Check for updates

RESEARCH ARTICLE

Functional Ecology   BRITISH ECOLOGICAL SOCIETY

Species responses to changing precipitation depend on trait plasticity rather than trait means and intraspecific variation

Bingwei Zhang[1,2,3] (iD) | Yann Hautier[4] (iD) | Xingru Tan[1,5] | Cuihai You[1,5] | Marc W. Cadotte[6] (iD) | Chengjin Chu[2] (iD) | Lin Jiang[7] (iD) | Xinghua Sui[2] (iD) | Tingting Ren[1,5] | Xingguo Han[1,5] (iD) | Shiping Chen[1,5] (iD)

[1]State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing, China; [2]Department of Ecology, State Key Laboratory of Biocontrol and School of Life Sciences, Sun Yat-sen University, Guangzhou, China; [3]Zhuhai Branch of State Key Laboratory of Earth Surface Processes and Resource Ecology, Beijing Normal University at Zhuhai, Zhuhai, China; [4]Ecology and Biodiversity Group, Department of Biology, Utrecht University, Utrecht, The Netherlands; [5]College of Resources and Environment, University of Chinese Academy of Sciences, Beijing, China; [6]Department of Biological Sciences, University of Toronto-Scarborough, Toronto, ON, Canada and [7]School of Biological Sciences, Georgia Institute of Technology, Atlanta, GA, USA

Correspondence
Bingwei Zhang
Email: zhangbw23@mail.sysu.edu.cn

Shiping Chen
Email: spchen@ibcas.ac.cn

Abstract

1. Trait-based approaches are key to develop mechanistic understanding of differences in plant species performance under environmental change. While mean trait values have been widely used to link functional traits to species performance, the contribution of intraspecific trait variation and trait plasticity remains unclear. Moreover, environmentally induced changes in species biomass are caused by changes in the number of individuals and individual growth rate, both of which should be influenced by trait differences and plasticity. Our goal in this study is to use trait-based information to explain species performance via changes in species abundance and individual weight.

2. We measured the mean, intraspecific variation and plasticity of nine above-ground plant traits, and a further three mean root traits from 10 common species in a precipitation manipulation experiment in semi-arid grassland. We used this trait information to explain differences in the responses of species biomass, abundance and mean individual weight to changing precipitation. Species responses were calculated as the normalised slopes of the regressions between species biomass, abundance and individual weight with the manipulated precipitation amount.

3. We found strong differences in species responses to changing precipitation for species biomass, abundance and mean individual weight. Reduced precipitation decreased biomass, abundance and mean individual weight for some species, but increased them for others. Biomass and mean individual weight of species with resource-acquisitive traits, such as shallow rooted species, showed stronger positive responses to changing precipitation compared to resource-conservative traits, like those with deep roots. For above-ground traits, trait plasticity was the strongest predictor of species responses compared to mean traits and intraspecific trait variation. In addition, trait plasticity regulated changes in species biomass more via changes in species abundance than mean individual weight.

4. These results indicate that trait plasticity is a key driver for determining species-specific responses to changing precipitation and needs more consideration for understanding and predicting ecosystem structure and functioning in future climate scenarios.

1 | INTRODUCTION

Altered precipitation as a consequence of global climate change will have important repercussions for terrestrial plant productivity and further ecosystem functions and services (Morecroft et al., 2004; Reichmann, Sala, & Peters, 2013; Zhang et al., 2017). Alteration of plant productivity driven by changing precipitation is jointly caused by direct plant physiological responses (Buckley, 2019; Chaves, Maroco, & Pereira, 2003) and indirect change in plant species richness and composition (Morecroft et al., 2004). These two aspects can be captured by changes in individual weight and the number of individual. The latter is increasingly important over time as individual species responses and fitness changes accumulate (Griffin-Nolan et al., 2018; Smith, Knapp, & Collins, 2009), which alters community structure and causes increasingly important and persistent influences on ecosystem functioning. While many studies have explored the influence of changing precipitation on species productivity, we still do not have a clear understanding about the relative contribution from changes in species individual weight and numbers. Considering these two aspects and evaluating the causes of their variation are important not only to reveal the mechanisms underlying species' responses to changing precipitation but also to enhance our prediction of community structure in the future and their consequences on ecosystem functioning.

Plant functional traits, that is, plant morphological, physiological and phenological characteristics, influence plant survival, growth and reproduction (Violle et al., 2007). Thus, species mean trait values, either measured in a given set of environmental conditions or obtained from a trait database (i.e. TRY, Kattge et al., 2020), have been widely used to link interspecific trait variation to species coexistence and performance under environmental change (Griffin-Nolan et al., 2018; Kraft, Godoy, & Levine, 2015; Soudzilovskaia et al., 2013; Suding et al., 2008). For example, recent studies suggest that species with resource-acquisitive traits (i.e. shallow roots and low leaf thickness) are more responsive to environmental change because they are able to acquire resources quickly and dominate species with resource-conservative traits (i.e. deep roots and thick leaf) when resources (i.e. water) are not limiting. In contrast, species with resource-acquisitive traits should suffer more than species with resource-conservative traits when resources become limiting (Conti et al., 2018; Flombaum & Sala, 2012). However, whether acquisitive traits favour these

species via increasing their individual number or individual weight remains unclear.

The justification of using mean trait values is based on the implicit assumption that evolutionary, physiological and genetic constraints reduce intraspecific variation as compared to interspecific variation (Garnier et al., 2001; Violle et al., 2007). Under this view, intraspecific trait variation is supposed to account for only a small fraction of the overall trait variability as compared to interspecific trait variation (Garnier et al., 2001). However, the expression of plant functional traits varies within species as a result of genetic variation among individuals and phenotypic plasticity in response to abiotic and biotic conditions (Conti et al., 2018; Osnas et al., 2018; Shipley et al., 2016; Siefert et al., 2015; Valladares, Gianoli, & Gómez, 2007; Violle et al., 2012). High intraspecific trait variation is considered to favour species acclimation, competition and persistence in different or variable environments and might be a key index for predicting plant species responses to changing environmental conditions (Benito Garzon, Robson, & Hampe, 2019; Conti et al., 2018; Valladares et al., 2007, 2014). Studies have also shown that the direction and magnitude of trait plasticity in response to environmental fluctuations differ considerably among species and traits considered (Arnold, Kruuk, & Nicotra, 2019; Roscher et al., 2018). Trait plasticity mainly results from variation of trait expression caused by environmental change (Arnold et al., 2019; Shipley et al., 2016; Stamp & Hadfield, 2020; Valladares et al., 2007), which can alter species performance and therefore affect predictions derived from mean trait values. Using a standardised response slope of trait–environment relationships allows to assess trait plasticity, including the direction and magnitude of change in plant functional traits under environmental changes (Arnold et al., 2019; Roscher et al., 2018; Valladares et al., 2007), and thus determine the contribution of trait plasticity on species performance (Shipley et al., 2016; Siefert et al., 2015; Violle et al., 2012).

While understanding the mechanisms driving species responses to environmental changes is critically important for sound management of ecosystems, thus far studies have not assessed the relative contribution of multiple facets of trait metrics, including species trait means, intraspecific trait variation across communities and trait plasticity. Here, we conducted a precipitation manipulation experiment with five levels in a semi-arid steppe in northern China between 2012 and 2016, to study the contribution of species-specific trait-based

responses to species biomass under altered precipitation. Since water is a major limiting factor in the studied region, we calculated these trait-based metrics using 12 traits related to plant water acquisition, water loss and growth. We used these trait-based metrics to quantify their single and combined influences on species response to changing precipitation. Our objectives were to answer (a) how plant functional traits regulate species-specific responses to changing precipitation via species abundance and mean individual weight? (b) What is the relative contribution of trait mean, intraspecific trait variation and trait plasticity to species responses to changing precipitation?

2 | MATERIALS AND METHODS

2.1 | Site description

This study was conducted at a semi-arid steppe (44°22′N, 117°35′E, 1,148 m), located in West Ujinmqin Banner, Inner Mongolia, Northern China. The site was fenced in 2011 with no grazing or other disturbance thereafter. Before being fenced, the site was mowed once every year during August. The mean annual temperature is 1.5°C, mean annual precipitation is 333 mm and with 87% (288 mm) occurring during the growing season (May–September). The community is dominated by C_3 perennial grasses and forbs, such as *Stipa grandis*, *Leymus chinensis*, *Anemarrhena asphodeloides*, etc.

2.2 | Experimental design

The experiment was established as a randomised block design in 2012. We established five levels of precipitation treatments: 60% (P-60) and 30% (P-30) decreased precipitation using passive rainout shelters (Zhang et al., 2017), ambient control (P), 30% (P + 30) and 60% (P + 60) increased precipitation. A total of 20 plots were assigned to four blocks; each block contained five randomly assigned treatment plots, which were subjected to fixed manipulation levels throughout the entire duration of the experiment. Each plot was 3 m × 4 m with 1 m space between them. We inserted tin sheets into the ground to a depth of 100 cm around each plot to prevent lateral water movements. All measurements were conducted in the central area (2 m × 3 m) to avoid edge effects. Pre-treatment measurements showed that there was no significant difference of species richness, Simpson diversity index and productivity among treatments, suggesting low background spatial heterogeneity in this study site.

Natural precipitation amounts were measured at a frequency of every 0.5 hr by an automatic weather station at our study site. Precipitation manipulations were carried out from May (June in 2012) to August every year. In P-30 and P-60 treatments, 30% and 60% rainfall was removed by using passive rainout shelters with 30% and 60% shelter area (Zhang et al., 2017). Although the shelters caused small interception of incoming light, this caused only minor influence on plant response (Zhang et al., 2017). In P + 30 and P + 60, 30% and 60% rainfall amount of each precipitation event was added

by a handheld irrigation system with a flowmeter immediately after each event that was >2 mm. All the added water was taken from the rainfall removed by the shelters. This gave us five levels of precipitation without modifying the pattern of seasonal precipitation.

2.3 | Species biomass, abundance and mean individual weight

During the peak growing season (10th–15th of August) in the 5th year of the experiment (2016), above-ground biomass was harvested and sorted by species in a 0.2 m × 0.8 m strip in each plot, and separated into current year biomass and previous years litter. Abundance of each species in the strip (individual number for solitary species or bundle number for tufty species) was also recorded. All the samples were oven-dried at 65°C for 48 hr and weighed to determine the species-level biomass in each plot. Mean weight of individual plants per plot was calculated as the ratio of species biomass to its abundance in each plot.

2.4 | Sampling of plant functional traits

We measured plant functional traits for 10 common species (with occurrence frequencies of more than 90% at the site; see Table S1). These species contributed about 86% of the total above-ground net primary productivity (ANPP) and 96% of the total abundance, and thus contributed the most to community structure and ecosystem functioning (Grime, 1998). Rare species were not included in the trait sampling and further analysis.

In July 2015, we measured three root-related traits for each of the 10 most common species by collecting three soil cores (40 cm × 40 cm in size, 60 cm in depth) in an adjacent field. Root-related traits were not measured in the experimental plot to avoid disturbance of the experimental plots. After washing the soil cores in water, 3–10 plant individuals with complete shoot and root were selected for each species. Roots and their branches were spread on a board in their natural angles to measure rooting depth, proportion of surface (0–10 cm) root biomass to total root biomass (surface root distribution) and ratio of root biomass to shoot biomass (root: shoot ratio; Table 1).

In July and August 2016, we measured nine above-ground traits for each of the 10 most common species in each experimental plot (Table 1). Maximum rate of leaf photosynthesis, transpiration, stomatal conductance and water use efficiency for one normal leaf and each species in each experimental plot were estimated using Li-6400 (Li-Cor Inc.) at the photosynthetically active radiation (PAR) of 1,500 μmol m^{-2} s^{-1}, in the later July. Previous studies have shown that a light intensity of 1,500 μmol m^{-2} s^{-1} is beyond the light saturation point of species in this region (Zhang et al., 2017). The gas exchange measurements were taken from 08:00 to 11:00 a.m. (local time), when ambient PAR ranged from 660 to 1,600 μmol m^{-2} s^{-1}. Before measurements, leaf was acclimated in

TABLE 1 The detail information of the 12 plant functional traits used in this study. 'No' means that we have no information for coefficient of variation (T_{CV}) and plasticity ($T_{plasticity}$) of the three root-related traits due to the absence of their trait samplings in the experimental plots

Plant functional traits	Abbreviation	Units	Measurement methods	$T_{CV}/T_{plasticity}$
Maximum rooting depth	Rootdepth	cm	Direct measurement	No
Surface root distribution	Rootsurface	%	Proportion of root in 0–10 cm soil	No
Root: Shoot ratio	RSR	unitless	Ratio of root to shoot biomass	No
Height	Height	cm	Direct measurement	Yes
Leaf: Stem ratio	LSR	unitless	Ratio of leaf to stem biomass	Yes
Leaf mass per area	LMA_leaf	mg/cm^2	Leaf mass of per unit of leaf area	Yes
Maximum rate of leaf photosynthesis	Pn_leaf	μmol CO$_2$ m^{-2} s^{-1}	PAR at 1,500 μmol m^{-2} s^{-1} by Li-6400	Yes
Transpiration	T_leaf	mmol H$_2$O m^{-2} s^{-1}	PAR at 1,500 μmol m^{-2} s^{-1} by Li-6400	Yes
Stomatal conductance	gs_leaf	mmol H$_2$O m^{-2} s^{-1}	PAR at 1,500 μmol m^{-2} s^{-1} by Li-6400	Yes
Water use efficiency	WUE_Leaf	μmol CO$_2$ mmol^{-1} H$_2$O	Ratio of leaf Pn to T	Yes
Leaf nitrogen concentration per area	N_leaf	mg Ncm^{-2}	Elemental analyzer	Yes
Leaf C:N ratio	CNR_leaf	unitless	Ratio of leaf C to N concentration	Yes

the chamber for 1–3 min until the records of gas exchange rates and stomatal conductance were stable. An airflow rate of 500 ml/min was used throughout the measurements. We did not control leaf temperature, water vapour or CO$_2$ concentrations, but used a 20-L plastic buffer to stabilise the gas concentrations of the input air. Before the above-ground biomass harvesting, mean height was recorded by averaging the height of five random individuals (or all individuals for species with less than five individuals) except the reproductive individuals. Individuals without flowers and fruits from the harvested above-ground samples were separated into leaf and stem parts for each species in each plot. Biomass of leaf and stem were used to calculate leaf: stem ratio. After measuring leaf area, leaf samples were over-dried and weighted, to determine leaf mass per area. Then the same leaf samples were used to determine leaf carbon and nitrogen concentration with a CHNOS Elemental Analyzer (Vario EL III, Elemental Inc.); after that, the ratio of leaf carbon to nitrogen concentration (leaf C:N ratio) was calculated.

2.5 | Calculation of trait variability and plasticity

For each species and each of the nine above-ground traits, we calculated trait means (T_{mean}) as the mean of species trait values in 20 experimental plots, and trait variability within intraspecific (T_{CV}) as the coefficient of variation of trait values within species across 20 experimental plots (Figure S1). To estimate trait plasticity ($T_{plasticity}$), we ran linear mixed-effects models (LME) for each trait and each species with trait as the response variable, precipitation as the explanatory variable (the fixed effect) and block as the random effect. Precipitation amount received in the five treatments was considered as a continuous variable. We did not control the intercept. The fixed slopes of linear regression between traits

and precipitation for each trait and each species was used to express trait plasticity in response to changing precipitation (Arnold et al., 2019). We used linear model as most relationships were linear (Tables S2 and S3). Before calculation of $T_{plasticity}$, each trait was standardised by the maximum observed value. To reduce the sensitivity of this method to spuriously high maximum value, we used the mean value of the four maximum trait values for each trait and species as the maximum value (Byrnes et al., 2014). We did not use other standardisation approaches including z-transformation, although z-transformation produced highly comparable trait plasticity as the method we used, it was affected by the spuriously high maximum value (Figure S2). For the three root-related traits (rooting depth, surface root distribution and root: shoot ratio), their trait variations and plasticity were not accounted for in this study since we have no detailed information from the individual plot for these traits (Table 1).

2.6 | Statistical analysis

We first calculated species-level responses to changing precipitation, and then used the means (T_{mean}), CVs (T_{CV}) and plasticity ($T_{plasticity}$) of plant functional traits to explain species responses to changing precipitation.

Species-specific responses of biomass, abundance and mean individual weight to changing precipitation were estimated as the fixed-effect linear regression slopes of the relationships of species biomass, abundance and mean individual weight with the precipitation amounts in 2016, using linear mixed-effect model with block as random factor. Again, we used linear model as most relationships were linear (Table S4). These response metrics were hereafter referred to as $RR_{biomass}$, $RR_{abundance}$ and $RR_{meanweight}$. Before calculating species-specific responses, species biomass,

abundance and mean individual weight were standardised by dividing each value by the average of the first four maximum values for each variable and each species. Community total biomass and abundance, and mean individual weight were used to calculate community-level responses using the same method as species-level responses. Note that the species response metrics were calculated using species-level data in 2016, to be consistent with the trait sampling year. Repeat measured ANOVA showed no significant interaction between precipitation treatments and years (Table S5), indicating that the species response metrics mainly reflect the species functional strategy but not legacy effect from previous precipitation conditions.

Pearson correlation analysis was used to examine correlations of T_{mean}, T_{CV} and $T_{plasticity}$ for all single trait with $RR_{biomass}$, $RR_{abundance}$ and $RR_{meanweight}$. To clearly capture plant resource strategies based on the multiple plant functional traits and to link them to species response, principle component analysis was applied to produce the principle components (PCs) of T_{mean}, T_{CV} and $T_{plasticity}$ for the nine above-ground plant functional traits (Table S6). For example, PC1 of T_{mean} represents the fast–slow species strategy from high leaf mass per area, leaf transpiration, leaf stomatal conductance, leaf nitrogen concentration and leaf C:N ratio, and low leaf water use efficiency to low leaf mass per area, leaf transpiration, leaf stomatal conductance, leaf nitrogen concentration and leaf C:N ratio, and high leaf water use efficiency; PC2 of T_{mean} represents the other fast–slow species strategy from high leaf: stem ratio and maximum rate of leaf photosynthesis to low leaf: stem ratio and maximum rate of leaf photosynthesis. Then PC1 (representing 53%, 45% and 38% of the variations for T_{mean}, T_{CV} and $T_{plasticity}$, respectively) and PC2 (representing 18%, 20% and 25% of the variations for T_{mean}, T_{CV} and $T_{plasticity}$, respectively) of the nine T_{mean}, T_{CV} and $T_{plasticity}$ were further used to analyse their influence on $RR_{biomass}$ through $RR_{abundance}$ and $RR_{meanweight}$, using Pearson correlation analysis and structural equation modelling (SEM) analysis. Since change in species biomass is fully contributed by changes in species abundance and mean individual weight, we did not add direct pathways linking trait metrics and species response of biomass. SEM analysis was also applied for each of the single trait to examine the mean, intraspecific variation and plasticity of trait on species responses. All analyses were conducted in R 3.3.4. We used packages CORRPLOT (Wei & Simko, 2013) and PIECEWISESEM which was suitable for SEM with small data size (Lefcheck, 2016).

3 | RESULTS

3.1 | Community and species-specific responses to changing precipitation

At the community level, total abundance ($RR_{abundance}$ = 0.101), mean individual weight ($RR_{meanweight}$ = 0.152) and total biomass ($RR_{biomass}$ = 0.224) increased with increasing precipitation (Figure 1). In
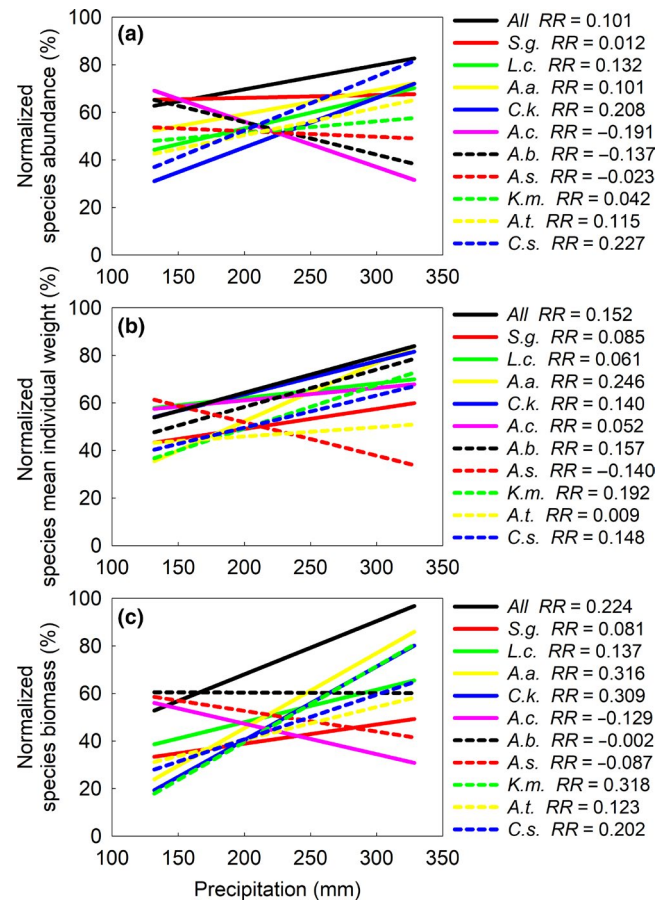

FIGURE 1 Response of species abundance, mean individual weight and biomass to changing precipitation. The fixed slope of the normalised species abundance (a, $RR_{abundance}$), mean individual weight (b, $RR_{meanweight}$) and biomass (c, $RR_{biomass}$) to the five precipitation treatments for the 10 common species, using linear mixed-effect model and with block as the random factor. The normalisation was performed by the mean abundance, mean weight or biomass of the four highest values for each species in the 20 plots. The response ratios (RR) are shown to the right of each panel and used in the further correlation and structural equation modelling analysis

contrast, our measures of diversity (species richness and Simpson diversity index) were not significantly altered by precipitation (Figure S3).

At the species level, species responses of abundance, mean individual weight and biomass (i.e. the normalised slopes in species–precipitation relationships) varied strongly among the 10 most common species (Figure 1). In other words, the direction and magnitude of species responses to changing precipitation varied among species, with some species increasing and others decreasing with different magnitudes as precipitation increased. Specifically, species responses of abundance ($RR_{abundance}$) ranged from −0.191 (*Agropyron cristatum*) to 0.227 (*Cleistogenes squarrosa*), responses of mean individual weight ($RR_{meanweight}$) ranged from −0.140 (*A. sibiricum*) to 0.246 (*A. asphodeloides*), and responses of biomass ($RR_{biomass}$) ranged from −0.129 (*Agropyron cristatum*) to 0.318 (*Koeleria macrantha*, Figure 1). The magnitude of $RR_{biomass}$ was positively correlated to both $RR_{abundance}$ and $RR_{meanweight}$ (Figure 2).

FIGURE 2 Relationships between traits metrics and species response. Linear regression relationships between PC1 and PC2 of T_{mean}, T_{CV} and $T_{plasticity}$ with the three species response metrics to precipitation ($RR_{abundance}$, $RR_{meanweight}$ and $RR_{biomass}$) for the 10 common species. Regression lines for non-significant relationships were not shown in subplots ($p \geq 0.1$, $n = 10$)
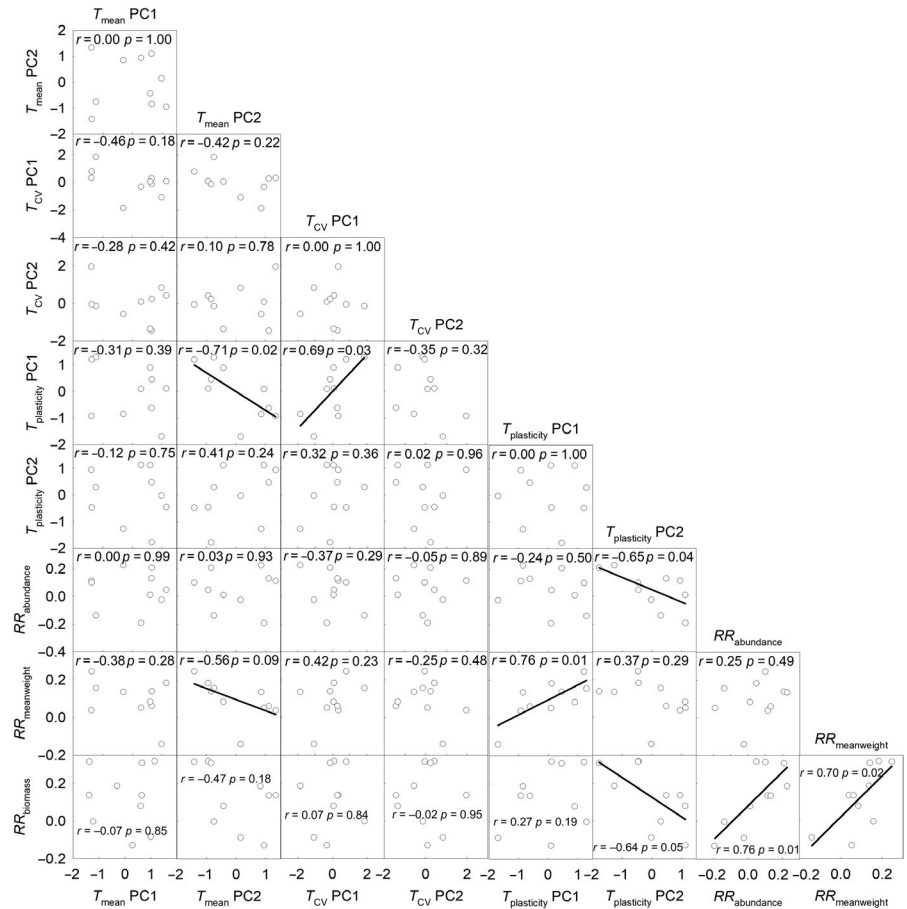

TABLE 2 Pearson correlation coefficients for the relationships between mean (T_{mean}), variation (T_{CV}) and plasticity ($T_{plasticity}$) of plant functional traits with three species-specific response metrics ($RR_{abundance}$, $RR_{meanweight}$ and $RR_{biomass}$) to changing precipitation across 10 common species

Traits	$RR_{abundance}$			$RR_{meanweight}$			$RR_{biomsss}$		
	T_{mean}	T_{CV}	$T_{plasticity}$	T_{mean}	T_{CV}	$T_{plasticity}$	T_{mean}	T_{CV}	$T_{plasticity}$
Rootdepth	−0.40	nd	nd	−0.56[#]	nd	nd	−0.69*	nd	nd
Rootsurface	0.22	nd	nd	0.74*	nd	nd	0.53	nd	nd
RSR	0.39	nd	nd	0.51	nd	nd	0.62[#]	nd	nd
Height	−0.17	0.30	0.28	−0.27	0.13	0.47	−0.22	0.34	0.48
LSR	0.27	0.03	−0.01	0.35	−0.16	0.23	0.63*	−0.02	0.20
LMA_leaf	−0.04	−0.15	−0.74*	−0.31	−0.59[#]	−0.48	−0.17	−0.50	−0.57[#]
Pn_leaf	0.45	−0.77**	−0.51	−0.45	0.03	0.55[#]	−0.04	−0.41	−0.08
T_leaf	0.06	−0.56[#]	−0.30	−0.26	0.31	0.65*	0.09	−0.10	0.21
gs_leaf	0.12	−0.47	−0.21	−0.31	0.13	0.85**	0.05	−0.26	0.32
WUE_leaf	0.26	−0.07	−0.02	0.26	0.12	−0.50	0.17	0.31	−0.36
N_leaf	−0.27	−0.03	−0.72*	−0.69*	−0.59[#]	−0.37	−0.56[#]	−0.45	−0.57[#]
CNR_leaf	0.15	0.03	0.25	0.17	−0.43	−0.23	0.23	−0.08	0.13

Abbreviation: nd, not determined.

[#], * and ** indicates significant relationship at the levels of $p < 0.1$, $p < 0.05$ and $p < 0.01$.

3.2 | Influence of mean trait values on species responses

The mean value (T_{mean}) of plant functional traits investigated showed strong interspecific differences, especially plant leaf: stem ratio and root: shoot ratio, with up to sevenfold difference among species (Figure S4). $RR_{meanweight}$ was positively correlated with T_{mean} of surface root distribution, and negatively correlated with T_{mean} of rooting depth and leaf nitrogen concentration. $RR_{biomass}$ was positively

correlated with T_{mean} of root: shoot ratio and leaf: stem ratio, but negatively correlated with T_{mean} of rooting depth and leaf nitrogen concentration (Table 2). We found no significant relationship between $RR_{abundance}$ and T_{mean} for any of the 12 traits investigated (Table 2). T_{mean} PC1 of the nine above-ground traits (mostly representing the positive effect of leaf mass per area, leaf transpiration rate, leaf stomatal conductance, leaf nitrogen concentration, leaf C:N ratio, and negative effect of leaf water use efficiency) had no significant influence on all species response metrics, T_{mean} PC2 of the nine above-ground traits (mostly representing the positive effect of maximum rate of leaf photosynthesis and leaf: stem ratio) showed a negative relationship with $RR_{meanweight}$ (Figure 2).

3.3 | Influence of intraspecific trait variation on species responses

Intraspecific trait variation (T_{CV}) also showed strong difference among species (Figure S5). In comparison with interspecific trait variation, T_{CV} of plant height, leaf: stem ratio, leaf mass per area, leaf nitrogen concentration and carbon: nitrogen ratio were smaller than their interspecific trait variations, while T_{CV} of maximum rate of leaf photosynthesis, transpiration rate, stomatal conductance and water use efficiency were greater than their interspecific trait variations (Figure S6). $RR_{meanweight}$ was negatively correlated with T_{CV} of leaf mass per area and leaf nitrogen concentration (Table 2). $RR_{abundance}$ was negatively correlated with T_{CV} of maximum rate of leaf photosynthesis and transpiration rates (Table 2). While the T_{CV} for multiple plant functional trait (PC1 and PC2) showed no significant relationships with all the species response metrics (Figure 2).

3.4 | Influence of trait plasticity on species responses

Trait plasticity ($T_{plasticity}$) in response to changing precipitation showed large species-specific and trait-specific differences (Figure S7). Leaf gas exchange traits (maximum rate of leaf photosynthesis, transpiration rate and stomatal conductance) exhibited much greater plasticity compared to other traits (0.29–0.32 vs. −0.002 to 0.14; Figure S7). For most traits, their plasticity had no significant relationship with T_{CV} or T_{mean} (Figure S8). $RR_{abundance}$ was negatively correlated with $T_{plasticity}$ of leaf mass per area and nitrogen concentration, $RR_{meanweight}$ was positively correlated with $T_{plasticity}$ of maximum rate of leaf photosynthesis, transpiration rate and stomatal conductance; $RR_{biomass}$ was negatively correlated with $T_{plasticity}$ of leaf mass per area and nitrogen concentration (Table 2). PC1 of $T_{plasticity}$ (mostly representing the positive effect from plasticity of maximum rate of leaf photosynthesis, transpiration rate, stomatal conductance and negative effect from leaf water use efficiency) had a positive relationship with $RR_{meanweight}$, while PC2 of $T_{plasticity}$ (representing the positive effect from plasticity of leaf nitrogen concentration and negative

effect from plant height) had a negative relationship with $RR_{abundance}$ and $RR_{biomass}$ (Figure 2).

3.5 | Pathways of influence of different trait variables on species responses

The nine above-ground plant functional traits for which we had species-level responses to changing precipitation fitted the structural equation modelling (SEM) well (Fisher' $C = 9.81$, $p = 0.46$, $df = 10$, AIC $= 29.81$, BIC $= 32.83$, $n = 10$), and provided deeper insights on our data (Figure 3). In contrast to when analysed separately, PC2 of T_{mean} was not related to $RR_{meanweight}$ in the final model. The results of SEM
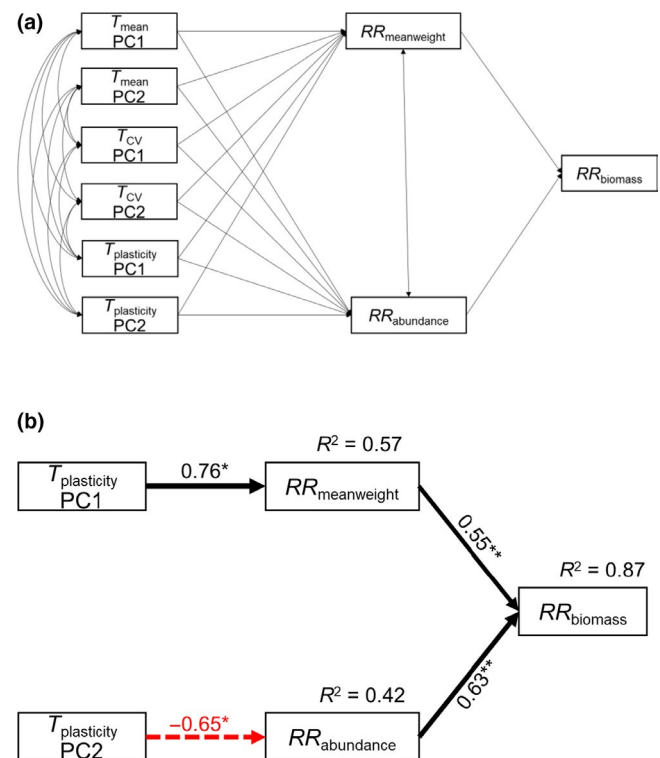

FIGURE 3 Structural equation modelling (SEM) for the influence of trait metrics on species responses. (a) Initial SEM analysis for the influence of T_{mean}, T_{CV} and $T_{plasticity}$ on species responses to changing precipitation. The first two PCs of T_{mean}, T_{CV} and $T_{plasticity}$ used in the SEM analysis contributed 71%, 65% and 63% variation of all the T_{mean}, T_{CV} and $T_{plasticity}$ except the root-related traits. (b) Final model only showed the influence of PC1 and PC2 of $T_{plasticity}$ on species responses, while T_{mean} and T_{CV} were removed due to their insignificant pathways with species responses. Note that we did not assess the direct influence of trait-based predictors on biomass because change in species biomass is fully contributed by species abundance and mean weight. The model fitted well with Fisher' $C = 9.81$, $p = 0.46$, $df = 10$, AIC $= 29.81$, BIC $= 32.83$. Black and red dashed arrows indicate significantly positive and negative effects, respectively. * and ** indicate significant relationship at the levels of $p < 0.05$ and $p < 0.01$, respectively. Values associated with the arrows represent standardised path coefficients. Widths of significant paths are scaled by standardised path coefficients. R^2 for each variable is reported next to the corresponding variable

confirmed that PC1 of T_{mean} and PC1 and PC2 of T_{CV} had no significant relationships with any of $RR_{meanweight}$, $RR_{abundance}$ and $RR_{biomass}$. PC1 of $T_{plasticity}$ was positively related to $RR_{meanweight}$ and explained 57% of its variation, PC2 of $T_{plasticity}$ was negatively related to $RR_{abundance}$ and explained 42% of its variation. $RR_{abundance}$ and $RR_{meanweight}$ jointly contributed to 87% variation of $RR_{biomass}$. SEM analysis for any of the single trait also showed similar results and supported the multiple traits analysis (Figure S9). For example, $T_{plasticity}$ of maximum rate of leaf photosynthesis, transpiration and stomatal conductance (the major components for PC1 of $T_{plasticity}$) all showed positive influence on $RR_{biomass}$ via $RR_{meanweight}$; while $T_{plasticity}$ of leaf nitrogen concentration (the major component for PC2 of $T_{plasticity}$) negatively affected $RR_{biomass}$ via $RR_{abundance}$ (Figure S9).

4 | DISCUSSION

Trait-based approaches have great potential to reveal the underlying mechanisms of species response to environmental changes (Griffin-Nolan et al., 2018; Kraft et al., 2015; Soudzilovskaia et al., 2013; Suding et al., 2008; Violle et al., 2007). Previous studies mostly focused on mean trait values, assuming that intraspecific trait variation and trait plasticity account for only a small fraction of the overall trait variability (Shipley et al., 2016; Siefert et al., 2015; Violle et al., 2012). Here, we assessed the relative contribution of multiple aspects of plant functional traits (trait means, intraspecific trait variation and trait plasticity) to species responses of mean individual weight, abundance and biomass to experimental manipulation of precipitation.

4.1 | Species respond differently to changing precipitation

Our study showed a wide range of species responses to experimental manipulation of precipitation, in terms of abundance, mean individual weight and biomass. Due to interspecific compensatory effects, the decrease in the response of some species was offset by the increase in other species (Bai, Han, Wu, Chen, & Li, 2004; Loreau & Mazancourt, 2013). Thus, community-level change was much weaker than that of the most responsive species, which favoured ecosystem stability under changing precipitation (Bai et al., 2004). Previous studies have repeatedly shown the contribution of species richness to ecosystem functioning and to the stability of ecosystem functioning under fluctuating environmental conditions or experimental manipulation of global change drivers (Hautier et al., 2014; Isbell et al., 2015). Our results suggest that fluctuations in community composition in response to environmental changes, rather than species diversity per se, could play an important role in ecosystem functioning and stability, especially over short time intervals (Jones, Ripplinger, & Collins, 2017; Loreau & Mazancourt, 2013; Smith et al., 2009). For example, *A. asphodeloides* and *Carex korshinskyi* (two common species with 23% and 41% contribution to community

total ANPP and abundance in the control plots) were the two most positively responsive species for biomass in these communities ($RR_{biomass}$: 0.309–0.318), their influence on the community-level response ($RR_{biomass}$: 0.224) is largely dragged down by two most negatively responsive species of *A. cristatum* and *A. sibiricum* (two common species with 13% and 31% contribution to community total ANPP and abundance, $RR_{biomass}$: −0.128 to −0.087). We also found that change in species biomass was jointly contributed by changes in mean individual weight and species abundance, but with more dependence on the latter (0.55 vs. 0.63 for mean individual weight vs. abundance, Figure 3b). In water-limited ecosystems, due to species adaptation to changing precipitation to live under different conditions (Chaves et al., 2003; Gilbert & Medina, 2016), the number of plant individuals of a species is generally less variable than its growth rate. Thus, changes in the abundance of a species could potentially cause greater legacy effect on ecosystem productivity than changes in mean plant individual weight (Reichmann et al., 2013; Smith et al., 2009). Note that this does not mean abundance is not responsive to changing precipitation for all species, for example, *C. Korshinskyi*, a short stature species in the community, shows small change in mean individual weight but large change in abundance, due to less stressful environment in the community understory. Our results highlight the importance of both species biomass and abundance for prediction of changes in community structure and their consequence on ecosystem functioning under future climate change.

4.2 | Mean trait value contributes to species change in individual weight and biomass

In the present study, specific differences in response to changing precipitation could be partially explained by the mean value of the investigated plant functional traits. In particular, mean differences in root-related traits were linked to species change in biomass and individual weight. This result confirms previous findings that the mean of plant functional traits is a determinant of species response to environmental change (Flombaum & Sala, 2012; Soudzilovskaia et al., 2013; Violle et al., 2007). Moreover, species with shallow rooting depth, high surface root distribution, high root: shoot ratio and high leaf: stem ratio, all indicating resource-acquisitive traits, had greater response based on biomass and individual weight to precipitation change. Similar result was also reported by Conti et al. (2018). In semi-arid ecosystems, soil water availability is a limited resource, especially in the surface soil (Zhang et al., 2017, 2019). Since these acquisitive traits are closely related to plant water uptake (shallow rooting depth, high surface root distribution, high root: shoot ratio) and water loss (high leaf: stem ratio), species with such trait values were more easily affected by changing precipitation than species with the opposite trait values (Flombaum & Sala, 2012; van Wijk, 2011; Zhang et al., 2019). While high leaf nitrogen concentration, another commonly referenced resource-acquisitive trait (Díaz et al., 2016; Reich, 2014), caused a small

response based on mean individual weight. This seems to be opposite to the above pattern that resource-acquisitive species are more responsive to precipitation. However, several recent studies also suggest that high nitrogen favours plant tolerance under drought stress (Iqbal et al., 2020; Weih, Bonosi, Ghelardini, & Rönnberg-Wästljung, 2011), which potentially reduces plant responses to precipitation. Further studies are still necessary to test this debate. In contrast to responses of species biomass and individual weight, we found no significant correlation between the response of species abundance and trait means to any of the 12 traits investigated. This suggests that the number of species individuals caused by changing precipitation might not be linked to the mean value of investigated plant functional traits.

Moreover, we did not observe significant correlations between any of the mean leaf traits measured and any of the response metrics except leaf nitrogen concentration (Table 2 and Figure S9). This result is surprising given that leaf mass per area and plant height have been widely used to explain species' responses to other climate changes, that is, warming and species invasion (Conti et al., 2018; Soudzilovskaia et al., 2013). Similarly, a recent review also suggests that several common leaf traits, that is, specific leaf area and leaf dry mass content, do not show consistent relationships with water availability and species performance (Griffin-Nolan et al., 2018). One possible explanation of this difference is that these measurements for leaf traits are all based on unit of leaf but their influence on species performance could be largely regulated by differences in leaf mass ratio among species (Yang, Cao, & Swenson, 2018). For example, *L. chinensis* and *A. asphodeloides* are two dominant species in this community; *L. chinensis* has a greater maximum rate of leaf photosynthesis (8.44 vs. 5.28), but a much smaller leaf: stem ratio (1.62 vs. 4.83) than *A. asphodeloides*, which results in its smaller $RR_{meanwight}$ (0.06 vs. 0.25) and $RR_{biomass}$ (0.14 vs. 0.32). These results indicate that the performances of plant in water-limited biomes under changing precipitation might depend more on root-related traits and whole plant traits rather than leaf-related traits.

4.3 | Trait plasticity contributes to species changes in individual number and biomass

Our results showed that $T_{plasticity}$ performed better than T_{CV} in explaining species responses to changing precipitation. Similar result was also observed from a diversity manipulative experiment (Roscher et al., 2018). The reason is that the responses of species performance to changing precipitation not only differ in intensity but also change in direction (positive vs. negative). While the scalar index, that is, T_{CV}, failed to capture the change direction and their consequences on species responses (Roscher et al., 2018; Valladares et al., 2007). Our findings suggest that $T_{plasticity}$ better reflects the role of intraspecific trait variation by capturing the direction of trait changes with environmental change (Arnold et al., 2019; Conti et al., 2018; Roscher et al., 2018; Valladares et al., 2007).

In contrast to the limited influence of mean trait value of leaf on species responses, plasticity of leaf traits greatly contributed

to species responses to changing precipitation. The first PC axis of $T_{plasticity}$ (mostly representing the positive effect of maximum rate of leaf photosynthesis, transpiration and stomatal conductance, and negative effect of water use efficiency) indirectly and positively influenced $RR_{biomass}$ through $RR_{meanweight}$ (Figure 3b, also see SEMs for single trait of these traits, Figure S9). These traits are related to leaf stomatal behaviour, and varied much more within than among species (Figure S6). High plasticity of these traits enable plants to rapidly close their stomata to prevent water loss under drought stress, and rapidly reopen the stomata to maximise CO_2 and H_2O exchange when water is not limited (Buckley, 2019; Martin-StPaul, Delzon, & Cochard, 2017; Zhang et al., 2017), thus, leading to a high response of plant growth rate (i.e. $RR_{meanweight}$). In contrast, trait plasticity along the second PC axis (positive effect of leaf nitrogen concentration, negative effect of plant height) had a negative effect on $RR_{biomass}$ via $RR_{abundance}$ (Figure 3b, also see SEMs for single trait of leaf nitrogen concentration, Figure S9). High plasticity provides plants with a way to deal with the local long-term environmental change and avoid the deleterious effects of adverse environments (Valladares et al., 2007, 2014); thus, species with higher plasticity of leaf nitrogen concentration and plant height are effective in maintaining their population size over changing precipitation, leading to smaller $RR_{abundance}$. Overall, our study shows that trait plasticity predominantly regulates species response to changing precipitation rather than the mean and intraspecific variation of traits, and demonstrates that measurements of plant functional traits in different environmental conditions is key to identify how plant functional traits may be altered by the environment and their consequences on ecosystem functioning (Valladares et al., 2007, 2014; Violle et al., 2012).

4.4 | Study limitations

There were two limitations of this study. One is that all of our analyses are based on 10 common species since the rest of rare species compromise so little to the community that sample sizes are too small. This small dataset might influence the general relationships between trait metrics and species response to changing precipitation, as any single species could have a strong influence on the results. A bootstrap resampling based on data of the ten species showed a very small bias on the regression coefficients and R^2 for three significant relationships between species responses and trait metrics in Figure 2: $RR_{biomass} - T_{plasticity}PC2$, $RR_{abundance} - T_{plasticity}PC2$ and $RR_{meanweight} - T_{plasticity}PC1$ relationships (Table S7), suggesting that our key conclusions are robust. Moreover, we acknowledge that the change in ambient environmental condition, such as, temperature and air humidity, during leaf gas exchange measurements might affect the calculation of trait plasticity. But we did our best to control for such potential variation with reasonable statistical analyses. Particularly, adding block as a random effect in the analyses partially controls for potential influence from the ambient environmental condition.

The other was that we were not able to quantify the plasticity of root traits because we wished to avoid distributing the treatment plots. There are several studies indicating that drought might reduce root length and root density, increase root diameter (Zhou et al., 2018), enhance the root: shoot ratio and reduce the surface root distribution and rooting depth (van Wijk, 2011; Zhang et al., 2019) while the influence of changing precipitation on root traits is obviously species-specific and trait-dependent (Zhou, Wang, Bai, Zhang, & Zhang, 2019). Such an ability to alter root traits could also have important influence on plant responses to changing precipitation (Flombaum & Sala, 2012). Future studies with pot planting or field root sampling at the individual level are needed to provide a more comprehensive understanding of the role of trait plasticity.

5 | CONCLUSIONS

With this precipitation experiment, we found that the mean value of root-related traits was an effective predictor of species-specific responses to changing precipitation, indicating the usefulness of trait-based approaches. For the nine above-ground traits investigated, we found that trait plasticity plays a predominate role in regulating species response to changing precipitation above mean traits and intraspecific trait variation. This plasticity effect comes mainly via the plasticity of leaf traits while mean leaf-related traits are not important for all species response metrics. This means that some traits might affect species response to environmental change via their mean value while others might rely on their plasticity.

Our study has two important implications. First, trait plasticity is an important component affecting species responses to environmental change, and should be considered in future studies that employ trait-based approaches. To consider trait plasticity, however, it means that we need to measure many traits for many species under various environmental conditions, which has limited the wide use of trait plasticity in previous studies. While recent studies suggest that remote sensing is a promising technique for field trait survey (Chadwick & Asner, 2016), which could thus help in the future to easily get this important trait plasticity information, and encourage the application of trait plasticity. Second, future increases in extreme climatic fluctuations could change plant community structure by selecting species with higher plasticity because they exhibit lower $RR_{abundance}$ to changing precipitation. The increase in the proportion of plastic species should have important implications for ecosystem functioning (Jones et al., 2017; Smith et al., 2009), and might lead to a relatively stable community in long term.

AUTHORS' CONTRIBUTIONS
S.C., B.Z. and X.H. conceived the ideas and designed methodology; B.Z., X.T., C.Y. and T.R. collected the data, B.Z., Y.H., M.W.C., C.C. and S.C. analysed the data and led the writing of the manuscript. All authors contributed critically to draft and gave final approval for publication.

DATA AVAILABILITY STATEMENT
Data deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.gtht76hjp (Zhang et al., 2020).

ORCID
Bingwei Zhang https://orcid.org/0000-0002-7858-4806
Yann Hautier https://orcid.org/0000-0003-4347-7741
Marc W. Cadotte https://orcid.org/0000-0002-5816-7693
Chengjin Chu https://orcid.org/0000-0002-0606-449X
Lin Jiang https://orcid.org/0000-0002-7114-0794
Xinghua Sui https://orcid.org/0000-0001-6076-4318
Xingguo Han https://orcid.org/0000-0002-1836-975X
Shiping Chen https://orcid.org/0000-0002-1934-2372

REFERENCES
Arnold, P. A., Kruuk, L. E. B., & Nicotra, A. B. (2019). How to analyse plant phenotypic plasticity in response to a changing climate. *New Phytologist*, *222*, 1235–1241. https://doi.org/10.1111/nph.15656

Bai, Y., Han, X., Wu, J., Chen, Z., & Li, L. (2004). Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature*, *431*, 181–184. https://doi.org/10.1038/nature02850

Benito Garzon, M., Robson, T. M., & Hampe, A. (2019). DeltaTraitSDMs: Species distribution models that account for local adaptation and phenotypic plasticity. *New Phytologist*, *222*, 1757–1765. https://doi.org/10.1111/nph.15716

Buckley, T. N. (2019). How do stomata respond to water status? *New Phytologist*, *224*, 21–36. https://doi.org/10.1111/nph.15899

Byrnes, J. E. K., Gamfeldt, L., Isbell, F., Lefcheck, J. S., Griffin, J. N., Hector, A., … Emmett Duffy, J. (2014). Investigating the relationship between biodiversity and ecosystem multifunctionality: Challenges and solutions. *Methods in Ecology and Evolution*, *5*, 111–124. https://doi.org/10.1111/2041-210X.12143

Chadwick, K., & Asner, G. (2016). Organismic-scale remote sensing of canopy foliar traits in lowland tropical forests. *Remote Sensing*, *8*, 87. https://doi.org/10.3390/rs8020087

Chaves, M. M., Maroco, J. P., & Pereira, J. S. (2003). Understanding plant responses to drought – From genes to the whole plant. *Functional Plant Biology*, *30*, 239–264. https://doi.org/10.1071/FP02076

Conti, L., Block, S., Parepa, M., Münkemüller, T., Thuiller, W., Acosta, A. T. R., … Carboni, M. (2018). Functional trait differences and trait plasticity mediate biotic resistance to potential plant invaders. *Journal of Ecology*, *106*, 1607–1620. https://doi.org/10.1111/1365-2745.12928

Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., … Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, *529*, 167–171. https://doi.org/10.1038/nature16489

Flombaum, P., & Sala, O. E. (2012). Effects of plant species traits on ecosystem processes: Experiments in the Patagonian steppe. *Ecology*, *93*, 227–234. https://doi.org/10.1890/11-0722.1

Garnier, E., Laurent, G., Bellmann, A., Debain, S., Berthelier, P., Ducout, B., … Navas, M.-L. (2001). Consistency of species ranking based on functional leaf traits. *New Phytologist*, *152*, 69–83. https://doi.org/10.1046/j.0028-646x.2001.00239.x

Gilbert, M. E., & Medina, V. (2016). Drought adaptation mechanisms should guide experimental design. *Trends in Plant Science*, *21*, 639–647. https://doi.org/10.1016/j.tplants.2016.03.003

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

Grime, J. P. (1998). Benefits of plant diversity to ecosystems: Immediate, filter and founder effects. *Journal of Ecology*, *86*, 902–910. https://doi.org/10.1046/j.1365-2745.1998.00306.x

Hautier, Y., Seabloom, E. W., Borer, E. T., Adler, P. B., Harpole, W. S., Hillebrand, H., … Hector, A. (2014). Eutrophication weakens stabilizing effects of diversity in natural grasslands. *Nature*, *508*, 521. https://doi.org/10.1038/nature13014

Iqbal, A., Dong, Q., Wang, X., Gui, H., Zhang, H., Zhang, X., & Song, M. (2020). High nitrogen enhance drought tolerance in cotton through antioxidant enzymatic activities, nitrogen metabolism and osmotic adjustment. *Plants (Basel, Switzerland)*, *9*, 178. https://doi.org/10.3390/plants9020178

Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., … Eisenhauer, N. (2015). Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature*, *526*, 574–577. https://doi.org/10.1038/nature15374

Jones, S. K., Ripplinger, J., & Collins, S. L. (2017). Species reordering, not changes in richness, drives long-term dynamics in grassland communities. *Ecology Letters*, *20*, 1556–1565. https://doi.org/10.1111/ele.12864

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., … Wirth, C. (2020). TRY plant trait database – Enhanced coverage and open access. *Global Change Biology*, *26*, 119–188. https://doi.org/10.1111/gcb.14904

Kraft, N. J. B., Godoy, O., & Levine, J. M. (2015). Plant functional traits and the multidimensional nature of species coexistence. *Proceedings of the National Academy of Sciences of the United States of America*, *112*, 797–802. https://doi.org/10.1073/pnas.1413650112

Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, *7*, 573–579. https://doi.org/10.1111/2041-210X.12512

Loreau, M., & Mazancourt, C. (2013). Biodiversity and ecosystem stability: A synthesis of underlying mechanisms. *Ecology Letters*, *16*, 106–115. https://doi.org/10.1111/ele.12073

Martin-StPaul, N., Delzon, S., & Cochard, H. (2017). Plant resistance to drought depends on timely stomatal closure. *Ecology Letters*, *20*, 1437–1447. https://doi.org/10.1111/ele.12851

Morecroft, M. D., Masters, G. J., Brown, V. K., Clarke, I. P., Taylor, M. E., & Whitehouse, A. T. (2004). Changing precipitation patterns alter plant community dynamics and succession in an ex-arable grassland. *Functional Ecology*, *18*, 648–655. https://doi.org/10.1111/j.0269-8463.2004.00896.x

Osnas, J. L. D., Katabuchi, M., Kitajima, K., Wright, S. J., Reich, P. B., Van Bael, S. A., … Lichstein, J. W. (2018). Divergent drivers of leaf trait variation within species, among species, and among functional groups. *Proceedings of the National Academy of Sciences of the United States of America*, *115*, 5480–5485. https://doi.org/10.1073/pnas.1803989115

Reich, P. B. (2014). The world-wide 'fast–slow' plant economics spectrum: A traits manifesto. *Journal of Ecology*, *102*, 275–301. https://doi.org/10.1111/1365-2745.12211

Reichmann, L. G., Sala, O. E., & Peters, D. P. C. (2013). Precipitation legacies in desert grassland primary production occur through previous-year tiller density. *Ecology*, *94*, 435–443. https://doi.org/10.1890/12-1237.1

Roscher, C., Gubsch, M., Lipowsky, A., Schumacher, J., Weigelt, A., Buchmann, N., … Schmid, B. (2018). Trait means, trait plasticity and trait differences to other species jointly explain species performances in grasslands of varying diversity. *Oikos*, *127*, 855–865. https://doi.org/10.1111/oik.04815

Shipley, B., De Bello, F., Cornelissen, J. H. C., Laliberté, E., Laughlin, D. C., & Reich, P. B. (2016). Reinforcing loose foundation stones in trait-based plant ecology. *Oecologia*, *180*, 923–931. https://doi.org/10.1007/s00442-016-3549-x

Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., … Wardle, D. A. (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, *18*, 1406–1419. https://doi.org/10.1111/ele.12508

Smith, M. D., Knapp, A. K., & Collins, S. L. (2009). A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. *Ecology*, *90*, 3279–3289. https://doi.org/10.1890/08-1815.1

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

Stamp, M. A., & Hadfield, J. D. (2020). The relative importance of plasticity versus genetic differentiation in explaining between population differences; a meta-analysis. *Ecology Letters*. https://doi.org/10.1111/ele.13565

Suding, K. N., Lavorel, S., Chapin, F. S., Cornelissen, J. H. C., Díaz, S., Garnier, E., … Navas, M.-L. (2008). Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. *Global Change Biology*, *14*, 1125–1140. https://doi.org/10.1111/j.1365-2486.2008.01557.x

Valladares, F., Gianoli, E., & Gómez, J. M. (2007). Ecological limits to plant phenotypic plasticity. *New Phytologist*, *176*, 749–763. https://doi.org/10.1111/j.1469-8137.2007.02275.x

Valladares, F., Matesanz, S., Guilhaumon, F., Araújo, M. B., Balaguer, L., Benito-Garzón, M., … Zavala, M. A. (2014). The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecology Letters*, *17*, 1351–1364. https://doi.org/10.1111/ele.12348

van Wijk, M. T. (2011). Understanding plant rooting patterns in semi-arid systems: An integrated model analysis of climate, soil type and plant biomass. *Global Ecology and Biogeography*, *20*, 331–342. https://doi.org/10.1111/j.1466-8238.2010.00601.x

Violle, C., Enquist, B. J., McGill, B. J., Jiang, L., Albert, C. H., Hulshof, C., … Messier, J. (2012). The return of the variance: Intraspecific variability in community ecology. *Trends in Ecology & Evolution*, *27*, 244–252. https://doi.org/10.1016/j.tree.2011.11.014

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, *116*, 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Wei, T., & Simko, V. (2013). *corrplot: Visualization of a Correlation Matrix*. R package version 0.73. Retrieved from http://CRAN.R-project.org/package=corrplot

Weih, M., Bonosi, L., Ghelardini, L., & Rönnberg-Wästljung, A. C. (2011). Optimizing nitrogen economy under drought: Increased leaf nitrogen is an acclimation to water stress in willow (*Salix* spp.). *Annals of Botany*, *108*, 1347–1353. https://doi.org/10.1093/aob/mcr227

Yang, J., Cao, M., & Swenson, N. G. (2018). Why functional traits do not predict tree demographic rates. *Trends in Ecology & Evolution*, *33*, 326–336. https://doi.org/10.1016/j.tree.2018.03.003

Zhang, B., Cadotte, M. W., Chen, S., Tan, X., You, C., Ren, T., … Han, X. (2019). Plants alter their vertical root distribution rather than

biomass allocation in response to changing precipitation. *Ecology*, *100*, e02828. https://doi.org/10.1002/ecy.2828

Zhang, B., Hautier, Y., Tan, X., You, C., Cadotte, M. W., Chu, C., ... Chen, S. (2020). Data from: Species responses to changing precipitation depends on trait plasticity rather than trait means and intraspecific variation. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.gtht76hjp

Zhang, B., Tan, X., Wang, S., Chen, M., Chen, S., Ren, T., ... Han, X. (2017). Asymmetric sensitivity of ecosystem carbon and water processes in response to precipitation change in a semiarid steppe. *Functional Ecology*, *31*, 1301–1311. https://doi.org/10.1111/1365-2435.12836

Zhou, G., Zhou, X., Nie, Y., Bai, S. H., Zhou, L., Shao, J., ... Fu, Y. (2018). Drought-induced changes in root biomass largely result from altered root morphological traits: Evidence from a synthesis of global field trials. *Plant Cell and Environment*, *41*, 2589–2599. https://doi.org/10.1111/pce.13356

Zhou, M., Wang, J., Bai, W., Zhang, Y., & Zhang, W.-H. (2019). The response of root traits to precipitation change of herbaceous species in temperate steppes. *Functional Ecology*, *33*, 2030–2041. https://doi.org/10.1111/1365-2435.13420

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.