

RESEARCH ARTICLE

Plant functional diversity modulates global environmental change effects on grassland productivity

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Abstract

1. Although much research has explored changes in ecosystem functions associated with global environmental changes, the mechanistic pathways behind the observed changes remain poorly understood.
2. Using an 11-year experiment that increased growing season precipitation and nitrogen deposition in a temperate steppe, we explored the relative importance of direct and indirect environmental change effects on plant primary productivity.
3. We show that increases in water and nitrogen availability influenced plant productivity via both direct and indirect pathways. While both treatments stimulated plant productivity, changes in plant productivity cannot be explained by observed changes in species or phylogenetic diversity. Instead, the indirect effects of water and nitrogen addition were through their positive effects on plant functional diversity. Importantly, while the increase in one component of functional diversity (community-level weighted mean of plant stature) resulted in increased productivity, the increase in another component of functional diversity (functional dispersion) resulted in decreased productivity.
4. *Synthesis.* Our study provides the first evidence for the opposite effects of community-weighted means and functional dispersion of plant functional traits on grassland productivity and highlights the importance of both traits of dominant species and trait distribution among species in modulating the effects of global changes on ecosystem functions.

KEYWORDS

functional dispersion, functional traits, global change ecology, nitrogen deposition, phylogenetic diversity, precipitation, species richness, temperate steppe

1 | INTRODUCTION

The past few decades have witnessed an ever-increasing influence of human activities on the biosphere (Vitousek, Mooney, Lubchenco, & Melillo, 1997). Ongoing global environmental changes, such as alterations of the nitrogen cycle (Vitousek, Aber, et al., 1997) and precipitation patterns (Zhang et al., 2007), have triggered two lines of productive research aiming to understand their consequences for

the Earth's ecosystems. Ecosystem ecologists have investigated how global change factors alter various ecosystem functions and services that are essential for the well-being of humanity (Cramer et al., 2001; Schröter et al., 2005). In parallel, community ecologists, concerned over the possibility that anthropogenic biodiversity loss may be detrimental to ecosystems, have strived to understand the relationships between biodiversity and ecosystem functioning (hereafter BEF; Cardinale et al., 2012; Tilman, Isbell, & Cowles, 2014). While these

efforts have proven fruitful, we still lack a mechanistic understanding of how ecosystems respond to global environmental changes (Cardinale et al., 2012), limiting our ability to project ecosystem performance under future global change scenarios.

Several factors have contributed to our limited knowledge on mechanisms underlying ecosystem responses to global changes. First, global environmental changes may influence ecosystem properties directly via altering species metabolism and physiology and indirectly via altering biodiversity (Díaz et al., 2007). Widespread ongoing changes in biodiversity, both globally (Pereira et al., 2010; Pimm et al., 2014) and locally (Gonzalez et al., 2016; Sax & Gaines, 2003), make it imperative to consider biodiversity-mediated global change effects (Díaz et al., 2007). However, few global change studies have explicitly considered both direct and indirect pathways (Díaz et al., 2007; Isbell et al., 2013). In fact, despite several notable exceptions (e.g. Reich et al., 2001), the fields of global change and BEF research have developed largely independent of each other, although they shared focus on anthropogenic changes in ecosystem functions. Consequently, the relative importance of direct vs. indirect global change effects remains largely unexplored. Second, while much BEF research has shown that declining biodiversity may erode ecosystem functions, the extent to which this finding, based largely on experimentally assembled communities, can apply to natural communities under environmental stressors remains controversial (Duffy, Godwin, & Cardinale, 2017; Wardle, 2016). Much of the BEF research has directly assembled communities differing in diversity, while assuming random species extinction and colonization; the assembly of natural communities, however, is not random, such that species abundance and distribution patterns in natural communities typically differ from those of synthetic communities in BEF studies (Jiang, Wan, & Li, 2009; Wardle, 2016). It is thus necessary for future BEF studies to study natural communities directly and integrate biodiversity changes with their environmental change drivers in these communities, in order to obtain accurate predictions of ecosystem functioning under environmental changes (De Laender et al., 2016). Third, both species responses to environmental changes and impacts on ecosystem functions are regulated by their functional traits, mandating a trait-based approach to studying ecological consequences of environmental changes (Díaz et al., 2007; Violle et al., 2007). The need for the trait-based approach is further necessitated by the fact that environmental changes may cause species turnover without influencing species diversity (Avolio et al., 2014; Hillebrand et al., 2018; Jones, Ripplinger, & Collins, 2017), which can be readily captured by changes in functional diversity. We thus expect environmental changes may frequently alter functional diversity, even in the absence of changes in species diversity, with ensuing consequences for ecosystem functioning. Recent BEF research has investigated the role of functional diversity and phylogenetic diversity, which accounts for species evolutionary relationships and serves as a proxy of overall functional diversity, for ecosystem functions (e.g. Cadotte, Cardinale, & Oakley, 2008; Cadotte, Cavender-Bares, Tilman, & Oakley, 2009; Flynn, Mirotnick, Jain, Palmer, & Naeem, 2011; but see Venail et al., 2015). However, their roles in modulating

the responses of ecosystems to global changes remain largely unexplored. Of particular interest is how different components of functional diversity, such as the traits of dominant species and trait distribution among species that are known to influence ecosystem properties (Cadotte, 2017; Gagic et al., 2015; Roscher et al., 2012), modulate global change effects.

Many terrestrial ecosystems are limited by the availability of water (DeMalach, Zaady, & Kadmon, 2017) and nitrogen (LeBauer & Treseder, 2008). Human activities have altered global precipitation patterns, with varying effects across different regions (Zhang et al., 2007). Likewise, human activities have fundamentally shaped the nitrogen cycle (Vitousek, Aber, et al., 1997), to the point where the magnitude of global nitrogen cycling has doubled over the past century (Fowler et al., 2013). Consistent with water and nitrogen being common limiting resources, many studies have reported positive response of terrestrial productivity to increased water (Sala & Parton, 1988; Yang, Fang, Ma, & Wang, 2008) and nitrogen (LeBauer & Treseder, 2008; Xia & Wan, 2008) input. It is largely unknown, however, whether the observed productivity increases were driven mainly by species physiological responses or mediated by changes in biodiversity.

The temperate steppe in North China constitutes an important part of the Eurasian grassland biome and provides diverse products and services for the local residents (Kang, Han, Zhang, & Sun, 2007). This ecosystem, limited by both water and nitrogen availability (Bai, Han, Wu, Chen, & Li, 2004; Niu et al., 2010), is projected to experience increases in summer precipitation (Sun & Ding, 2010) and atmospheric nitrogen deposition (Liu et al., 2011) in the coming decades. Using an 11-year field experiment that manipulated water and nitrogen availability in this ecologically and economically important ecosystem, we explored the relative importance of direct and indirect (mediated through multiple dimensions of biodiversity) global change effects on plant primary productivity. Our study aimed at answering two questions. First, does plant functional diversity play an indispensable role in modulating environmental change effects on productivity? Second, do anthropogenic changes in the traits of dominant species and changes in functional dispersion (FD) among species have similar effects on productivity?

2 | MATERIALS AND METHODS

2.1 | Study sites and experimental design

Our study was conducted at the field station (116°17'E and 42°02'N, elevation 1,324 m a.s.l.) of the Institute of Botany of Chinese Academy of Sciences, located in Duolun county of Inner Mongolia, China. Mean annual precipitation is 379 mm and mean annual temperature is 2.1°C, with mean monthly temperatures ranging from -17.5°C (January) to 18.9°C (July). Soil is chestnut according to the Chinese classification and Calcis-orthic Aridisol in the US soil taxonomy classification. The dominant species in our study grassland include two grasses *Stipa krylovii* and *Agropyron cristatum* and one forb *Artemisia frigida*.

In early April 2005, we established seven blocks containing naturally assembled communities using a split-plot experimental design. Each block was divided into two main plots subjected to either ambient precipitation or water addition treatment. From June to August of each year, the water addition plots were sprinkled with 15 mm of groundwater weekly, resulting in a total of 180 mm additional precipitation during each growing season. Increased precipitation of similar magnitude has been observed in previous years (Xu et al., 2015) and is projected to occur more frequently in the future (Sun & Ding, 2010). Each main plot was divided into two 8 m × 8 m subplots, with each subplot randomly assigned to one of two nitrogen treatments: ambient or additional nitrogen. The nitrogen addition plots received granular urea (10 g nitrogen m⁻² year⁻¹) twice a year, each with equal amount in early May and late June; the amount of nitrogen addition is comparable to the estimated atmospheric nitrogen deposition rate in northern China (He, Liu, Fangmeier, & Zhang, 2007). This study thus contained four treatments: control (no water or nitrogen addition), nitrogen addition, water addition and nitrogen plus water addition. Both the blocks and subplots were separated by a 1 m wide buffer zone.

2.2 | Plant community survey and biodiversity calculations

In May 2005, a permanent quadrat of 1 m × 1 m was established in each subplot. In mid-July from 2005 to 2015, each plant species within the quadrat was recorded. Species richness of each subplot was defined as the total number of species recorded in the permanent quadrat. To estimate plant community productivity, above-ground biomass was harvested at its peak in early September each year within a randomly selected 0.15 m × 2 m strip in each subplot outside the permanent quadrat. The harvest was sorted by species and dried at 65°C for 48 hr before weighing for dry biomass.

To estimate the phylogenetic relations between the 114 plant species present in the experimental region, we first constructed a maximum likelihood (ML) phylogenetic tree. We constrained the family-level phylogeny to that in the APG III classification system. Then, we acquired the ITS gene sequences, which are commonly used in angiosperm phylogeny, of the studied species. The ITS gene sequences (ITS1-ITS4 region) of 79 species were obtained from GenBank (<http://www.ncbi.nlm.nih.gov>) and fresh leaves of the other 35 species, for which GenBank sequences are not available, were collected from our study site to determine their ITS gene sequences according to published protocols (Lin, Fleming, Kuo, Matthews, & Saunders, 2000). After aligning the sequences with ClustalX, we constructed one ML tree for each family in PhyML (Guindon et al., 2010) to improve the resolution of our phylogeny (see Figure S1 for a list of all species on the tree). We also constructed a phylogenetic tree for the 114 species according to Zanne et al. (2014). We used Mantel's test to compare the species-wise phylogenetic distance matrices between the two versions of trees; the results indicated that results based on the two trees were similar ($r = .921$,

$p < .001$). Here, we only reported the results based on the ITS tree. For each subplot in each year, we quantified community phylogenetic diversity using the net relatedness index (NRI), following Webb, Ackerly, McPeck, and Donoghue (2002). Results based on the nearest taxon index, another commonly used metric of phylogenetic diversity (Webb et al., 2002), were qualitatively similar.

In July 2008 and 2014, we measured five plant functional traits: plant stature (S), leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC) and leaf nitrogen concentration (LN), for each species within a 0.5 m × 0.5 m quadrat in each subplot. These traits are known to be important for acquiring sources and determining species abundance in grasslands (Ansquer, Duru, Theau, & Cruz, 2009; Laliberté, Shipley, Norton, & Scott, 2012). The stature of each species was determined as the mean values of five randomly selected individuals; all observed individuals were measured for species with less than five individuals. Afterwards, all the above-ground living tissues in the quadrat were clipped by species to determine leaf area (using Sigmascan 4.1) and to measure leaf fresh mass; plant leaves were then dried at 70°C for 24 hr and weighed for the calculation of SLA and LDMC. The dry leaf materials were ground and sieved through a 0.25 mm screen to determine total nitrogen concentration using a Vario MICRO Cube elemental analyzer (Elementar, Hanau, Germany).

We quantified functional diversity of our study communities using two metrics: community-weighted mean (CWM) and functional dispersion (FD_{is}), following Díaz et al. (2007). CWM for each of the five plant functional traits was calculated as:

$$\text{CWM} = \sum p_i \times \text{trait}_i \quad (1)$$

where p_i is the relative abundance of species i in the community, and trait_i is the trait value of species i (Lavorel et al., 2008). CWM represents the expected trait value of a randomly sampled individual from a community (Garnier et al., 2004) and is strongly driven by the trait values of the dominant species. A significant effect of CWM on ecosystem functions would thus indicate that ecosystem processes are largely driven by the traits of dominant species (Díaz et al., 2007; Garnier et al., 2004). We calculated FD_{is} for all traits together, following (Laliberté & Legendre, 2010):

$$\text{FD}_{\text{is}} = \sum (a_{ij}z_j) / \sum a_j \quad (2)$$

where a_j is the abundance of species j and z_j is the distance of species j to the weighted centroid \mathbf{c} , calculated as

$$\mathbf{c} = \sum (a_{ij}x_{ij}) / \sum a_j \quad (3)$$

where x_{ij} is the trait value of species j for trait i . FD_{is} measures the variation in trait values among species within a community and has several advantages over other metrics of functional diversity, including its insensitivity to species richness and ability to incorporate species relative abundance (Laliberté & Legendre, 2010). A significant effect of FD_{is} for ecosystem processes suggests that multiple species with different traits contribute to these processes (Roscher et al., 2012).

2.3 | Soil water and nitrogen concentration

Two soil cores (3 cm in diameter and 10 cm in depth respectively) were collected from each subplot biweekly between May and September of each year (2007–2015). The soil cores were weighed and dried to constant weight to determine soil water concentration, calculated as the percentage of weight loss from fresh to dry soil. In early August of each year, soil samples (10 cm in depth) were collected from five randomly selected locations in each subplot and mixed. The mixed samples were used to measure soil inorganic nitrogen concentration using a flow-injection autoanalyser (FIAstar 5000 Analyzer, Foss Tecator, Denmark), following extraction with solutions of 2 M KCl.

2.4 | Statistical analyses

Data on plant productivity, species richness and NRI were square-root transformed and data on soil inorganic nitrogen and CWM values of leaf area (CWM_{LA}) were ln-transformed to meet the normality assumption. Linear mixed-effects models with a split-plot design were used to assess the effects of water and nitrogen addition on plant community productivity, plant diversity (including species richness, phylogenetic diversity [NRI], CWM of each trait and FD_{is}) and soil water and inorganic nitrogen. Year was included as a random effect in the models. We checked the bivariate relationships among soil conditions, biodiversity metrics and community productivity, using data across the four treatments and the two sampling years (2008 and 2014) when species trait data are available. Then, we constructed an a priori piecewise structural equation model (piecewise SEM; Lefcheck & Duffy, 2015) based on the bivariate relationships to understand the causal pathways through which soil water and nitrogen availability influences productivity, where both direct and indirect (via changing various aspects of plant diversity) pathways were considered (see Figure S2). We simplified the initial model by eliminating non-significant pathways and state variables based on regression weight estimates. Overall fit of the piecewise SEM was evaluated using Shipley's test of d-separation, Fisher's C statistic and AIC. The above analyses were also conducted using the 11-year (2005–2015) data collected for measures other than species traits; the results are qualitatively the same as those based on the 2-year

(2008 and 2014) data; thus, we only report the latter results here. The piecewise SEM was constructed using the piecewise SEM package in R (R Development Core Team, 2013). The remaining statistical analyses were conducted using SPSS 13.0 (SPSS, Inc., Chicago, IL, USA).

3 | RESULTS

3.1 | Effects of water and nitrogen addition on productivity and biodiversity

Plant community productivity showed similar, marked increases in response to water and nitrogen addition; the effects of the two treatments were additive, resulting in the largest productivity increase in plots amended with both water and nitrogen (Table 1; Figure 1). By contrast, water and nitrogen addition had opposite

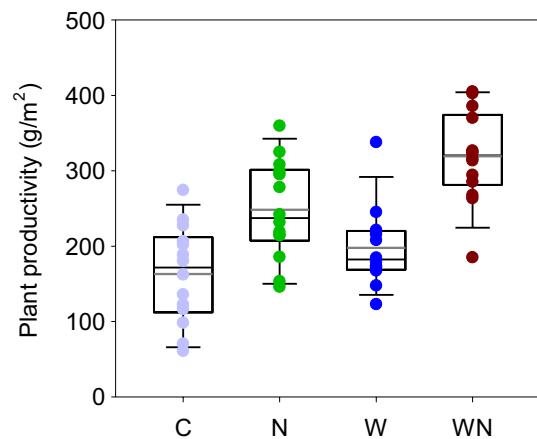


FIGURE 1 Boxplot showing the differences in plant community productivity among nitrogen and water treatments. C: control, N: nitrogen addition, W: water addition, WN: water plus nitrogen addition. The black and grey lines within the box represent the median and mean of plant productivity, respectively, across the two sampling years (2008 & 2014); box limits indicate the plant productivity in the 25–75th percentile range. Error bars indicate the 10th and 90th percentiles. The closed dots show the distribution of plant productivity data in each treatment. Water and nitrogen addition stimulated plant productivity additively, with the WN subplots yielding the highest productivity

TABLE 1 Results (F -values) of linear mixed-effects models with a repeated-measures split-plot design on the effects of block, water (W) and nitrogen (N) addition, and their interactions on plant community productivity (ANPP), species richness (SR), the net relatedness index (NRI), the community-weighted mean values of plant stature (CWM_S), leaf area (CWM_{LA}), specific leaf area (CWM_{SLA}), leaf nitrogen concentration (CWM_{LN}) and the leaf dry matter content (CWM_{LDMC}), functional dispersion (FD_{is}), soil water (SW) and soil inorganic nitrogen concentration (IN). Plant traits were measured based on five replicates. See Table S1 for the degrees of freedom for each variable

Source	Productivity	SR	NRI	CWM_S	CWM_{LA}	CWM_{SLA}	CWM_{LN}	CWM_{LDMC}	FD_{is}	SW	IN
Block	0.34	3.76**	1.57	0.59	0.54	0.01	0.54	1.08	0.07	0.02	0.22
W	13.54***	6.82*	1.68	3.22*	16.51***	12.99**	5.15*	6.82*	1.78	209.26***	3.34
N	50.16***	11.21**	0.33	15.59***	4.67*	7.37*	152.13***	0.23	4.64*	0.74	86.23***
W × N	0.53	0.59	0.39	1.96	0.97	1.90	0.04	0.54	0.00	5.61*	10.71**

* $p < .05$, ** $p < .01$, *** $p < .001$.

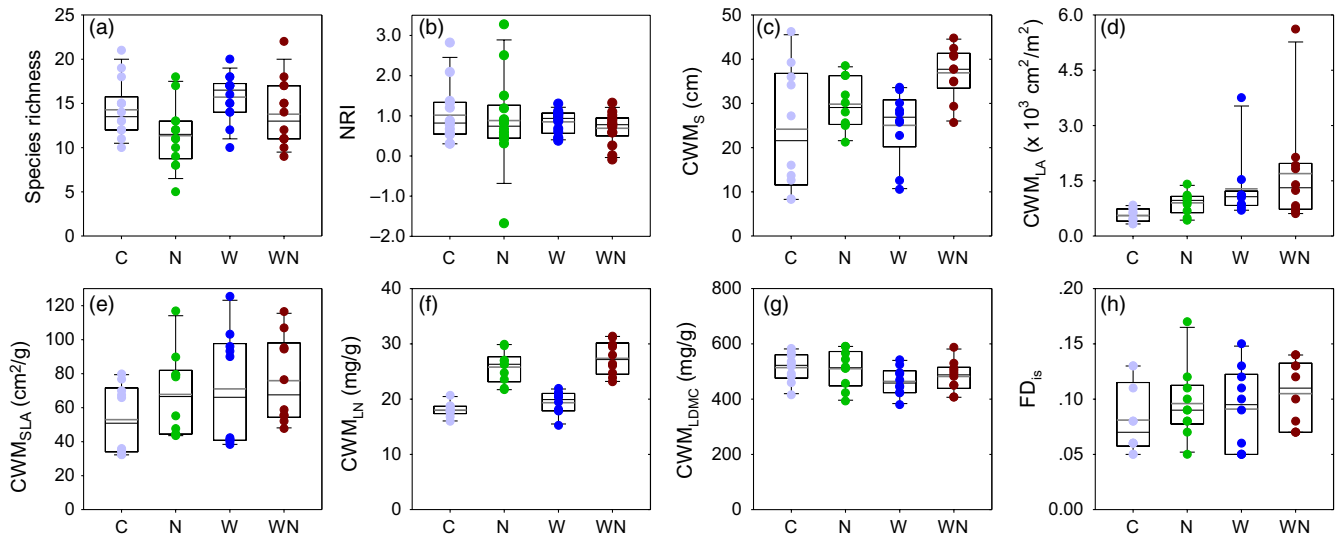


FIGURE 2 Boxplots showing the differences in plant diversity among nitrogen and water treatments across the sampling years. a) species richness, b) the net relatedness index (NRI), and on community weighted mean values for c) plant stature (CWM_S), d) leaf area (CWM_{LA}), e) specific leaf area (CWM_{SLA}), f) leaf nitrogen (CWM_{LN}) and g) leaf dry matter content (CWM_{LDMC}), and on h) functional dispersion (FD_{is}). C: control, N: nitrogen addition, W: water addition, WN: water plus nitrogen addition. The black and grey lines within the box represent the median and mean of plant diversity, respectively, across the two sampling years (2008 & 2014); box limits indicate the 25–75th percentile range. Error bars indicate the 10th and 90th percentiles. The closed dots show the distribution of plant diversity data in each treatment

effect on species richness, with the former effect being positive and the latter effect being negative (Table 1; Figure 2a). Neither treatment affected NRI as the measure of phylogenetic diversity (Table 1; Figure 2b). Water and nitrogen addition had similar positive effects on the CWM of the five functional traits we measured (Figure 2c–f), except for CWM_{LDMC} , which declined under water but not nitrogen enrichment (Table 1; Figure 2g). Nitrogen, but not water, addition increased FD_{is} (Table 1; Figure 2h).

3.2 | Relationships between soil water, soil nitrogen concentration, biodiversity and productivity

As expected, water addition increased soil water concentration and nitrogen addition increased soil inorganic nitrogen concentration (Table 1; Figure S3). Also as expected, plant community productivity showed positive bivariate relationships with soil water and nitrogen concentration (Figure S4a,b). Somewhat unexpectedly, plant community productivity was not related to species richness and showed a negative bivariate relationship with NRI (Figure S4c,d). Functional diversity measures, including FD_{is} and CWM of most functional traits, showed positive bivariate relationships with community productivity (Figure S4e–i); CWM_{LDMC} , however, was unrelated to community productivity (Figure S4j).

When considering multivariate causal relationships with SEM, we found that soil water and nitrogen concentration influenced plant community productivity both directly as well as indirectly via changing plant functional diversity. The best SEM model retained CWM_S and FD_{is} as the additional explanatory variables for community productivity, while eliminating all other biodiversity measures (species

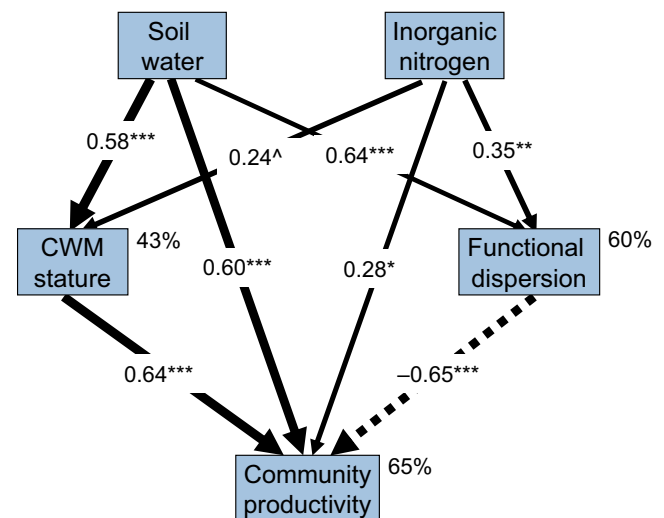


FIGURE 3 The final structural equation model relating soil water, inorganic nitrogen concentration, community-weighted mean (CWM) of plant stature and functional dispersion to plant community productivity. The final model adequately fitted the data: Fisher C = 5.82, $p = .054$, $df = 2$; AIC = 33.82. Solid and dashed arrows indicate significant ($^{\wedge}p < .10$, $*p < .05$, $**p < .01$, $***p < .001$) positive and negative pathways respectively. Arrow width is proportional to the strength of the relationship. Numbers along the arrows are standardized path coefficients indicating the effect size of the relationship. The proportion of variance explained (R^2) appears alongside response variables in the model

richness, NRI and CWM of the four other functional traits) (Figure 3). Besides directly benefiting community productivity, increasing soil

water and nitrogen concentration also caused the increase in CWM_S and FD_{is} , which in turn influenced community productivity. The effects of CWM_S and FD_{is} , however, were opposite of each other; whereas increasing CWM_S increased community productivity, increasing FD_{is} reduced community productivity (Figure 3).

4 | DISCUSSION

Our study differs from the majority of previous work on global change effects on ecosystems by considering the role of biodiversity, allowing us to assess the relative importance of direct and indirect pathways through which global environmental changes influence ecosystem properties. Our study also differs from the majority of existing BEF studies by examining BEF relationships in natural communities and by linking environmental drivers of biodiversity changes with the functional consequences of biodiversity changes, echoing recent call for this type of research (De Laender et al., 2016). By explicitly considering plant functional diversity in relation to global change factors and plant community productivity, our study provides the rare demonstration that global environmental changes influence plant productivity both directly and indirectly, with the latter effect via altering different components of plant functional diversity. Therefore, plant functional diversity plays an important role in modulating global change effects on the productivity of the natural steppe we studied.

Consistent with many other studies of grassland ecosystems (DeMalach et al., 2017; Stevens, Dise, Mountford, & Gowing, 2004), increase in soil water and nitrogen availability increased plant community productivity in our experiment. Water serves as the reactant in various biochemical processes, and as the medium transporting mineral nutrients between soil and plants and transporting nutrients and photosynthetic products between plant tissues. Water addition in water-limited systems thus increases nutrient uptake and transport, promoting plant physiology and growth (Kozłowski, 1968; Patrick et al., 2007). Increased water supply may also enhance plant productivity by promoting litter decomposition (Wang et al., 2017) and mineralization (Kozłowski, 1968), which results in improved soil nutrient availability. Accordingly, in our water-limited study, grassland water addition increased plant leaf production (Ren et al., 2011) as well as the production of plant tillers (Xu, Wan, Zhu, Ren, & Han, 2010), contributing to increased plant productivity. Nitrogen is essential for the synthesis of structural and enzymatic proteins as building blocks of plant tissues (Lawlor, 1995; Lawlor, Lemaire, & Gastal, 2001; Lemaire et al., 1992). Nitrogen application in nitrogen-limited systems is known to enhance plant CO_2 assimilation (Theobald, Mitchell, Parry, & Lawlor, 1998), tissue formation (Lawlor & Young, 1989) and leaf production (Lemaire et al., 1992). Accordingly, nitrogen enrichment has been found to stimulate net carbon sequestration and increase leaf area and biomass in our study grassland (Niu et al., 2010; Ren et al., 2011), contributing to increased plant productivity.

Our most important findings are that both components of functional diversity, CWM_S and FD_{is} , modulated the effects of water and nitrogen amendment on plant community productivity and that their effects were opposite to each other. SEM revealed that water and nitrogen amendment had indirect positive effects on community productivity, primarily through increasing the CWM of stature (CWM_S), a crucial trait that influences plant carbon sequestration capacity, competitive ability and multiple aspects of plant ecological strategies (Moles et al., 2009). Note that CWM of several other traits, including leaf area, SLA and LN, also increased with water and nitrogen addition, reflecting the overall increased fitness of study species under improved water and nitrogen conditions. The CWM of these traits also showed positive relationships with plant community productivity in bivariate regressions but were eliminated from the final SEM model because they tend to be closely associated with plant height (sensu Falster & Westoby, 2003). The importance of CWM for ecosystem functioning is a quantitative translation of the mass ratio hypothesis (Spasojevic & Suding, 2012), which states that ecosystem functions are relatively insensitive to changes in species richness, but determined, to a large extent, by the traits of the dominant species (Grime, 1998). The dependence of community productivity on community-weighted means of the measured traits, together with the independence of community productivity from species richness, provide strong support for the mass ratio hypothesis. In our experiment, dominant species (e.g. *S. krylovii*, *A. cristatum*) attained the largest biomass and the tallest stature, both of which increased under improved water and nitrogen conditions, contributing significantly to increased overall ecosystem productivity.

Concurrent with changes in CWM of the measured functional traits, SEM also identified a second indirect pathway in which water and nitrogen availability influenced productivity by altering the dispersion of these functional traits. Strikingly, the net effect on productivity through this indirect pathway is negative; whereas FD increased under improved soil water and nitrogen conditions, increased FD had a negative effect on productivity. The increase in FD in a community could arise from the extinction of species with similar traits or the colonization of species with distinct traits. Inspection of species trait data reveals that the latter scenario drove the increase in FD under water/nitrogen amendment. For example, water enrichment promoted the colonization of *Dysphania aristata*, which had the lowest stature, smallest leaf area and second highest LDMC among all species present in the water amendment plots, and *Poa subfastigiata* which was the second lowest in both leaf area and LDMC in the water amendment plots. Even in nitrogen amendment plots where species richness declined (i.e. the number of extinct species greater than colonized species), some of the successful colonizers possessed distinct traits than their neighbouring species (e.g. *Allium neriniflorum* being the smallest in leaf area, lowest in LDMC and second smallest in SLA; *Salsola collina* being the second smallest in leaf area and third smallest in SLA). The successful colonization of these species under nitrogen/water amendment may have been made possible by the improved resource availability (Davis, Grime, & Thompson, 2000) as well as their distinct niches

that allow them to escape strong competition from the resident species (Li et al., 2015).

It has been suggested that the increase in the variety of functional traits in a community may allow the community to utilize a greater variety of resources, leading to greater ecosystem functioning (Díaz & Cabido, 2001; Petchey & Gaston, 2006). This intuitively appealing idea has received considerable support from BEF experiments, including those that manipulated functional group richness (e.g. Tilman et al., 1997) and those that considered continuous measures of function trait distribution (e.g. Petchey, Hector, & Gaston, 2004). Some recent BEF studies have explicitly linked functional trait distribution to niche complementarity and selection effects, demonstrating that greater niche complementarity in communities with broader trait distribution contributes to increased ecosystem functioning (e.g. Cadotte, 2017; Roscher et al., 2012). By contrast, our study showed that increasing FD, as a result of global environmental changes, could have a negative effect on natural ecosystem productivity. While seemingly puzzling at first, this result may be explained by the non-random assembly of our study communities. Specifically, while water/nitrogen addition promoted the colonization of functionally distinct species, resulting in increased FD, these functionally distinct species generally attained little biomass (accounting for 5.7% and 2.8% of the total community biomass in water and nitrogen addition plots respectively) and, therefore, contributed little to overall ecosystem productivity. The presence of these low-biomass species leaves less space and fewer resources for species with potential for large biomass production, causing productivity to decline (see Norberg et al., 2001 for a prediction of this pattern). This non-random community assembly may also be the reason that the productivity was not related to species or phylogenetic diversity in our SEM. Note that this scenario is akin to the dilution effect in disease ecology, where the presence of suboptimal hosts reduces the transmission and prevalence of vector-borne diseases (Ostfeld & Keesing, 2000). Our result thus casts an important cautionary note on the perceived importance of functional diversity for the functioning of natural communities.

We found contrasting effects of nitrogen enrichment and water addition on grassland plant species richness, a finding also reported by several previous studies (Stevens, Shirk, & Steiner, 2006; Yang et al., 2011; Zavaleta et al., 2003). The decline in species richness with nitrogen enrichment has been attributed to a host of mechanisms, including soil acidification (Lu, Jiangming, Franks, Zhou, & Fang, 2010), exacerbated water limitation due to elevated transpiration (Zavaleta et al., 2003), increased competition for light (Hautier, Niklaus, & Hector, 2009) and reduced niche dimensionality (Harpole & Tilman, 2007). Our experiment, however, was not designed to identify the exact mechanism(s) driving species diversity decline under nitrogen enrichment. Although water addition also increased above-ground biomass, resulting in greater competition for light, water addition had a positive effect on species richness. This result may be explained by at least two mutually non-exclusive mechanisms. First, water addition may have promoted plant germination and establishment, as indicated by the increase in the number of

plant individuals under water addition in our experiment (Xu et al., 2010). Second, increased water availability favoured shallow-rooted forbs that were generally disadvantaged in dry soils (Xu et al., 2015; Yang et al., 2011), preventing their competitive exclusion by dominant grasses.

Despite significant treatment effects on plant species richness, plant species richness is not a significant predictor of productivity in either bivariate regression or SEM. This is at odds with plant species richness often being positively related to productivity in BEF experiments (Cardinale et al., 2006; Spehn, Joshi, Schmid, Diemer, & Korner, 2000; Tilman et al., 2001, 2014). One possible explanation for this discrepancy is the difference in the assembly of natural communities vs. synthetic communities in BEF studies. Random community assembly in BEF experiments facilitates the operation of complementarity and positive selection effects (Jiang et al., 2009; Wardle, 2016), two primary mechanisms contributing to positive diversity–productivity relationships (Loreau & Hector, 2001). However, these two mechanisms tend to be much less important in natural communities where abundant species contribute most to community productivity but rarely experience extinction (Jiang et al., 2009; Wardle, 2016). Although rarely mentioned, this explanation could also potentially account for the weak relationship between species richness and productivity reported for other natural grassland communities (Adler et al., 2011; Grace et al., 2007).

Phylogenetic diversity has recently been proposed as a convenient proxy of species functional trait distribution, on the ground that more closely related species tend to share more similar traits (Cadotte et al., 2008). A number of BEF experiments have reported positive relationships between plant phylogenetic diversity and community productivity (summarized in Venail et al., 2015), and some of these studies have shown that phylogenetic diversity better predicts productivity than species richness (e.g. Cadotte et al., 2008; Flynn et al., 2011). However, phylogenetic diversity is also not a significant predictor of productivity in our experiment. This result may again be explained by non-random community assembly (see last paragraph). However, a more parsimonious explanation is that phylogenetic diversity may not necessarily be an effective proxy of functional trait diversity as often assumed. Consistent with this idea, when examining the phylogenetic signal of the five measured traits using plants grown in our control plots with Blomberg's K , we found that only two (leaf area and LDMC) exhibited a significant signal (leaf area: Blomberg's $K = 0.44$, $p = .01$; LDMC: Blomberg's $K = 0.35$, $p = .017$).

In conclusion, our results show that increase in growing season precipitation and nitrogen deposition increased plant community productivity directly as well as indirectly in the affected temperate grassland. The indirect effect on productivity, however, comes from water- and nitrogen-induced changes in functional diversity, not species or phylogenetic diversity. Importantly, while the two components of plant functional diversity, CWMs and FD, showed similar positive responses to water and nitrogen addition, their effects on productivity were opposite. When combined together, the overall indirect effect of water addition on productivity is positive

(i.e. positive changes via CWMs outweigh negative changes via FD), and the overall indirect effect of nitrogen addition is almost non-existent as the two indirect pathways cancel out each other (Figure 3). Overall, our study demonstrates the importance of both the traits of dominant species and functional trait distribution among species in modulating the effects of global changes on plant community productivity. It remains to be seen whether the observed negative effect of anthropogenic increases in FD on productivity, which challenges the paradigm of positive relationships between the two, could be generalized to other natural ecosystems experiencing global environmental changes.

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AUTHORS' CONTRIBUTIONS

Z.X., Y.J. and X.H. conceived the project; Z.X. and H.R. performed the field experiment; Z.X. and S.-P.L. analysed the data; Z.X. and L.J. wrote the paper. All authors contributed to manuscript revision and gave final approval for publication.

DATA ACCESSIBILITY

Data associated with this study are archived in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.689hp02> (Xu et al., 2018).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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