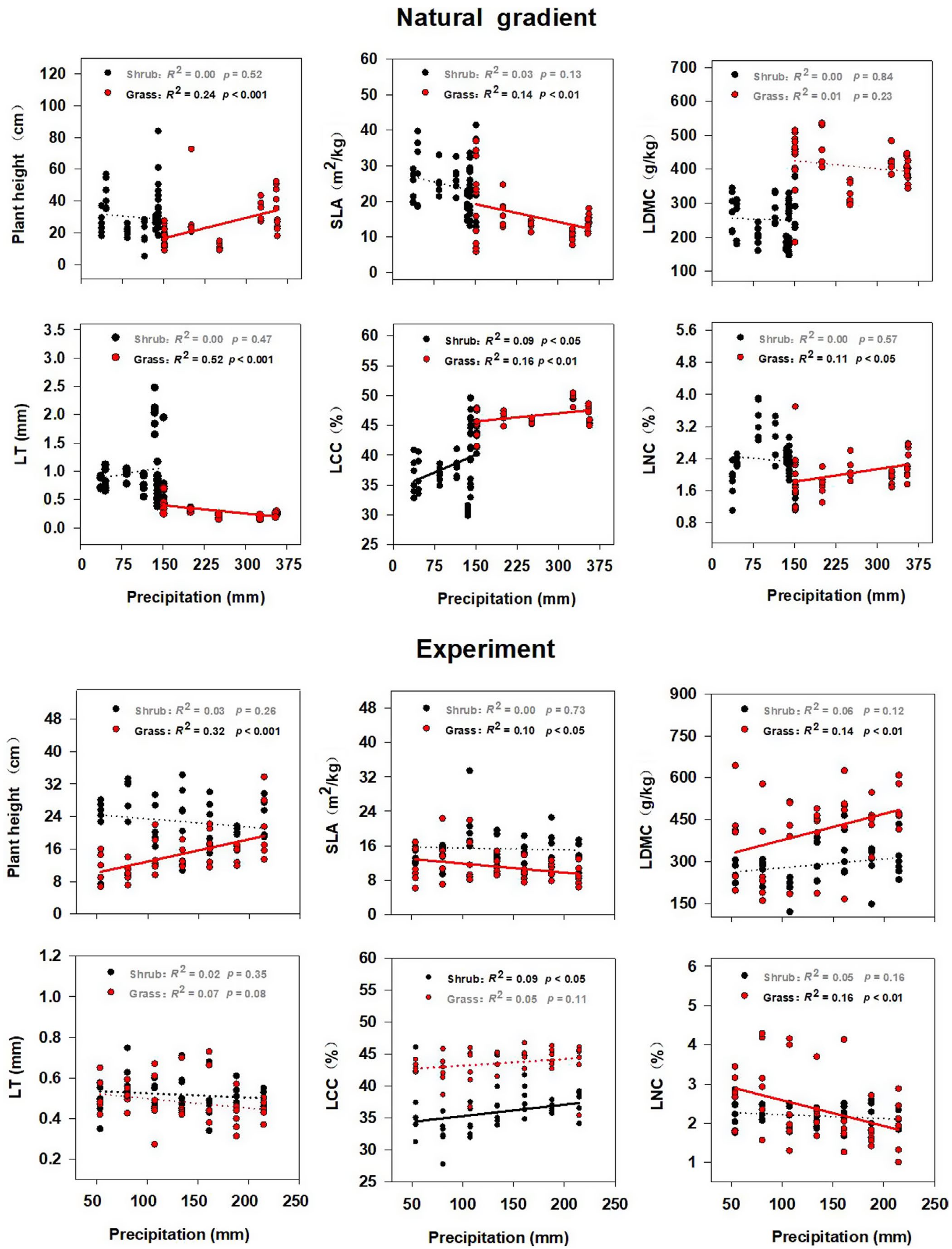

FIGURE 2 Relationship between community-weighted mean of single trait and precipitation changes along a natural gradient and in experiment. LCC, leaf carbon content, LDMC, leaf dry matter content; LNC, leaf nitrogen content. LT, leaf thickness. Shrub- and grass-dominated communities are indicated by black and red dots respectively. Non-significant regression is indicated by the dashed line

shrub communities to the natural precipitation gradient had the higher sensitivity than in experiment.

Along the natural gradient in grass communities, species turnover variation was significant for plant height, LDMC, LT and LCC, and the intraspecific variation was significant for plant height, LT, LCC and LNC ($p < 0.05$, Table S2; Figure 5). However, in the experiment, species turnover variation was marginally significant for plant height ($p < 0.10$) and significant for SLA ($p < 0.05$), and the intraspecific variation was significant for plant height and LNC in the experiment ($p < 0.05$). So, both species turnover and intraspecific variations contributed to trait mean differences in grass communities along the natural or experimental precipitation gradients.

In contrast, along the natural gradient in shrub communities, species turnover and intraspecific variations were marginally significant ($p < 0.10$) or significant for ($p < 0.05$) for all FDvar of single trait and FDis except for FDvar of LDMC and LT (Table S3; Figure 5). In the experiment, species turnover variation was significant for FDvar of plant height, LCC and LNC and FDis ($p < 0.05$) and marginally significant for FDvar of LT ($p < 0.10$), while the intraspecific variation was only significant for FDvar of LCC ($p < 0.05$, Table S4; Figure 5). So, both species turnover and intraspecific variations contributed to differences of FDvar of single trait and FDis in shrub communities along the natural precipitation gradient, while species turnover contributed more along the experimental precipitation gradient.

4 | DISCUSSION

4.1 | Experimental versus natural precipitation gradient

Contrary to the first hypothesis, we found the better concordance between the effects of naturally and experimentally increased precipitation on functional trait and diversity of plant communities in northern China. This contrasts with the effects of geographic and experimental precipitation gradients on plant community traits in the United States (Sandel et al., 2010). Potentially, this can be attributed to differences in species identities, abundances and phylogenetic histories in plant communities between northern China and the United States, and the larger precipitation ranges across the natural gradient in the United States (280–1,450 mm) than in China (37–354 mm). Here, we show that the shifts of CWM of plant height, SLA and LT in grassland communities with increasing precipitation are consistent between the experimental and natural gradients. This suggests that CWMs of plant height, SLA and LT are good predictor for short- or long-term responses of grass communities to precipitation changes, which is supported by the other studies in desert steppe (Ma et al., 2019). Similarly, the CWM of LCC, FDvar of LT and LCC and FDis are good predictors for short- or long-term responses of shrub communities to precipitation changes. These results further suggest that incorporating plant size and leaf morphology or functional dispersion into grass or shrub community-scale surveys should enhance our understanding of how plant community responds to precipitation changes.

The slope evaluation of the relationship between precipitation and functional diversity has shown that the responses of functional traits and diversity in grass and shrub communities to natural precipitation gradient have the higher sensitivity than in experiment. This can be explained by the differences in spatial scale between the natural and experimental gradients. The broad spatial scale along the natural precipitation gradient is likely to favour functional trait shifts due to the resource availability changes (Le Bagousse-Pinguet et al., 2017; Oyarzabal et al., 2008; Sandel et al., 2010), while the small spatial scale in experiment may decrease functional trait shifts due to the lower species turnover rates (Adler et al., 2013; Sandel et al., 2010). Although the response sensitivity is different between the natural and experimental gradients, some key functional traits and diversity of grass or shrub are likely to be advantageous when precipitation resources will be abundant whatever at the large or small spatial scale. This functional diversity–precipitation relationship has the important implication for the prediction of long-term vegetation dynamics in response to climate changes. Firstly, when we predict climate change effects on shrub or grass communities, we can use data from the natural and experimental gradients due to their better concordance. The responses of shrub or grass communities to experimental precipitation changes is predictive of long-term changes at spatial scale. Secondly, climate change effects on vegetation differ depending on plant community types, and the magnitude of climate change determines plant community shifts by the competitive interactions for assembly patterns of functional trait and diversity. So, to consider multiple communities-climate relationship studies are important for understanding the generalities of plant community response to climate changes.

4.2 | Grass- versus Shrub-dominated communities

Interestingly, we found that along both the natural and experimental precipitation gradients, CWM of most single trait in grass communities showed significant shifts, while FDvar of most single-trait and multi-trait dispersion in shrub communities consistently increased. These results indicate that the responses of CWM, FDvar of single-trait and multi-trait functional diversity to precipitation changes are different between shrub and grass communities, thus suggesting that shrub and grass communities display the different adaptive strategies to altered precipitation by modulating the expression of trait mean fitness or trait variation and dispersion. These differences in shrub and grass species responses to precipitation changes should correlate with differences in their traits or trait's variation in a similar way. This further provides an evidence that plant community responses to climate changes may vary across and within biomes due to the idiosyncratic nature of community or species adaption to climate changes (Byrne et al., 2017). Especially two plant communities located within the same location but dominated by shrub or grass have quite different responses to the similar precipitation changes.

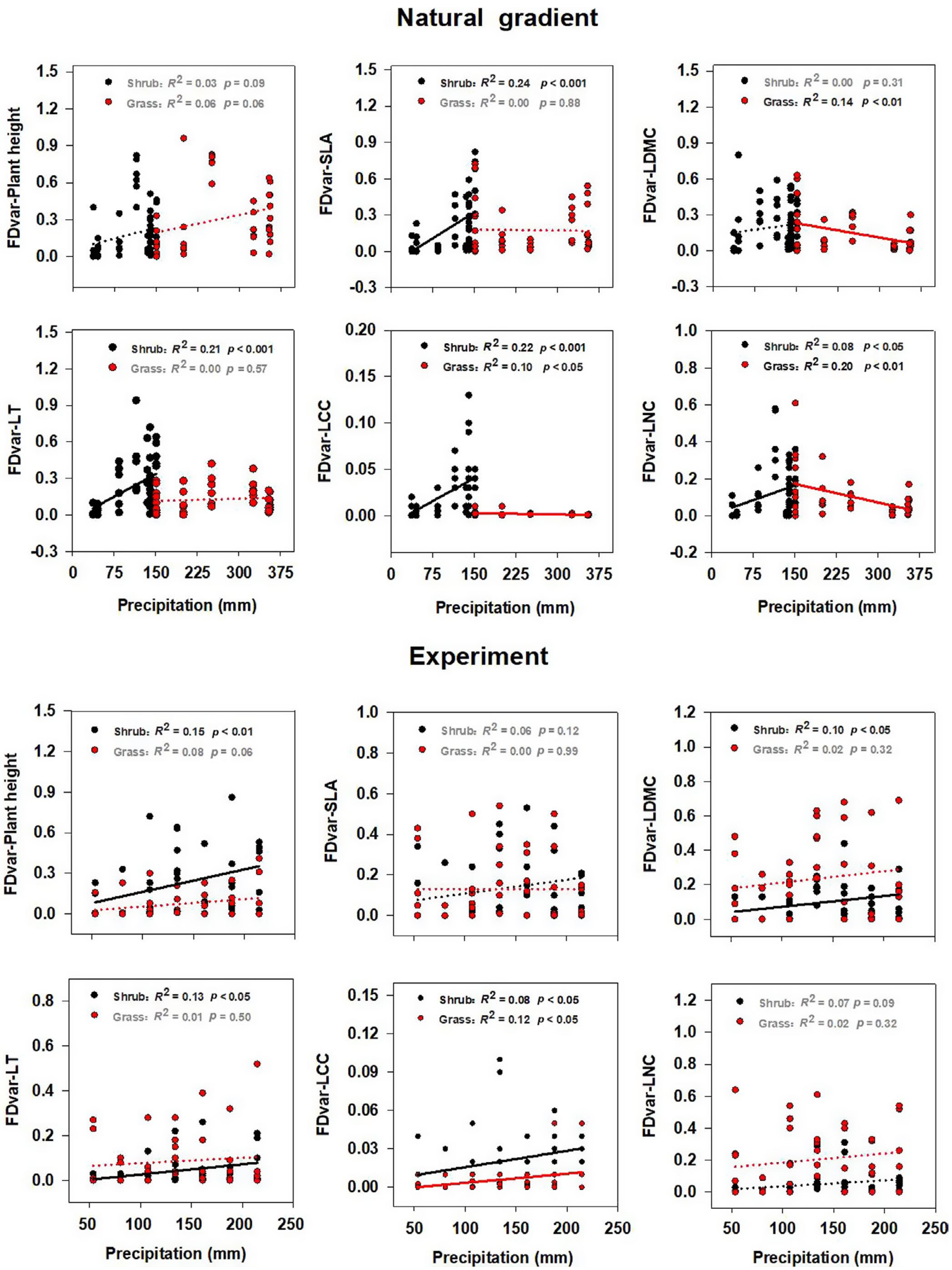

FIGURE 3 Relationship between the functional divergence of single trait and precipitation changes along a natural gradient and in experiment. LCC, leaf carbon content, LDMC, leaf dry matter content; LNC, leaf nitrogen content. LT, leaf thickness. Shrub- and grass-dominated communities are indicated by black and red dots respectively. Non-significant regression is indicated by the dashed line

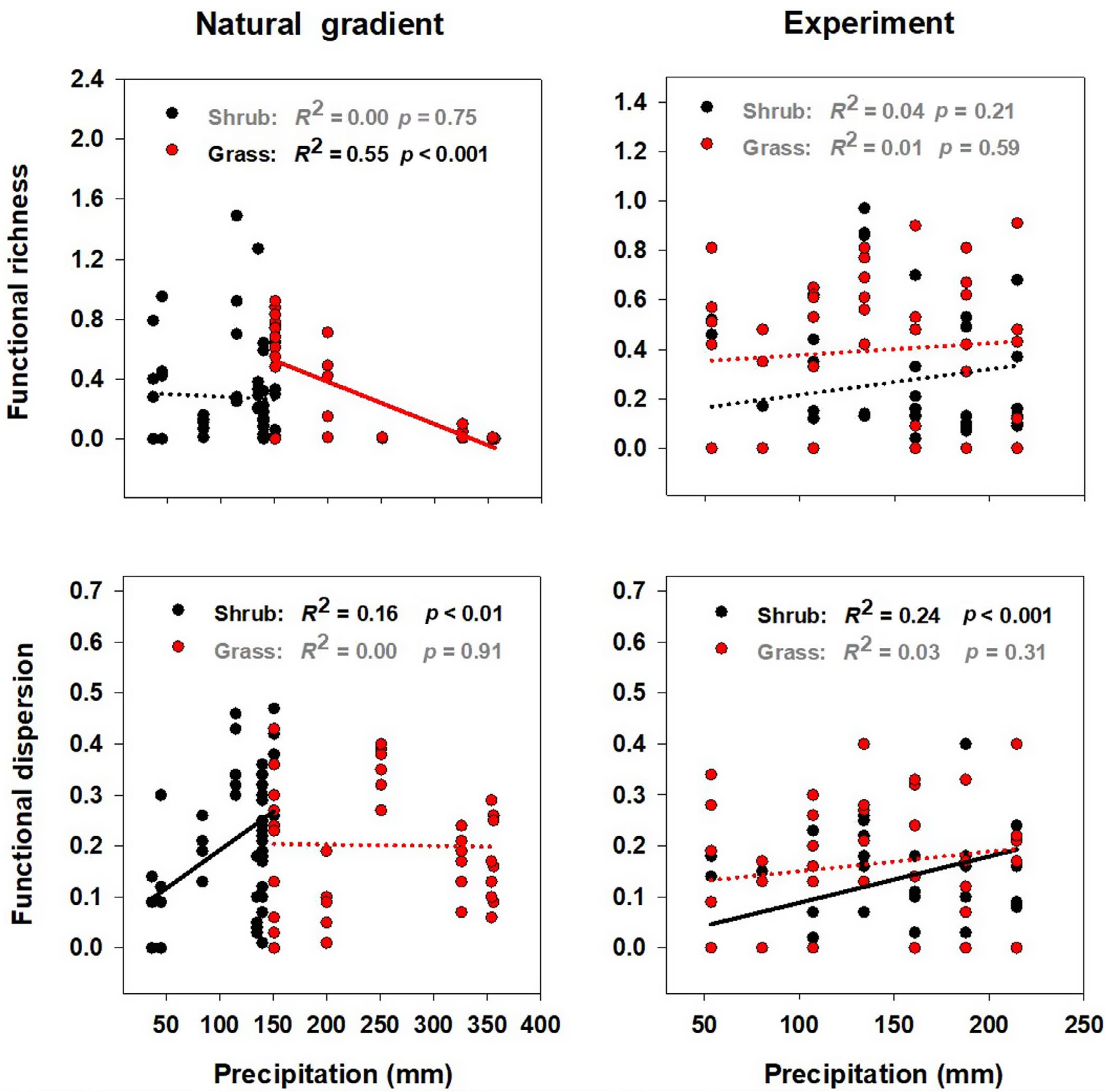

FIGURE 4 Relationship between plant functional richness and dispersion and precipitation changes along a natural gradient and in experiment. Shrub- and grass-dominated communities are indicated by black and red dots respectively. Non-significant regression is indicated by the dashed line

Grass communities can adapt to altered precipitation by their trait differences, while shrub communities are through the niche differentiation form multi-trait dispersion.

Five key traits in grass communities tended to alter along the natural precipitation gradient, which is consistent with plant trait patterns in grasslands observed at the spatial scale (Le Bagousse-Pinguet et al., 2017; Oyarzabal et al., 2008; Sandel et al., 2010). The positive associations of plant height, LCC and LNC with increased precipitation along the natural gradient suggest species composition shifts from the slow-growing stress-tolerant plants to fast-growing plants with high nutrient acquisition rates. The negative associations of SLA and LT with increased precipitation can reflect species with high height and nutrient acquisition rates to reduce transpiration due to the competition effects of abundant species for soil water availability (Lang et al., 2018; Zheng et al., 2011). Similarly, from high precipitation to extreme drought, the shift in grass community tended towards species with low plant height, as well as high SLA and LT, indicating that these species with different average traits have the competitive advantage to low precipitation (Lang et al., 2018; Sandel et al., 2010). These results further support that herbaceous plants with different morphological and reproductive traits have the strong adaptability to a wide range of

TABLE 1 Slope of linear regression of functional trait, divergence and diversity with precipitation changes along a natural gradient and in experiment

	Natural gradient				Experiment			
	Shrub		*Grass*		*Shrub*		*Grass*	
	Slope	*p*	Slope	*p*	Slope	*p*	Slope	*p*
Plant height	−0.029	0.52	0.086	<0.001	−0.02	0.27	0.055	<0.001
SLA	−0.035	0.13	−0.033	0.009	−0.004	0.73	−0.021	0.041
Leaf dry matter content	−0.050	0.84	−0.157	0.23	0.316	0.13	0.942	0.011
Leaf thickness	0.002	0.47	−0.001	<0.001	−0.0002	0.36	−0.0005	0.092
Leaf carbon content	0.039	0.018	0.009	0.006	0.018	0.049	0.010	0.121
Leaf nitrogen content	−0.001	0.57	0.002	0.020	−0.001	0.165	−0.007	0.009
FDvar-plant height	0.001	0.094	0.001	0.065	0.002	0.011	0.0005	0.071
FDvar-SLA	0.003	<0.001	−0.0001	0.88	0.0007	0.12	0.0000	0.993
FDvar-leaf dry matter content	0.001	0.31	−0.001	0.008	0.0006	0.037	0.007	0.322
FDvar-leaf thickness	0.003	<0.001	0.0001	0.57	0.0005	0.016	0.0002	0.51
FDvar-leaf carbon content	0.0003	<0.001	−0.0001	0.02	0.0001	0.05	0.0001	0.024
FDvar-leaf nitrogen content	0.001	0.023	−0.001	0.002	0.0004	0.099	0.0006	0.325
Functional richness	−0.0003	0.75	−0.003	<0.001	0.001	0.21	0.0005	0.59
Functional dispersion	0.002	0.002	−0.0001	0.91	0.001	0.001	0.0004	0.31

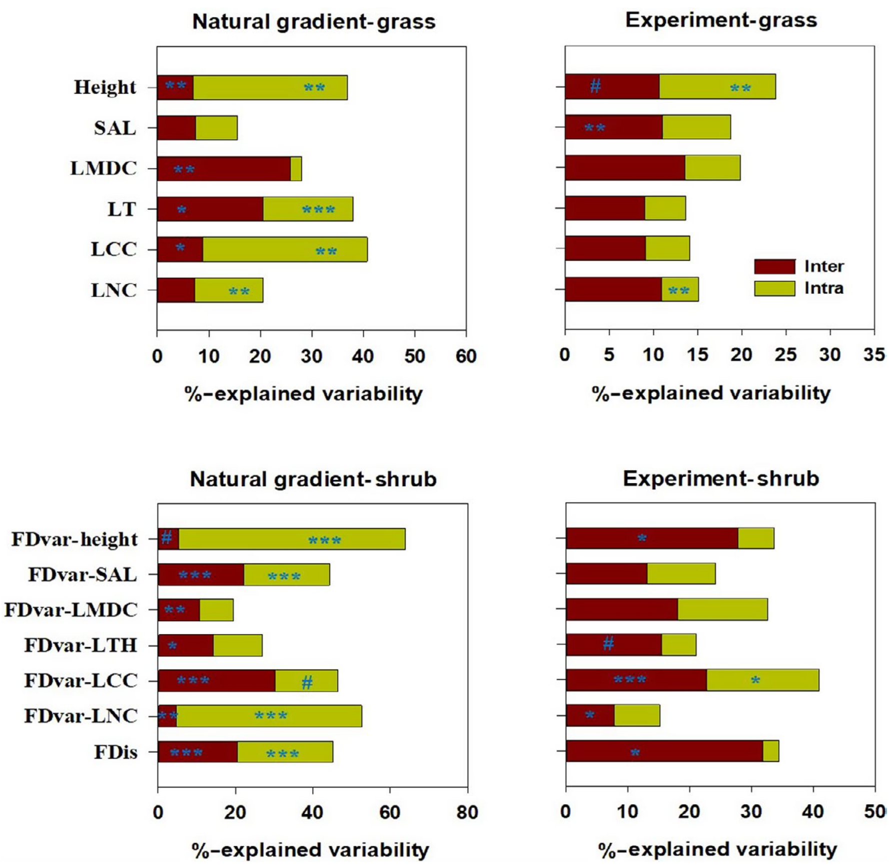

FIGURE 5 Contributions of inter- and intraspecific variability effects to grass community traits along the natural precipitation gradient and to functional divergence (FDvar) of single trait and functional dispersion (FDis) in shrub community in the experiment. LDMC, leaf dry matter content; LT, leaf thickness; LCC, leaf carbon content; LNC, leaf nitrogen content. The statistical significance ($^{\#}p < 0.10$, $^{*}p < 0.05$, $^{**}p < 0.01$ and $^{***}p < 0.001$, inside histograms) are presented on the graph for the inter- and intraspecific effects

precipitation changes by reducing niche overlap due to stronger trade-offs in resource requirements (Adler et al., 2013; Oyarzabal et al., 2008; Perez-Ramos et al., 2019). Altered precipitation pattern can promote herbaceous plant coexistence when different traits or trait specialization are favoured in different precipitation conditions.

In contrast, for shrub communities, precipitation changes along the natural and experimental gradients did not relate to most single trait at community level, but positively related to the LCC, FDvar of most single trait and FDis. This can support other studies that community trait variations can be altered by long-term drought (Luo et al., 2019) and FDis of multi-trait related to plant growth can be increased by increasing precipitation (Schellenberger Costa et al., 2017). These results further suggest that desert shrubs might have a wide trait variation ranges to adapt to precipitation changes through single-and multi-trait variation, so that their means of plant size and leaf traits at community level express a relative high resistance to precipitation changes in space and time. High shrubs with deeper roots in desert can survive and grow in arid and barren environment by maximizing the resources uptake as long as the water and nutrient are available (Morales et al., 2015), which may be caused by the high niche differentiation due to the high multi-trait dispersion. Also, shrubs with higher LT are generally linked to higher proportion of sclerified tissues and compactness of cells (Castro-Diez et al., 2000), thus having a strong endurance in arid and barren environment. The slow-growing desert shrubs can respond to precipitation variations through changes in carbon allocation or accumulation rather than changes in community-level traits (Reinhardt et al., 2018).

4.3 | Effects of species turnover versus intraspecific variation

We found that different contributions of species turnover and intraspecific variation effects led to the contrasting responses of community-level trait means to precipitation changes between shrub and grass. Changes in grass community traits could be explained by the effects of species turnover and intraspecific variations induced by altered precipitation along the natural and experimental gradients. Similarly, species turnover and intraspecific variations contribute to responses of FDvar of traits and functional dispersion in shrub community to precipitation changes along the natural gradient. These results agree with other empirical studies that species turnover and within-species trait variations can play an important role in mediating the responses of community traits to precipitation changes (Jung et al., 2014; Luo et al., 2018). The previous studies in this area have shown that soil water availability determined by precipitation changes can induce both of species turnover and intraspecific trait variations (Luo et al., 2018; Zheng et al., 2015), thus contributing the responses of community-level traits, trait divergence or dispersion to precipitation changes.

In contrast, species turnover variation had a greater contribution to responses of FDvar of traits and functional dispersion in shrub community to precipitation changes than intraspecific variation in experiment, supporting other studies that species turnover variation can play the key role in the responses of community traits to environmental gradients (Kichenin et al., 2013; Zuo et al., 2017). This may be because that shrub–grass competitions for precipitation changes are as the driver of grassland-to-shrubland transitions, thus leading to species turnover variation (Pierce et al., 2019). More importantly, extreme drought in experiment, which can exceed the tolerance thresholds for even relatively stress-tolerant species, can also cause the important trait variations with species turnover (Luo et al., 2018; de la Riva et al., 2016).

5 | CONCLUSIONS

This is one of the first study showing that shrub and grass communities display marked differences in their responses and adaptions to precipitation changes. Precipitation changes along the natural and experimental gradients can alter the means of most single trait in grass community, as well as the variations of most single-trait and multi-trait dispersion in shrub community. These results suggest the similar effects of altered precipitation along both the natural and experimental gradients on functional trait and diversity of plant community. Grass communities are tending to respond and adapt to precipitation changes through the trait shifts resulted from the effects of intraspecific variations or its combination with species turnover. However, precipitation reduction or prolonged drought may drive the decline in single-trait divergence and the loss of multi-trait functional diversity of shrub community, thus possibly enhancing the dominance of shrub plants due to its high resistance. Our study clearly demonstrates that short-term responses of some measures in functional diversity of plant community to experimental precipitation changes can predict long-term patterns to precipitation changes at spatial scale. These findings provide an empirical evidence that some single- and multi-trait indices in plant functional diversity can be used to predict plant community responses to future climate changes. Our study also highlights that the approach of incorporating the observation and experimental studies can provide the deep insight to understand or predict the response or adaption of plant community to future climate changes.

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AUTHORS' CONTRIBUTIONS

X.Z. designed the research, collected and analysed the data and wrote the paper; S.Z., H.C., Y.H., S.W. and P.Y. assisted with data collection and did some laboratory analysis; R.L., A.K.K., M.D.S. and S.E.K. assisted with paper revision; Q.Y. assisted with research design and paper revision. The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available from Dryad Digital Repository https://doi.org/10.5061/dryad.r7sqv9sc2 (Zuo et al., 2021).

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REFERENCES

Adler, P. B., Fajardo, A., Kleinhesselink, A. R., & Kraft, N. J. B. (2013). Trait-based tests of coexistence mechanisms. *Ecology Letters*, *16*, 1294–1306. https://doi.org/10.1111/ele.12157

Bahn, M., Reichstein, M., Dukes, J. S., Smith, M. D., & McDowell, N. G. (2014). Climate–biosphere interactions in a more extreme world. *New Phytologist*, *202*, 356–359. https://doi.org/10.1111/nph.12662

Bai, Y. F., Wu, J. G., Clark, C. M., Pan, Q. M., Zhang, L. X., Chen, S. P., Wang, Q. B., & Han, X. G. (2012). Grazing alters ecosystem functioning and C:N:P stoichiometry of grasslands along a regional precipitation gradient. *Journal of Applied Ecology*, *49*, 1204–1215. https://doi.org/10.1111/j.1365-2664.2012.02205.x

Byrne, K. M., Adler, P. B., & Lauenroth, W. K. (2017). Contrasting effects of precipitation manipulations in two Great Plains plant communities. *Journal of Vegetation Science*, *28*, 238–249. https://doi.org/10.1111/jvs.12486

Carvajal, D. E., Loayza, A. P., Rios, R. S., Gianoli, E., & Squeo, F. A. (2017). Population variation in drought-resistance strategies in a desert shrub along an aridity gradient: Interplay between phenotypic plasticity and ecotypic differentiation. *Perspectives in Plant Ecology Evolution and Systematics*, *29*, 12–19. https://doi.org/10.1016/j.ppees.2017.10.001

Casanoves, F., Pla, L., Di Rienzo, J. A., & Díaz, S. (2011). FDiversity: A software package for the integrated analysis of functional diversity. *Methods in Ecology and Evolution*, *2*, 233–237. https://doi.org/10.1111/j.2041-210X.2010.00082.x

Castro, H., & Freitas, H. (2009). Above-ground biomass and productivity in the Montado: From herbaceous to shrub dominated communities. *Journal of Arid Environments*, *73*, 506–511. https://doi.org/10.1016/j.jaridenv.2008.12.009

Castro-Diez, P., Puyravaud, J. P., & Cornelissen, J. H. C. (2000). Leaf structure and anatomy as related to leaf mass per area variation in seedlings of a wide range of woody plant species and types. *Oecologia*, *124*, 476–486. https://doi.org/10.1007/PL00008873

Cleland, E. E., Collins, S. L., Dickson, T. L., Farrer, E. C., Gross, K. L., Gherardi, L. A., Hallett, L. M., Hobbs, R. J., Hsu, J. S., Turnbull, L., & Suding, K. N. (2013). Sensitivity of grassland plant community composition to spatial vs. temporal variation in precipitation. *Ecology*, *94*, 1687–1696. https://doi.org/10.1890/12-1006.1

Conti, G., & Díaz, S. (2013). Plant functional diversity and carbon storage – An empirical test in semi-arid forest ecosystems. *Journal of Ecology*, *101*, 18–28. https://doi.org/10.1111/1365-2745.12012

Cornelissen, J. H. C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D. E., Reich, P. B., Steege, H. T., Morgan, H. D., Heijden, M. G. A. V. D., Pausas, J. G., & Poorter, H. (2003). A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, *51*, 335–380. https://doi.org/10.1071/BT02124

de la Riva, E. G., Perez-Ramos, I. M., Tosto, A., Navarro-Fernandez, C. M., Olmo, M., Maranon, T., & Villar, R. (2016). Disentangling the relative importance of species occurrence, abundance and intraspecific variability in community assembly: A trait-based approach at the whole-plant level in Mediterranean forests. *Oikos*, *125*, 354–363. https://doi.org/10.1111/oik.01875

Deleglise, C., Meisser, M., Mosimann, E., Spiegelberger, T., Signarbieux, C., Jeangros, B., & Buttler, A. (2015). Drought-induced shifts in plants traits, yields and nutritive value under realistic grazing and mowing managements in a mountain grassland. *Agriculture Ecosystems & Environment*, *213*, 94–104. https://doi.org/10.1016/j.agee.2015.07.020

Du, P. Z., Arndt, S. K., & Farrell, C. (2018). Relationships between plant drought response, traits, and climate of origin for green roof plant selection. *Ecological Applications*, *28*, 1752–1761. https://doi.org/10.1002/eap.1782

Eugenio, C. U. O., Munhoz, C. B. R., & Felfili, J. M. (2011). Temporal dynamics of the shrub and herbaceous layer of an area of moist grassland in Alto Paraiso de Goias, Brazil. *Acta Botanica Brasilica*, *25*, 497–507.

Forrestel, E. J., Donoghue, M. J., Edwards, E. J., Jetz, W., du Toit, J. C. O., & Smith, M. D. (2017). Different clades and traits yield similar grassland functional responses. *Proceedings of the National Academy of Sciences of the United States of America*, *114*, 705–710. https://doi.org/10.1073/pnas.1612909114

Frenette-Dussault, C., Shipley, B., Meziane, D., & Hingrat, Y. (2013). Trait-based climate change predictions of plant community structure in arid steppes. *Journal of Ecology*, *101*, 484–492. https://doi.org/10.1111/1365-2745.12040

Gao, Q., & Reynolds, J. F. (2003). Historical shrub–grass transitions in the northern Chihuahuan Desert: Modeling the effects of shifting rainfall seasonality and event size over a landscape gradient. *Global Change Biology*, *9*, 1475–1493. https://doi.org/10.1046/j.1365-2486.2003.00676.x

Griffin-Nolan, R. J., Blumenthal, D. M., Collins, S. L., Farkas, T. E., Hoffman, A. M., Mueller, K. E., Ocheltree, T. W., Smith, M. D., Whitney, K. D., & Knapp, A. K. (2019). Shifts in plant functional composition following long-term drought in grasslands. *Journal of Ecology*, *107*, 2133–2148. https://doi.org/10.1111/1365-2745.13252

Griffin-Nolan, R. J., Bushey, J. A., Carroll, C. J. W., Challis, A., Chieppa, J., Garbowski, M., Hoffman, A. M., Post, A. K., Slette, I. J., Spitzer, D., Zambonini, D., Ocheltree, T. W., Tissue, D. T., & Knapp, A. K. (2018). Trait selection and community weighting are key to understanding ecosystem responses to changing precipitation regimes. *Functional Ecology*, *32*, 1746–1756. https://doi.org/10.1111/1365-2435.13135

Guittar, J., Goldberg, D., Klanderud, K., Telford, R. J., & Vandvik, V. (2016). Can trait patterns along gradients predict plant community responses to climate change? *Ecology*, *97*, 2791–2801. https://doi.org/10.1002/ecy.1500

Huang, J., Xue, Y., Sun, S. L., & Zhang, J. C. (2015). Spatial and temporal variability of drought during 1960–2012 in Inner Mongolia, north China. *Quaternary International*, *355*, 134–144. https://doi.org/10.1016/j.quaint.2014.10.036

Huxman, T. E., Smith, M. D., Fay, P. A., Knapp, A. K., Shaw, M. R., Loik, M. E., Smith, S. D., Tissue, D. T., Zak, J. C., Weltzin, J. F., Pockman, W. T., Sala, O. E., Haddad, B. M., Harte, J., Koch, G. W., Schwinning, S., Small, E. E., & Williams, D. G. (2004). Convergence across biomes to a common rain-use efficiency. *Nature*, *429*, 651–654. https://doi.org/10.1038/nature02561

Jung, V., Albert, C. H., Violle, C., Kunstler, G., Loucougaray, G., & Spiegelberger, T. (2014). Intraspecific trait variability mediates the response of subalpine grassland communities to extreme drought events. *Journal of Ecology*, *102*, 45–53. https://doi.org/10.1111/1365-2745.12177

Kichenin, E., Wardle, D. A., Peltzer, D. A., Morse, C. W., & Freschet, G. T. (2013). Contrasting effects of plant inter- and intraspecific variation on community-level trait measures along an environmental gradient. *Functional Ecology*, *27*, 1254–1261. https://doi.org/10.1111/1365-2435.12116

Kimball, S., Funk, J. L., Spasojevic, M. J., Suding, K. N., Parker, S., & Goulden, M. L. (2016). Can functional traits predict plant community response to global change? *Ecosphere*, *7*, e01602. https://doi.org/10.1002/ecs2.1602

Knapp, A. K., Hoover, D. L., Wilcox, K. R., Avolio, M. L., Koerner, S. E., La Pierre, K. J., Loik, M. E., Luo, Y. Q., Sala, O. E., & Smith, M. D. (2015). Characterizing differences in precipitation regimes of extreme wet and dry years: Implications for climate change experiments. *Global Change Biology*, *21*, 2624–2633. https://doi.org/10.1111/gcb.12888

Lang, B., Geiger, A., Oyunbileg, M., Ahlborn, J., von Wehrden, H., Wesche, K., Oyuntsetseg, B., & Römermann, C. (2018). Intraspecific trait variation patterns along a precipitation gradient in Mongolian rangelands. *Flora*, *254*, 135–146. https://doi.org/10.1016/j.flora.2018.11.008

Le Bagousse-Pinguet, Y., Gross, N., Maestre, F. T., Maire, V., de Bello, F., Fonseca, C. R., Kattge, J., Valencia, E., Leps, J., & Liancourt, P. (2017). Testing the environmental filtering concept in global drylands. *Journal of Ecology*, *105*, 1058–1069. https://doi.org/10.1111/1365-2745.12735

Li, X. Y., Yue, P., Cheng, H., Guo, X. X., Zhao, S. L., Zhang, S. X., Wang, S. K., & Zuo, X. A. (2020). Biomass prediction model for *Reaumuria soongorica* in the Urat desert steppe in Inner Mongolia. *Arid Zone Research*, *37*, 462–469.

Luo, W. T., Zuo, X. A., Griffin-Nolan, R. J., Xu, C., Ma, W., Song, L., Helsen, K., Lin, Y. C., Cai, J. P., Yu, Q., Wang, Z. W., Smith, M. D., Han, X. G., & Knapp, A. K. (2019). Long term experimental drought alters community plant trait variation, not trait means, across three semiarid grasslands. *Plant and Soil*, *442*, 343–353. https://doi.org/10.1007/s11104-019-04176-w

Luo, W. T., Zuo, X. A., Ma, W., Xu, C., Li, A., Yu, Q., Knapp, A. K., Tognetti, R., Dijkstra, F. A., Li, M. H., Han, G. D., Wang, Z. W., & Han, X. G. (2018). Differential responses of canopy nutrients to experimental drought along a natural aridity gradient. *Ecology*, *99*, 2230–2239. https://doi.org/10.1002/ecy.2444

Ma, Q. H., Liu, X. D., Li, Y. B., Li, L., Yu, H. Y., Qi, M., Zhou, G. S., & Xu, Z. Z. (2019). Nitrogen deposition magnifies the sensitivity of desert steppe plant communities to large changes in precipitation. *Journal of Ecology*, *108*, 598–610. https://doi.org/10.1111/1365-2745.13264

Mao, W., Zhao, X. Y., Sun, Z. B., Felton, A. J., Zhang, T. H., Li, Y. L., & Smith, M. D. (2018). Limiting similarity mediates plant community niche hypervolume across a desert-steppe ecotone of Inner Mongolia. *Environmental and Experimental Botany*, *153*, 320–326. https://doi.org/10.1016/j.envexpbot.2018.06.011

Morales, J., Squeo, F. A., Tracol, Y., Armas, C., & Gutierrez, J. R. (2015). Resource economics and coordination among above- and below-ground functional traits of three dominant shrubs from the Chilean coastal desert. *Journal of Plant Ecology*, *8*, 70–78. https://doi.org/10.1093/jpe/rtu010

Moreno, L., Bertiller, M. B., & Carrera, A. L. (2010). Changes in traits of shrub canopies across an aridity gradient in northern Patagonia, Argentina. *Basic and Applied Ecology*, *11*, 693–701. https://doi.org/10.1016/j.baae.2010.09.002

Nguyen, Q. N., Polle, A., & Pena, R. (2017). Intraspecific variations in drought response and fitness traits of beech (*Fagus sylvatica* L.) seedlings from three provenances differing in annual precipitation. *Trees-Structure and Function*, *31*, 1215–1225. https://doi.org/10.1007/s00468-017-1539-1

Oyarzabal, M., Paruelo, J. M., Federico, P., Oesterheld, M., & Lauenroth, W. K. (2008). Trait differences between grass species along a climatic gradient in South and North America. *Journal of Vegetation Science*, *19*, 183–192. https://doi.org/10.3170/2007-8-18349

Perez-Ramos, I. M., Matias, L., Gomez-Aparicio, L., & Godoy, O. (2019). Functional traits and phenotypic plasticity modulate species coexistence across contrasting climatic conditions. *Nature Communications*, *10*, 2555. https://doi.org/10.1038/s41467-019-10453-0

Pierce, N. A., Archer, S. R., Bestelmeyer, B. T., & James, D. K. (2019). Grass-shrub competition in arid lands: An overlooked driver in grassland–shrubland state transition? *Ecosystems*, *22*, 619–628. https://doi.org/10.1007/s10021-018-0290-9

Reinhardt, K., McAbee, K., & Germino, M. J. (2018). Changes in structure and physiological functioning due to experimentally enhanced precipitation seasonality in a widespread shrub species. *Plant Ecology*, *220*(2), 199–211.

Sandel, B., Goldstein, L. J., Kraft, N. J., Okie, J. G., Shuldman, M. I., Ackerly, D. D., Cleland, E. E., & Suding, K. N. (2010). Contrasting trait responses in plant communities to experimental and geographic variation in precipitation. *New Phytologist*, *188*, 565–575. https://doi.org/10.1111/j.1469-8137.2010.03382.x

Schellenberger Costa, D., Gerschlauer, F., Pabst, H., Kühnel, A., Huwe, B., Kiese, R., Kuzyakov, Y., & Kleyer, M. (2017). Community-weighted means and functional dispersion of plant functional traits along environmental gradients on Mount Kilimanjaro. *Journal of Vegetation Science*, *28*, 684–695. https://doi.org/10.1111/jvs.12542

Schooley, R. L., Bestelmeyer, B. T., & Campanella, A. (2018). Shrub encroachment, productivity pulses, and core-transient dynamics of Chihuahuan Desert rodents. *Ecosphere*, *9*, e02330. https://doi.org/10.1002/ecs2.2330

Spasojevic, M. J., Grace, J. B., Harrison, S., & Damschen, E. I. (2014). Functional diversity supports the physiological tolerance hypothesis for plant species richness along climatic gradients. *Journal of Ecology*, *102*, 447–455. https://doi.org/10.1111/1365-2745.12204

Valencia, E., Maestre, F. T., Le Bagousse-Pinguet, Y., Quero, J. L., Tamme, R., Börger, L., García-Gómez, M., & Gross, N. (2015). Functional diversity enhances the resistance of ecosystem multifunctionality to aridity in Mediterranean drylands. *New Phytologist*, *206*, 660–671.

Wellstein, C., Poschlod, P., Gohlke, A., Chelli, S., Campetella, G., Rosbakh, S., Canullo, R., Kreyling, J., Jentsch, A., & 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*. https://doi.org/10.1111/gcb.13662

Xin, Z. M., Liu, M. H., Lu, Q., Busso, C. A., Zhu, Y. J., Li, Z., Huang, Y. R., Li, X. L., Luo, F. M., Bao, F., Qian, J. Q., & Li, Y. H. (2018). Responses of leaf delta C-13 and leaf traits to precipitation and temperature in arid ecosystem of northwestern China. *Phyton-International Journal of Experimental Botany*, *87*, 144–155.

Xu, Z. W., Li, M. H., Zimmermann, N. E., Li, S. P., Li, H., Ren, H. Y., Sun, H., Han, X. G., Jiang, Y., & Jiang, L. (2018). Plant functional diversity modulates global environmental change effects on grassland productivity. *Journal of Ecology*, *106*, 1941–1951. https://doi.org/10.1111/1365-2745.12951

Zhang, R., Zhao, X. Y., Zuo, X. A., Qu, H., Degen, A. A., Luo, Y. Y., Ma, X. J., Chen, M., Liu, L. X., & Chen, J. L. (2019). Impacts of precipitation on ecosystem carbon fluxes in desert-grasslands in inner Mongolia, China. *Journal of Geophysical Research-Atmospheres*, *124*, 1266–1276. https://doi.org/10.1029/2018JD028419

Zheng, S. X., Lan, Z. C., Li, W. H., Shao, R. X., Shan, Y. M., Wan, H. W., Taube, F., & Bai, Y. F. (2011). Differential responses of plant functional trait to grazing between two contrasting dominant C3 and C4 species in a typical steppe of Inner Mongolia, China. *Plant and Soil*, *340*, 141–155. https://doi.org/10.1007/s11104-010-0369-3

Zheng, S. X., Li, W. H., Lan, Z. C., Ren, H. Y., & Wang, K. B. (2015). Functional trait responses to grazing are mediated by soil moisture and plant functional group identity. *Scientific Reports*, *5*, 18163. https://doi.org/10.1038/srep18163

Zuo, X., Cheng, H., Zhao, S., Yue, P., Liu, X., Wang, S., Liu, L., Xu, C., Luo, W., Knops, J. M. H., & Medina-Roldán, E. (2020). Observational and experimental evidence for the effect of altered precipitation on desert and steppe communities. *Global Ecology and Conservation*, *21*, e00864. https://doi.org/10.1016/j.gecco.2019.e00864

Zuo, X. A., Yue, X. Y., Lv, P., Yu, Q., Chen, M., Zhang, J., Luo, Y. Q., Wang, S. K., & Zhang, J. (2017). Contrasting effects of plant inter- and intraspecific variation on community trait responses to restoration of a sandy grassland ecosystem. *Ecology and Evolution*, *7*, 1125–1134.

Zuo, X., Zhao, S., Cheng, H., Hu, Y., Wang, S., Yue, P., Liu, R., Knapp, A. K., Smith, M. D., Yu, Q., & Koerner, S. E. (2021). Data from: Functional diversity response to geographic and experimental precipitation gradients varies with plant community type. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.r7sqv9sc2

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