

# Direct and Indirect Effects of Precipitation Change and Nutrients Addition on Desert Steppe Productivity in Inner Mongolia, Northern China

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## Research Article

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# Abstract

**Background and Aims** Global changes profoundly impact on structure and function of grassland ecosystem. However, it remains unclear on the mechanism of how multiple limiting resources affect plant community primary productivity (ANPP) in desert steppe.

**Methods** Here, we conducted an experiment to examine the effects of precipitation changes (natural and  $\pm 50\%$  precipitation) and nutrient addition (=N:  $0 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ; +N:  $10 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ; +NPK: N/P/K each for  $10 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ) on species diversity, ANPP, functional traits and soil properties. We used structural equation model (SEM) to evaluate the effects of precipitation changes and nutrient addition on ANPP.

**Results** Increased precipitation increased species diversity and ANPP under NPK addition, NPK addition increased ANPP under increased precipitation, and the interaction of precipitation changes and nutrient addition was significant for ANPP. Drought reduced plant height and leaf dry matter content (LDMC), but increased leaf nitrogen content (LNC). ANPP was positively correlated with species richness, abundance, height and LDMC, but negatively correlated with specific leaf area (SLA) and LNC. The SEM showed increased precipitation and nutrient addition directly increased ANPP. Altered precipitation indirectly affected ANPP through its effect on abundance and SLA, while nutrient addition indirectly affected ANPP only through its effect on abundance.

**Conclusion** The combined limitations of precipitation and multiple nutrients deserves more attention in studying the effect of global changes on productivity in arid steppe. Our results highlight the importance of species diversity and functional traits in driving short-term responses of ANPP to environmental factors in desert steppe ecosystems.

## Introduction

Under the influence of human activities, global change has an appreciable impact on terrestrial ecosystems (Chen et al. 2013; Hautier et al. 2009; Zhang et al. 2020). There are increasing evidences that extreme drought and extreme precipitation events occur frequently in arid areas of northern China (Kim et al. 2020; Luo et al. 2019; Naumann et al. 2018). Precipitation is the most important driving force of plant productivity in steppe (Lu et al. 2018b; Wilcox et al. 2016). Many studies have shown that productivity of steppe is positively correlated with precipitation (Bin et al. 2014; DeMalach et al. 2017). However, increased precipitation also causes soil erosion and organic matter loss, thus reducing productivity of steppe (Gao et al. 2013). Further study is needed to explore the impact of precipitation changes on the productivity of grassland ecosystems. In addition, human industrial and agricultural activities led to a sharp increase in atmospheric nitrogen (N) deposition (Fowler et al. 2013; Galloway et al. 2008), resulting in the accumulation of available nitrogen, which is gradually improving productivity (Dziedek et al. 2017; Epstein et al. 2002). The restriction of other elements caused by nitrogen enrichment further counteracts the positive effect of nitrogen increase on plant growth (Wang et al. 2018; Zhan et al. 2019). Phosphorus (P) is an essential element for plant energy transmission and growth (Baldarelli et al. 2021; Falkowski et

al. 2000), while potassium (K) can not only improve the uptake and utilization of nitrogen, but also enhance the resistance of plants (Deng et al. 2017; Hooper and Johnson 1999; Mao et al. 2020; Vitousek et al. 2010). Human disturbance (such as deforestation and fertilization) leads to soil erosion and acidification, which in turn leads to loss of available P and K from plants to eutrophication of rivers and lakes (Cloern 2001; Conley 1999; Rader and Richardson 1994). Previous studies have focused on the effects of P and K on aquatic and agro-ecological system (Moura et al. 2016; Obersteiner et al. 2013; Perini and Bracken 2014; Shin 2014). However, there is still a lack of research on the effects of precipitation change, different nutrient addition types and their interaction on terrestrial grassland ecosystem.

Community vegetation characteristics and function traits are the adaptation characteristic of internal physiology and external form formed by plants in response to environmental change (Butterfield and Suding 2013; Cleland and Harpole 2010; Ma et al. 2019). Species diversity reflects vegetation characteristics and biological distribution dynamics (Hooper et al. 2005). Most studies suggested that resource enhancement reduces species diversity (Harpole et al. 2016; Isbell et al. 2013; Siddique et al. 2010; Soons et al. 2017; Suding et al. 2005). Yet classical ecological theory predicts that resource-rich environments can accommodate more species. In addition, evidence is growing that nitrogen additions may alleviate ecosystem N limitation leading to increased species diversity in degraded, resource-poor communities (Bai et al. 2010). A study of the desert steppe in North America indicated species richness varied with seasonal precipitation but was not affected by N addition (Ladwig et al. 2012). Community weighted mean values (CWM) reflects the impact of dominant species on ecosystem function (Cadotte 2017). Most scholars deemed that light acquisition traits (such as plant height and SLA) were positively correlated with precipitation and N addition (Zhan et al. 2019; Zhang et al. 2019a). Nutrient acquisition traits, such as LNC, increased with drought and N application (Lu et al. 2018a). While another study shown SLA remained constant but LDMC decreased with increasing aridity in temperate steppe (Luo et al. 2019). It is crucial to study the responses of species diversity and community functional traits to the change of precipitation and nutrients for understanding the structure and function of desert steppe.

Soil physical and chemical environment is the main source of water and nutrients needed for plant growth. The response of soil properties to precipitation changes and nutrient addition further affects the vegetation structure and function. Growing studies shown that N addition leads to soil acidification (Lu et al. 2014; Tian and Niu 2015). Whereas buffering capacity on the soil acid was detected from phosphorus and water addition (Cai et al. 2017; Mao et al. 2017; Wang et al. 2020). However, it is rarely reported how the soil system responds to precipitation change and multiple nutrient additions, as well as whether it further affects plant productivity of desert steppe.

Above-ground net primary productivity (ANPP) is the most basic and important function of grassland ecosystem (Foley 1994; Gower et al. 1999). Recent studies have suggested that plant functional traits can serve as a bridge between environmental change and ecosystem productivity (Forrestel et al. 2017; Lavorel and Grigulis 2012). For example, a meta-analysis highlighted the addition of water increased productivity by promoting the growth of forb (DeMalach et al. 2017). N addition has direct and indirect

effects on community primary productivity by influencing community specific leaf area and leaf phosphorus content (Zhan et al. 2019). Another study conducted N-induced stimulated community functional traits by increasing canopy light retention and decreasing resource utilization, sequentially actuated alpine grassland ecosystem productivity (Zhan et al. 2019). Furthermore, species richness, plant height and soil properties had significant effects on plant productivity in sandy grassland (Zuo et al. 2016). However, it still unknown whether precipitation and nutrient addition affect ANPP through regulating species diversity or community functional traits in desert steppe.

The desert steppes, a kind of transitional grassland from grassland to desert, are located in the interior of Eurasia. As an important part of temperate grassland ecosystem, it owns uniqueness in ecological geographical conditions, community structure and function (Luo et al. 2020; Zhang et al. 2019b). However, there are few studies on the interaction between water and nutrients in desert steppe. A N addition experiment in desert grassland in central New Mexico, USA found that species richness was only affected by inter-annual rainfall changes and not altered by N enrichment, while ANPP was related to the interaction between inter-annual and N addition (Ladwig et al. 2012). But in many grassland ecosystems, the addition of water and nutrients tended to reduce community heterogeneity and increase ANPP (Chalcraft et al. 2008; Isbell et al. 2013; Kimmel et al. 2020). The Urat desert grassland is located in an arid and semi-arid marginal area of northwest Inner Mongolia (Luo et al. 2020; Luo et al. 2018). Previous studies just focused on the response of the desert steppe ecosystem to precipitation change (Luo et al. 2018). Compared with grassland, the nitrogen content of plant canopy in Urat desert steppe was less sensitive to drought (Luo et al. 2019). The carbon absorption capacity of desert steppe ecosystem enhanced with the increase of precipitation (Zhang et al. 2019b). A little is known the effects of water and multiple nutrients coupling on the structure and function of plant community in the desert steppe.

In this study, we asked the following questions: (1) How do species diversity, functional traits and soil properties respond to precipitation change and nutrient addition in desert steppe? (2) Which indicators of vegetation and soil systems drive variation in ANPP?

## Materials And Methods

### Site description

The experimental site is located in the central part of Urat Rear Banner, Inner Mongolia, China (41°25' N, 106°58' E, 1650 m a.s.l.). This area has a continental arid climate with mean annual temperature of 5.3 °C and mean annual precipitation of 151 mm (falling mainly in July and August, accounting for about 70% of total precipitation). The vegetation in this region is mainly desert shrub and desert steppe plant community (Zhang et al. 2019b). The soil is mainly grey brown desert soil and brown calcium brown soil following Chinese soil taxonomy system (<http://www.resdc.cn>).

The sampling site is placed in the comprehensive experimental field of Urat Desert Grassland Research Station of Chinese Academy of Sciences. The experimental field (350 hm<sup>2</sup>) has been enclosed since

2010, which is divided into *Stipa glareosa*, *Achnatherum splendens* and *Reaumuria soongarica* community from south to north (Du et al. 2019). The *Stipa glareosa* community is dominated by perennial species including *Stipa glareosa*, *Allium polyrhizum* and *Peganum harmala*. Additionally, several subordinate plant species includes *Allium mongolicum*, *Corispermum hyssopifolium*, *Salsola collina*, *Bassia dasyphylla*, etc.

## Experimental design

This experiment was carried out based on the Global Change Network platform established in July 2017, which is a manipulative experiment that simulates elements (such as precipitation change and nitrogen deposition) of global change. This platform is mainly used to study the effects of precipitation changes and nutrient addition and their interactions on *Stipa glareosa* communities. We monitored the rainfall of the growing season through the weather station of the experimental station. The increased precipitation treatment was watered by 50% using the underground water every week from April to August. The decreased precipitation treatment was manipulated to cover 50% of the precipitation in the experimental plot by using a strip-grooved flashing board arranged at equal intervals at the top of the canopy. The board was made of high-light transmittance polycarbonate permitted nearly 90% effective light radiation (Yue et al. 2019). Furthermore, we separated each plot by a metal partition (1 m deep) covered with plastic paper to reduce the lateral interference of water. The amount of nutrient (nitrogen (N), phosphorus (P), potassium (K)) addition was consistent with that of the Global Nutrient Addition Research network(<http://www.nutnet.org/>), which were applied by  $10 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  at the beginning of May each year. N fertilizer was added using resin coated urea (pure N content of 44%), P fertilizer was added using heavy calcium superphosphate ( $\text{P}_2\text{O}_5$  content is 40%, including 17% pure P), K fertilizer was added using potassium sulfate ( $\text{K}_2\text{O}$  content is 50%, pure K content of 40%).

Using a randomized complete block design with six blocks, we conducted three level water (Cont: natural precipitation; +50%: increased precipitation by 50%; -50%: decreased precipitation by 50%) and nutrient (= N:  $0 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ ; +N:  $10 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ ; +NPK: N/P/K each for  $10 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ ) treatment, respectively. Namely, there were 9 treatments (-50% × =N, -50% × +N, -50% × +NPK, Cont × =N (control), Cont × +N, Cont × +NPK, +50% × =N, +50% × +N, +50% × +NPK) randomly assigned in 6 × 6 m plots. Between each adjacent plot, a 2 m buffer strip was seated to avert interference with each other (Zhan et al. 2019).

## Sampling and measurement

During peak biomass in early August 2019, number of species was checked in one 100 cm × 100 cm quadrat randomly selected in each plot. Besides, the height of each species was measured with a tape. After that, the aboveground net primary production (ANPP) in the quadrat was harvested by species. Then it was dried at 65°C for 48 hours to a constant weight and weighed separately (Zhao et al. 2016).

At the same time, mature leaves of comparatively dominant species, which accumulatively represented over 90% of the total plant cover in each plot, were collected for the determination of leaf function traits (Luo et al. 2019). The plant function traits was measured using the handbook advocated by cornelissen

et al. (Cornelissen et al. 2003). In short, specific leaf area (SLA) is the one-sided area of a fresh leaf divided by its oven-dry mass. Therein, leaf area was scanned by tiling the leaves on the scanner and calculated with WinRHIZO software. Leaf dry matter content (LDMC) is leaf dry weight divided by leaf saturated fresh weight. Moreover, the carbon and nitrogen content of leaves were determined by elemental analyzer (vario Macro cube, Elementar, Hanau, Germany).

After removing the ground debris, three random soil cores (0–10 cm depth) were collected within each plot using a soil auger (3 cm-diameter). Then we evenly mixed the impurity removed soil samples and divided them into two (Zuo et al. 2016). One of the soil samples was air-dried and screened with a pore diameter 2 mm, which was used for the analysis and determination of soil physical and chemical properties. Soil pH and electrical conductivity (EC) were measured in a 1:5 soil-water supernatant (Multiline F/SET-3, Germany). Soil carbon and nitrogen content were assayed by elemental analyzer (Zuo et al. 2017). Another soil sample was used to quantify gravimetric soil water content (Luo et al. 2018). The soil bulk density was obtained by drying soil samples collected with ring knife (a 100 cm<sup>3</sup>) in an oven at 105°C for 48 hours.

## Statistical analysis

Based on the quantitative characteristics of the plant community recorded in August 2019, we analyzed the vegetation characteristics, functional traits, soil properties and other changes of the desert grassland community under different water and nutrient treatments. The calculation formulas of Shannon-Wiener

$$H = - \sum_{i=1}^S N_i \ln N_i$$

diversity index (H) is as follows: , where  $N_i$  is the relative important traits value of species  $i$  ( $N_i = ((\text{relative height} + \text{relative cover} + \text{relative biomass})/3)$ ) (Luo et al. 2019). While weighted-mean values of community functional traits (CWM) was calculated using the relative biomass of species as a weighting factor (Leps et al. 2011; Lu et al. 2018a). The linear correlation analysis was used to study the relationship between ANPP and species diversity, community functional traits and soil physical and chemical properties. Based on the correlations, a structural equation models (SEM) was constructed, in which precipitation change and nutrient addition were treated as exogenous variables; species diversity, community functional traits and soil properties were considered as endogenous variables; ANPP was regarded as response variable. By screening the related variables, we finally obtained a model with the lowest AIC value, Chi-square test ( $p > 0.05$ ), root mean square error of approximation (RMSEA  $< 0.05$ ) and goodness-of-fit index (GFI  $> 0.95$ ) (Zuo et al. 2016). Then we investigated the paths of the influence of precipitation change and nutrient addition on ANPP.

All data were presented as mean  $\pm$  1 SE ( $n = 6$ ). A mixed effect model was used to analyze the response of each variable to habitat change, in which water and nutrient addition were fixed factors and block was random factors. Community traits difference between water and nitrogen treatments was compared by using two - way ANOVAs, with Duncan's test performing multiple comparisons when ANOVA tests were considered significant ( $p < 0.05$ ). The functional diversity were calculated with FDiversity software

(Casanoves et al. 2011). SPSS22 and AMOS25.0 were used to analyze data and the structural equation model, respectively. SigmaPlot12.5 software and the basic Trendline package in R were used for drawing.

## Results

The species diversity was only positively correlated with precipitation, while aboveground net primary production (ANPP) was affected by positively correlated with precipitation and nutrient addition ( $p < 0.05$ , Table S1, Fig. 1a-d). However, species richness, relative abundance (density) and Shannon index were all enhanced by increased 50% precipitation under the treatment of NPK addition (Fig. 1a-c). Specifically, the interaction between precipitation and nutrient addition had a marginally positive effect on the Shannon index ( $p = 0.077$ , Table S1). The increase of precipitation improved ANPP on the whole ( $p < 0.001$ , Table S1, Fig. 1d), but the change of ANPP with precipitation gradient is slightly different under different nutrient treatments. Compared with natural precipitation, under ambient nutrients (= N) and NPK addition (+ NPK) conditions, decreased 50% precipitation (-50%) did not significantly reduced ANPP, but increased 50% precipitation (+ 50%) increased ANPP by 115% and 187%, respectively. With nitrogen addition (+ N), decreased 50% precipitation reduced ANPP by 46%, but increased 50% precipitation did not significantly enhanced ANPP. In addition, there was no conspicuous difference in the response of ANPP to nutrient addition types under natural and decreased 50% precipitation. Under the treatment of increased 50% precipitation, ANPP under NPK addition was 80.62% and 110.62% higher than that under = N and + N, respectively (Fig. 1d). Moreover, the interaction of water and nutrients had a significant effect on ANPP ( $p < 0.05$ , Table S1), and the coupling of increased 50% precipitation and NPK addition led ANPP to soar to the maximum at  $95.8205 \text{ g} \cdot \text{m}^{-2}$ .

CWM.height and CWM.LDMC were highly responsive to precipitation change ( $p < 0.001$ , Fig. 2a-b). Overall, decreased 50% precipitation reduced CWM.height and CWM.LDMC. But under the treatment of NPK addition, CWM.LDMC did not changed significantly with the precipitation gradient. CWM.SLA and CWM.LT had no significant response to precipitation change and nutrient addition ( $p > 0.05$ , Fig. 2c-d). LCC was positively correlated with precipitation ( $p < 0.05$ ), while LNC was negatively correlated with precipitation ( $p < 0.01$ ) and positively correlated with nutrient addition ( $p < 0.01$ , Table S2, Fig. 2e-f). However, under N addition, LCC was not significantly reduced by precipitation reduction. In addition, the effect of NPK addition on LNC was not significantly different from that of ambient nutrients under the treatment of decreased 50% precipitation. Nutrient addition types regulated the influence of precipitation change on community level functional traits.

Under ambient nutrients condition (= N), the change of precipitation had no effect on soil pH, but under added fertilizers conditions, decreased 50% precipitation reduced soil pH. Besides, NPK addition significantly decreased soil pH ( $p < 0.001$ , Table S2, Fig. 3a). EC was very sensitive to NPK addition. Compared with = N, EC increased by 304.30% ( $205.10 \text{ s} \cdot \text{cm}^{-1}$ ) and 276.12% ( $141.05 \text{ s} \cdot \text{cm}^{-1}$ ) with NPK addition at decreased 50% and natural precipitation, respectively. However, the effect of N addition on EC was not observed with increased 50% precipitation (Fig. 3b). In other words, increased precipitation diluted the effect of NPK addition on EC. Nonetheless, short-term water and nutrients manipulation did

not observably change soil bulk density, carbon and nitrogen content ( $p > 0.05$ , Table S1, Fig. 3d-f). Soil moisture content was positively correlated with precipitation ( $p < 0.01$ , Table S2, Fig. 3c), and reached the lowest value (3.27%) with decreased 50% precipitation  $\times$  nitrogen addition.

Species richness, density (abundance), height and LDMC were positively correlated with ANPP, but SLA and LNC were negatively correlated with ANPP ( $p < 0.05$ , Fig. 4). However, no significant correlation was found between soil properties and ANPP (Table S2). It is worth mentioning that the three indicators with high interpretation rate of ANPP were density ( $R^2 = 0.439$ ,  $p < 0.0001$ ), CWM.height ( $R^2 = 0.282$ ,  $p < 0.0001$ ) and CWM.SLA ( $R^2 = 0.182$ ,  $p < 0.01$ ) respectively. We established a structural equation model (SEM) ( $\chi^2 = 0.268$ , d. f. = 3,  $p = 0.966$ , RMSEA = 0.000, GFI = 0.998) fitted the variance best and explained 69% variances in ANPP (Fig. 5). The SEM showed that both precipitation change and nutrient addition had direct and indirect effects on ANPP. Specifically, nutrient addition indirectly affected ANPP through a weak positive effect on abundance (density). Accordingly, increased precipitation indirectly positively affects ANPP by increasing abundance and regulating SLA (Table 2, Fig. 5).

## Discussion

Species diversity and aboveground net primary productivity (ANPP) were more sensitive to increased precipitation under NPK addition. Richness is generally positively correlated with precipitation in temperate grasslands (White et al. 2014) (Yang et al. 2011). However, a globally distributed nutrient addition experiment indicated the addition of multiple limiting resources reduces the diversity of grassland (Harpole et al. 2016). In contrast, an increase in diversity with increased precipitation was observed only with the treatment of NPK addition in our study (Fig. 1). One possible explanation is that in the Urat desert steppe, light resources are abundant and the surface vegetation cover is low, resulting in less competition for light resources among plants. Therefore, removal of nutrient constraints results in increased precipitation providing niches for more species and also increasing density of vegetation (Lu et al. 2018b). It also verified the physiological tolerance hypothesis, which suggests that benign environments support more species (Spasojevic et al. 2014). Moreover, the relief of water stress enabled NPK addition to exert the enhancement effect on ANPP (Kuchenbuch et al. 1986; Liu et al. 2018; Yang et al. 2008). And the effect of NPK addition on ANPP was dramatically more significant than that of single N addition. The addition of P and K can remove the P limitation caused by single N application, thus allowing plants to make better use of N fertilizer (Perini and Bracken 2014; Vitousek et al. 2010).

Decreased precipitation reduced community plant height and leaf dry matter content (LDMC). Height and LDMC, as important light acquisition traits, reflect the ability of plant to acquire resources and adapt to the environment change (Wilson et al. 1999; Zhan et al. 2019). Water is the most important limiting factor in arid desert steppe, the decrease of precipitation affected the dry matter accumulation and photosynthetic capacity of plant communities (Ma et al. 2019). A research manifested that the drier grassland ecosystem was more sensitive to drought and its resistance was weaker (Knapp et al. 2015). However, SLA has no obvious response to water and nutrient addition, which was different from previous research results that N enrichment increased SLA (Zhan et al. 2019). This may be because precipitation



enhancement affects the species composition of the *Stipa glareosa* community, which makes the *Stipa glareosa* dominant position prominent. Our previous studies have shown that *Stipa glareosa* adopted a relatively conservative strategy to cope short-term environmental changes (Hu et al. 2020). LNC was diluted by increased precipitation, which is mutually verified with the result that drought led to increased LNC (Luo et al. 2020).

Increased precipitation reduced the effects of nutrient addition on soil pH and EC (Fig. 3). Our research displayed the addition of NPK significantly reduced soil pH and enhanced EC under natural and decreased 50% precipitation. Increased precipitation could enhance the exchange ability of soil basic cations thus diluted the influence of nutrients on pH (Cai et al. 2017). Furthermore, increased precipitation reduced the surface (0–10 cm) salinity by soil fully leaching (Akther et al. 2021). N addition mediates the effect of drought on soil water content reduction. The response of arid grassland to drought is stronger (Dziedek et al. 2016), and N addition could decrease plants' drought resistance (Yu et al. 2019). However, the carbon and nitrogen content and bulk density of soil did not respond significantly to such short-term habitat changes. This may be attributed that the nutrient release rate of slow-acting resin coated urea is limited by the amount of fertilizer applied and the number of years of application. Alternatively, it may be because these three soil properties were relatively stable in desert grasslands with sparse vegetation in the short-term experiments. This has yet to be confirmed by long-term observations.

The above-ground net primary productivity (ANPP) is comprehensive embodiment of the structure and function of grassland ecosystem. Previous studies in temperate sandy grasslands have shown that plant height and species richness significantly affected plant biomass (Zuo et al. 2016). But CWM.height, although strongly correlated with ANPP, was not retained in the final SEM in our experiment. This difference may be due to nutrient addition and regional heterogeneity. Besides, ANPP was weakly correlated with species richness ( $R^2 = 0.0758$ ,  $p < 0.05$ ), which is similar to the experimental results of N addition in the alpine meadow of Tibet Plateau (Zhan et al. 2019). The difference with their results is that, in our SEM, precipitation, rather than nutrient addition, induced CWM.SLA to have a negative effect on ANPP. It may be due to the phenotypic plasticity of desert steppe plants (Gabriel 2006; Kreyling et al. 2019). With the increase of precipitation, plants adopt the growth strategy of rapidly acquiring and utilizing resources, low SLA of new leaves is conducive to preventing excessive water loss and improving photosynthetic capacity of leaves (Luo et al. 2019). Therefore, altered precipitation maximized ANPP by regulating the amount and biomass proportion of plants with low SLA in the community. The reason why soil properties were not selected into the SEM may be related to the short term in our experiment.

## Conclusion

This study demonstrates how precipitation changes and nutrient addition affect species diversity, community-level functional traits, ANPP and their relationship in desert steppe. Our results suggest ANPP responds strongly to the interaction between increased precipitation and NPK addition. Both increased precipitation and nutrient addition not only have direct positive effects on ANPP, but also indirectly increase ANPP by increasing plant density. Community-level SLA mediates the effect of altered

precipitation on ANPP. Longer term field observations are needed to more definitively determine how changes in limiting resources induce community composition and functional traits to affect productivity in desert steppe. Our study provides a theoretical basis for predicting the response of vegetation structure and function of desert steppe to multiple global change factors. It is critical to understand the influence mechanism of precipitation and soil nutrients changes on productivity for the management of arid grassland ecosystems.

## Declarations

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**Conflicts of Interest** The authors declare no conflict of interest.

**Author Contributions** X.Z. and X.G. designed experiments; X.G., X.L., and Y.H. conducted the experiments and analyzed the data; X.G. wrote the manuscript; X.Z. and P.Y. revised the manuscript. All authors have read and agreed to the published version of the manuscript.

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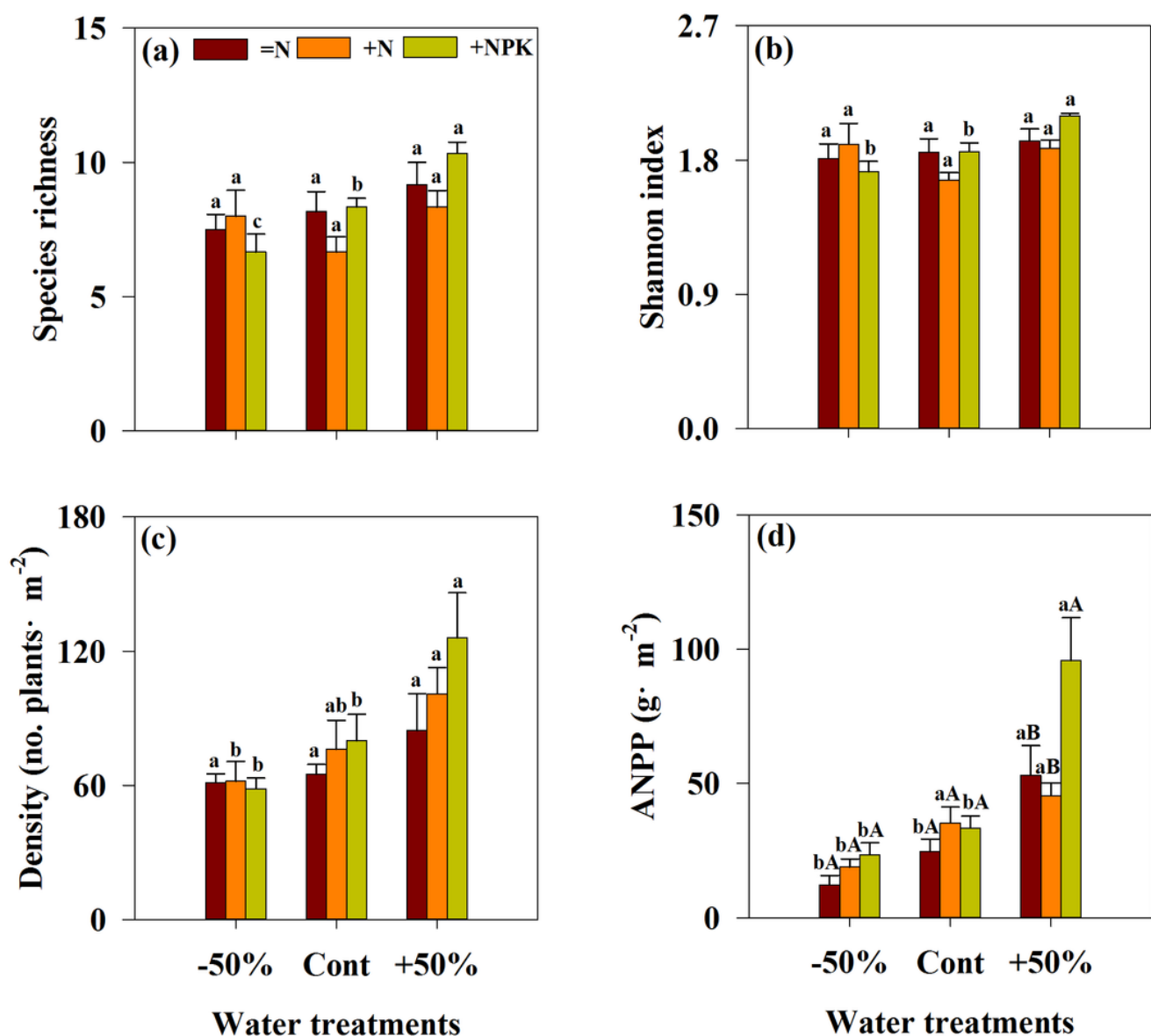
## Tables

Table 1 Direct, indirect and total effects on above-ground net primary productivity (ANPP) on standardized values of statistically significant SEM paths ( $p < 0.05$ ). Direction of relationship indicated by + (positive relationship) or – (negative relationship)

Predictor	Pathway to ANPP	Effect
Precipitation	Direct	0.384
	Indirect	0.266
	Total	0.65
Nutrient	Direct	0.229
	Indirect	0.08
	Total	0.309
CWM.SLA	Direct	-0.287
	Indirect	NS
	Total	-0.287
Abundance	Direct	0.368
	Indirect	NS
	Total	0.368

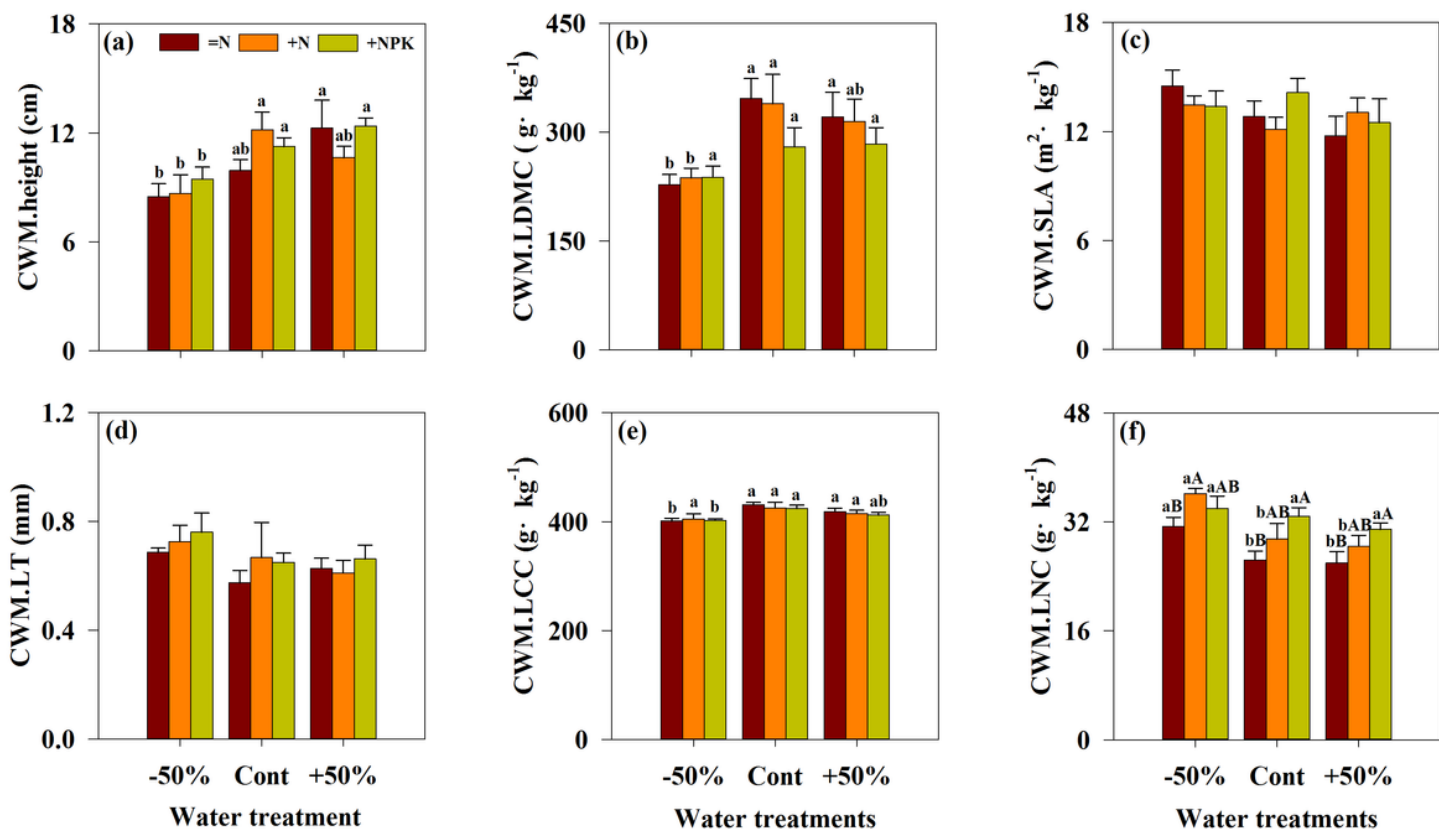
NS, no significant relationships.

## Figures



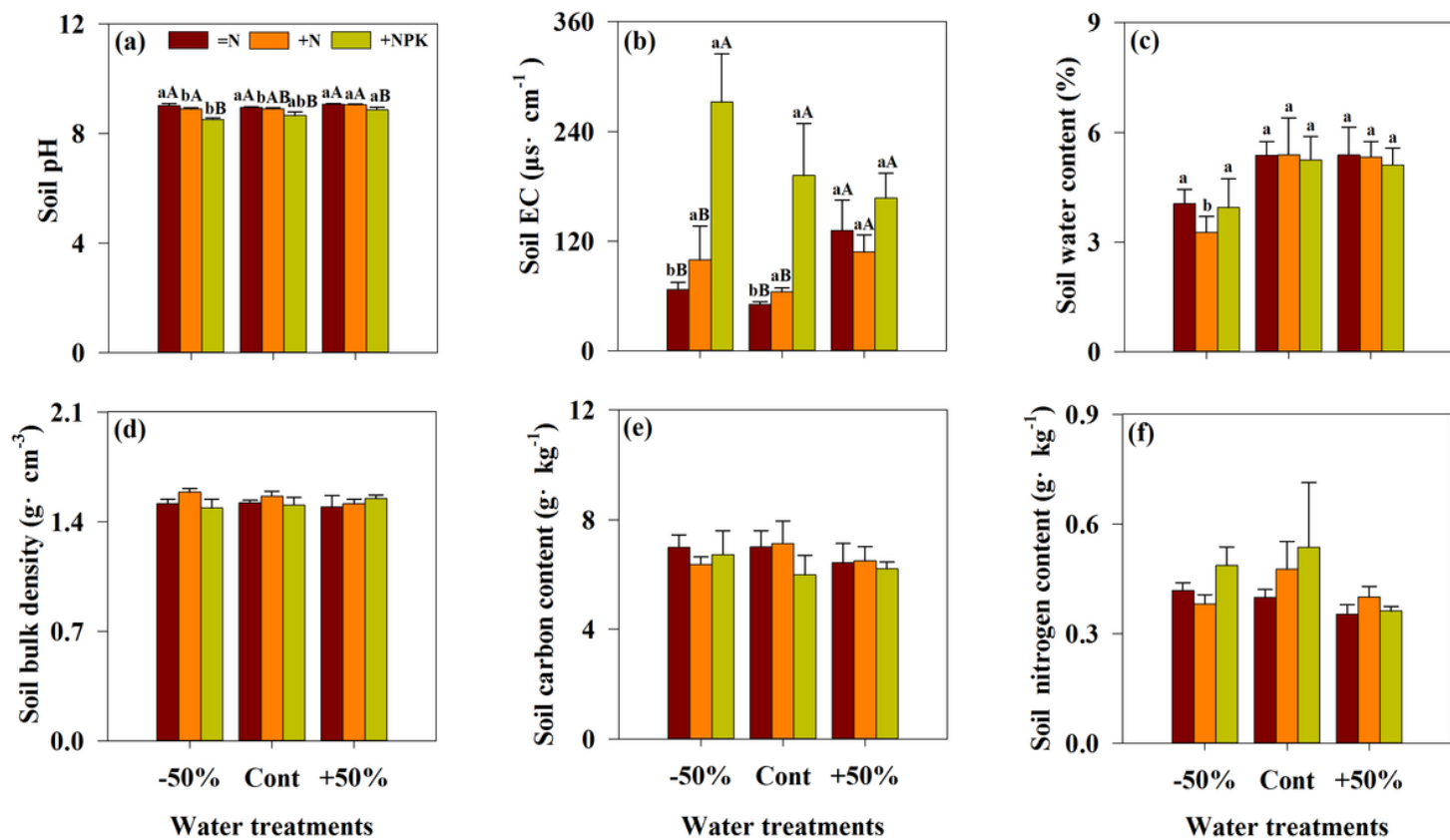
**Figure 1**

Response of community vegetation characteristics to precipitation change and nutrient addition. Water treatments: Cont: natural precipitation; +50%: increased precipitation by 50%; -50%: decreased precipitation by 50%. Nutrient treatments: =N: 0 g·m<sup>-2</sup>·yr<sup>-1</sup>; +N: N 10 g·m<sup>-2</sup>·yr<sup>-1</sup>; +NPK: N/P/K each for g·m<sup>-2</sup>·yr<sup>-1</sup>. Lowercase letters indicate the difference between different water treatment under the treatment of same nutrient addition; Capital letters indicate the difference between different nutrient addition treatment under same water condition ( $n = 6$ ,  $p \leq 0.05$ ). The same below.



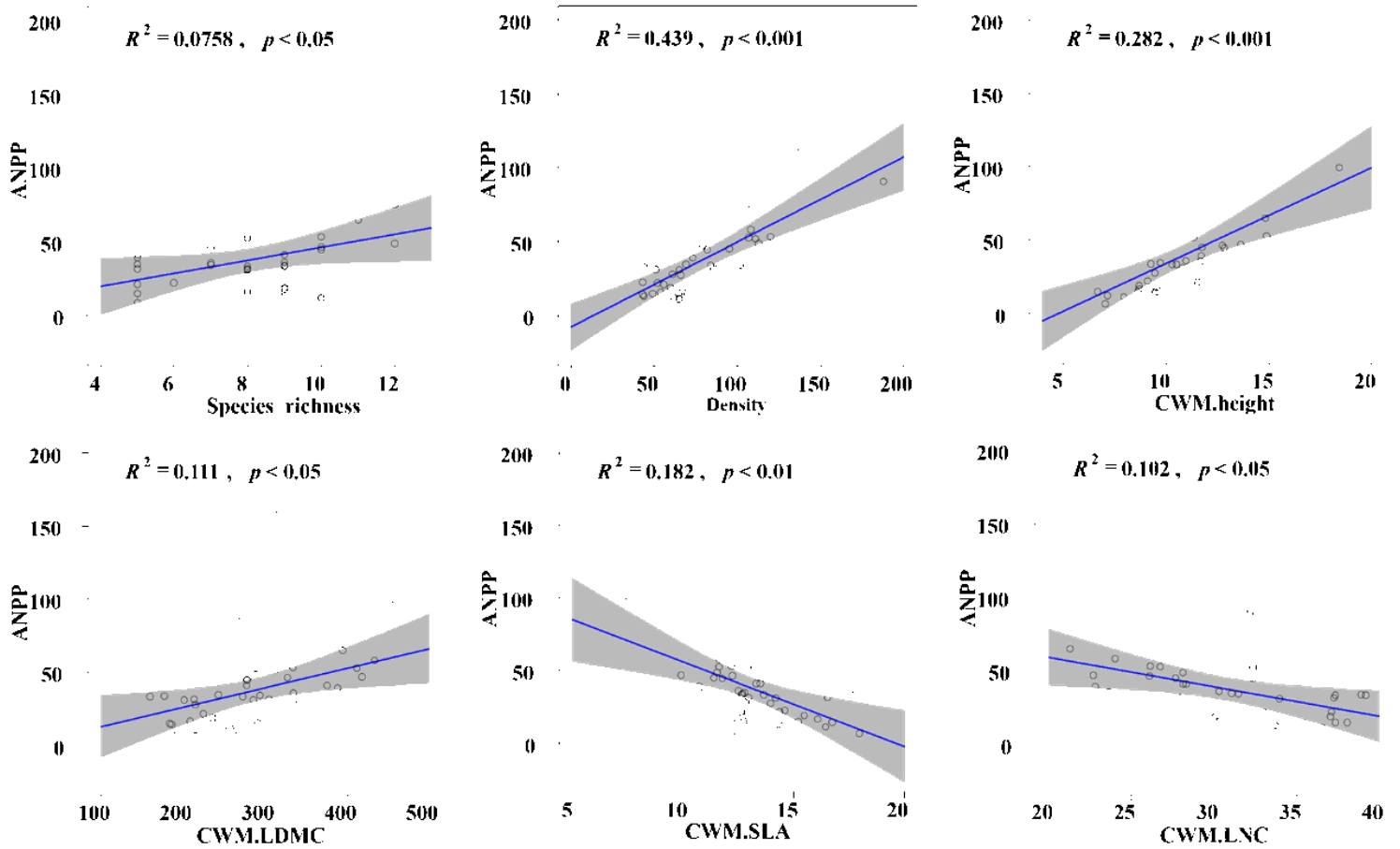
**Figure 2**

Response of community weighted mean of functional traits to precipitation change and nutrient addition. CWM, community weighted mean; LDMC, leaf dry matter content; LCC, leaf carbon content; LNC, leaf nitrogen content; SLA, specific leaf area; LT, leaf thickness.



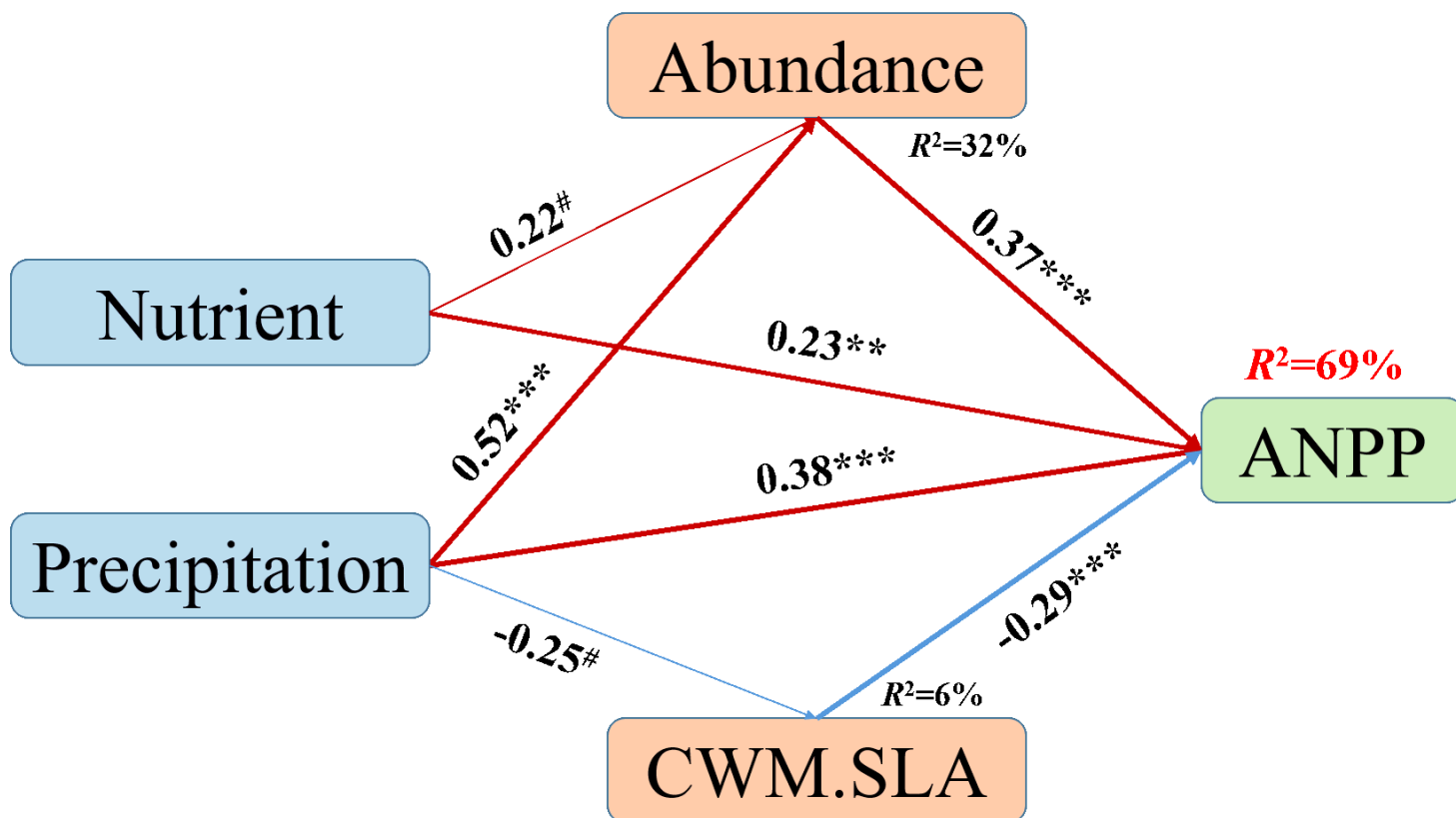
**Figure 3**

Response of community soil properties to precipitation change and nutrient addition. Soil EC: soil electrical conductivity.



**Figure 4**

Simple linear regression analyses between ANPP (aboveground net primary production) and species richness, abundance (density), CWM.height, CWM.LDMC, CWM.SLA, and CWM.LNC. Regression coefficients ( $R^2$ ) and  $p$  values are given for simple linear model regressions of community vegetation characteristics and community weighted mean values of functional traits by ANPP. CWM, community weighted mean; LDMC, leaf dry matter content; SLA, specific leaf area; LCC, leaf carbon content. Indicators with insignificant linear relationship with ANPP are not listed, and the specific data can be seen in Table S2.



**Figure 5**

Structural equation model showing all interaction pathways of ANPP (aboveground net primary production) and nutrient, water, abundance (density), CWM.SLA (specific leaf area). (a) The single-headed arrows represent paths in this conceptual model. The red and blue arrows separately indicate positive and negative pathways. The arrow width is proportional to the strength of the relationship. (b) Standardized regression weights (along path) and total variance explained as a result of all predictors pointing to that variable (top right corner of rectangle). #, \*\* and \*\*\* indicate statistically significant paths at  $0.1 < p < 0.05$ ,  $p < 0.01$  and  $p < 0.001$ , respectively.

## Supplementary Files

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