


## Research Article

# Plant functional groups mediate effects of climate and soil factors on species richness and community biomass in grasslands of Mongolian Plateau

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## Abstract

**Aims** Functional group composition of a plant community is mainly driven by environmental factors and is one of the main determinants of grassland biodiversity and productivity. Therefore, it is important to understand the role of plant functional groups (PFGs) in mediating the impact of environmental conditions on ecosystem functions and biodiversity.

**Methods** We measured plant biomass and species richness (SR) of grasslands in 65 sites on the Mongolian Plateau and classified 157 perennial herbaceous plants into two main PFGs (namely grasses and forbs). Using the random forest model and ordinary least squares regression, we identified that environmental factors (i.e. aridity index, soil total nitrogen [STN] and pH) were significantly related to the SR and aboveground biomass (AGB) of PFGs. We then used structural equation modeling to explore the relationship between the identified environmental factors and community SR and biomass, and the role of PFGs in driving this relationship.

**Important Findings** We found that aridity index had unimodal relationships with both AGB and SR of the PFGs and the whole community. All SR and biomass metrics were significantly related to STN and pH. The relationship between aridity index and community biomass was mediated by an increase in the AGB of grasses. The influence of STN and pH on community SR was mainly due to their regulation in the SR of forbs. Our results

indicate that community composition and the identity of the PFGs play a key role in linking environmental factors to ecosystem functioning.

**Keywords** climate, community composition, plant functional groups, Mongolian Plateau, soil properties

### 植物功能群在调控气候和土壤因子对蒙古高原草原群落物种丰富度和生物量影响中的作用

**摘要：**植物功能群组成主要受环境因素驱动，同时植物功能群组成也是影响草地生物多样性和生产力的主要因素之一。因此，理解植物功能群在调控环境因素对生态系统功能和生物多样性影响中可能发挥的作用至关重要。通过对蒙古高原草原65个样点的植物生物量和物种丰富度的调查，将157种多年生草本植物分为两种植物功能群(即禾草和杂类草)。通过随机森林模型和普通最小二乘回归，确定与植物功能群物种丰富度和地上生物量显著相关的环境因素(即干燥度、土壤总氮和pH)，并利用结构方程模型探讨筛选出的环境因素与群落物种丰富度和生物量间的关系，以及植物功能群在驱动这种关系中发挥的作用。干燥度与禾草、杂类草以及整个群落的地上生物量和物种丰富度均呈显著的单峰关系。所有的物种丰富度和生物量指标均与土壤总氮和pH值显著相关。禾草在维持蒙古高原草原生态系统群落生物量中起着关键作用，并受气候因素的直接影响。而杂类草物种丰富度决定了群落总丰富度，并受到土壤因素直接的调控。因此，群落组成在调控环境因素对群落生物量和植物多样性的影响中起着关键作用。

**关键词：**气候，群落组成，植物功能群，蒙古高原，土壤性质

## INTRODUCTION

Community composition is one of the fundamental factors affecting the relationship between environmental conditions and ecosystem functioning. The identity of plant functional groups (PFGs, a group of species with the same or similar functional traits in a community) substantially determines ecosystem functions and services (Hooper and Vitousek 1997; McLaren and Turkington 2010; Tilman *et al.* 1997). Mass loss of the dominant PFGs in a given community results in considerable declines in various ecosystem functions (Smith and Knapp 2003; Smith *et al.* 2020). The 'mass ratio' theory suggests that the traits and functional diversity of dominant plants are proportional to the input of primary productivity (Grime 1998), and that dominant PFGs play a central role in maintaining the temporal stability of community biomass (Ma *et al.* 2017; Sasaki and Lauenroth 2011). However, a large body of studies has focused on the dominant PFGs, leading researchers to underestimate or even ignore the role of subordinate PFGs in biodiversity and ecosystem functioning (Mariotte *et al.* 2013). The niche complementarity hypothesis suggests that differences between PFGs can greatly increase community biomass through diversification of resource acquisition strategies (Gross *et al.* 2007; Sanaei and Ali 2019; Tilman *et al.* 2001).

Subordinate species could primarily increase species richness (SR) and turnover (Cleland *et al.* 2013) and increase community resistance by enhancing their aboveground biomass (AGB) (Mariotte *et al.* 2013). This suggests that subordinate species have the potential to buffer climate change effects on ecosystem functioning (Kardol *et al.* 2010; Mariotte *et al.* 2013). As such, they are critical in determining overall community dynamics (Avolio *et al.* 2019; Grime 1998; Smith and Knapp 2003). Therefore, assessment of how PFGs (e.g. dominant vs. subordinate) affect ecosystem functions is essential to advance our understanding of the drivers of biodiversity and ecosystem functioning.

Manipulative experiments have greatly improved our understanding of the role of PFGs in ecosystem functioning at a relatively small scale (e.g. study plots) (Hooper and Vitousek 1997; Smith *et al.* 2020). Most previous studies focusing on the effects of community composition and PFGs on AGB and SR have been based on functional group removal experiments (Grace *et al.* 2016; McLaren and Turkington 2010; Symstad 2000) or manipulation of SR within functional groups. However, much less is known about how changes in the identity of dominant and subordinate species or PFGs impact ecosystem functions in natural ecosystems and at larger scales (Avolio *et al.* 2019; Mariotte 2014; Smith *et al.* 2020). In nature, ecosystem processes become

more complex and less predictable than in artificial experiments. Therefore, the explicit influence of PFGs and their contribution to biodiversity and ecosystem functioning at the regional scale are still unclear.

Habitat heterogeneity is generally larger at the regional scale than at the local scale and varies with environmental gradients. Environmental conditions mainly affect ecosystem primary productivity and nutrient cycling (Hautier *et al.* 2015; Hooper *et al.* 2005; Winfree *et al.* 2015). In arid and semi-arid environments, climatic factors, especially the increase in temperature and decrease in precipitation during the growing season, drive the directional loss of community species diversity (Harrison *et al.* 2015), which in turn may lead to a decline in community biomass. Grasslands in mid-northern hemisphere latitudes are more sensitive to variations in water availability (Seddon *et al.* 2016), and there is a strong positive correlation between grassland plant community biomass and precipitation (Bai *et al.* 2008; Cleland *et al.* 2013; Knapp and Smith 2001). Precipitation determines the availability of water resources and is the most important factor limiting plant survival, growth and distribution in temperate ecosystems (Bai *et al.* 2008; Guo *et al.* 2019; Peters *et al.* 2012). Moreover, increasing temperature and decreasing rainfall during the growing season may exacerbate drought and cause shifts in community composition (Dai 2013). For example, long-term monitoring in an Inner Mongolia grassland showed that drought reduced the abundance of forbs but enhanced that of grasses (Li *et al.* 2015). Similarly, drought-induced changes in community composition have also been found in alpine meadows on the Tibetan Plateau (Liu *et al.* 2018). The intensification of aridity has further led to systemic and abrupt changes in multiple ecosystem attributes, such as a sharp decline in plant productivity, soil fertility and SR of ecosystems worldwide (Berdugo *et al.* 2020; Zhao and Running 2010).

Soil characteristics with significant spatiotemporal heterogeneity are particularly important in determining the spatial distribution pattern of plant communities (García-Palacios *et al.* 2012; Stein *et al.* 2014; Ulrich *et al.* 2014). Increasing soil bulk density generally inhibits plant root growth and penetration and it simultaneously suppresses soil water availability for plant growth and colonization, thereby affecting all soil biochemical processes. A series of nutrient addition experiments conducted in grasslands showed that soil nitrogen enrichment significantly increased community biomass and

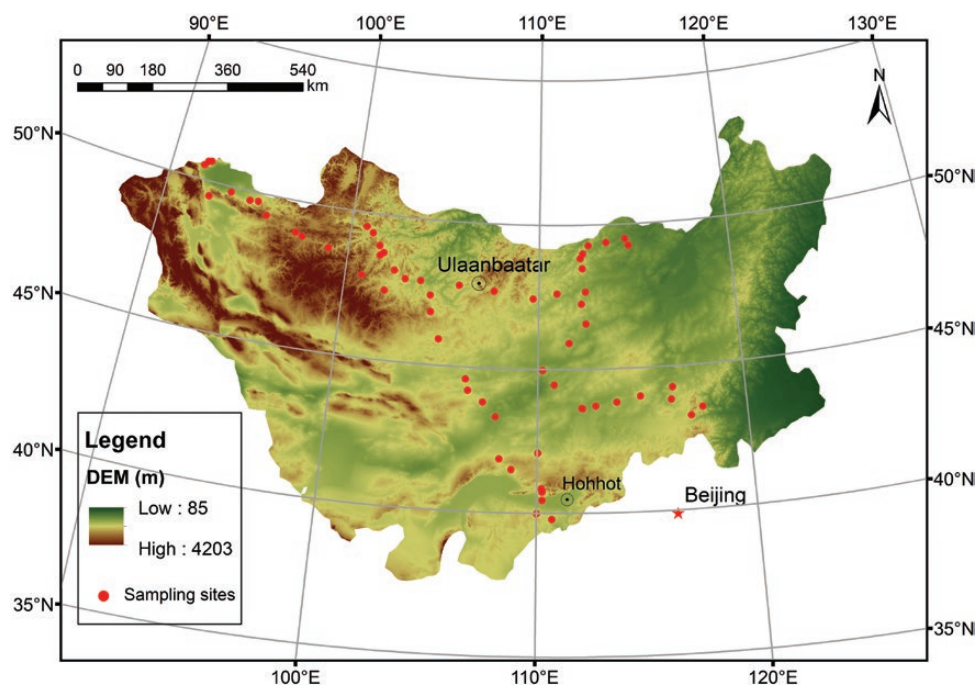
reduced SR (Bai *et al.* 2010; Hautier *et al.* 2009; Isbell *et al.* 2013). Previous studies emphasized that multiple environmental factors could simultaneously shape biodiversity and ecosystem function in local communities (Cardinale *et al.* 2006; Duffy *et al.* 2017; Tilman *et al.* 2012), and the impact of soil on biodiversity was mediated by climate. For example, with the decrease of precipitation in Eurasian grasslands, the relationship between SR and soil pH changes from unimodal, through negative, to none (Palpurina *et al.* 2017). Additionally, the response of PFGs to edaphic factors is identity dependent and is generally regulated by climate factors (e.g. precipitation and temperature) (Maestre and Reynolds 2006; Yang *et al.* 2011), which is likely one of the underlying mechanisms through which PFGs shape the relationships between biodiversity and ecosystem function at different spatial scales (Avolio *et al.* 2019; Liu *et al.* 2018; Palpurina *et al.* 2017). Therefore, how these environmental factors regulate the contribution of PFGs to biodiversity and ecosystem function remains to be explored.

The Mongolian Plateau is located in Asia and has been recognized as a major component of global rangeland systems, with important contributions to global livestock production and ecosystem services (Wu *et al.* 2015). Understanding how environmental factors influence biodiversity and ecosystem functioning via mediating PFGs in natural ecosystems at the regional scale is critical to predicting the dynamics of plant communities under global change. Grasslands on the Mongolian Plateau are naturally distributed along environmental gradients along an east–west axis. Grasses and forbs constitute the two main PFGs in the Mongolian Plateau steppe. Therefore, we conducted 65 sites in natural grasslands on the Mongolian Plateau in 2015 and 2016, investigating biodiversity, AGB and soil properties. We aimed to answer the following questions: (i) What is the relationship between environmental conditions (i.e. climate and soil factors), SR and the productivity of communities or PFGs (grasses vs. forbs)? and (ii) how do climate and soil factors influence patterns of biodiversity and biomass via regulating grasses and forbs?

## MATERIALS AND METHODS

### Study area

The study was conducted on the Mongolian Plateau in the eastern part of the Eurasian steppe at latitudes from 39.79° to 50.66° N and longitudes from 91.72° to



**Figure 1:** The study area and sampling sites on the Mongolia Plateau.

117.9° E (Fig. 1). A total of 65 vegetation sites located in central and eastern Mongolia and Inner Mongolia were surveyed. The average elevation of the sites was 1200 m. The study region is characterized by a dry, temperate continental climate with mean annual temperature (MAT) ranging from  $-6.5$  to  $6.3$  °C, mean annual precipitation (MAP) from 108 to 408 mm and mean de Martonne's aridity index from 7 to 66.

The major vegetation types in the study area include temperate meadow steppe dominated by *Stipa baicalensis*, *Filifolium sibiricum* and *Leymus chinensis*, typical steppe dominated by *S. grandis*, *S. krylovii* and *S. sareptana*, and desert steppe dominated by *S. klemenzi*, *S. glareosa*, *S. breviflora* and *Allium polyrhizum*. The soil types are predominately chernozem or dark chestnut (meadow steppe), typical chestnut (typical steppe) and calcic brown soil (desert steppe).

## Data collection

### Field sampling design

During the growing season in 2015 and 2016, we investigated 65 sites on the Mongolian Plateau (Fig. 1). At each site, a 10 m  $\times$  10 m plot was randomly chosen. Within each plot, five 1 m  $\times$  1 m quadrats were placed at the four corners and the center of the plot (with three quadrats along the diagonal line of the plot in four sites) to survey vegetation and soil. In total, 317 quadrats were sampled and 215 plant

species were recorded. The geographical coordinates and elevation were also recorded for each plot.

### Vegetation survey

We investigated plant attributes, including species identity, height, density and standing biomass of each species in each quadrat. Density (i.e. the number of individuals per square meter) was measured either by counting the number of clusters for bunchgrasses or by counting individuals for species with distinct stems. AGB of each plant species was clipped and put into a separate envelope in each quadrat. The plant samples were brought to the laboratory, oven-dried to constant weight at 65 °C and weighed.

### Soil sampling and measurements

Soil samples were collected from seven layers of the soil profile (i.e. 0–5, 5–10, 10–20, 20–30, 30–50, 50–70 and 70–100 cm) in each plot, including samples used for determining soil bulk density (BD) with a BD corer (100 cm<sup>3</sup>). For shallow soil layers, the soil profile was dug to the top of the parent materials. Composite samples from the top four layers (i.e. 0–5, 5–10, 10–20 and 20–30 cm) along the diagonal in each quadrat were used in this study. After plant roots and gravel were removed, the samples were air-dried, passed through a 2 mm sieve, and used to determine soil physical and chemical properties, including soil texture, pH, soil total carbon (STC) and soil total nitrogen (STN).



Soil texture was measured with a Laser Particle Size Analyzer (Microtrac-S3500) and particles were divided into three grades of sand (2–0.05 mm), silt (0.05–0.002 mm) and clay (<0.002 mm) based on the United States Department of Agriculture System particle size classification criteria. Soil pH was obtained with a calibrated pH meter (Mettler Toledo, Shanghai, China) after 30 min of extraction in distilled water (soil:water ratio of 1:2.5). STC and STN were determined through elemental analysis (VARIO ELIII, Elementary, Hanau, Germany) at the Institute of Botany, Chinese Academy of Sciences.

### Climate data

MAT (°C) and MAP (mm) at each surveyed site were downloaded from CHELSA (Climatologies at high resolution for the earth's land surface areas, <http://chelsa-climate.org/>), which is a global climate data set based on the period from 1979 to 2013. All data resolution was 30 s × 30 s. The de Martonne's aridity index (Tuhkanen 1980) was calculated as follows:  $I_{\text{dM}} = \text{MAP}/(\text{MAT} + 10)$ , with higher  $I_{\text{dM}}$  values indicating higher humidity.

### Calculation and statistics

#### Plant AGB and diversity

The AGB of each species in each quadrat was summed to plant community AGB in the quadrat ( $\text{g m}^{-2}$ ), and the average ABG of all quadrats at each site was calculated to represent plant community ABG at each site ( $\text{AGB}_{\text{com}}$ ). SR (species  $\text{m}^{-2}$ ) was the average number of species per square meter at each study site. The 215 recorded plant species were classified into four PFGs primarily based on plant growth form, namely grasses (including perennial graminoids and perennial sedges), forbs (perennial forbs), annuals and biennials and shrubs and subshrubs (Supplementary Table S1). The average SR of the four PFGs in the community was  $3.86 \pm 1.78$ ,  $6.14 \pm 4.49$ ,  $1.76 \pm 1.39$  and  $0.74 \pm 0.60$  species  $\text{m}^{-2}$ , and the average biomass values were  $41.33 \pm 35.32$ ,  $23.46 \pm 22.75$ ,  $4.59 \pm 10.08$  and  $8.25 \pm 18.64$   $\text{g m}^{-2}$ , respectively (Supplementary Table S2). The annuals and biennials group and the shrubs and subshrubs group were excluded in functional group analysis due to their relatively low AGB or SR (Supplementary Table S2 and Fig. S1). We denote the ABG and SR of grasses and forbs as  $\text{AGB}_{\text{grass}}$ ,  $\text{AGB}_{\text{forb}}$ ,  $\text{SR}_{\text{grass}}$  and  $\text{SR}_{\text{forb}}$ , respectively.

#### Statistics

We first performed the random forest model (RFM) (Breiman 2001) to screen the important

environmental factors that drove  $\text{SR}_{\text{com}}$  and  $\text{AGB}_{\text{com}}$ , and then performed ordinary least squares regression to test whether the influence of these factors on the community was related to PFGs (grasses and forbs). RFM is an extension of the traditional regression tree analysis (RTA) method, which creates a collection of classification trees with binary splits (Cutler *et al.* 2007). An advantage of RFM is that it can alleviate multicollinearity problems in multiple regression and can model complex interactions among predictors rather than make a distribution hypothesis for predictors or response variables (Cutler *et al.* 2007; Delgado-Baquerizo *et al.* 2017). The environmental factors examined in RFM included climate factors (MAT, MAP and  $I_{\text{dM}}$ ) and soil factors (soil pH, BD, STC, STN, sand, silt and clay; Supplementary Table S2). Five thousand regression trees were established in RFM, and each tree was fitted using random data (2/3 of the data). The other 1/3 of the data was called out-of-bag data (OOB) and was used to estimate the importance of each predictor, which was the increase in the mean square error between the observed value and the OOB prediction value. In the establishment of each decision tree, the model searched a few predictors from all the variables to determine the best split of the decision tree. The number of random predictors that determined the best split was set to 1/3 of all variables (three predictors in this study). RFM was implemented using the 'randomForest' package for R (Liaw and Wiener 2002). The significance ( $P$  value) of each predictor was assessed by using the 'rfPermute' package in R (Archer 2020). The cross-validated  $R^2$  and significance of the model were assessed with 5000 permutations of the response variable using the 'A3' package in R (Fortmann-Roe 2015).

Based on the results of RFM, we identified the climate and soil factors that significantly affected community biomass and diversity, respectively. Then, we performed least square regression to further determine the identified variables that have significant relationships with the biomass and SR of functional groups. We first built a polynomial regression including the linear and quadratic terms of the predictor variables. The final model was selected by determining whether the quadratic term was significant and whether the polynomial regression had a better fit and explanatory power than a linear regression (standard  $P < 0.05$  in the  $F$ -ratio test).

Second, to examine how environmental factors influence  $\text{AGB}_{\text{com}}$  and  $\text{SR}_{\text{com}}$  by regulating different PFGs, we constructed structural equation models

(SEMs) using climate and soil factors that significantly affected both communities and PFGs in the regression. We first considered a complete model that included all possible pathways (Supplementary Fig. S2), and then sequentially excluded nonsignificant pathways until the final model was obtained. We used the  $\chi^2$  test ( $P > 0.05$ ) and standardized root mean square residual (SRMR, where  $\text{SRMR} < 0.10$ ) to evaluate the fitness of the model and Akaike information criteria to select the best model. We used standardized path coefficients to measure the direct, indirect and total effect sizes of climate, soil factors and functional groups on  $\text{AGB}_{\text{com}}$  and  $\text{SR}_{\text{com}}$  (Grace and Bollen 2005). The SEMs were developed using the 'lavaan' package in R (Rosseel 2012).

Before all statistical analyses, AGB and SR of community and PFGs,  $I_{\text{dm}}$  and STN were square-root transformed, and STC was log-transformed (based on *e*) so that the residuals of the models followed a normal distribution. Pearson's correlation analysis was carried out for pairwise correlations between all climate and soil variables (Supplementary Fig. S3). All analyses were programmed in R x64 v 3.6.1 (R Development Core Team).

## RESULTS

### Environmental factors influencing biomass and SR

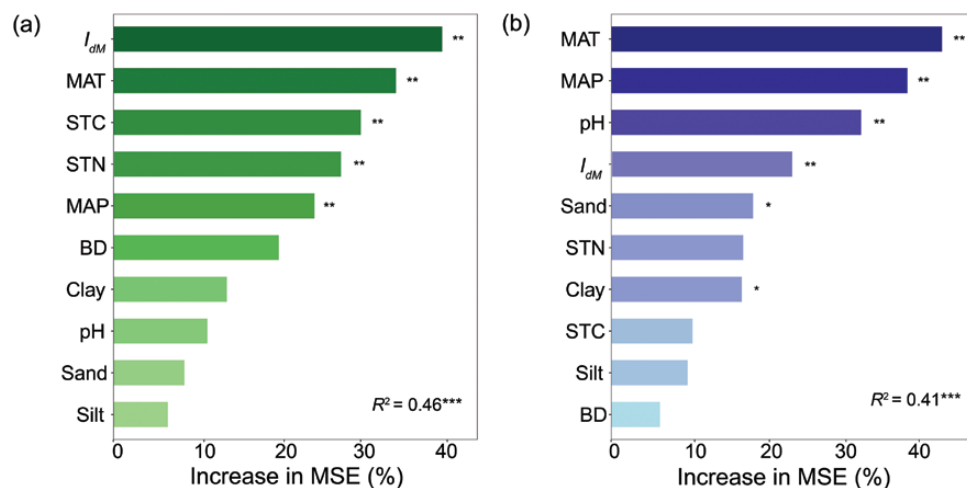
Environmental factors explained 46% and 41% of the variance in AGB ( $\text{AGB}_{\text{com}}$ , Fig. 2a, cross-validation  $R^2 = 0.46$ ,  $P < 0.001$ ) and SR ( $\text{SR}_{\text{com}}$ , Fig. 2b, cross-validation  $R^2 = 0.41$ ,  $P < 0.001$ ) of the community,

respectively. Climate factors (i.e.  $I_{\text{dm}}$ , MAT and MAP) significantly affected both  $\text{AGB}_{\text{com}}$  and  $\text{SR}_{\text{com}}$  (Fig. 2). Interestingly, soil factors were more important in regulating  $\text{SR}_{\text{com}}$  than  $\text{AGB}_{\text{com}}$ , showing significant effects of soil pH, sand and clay on  $\text{SR}_{\text{com}}$  but not on  $\text{AGB}_{\text{com}}$  (Fig. 2b). STC and STN had significant effects on  $\text{AGB}_{\text{com}}$  (Fig. 2a).

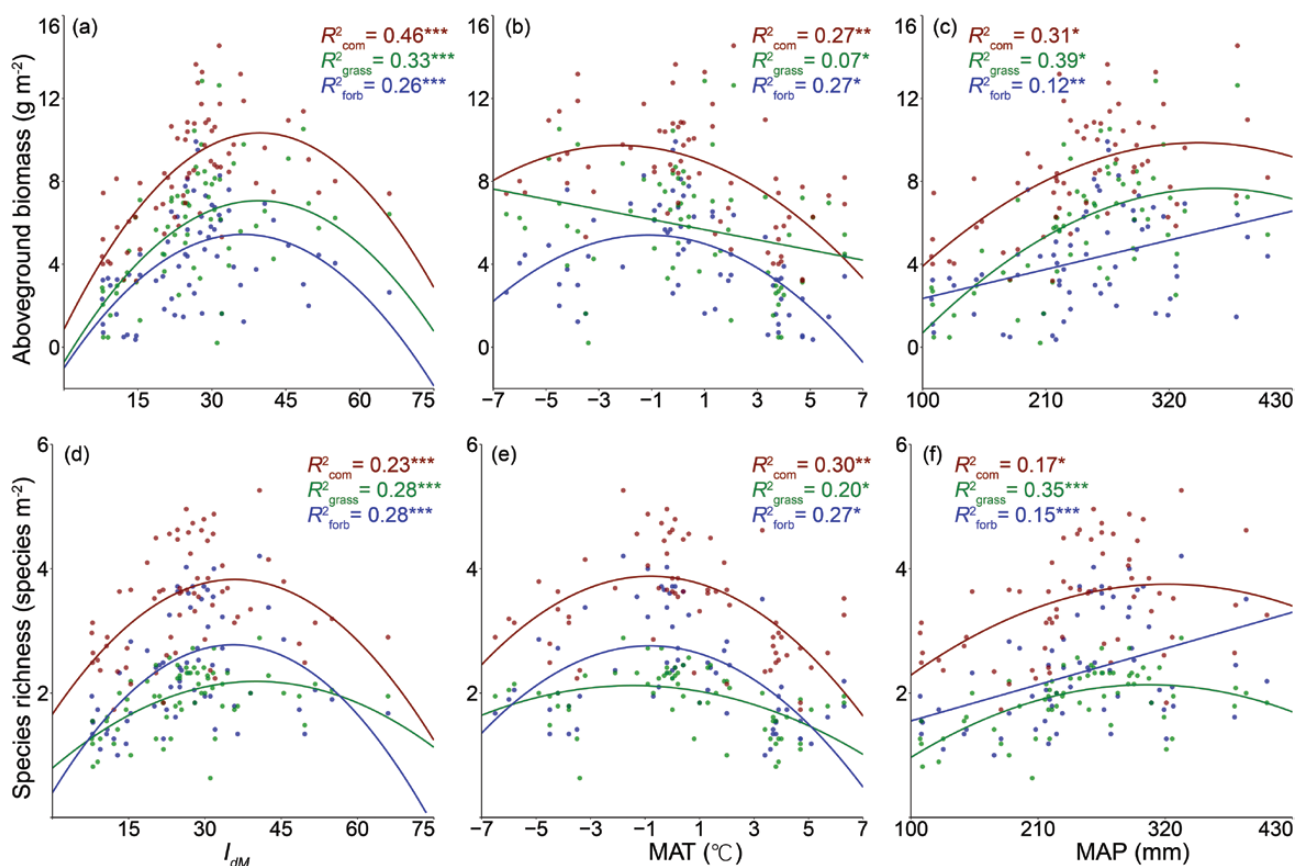
The best-fitting models for the two PFGs and the whole community included unimodal relationships of  $I_{\text{dm}}$  with both AGB ( $R^2_{\text{com}} = 0.46$ ,  $R^2_{\text{grass}} = 0.33$ ,  $R^2_{\text{forb}} = 0.26$ ;  $P < 0.001$  in all cases) and SR ( $R^2_{\text{com}} = 0.23$ ,  $R^2_{\text{grass}} = 0.28$ ,  $R^2_{\text{forb}} = 0.28$ ,  $P < 0.001$  in all cases, Fig. 3a and d). For functional groups,  $I_{\text{dm}}$  had a greater explanatory value than the individual contributions of MAT or MAP (except for the relationships between MAT and  $\text{AGB}_{\text{forb}}$ , MAP with  $\text{AGB}_{\text{grass}}$  and  $\text{SR}_{\text{grass}}$ , Fig. 3b, c, e and f). Moreover, both AGB and SR metrics were significantly related to STN (Fig. 4a and d,  $P < 0.05$  in all cases) and pH (Fig. 4c and f,  $P < 0.05$  in all cases), rather than STC (Fig. 4b and e), clay or sand (Supplementary Fig. S4). Following the results of the RFM and the least square regression, the  $I_{\text{dm}}$ , STN and pH were applied in the SEM.

### Environmental factors influencing biomass and SR by mediating functional groups

The SEM explained 81% of the variance in  $\text{AGB}_{\text{com}}$  ( $R^2 = 0.81$ ), which was mainly due to the direct positive effects of  $\text{AGB}_{\text{grass}}$  ( $r_{\partial} = 0.74$ ,  $P < 0.001$ ) and AGB of forbs ( $\text{AGB}_{\text{forb}}$ ,  $r_{\partial} = 0.46$ ,  $P < 0.001$ , Figs 5 and 6a, b). The direct effect of SR of grasses ( $\text{SR}_{\text{grass}}$ ,  $r_{\partial} = -0.33$ ,  $P < 0.001$ , Fig. 5) on community biomass was negative, but this effect was offset by its positive



**Figure 2:** The importance of environmental factors driving (a) AGB and (b) SR. Increase in MSE denotes an increase in the percentage mean square error. Abbreviations:  $I_{\text{dm}}$  = de Martonne index. Significance levels are as follows: \* $P < 0.05$ , \*\* $P < 0.01$  and \*\*\* $P < 0.001$ .



**Figure 3:** The relationships of climate factors with AGB and SR on the Mongolian Plateau. Lines represent the least square regression of AGB and SR for  $I_{dm}$  (a and d), MAT (b and e) and MAP (c and f). Red, green and blue points and lines represent these metrics in the community, grasses and forbs, respectively. Abbreviations:  $I_{dm}$  = de Martonne index. Significance levels are as follows: \* $P < 0.05$ , \*\* $P < 0.01$  and \*\*\* $P < 0.001$ .

indirect effect on community biomass, and the total effect of  $SR_{grass}$  on  $AGB_{com}$  was only 0.5% (Fig. 6a and b).  $AGB_{grass}$  accounted for the largest proportion of variation in community biomass (i.e. 31.2%), followed by  $I_{dm}$  at 24.6% (Fig. 6b). The indirect effect of  $I_{dm}$  on  $AGB_{com}$  was greater than the direct effect ( $r_{\partial} = 0.18$ ,  $P < 0.001$ , Fig. 6a).  $I_{dm}$  affected  $AGB_{com}$  by directly affecting  $AGB_{grass}$  ( $r_{\partial} = 0.33$ ,  $P < 0.001$ , Fig. 5). The indirect effects of STN and pH on  $AGB_{com}$  were relatively small (4.6% and 5.1%, respectively, Fig. 6b).

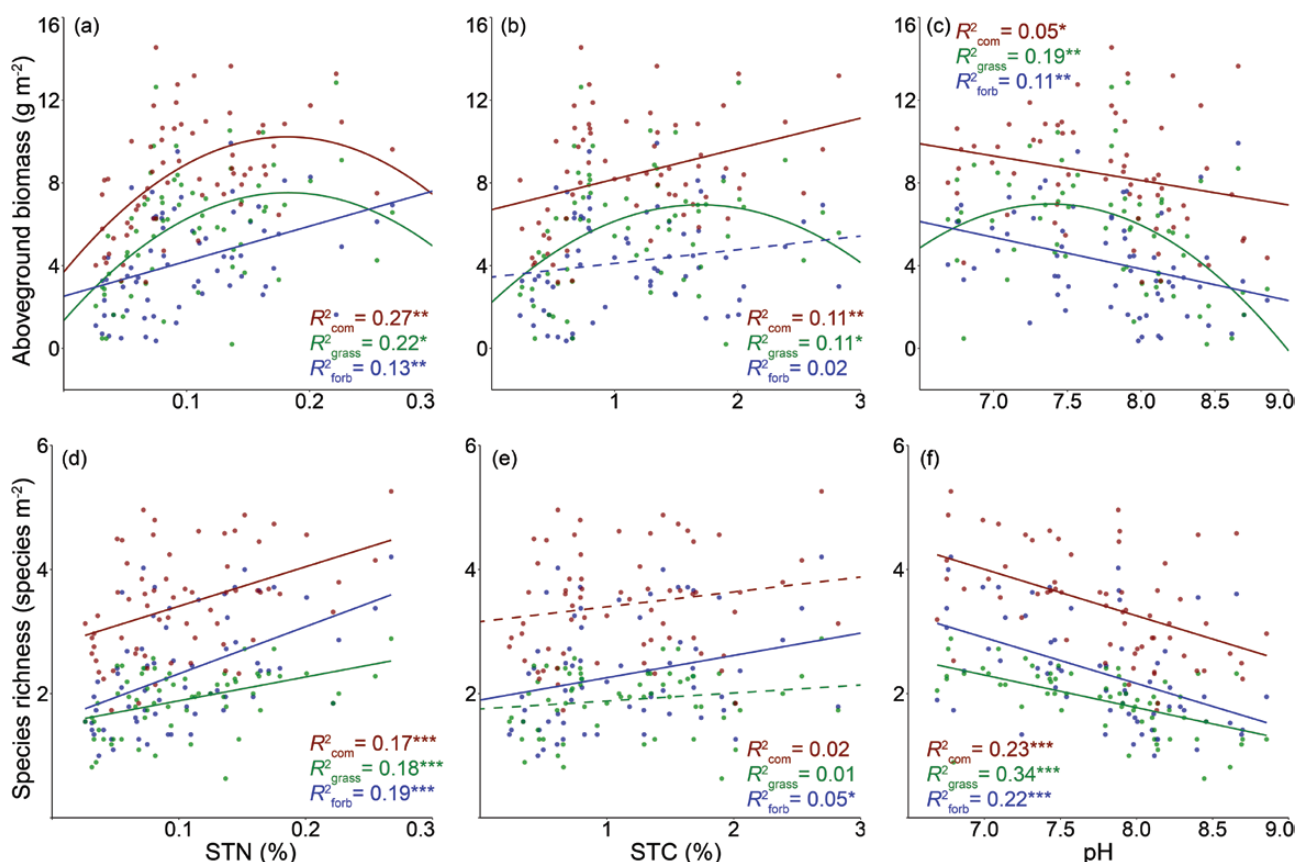
The SEM explained 91% of the variance in  $SR_{com}$  ( $R^2 = 0.91$ ). The direct effect of  $SR_{forb}$  ( $r_{\partial} = 0.64$ ,  $P < 0.001$ ) on  $SR_{com}$  was stronger than that of  $SR_{grass}$  ( $r_{\partial} = 0.38$ ,  $P < 0.001$ , Figs 5 and 6c). The relative contribution of  $SR_{forb}$  to the variance in  $SR_{com}$  was 30.6% (Fig. 6d). Environmental factors had indirect effects on  $SR_{com}$ . The positive indirect effect of  $I_{dm}$  on  $SR_{com}$  was due to the regulation of soil factors and functional groups (Fig. 5). STN directly affected  $SR_{forb}$  ( $r_{\partial} = 0.32$ ,  $P < 0.01$ ) and  $SR_{grass}$  ( $r_{\partial} = 0.28$ ,  $P < 0.01$ ),

and thus had a positive indirect effect on  $SR_{com}$  (Figs 5 and 6c). The effect of soil pH on  $SR_{com}$  was negative and indirect, mainly because pH had a negative direct effect on  $SR_{grass}$  ( $r_{\partial} = -0.49$ ,  $P < 0.001$ ) and  $SR_{forb}$  ( $r_{\partial} = -0.36$ ,  $P < 0.001$ , Fig. 5).

## DISCUSSION

### Climate indirectly affects community biomass by regulating grasses

Our results demonstrated that grasses contributed a majority of community biomass ( $AGB_{com}$ ) in grasslands on the Mongolian Plateau. This is likely because grasses are the dominant PFG in the study area, which supports the ‘mass ratio’ hypothesis in which it is generally recognized that the high biomass plant species (i.e. dominant species or PFGs) in grasslands have greater relative contributions to ecosystem functioning (Avolio *et al.* 2019; Grime 1998; Polley *et al.* 2003). This occurs mostly as the



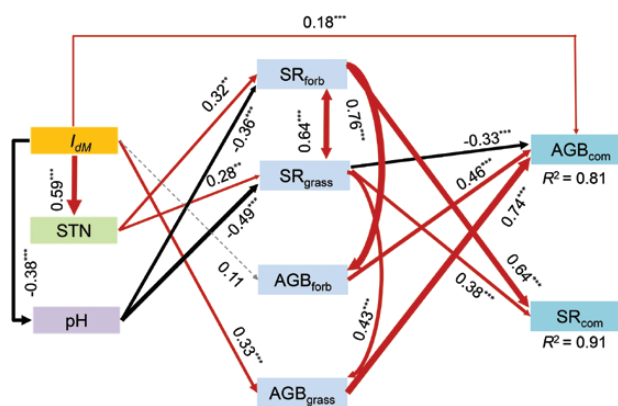
**Figure 4:** The relationships of soil factors with AGB and SR on the Mongolian Plateau. Lines represent the least square regression of AGB and SR for STN (a and d), STC (b and e) and pH (c and f). Red, green and blue points and lines represent these metrics in the community, grasses and forbs, respectively. Solid and dashed lines indicate significant and nonsignificant relationships, respectively. Significance levels are as follows: \* $P < 0.05$ , \*\* $P < 0.01$  and \*\*\* $P < 0.001$ .

result of their long-term evolutionary history and resilience to environmental perturbations in the region. Grasses of the Mongolian Plateau include mainly *Stipa* spp., which are much larger than other species and more efficiently intercept light at the top of the canopy. Dominant species or PFGs have an important impact on community biomass mainly because of their capacity to capture resources (Hooper *et al.* 2005), and *Stipa* spp. are acquisitive-conservative for resources using a conservative resource utilization strategy during their long-term evolution and adaptation (Bai *et al.* 2004; Zheng *et al.* 2015). Moreover, under disturbance (e.g. grazing) or stress (e.g. drought), grass species could facilitate each other but compete with other PFGs (i.e. forbs) (Liang *et al.* 2018). Results of a warming and drought experiment also suggested that grasses could increase at the expense of other PFGs (Liu *et al.* 2018). However, we found that the negative direct impact of grass SR on community biomass was offset by its positive indirect effect, so the total effect of grass SR on community biomass was weak,

which indicates that the 'mass ratio effect' of the dominant species may be more important than its richness.

Furthermore, our results indicated that the effect of climate on AGB<sub>com</sub> was mainly because of the indirect regulation of AGB of grasses (AGB<sub>grass</sub>), and that climate directly affected AGB<sub>grass</sub>. This is probably generally the case in arid and semi-arid grasslands where plant biomass is primarily driven by climate factors (Isbell *et al.* 2015; Li *et al.* 2020; Seddon *et al.* 2016). The response of plant biomass to environmental factors varies between grasses and forbs. As water availability increases, AGB<sub>grass</sub> increases faster than that of forbs (AGB<sub>forb</sub>) (Yang *et al.* 2011). Grasses are generally tall and erect on the Mongolian Plateau (Liang *et al.* 2018), and most of the grasses grow at the top of the vertical architecture in the community. When habitats provide high water availability (e.g. with an increase in rainfall), grasses could preferentially photosynthesize via capturing the solar energy at the top of the plant canopy, maintaining high AGB. Furthermore, despite some





**Figure 5:** SEM of the effects of environmental drivers on AGB and SR via PFGs. Numbers are the standardized path coefficients ( $r_j$ ).  $R^2$  denotes the total variation of the dependent variable explained by the combined independent variables. Red and black arrows indicate positive and negative paths, respectively. Solid and dashed arrows represent significant and nonsignificant paths, respectively. Abbreviations:  $AGB_{grass/forb}$  = functional groups aboveground biomass,  $I_{DM}$  = de Martonne index,  $SR_{grass/forb}$  = functional groups species richness. Significance levels are as follows:  $**P < 0.01$  and  $***P < 0.001$ .  $P_{\text{Chi-square}} = 0.115$ ;  $SRMR = 0.064$ ; Akaike information criteria (AIC) = 871.288.

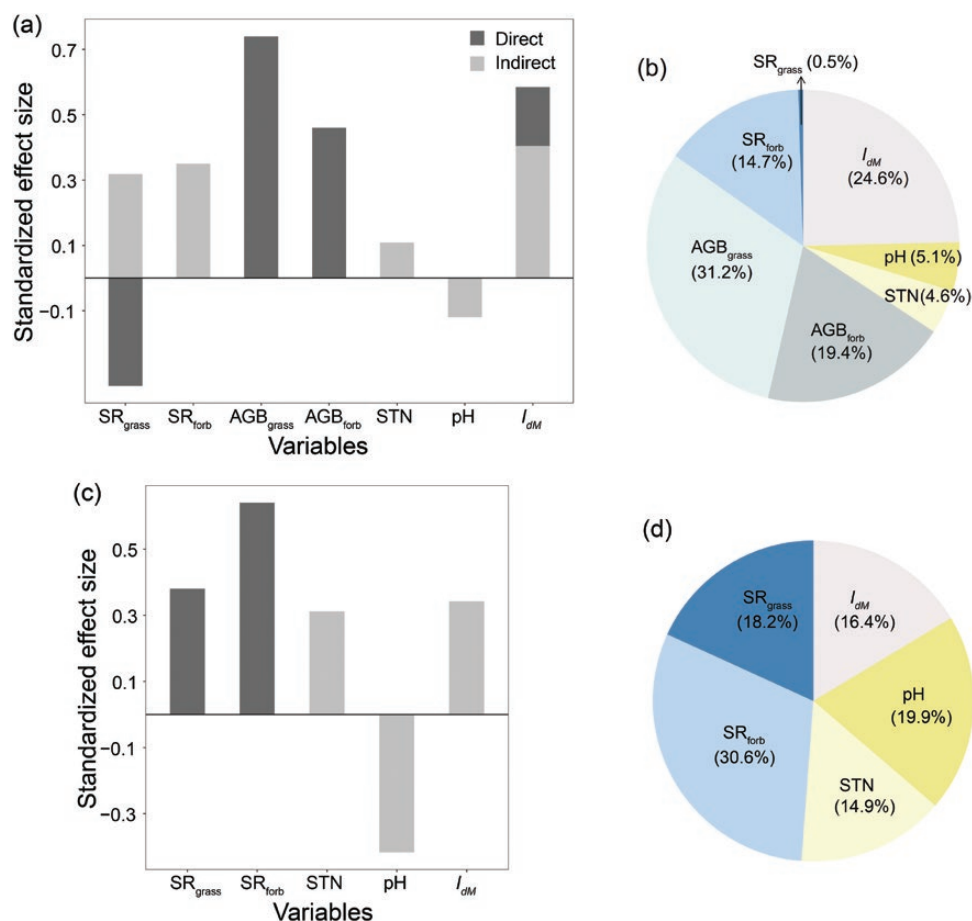
$C_4$  grasses being of small and prostrate structure, they are capable of maintaining a high photosynthetic rate and biomass because of a physiological buffering capacity for water variability (Fay *et al.* 2002; Li *et al.* 2015). In addition, the water use efficiency of plant species is driven by the root system (i.e. root depth) (Fry *et al.* 2018). Therefore, grasses have higher water use efficiency due to the difference in the root system between grasses and forbs. For example, the root systems of grasses are shallow and have many fibrous roots (Nippert and Knapp 2007), which means they have a large distribution area in the soil and can preferentially and quickly use the water on the soil surface to grow and maintain biomass. By contrast, root systems of forbs are straight and are usually deeper than those of grasses, and need to absorb deep soil water (Nippert and Knapp 2007). In conclusion, aridity affects community biomass mainly by regulating grasses in the steppe.

### Soil factors indirectly affect community SR through mediating functional groups

Our results demonstrated that the SR of PFGs, especially SR of forbs ( $SR_{forb}$ ), contributed considerably to variability in plant community biodiversity (i.e.  $SR_{com}$ ) in grasslands on the Mongolian Plateau. A long-term species removal experiment has shown that nonrandom loss of uncommon/rare species or a

single dominant species is an important factor leading to significant decline in  $SR_{com}$  (Smith *et al.* 2020). The impact of dominant PFGs on  $SR_{com}$  may depend on whether the dominant species played a facilitative or competitive role in the community (Smith *et al.* 2020). A facilitative role means that dominant species affect the local environment on which a variety of other species depend, allowing greater species coexistence (Ellison *et al.* 2005). The competition effect is mainly manifested as the inhibitory effect of the existence of a dominant species on other species (Avolio *et al.* 2019). However, the effects of forbs on  $SR_{com}$  might be attributed to their niche partitioning and trait characteristics. Forbs are usually subdominant PFGs on the Mongolian Plateau. Generally, subdominant PFGs are smaller in stature than dominants (Grime 1998). Forbs with low canopy height could occupy canopy space below the dominant species (Monsi and Saeki 2005), which allows more species to survive.

Interestingly, our results suggested that SR in grasslands was indirectly affected by edaphic factors, mainly through the effect of soil on the SR of PFGs, and that SR had a nonsignificant direct relationship with climate. One possible reason is that in arid and semi-arid climates, soil differences in microhabitats affected by climate may have a more significant impact on SR. A reduction of subordinates in dryland ecosystems typically results from low availability of soil nutrients (Ulrich *et al.* 2014), which is similar to the role of forbs in grasslands on the Mongolian Plateau. Our results showed that STN could promote  $SR_{com}$  by directly affecting the SR of PFGs. This is mainly because the growth of vegetation in natural ecosystems is limited by nitrogen (LeBauer and Treseder 2008), especially in temperate grasslands of the Mongolian Plateau (Bai *et al.* 2010), so SR increases with increasing nitrogen. Alternatively, saturated soil nutrients could also decrease SR (Clark and Tilman 2008; Harpole and Tilman 2007; Isbell *et al.* 2013; Stevens *et al.* 2004). Chronic nitrogen addition results in reduced stability of dominant species (Wu *et al.* 2020), and the combined effects of soil acidification (Bai *et al.* 2015; Tian *et al.* 2016) and light competition (Hautier *et al.* 2009) caused by nitrogen addition significantly inhibit the photosynthetic rate of forbs, leading to a reduction in  $SR_{com}$ . Additionally, our findings show that soil pH has a negative indirect effect on  $SR_{com}$  by affecting PFGs. The soils of the Mongolian Plateau grassland are mostly alkaline. In high pH soils (pH > 7), because of the reduced solubility of phosphorus



**Figure 6:** The relative contribution of environmental drivers and PFGs in the SEM. Bar plots show the summed direct and indirect effects of abiotic and biotic drivers on (a) AGB and (c) SR in the SEM. Pie charts show the relative contributions of predictors to the explained variations in (b) AGB and (d) SR. Abbreviations: AGB<sub>grass/forb</sub> = functional groups aboveground biomass, I<sub>dM</sub> = de Martonne index, SR<sub>grass/forb</sub> = functional groups species richness.

and iron, they become limiting nutrients, which might lead to a decline in SR<sub>com</sub> (Zohlen and Tyler 2000). There was a negative correlation between pH and the SR of PFGs. This might be because physiological stress affecting plants limits the number of species, which in turn reduces SR<sub>com</sub>. Overall, STN and pH affect the SR<sub>com</sub> by mediating the SR of both grasses and forbs.

Our results suggested that the regulation by soil factors of SR<sub>com</sub> was also climate related. A study of the Eurasian steppe showed that the relationship between plant SR and soil pH gradually vanished as the increasingly dry climate, indicating the important role of climate in driving soil characteristics and SR (Palpurina *et al.* 2017). Climate had an indirect effect on plant community composition by changing soil water availability (Yang *et al.* 2011). This might be because the climate-related soil characteristics show obvious spatiotemporal heterogeneity, which increases with the intensification of drought (D'Odorico *et al.* 2007) and in turn affects community attributes.

## CONCLUSIONS

Overall, we found that grasses played a key role in maintaining the community biomass of grasslands on the Mongolian Plateau in the eastern Eurasian Steppe, and that this relationship was regulated by climate factors. Furthermore, the SR of PFGs, especially forbs, determined plant SR in the community, and this was indirectly affected by soil factors. Our results highlight that environmental factors (i.e. aridity index, STN and pH) are fundamental drivers of ecosystem functioning and their impacts on plant SR and community biomass are indirectly expressed through the promotion of PFGs. Therefore, community composition plays an important role in regulating the effects of environmental factors on community biomass and plant diversity.

## Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

Figure S1: Variations of aboveground biomass (**a**) and species richness (**b**) of steppe communities and their plant functional groups.

Figure S2: A conceptual model assumed that climate and soil factors affect  $AGB_{com}$  and  $SR_{com}$  by regulating different functional groups.

Figure S3: Pearson's correlation matrix of climate and soil factors in Mongolian Plateau grassland.

Figure S4: The relationships of soil particle size with aboveground biomass and species richness on the Mongolian Plateau.

Table S1: The list of species (total = 215) and their trait information recorded in 65 vegetation sites on the Mongolian Plateau.

Table S2: Descriptive statistics of environment factors, biodiversity and aboveground biomass of the steppes on the Mongolian Plateau grasslands.

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*Conflict of interest statement.* The authors declare that they have no conflict of interest.

### Authors' Contributions

Z. Li analyzed the data and wrote the first draft of the manuscript. M. Liang, Zh. Li, F.Y. Li, P. Mariotte, E.S. Gornish, C. Liang and Zh. Dang contributed to later versions of the manuscript and all authors provided constructive comments to improve the manuscript. F.Y. Li and C. Liang designed and led the field survey. Z. Li, Zh. Li, X. Tong, J. Zhang, L. Dong, Y. Zheng, W. Ma, L. Zhao, L. Wang, L. Wen, I. Tuvshintogtokh, C. Liang and F.Y. Li conducted the experiment and collected the data.

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