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Impact of climate change on plant species richness across drylands in China: From past to present and into the future

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A R T I C L E   I N F O

A B S T R A C T

It is commonly believed that climate plays an important role in shaping the patterns of plant species richness. However, it remains unclear how climate may affect plant richness across large spatial scales and also over long-terms, for example across massive arid regions during the Quaternary and into the future. To fill this knowledge gap, we examined the long-term trends in plant species richness across vast drylands in China based on our newly developed climate-species richness models. We first generated optimal random forest models based on the relationships between the current (CUR, 1970–2000) annual, perennial, woody and total species richness and climatic variables. We subsequently hindcasted and forecasted plant species richness in five other periods: last interglacial (LIG, 120,000–140,000 years BP), last glacial maximum (LGM, about 22,000 years BP), mid-Holocene (MH, about 6000 years BP), 2041–2060 (2050), and 2061–2080 (2070). Our results showed that total and herbaceous species richness exhibited similar patterns that were driven by temperature and precipitation. Both groups of species formed a transition zone between arid and semi-arid regions in all periods except LIG. In contrast, woody species richness did not form any transition zone because it was regulated mainly by temperature. Furthermore, the mean richness of herbaceous, woody and all species exhibited gradually increasing trends from LIG to 2070 across drylands in China. On the one hand, herbaceous species were much more sensitive to climate change than woody species. On the other hand, plant species richness in mountain-basin systems and Taklamakan Desert regions were more sensitive to climate change than in meadows and steppes. These results shed new insights into the past and future changes in plant species richness over vast drylands and provide valuable information for future conservation efforts under global warming.

1. Introduction

Plant species richness offers critical support to the multi-functionality of terrestrial ecosystems (Hooper et al., 2012; Maestre et al., 2012; Sasaki et al., 2019). Climate change could pose varying effects on plant diversity, and any negative effects could impair ecosystem functioning and diminish the capacity of ecosystem services

(Cardinale et al., 2012). But how climate change may influence biodiversity in different habitats and across different spatial and temporal scales remains elusive (Francis and Currie, 2003; Dawson et al., 2011; Root et al., 2003; Yao et al., 2021). To date, most related studies have examined short-term effects (i.e., over a few years to decades; e.g., Becker-Scarpitta et al., 2019). It is not clear how plant species richness may respond to climate change over much longer time scales (for

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example, 100,000 years).

Paleoclimate records show that the Quaternary experienced many oscillations of glacial and interglacial periods and a series of abrupt cooling/warming events since the last interglacial (LIG, 120,000–140,000 years BP) period (Shakun et al., 2012), causing formation, migration, and extinction of many plant species (Blach-Overgaard et al., 2013). During the past several decades, dramatic climate warming has occurred (IPCC, 2014), leading to shifts in the distribution of numerous species (Parmesan, 2006). Such responses are likely to continue or even be intensified in the near future (Bellard et al., 2012; Humphreys et al., 2019). In addition, climate warming may cause an increase in plant species richness in temperate or cool regions and a decrease in dry or tropical regions (Harrison et al., 2015; Sommer et al., 2010).

The majority of past palaeo-ecological studies on plant species richness relied primarily on pollen data (Reitalu et al., 2019). However, this method has limitations because of restricted spatial coverage in pollen surface samples, difficulties in species identification (Wang et al., 2017), and difficulties in determining accurately the temporal change in plant species richness from pollen (Goring et al., 2013). Recently, researchers have concluded that the random forest model is an appropriate approach to estimate the species richness or distribution under global climate changes (Divíšek and Chytrý, 2018). Random forest models are a combination of multiple individual regression trees derived from re-sampled data, in which each tree consists of a randomized subset of predictors (Breiman, 2001). It has been reported to be extremely powerful in overcoming problems associated with multi-collinearity among variables (Siroky, 2009). However, compared to humid regions, only a few studies have systematically documented spatial and temporal variations in species richness in drylands under various climate change scenarios, particularly over extended periods in the past (e.g., since the LIG) and predictions into the future (Xiao et al., 2019).

Drylands in China are integral parts of the global middle-latitude drylands, covering a massive land area of ca. 3.57 million km^2. The region is characterized by low precipitation and low vegetation cover, and is more prone to accelerating warming rates than humid lands (Huang et al., 2017). Consequently, plants in this region are likely to be more sensitive to continuous warming in the future. Additionally, using surface pollen samples, Lu et al. (2020) demonstrated that ancient and modern vegetation composition did not differ at the genus level in drylands of China since the Quaternary, suggesting a weak effect of genetic divergence on plant species composition and richness. Thus, drylands in China provide an ideal habitat to evaluate how plant species richness responds to climate change on a large scale since the Quaternary.

It is expected that different plant lifeforms would display different responses to climate change. To estimate long-term trends in species richness of different plant lifeforms, we compiled datasets of 9,514 standing plant species, including annual herbs, perennial herbs, and woody plants, and the climatic variables from LIG to 2070 (projections) across drylands in China. Based on previous studies, we hypothesized that (i) long-term trends in plant species richness are regulated mainly by climate variables, followed by soil properties and human activities (Francis and Currie, 2003); and, (ii) richness of different lifeforms is affected by different climatic variables as herbs and woody species have certain distinct adaptive strategies in drylands (Chen et al., 2019). To test these hypotheses, we firstly compared the effects of climate, soil and human activity on the spatial patterns of the total, herbaceous and woody species richness to determine which factors should be included in the model. Subsequently, according to the developed optimal random forest models, we examined the spatiotemporal diversity patterns and trends of different plant lifeforms since LIG and possible underlying mechanisms. We expected that plant species richness is influenced mainly by climatic variables, although the key factors are likely to differ between herbs and woody plants.

2. Materials and methods

2.1. Study region

The study region was located in northwestern China (31.54°N to 53.33°N and 73.47°E to 126.08°E), characterized by diverse landscapes of mountains, plateaus, deserts, and basins (Fig. 1). The plant species richness is relatively low and vegetation types are mainly desert, meadow and steppe. Since LIG, the mean annual temperature (MAT) in the region has increased by 1 °C (Table S1) and it is predicted that by 2070 the MAT will increase by about 1.8 °C under RCP2.6 and 4.4 °C under RCP8.5 compared to 1970–2000 (CUR). From LIG to 2070, the mean annual precipitation (MAP) will only increase slightly. Moreover, climate seasonality, represented by temperature seasonality (TSN) or precipitation seasonality (PSN), was highest during LIG and then decreased gradually.

2.2. Plant species richness data

We used the current plant richness data from Lu et al. (2018), who assembled the spatial distribution data of angiosperms from published national and provincial floras, as well as from local floras, checklists, and herbarium records from 2,377 counties. They divided the map of China into 100 km × 100 km grid cells to minimize the sampling bias of unequal sampling areas. Using these data, we calculated the species richness per grid and divided the plants into three groups according to their lifeforms, namely, annual herbs, perennial herbs, and woody plants (i.e., shrubs and trees). Our final dataset had a total of 9,514 species (annual herbs = 1,021, perennial herbs = 6,028, and woody plants = 2,465).

2.3. Climate data

We extracted paleo-climatic and future climatic data from the simulation of the models CCSM4 (Community Climate System Model version 4) (Gent et al., 2011) and downloaded contemporary climatic data from WorldClim. These data were from 19 bioclimatic variables (Bio1 to Bio19) and mean monthly temperature and precipitation records (Fick and Hijmans, 2017; Hijmans et al., 2005; Otto-Bliesner et al., 2006). All the layers had a resolution of 30-arc-second (~1 km at the equator) except for 2.5-arc-minutes (~4.5 km at the equator) in the LGM, as this was the highest resolution available for this period. We only considered the 2.6 and 8.5 RCPs (Representative Concentration Pathways) for 2050 and 2070, because they represent two extreme future greenhouse gas concentration scenarios, that is RCP2.6 and RCP8.5 for 2050 and RCP2.6 and RCP8.5 for 2070 (hereafter called 2050RCP26, 2050RCP85, 2070RCP26, and 2070RCP85, respectively). Owing to strong correlations between climate variables in the warmest/coldest and wettest/driest quarters, four variables (i.e., mean temperatures and precipitations of warmest and coldest quarters) were removed from the analyses. To match the resolution of species geographic range data, climatic data were re-gridded to a 100 km resolution grid using 'zonal statistics as table tool' in ArcGIS 10.5 (ESRI, Redlands, California, USA).

We used the mean monthly temperature and precipitation to calculate the hydrothermal synthesis index (HSI), which reflects the degree of drought (Bailey, 1979). Generally, the aridity index (AI, the ratio of mean annual precipitation and mean annual potential evapo-transpiration) indicates the degree of drought; however, due to a lack of data on the mean annual potential evapo-transpiration during the Quaternary Ice Age, we used HSI (closely related to AI) defined as:

$$\text{HSI} = \sum_{t=1}^{12} p/1.045^t$$

Where p is mean monthly precipitation (cm) and t is mean monthly temperature (℃). Six levels of aridity were defined for HSI: arid (HSI of < 2.5), semi-arid (HSI of 2.5 to < 4.7), dry-subhumid (HSI of 4.7 to <
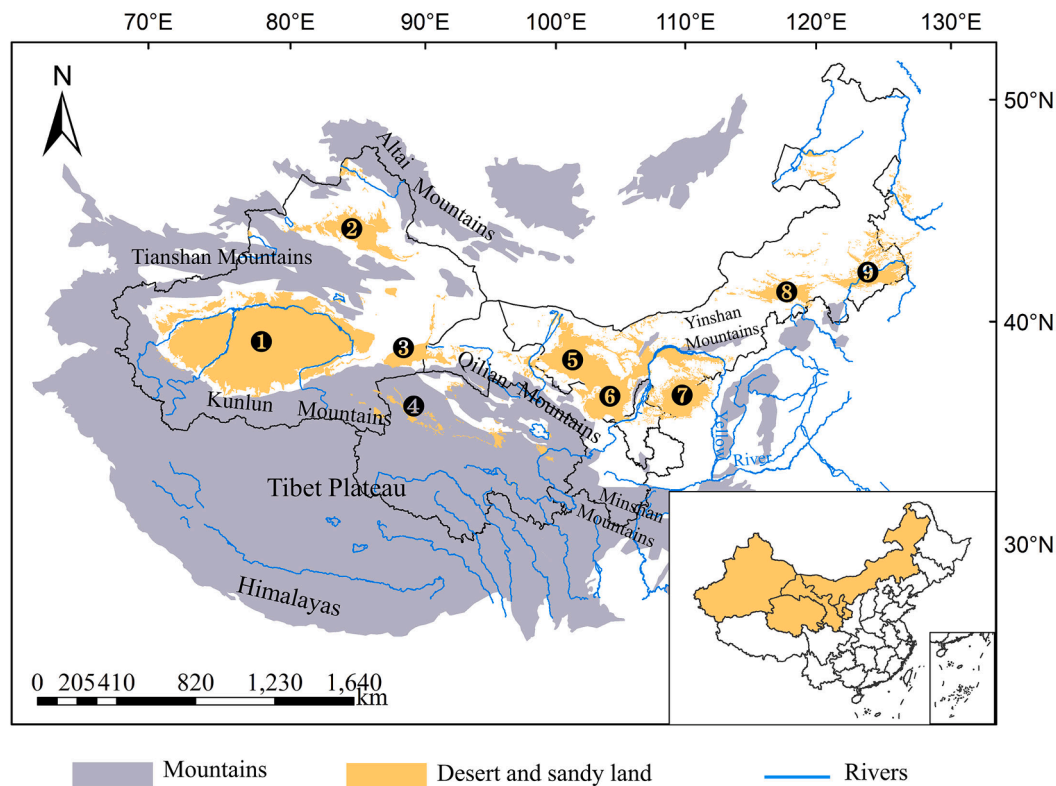
Fig. 1. The landscape structure of the study region. 1, Taklamakan Desert; 2, Gurbantunggut Desert; 3, Kumtag Desert; 4, Chaidamu Desert; 5, Badain Jaran Desert; 6, Tengger Desert; 7, Maowusu sandy lands; 8, Hunshandake sandy land; 9, Horqin sandy land (modified from Yang et al., 2011).

6.37), moist-subhumid (HSI of 6.37 to < 8.7), humid (HSI of 8.7 to < 16.2), and hyper-humid (HSI ≥ 16.2).

2.4. Soil and human activity variables

To test whether soil properties and human activities influence the current plant species richness distribution patterns, we used soil organic carbon (SOC), soil total nitrogen (STN), sand content (Sand%) and pH (all extracted from ISRIC-WISE Soil Property Database; Batjes, 2016) and the human influence index (HII). The HII was calculated by adding influence scores of all eight input variables (i.e., population density, built-up areas, nighttime lights, land use/land cover, coastlines, roads, railroads, navigable rivers; Wildlife Conservation Society - WCS and Center for International Earth Science Information Network - CIESIN - Columbia University, 2005).

2.5. Statistical analyses

2.5.1. Optimal random forest models construction

As the evaluation of plant species richness distribution pattern from past to future was based only on climate variables, variation partitioning was used to determine whether the effects of climatic variables on species richness were higher than those of soil and human factors. Some variables were correlated strongly with other variables ($r > 0.8$, Katz, 2011), including MTMWarmest, MTCM, TAR, MTQWettest, MTDQ, PWM, PDM, PQWettest (Abbreviation of climatic variables are available in Table S1) and STN, and thus, were excluded. The remaining variables were: (1) climate (MAT, MDR, ISO, TSN, MAP, PSN, PDQ), (2) soil (SOC, Sand%, and pH), and (3) human influence index (HII).

Our final random forest models used contemporary plant species richness as response variables and 15 climatic variables as predictors. Soil properties and human activities were poor predictors of plant richness compared with climate variables (Fig. S1) and, therefore, they

were not considered in our subsequent optimal model development. As the predictive power of random forest is not influenced by multi-collinearity issues (Dormann et al., 2013), we used all 15 climate variables in the random forest models. Initially, we randomly selected 80% of the data for generating the models and the remaining 20% for validating the models (Araújo and New, 2007). Then, the optimal model was selected based on the coefficient of determination (R^2) of the test data to derive optimal model parameters (ntree, the total number of trees to be grown in the model run and mtry, the number of predictors for splitting at each node). The precision of the optimal models was also evaluated using standard residuals and slopes between predicted and observed values. The optimal forest models were then used to reconstruct plant species richness for other periods, namely, LIG, LGM, MH, 2050RCP26, 2050RCP85, 2070RCP26, and 2070RCP85. Each random forest model was iterated 1,000 times and we obtained the predicted values by averaging results of 1000 models. Furthermore, we remodeled the random forest model based on climate, soil and human activity variables and compared the plant species richness obtained from the two models using the Mann-Whitney U test and Pearson test. Interestingly, the calculation of plant species richness based on climatic variables was similar to that based on factors of climate, soil properties, and human activities (Table S2).

2.5.2. Measurement of change trends

To examine the changes in trends in plant species richness from LIG to 2070, the linear relationships between plant species richness and time were tested for each lifeform. The slope < 0 indicated a decreasing trend while a slope > 0 indicated an increasing trend in plant species richness. Note that the time 120,000 years was regarded as an independent variable for the LIG in the model. We, then, examined the proportion of change in plant species richness between two adjacent periods. The proportion of change was calculated by the difference in plant species richness between two adjacent periods divided by the plant species

richness in the previous period.

2.5.3. Predictor importance assessment

To detect the dominant climatic drivers of plant species richness, the importance of each variable was estimated based on its percentage increase in mean square error (%IncMSE) using the random forest model.

To identify the effects of magnitude of change in each climatic variable on plant species richness, all-subsets regression was performed based on the difference of plant species richness and climatic variables between every two adjacent periods. All-subsets regression is similar to stepwise regression used to select a final set of predictor variables from a larger pool of candidate variables (Kabacoff, 2011). In the process, the variance inflation factor (VIF) was used to test for multi-collinearity; a value of less than five was acceptable (Wang et al., 2011). To further clarify whether different regions responded differently to climate change, we divided the vegetation in the region into 4 major groups (desert, meadow, steppe and forest) according to the "Vegetation Atlas of China 1:1,000,000" (Chinese Academy of Sciences, 2001). To generate a database for modeling, each grid contained only one vegetation type (Fig. S2).

We used ArcGIS 10.5 (ESRI, Redlands, California, USA) to map plant species richness. All statistical analyses were performed in R 3.6.0 (R Development Core Team, 2014). The random forest models and % IncMSE employed the 'randomForest', 'rfUtilities', and 'rfPermute' packages in R (Liaw and Wiener, 2002). Variation partitioning analyses used the R package 'vegan' (Oksanen et al., 2019), and all-subsets regression used the 'leaps' package in R.

3. Results

3.1. Model performance

The random forest models had high predictive power as they explained 70.4%, 61.7%, 70.4%, and 73.1% of the total variation in all plants, annual herbs, perennial herbs, and woody species richness, respectively (Table 1). The slope between the observed and predicted richness was close to 1, indicating that the random forest models were unbiased (Fig. S3).

3.2. Geographical patterns of plant species richness during each period

From LIG to 2070, total species richness displayed a similar pattern in each period, with highest plant species richness in the Tianshan and Minshan Mountains and north of the Tibetan Plateau, and lowest richness in the Taklamakan, Badain Jaran and Tengger Deserts (Fig. 2). After LIG, that is, from LGM to 2070, the spatial distribution patterns of total species richness formed a transition zone between arid and semi-arid regions near the 2.5 isolines of HSI (Fig. 2b-h).

The species richness patterns of annual and perennial herbs were similar to total species richness patterns and they also formed a boundary consistent with the 2.5 isolines of HSI (Fig. S4-5); however, the spatial richness patterns of woody species differed from those of herbaceous species. Specifically, the woody species richness peaked only in the southeastern study region and did not form any transition zones. Also, woody species richness was projected to increase slightly in the Taklamakan Desert in 2050–2070, especially under RCP 8.5 (Fig. S6).

Table 1
The optimal random forest models for plant species richness (all plants and each lifeform) across drylands in China.

Plant	ntree	mtry	R^2	*p*-values
All plants	4500	3	0.704	<0.001
Annual plant	3500	5	0.617	<0.001
Perennial plant	3000	1	0.704	<0.001
Woody plant	1000	3	0.731	<0.001

3.3. Spatiotemporal variations of plant species richness from LIG to 2070

During LIG, the mean total species richness was significantly lower than in other periods ($p < 0.05$), and then gradually increased from LIG to 2070 across the drylands in China (Fig. 3a). Likewise, the mean species richness of herbaceous and woody plants increased slightly from LIG to 2070 (Fig. 3e, i and m). However, plant species richness displayed different trends in different regions; namely, a decreasing trend in the southwest, but an increasing trend in other regions of the study region (Fig. 3b-c, f-g, j-k, n-o).

Plant species richness also showed noticeable changes between each two adjacent periods (Fig. 3d, h, l and p). From LIG to LGM, the richness of all plants and each lifeform increased in mountain-basin systems (Tianshan, Qilian, and Minshan Mountains). From LGM to MH, the regions with increasing total species richness declined substantially and richness of all plants (especially perennial herbs and woody plants) decreased mainly in the Taklimakan Desert (Fig. 3d, l and p). From MH to CUR, the plant species richness increased in mountain-basin systems but decreased in the Taklimakan Desert (Fig. 3d, h, l and p). From CUR to 2050, an interesting reversal in plant species richness occurred, that is, the total species richness, particularly woody plant richness, was projected to decrease in the Mountains but to increase in the Taklamakan Desert (Fig. 3d and p). Moreover, plant species richness exhibited the same trends under both the low emission concentration (RCP2.6) and the high emission concentration (RCP8.5) scenarios. From 2050 to 2070, the amplitude of increase or decrease in plant species richness is predicted to be small (Fig. 3d, h, l and p). However, for RCP2.6 and RCP8.5, the variations of plant species richness displayed distinct differences from 2050 to 2070; plant species richness decreased in RCP2.6 but increased in RCP8.5, particularly annual herbs and woody plants (Fig. 3l and p).

3.4. The drivers of plant species richness

Herbaceous species richness was affected jointly by precipitation and temperature, while woody species richness was influenced mainly by temperature-related factors (Fig. 4). However, changes in plant species richness were driven jointly by the magnitude of changes in temperature and precipitation from LIG to CUR and were projected to be regulated mainly by the rapidly increasing temperature in the future (Fig. S7). Specifically, increasing temperature would decrease but increasing PDQ would increase total plant richness (Fig. 5). Furthermore, a low magnitude of climate change could cause large changes in species richness, indicating the high sensitivity of desert vegetation, especially in the mountain-basin system and Taklamakan Desert (Fig. 5 and S8).

4. Discussion

This study demonstrated how climate change influences plant species richness across drylands in China. Long-term trends in plant species richness are driven mainly by climate variables rather than soil properties and human activities (Fig. S1 and Table S2). This may be because: i) the effects of soil properties and human activities on plant species richness may be restricted to small spatial scales or microhabitats; and, ii) ecological restoration projects in degraded ecosystems in China (Ouyang et al., 2016) may have offset human effects on plant species richness. Generally, the random forest models were able to describe the plant species richness response to climate change on large scales. More importantly, the determination of plant species richness patterns from LIG to 2070 helps to identify regions at risk of species range shifts and species richness loss under global climate change.

4.1. Geographic patterns of plant species richness across drylands in China

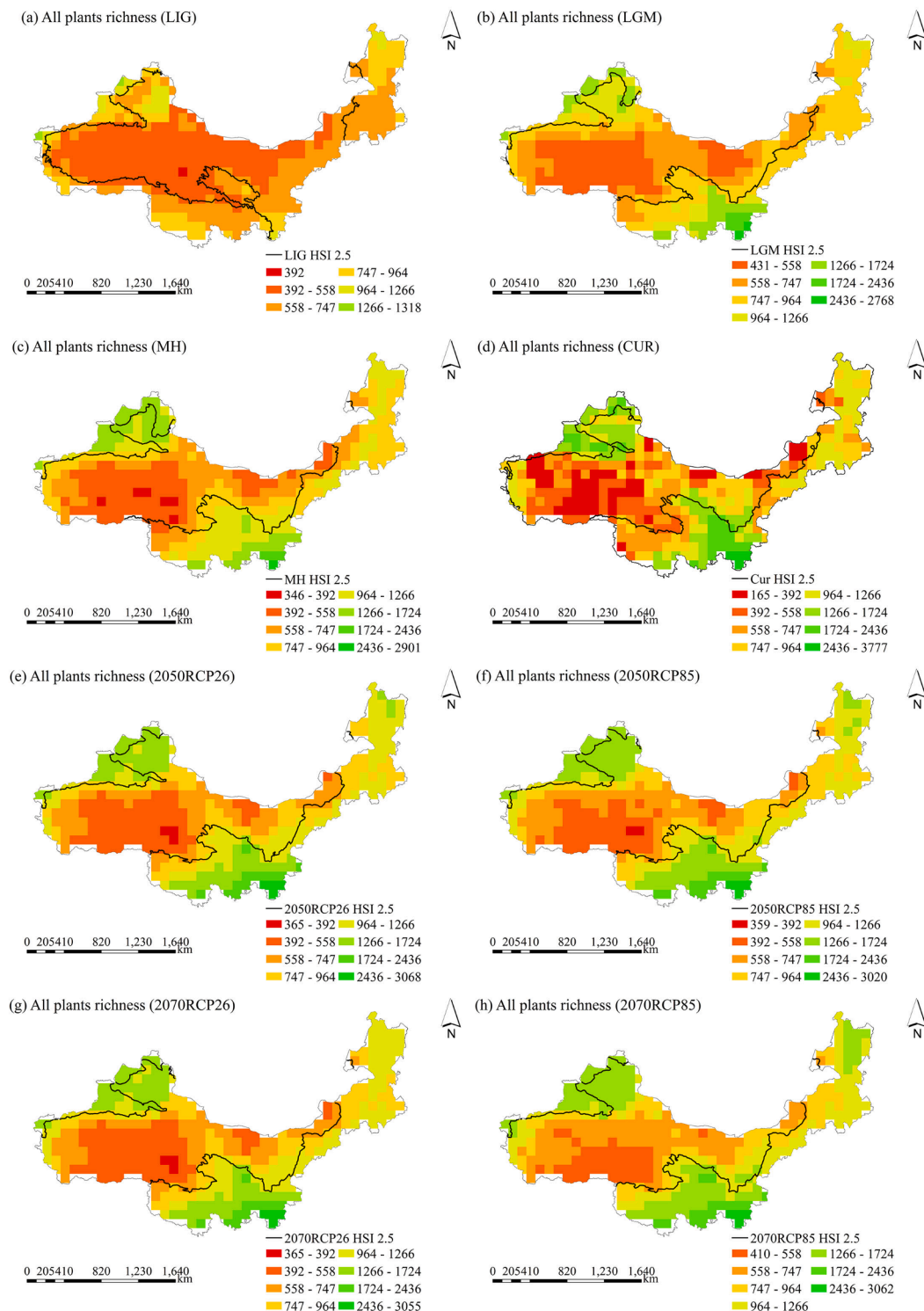Both total and herbaceous species richness changed little from LIG to

Fig. 2. The total species richness patterns in each period across drylands in China based on the random forest models. (a) LIG: last interglacial, 120,000–140,000 years BP; (b) LGM: last glacial maximum, about 22,000 years BP; (c) MH: mid-Holocene, about 22,000 years BP; (d) CUR: Current, 1970–2000; (e) 2050RCP26: RCP2.6 during 2041–2060; (f) 2050RCP85: RCP8.5 during 2041–2060; (g) 2070RCP26: RCP2.6 during 2061–2080; (h) 2070RCP85: RCP8.5 during 2061–2080. The RCP means Representative Concentration Pathways. The black line indicates the 2.5 S isoline, which is, the transition between arid and semi-arid regions. The color legends indicate the number of species in each grid.

2070, although climatic conditions fluctuated considerably. Generally, richness hotspots were located in mountainous regions, possibly due to the higher heterogeneity, steady water sources from meltwater and headwaters (Liu et al., 2019), and relatively more stable climates (Brown et al., 2020). Furthermore, local plant species richness was

affected by regional species-pool size (Eriksson, 1993; Taylor et al., 1990). Regions with higher plant species richness harbored more opportunities for speciation, adaptation, and distribution (Ron et al., 2018); whereas, deserts were characterized by low plant species richness, mostly due to severe drought stress.
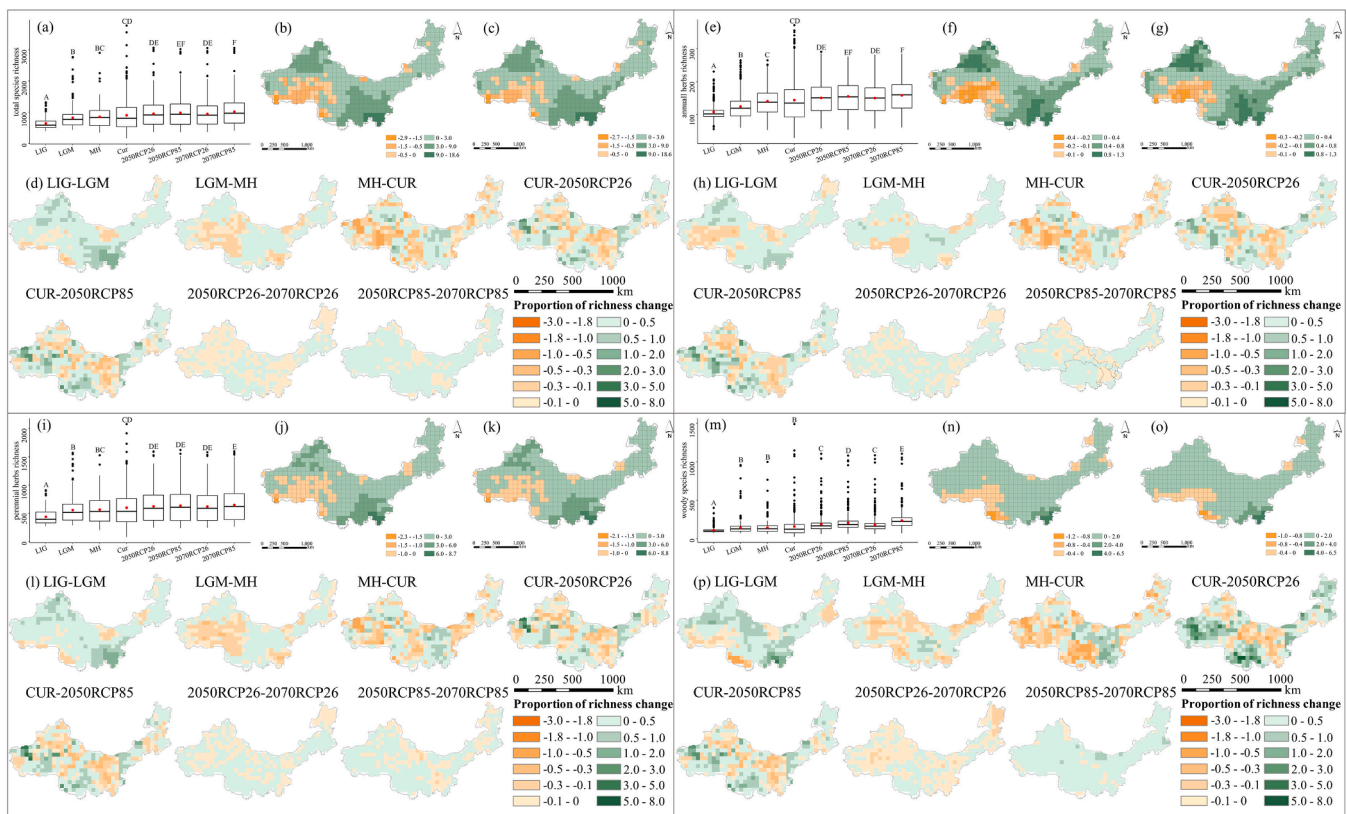
Fig. 3. Spatiotemporal changes in species richness of all plants (a-d), annual herbs (e-f), perennial herbs (i-l) and woody plants (m-p) across drylands in China from LIG to 2070. (a, e, i, m) the species richness in each period, the red dots indicate mean species richness across drylands in China during each period. Means with different uppercase differ from each other ($p < 0.05$; Duncan test). Change in trends in plant species richness under (b, f, j, n) low-emission scenario (RCP2.6) and (c, g, k, l) high-emission scenario (RCP8.5). The number in the legend indicates the 10,000*slope. (d, h, l, p) the proportion of change in plants species richness between two adjacent periods across drylands in China. The colors indicate the proportions of species richness change in each grid. Here the full names of all abbreviations are shown in Fig. 2.

In contrast to herbaceous species, richness hotspots for woody plants from LIG to 2070 were located in the southern part of the entire study region, especially in the Minshan Mountains. The Minshan Mountains had a higher MAT than other areas and, thus, contained more diverse plant types. Moreover, previous studies showed that woody plants were affected mainly by temperature-related variables, but that herbaceous species were affected mainly by precipitation-related variables (Chen et al., 2015; Yao et al., 2021). Our study demonstrated that the spatiotemporal patterns of woody species richness were affected mainly by temperature variables, especially the minimum temperature in the coldest month (MTCM) and the temperature annual range (TAR) (Fig. 4). However, woody species richness was relatively low and exhibited weak changes in more arid regions from LIG to CUR compared with herbs (Fig. S4, S5 and S6). A possible reason could be that the life-history strategies of different lifeforms play important roles. For example, herbaceous species have a short generation time, which enables them to be more flexible during climate change (Smith and Beaulieu, 2009). Woody plants, in contrast, have deeper root systems, allowing them to better adapt to a wider range of climatic conditions by their ability to obtain groundwater (Chen et al., 2019; Chen et al., 2021; Yao et al., 2021), but their longer lifespans limit genetic divergence and speciation rates, which could reduce their area of potential distribution (Albuquerque et al., 2011). In our projections, woody species are expected to expand towards the Taklamakan Desert in the future, which could be attributed to the possible better hydrothermal conditions under global warming.

4.2. Possible climate effects on plant species richness from LIG to 2070

Total plant species richness in the region has increased continuously since LIG. The lowest richness in LIG could be due to low precipitation of the driest quarter (PDQ) and low minimum temperature of the coldest month (MTCM) (Table S1). Furthermore, greater temperature seasonality (TSN) and precipitation seasonality (PSN) during LIG (Table S1) could also lead to a reduction of suitable habitats (Dakhil et al., 2019; Liu et al., 2019), thus causing low plant species richness.

Van der Hammen and Hooghiemstra (2000) stated that dryness and low temperature may have caused the extinction of some species in Amazonia during LGM. However, the present study indicated that the total species richness, particularly perennial herbs and woody plants across drylands in China, actually increased from LIG to LGM. This may be due to the increased precipitation in the driest quarter (PDQ, Fig. S7 and S8), which stimulated plant growth and reproduction (Ogle and Reynolds, 2004). The HSI displayed an increasing trend during LGM compared to LIG (Fig. S9), that is, the decreased aridity enhanced richness in this region. Similarly, total species richness also exhibited an increasing trend in the region from LGM to MH, especially in the mountain-basin systems (e.g., Tianshan, Qilian, and Minshan Mountain regions). This was consistent with the findings of Zhao et al. (2014), who reported that plant species richness increased from LGM to the Holocene Optimum due to warming and increased rainfall from East Asian summer monsoons.

The decrease in total species richness from CUR to 2050 may be due to intensified aridity (Fig. S9, HSI decreased). Interestingly, from 2050 to 2070, total species richness is expected to decrease slightly in RCP2.6 but to increase in RCP 8.5. If plant growth was primarily water-limited,
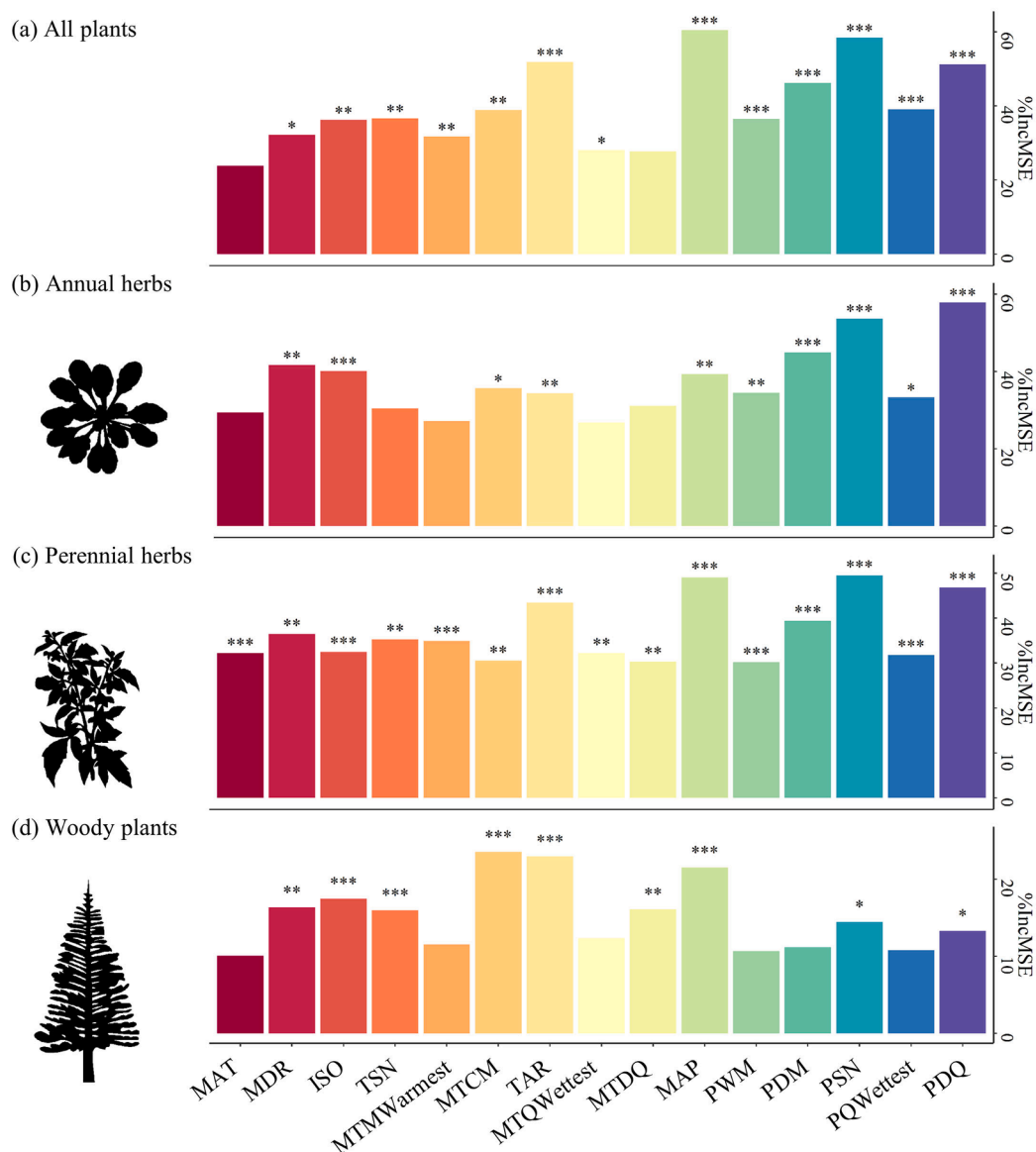
Fig. 4. Relative contributions of various climate variables as drivers of plant species richness across drylands in China. *$p <= 0.05$, **$p <= 0.01$, ***$p <= 0.001$. % IncMSE: the percentage increase in mean square error indicates the importance of each variable (high %IncMSE means greater importance). The climatic variables include MAT (mean annual temperature), MDR (mean diurnal range), ISO (isothermality), TSN (temperature seasonality), MTMWarmest (maximum temperature of warmest month), MTCM (minimum temperature of coldest month), TAR (temperature annual range), MTQWettest (mean temperature of wettest quarter), MTDQ (mean temperature of driest quarter), MAP (annual precipitation), PWM (precipitation of wettest month), PDM (precipitation of driest month), PSN (precipitation seasonality), PQWettest (precipitation of wettest quarter) and PDQ (precipitation of driest quarter).

plant species richness would decline under global warming (Harrison, 2020). In this study, MAP was lower under RCP2.6 than RCP8.5 (Fig. S9), which could limit water availability and, thus, lead to reduced richness under RCP2.6. Furthermore, the increase in total species richness under RCP 8.5 was mainly due to the increase of annual herbs and woody plant richness based on the future possible scenario of warming and increased precipitation. These results illustrated that annual herbs may have better opportunities to expand under the forecasted scenarios; thus, annual herb richness would increase with the increasing water availability (Sun et al., 2019). For woody species, the projected higher temperature could promote woody plant expansion and, thus, increase the local and regional richness (Wu et al., 2019). Moreover, increased air CO_2 concentrations projected for RCP8.5 may also promote the expansion of woody plant species (Bastin et al., 2019).

It is important to note that the projections of future plant species richness (up to 2070) did not specifically include the possible effects of

changes in human activities. Many plant species could be threatened and possibly become extinct if there is a drastic increase in human population and land use, which could result in habitat loss and fragmentation (Giam et al., 2010). Therefore, adaptive conservation planning should be considered if human disturbances are indeed increasing.

4.3. Implications for plant conservation under climate change

It is evident that plants in the mountainous regions (i.e., Tianshan, Qilian and Minshan Mountains) and deserts (i.e., Taklamakan Desert) respond differently to climate change. Mountainous regions provided biological refugia for plant species during the Quaternary ice ages (Zhang and Zhang, 2014). The projected decrease in plant species richness in the mountainous regions by 2050 indicates that protection for plants by mountains may be weakening, possibly due to the reduced precipitation in the driest quarter (PDQ) from CUR to 2050 and increase
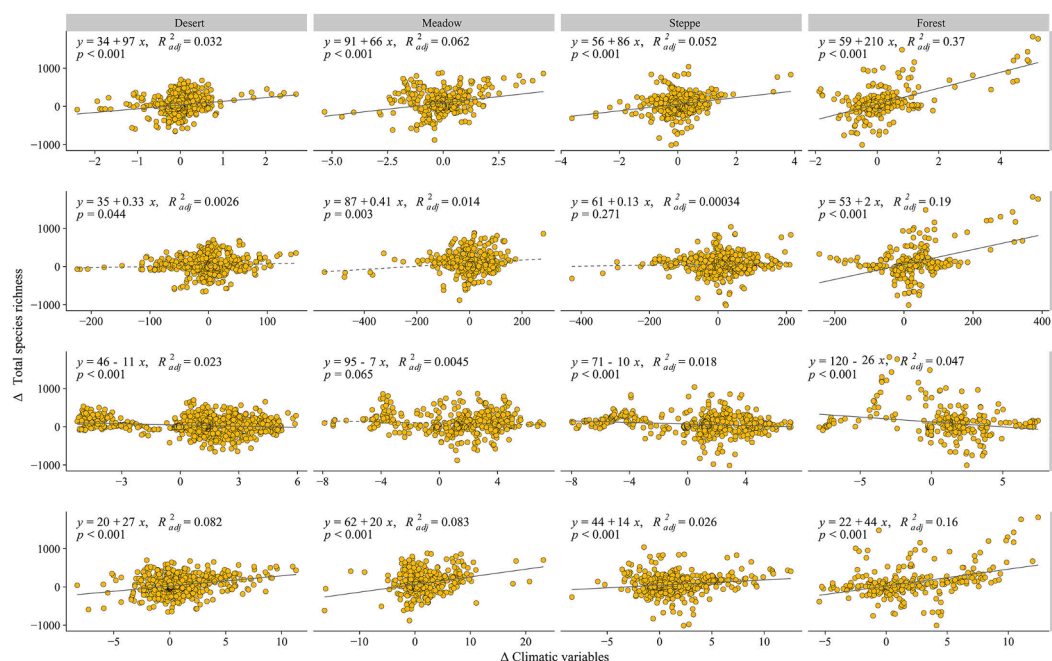
Fig. 5. The climate-total plant richness relationships for each vegetation type between every two adjacent periods across drylands in China. Where Δ total species richness represents difference of total species richness between every two adjacent periods; Δ climatic variables represent difference of climatic variables between every two adjacent periods. The HSI, MAP, MAT and PDQ are hydrothermal synthesis index, annual precipitation, mean annual temperature and precipitation of driest quarter, respectively.

in temperature (Fig. S9). Compared with mountains, deserts are less heterogeneous and, therefore, have less possibilities of increasing richness. However, the models project an increase in plant species richness in the Taklamakan Desert in the future, probably due to a decrease in aridity in the entire desert.

In conservation, special attention should be given to regions where plant species richness could decline under global warming in the future, including the Tianshan, Qilian and Minshan Mountains. This is consistent with Xu et al. (2017), who concluded that the Tianshan and Minshan Mountains are important regions for biodiversity conservation. In addition, less heterogeneous deserts should be preserved as they support different species and climate change may cause the extinction of species (Li et al., 2013; Román-Palacios and Wiens, 2020). The Taklamakan Desert, the largest desert in China, with a long history (about 0.5–0.7 Ma) in forming a permanent desert landscape (Liu et al., 2020), is such a region that deserves special attention for biological conservation.

5. Conclusions

The findings in this study, based on contemporary climate-plant diversity relationships, enhance our understanding of past and present dynamics of plant species richness across drylands in China as driven by climate change. The mean plant species richness has increased in the recent past and is projected to increase in the future. The spatiotemporal variations in plant species richness are determined by joint effects of precipitation and temperature (i.e., the hydrothermal hypothesis reflecting water availability) rather than by temperature as predicted by metabolic theory on large scales (Allen et al., 2002; Brown et al., 2004; Zhang et al., 2011), especially for annual and perennial herbs. Moreover, plant species richness in mountain-basin systems and Taklamakan Desert regions were more sensitive to global climate change than other regions. Therefore, both the mountain-basin regions and deserts should be preserved and diversity hotspots should be given high priority for conservation, as many species may be at high risk of extinction under warming and drying climates. Additionally, it may be necessary to develop a new theoretical framework to predict how plant species

richness varies with climatic variables in drylands at ecoregion levels.

CRediT authorship contribution statement

Ying Sun: Methodology, Software, Data curation, Writing – original draft, Investigation, Validation. **Yuan Sun:** Data curation, Investigation, Validation. **Shuran Yao:** Conceptualization, Validation. **Muhammad Adnan Akram:** Validation, Writing – review & editing. **Weigang Hu:** Funding acquisition, Validation. **Longwei Dong:** Data curation, Validation. **Hailing Li:** Data curation, Validation. **Maohong Wei:** Data curation, Validation. **Haiyang Gong:** Data curation, Validation. **Shubin Xie:** Data curation, Validation. **Muhammad Aqeel:** Validation, Writing – review & editing. **Jinzhi Ran:** Conceptualization, Supervision, Visualization, Funding acquisition, Validation. **Abraham Allan Degen:** Validation, Writing – review & editing. **Qinfeng Guo:** Validation, Writing – review & editing. **Jianming Deng:** Conceptualization, Supervision, Visualization, Funding acquisition, Validation, Writing – review & editing.

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Data accessibility

Data that support the findings of this study can be requested from the corresponding author.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.108288.

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