

# Intraspecific trait variation drives grassland species richness and productivity under changing precipitation

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**Abstract.** It has been increasingly recognized that plant traits and their intraspecific variation play pivotal roles in determining how ecosystem structure and function respond to a changing environment. Yet, it remains unclear how and which plant traits regulate the assembly process and thus affect ecosystem structure and function under climate changes. Here, we selected six steppe sites with snow fences along a precipitation gradient in inner Mongolia. We measured traits including plant height and leaf carbon, nitrogen, and phosphorus concentrations. We incorporated intraspecific trait variation to quantify the strength of external filters (assembly processes outside the community at a larger spatial scale), the strength of internal filters (assembly processes within the local community), and functional redundancy (the number of species having a similar function to an ecosystem). We applied these assembly rules to explain the changes in biodiversity and productivity in response to changing precipitation. We found that increased rainfall reduced plant carbon (C), nitrogen (N), and phosphorous (P) concentrations, but did not affect plant height. High snowfall increased phosphorous concentration, but did not affect other traits. Latent variable models identified climate (rainfall) and soil nutrient conditions (soil total N and P content) were more important than external filtering processes in predicting species richness. However, external filtering processes were the most important predictor of productivity. More specifically, we found with the increase in steppe productivity, the strength of the external filtering on leaf N increased and on plant height decreased, leading to leaf N converging into a small range but broadening the range of plant height. The internal filters had no significant effects on species richness or productivity. Additionally, we found that low precipitation reduced functional redundancy. We emphasize that intraspecific trait-variation drives plant productivity and richness responses to precipitation changes by regulating community assemblage. Our finding also underlines the importance to separate the contributions of different functional traits in regulating the responses of ecosystem structure and function to climate changes.

**Key words:** biodiversity and productivity; community assembly; drylands; external and internal filtering; functional redundancy; grasslands; intraspecific trait variation; precipitation change.

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## INTRODUCTION

Precipitation is one of the most important drivers in shaping ecosystem structure and maintaining ecosystem multifunctionality in drylands, which cover approximately 40% of the global terrestrial surface and continue to expand (Huang et al. 2016, Maestre et al. 2016). Because climate changes alter the rainfall and snowfall patterns during the growing season and non-growing season, respectively (Peng et al. 2010, Berghuijs et al. 2014), changes in precipitation regimes can induce significant variation in species richness and productivity in dryland (McCluney et al. 2012, Huang et al. 2016). Soil fertility is another important factor shaping the structure and function of dryland ecosystems, mainly by influencing plant nutrient traits (Ceulemans et al. 2013). For example, plants grow in fertile soil often have high leaf N concentrations, which promotes photosynthesis and thus increases ecosystem productivity (Grace et al. 2016). Recent studies have indicated that incorporating functional trait variation into community assembly rules could improve our capacity to predict ecosystem functions under climate changes (HilleRisLambers et al. 2012, Violle et al. 2012). Despite considerable research, few studies have addressed their relative contributions on species richness and productivity compared with climate and soil nutrient, which are considered as the most important driver (Grace et al. 2016). Studying this process helps advance our understanding of how trait-based assembly processes affect the dynamics of species richness and productivity in response to precipitation changes.

The shift in community traits in response to precipitation changes can be induced by changes in intraspecific trait variation (IV) and species turnover (Sandel et al. 2010, Albert et al. 2011). Recent studies found that IV effects showed comparable to, and sometimes even stronger than species effects on community composition (Des Roches et al. 2018). IV arises from phenotypic plasticity and genetic differences, and is important for adaptation in response to changes in environmental conditions (Henn et al. 2018). Low levels of IV would threaten the survival of the species in a changing environment (Henn et al. 2018). A meta-analysis on 36 plant traits has

shown that IV accounted for an average of one-fourth of the total within-community trait variance (Siefert et al. 2015). Under resource limitation condition, the superior competitors are found to express higher IV compared with competitively inferior species (Ashton et al. 2010), and the exploitative species often display a higher level of IV (e.g., leaf N content and specific leaf area) than the conservative species (Grassein et al. 2010). Therefore, IV is considered a more important driver than species turnover in community functional response to climate change on a short-term timescale (Sandel et al. 2010, Jung et al. 2014).

Compared with mean trait values, IV provides important information about the niche breadth and overlap among the coexisting species (Laughlin and Messier 2015, Carmona et al. 2016). Various abiotic (such as environmental conditions) and biotic (such as competition and parasitism) factors can induce intraspecific variation, which provides the rough material for natural selection by filtering processes (Violle et al. 2012, Abakumova et al. 2016). Therefore, in a given community, a group of species is the result of external and internal filtering on community traits variation (Chesson 2000, Violle et al. 2012, Jung et al. 2014, Mao et al. 2017). Generally, external filtering involves assembly processes that operate at a larger spatial scale including climate and soil conditions, and tends to select species with similar functional traits in similar habits, which leads to community traits converging into a small range (Laughlin et al. 2012, Kraft et al. 2015) (Fig. 1a). However, internal filtering involves assembly processes that mainly regulates species interaction within the local community, such as competition and parasitism, and tends to broaden the range of community trait variation (Fig. 1b), which will produce diverse traits and promote species coexistence by increasing niche differences, although in some cases it leads to trait convergence (Laughlin et al. 2012, Kraft et al. 2015, Hart et al. 2016). Although numerous studies have used trait and IV to predict community composition, few studies have explored how trait-based external and internal filtering respond to environmental change, and how this response further influences community assembly and ecosystem function (Asner et al. 2016, Kuczyński and Grenouillet 2018).

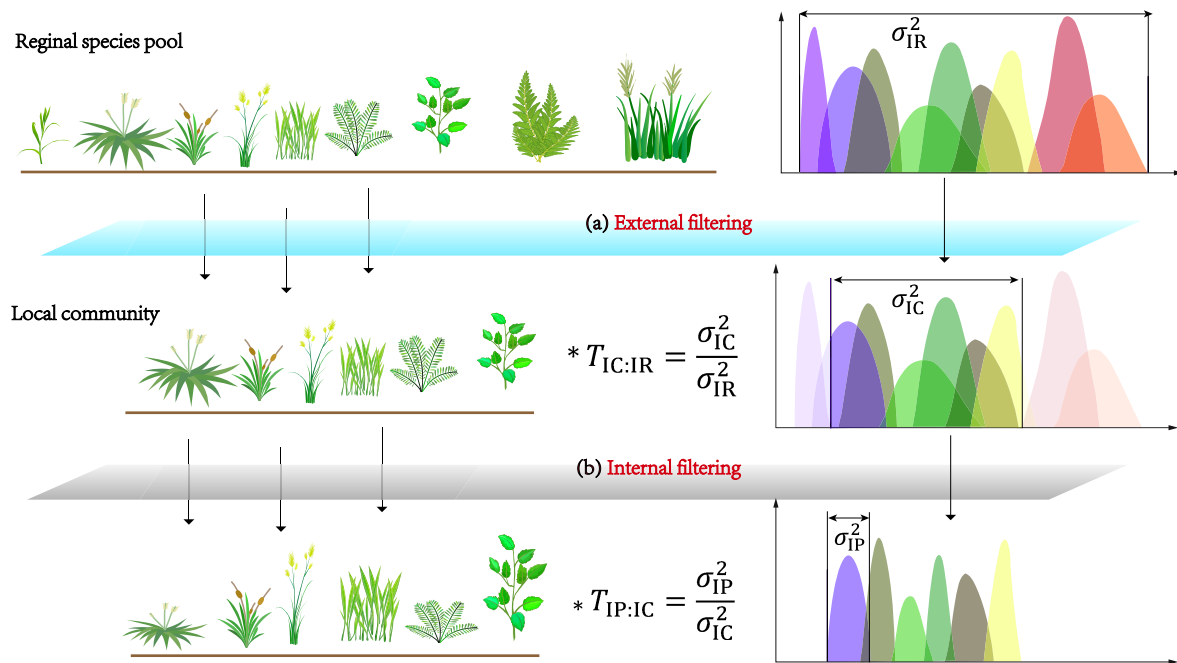


Fig. 1. The conceptual model of how external and internal filtering processes affect community assembly. Here, “ $T$ ” represents a specific plant trait,  $\sigma_{IR}^2$  represents the total variance of the trait in the regional pool,  $\sigma_{IC}^2$  represents community variance of the trait, and  $\sigma_{IP}^2$  represents population variance of the trait. \* The formulas were from Violle et al. (2012).

IV is often used to quantify niche overlap, which can be used to characterize the degree of functional redundancy (FRed) of the ecosystem (Carmona et al. 2016). Communities with high FRed generally have more species that can be replaced by a functionally similar species, which can provide the community with insurance against ecosystem function loss in the face of environmental changes (Ricotta et al. 2016, McWilliam et al. 2018). Because drylands are sensitive to climate changes, understanding how communities with different FRed change with changes in precipitation is critical to predicting future ecosystem stability.

Recent research found that three-quarters of trait variation is captured by the size of whole-plants (e.g., plant height) and the leaf economics spectrum (Siefert et al. 2015, Díaz et al. 2016). Plant height and leaf nutrient traits show the difference in plant ecological strategy relevant to growth, survival, and reproduction (Díaz et al. 2016). Plant height is one of the most important whole-plant traits related to how plant acquire, conserve, and compete for resources (Violle et al.

2007). Leaf nutrients, especially leaf nitrogen (N) and phosphorus (P) concentrations, are the most important leaf traits that regulate photosynthesis and plant growth (Wright et al. 2004). The leaf economics spectrum suggests that species with high leaf N and P concentrations have a quick return on productivity (Wright et al. 2004). Accordingly, it is expected that ecosystems with high productivity would support species riched in N and P. However, it remains unknown which traits play a vital role in driving the community dynamics during assembly processes, and what the potential mechanisms are.

In this work, we investigate the mean and IV of plant height, leaf nutrient traits, and soil nutrient contents in typical (dry) and meadow (wet) steppe in Inner Mongolia. Based on grasslands spanning a rain precipitation gradient with four snowfall treatments in Inner Mongolia, this investigation focuses explicitly on testing the following three hypotheses. First, the steppes with higher precipitation will favor plants with higher plant height and higher leaf N and P concentrations, thereby supporting higher productivity

and species richness. Second, the external and internal filtering on plant height and foliar nutrients have different effects on species richness and productivity. Third, the filter processes are less important than climate and soil nutrient in explaining species richness and productivity.

## METHODS

### Study system

Six grassland sites were selected along a precipitation gradient across a 440 km transient in Inner Mongolia (N 43.62°–N 45.83°; E 115.78°–E 119.72°), where the mean annual precipitation (MAP) ranged from 216 to 539 mm and the mean annual temperature (MAT) spanned from 0.98 to 3.75°C between 2013 and 2016. In the present climate, ~8% of the local precipitation falls as snow in these cold, dry grasslands (Liu et al. 2018). In 2003, the Inner Mongolia Department of Transportation built 2-m high snow fences along several highways, ~150–200 m away from the roads. We selected 6 snow fences that had not been grazed by large herbivores for at least 10 yr from the two types of steppes, typical ( $n = 3$ ) and meadow steppes ( $n = 3$ ). The typical steppe soil consists of typical chestnut soil, and the vegetation is dominated by *Leymus chinensis* (Trin.) Tzvel., *Carex enervis* C. A. Mey., *Cleistogenes squarrosa* (Trin.) Keng, and *Stipa grandis* P.A. Smirn. The meadow steppe soil was dark chestnut soil, and the dominant species were *Leymus chinensis* (Trin.) Tzvel., *Carex enervis* C. A. Mey., *Cleistogenes squarrosa* (Trin.) Keng, *Agropyron cristatum* (L.) Gaertn., *Stipa grandis* P. Smirn., *Serratula centauroides* L., and *Heteropappus altaicus* (Willd.) Novopokr., *Melissilus ruthenicus* (L.) Peschkova. The geographical coordinates and climate conditions for the six fences are given in Appendix S1: Table S1.

### Snow depth gradient experiment

The snow fences for the six sites were oriented approximately south-north or southwest-northeast, in a direction perpendicular to their prevailing wind directions in winter. The depth of snow accumulation decreased with increasing distance from the fence. Therefore, the snow fence delineated the beginning of a snow depth gradient. Here, we focused on 3 sampling transects on the windward sides of each fence: The

distances were 10, 7, and 3 m from sampling transects to fences, which represented mildly increased snow depth, moderately increased snow depth, and heavily increased snow depth, respectively. We established another transect at 100 m from each fence as ambient snow depth. For each sampling transect, we established 3 replicate plots 50 m away from each other, resulting in a total of 12 sampling plots per site. During our experiments from 2013 to 2016, the snow precipitation in the ambient plots for the 6 sites was estimated by the summary of precipitation during the whole winter (including November, December, January, February, and March). The precipitation data were obtained from the National Meteorological Information Center (<http://data.cma.cn/>). The snow precipitation in snow treatment plots was estimated by the depth ratio of the snow treatment to ambient plots measured in 2016. Snow depths (including the ambient snow depth and the 3 increasing snow depths) of the 6 sites were measured during February 15–28, 2016, using poles pushed through the snow to the soil surface. Three replicates were measured to get the mean snow depth for each transect.

### Community and soil measurements

From 2013 to 2016, plant and soil samples were collected from a 1-m<sup>2</sup> quadrat at each plot in six sites. In total, we sampled 276 plots during August of each year, corresponding to the annual peak period of standing biomass (Bai et al. 2008). All live plants in each quadrat were clipped at ground level and sorted by species. Species richness was determined by the number of species in the 1-m<sup>2</sup> quadrat. The aboveground biomass (AGB), both total and species-specific, was determined after the samples were oven-dried at 65°C to constant weight. Three soil cores were randomly collected within each plot using a 7 cm diameter soil corer to a depth of 5 cm, and mixed *in situ* to form one composite sample. After removal of roots and stones, the mixed moist soil samples were sieved through a 2-mm mesh. Part of the soil samples was air-dried to measure total soil C, N, and P.

### Plant traits

In order to test the effect of trait variation on species richness and productivity of grassland

ecosystems, we measured plant trait values of eight dominant species that accounted for about  $78 \pm 23\%$  aboveground biomass across our study regions. The eight species included *Agropyron cristatum*, *Leymus chinensis*, *Carex enervis*, *Cleistogenes squarrosa*, *Stipa grandis*, *Serratula centauroides*, *Heteropappus altaicus*, and *Melissitus rutenica*. For each plot, all individuals of each species in a 1-m<sup>2</sup> quadrat were selected and mixed into one sample. Leaf samples were then ground with a ball mill for further chemical analysis. In all, a total of 1200 plant samples were analyzed. The concentrations of foliar C and foliar N were analyzed using a CN elemental analyzer (Vario EL III; Elementar Analysensysteme GmbH, Hanau, Germany). To determine foliar P concentration, the plant samples were wet-combusted in nitric acid: perchloric acid mixture (2.5:1). The P concentration of plant samples was measured using an iCAP 6300 inductively coupled plasma emission spectrometer (ICP; Thermo Scientific, West Palm Beach, Florida, USA). For each plot, plant height for each species was estimated by the mean values of three to five random measurements, when the number of individuals of a species exceeded three.

#### Measure of functional redundancy

FRed could be calculated as the average number of species sharing the same trait values within the community (Carmona et al. 2016). The FRed calculation was based on trait probability density (TPD). We divided  $N$  cells within the distribution range of traits. For each cell, we counted the number of species with a trait probability density value greater than zero and calculated the FRed as:

$$\text{FRed} = \left( \sum_{i=1}^N M_i \text{TPD}_i \right) - 1 \quad (1)$$

where FRed was functional redundancy,  $N$  was the number of divided cells,  $i$  was from 1 to  $N$ , and  $M_i$  was the number of species of each cell for each trait probability density ( $\text{TPD}_i$ ). To ensure that each bin had at least 3 data, the number of bins ( $N$ ) is set to 15. The robustness of the analyses was further tested by using different number of bins (Appendix S1: Table. S2).

#### Quantification of the strength of external and internal filtering on traits

The strength of external filtering that represented the overlap of intraspecific trait variation at the level of community can be estimated by the ratio of the variance within the community relative to the total variance of the regional pool. Follow the equation given by Violle et al. (2012), we calculated the strength of external filtering as (Fig. 1):

$$T_{\text{IC:IR}} = \frac{\sigma_{\text{IC}}^2}{\sigma_{\text{IR}}^2} \quad (2)$$

where  $T_{\text{IC:IR}}$  was the strength of external filtering ("T" for various traits),  $\sigma_{\text{IC}}^2$  was the trait variance of each snow treatment in each site (community level), and  $\sigma_{\text{IR}}^2$  was the total trait variance in the regional pool (all six sites). A higher  $T_{\text{IC:IR}}$  ratio indicated a lower external filtering strength.

Meanwhile, the strength of internal filtering that represented the overlap of intraspecific trait variation within local community was an estimation of the variance within a single species relative to the total variance of the local community. Again, following the equation given by Violle et al. (2012), we calculated the internal filtering strength on various traits as:

$$T_{\text{IP:IC}} = \frac{\sigma_{\text{IP}}^2}{\sigma_{\text{IC}}^2} \quad (3)$$

where  $T_{\text{IP:IC}}$  was the internal filtering strength ("T" for various traits),  $\sigma_{\text{IP}}^2$  was the trait variance within a single species (population level) of each snow treatment in each site, and  $\sigma_{\text{IC}}^2$  was the trait variance of each snow treatment in each site (local community level). A higher  $T_{\text{IP:IC}}$  ratio indicated a higher internal filtering strength.

#### Statistical analysis

We used linear fixed-effect models to simulate a linear relationship between the external and internal filtering strength on four traits (including foliar C concentration, foliar N concentration, foliar P concentration, and plant height), and climate variables, such as rain precipitation, snow precipitation, and their interaction. The  $t$ -test performed to identify differences in these four traits between typical and meadow steppes. Differences in species richness and productivity among

sites, snow treatment, and year were tested by multi-ANOVA. In addition, a two-way ANOVA was employed to identify differences in these four traits between sites (snow treatment) and species. To compare the  $T_{IP:IC}$  and  $T_{IC:IR}$  effects of the four traits (including foliar C concentration, foliar N concentration, foliar P concentration, and plant height) on species richness and productivity, we scaled the dependent variables from 0 to 1. Productivity was  $\log_{10}$ -transformed to improve data normality before analysis.

Compared with the conventional SEM, by introducing both continuous and categorical latent variables, the modeling capability of the latent variable modeling (LVM) is vastly enhanced (Collins and Sayer 2001). In this study, we used LVM to examine the direct and indirect effects of environmental variables, trait mean, trait variation, internal filters, and external filters on species richness and productivity. The mean value, coefficient of variance, internal filters  $T_{IP:IC}$  and  $T_{IC:IR}$  of four traits, including foliar C, N, P, and plant height, were used to represent the latent variables for the trait mean, trait variation, internal filters, and external filters, respectively. Before fitting the latent variable models, richness was transformed with root square and productivity was transformed with logarithm to ensure normal distribution. Latent variable models were fitted using the *lavaan* package in R. We used the chi square statistics,  $P$  value ( $P > 0.05$ ), comparative fit index (CFI  $> 0.95$ ), the root mean square error of approximation (RMSEA  $< 0.06$ ), and standardized root mean square residual (SRMR  $< 0.08$ ) to assess model fit. The first latent variable models tested included all the four latent constructs (trait mean, trait variation, internal filters, and external filters), and the models did not fit the data well ( $P < 0.05$ , CFI  $< 0.95$ , RMSEA  $> 0.06$ , SRMR  $> 0.08$ ). We then reduced models by using modification indices and removing variables that had a relatively low contribution to the endogenous variables. We further conducted the Likelihood Ratio Test (LRT) to compare the candidate models and chose the best model with the lowest AIC scores (Fig. 4; Appendix S1: Fig. S9).

All statistical analyses were performed using the R statistical software package (ver. 3.6.0), and statistical tests were considered significant at  $P < 0.05$ .

## RESULTS

### *Effects of precipitation on plant traits*

Plant height and nutrient traits exhibited different responses to increasing rain precipitation; plant C, N, and P concentrations declined ( $P < 0.05$ ; Appendix S1: Table S3), but no change in plant height was observed (Figs. 2, 3; Appendix S1: Figs. S2, S3). The additional snow precipitation led to an increase in plant P concentration ( $P < 0.05$ ), but had no effect on plant C or N concentrations, or plant height. In addition, the effects of snowfall on plant P concentration were stronger in the dry region than in the wet region (Appendix S1: Fig. S3). Based on intraspecific trait variations, FRed of plant C (1.73:2.22) and P (2.20:3.33), as well as plant height (2.13:3.40) in typical steppes, were lower than those in meadow steppes (Fig. 2). However, the difference in FRed of plant N between typical (3.40) and meadow steppes (3.27) was small (Fig. 2). The sensitivity analysis proved that the results of FRed were not altered by the number of bins (Appendix S1: Table S2).

### *Effects of external and internal filters on species richness and productivity*

To investigate the effects of plant intraspecific trait variations on ecosystem structure and function, we examined the external filters ( $T_{IC:IR}$ ) and internal filters ( $T_{IP:IC}$ ) strength of four traits, including plant height, plant C, foliar N, and foliar P concentrations on species richness and productivity. Results showed that only the  $T_{IC:IR}$  of foliar P ( $P < 0.05$ ) had significant negative effects on species richness (Figs. 4a, 5a); however, the  $T_{IC:IR}$  of all the four traits significantly influenced productivity ( $P < 0.05$ ; Figs. 4c, 5b).

Furthermore, the  $T_{IC:IR}$  of plant height ( $P < 0.05$ ) depicted positive effects on productivity, while the plant nutrient traits showed negative effects. With regard to the relationships between the  $T_{IP:IC}$  of the four traits and the two variables (Figs. 4b, d, and 5), we found species richness showed a significantly negative correlation with the  $T_{IP:IC}$  of plant N concentration ( $P < 0.05$ ), but a positive correlation with the  $T_{IP:IC}$  of plant height ( $P < 0.05$ ). Productivity showed a significant positive response to the  $T_{IP:IC}$  of plant height and plant C concentration ( $P < 0.05$ ).

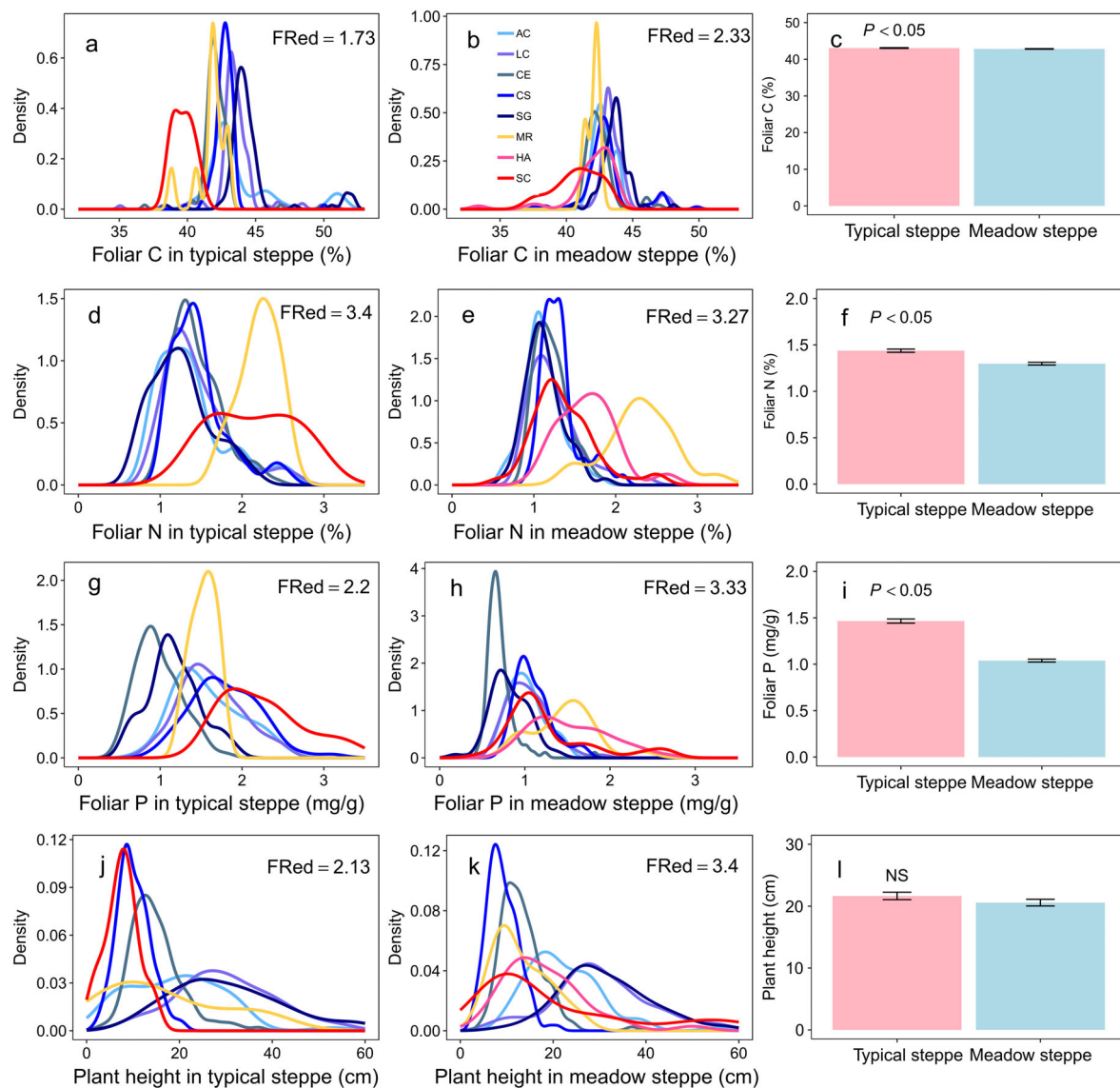


Fig. 2. Precipitation changes affect community traits in typical steppes and meadow steppes. a-d, (a) the distribution of leaf C, (d) leaf N, (g) leaf P, and (j) plant height for the seven species in typical steppes. e-h, the distribution of (b) leaf C, (e) leaf N, (h) leaf P, and (k) plant height for the eight species in meadow steppes. i-l, the results of ANOVA for (c) leaf C, (f) leaf N, (i) leaf P, and (l) plant height in two types of different steppes. FRed represents functional redundancy based on intraspecific trait variation. AC, *Agropyron cristatum*; LC, *Leymus chinensis*; CE, *Carex enervis*; CS, *Cleistogenes squarrosa*; SG, *Stipa grandis*; MR, *Melissilus ruthenicus*; HA, *Heteropappus altaicus*; and SC, *Serratula centauroides*. The error bars represent standard errors.

#### The effects of climate, soil nutrients, external, and internal filtering on species richness and productivity

The best-fitting models contained the latent constructs of internal filters and external filters explained 82% and 80% variation for species

richness ( $\chi^2 = 31.5$ ,  $P = 0.35$ ) and productivity ( $\chi^2 = 22.4$ ,  $P = 0.32$ ), respectively (Figs. 5a, b). We compared the relative influence of the variables by their standardized coefficients. The model identified rainfall ( $r = 0.79$ ), soil total N ( $r = 0.060$ ), and P concentrations ( $r = -0.56$ ) as

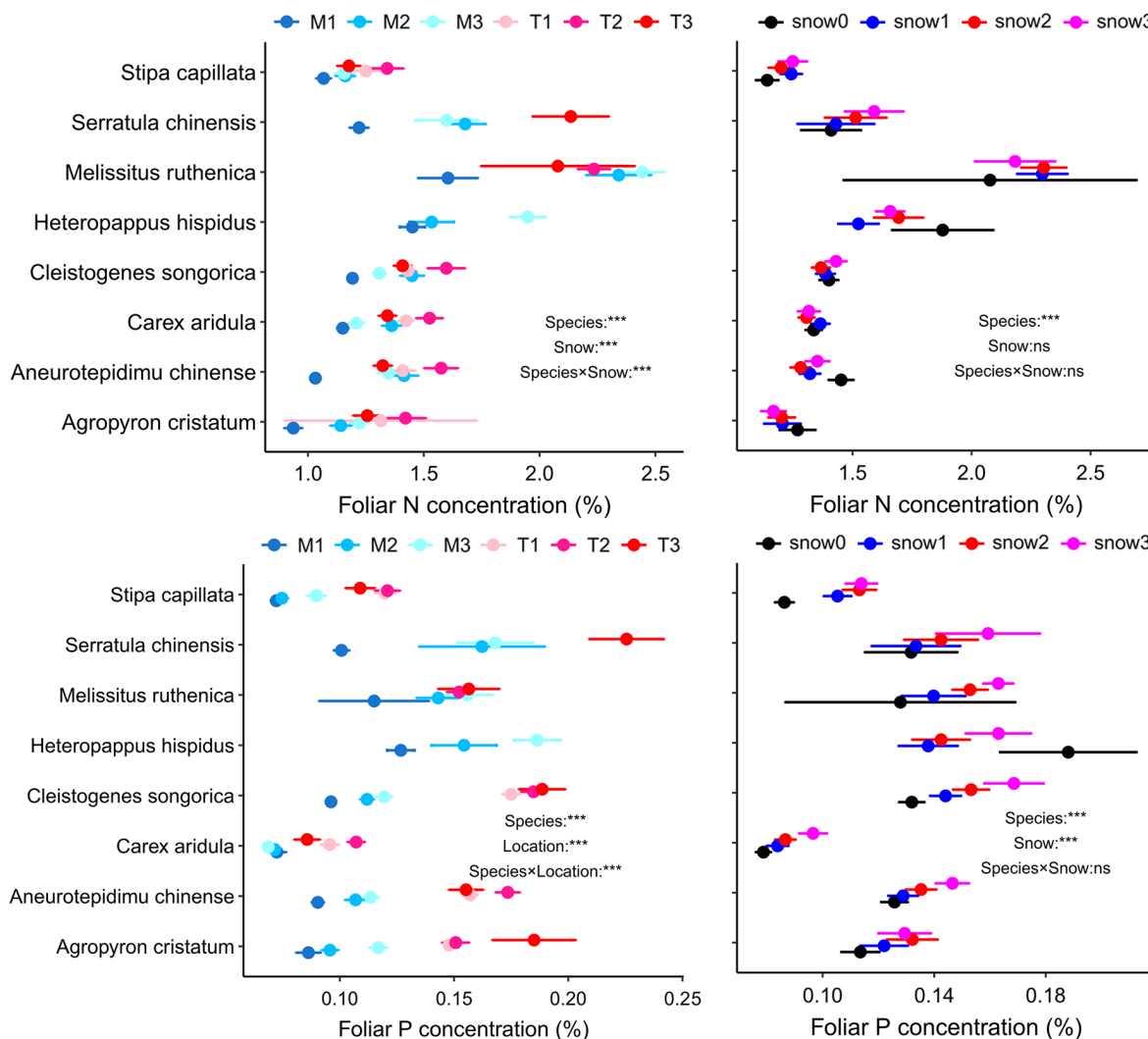


Fig. 3. Foliar N and P concentrations of the eight species at different levels of precipitation. Foliar N and P concentrations are different among the eight species. Higher precipitation in meadow steppes resulted in (a) lower foliar N and (b) lower foliar P concentrations as compared to lower precipitation in typical steppes. (c) Snow precipitation had no effect on foliar N concentration for the species, (d) increased snow precipitation resulted in high foliar P concentration. *P* values (*P* levels: \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ , ns, not significant) show the results of two-way ANOVA for foliar N concentration and foliar P concentration. The distances were 30, 10, 7, and 3 m from sampling transects to fences, which represented ambient snow depth (snow0), mildly increased snow depth (snow1), moderately increased snow depth (snow2), and heavily increased snow depth (snow3), respectively. M1, M2, and M3 indicate Meadow steppes; T1, T2, and T3 indicate typical steppes. Data are presented as means  $\pm$  SE.

the more important predictors than the external filtering ( $r = -0.43$ ) on species richness (Fig. 5a). MAP and soil N concentration had direct and positive effects on species richness, but snowfall and soil P concentration had direct and negative effects on species richness (Appendix S1: Fig. S8,

Table S3). MAT indirectly positively influenced species richness via reducing the effects of external filters.

The model revealed that the strength of the external filtering ( $r = -0.78$ ) is the most important predictor of productivity (Fig. 5b). Soil TN

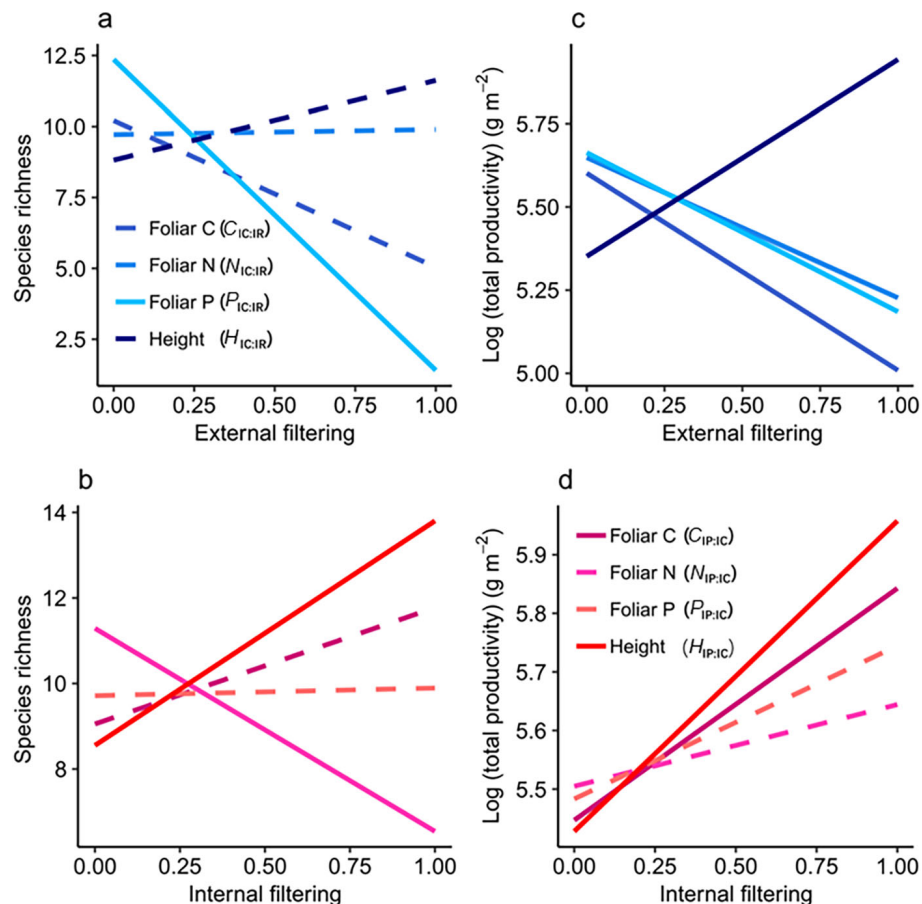


Fig. 4. External filtering ( $T_{IC:IR}$ ) and internal filtering ( $T_{IP:IC}$ ) on four traits influenced species richness and productivity with the change of the precipitation in grasslands. The lines represent ordinary least squares regression fits for external and internal filtering on foliar C, foliar N, foliar P, and plant height to species richness (a, b) and productivity (c, d) after scaling data from 0 to 1. Solid lines indicate that linear regression fits data that are significant at the  $P < 0.05$  level, and dashed lines indicate that linear regression fits data that are not significant at the  $P \geq 0.05$  level.

( $r = 0.43$ ) had a direct positive effect on productivity, while MAT ( $r = -0.48$ ) had a direct negative impact on productivity but has an indirect positive effect ( $r = -0.39$ ) on productivity. MAP indirectly and negatively influenced productivity via increasing the effects of external filters, but snowfall indirectly and positively influenced productivity via reducing the effects of external filters. Soil P concentration had nonsignificant and indirect effects on species richness and productivity. The factor loading of  $H_{IC:IR}$  of plant height included in external filtering was negative, while the loading of  $N_{IC:IR}$  of foliar N concentration included in external filtering was positive. Thus,

the ecosystem with more converge plant height but diverse foliar N concentration had a higher “score” on external filter indicators, and consequently had lower species richness and productivity (Fig. 5). Internal filters had a weak influence on either species richness or productivity.

## DISCUSSION

### *Precipitation regime shaping the regional pattern of plant traits in drylands*

This study showed that plants in dry typical steppes produce foliage rich in N, P, and C

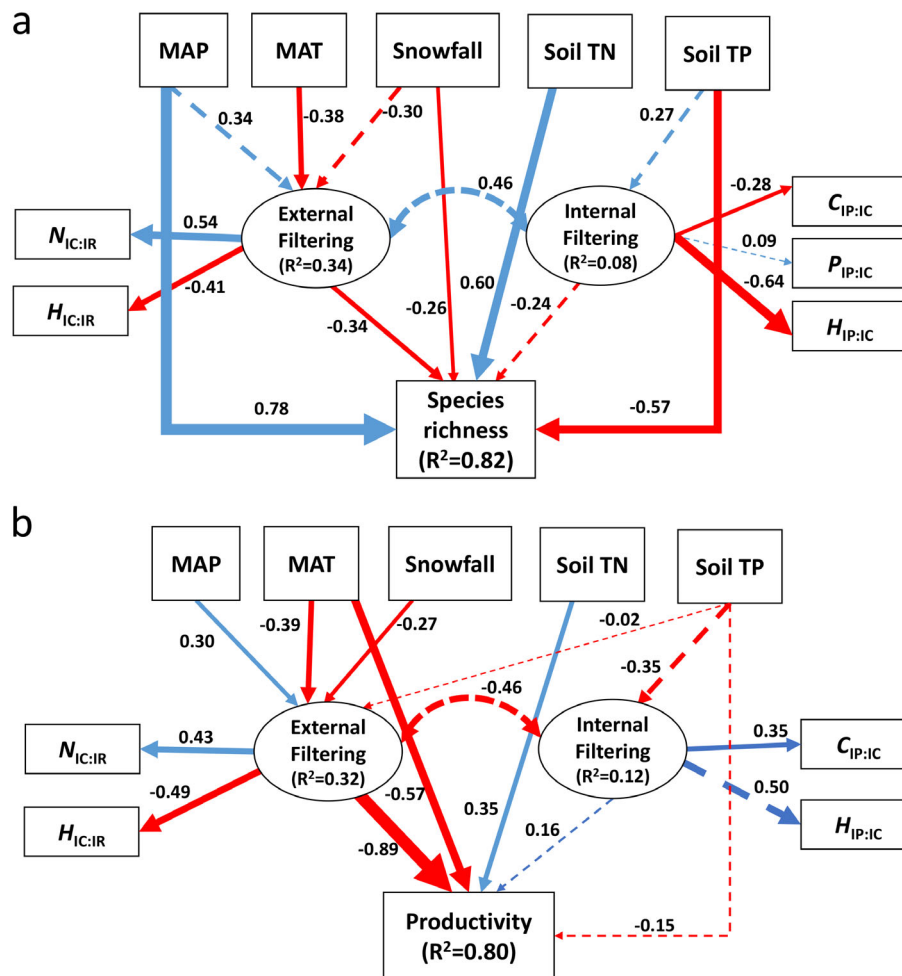


Fig. 5. Latent variable models depicting the direct and indirect influences of MAP, MAT, snowfall, soil total N content, soil total P content, external filtering, and internal filtering on the effects of species richness (a.  $\chi^2 = 31.5$ ,  $P = 0.35$ ,  $df = 29$ ,  $AIC = 632.5$ ,  $CFI = 0.99$ ,  $RMSEA = 0.03$ ,  $SRMR = 0.06$ ) and productivity (b.  $\chi^2 = 22.4$ ,  $P = 0.32$ ,  $df = 20$ ,  $AIC = 528.3$ ,  $CFI = 0.99$ ,  $RMSEA = 0.04$ ,  $SRMR = 0.06$ ). Variables in the rectangle are manifest variables, and variables in the oval are latent variables. Arrows represent the flow of causality. Arrow width is proportional to the standardized coefficient estimate and could be interpreted as the relative importance of each factor. Solid arrows indicate a significant relationship ( $P < 0.05$ ), dashed arrows indicate a non-significant relationship. "N" represents leaf N concentration, "P" represents leaf P concentration, "C" represents leaf C concentration, and "H" represents plant height. The subscript of IC:IR represents external filtering, and IP:IC represents internal filtering.

relative to those in wet meadow steppes (Figs. 2, 3; Appendix S1: Figs. S1, S2). This was inconsistent with our hypothesis that wet meadow steppes would have higher N and P concentration. In addition, we had not observed the positive effects of foliar N and P concentrations on productivity (Appendix S1: Fig. S4). Trait intraspecific variations ensured that plants could

grow, survive, and reproduce more successfully in a changing environment (Díaz et al. 2016). Although the high N and P concentrations in dry typical steppes did not result in a high biomass production (Appendix S1: Fig. S4), they helped plants survive in water-limited environments; as many findings suggested that overinvestment in N enhances plant water use efficiency in

drylands, and facilitated seed spreading by remobilizing nutrients from leaves to seeds (Schiltz et al. 2005, Adams et al. 2016). Our results suggested that future dryland expansion could lead to a shift in plant community that exhibits more N and P demanding species, which would subsequently have a profound impact on productivity and nutrient cycles.

The whole plant's height played an important role in ecosystem functioning because it not only altered light condition below vegetation canopy, but also influenced soil moisture by changing the amount of radiation incident on the soil surface and vegetation boundary-layer thickness (Violle et al. 2007, Hautier et al. 2009, Funk et al. 2017). We hypothesized that species in wet meadow steppes would have higher plant height than dry typical steppes (Moles et al. 2009). However, our results indicated that there was no difference in plant height between dry typical steppes and wet meadow steppes (Fig. 2; Appendix S1: Figs. S1, S3), which was consistent with the findings in African grasslands (Forrestel et al. 2017). In drylands, the increasing plant height would increase the difficulty of supplying water to the leaves, and consequently, stomata would be forced to close (Moles et al. 2009). Therefore, despite the higher precipitation in the wetland steppes, soils there could not support vegetation with a high canopy.

Changes in snow depth on a short-time scale also altered plant traits, although the impact was relatively small compared to the effects of rainfall on a long-timescale (Appendix S1: Fig. S3). Leaf P concentration increased with snow depth, while no significant changes were observed for leaf N concentration and plant height (Fig. 3; Appendix S1: Figs. S2, S3). Winter snowfall was an important water source for early spring plant growth (Barnett et al. 2005, Peng et al. 2010) and could also enhance nutrient supply by increasing winter soil temperature and soil nutrient mineralization (DeMarco et al. 2011). Interestingly, our results showed that only soil available P, but not soil available N, increased in response to the rising snow depth (Appendix S1: Fig. S5), which was consistent with the leaf N and P concentration responses. There was an increasing trend of winter snowfall in our study area (Peng et al. 2010). Our research indicated that the increase in the soil available P under deepened snow

conditions would increase the P supply, which was beneficial to high P demand species in the grasslands (Appendix S1: Fig. S3).

#### *Intraspecific trait variation drives community assemblage and ecosystem productivity*

Our results showed that FRed calculated by intraspecific-variation of leaf C (1.73:2.33), leaf P (2.20:3.33), and plant height (2.13:3.40) in dry typical steppes was lower than that in wet meadow steppes (Fig. 2). Given the importance of FRed to ecosystem resistance and recovery (Loreau et al. 2004, Laliberté et al. 2010), our findings suggested that ecosystem functions in drier grassland regions, for example, typical steppes, were more vulnerable and will face heightened threats in future climate scenarios with high drought probability. However, we observed small differences in the leaf N concentration FRed between typical and meadow grasslands (3.40:3.27, Fig. 2). Higher FRed of leaf N concentration indicated that species in grasslands share higher N niche overlap, which strengthened the strong competition for N acquisition (Geange et al. 2011, Fetzer et al. 2015, Carmona et al. 2016). The different FRed value between the assessed traits implied that ecosystem resistance and recovery in the grasslands could be more affected by N supply than P supply or light acquisition.

To explore the mechanisms that regulated grassland ecosystem functions undergoing precipitation changes, we incorporated trait intraspecific variation into assembly rules (external and internal filtering) to explain the effect of community assembly on ecosystem productivity and species richness. Because precipitation (Appendix S1: Table S1), soil conditions, and species pool differed between sites, plants in the varying sites faced different limited resources. Thus, the direction and strength of ecological filters in different traits were unique. Our findings showed that rainfall enhanced the strength of the external filtering on foliar P (low  $T_{IC:IR}$ ), but reduced the strength of the external filtering on foliar N (high  $T_{IC:IR}$ ) across our study regions (Appendix S1: Fig. S6). Snowfall mainly altered the strength of internal filtering on foliar P and plant height (Appendix S1: Fig. S7).

Furthermore, it was observed that the intraspecific variation of different traits related to

assembly rules showed varying effects on species richness and productivity (Fig. 4). The simple correlation analyses found that species richness and productivity were influenced by both internal and external filters (Fig. 4). However, the effects of internal filters on species richness and productivity were no longer significant once the climate and soil nutrient condition were taken into account (Fig. 5). Our latent variable models showed climate (rainfall and snowfall) and soil nutrient conditions (soil TN and TP content) as the major controls on species richness, which was consistent with previous findings (Grace et al. 2016). Noticeably, our study also firstly proved that the external filtering on plant traits influenced species richness (Fig. 5a). More importantly, we found that external filters had a stronger impact on community productivity than climate or soil nutrient conditions (Fig. 5b).

Strong external filtering caused by environmental changes often leads to traits converging into a small range (low  $T_{IC:IR}$  value), while weak external filtering broadened the range of trait variation and resulted in more diverse traits (high  $T_{IC:IR}$  value). Our latent models found that as species richness and productivity increased, the strength of the external filters on leaf N decreased, while the external filters on plant height increased (Fig. 5). This indicated that more species richness and productive grasslands favored species with converged N content and diverged plant heights, and this was consistent with our hypotheses. Plant growth was mainly co-limited by light and N in grasslands (Hautier et al. 2009). With the increase of species richness and productivity, the intensified competition for N and light might be the major reason for the formation of community trait with the converged leaf N concentration and diverged plant height.

In summary, our findings suggested that the increasing global aridity could facilitate the transformation of the plant community to high N and P-demanding species, and those species were often more resistant to drought stress by consuming more nutrients (Adams et al. 2016). Furthermore, drought stress decreased functional redundancy and reduced ecosystem recovery capacity against species loss caused by disturbance. Our results also indicated that ecosystems with high richness and productivity were characterized by: (1) a small range of leaf

N variation—the result of high competition for N, and (2) a broad range of height variation, which was associated with high competition for light. Our study provided an empirical context for testing the theory that community assembly through ecological filters played important roles in regulating ecosystem species richness and productivity. We highlighted that trait-based community assembly rules should be integrated into models for predicting community structure and ecosystem function under climate changes.

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## DATA AVAILABILITY STATEMENT

Data are available in Figshare: <http://doi.org/10.6084/m9.figshare.14252846>

## SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3707/full>