Research paper

# Distribution, species richness, and relative importance of different plant life forms across drylands in China

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## ARTICLE INFO

## ABSTRACT

Studies on plant diversity are usually based on the total number of species in a community. However, few studies have examined species richness (SR) of different plant life forms in a community along large-scale environmental gradients. Particularly, the relative importance (RIV) of different plant life forms in a community and how they vary with environmental variables are still unclear. To fill these gaps, we determined plant diversity of ephemeral plants, annual herbs, perennial herbs, and woody plants from 187 sites across drylands in China. The SR patterns of herbaceous plants, especially perennial herbs, and their RIV in plant communities increased with increasing precipitation and soil nutrient content; however, the RIV of annual herbs was not altered along these gradients. The SR and RIV of ephemeral plants were affected mainly by precipitation seasonality. The SR of woody plants had a unimodal relationship with air temperature and exhibited the highest RIV and SR percentage in plant communities under the harshest environments. An obvious shift emerged in plant community composition, SR and their critical impact factors at 238.5 mm of mean annual precipitation (MAP). In mesic regions (> 238.5 mm), herbs were the dominant species, and the SR displayed a relatively slow decreasing rate with increasing aridity, which was mediated mainly by MAP and soil nutrients. In arid regions (< 238.5 mm), woody plants were the dominant species, and the SR displayed a relatively fast decreasing rate with increasing aridity, which was mediated mainly by climate variables, especially precipitation. Our findings highlight the importance of comparative life form studies in community structure and biodiversity, as their responses to gradients differed substantially on a large scale.

## 1. Introduction

Determining large-scale patterns and underlying mechanisms of plant biodiversity are central goals in ecology because they are essential in understanding and modeling ecosystem functions (Hooper et al., 2012; Maestre et al., 2012). The majority of previous studies on this subject focused on plant species richness (SR), which advances our knowledge of how plant communities adapt to continuous environmental change such as climate variables or environmental gradients (Adler and Levine, 2007; Sun et al., 2021;

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Yao et al., 2021). However, community structure, including species composition and abundance, are usually more sensitive to environmental changes (such as aridity and soil pH) than SR, and, thus, can further affect ecosystem function (Ulrich et al., 2014; Berdugo et al., 2017, 2019; Spaak et al., 2017). Therefore, the relative importance (RIV) of plant species or various species types can be altered within the community with changes in environmental conditions, which can result in changes in community structure (Ulrich et al., 2014; Berdugo et al., 2017; Spaak et al., 2017). Consequently, it would be beneficial to determine the environmental factors that influence both the RIV and the SR of various species types.

Studies have demonstrated that climate change is expected to result in substantial changes in the amount and pattern of precipitation and evapotranspiration in drylands (Huang et al., 2017; Li et al., 2021). These changes can affect soil nutrients and reduce vegetation coverage, likely causing the extinction of many important species and, thus, shifting their distribution patterns (Parmesan, 2006; Delgado-Baquerizo et al., 2013; Li et al., 2021; Sun et al., 2021). However, most studies on the distribution of plant SR focused on wet environments, such as forests and grassland ecosystems (Fang et al., 2012; Liu et al., 2018). In contrast, drylands, although they are the largest terrestrial ecosystem on Earth (Schimel, 2010) and one of the most sensitive ecosystems to global climate change (Reed et al., 2012), have received relatively less attention (Hu et al., 2021, 2022; Sun et al., 2021; Yao et al., 2021).

Plant communities on land are a complex composition of diverse species functional groups, that is, woody, annual, and perennial species. In addition, in temperate deserts, apart from "drought-tolerant" herbaceous plant species (annual and perennial herbs in the present study), dryland ecosystems include a special group of "drought-avoiding" herb species, called ephemeral plants, which have very short growth cycles and are derived from the xerothermic relic flora (Li et al., 2019). Ephemeral plants complete their life histories quickly during brief "windows of opportunity", when both air temperature and moisture conditions are conducive to growth and reproduction (Li et al., 2019; Tao et al., 2022). In contrast, the "drought-tolerant" herbaceous plants had a relatively longer evolutionary history to adapt to the extreme environment in drylands than ephemeral plants, as their speciation and diversification were driven mainly by aridification and desertification during the Quaternary period (Meng et al., 2015; Li et al., 2019). In particular, annual herbs can avoid cold and dry stress in winter through seed dormancy (Facelli et al., 2005; Harrison et al., 2015). However, perennial species display diverse strategies to adapt to cold and dry environments in drylands, for example, allocating more material and energy to the growth of roots, and reproducing by both tillering and seed production (Husáková et al., 2018). In addition, woody plants usually have well-developed stems and extensive root systems (Hageer et al., 2017; Chen et al., 2019), and tend to produce small leaves with thick-walled cells as an adaptation to water and temperature stress in desert ecosystems (Wright et al., 2004; Deng et al., 2006, 2008). Therefore, different plant life forms have evolved different mechanisms to cope with the extreme environmental stresses in drylands. However, most studies to date have focused on overall plant diversity (Francis and Currie, 2003; Palpurina et al., 2017), and very few have examined SR and RIV of different life forms in plant communities.

Given that different plant life forms display different adaptation strategies, we hypothesized that: i) their responses to environmental changes differ, and ii) their relative ecological importance with respect to the plant community composition varies along environmental gradients. Recent findings reported a shift in biodiversity-soil multifunctionality relationships at an aridity level of approximately 0.8 in China's drylands (Hu et al., 2021). Based on

this finding, we also hypothesized that iii) the variations in plant community composition, SR, and their environmental determinants would exhibit a threshold along an aridity gradient in China's drylands. Based on these hypotheses, we asked the following key questions: i) how do plant SR, community species compositions (e.g., woody, perennial, annual and ephemeral species) and their RIVs vary along an environmental gradient in drylands? and ii) what are the crucial drivers that determine the spatial patterns of plant species richness, community species compositions, and their RIVs across drylands? To test our hypotheses and address these questions, we collected large-scale datasets in plant communities and soil attributes from 187 sites in China's drylands.

## 2. Material and methods

### 2.1. Study region

Measurements were made in northern China (36.00−50.71° N and 76.61−122.40° E) in the interior of the Eurasia continent where shrubs, semi-shrubs, and herbs dominated the plant communities. This large study region covered dry sub-humid, semi-arid, arid, and hyper-arid regions, with an aridity index (AI) ranging from 0.01 to 0.62. This region is characterized by a dry temperate continental climate, with the mean annual air temperature ranging from −3.8 to 12.6 °C and the annual precipitation ranging from 25 to 485 mm.

### 2.2. Sampling survey

Owing to the patchiness of the dryland ecosystems, a nested sampling design was employed ranging from 0.5 m × 0.5 m to 30 m × 30 m for sites dominated by herbaceous species, and increasing to 100 m × 100 m for sites dominated by large woody species, such as *Haloxylon ammodendron* and *Tamarix chinensis* (Fig. S1). To address the scale-dependence of biodiversity, we determined the SR in 30 m × 30 m at each site. In addition, the latitude, longitude, and elevation were recorded along with species composition and abundance. All plants in the community were categorized into four different plant life forms, namely, ephemeral plants, annual herbs, perennial herbs, and woody plants, according to the Flora Reipublicae Popularis Sinicae (http://www.iplant.cn/frps), and the height and crown width of each individual plant were measured in each plot. A total of 1057 plots at 187 sites were sampled during the growing season (June to August) from 2013 to 2018.

### 2.3. Environmental factors

To determine the effects of climate on diversity distribution and the RIV of plants in drylands, we selected 18 climatic variables at each site (Table S1). Specifically, air temperature variables (mean annual temperature, wettest quarter, driest quarter, warmest quarter, and coldest quarter), precipitation variables (annual precipitation, driest quarter, coldest quarter, wettest quarter, and warmest quarter), temperature seasonality (TSN) and precipitation seasonality (PSN, %) were obtained from the WorldClim website (http://worldclim.org/version2) (Fick and Hijmans, 2017). Annual potential (PET) and actual evapotranspiration (AET) in mm and aridity index (AI) were obtained from the Consortium for Spatial Information (CGIAR-CSI) website (http://www.cgiar-csi.org/data). The air temperature and precipitation during the growing season (May to September) (GST, °C and GSP, mm) and the annual rainfall (RAIN, mm, the sum of monthly precipitation when mean monthly temperatures were above 0 °C) were calculated from monthly air temperature and precipitation provided by the WorldClim website.

All climatic variables were extracted at a resolution of 30 s $\times$ 30 s (*ca*. 1 km $\times$ 1 km at the equator).

Besides climate variables, soil variables are also major factors influencing species distribution, in particular, soil nutrient contents (Hageer et al., 2017; Wang et al., 2017). Therefore, soil variables, including soil organic carbon (SOC, g/kg), total nitrogen (TN, g/kg), total phosphorus (TP, g/kg), available phosphorus (AP, mg/kg), pH, and electrolytic conductivity (EC, μs/cm), were measured at all field sites (in 30 m $\times$ 30 m plots) in the top 10 cm soil layer. To obtain site-level estimates, the data between the bare ground and vegetated areas were weighted by vegetation coverage at each site as:

$$Soil_{site-level} = Soil_{vegetated} \times Coverage + Soil_{bare} \times (1 - Coverage) \quad (1)$$

Where $Soil_{site-level}$ was the weighed-value for a given soil variable at each quadrat, which was estimated by the corresponding measure values of soil from under the plant canopy ($Soil_{vegetated}$) and bare ground ($Soil_{bare}$), and percentage of vegetation coverage together.

### 2.4. Calculation of relative importance value

We calculated the RIV (Curtis and McIntosh, 1951) and the SR percentage for each life form at each site to determine changes along environmental gradients. The RIV of each life form was calculated using the equation:

$$RIV = (RH + RC + RA) / 3 \quad (2)$$

where RH, RC and RA were the relative height, relative crown width, and relative abundance (percent) of each life form in the plant community, respectively. RH was calculated as the percentage of the sum of heights of each life form to the sum of heights of all plants in the sampling plant community, as were the algorithms of RC and RA.

The SR percentage for each life form was calculated using the equation:

$$The\ percentage = (SR_{life\ forms} / SR_{all\ plants}) \times 100\% \quad (3)$$

$SR_{life\ forms}$ was the SR of each life form in each sampling site, and $SR_{all\ plants}$ was the SR of all plants in each sampling site.

### 2.5. Statistical analyses

Because strongly correlated environmental variables (i.e., $r > 0.7$) led to multicollinearity (Table S2), principal components analysis (PCA) was applied separately for temperature variables, water availability variables, and soil nutrient variables to eliminate multicollinearity within groups. We retained the first PCA axis as synthetic predictors for each group of variables because the first principal components explained the greatest percentage of variance for the group of temperature variables (PC1temp), water availability (PC1water), and soil nutrients (PC1nutrients) (Table S3) (Borvka et al., 2005; Xu et al., 2016).

We used linear regressions to determine the relationships between environmental variables and the SR and RIV of each life form, and the SR of all plants. Quadratic models were used if they had better fits than linear models according to Akaike information criterion (AIC). We transformed SR by taking its square root to obtain a normal distribution (Palpurina et al., 2017). Linear mixed-effects models (R package lme4) were used to identify the most important climate and soil variables using the AIC and variance inflation factors (VIF) (Wang et al., 2010; Kuznetsova et al., 2017). In these models, climate variables (PC1water, PC1temp, PSN, and TSN) and soil variables (PC1nutrients, pH, and EC) were treated as fixed

variables. To eliminate the potential annual variability on plants that may result from sampling in different years, "year" was used as a random intercept in the models. Variables with a multicollinearity value of less than five were accepted (Wang et al., 2010). Models with minimal AIC were used to test each regression using F- and T-tests (Kuznetsova et al., 2017; Palpurina et al., 2017). The initial models and the final models selected are presented in Table S4.

Structural equation models (SEM) were generated to identify the direct and indirect drivers of the overall SR and of the SR and RIV of the four plant functional groups. Here, it is reasonable to assume that the plant SR and RIV are affected by both climate variables and soil variables, and that soil attributes (e.g., soil nutrients, soil physical and chemical properties) are controlled mainly by climate conditions (Reed et al., 2012; Delgado-Baquerizo et al., 2013; Palpurina et al., 2017; Wang et al., 2017; Dong et al., 2022). Moreover, climate variables change with latitude, longitude, and altitude, which were considered to account for the spatial structure of the SEMs (Hu et al., 2021). As a result, a *priori* model was tested according to the relationships among geographical space, climate, and soil variables (Fig. S2). SEM goodness of fit was determined using the comparative fit index (CFI), the goodness of fit index (GFI), the normed fit index (NFI), the root mean square error of approximation (RMSEA), and $X^2$ tests (Table S5). SEMs were generated with the AMOS software (v. 21) (Blunch, 2008).

To identify region-specific responses to environmental variables and the presence of environmental thresholds in SR of plants in drylands, we used regression tree analysis with the "*rpart*" package (Therneau and Atkinson, 2019) and step regression with the "*chngpt*" package (Fong et al., 2017) in R software. A threshold can occur only when a nonlinear regression fits the data better than a linear regression. The advantage of regression tree analysis is that it allows complex collinearity, interactions, and nonlinear relationships among variables (De'ath and Fabricius, 2000). It is a binary recursive variance partitioning method that builds the tree model in a forward stepwise search. Trees explain variation of the response variable by repeatedly splitting the data into more homogeneous groups. In general, the parameters at the top of the regression tree analysis are the most important contributors to the variation of the dependent variables (De'ath and Fabricius, 2000; Therneau and Atkinson, 2019). Step regression helps to determine whether there is an environmental threshold at which the plant SR step changes (such as a significant increase or decrease) (Fong et al., 2017; Hu et al., 2021). A one-way ANOVA and a non-parametric Mann-Whitney U-test were used to compare both sides of the environmental threshold (Ulrich et al., 2014; Hu et al., 2021).

The spatial distributions of SR and RIV were visualized using ordinary kriging in ArcMap10.3 (ESRI, Redlands, CA, USA).

## 3. Results

### 3.1. Geographical patterns of SR and RIV and their environmental thresholds

Plant SR increased gradually from the southwest desert ecosystems to the northeast grassland ecosystems across the drylands of China, with a boundary in SR variations along the 238.5 mm MAP (Fig. 1a). Moreover, SR was greater ($p < 0.001$) in sites receiving a MAP of more than 238.5 mm than in sites receiving less than 238.5 mm (Fig. 1b, Fig. S3a). In sites with MAP > 238.5 mm, SOC was the main driver of SR distribution; while in sites with MAP < 238.5 mm, climate variables, especially water variables, were key drivers (Fig. 1b). The stepwise regression showed that approximately 236 mm of MAP was the environmental threshold at which the plant SR step changed significantly ($p < 0.001$; Fig. 1c, Fig. S4a).
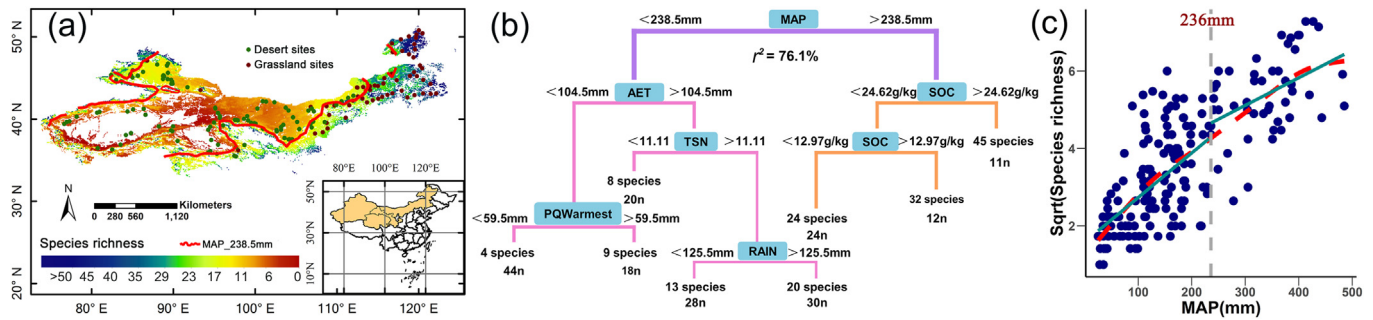
**Fig. 1.** (a) The geographical species richness patterns of all plants in China's drylands based on data from 187 sites (30 m × 30 m in each site) by ordinary kriging, (b) regression tree analysis based on binary recursive variance partitioning, and (c) nonlinear environmental response and environmental threshold of SR for all plants in China's drylands. The base map does not include mountains and the interior of the Taklimakan Desert (the largest sandy desert in China). The spatial resolution is 30 s × 30 s (ca 1 km × 1 km at the equator). For the regression tree analysis, predictors and their split values are presented at each node, and mean values of plant species richness and the number of observations are presented at each terminal. Environmental threshold (MAP = 236 mm, the gray dashed line) was obtained by step regression. Red dashed line and dark cyan solid line represent the smoothed trend fitted by a generalized additive model (GAM) and the linear fits at both sides of environmental threshold, respectively. MAP, mean annual precipitation; AET, annual actual evapotranspiration; TSN, temperature seasonality; PQWarmest, precipitation of warmest quarter; RAIN, annual rainfall; SOC, soil organic carbon.

Different plant life forms had different SR distributions and RIVs in the plant communities (Fig. 2). The distribution of SR in herbaceous species, especially perennials, was similar to the pattern for all plant species (Figs. 1a, 2b and 2c). Woody species did not display an obvious trend in SR, whereas ephemerals were concentrated mainly in the northwest drylands (Fig. 2a and d). Interestingly, the RIV of each life form did not always correspond to its geographical SR pattern. Specifically, the RIV and SR patterns of ephemeral plants and perennial herbs were similar (Fig. 2a, c, e and g). The RIV of annual herbs did not follow a geographical pattern (Fig. 2f), while woody species and perennial herbs exhibited opposite RIV patterns (Fig. 2g and h). In addition, the SR and RIV of different plant life forms exhibited different environmental thresholds (Table S6; Figs. S3−S4).

### 3.2. Relationships between SR and environmental variables

The SR of annual and perennial herbs increased strongly and linearly with PC1water (Fig. 3c2 and d2), but perennials decreased linearly with PC1temp (Fig. 3d1), and ephemerals decreased linearly with PSN (Fig. 3b4). The SR of woody plants displayed a unimodal relationship with PC1temp and TSN (Fig. 3e), as did the SR-PC1temp with all plants in sites with MAP < 238.5 mm (Fig. 3a1). PC1nutrients, especially SOC, was correlated most strongly with perennial herb SR and all plant SR in sites with MAP > 238.5 mm, but much less so in sites with MAP < 238.5 mm (Fig. 3a5 and d5, Fig. S5).

We also examined the effects of environmental variables on the SR of dryland plants by multiple regressions (Tables 1 and S4). Results were similar to those of bivariate regression analyses (Table 1), which strengthened our hypothesis that the SR of different plant life forms responds differently to environmental variables.

Structural equation models (SEMs) also indicated that PC1water had a direct and positive effect on all plant SR in all drylands and at sites with MAP < 238.5 mm, as well as on the SR of annual and perennial herbs (Fig. 4a, b, e and f). PC1water, through its effect on PC1nutrients, had an indirect effect on the SR of all plants in all drylands and sites with MAP > 238.5 mm and the SR of perennial herbs (Fig. 4a, c and f). PSN and the quadratic term of PC1temp had significant, negative, direct effects on the SR of ephemerals and woody plants, respectively (Fig. 4d and g).
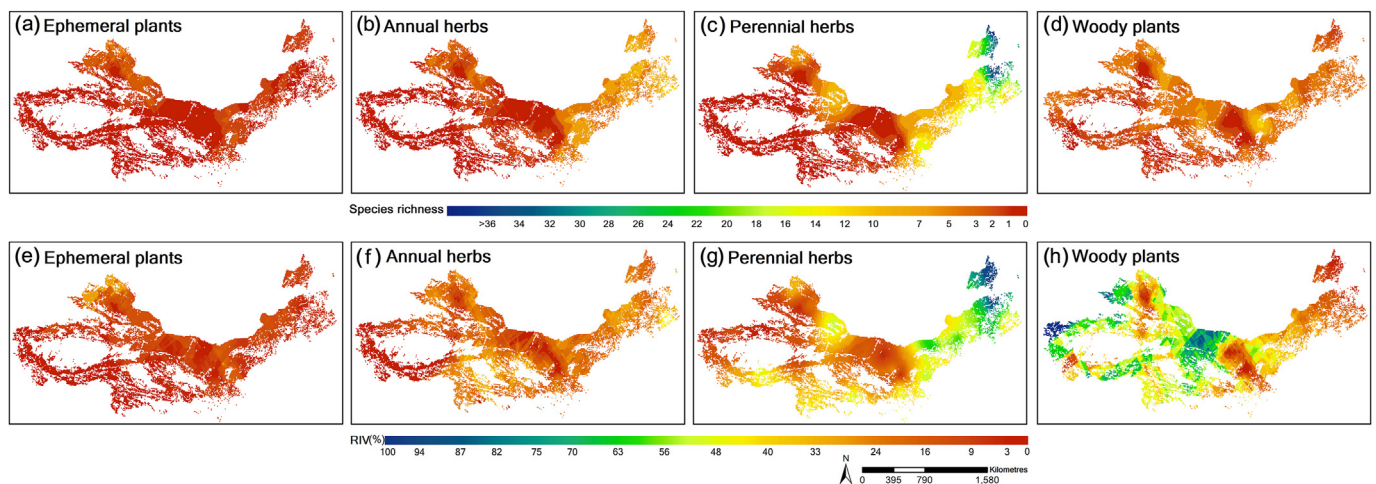


**Fig. 2.** The spatial patterns in (a−d) species richness and (e−h) relative importance value (RIV, %) of different plant life forms in China's drylands based on data from 187 sites (30 m × 30 m in each site) by ordinary kriging. The base map does not include mountains and the interior of the Taklimakan Desert (the largest sandy desert in China). The spatial resolution is 30 s × 30 s (ca. 1 km × 1 km at the equator).
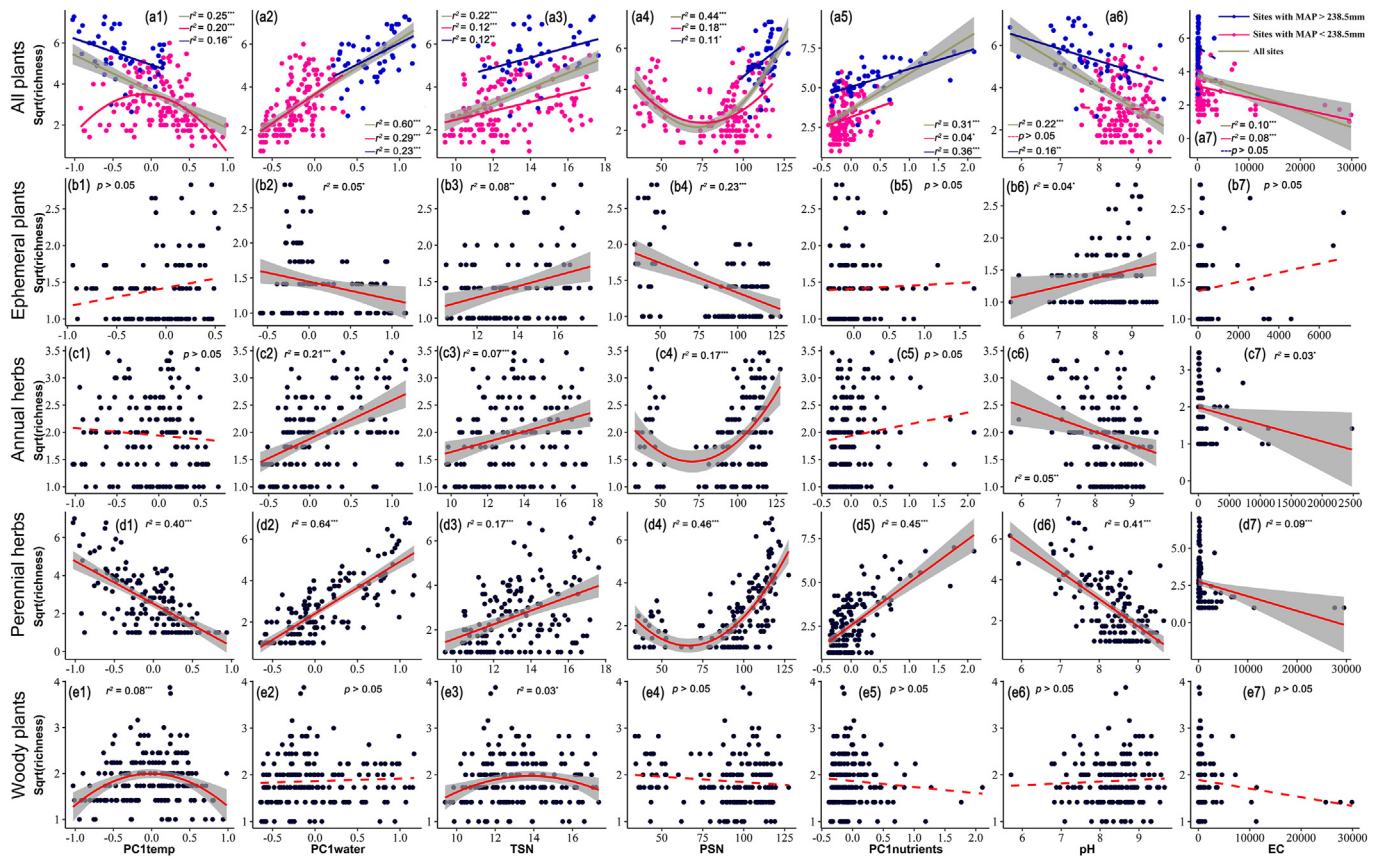
**Fig. 3.** Relationships between environmental variables and species richness of all plants and four life forms in China's drylands. In a1-a7, the blue dots and lines represent plant species richness and their fitting lines in sites with MAP > 238.5 mm; the pink dots and lines represent plant species richness and their fitting lines in sites with MAP < 238.5 mm; the gray lines represent fitting lines for species richness of all plants in all sites. The square root of plant species richness is used in the models and $r^2$ is the adjusted coefficient of determination. Solid lines represent significant fits (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$), whereas dashed lines represent non-significant fits ($p > 0.05$). Shaded areas represent the 95% confidence intervals of the regression lines.

**Table 1**
Stepwise multiple regression relationships between environmental variables and plant species richness in all plants and different plant life forms, and between environmental variables and relative importance of different plant life forms in dryland ecosystems using linear mixed-effects models.

| Groups | Response variables | Models | AIC | Fixed $r^2$ | Full $r^2$ | Standardized coefficients (mean ± s.d) | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | coefficient1 | coefficient2 | coefficient3 | coefficient4 |
| **All plants** (All sites) | SR | PC1water + TSN + PC1nutrients + EC | 300.14 | 0.43 | 0.67 | 0.34 ± 0.13 | 0.14 ± 0.09 | 0.15 ± 0.09 | −0.15 ± 0.08 |
| **All plants** (Sites with MAP < 238.5 mm) | SR | PC1water + TSN + EC | 308.74 | 0.26 | 0.56 | 0.36 ± 0.13 | 0.21 ± 0.13 | −0.20 ± 0.12 | |
| **All plants** (Sites with MAP > 238.5 mm) | SR | PC1water + PC1nutrients | 101.37 | 0.14 | 0.87 | 0.21 ± 0.18 | 0.49 ± 0.18 | | |
| **Ephemeral plants** | SR | PSN + EC | 267.43 | 0.19 | 0.44 | −0.50 ± 0.27 | −0.09 ± 0.17 | | |
| | RIV | PC1temp$^2$+TSN + PC1nutrients + PSN | 504.29 | 0.18 | 0.24 | −0.24 ± 0.15 | 0.21 ± 0.16 | 0.06 ± 0.16 | −0.28 ± 0.18 |
| **Annual herbs** | SR | PC1water + PC1nutrients | 370.38 | 0.08 | 0.27 | 0.33 ± 0.23 | −0.19 ± 0.16 | | |
| | RIV | PC1temp + PC1nutrients | 523.76 | 0.04 | 0.04 | −0.23 ± 0.17 | −0.23 ± 0.18 | | |
| **Perennial herbs** | SR | PC1water + PC1nutrients | 212.58 | 0.53 | 0.72 | 0.37 ± 0.12 | 0.34 ± 0.09 | | |
| | RIV | PC1water + PC1nutrients + PSN | 412.76 | 0.47 | 0.48 | 0.30 ± 0.15 | 0.30 ± 0.12 | 0.25 ± 0.13 | |
| **Woody plants** | SR | PC1temp$^2$+PSN | 499.67 | 0.15 | 0.31 | −0.33 ± 0.14 | −0.19 ± 0.18 | | |
| | RIV | PC1temp + PC1water + EC | 424.86 | 0.34 | 0.43 | 0.25 ± 0.14 | −0.37 ± 0.18 | −0.13 ± 0.11 | |

Coefficients 1 to 6 correspond to standardized coefficients. In these models, environmental variables (PC1water, PC1temp, PC1nutrients, PSN, TSN, pH, EC) are fixed variables, and sampling years are random factors; $r^2$ values of models are given for fixed and full (fixed + random) effects. Significant levels at $p < 0.05$. SR, species richness; RIV, relative importance value; TSN, temperature seasonality; PSN, precipitation seasonality; EC, electrolytic conductivity.

### 3.3. RIV of different plant life forms

The RIVs and the SR percentages of perennial herbs and woody plants were the most affected by climate and soil variables but displayed opposite trends (Table 1; Fig. 5c and d, Figs. S6−S7).

Furthermore, perennial herbs, which are dominant species in mesic areas with the lowest aridity and least environmental stress, had the highest RIV and the largest SR percentage (Figs. 2g and 5c, Figs. S6−S7). In contrast, woody plants, which are dominant species in deserts with the highest aridity and most environmental stress,
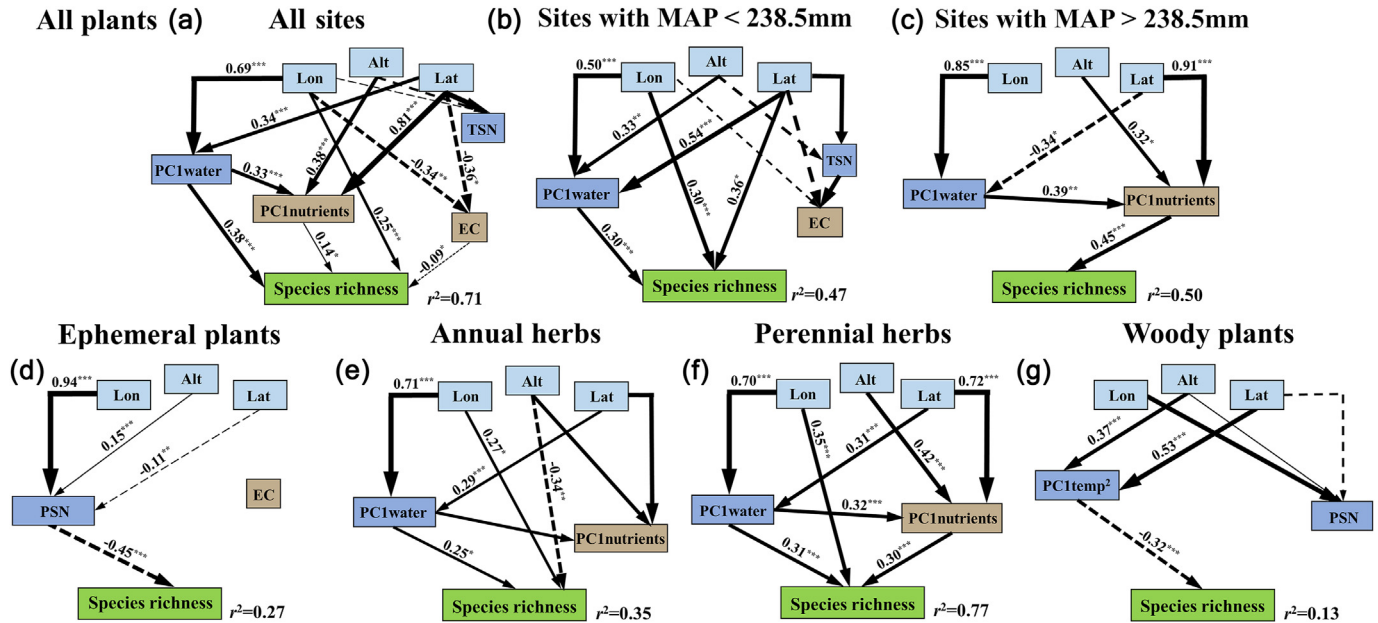
**Fig. 4.** Structural equation models (SEM) displaying the direct and indirect drivers of spatial variables, climate drivers, and soil attributes on plant species richness of **(a–c)** all plants and **(d–g)** different plant life forms across China's drylands. Dashed lines represent significant negative effects, while solid lines indicate significant positive effects. Non-significant (*p* > 0.05) paths were eliminated to simplify the graph. Numbers adjacent to arrows are standardized path coefficients, and the thickness of the line is proportional to the strength of path coefficients. *r²* is the proportion of variance explained. Significant levels: **p* < 0.05; ***p* < 0.01; ****p* < 0.001. Lon, longitude; Lat, latitude; Alt, altitude; TSN, temperature seasonality; PSN, precipitation seasonality; EC, electrolytic conductivity. All of the SEM models provided good fits (see Supporting information for the goodness of SEM fits).
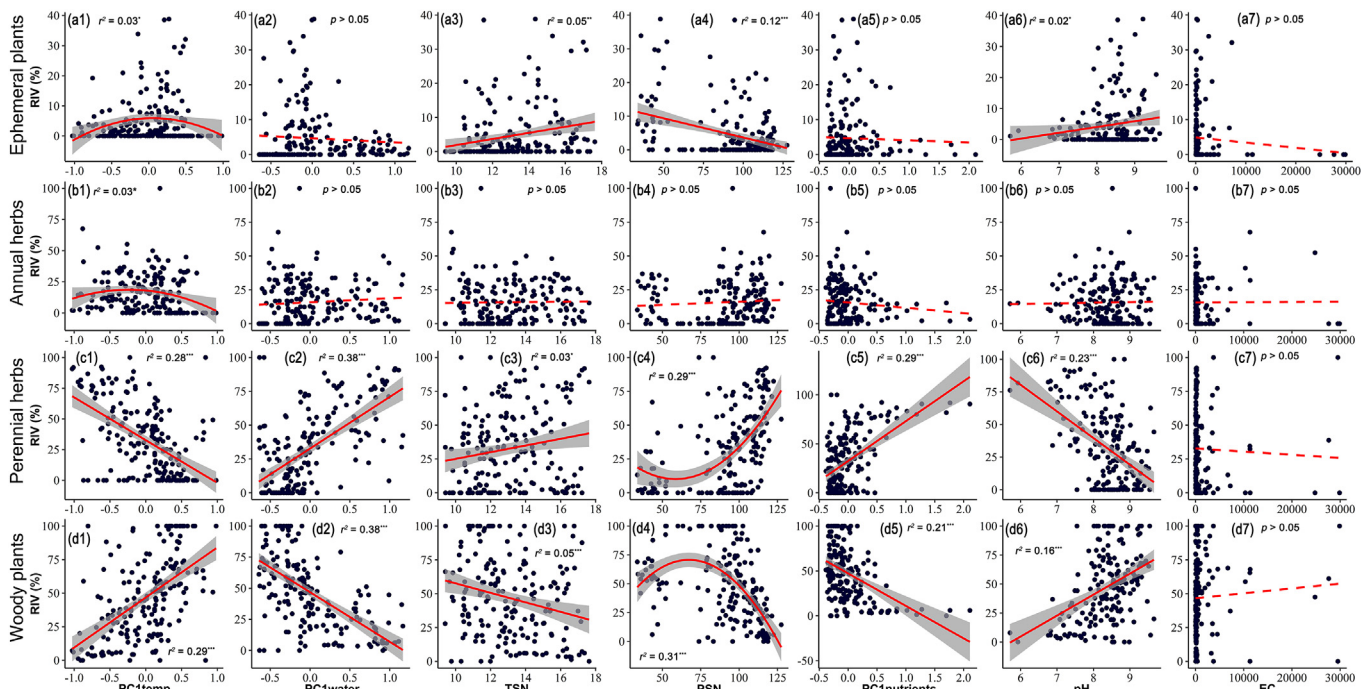


**Fig. 5.** Relationships between environmental variables and relative importance value (RIV, %) of four life forms in the plant communities of China's drylands. Solid lines represent significant fits at **p* < 0.05, ***p* < 0.01, ****p* < 0.001, whereas dashed lines represent non-significant fits at *p* > 0.05. Shaded areas represent the 95% confidence intervals of the regression lines.

had the highest RIV and the largest SR percentage (Figs. 2h and 5d, Figs. S6–S7). PC1water displayed a direct, positive effect on RIV of perennial herbs (standardized coefficient = 0.24; Fig. 6c), but a direct, negative effect on woody plants (standardized coefficient = −0.21; Fig. 6d). Moreover, PC1water, through its effect

on PC1nutrients, had a positive, indirect effect on the RIV of perennial herbs (Fig. 6c), while PC1temp had a direct, positive effect on the RIV of woody plants (standardized coefficient = 0.28; Fig. 6d). The SR percentage and the RIV of annual herbs were not affected, while ephemeral plants were affected weakly by climate
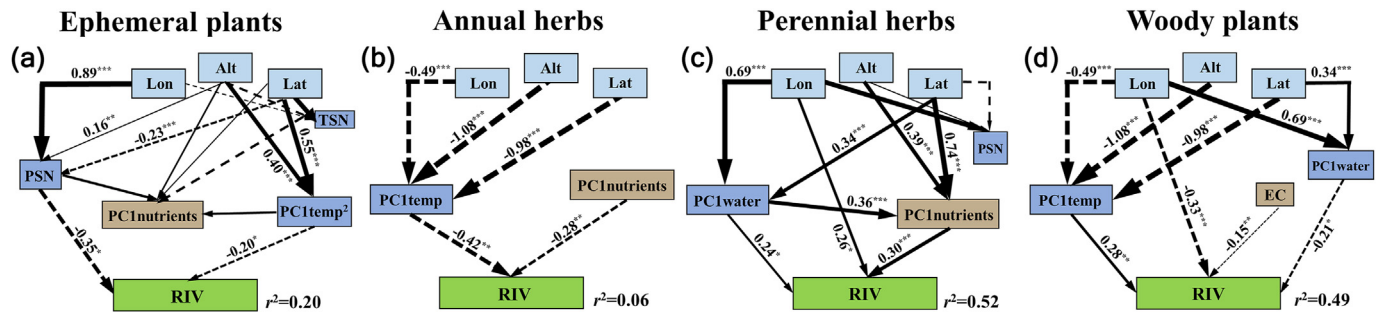
**Fig. 6.** Structural equation models (SEM) displaying the direct and indirect drivers of spatial variables, climate drivers, and soil attributes on the relative importance (RIV) of different plant life forms across China's drylands. Dashed lines represent significant negative effects, while solid lines indicate significant positive effects. Non-significant ($p > 0.05$) paths were eliminated to simplify the graph. Numbers adjacent to arrows are standardized path coefficients, and the thickness of the line is proportional to the strength of path coefficients. $r^2$ is the proportion of variance explained. Significant levels: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$. Lon, longitude; Lat, latitude; Alt, altitude; TSN, temperature seasonality; PSN, precipitation seasonality; EC, electrolytic conductivity. All of the SEM models provided good fits (see Supporting information for the goodness of SEM fits).

and soil factors across all drylands except PSN (Fig. 5a and b, Figs. S6—S7). PSN had a significant, direct, negative effect on the RIV of ephemeral plants (standardized coefficient = −0.35; Fig. 6a).

## 4. Discussion

### 4.1. Spatial patterns of plant species richness and a shift phenomenon across drylands

Overall, the plant SR in China's dryland ecosystems exhibited a pronounced geographical gradient and was lower than in wet regions (Tang et al., 2006; Wang et al., 2010; Fang et al., 2012). Climatic variables, especially precipitation, explained more of the variation in dryland SR patterns than soil variables, which was consistent with previous studies (Francis and Currie, 2003; Li et al., 2017; Palpurina et al., 2017).

The SR, dominant species in plant communities, and environmental determinants of SR displayed divergence on both sides of MAP at approximately 238.5 mm. In areas with MAP less than 238.5 mm (arid regions), climate variables, especially available water, were the main direct drivers of SR, while soil nutrients only had a minor effect, which suggests that drought stress is the bottleneck for plant growth and development in arid regions. Hence, aridity acts as an environmental filter, leaving only a few drought-tolerant species, such as woody plants with deep root systems, that are able to survive under such conditions (Ulrich et al., 2014; Le Bagousse-Pinguet et al., 2017). In areas with MAP greater than 238.5 mm (mesic regions), soil nutrients were the main drivers for SR, while water had only an indirect impact by its effect on the uptake of soil nutrients. Water increases soil nutrient cycling by enhancing soil microbial activity and soil nutrient availability (Zhang et al., 2015; Palpurina et al., 2017; Wang et al., 2017; Ochoa-Hueso et al., 2018; Dong et al., 2022). Therefore, precipitation mitigates drought stress on plants (Yao et al., 2021), and soil fertility becomes the bottleneck for plant growth in mesic regions. In addition, soil nutrients are concentrated in the surface (Dong et al., 2022), and, thus, herbaceous species with shallow roots are the dominant species in mesic areas. Several studies reported that the biodiversity-soil multifunctionality relationships, soil fertility, nutrient capture, and nutrient cycling shift abruptly at a certain threshold (Berdugo et al., 2017; Huang et al., 2017; Hu et al., 2021). This shift phenomenon also occurred in the present study at a MAP of approximately 238 mm, that is, at an AI ≈ 0.24, which was slightly greater than the AI of 0.2 reported for the biodiversity-soil multifunctionality relationships in China's drylands (Hu et al., 2021). This difference in threshold may be due to the lagging effect of biodiversity on ecosystem function.

### 4.2. Species richness and relative importance of the various plant life forms across drylands

As hypothesized, different plant life forms had different SRs, RIVs, and key drivers along environmental gradients. Ephemeral plants had high SR and RIV in the Gurbantunggut Desert located in the northern Xinjiang Province of China. This can be attributed, at least partially, to climatic characteristics in this region, where winter snowfall is greater than in other drylands in China. Water in the form of snow- and ice melt provides a humid environment for the survival of ephemeral plants after air temperature rises (Fan et al., 2014; Jia et al., 2020). In the present study, ephemeral species referred mainly to spring ephemeral plants, which are particularly sensitive to precipitation during the dry and cold seasons and to air temperature in warm and wet growing seasons (Figs. S5—S7). The most vital environmental variable for the survival of ephemeral plants in China's dryland ecosystems was PSN rather than MAP. Ephemeral species are a special group of herbaceous plants adapted to dry and hot environments by avoiding drought rather than by coping with it (Li et al., 2019). These species tend to have high water-use efficiencies, are highly sensitive to available water, and complete their life history quickly in a few weeks (Chen et al., 2019; Li et al., 2019; Tao et al., 2022). Hence, they depend more on short-term soil moisture content than on annual precipitation. The smaller PSN indicates that precipitation tends to be distributed more evenly throughout the year, and, thus, relatively abundant precipitation in winter is more helpful for ephemerals in drylands.

The SR of the annual and especially the perennial herbaceous life forms displayed increasing trends with increasing precipitation and soil nutrient content, whereas woody plants did not. Herbaceous plants tend to have shallow roots and rely mainly on upper layer soil water provided by precipitation (Harrison et al., 2015; Chen et al., 2019), whereas woody plants have developed secondary tissues and deep roots that can reach deep groundwater (Zhu et al., 2013; Hageer et al., 2017; Chen et al., 2019). Soil nutrient cycling is much faster in herbaceous species than in woody plant species (Ochoa-Hueso et al., 2018; Hu et al., 2021). Consequently, it is not surprising that the variation in SR of herbs, especially perennial herbs, is more sensitive to precipitation and soil nutrients than in woody species. Moreover, woody plants have greater tolerance to environmental stress than herbaceous species because of these physiological and developmental differences. In the harshest environments, woody plants have the highest RIV and the largest SR percentage, and play an important role in maintaining plant SR and community stability. In contrast to long-living woody plants, perennial herbs have shorter generation times, leading to a faster turnover rate. Thus, they respond faster to climate change,

occupy blank ecological niches, and diversify quicker than woody plants (Liu et al., 2018; Sun et al., 2021). As a result, perennial herbs become the dominant life forms in favorable climatic areas. However, the RIV of annual herbs was not evident across the entire drylands of China. This may be partly attributed to the fact that the persistence of annual herbs depends on the vigor of soil seed banks (Facelli et al., 2005; Adler and Levine, 2007); seed germination relies on environmental conditions (Ladwig et al., 2016), and thus tends to exhibit high intra- and inter-annual variability (Maestre et al., 2012).

The current study indicated that the SR of woody species displayed a unimodal relationship with temperature across China's drylands. The SR of woody plants is affected by low air temperature in winter in colder regions, while being restricted by high temperature in summer in hot regions with increasing temperature. This is because the developed secondary tissues of woody plants enable them to tolerate frost and high air temperatures (Yao et al., 2021). By contrast, herbaceous species can mitigate the effects of frost by their roots or seeds (Harrison et al., 2015; Xu et al., 2016; Yao et al., 2021). Therefore, the SRs of annual and perennial herbaceous species in China's drylands were correlated negatively with most temperature variables, suggesting that dryland temperatures are high for most herbaceous plants. The SR of herbaceous species is not affected by low winter temperature, but by high summer temperature which limits plant growth and development primarily by enhancing water evaporation in China's drylands (Yao et al., 2021). Therefore, except for woody plants in colder regions, low temperature in severely cold winters is not detrimental for plant SR in China's drylands (Fig. S5). This is inconsistent with the "freezing tolerance hypothesis," which postulates that low air temperature in winter limits SR (Currie et al., 2004; Wang et al., 2010).

## 5. Conclusions

Climate change, including changes on patterns of precipitation and temperature, is a serious threat to China's dryland ecosystems (Li et al., 2021), and can lead to fundamental changes in the plant community composition and ecosystem structure (Adler and Levine, 2007; Fang et al., 2018; Roberts, 2020). Previous studies demonstrated that the turnover in species composition plays a key role in determining plant SR patterns (Adler and Levine, 2007; Saiz et al., 2018; Dornelas et al., 2023; Šímová et al., 2023), as the patterns depend largely on the colonization rates of individual species as they adapt to climate change (Adler and Levine, 2007; Šímová et al., 2023). The present study demonstrated that the different plant life forms have distinct SR patterns, different RIVs for plant communities, and respond differently to multiple environmental gradients, indicating that they will continue to develop different responses when adapting to climate change. Interestingly, the change in the pattern of all plant SR across drylands resulted mainly from a rapid decrease in perennial herb SR and RIV as a consequence of increasing drought stress. However, woody plants maintained plant SR and stability in plant communities in the harshest environments, such as deserts. A clear shift phenomenon occurred in SR, community composition and dominant species (i.e., herbaceous and woody plants) at an annual precipitation of ~238 mm. In addition, plant diversities in herb- and woody plant-dominated communities were regulated mainly by water-soil nutrients and precipitation, respectively. Generally, our findings highlighted the importance of considering biodiversity as a delicate balance of different life forms coping with the increased pressures of global climate change, and emphasized the importance of comparative life-form studies in plant communities.

## CRediT authorship contribution statement

**Shuran Yao:** Writing − review & editing, Writing − original draft, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization, Funding acquisition, Validation, Visualization. **Weigang Hu:** Writing − review & editing, Investigation, Conceptualization, Funding acquisition. **Mingfei Ji:** Investigation, Data curation, Formal analysis, Visualization. **Abraham Allan Degen:** Writing − review & editing, Conceptualization, Visualization. **Qiajun Du:** Methodology, Investigation, Data curation. **Muhammad Adnan Akram:** Writing − review & editing, Formal analysis. **Yuan Sun:** Investigation, Software. **Ying Sun:** Formal analysis, Investigation. **Yan Deng:** Data curation, Formal analysis. **Longwei Dong:** Methodology, Investigation. **Haiyang Gong:** Investigation, Software. **Qingqing Hou:** Investigation, Software. **Shubin Xie:** Investigation, Formal analysis. **Xiaoting Wang:** Investigation, Formal analysis. **Jinzhi Ran:** Conceptualization, Funding acquisition, Supervision. **Bernhard Schmid:** Writing − review & editing, Conceptualization. **Qinfeng Guo:** Writing − review & editing, Conceptualization. **Karl J. Niklas:** Writing − review & editing, Visualization. **Jianming Deng:** Writing − review & editing, Visualization, Supervision, Resources, Project administration, Conceptualization, Formal analysis, Funding acquisition, Methodology.

## Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Jianming Deng is an editorial board member for Plant Diversity and was not involved in the editorial review or the decision to publish this article. All authors declare that there are no competing interests.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pld.2024.09.007.

## References

Adler, P.B., Levine, J.M., 2007. Contrasting relationships between precipitation and species richness in space and time. Oikos 116, 221−232. https://doi.org/10.1111/j.2006.0030-1299.15327.x.

Berdugo, M., Kefi, S., Soliveres, S., et al., 2017. Plant spatial patterns identify alternative ecosystem multifunctionality states in global drylands. Nat. Ecol. Evol. 1, 3. https://doi.org/10.1038/s41559-016-0003.

Berdugo, M., Maestre, F.T., Kéfi, S., et al., 2019. Aridity preferences alter the relative importance of abiotic and biotic drivers on plant species abundance in global drylands. J. Ecol. 107, 190−202. https://doi.org/10.1111/1365-2745.13006.

Blunch, N., 2008. Introduction to Structural Equation Modeling Using SPSS and AMOS. SAGE Publications Ltd. https://doi.org/10.4135/9781446249345.

Borvka, L., Vacek, O., Jehlika, J., 2005. Principal component analysis as a tool to indicate the origin of potentially toxic elements in soils. Geoderma 128, 289−300. https://doi.org/10.1016/j.geoderma.2005.04.010.

Chen, R., Ran, J., Huang, H., et al., 2019. Life history strategies drive size-dependent biomass allocation patterns of dryland ephemerals and shrubs. Ecosphere 10, e02709. https://doi.org/10.1002/ecs2.2709.

Currie, D.J., Mittelbach, G.G., Cornell, H.V., et al., 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecol. Lett. 7, 1121–1134. https://doi.org/10.1111/j.1461-0248.2004.00671.x.

Curtis, J.T., McIntosh, R.P., 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology 32, 476–496. https://doi.org/10.2307/1931725.

De'ath, G., Fabricius, K.E., 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology 81, 3178–3192. https://doi.org/10.1890/0012-9658(2000)081[3178:CARTAP]2.0.CO;2.

Delgado-Baquerizo, M., Maestre, F.T., Gallardo, A., et al., 2013. Decoupling of soil nutrient cycles as a function of aridity in global drylands. Nature 502, 672–676. https://doi.org/10.1038/nature12670.

Deng, J., Wang, G., Morris, E., et al., 2006. Plant mass-density relationship along a moisture gradient in north-west China. J. Ecol. 94, 953–958. https://doi.org/10.1111/j.1365-2745.2006.01141.x.

Deng, J., Li, T., Wang, G., et al., 2008. Trade-offs between the metabolic rate and population density of plants. PLoS One 3, e1799. https://doi.org/10.1371/journal.pone.0001799.

Dong, L., Sun, Y., Ran, J., et al., 2022. Ecosystem organic carbon storage and their drivers across the drylands of China. Catena 214, 106280. https://doi.org/10.1016/j.catena.2022.106280.

Dornelas, M., Chase, J.M., Gotelli, N.J., et al., 2023. Looking back on biodiversity change: lessons for the road ahead. Phil. Trans. R. Soc. B. 37820220199. https://doi.org/10.1098/rstb.2022.0199.

Facelli, J.M., Chesson, P., Barnes, N., 2005. Differences in seed biology of annual plants in arid lands: a key ingredient of the storage effect. Ecology 86, 2998–3006. https://doi.org/10.1890/05-0304.

Fan, L., Tang, L., Wu, L., et al., 2014. The limited role of snow water in the growth and development of ephemeral plants in a cold desert. J. Veg. Sci. 25, 681–690. https://doi.org/10.1111/jvs.12121.

Fang, J., Shen, Z., Tang, Z., et al., 2012. Forest community survey and the structural characteristics of forests in China. Ecography 35, 1059–1071. https://doi.org/10.1111/j.1600-0587.2013.00161.x.

Fang, J., Yu, G., Liu, L., et al., 2018. Climate change, human impacts, and carbon sequestration in China. Proc. Natl. Acad. Sci. U.S.A. 115, 4015–4020. https://doi.org/10.1073/pnas.1700304115.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37, 4302–4315. https://doi.org/10.1002/joc.5086.

Fong, Y., Huang, Y., Gilbert, P.B., et al., 2017. Chngpt: threshold regression model estimation and inference. BMC Bioinformatics 18, 454. https://doi.org/10.1186/s12859-017-1863-x.

Francis, A.P., Currie, D.J., 2003. A globally consistent richness-climate relationship for angiosperms. Am. Nat. 161, 523–536. https://doi.org/10.1086/368223.

Hageer, Y., Esperón-Rodríguez, M., Baumgartner, J.B., et al., 2017. Climate, soil or both? Which variables are better predictors of the distributions of Australian shrub species? PeerJ 5, 1–22. https://doi.org/10.7717/peerj.3446.

Harrison, S.P., Gornish, E.S., Copeland, S., 2015. Climate-driven diversity loss in a grassland community. Proc. Natl. Acad. Sci. U.S.A. 112, 8672–8677. https://doi.org/10.1073/pnas.1502074112.

Hu, W., Ran, J., Dong, L., et al., 2021. Aridity-driven shift in biodiversity-soil multi-functionality relationships. Nat. Commun. 12, 1–15. https://doi.org/10.1038/s41467-021-25641-0.

Hu, W., Hou, Q., Delgado-Baquerizo, M., et al., 2022. Continental-scale niche dif-ferentiation of dominant topsoil archaea in drylands. Environ. Microbiol. 24, 5483–5497. https://doi.org/10.1111/1462-2920.16099.

Huang, J., Li, Y., Fu, C., et al., 2017. Dryland climate change: recent progress and challenges. Rev. Geophys. 55, 719–778. https://doi.org/10.1002/2016RG000550.

Husáková, I., Weiner, J., Münzbergová, Z., 2018. Species traits and shoot-root biomass allocation in 20 dry-grassland species. J. Plant Ecol. 11, 273–285. https://doi.org/10.1093/jpe/rtw143.

Hooper, D.U., Adair, E.C., Cardinale, B.J., et al., 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486, 105–108. https://doi.org/10.1038/nature11118.

Jia, Y., Sun, Y., Zhang, T., et al., 2020. Elevated precipitation alters the community structure of spring ephemerals by changing dominant species density in Central Asia. Ecol. Evol. 10, 2196–2212. https://doi.org/10.1002/ece3.6057.

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest package: tests in linear mixed effects models. J. Stat. Softw. 82, 1–26. https://doi.org/10.18637/jss.v082.i13.

Ladwig, L.M., Ratajczak, Z.R., Ocheltree, T.W., et al., 2016. Beyond arctic and alpine: the influence of winter climate on temperate ecosystems. Ecology 97, 372–382. https://doi.org/10.1890/15-0153.1.

Le Bagousse-Pinguet, Y., Gross, N., Maestre, F.T., et al., 2017. Testing the environ-mental filtering concept in global drylands. J. Ecol. 105, 1058–1069. https://doi.org/10.1111/1365-2745.12735.

Li, X., Song, G., Hui, R., et al., 2017. Precipitation and topsoil attributes determine the species diversity and distribution patterns of crustal communities in desert ecosystems. Plant Soil 420, 163–175. https://doi.org/10.1007/s11104-017-3385-8.

Li, Y., Zhang, X., Lv, G., 2019. Phylogeography of *Ixiolirion songaricum*, a spring ephemeral species endemic to Northwest China. Plant Syst. Evol. 305, 205–221. https://doi.org/10.1007/s00606-018-1563-7.

Li, C., Fu, B., Wang, S., et al., 2021. Drivers and impacts of changes in China's dry-lands. Nat. Rev. Earth Environ. 2, 858–873. https://doi.org/10.1038/s43017-021-00226-z.

Liu, Y., Su, X., Shrestha, N., et al., 2018. Effects of contemporary environment and Quaternary climate change on drylands plant diversity differ between growth forms. Ecography 42, 334–345. https://doi.org/10.1111/ecog.03698.

Maestre, F.T., Quero, J.L., Gotelli, N.J., et al., 2012. Plant species richness and ecosystem multifunctionality in global drylands. Science 335, 214–218. https://doi.org/10.1126/science.1215442.

Meng, H., Gao, X., Huang, J., et al., 2015. Plant phylogeography in arid Northwest China: retrospectives and perspectives. J. Syst. Evol. 53, 33–46. https://doi.org/10.1111/jse.12088.

Ochoa-Hueso, R., Eldridge, D.J., Delgado-Baquerizo, M., et al., 2018. Soil fungal abundance and plant functional traits drive fertile island formation in global drylands. J. Ecol. 106, 242–253. https://doi.org/10.1111/1365-2745.12871.

Palpurina, S., Wagner, V., von Wehrden, H., et al., 2017. The relationship between plant species richness and soil pH vanishes with increasing aridity across Eurasian dry grasslands. Global Ecol. Biogeogr. 26, 425–434. https://doi.org/10.1111/geb.12549.

Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. Syst. 37, 637–669. https://doi.org/10.1146/ecolsys.2006.37issue-110.110annurev.ecolsys.37.091305.110100.

Reed, S.C., Coe, K.K., Sparks, J.P., et al., 2012. Changes to dryland rainfall result in rapid moss mortality and altered soil fertility. Nat. Clim. Change 2, 752–755. https://doi.org/10.1038/nclimate1596.

Roberts, D.W., 2020. Comparison of distance-based and model-based ordinations. Ecology 101, e02908. https://doi.org/10.1002/ecy.2908.

Šímová, I., Ordonez, A., Storch, D., 2023. The dynamics of the diversity–energy relationship during the last 21,000 years. Global Ecol. Biogeogr. 32, 707–718. https://doi.org/10.1111/geb.13649.

Saiz, H., Gómez-Gardeñes, J., Borda, J.P., et al., 2018. The structure of plant spatial association networks is linked to plant diversity in global drylands. J. Ecol. 106, 1443–1453. https://doi.org/10.1111/1365-2745.12935.

Schimel, D.S., 2010. Drylands in the earth system. Science 327, 418–419. https://doi.org/10.1126/science.1184946.

Spaak, J.W., Baert, J.M., Baird, D.J., et al., 2017. Shifts of community composition and population density substantially affect ecosystem function despite invariant richness. Ecol. Lett. 20, 1315–1324. https://doi.org/10.1111/ele.12828.

Sun, Y., Sun, Y., Yao, S., et al., 2021. Impact of climate change on plant species richness across drylands in China: from past to present and into the future. Ecol. Indicat. 132, 108288. https://doi.org/10.1016/j.ecolind.2021.108288.

Tang, Z., Wang, Z., Zheng, C., et al., 2006. Biodiversity in China's mountains. Front. Ecol. Environ. 4, 347–352. https://doi.org/10.1890/1540-9295(2006)004[0347:BICM]2.0.CO;2.

Tao, Y., Qiu, D., Gong, Y., et al., 2022. Leaf-root-soil N:P stoichiometry of ephemeral plants in a temperate desert in Central Asia. J. Plant Res. 135, 55–67. https://doi.org/10.1007/s10265-021-01355-8.

Therneau, T.M., Atkinson, E.J., 2019. An introduction to recursive partitioning using the RPART routines. Rochester, M.N: Division of Biomedical Statistics and Informatics. Mayo Clinic, 2018. https://cran.r-project.org/web/packages/rpart/vignettes/longintro.pdf.

Ulrich, W., Soliveres, S., Maestre, F.T., et al., 2014. Climate and soil attributes determine plant species turnover in global drylands. J. Biogeogr. 41, 2307–2319. https://doi.org/10.1111/jbi.12377.

Wang, C., Wang, S., Fu, B., et al., 2017. Precipitation gradient determines the tradeoff between soil moisture and soil organic carbon, total nitrogen, and species richness in the Loess Plateau. China. Sci. Total Environ. 575, 1538–1545. https://doi.org/10.1016/j.scitotenv.2016.10.047.

Wang, Z., Fang, J., Tang, Z., et al., 2010. Patterns, determinants and models of woody plant diversity in China. Proc. R. Soc. B-Biol. Sci. 278, 2122–2132. https://doi.org/10.1098/rspb.2010.1897.

Wright, I.J., Reich, P.B., Westoby, M., et al., 2004. The worldwide leaf economics spectrum. Nature 428, 821–827. https://doi.org/10.1038/nature02403.

Xu, X., Wang, Z., Rahbek, C., et al., 2016. Geographical variation in the importance of water and energy for oak diversity. J. Biogeogr. 43, 279–288. https://doi.org/10.1111/jbi.12620.

Yao, S., Akram, M.A., Hu, W., et al., 2021. Effects of water and energy on plant di-versity along the aridity gradient across dryland in China. Plants 10, 636. https://doi.org/10.3390/plants10040636.

Zhang, R., Liu, T., Zhang, J., et al., 2015. Spatial and environmental determinants of plant species diversity in a temperate desert. J. Plant Ecol. 9, 124–131. https://doi.org/10.1093/jpe/rtv053.

Zhu, J., Yu, G., Wang, P., et al., 2013. Distribution patterns of groundwater-dependent vegetation species diversity and their relationship to groundwater attributes in northwestern China. Ecohydrology 6, 191–200. https://doi.org/10.1002/eco.1258.