



# Long term experimental drought alters community plant trait variation, not trait means, across three semiarid grasslands

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## Abstract

**Background and aims** Grasslands are expected to experience droughts of unprecedented magnitude and duration in this century. Plant traits can be useful for understanding community and ecosystem responses to climate extremes. Few studies, however, have investigated the response of community-scale traits to extreme drought on broad spatial/temporal scales, with even less research on the relative contribution of species turnover vs. intraspecific trait variation to such responses.

**Methods** We experimentally removed ~66% of growing season rainfall for three years across three semi-arid

grasslands of northern China and tracked changes in community functional composition, defined as the community mean and variation of several leaf economic traits.

**Results** Community trait variations were more sensitive to drought than community trait means, which suggests this component of functional composition may be a better indicator of initial community drought responses than trait values themselves. The greatest change in trait variation was observed at the high aridity site and was driven largely by intraspecific trait variability. Apart from specific leaf area, trait variability increased with

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increasing aridity across sites, largely due to species turnover. Variations in soil moisture and fertility likely mediated the responses of community trait variations to water stress.

**Conclusions** These results highlight the importance of measuring community trait variability in response to drought and support the well-documented pattern of increased community drought sensitivity of more arid ecosystems.

**Keywords** Climate change · Plant functional traits · Grasslands · Intraspecific trait variability · Species turnover

## Introduction

Plant traits are useful proxies of plant strategies for coping with biotic and abiotic stress (Bruehlheide et al. 2018; He et al. 2018; Wright et al. 2004). When the appropriate traits are measured at the community level, they have the potential to greatly improve predictions of ecosystem responses to environmental change (Bruehlheide et al. 2018; Griffin-Nolan et al. 2018a; Suding et al. 2008). Quantification of community functional composition (i.e., community plant trait means and variation) is therefore expected to provide valuable insights into community assembly processes in response to climate change (Bruehlheide et al. 2018; Cornwell and Ackerly 2009; Grime 2006). The magnitude and frequency of extreme climatic events, such as summer drought, are projected to increase in arid and semiarid ecosystems with climate change (Dai 2011; Handmer and Kundzewicz 2012); however, few studies assess the response of functional composition to climate extremes at broad spatial and temporal scales.

Extreme drought can act as an environmental filter, whereby only certain trait combinations confer survival/fitness leading to trait convergence and a reduction in the trait diversity at the community level (Cornwell and Ackerly 2009). Shifts in functional composition may be due to species turnover (i.e., species migration) and/or intraspecific variation (i.e., phenotypic plasticity or shifts in genotypic composition) (Albert et al. 2010). Quantifying the relative contribution of each of these processes is critical to a mechanistic understanding of how drought alters community functional composition (Ackerly and Cornwell 2007; Lepš et al. 2011; Violle et al. 2012).

Precipitation manipulation experiments and observations along aridity gradients are two approaches to determine the short- and long-term impacts of water-limitation on community functional composition, respectively (Elmendorf et al. 2015; Knapp et al. 2018; Luo et al. 2011; Yuan et al. 2017). Experimental approaches allow ecologists to study shifts in functional composition following short-term precipitation change (Dunne et al. 2004; Sandel et al. 2010), while natural aridity gradients allow for studies on community assembly processes in response to long-term water limitation (Elmendorf et al. 2015; Hewitt et al. 2007). Previous drought experiments have been performed at a single site, with the implicit assumption that the responses can represent the entire ecosystem type (Cherwin and Knapp 2012); However, community responses to climate extremes can vary greatly among different sites, even within the same ecosystem (i.e., grasslands) (Griffin-Nolan et al. 2018b; Grime et al. 2000; Luo et al. 2018). Thus, coordinated distributed experiments across multiple sites with contrasting climatic conditions are needed to accurately predict the responses of plant communities to drought (Cherwin and Knapp 2012).

We experimentally reduced growing season precipitation (66% reduction) within three grassland sites along an aridity gradient in northern China and tracked changes in functional composition (i.e., community trait means and variation). We focus on four leaf economic traits, namely specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen content (LNC) and leaf phosphorus content (LPC), all of which reflect plant performance and fast vs. slow strategies for coping with limiting resources (Reich 2014; Wright et al. 2004). We test the following hypotheses: (1) community-level trait mean and variation will decrease in response to experimental drought and with increasing aridity due to environmental filtering; (2) the response of community functional composition to experimental drought will differ from the spatial trends observed along the natural aridity gradient with the response driven primarily by species turnover at a spatial scale (aridity gradient) and intra-specific trait variation at a temporal scale (experimental drought); and (3) community functional composition will be more sensitive to experimental drought with increasing aridity (Huxman et al. 2004).

## Materials and methods

### Experimental sites

In 2014, we selected three sites that represent much of the east-west extent of the arid and semi-arid grasslands of northern China (Fig. S1a). All experimental plots for each site were established across areas with homogeneous soils and uniform vegetation to exclude the potential influence of small-scale heterogeneity. The three sites, as part of the ‘Extreme Drought in Grassland Experiment’ (EDGE) (<http://edge.biology.colostate.edu/EDGEchina.html>) vary in plant species composition as well as climatic and edaphic properties (Table 1). The low aridity site, located at the Inner Mongolia Grassland Ecosystem Research Station (116°33'E, 43°32'N), receives about 346 mm of mean annual precipitation (MAP) and has a mean annual temperature (MAT) of 1.9 °C. The medium aridity site, located in Sheila MuRen (111°53'E, 41°47'N), is drier and hotter than the low aridity site (MAP = 251 mm; MAT = 4.5 °C). The high aridity site, located at the Urat Desert-

Grassland Research Station (106°58'E, 41°25'N), receives an average of 175 mm of precipitation annually and is the hottest of the three sites (MAT = 5.6 °C) (see Table 1 for more detailed information about each site).

### Experimental treatments

In the summer of 2015, drought was imposed at each site using large rainout shelters (Fig. S1b), which reduced each precipitation event by 66% for the entire growing season (May to August) – this is roughly equivalent to a 50% reduction in annual precipitation. The experimental design was a randomized complete block design with six replications, and treatments were applied during three consecutive years (2015–2017). The 12 (6 m × 6 m) plots (control and drought) were randomly assigned with at least 2 m between plots. Each plot was hydrologically isolated from the surrounding soil matrix by aluminum flashing installed to a depth of 1 m around the perimeter. In the center of each plot, one 16 m<sup>2</sup> (4 m × 4 m) subplot was established with a 1 m buffer with the edge of the sampling plots and adjacent

**Table 1** Climate, soil, and vegetative characteristics of the three study sites in arid and semiarid grasslands of northern China

	Low aridity site	Medium aridity site	High aridity site
General			
Latitude	43°32'N	41°47'N	41°25'N
Longitude	116°33'E	111°53'E	106°58'E
Grassland type	Typical steppe	Transition zone	Desert steppe
Climate			
MAP (mm)	346	251	175
GSP (mm)	249	183	133
MAT (°C)	1.9	4.5	5.6
Aridity index	0.40	0.25	0.17
Soil			
SOC (g kg <sup>-1</sup> )	21.35	16.45	8.68
STN (g kg <sup>-1</sup> )	2.94	2.83	0.38
Vegetation			
ANPP (g m <sup>-2</sup> )	133	55	23
Dominant species	<i>S. grandis</i> and <i>L. chinensis</i>	<i>S. breviflora</i> and <i>L. chinensis</i>	<i>S. glareosa</i> and <i>Peganum harmala</i>
Species richness	4.5	8.5	5.4

All soil and vegetation characteristics (e.g., biomass and species richness) were calculated using the data from 2015 to 2017 in control plots of the experiment. Climatic variables are calculated from a 32-year record (1982–2014) for the low aridity site, and a 44-year record (1971–2014) for the medium and high aridity sites. MAP, mean annual precipitation; GSP, growing season precipitation; MAT, mean annual temperature; SOC, soil organic carbon; STN, soil total nitrogen; ANPP, aboveground net primary production. Species richness was calculated as the number of species. Aridity index was calculated as the ratios of MAP to potential evapotranspiration (PET), with values closer to 0–denoting greater aridity

treatment subplots. Rainfall was passively removed from drought plots to maintain the frequency and timing of natural rainfall events (Knapp et al. 2016) using roofs composed of strips of clear polycarbonate plastic (Beijing Plastics Research Institute, Beijing, China). Untreated control subplots were also trenched yet lacked rainout shelters and received ambient precipitation. The drought shelters were 0.5 m and 2 m above the ground at the lowest and highest point, respectively, which allowed for air circulation and prevented microclimatic changes. The shelters had minimal shading effects (<10% reduction in photosynthetically active radiation) and are known to have little influence on ecosystem functions in grasslands. Species richness, diversity and evenness were similar between control and treatment plots at each site prior to imposing experimental drought (Luo et al. 2018). Soil moisture was measured at 0–10 cm (>70% of root biomass allocated to this soil layer, Matthew et al. 2001) every hour from May through August in 2016 and 2017 (PG-110, Jingchuang Electronic Technology Co., Handan, China) with measurements averaged to produce daily mean values at each site. Identical protocols were used across all three sites to avoid confounding results from methodological differences (Smith et al. 2017). Further details on the experimental design can be found in Luo et al. (2018).

Growing season precipitation (GSP) varied at each site over the three-year study period but was within the expected climatic range (approx. 50th percentile of historic amounts) (Fig. S2). Also note that, at the high aridity site, GSP was below the normal season precipitation values in 2015 and 2017 (Fig. S2). In each year, the drought treatment reduced rainfall close to the 10th percentile of an estimated probability function calculated from 32-year record of GSP for the low aridity site and 44-year records for the medium and high aridity sites (Fig. S2). Soil moisture was greatly reduced by the imposed drought but effects on soil and air temperature, and relative humidity were minimal (Luo et al. 2018). The drought treatment reduced mean soil moisture by 33%, 38%, and 30% at the low, medium, and high aridity site, respectively, during 2016–2017 growing seasons (Fig. S3).

### Community sampling

Plant community composition was surveyed from a 2 m × 2 m permanent plot at the beginning and middle of the growing season (June and August, respectively)

during each year of the 4-year study (1 year of pre-treatment, 3 years of treatment). The 2 m × 2 m permanent species composition plot was divided into four 1 m × 1 m sub-plots, and aerial coverage (to the nearest 1%) of each sub-plot was recorded. Aboveground net primary production (ANPP) was measured during peak biomass (early August) in each treatment year by clipping all aboveground plant parts of all species in two 0.25-m<sup>2</sup> quadrats located adjacent to the permanent plot. Simultaneously, leaves were collected from all species in another two separate 0.25 m<sup>2</sup> quadrats during each treatment year for plant trait measurements. Three recently emerged and fully expanded leaves were collected from three sun-exposed individuals of each species per plot and traits were measured following standard protocols (Pérez-Harguindeguy et al. 2013). Biomass and trait values were averaged across the quadrats for each plot. The harvested species cumulatively represented 90% (or more) of total plant coverage in each plot. Rare species were not sampled unless enough leaf material was available for each trait measurement. Further details on the sampled species can be found in supporting information.

We focus on four leaf economic traits expected to be involved in drought filtering and niche differentiation in our study. Plant SLA and LDMC are useful traits related to plant economics, including plant responses to water stress (Reich 2014; Wright et al. 2004). Plant LNC and LPC are not often related to plant responses to water; however, they are linked with plant economics and highly predictive of ecosystem functions such as aboveground net primary productivity (ANPP) (Wright et al. 2004; Luo et al. 2015, 2018). Leaf area was measured using Image J (<https://imagej.nih.gov/ij/>) after fully rehydration. Leaf dry weight was measured after drying all the leaves at 65 °C for 48 h to calculate both SLA (m<sup>2</sup> kg<sup>-1</sup>) and LDMC (mg g<sup>-1</sup>) following standardized protocols (Garnier et al. 2001). Then, these leaves were ground for measurements of leaf chemistry. We measured LNC (mg g<sup>-1</sup>) using an elemental analyzer (2400II CHN elemental analyzer, Perkin-Elmer, USA) and LPC (mg g<sup>-1</sup>) using inductively coupled plasma atomic emission spectrometry (OPTIMA 3000 DV, Perkin Elmer, USA) after H<sub>2</sub>SO<sub>4</sub>-H<sub>2</sub>O<sub>2</sub> digestion.

After removing the litter layer, one composite soil core (0–10 cm depth) was obtained from five randomly selected locations in each of the two quadrats of each plot, using a soil gauge (2.5 cm diameter). Subsamples of each soil sample were used to quantify gravimetric

soil water content. Subsamples were air-dried, ground and filtered through a 1 mm sieve (NM200, Retsch, Haan, Germany). Soil organic carbon and total nitrogen content were measured using an elemental analyzer (2400II CHN elemental analyzer, Perkin-Elmer, USA). Soil carbon: nitrogen (C:N) ratios were estimated and used to explore the indirect effects of drought on community functional composition through changes in soil fertility.

### Data analysis

For each sampled plot, community-level trait variability, defined as the degree of dissimilarity in traits among all species in a community, was quantified for each of the four traits separately. Community trait variation, the coefficient of variation of trait values, was calculated as the ratio of community trait standard deviation ( $\sigma$ ) to

the community trait mean ( $t$ ); with  $t = \frac{\sum_{i=1}^S ti}{S}$  and  $\sigma = \sqrt{\frac{\sum_{i=1}^S (ti-t)^2}{S}}$ , where  $ti$  is the trait values of species  $i$ , and  $S$  is the total number of species in the community plot. All species are weighted equally in trait variation calculation, thus changes in the measure of community-level trait variability are driven by species presence or absence, reflecting responses of species turnover to environmental changes (Jung et al. 2010; Mason et al. 2012). Trait variability is minimized when all resident species have similar trait values and is maximized when trait values are dispersed and clustered along the trait axis.

Repeated-measures linear mixed models were applied to examine the effects of experimental treatment (control vs. drought) on community trait mean and variation, with treatment as fixed factors and block as a random factor for each site separately in each year. The community trait mean and variation at the three sites were compared using one-way ANOVAs, with Duncan's Test as the post-hoc test for multiple comparisons in each year.

Changes in community-level trait variability in response to drought is attributable to either species turnover (i.e., species presence/absence) and/or intraspecific variation in trait values. The relative contribution of species turnover ( $C_{\text{turn}}$ ) vs. intraspecific trait variation ( $C_{\text{intra}}$ ) to the drought response of community-level trait variability was calculated as:  $C_{\text{turn}} = H_{\text{dr}*} - H_{\text{co}}$ , and  $C_{\text{intra}} = H_{\text{dr}} - H_{\text{dr}*}$ , where  $H_{\text{dr}}$  and  $H_{\text{co}}$  are the observed

community trait variation in drought and control plots, respectively, and  $H_{\text{dr}*}$  is community trait variation recalculated in drought plots using species trait values from control plots within each block (Jung et al. 2014). We used these same methods to calculate  $C_{\text{turn}}$  and  $C_{\text{intra}}$  of trait variability trends along the natural aridity gradient (Kichenin et al. 2013). We recalculated  $H_{\text{dr}*}$  from the species in the control plots at each site, but now using the mean species trait values in the control plots across all three sites under the hypothesis of a lack of intraspecific variation (Kichenin et al. 2013).

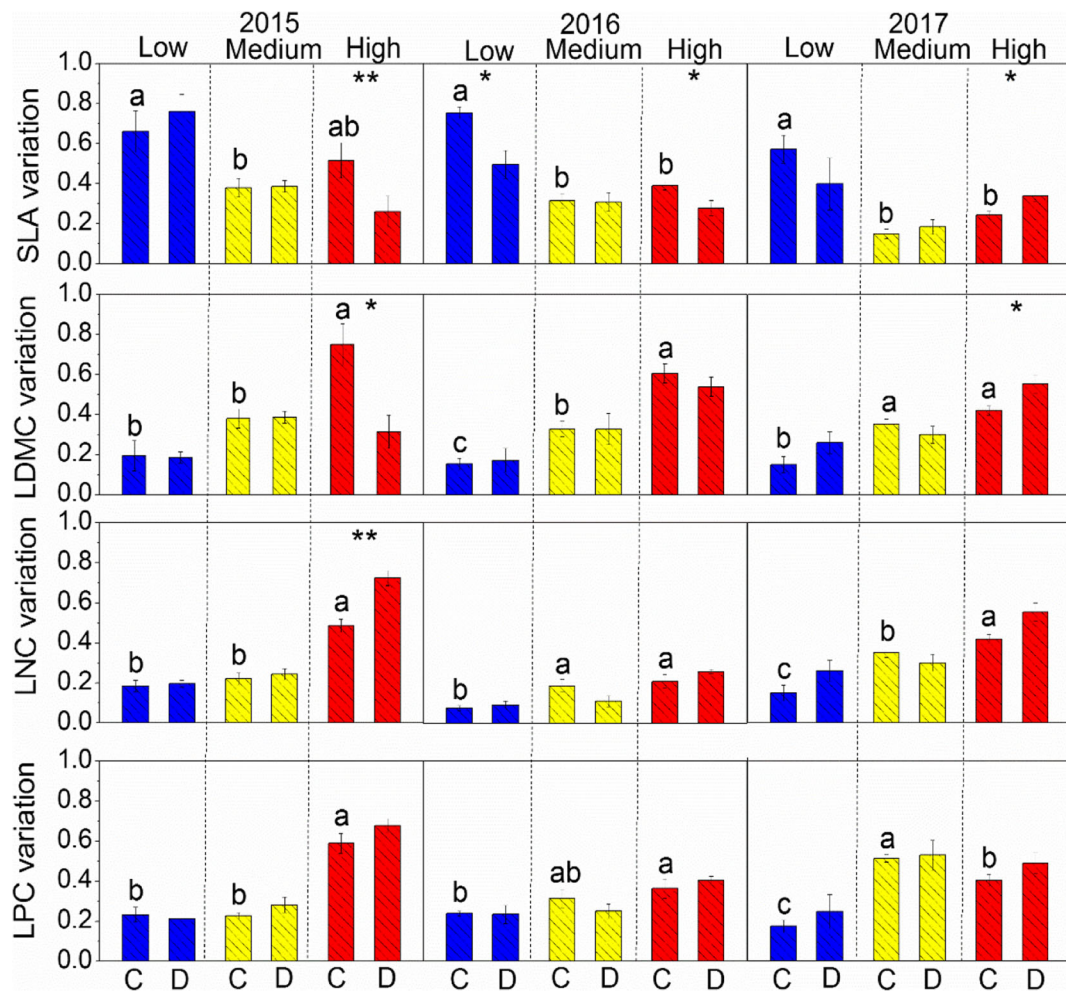
Linear mixed effects models were used to assess the relationship between community trait variation and both soil fertility (i.e., soil C:N ratio) and moisture content. Across sites, mixed effects models included soil fertility or moisture as fixed effects with block, site, and year as random effects. Within sites (i.e., experimental drought), random effects included only block and year.

Data were tested for normality using the Kolmogorov-Smirnov test and for equality of error variance using Levene's test. As all the data met model assumptions, we used untransformed data for statistical analyses. All statistical analyses were performed using the *lme* function in the *nlme* package of R software (v3.2.3, R Core Team, 2015).

### Results

Experimental drought significantly altered community trait variation, particularly at the high aridity site (Fig. 1). Surprisingly, the loss/addition of species due to following three years of drought (Table S1 and Fig. 2) did not impact community mean trait values (Fig. S4). Community trait variation varied considerably along the natural aridity gradient with trait-specific trends ( $p < 0.05$ ; Fig. 1). While community mean SLA remained constant (Fig. S4), SLA variation decreased generally with increasing aridity ( $p < 0.05$ ; Fig. 1), indicating that species are more likely to converge upon a mean value of SLA in arid sites. Community mean LDMC decreased with increasing aridity ( $p < 0.05$ ; Fig. S4), yet trait variation increased ( $p < 0.05$ ; Fig. 1), possibly due to unequal reductions among species (Fig. 2). Community means and variations for both LNC and LPC increased with increasing aridity ( $p < 0.05$ ; Figs. 1 and S4), due to unequal increases among species along the aridity gradient (Fig. 2).



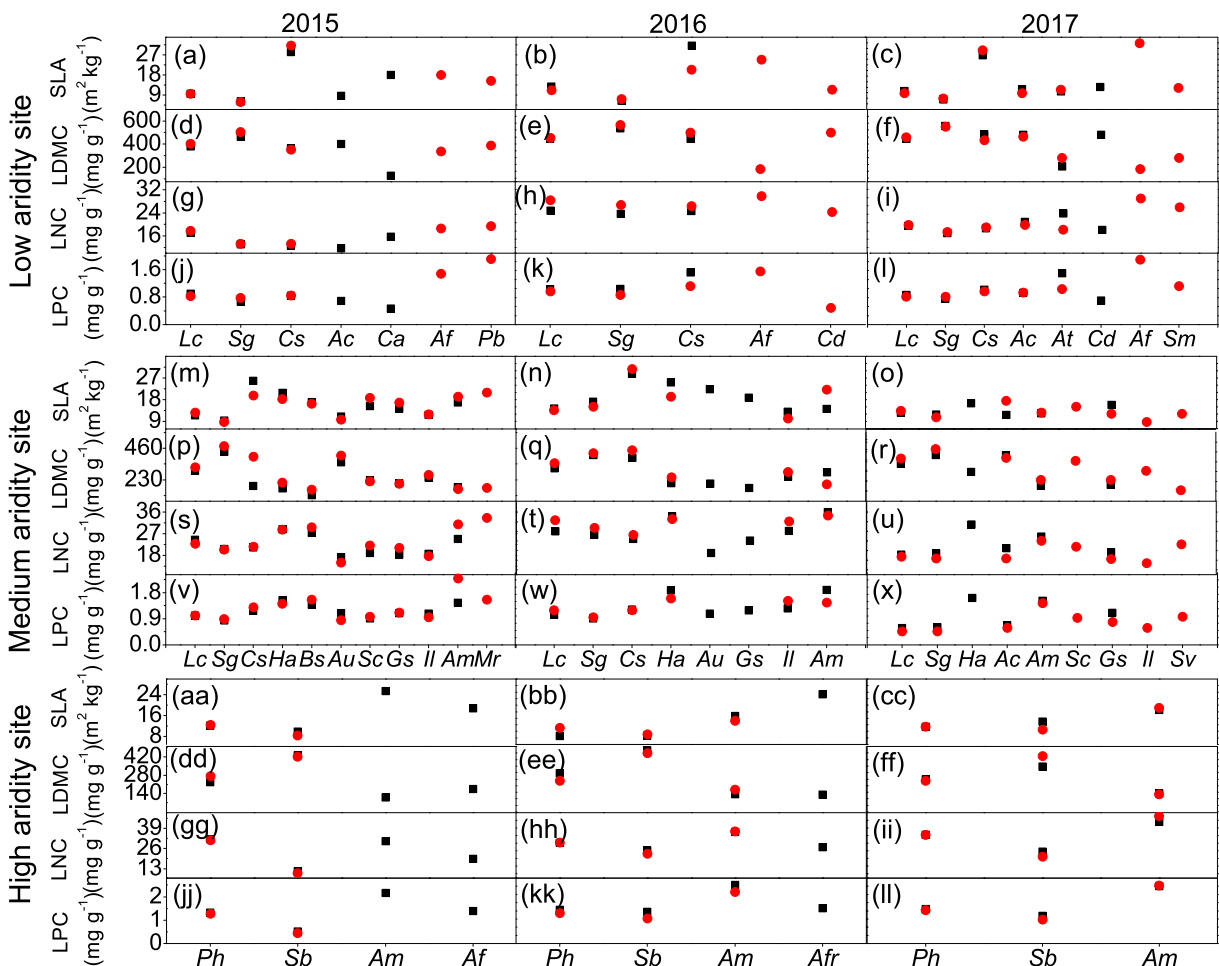


**Fig. 1** Effects of drought (C, control; D, drought) and site (low, medium and high aridity site) on plant community trait variation during the treatment years (2015–2017). SLA, specific leaf area; LDMC, leaf dry matter content; LNC, leaf nitrogen content; LPC, leaf phosphorus content. Each bar represents the mean trait

variation with error bars indicating standard errors calculated from replicate plots for each treatment. Different letters indicate significant differences among controls in different sites in each year at  $p < 0.05$ . Statistical significance of drought effect in each year is depicted as \*\*  $p < 0.01$  and \*  $p < 0.05$

Both species turnover (i.e., species presence-absence) and intraspecific trait variation played a key role in driving community trait variation at each site (Table 2). For community trait variation, species turnover had a more important role than intraspecific trait variation at the low and medium aridity site, while intraspecific trait variability played a more important role at the high aridity site (Table 2). Moreover, in many cases, intraspecific trait variation explained about 100% of the variability in community trait variation in response to experimental drought at the high aridity site (Table 2). Along the natural aridity gradient, intraspecific trait variation only explained about 10% of the variability in community trait variation across sites (Table 2).

Soil moisture and fertility were significantly correlated with the variation of certain traits, depending on site. At the low aridity site, variation in SLA was positively correlated with soil water content ( $p = 0.007$ ), while community variation in LNC was negatively correlated with soil C:N ratio ( $p = 0.023$ ; Fig. 3). At the medium aridity site, variations of community SLA and LDMC were significantly and positively correlated with soil water content ( $p = 0.002$  and  $0.021$ , respectively), while variation of community LPC was negatively correlated to soil water content ( $p = 0.001$ ; Fig. 3). Variations of community SLA and LPC were negatively ( $p = 0.06$ ) and positively ( $p = 0.02$ ) correlated with soil C:N ratio at the medium aridity site, respectively (Fig. 3). At the high



**Fig. 2** Species trait means in control (black circle) and drought (red square) plots during the treatment years (2015–2017) across three grassland sites along an aridity gradient in northern China.

SLA, specific leaf area; LDMC, leaf dry matter content; LNC, leaf nitrogen content; LPC, leaf phosphorus content. Abbreviations for species can be found in Table S1

aridity site, community variation in LNC and LPC were both negatively correlated with soil moisture content (both  $p < 0.001$ ; Fig. 3) and with soil C: N ratio ( $p < 0.01$ ; Fig. 3). Again, at the high aridity site, community variation in LDMC was positively correlated with soil C:N ratio ( $p = 0.025$  and  $0.012$ , respectively).

The spatial patterns in trait variation observed along the aridity gradient were also partially explained by soil moisture and fertility. Community SLA variation was positively correlated with soil water content ( $p = 0.002$ ), while community variation in LDMC and LPC were both negatively correlated with soil water content ( $p = 0.019$  and  $0.029$ , respectively; Fig. 3). Community variations in LDMC, LNC and LPC were all positively correlated with soil C:N ratio along the aridity gradient ( $p < 0.05$ ; Fig. 3).

## Discussion

Ecosystem responses to climate extremes are in part driven by the functional composition of plant communities. Thus, understanding the drought sensitivity of community-scale plant traits may improve predictions of ecosystem responses to climate change. Here, three years of experimental drought had no effect on community trait means and had variable effects on trait variability, especially at the most arid site (Figs. 1 and S4). This difference implies that community functional responses to drought are not only reflected in the average trait values, but also in the variation and distribution of traits (Benedetti-Cecchi 2003), with variability perhaps responding more rapidly to climate extremes than

**Table 2** The relative contributions of species turnover and intraspecific trait variation on changes in plant community trait variation under drought conditions within and among three grassland sites along an aridity gradient over three years in northern China

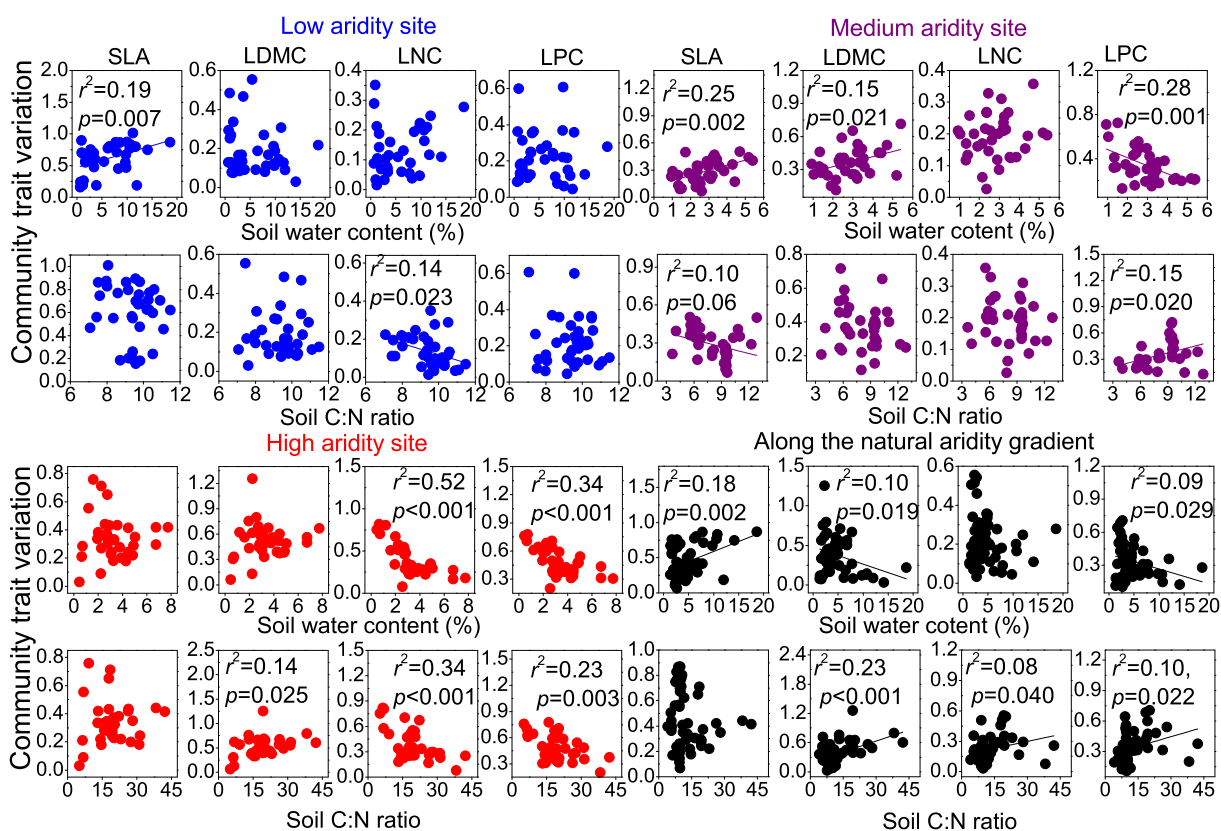
	Experiment manipulation									Gradient experiment		
	Low aridity site			Medium aridity site			High aridity site			2015	2016	2017
	2015	2016	2017	2015	2016	2017	2015	2016	2017			
SLA	53	68	17	69	44	96	21	97	100	8	10	15
LDMC	46	18	5	47	49	23	59	55	100	20	10	7
LNC	58	20	46	70	9	38	20	87	100	6	18	14
LPC	57	67	37	52	20	53	61	85	100	7	7	8

SLA specific leaf area; LDMC leaf dry matter content; LNC leaf nitrogen content; LPC leaf phosphorus content

The contribution of intraspecific trait variation is given as a percent (%) for community trait variation, while the remaining percent (not shown) represents the contribution of species turnover

community means. Further assessments of community-level trait variability may thus increase the detection of environmental filtering and improve model predictions of vegetation dynamics in

response to climate change. Variable effects of drought on trait variability can be attributed to differences in the relative contribution of intraspecific trait variability and species turnover.



**Fig. 3** Relationships between plant community trait variation and soil water content and fertility (soil C:N ratio) under drought conditions within and among three grassland sites along an aridity gradient during the treatment years (2015–2017). SLA, specific

leaf area; LDMC, leaf dry matter content; LNC, leaf nitrogen content; LPC, leaf phosphorus content.  $P$ -values and  $R^2$  are shown for statistically significant regressions



The highest absolute differences in community trait variation between control and drought plots were found at the driest site, suggesting that species trait distributions are more sensitive to drought in drier vs. moister environments. This result is consistent with our hypothesis, and in line with many previous studies which suggest that ecosystem properties, such as plant productivity (Huxman et al. 2004), CO<sub>2</sub> flux (Hoover et al. 2014) and plant species richness (Cleland et al. 2013), are more sensitive to drought in arid ecosystems. One potential explanation for this differential sensitivity could be the greater contribution of intraspecific trait variation to the functional response of the high aridity site compared to the other sites (Table 2). The stability of community-level trait variability is driven by both species turnover/re-ordering and intraspecific trait variability (Lepš et al. 2011; Violle et al. 2012). The extent to which populations of species can adjust trait values (either through phenotypic plasticity or shifts in genotypic abundance) can determine whether they are out-competed by other species with more environmentally suitable traits (i.e., lower SLA with decreased soil moisture). Species composition has been shown to be insensitive to rainfall manipulation in some arid sites (Tielbörger et al. 2014), which may explain why species turnover contributed less to the functional response observed at the high aridity sites. Trait adjustments of certain species along with survival of other species incapable of adjustment led to increased trait variation. It is worth noting, however, that trait variation was calculated using presence/absence data, thus, any change in abundance of species unable to acclimate to drought (i.e., trait plasticity) was not captured in these calculations.

Contrary to our hypothesis, we did not observe a decline in trait variability towards a limited set of trait values in response to experimental drought. This may simply be because our drought treatments did not cause significant species loss across all sites. Moreover, functional traits do not respond to resource limitation in the same way (especially not for every species), thus, it is not surprising that convergence did not occur for all traits simultaneously. Additionally, hydraulic traits and/or traits related to plant phenology or reproductive strategy (e.g., onset of flowering) may have been more responsive to drought treatments (Anderegg et al. 2016; Reich 2014; Nogueira et al. 2018). Across sites, we did observe convergence towards a common community SLA (i.e., decreased variability) with increasing aridity, largely due to species turnover.

Community responses to the drought treatment did not mirror spatial trends observed along the aridity gradient. The discrepancies between the spatial and temporal responses of communities and ecosystems to environmental change have been observed in many climate change experiments (Blume-Werry et al., 2016). For example, Sandel et al. (2010) contrasts the trends in plant trait distributions along a precipitation gradient with those observed in response to short-term water addition. The response of plant community-level trait variability to experimental drought vs. a spatial gradient in aridity is codetermined by species turnover and intraspecific trait variation. This co-determination likely played a large role in the discrepancy between spatial and temporal responses (Auger and Shipley 2013; Smith 2011). Indeed, 90% of variability in trait variability along the natural gradient was determined by species turnover whereas intraspecific trait plasticity played a larger role in within-site responses (Table 2). Compared to the long-term influence of aridity, the drought treatments imposed here reflect a novel environmental stress, which is more likely to cause variable responses in functional composition. This explanation is supported by the differential responses of community-level trait variability to experimental drought among years, yet consistent trends along the natural aridity gradient throughout the observational period (Fig. 2).

Lastly, spatial differences in soil moisture and fertility likely played a role in changes in functional composition observed here. Drought, and aridity more broadly, can have indirect effects on community trait variability by reducing N-mineralization rates and thus soil fertility (Bernard-Verdier et al. 2012; Nogueira et al. 2018). Here, we show that differences in soil fertility between sites (i.e., lower fertility with increased aridity) at least partially drive the spatial trends in community trait variability. Drought treatments had a similar influence on community trait variability; however, spatial relationships between trait responses and soil moisture/fertility were stronger than the within-site temporal models comparing drought and control plots (Fig. 3). The response of community-level trait variability to drought may converge on trends observed along a natural gradient if the duration and/or intensity of drought were to increase (Smith et al. 2009). Long-term drought experiments are thus needed to test whether species substitution and acclimation in drought plots will lead to community shifts proportional to those observed along natural aridity gradients.

## Conclusion

Long-term drought altered community trait variability with little effect on community-level trait means. Trait variability, and functional diversity more broadly, may thus be a better indicator of initial community drought responses than community trait values themselves. Community-level trait variability generally remained constant in response to drought at the low aridity sites and was more sensitive to drought at the high aridity site. In contrast, community-level trait variability declined for SLA but increased for the other traits along the aridity gradient. Thus, site-level responses to drought do not mirror the trends observed along natural aridity gradients. While this was not entirely unexpected, we urge caution when using broad aridity gradients to make predictions concerning site-specific responses to drought.

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