



Geographical divergence of species richness and local homogenization of plant assemblages due to climate change in grasslands

Yu Peng¹ · Jinchao Feng¹ · Weiguo Sang¹ · Jan Christoph Axmacher²

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Abstract

In arid and semi-arid regions worldwide, grassland plant species richness is highly sensitive to climate change. Studies assessing local grassland richness patterns have yielded inconsistent trends toward climate change, partly due to differences in recording approaches, environmental conditions, and local flora. Remote sensing presents a valuable opportunity to investigate plant richness–climate change relationships in grasslands across large environmental gradients. Based on spectral diversity indices extracted from Landsat satellite imagery, we explore how plant diversity responds to climate change and aim to determine the major climatic drivers of plant diversity patterns in ten grassland nature reserves worldwide. Plot-level plant richness was correlated with 19 bioclimatic variables through stepwise linear regression for each climate change scenario in every nature reserve. The performance of the models was assessed according to the model accuracy. We used the fitted models between climatic variables and plant richness from 1990 to 2000 to predict plant richness in 2050 and 2070 under 33 climatic change scenarios for 1120 plots in each reserve. A general tendency toward a decrease in the plot-level plant richness and beta (β)-diversity in the future decades were observed in most cases, although there also were some opposite trends in plant richness. The dominant bioclimatic predictors involved in predictive models varied across sites. Spectral plant richness responses diverge geographically, while β -diversity generally declines under climate change scenarios. Over the next decades, the expected homogeneities in plant species across grasslands encountered on different continents will likely lead to the dominance of climate generalist species. Policy-makers and conservationists therefore need to urgently develop strategies to ensure plant survival, particularly that of locally endemic species under predicted climatic scenarios; human assistance may be required when adjusting their distribution ranges.

Keywords Grasslands · Plant species richness · Beta diversity · Climate change · Remote sensing

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Extended author information available on the last page of the article

Introduction

Currently, the loss of biodiversity and associated ecosystem services has caused widespread concern (Gaston 2000; Kreft and Jetz 2007; Bellard et al. 2012). Driving factors of biodiversity loss include climate and land-use change as well as pollution and the invasion of alien species (Burns et al. 2016; Cardoso et al. 2020; Wagner 2020). Among these drivers, climate change is becoming increasingly important and may be the most important factor in the future (Bellard et al., 2014; Aguilos et al. 2021). Grasslands occur naturally in semi-arid regions and mainly locate at low latitudes accounting for one-third of the world's land, are sensitive to climatic change (Seager et al. 2007; Dobrowski et al. 2013). However, studies on grassland diversity and climate have reported inconsistent results on the exact impact of climate change on vegetation. An accelerated enrichment in plant species richness in the last 50 years was found in 302 mountain summits across Europe using a dataset of repeated plant surveys, demonstrating the effects of global warming (Steinbauer et al. 2018), although other influencing factors as inter or intral species interactions may also work. However, the opposite trend was observed in 10 European mountain summit regions, where warming has led to more severe climatic water deficits (Pauli et al. 2012). In a heterogeneous California grassland, a decline in plant diversity from 2000 to 2014 at both the local community (5 m²) and landscape (27 km²) scales was found (Harrison et al. 2015). In Northern America, warming was found to directly cause species loss at all experimental sites across the three temperate grasslands (White et al. 2014).

Inconsistencies in vegetation type, sampling method, and plot size across grasslands may lead to different results in studies of climate–plant richness correlations (Scheiner et al. 2011; Jiménez-Alfaro et al. 2018; Soininen et al. 2018). The studied grasslands extend over broad ranges, from tropical to Arctic Tundra and hot desert, with different community compositions and spatial distributions. In addition, the plot sizes used in species diversity surveys are greatly different across sites, ranging from 1 km² (Cowling et al. 2015; Li et al. 2015; Luo et al. 2015), to 5 km² (Irl et al. 2015), and even 50 km² (Vazquez-Rivera and Currie 2015). To achieve a series of comparable studies on climate change affecting plant diversity, differences in time and spatial scales, site dependence (i.e. different performances across different sites), and scaling effects (i.e. different performances along a series of spatial scales) should be avoided. In the light of the above-mentioned previous studies, the plant diversity of grasslands may demonstrate a general decreased trend in species richness in most cases, since only the species suitable to relatively high temperature and water deficit which occurred in most future climate projections can survive and consequently lead to a biological homogenous. In some local sites, such as mountain summits, where more energy may support more species. However, it is still hard to confirm such hypothesis, since we lack a series of comparable studies world widely which using identical sampling size, method and diversity indices.

Recently, remote sensing techniques have been intensively applied in plant diversity estimation. Spectral diversity, based on the hypothesis that different plant species has different spectral information has been employed to indicate plant species diversity (Rocchini et al. 2007; Wang et al. 2018a). Owing to the spatially continuous and temporally frequent capture of spectral data, the approaches of spectral plant diversity generated from Landsat imagery have been proved more effective and accurate pathways for assessing and predicting worldwide grassland ecosystem species diversity (Qi et al. 1994; Castillo-Riffart et al. 2017; Wang et al. 2018a, 2018b; Gholizadeh et al. 2018). This approach can overcome the inconsistencies in plot size, sampling time, and sampling method. Biodiversity indices are

also calculated using the same method and can be compared across different study sites. Grasslands have been shown to be more vulnerable to climatic change than other vegetation types (White et al. 2014; Harrison et al. 2015). Moreover, the relatively simple structure and layering of grasslands allows for a particularly effective assessment of diversity patterns using remotely sensed imagery. It is not feasible using traditional approaches in the field setting, yet that remote sensing platforms provides a unique opportunity to achieve this. Consequently, we select grassland ecosystem as the object in the present study and use remote sensing techniques to explore the variation of plant diversity under climate change.

We used spectral plant diversity indices extracted from Landsat Thematic Mapper (TM) images to characterize global vascular plant diversity at 30-m resolution. We selected a number of protected grassland areas around the globe to explore the influence of climatic change on community diversity, since the strict protection of the sites allows us to distill climate change effects in areas lacking human disturbances. In this study, we want to test the following hypotheses: (1) there exists a general decreased trend in plant diversity under future climate change across the world's grasslands; (2) beta (β)-diversity has declined across global grasslands, with communities becoming increasingly homogenous within each protected area. In achieving these objects, we generated two-stage biodiversity dynamics at a 1-km² grid scale across world grasslands through extracting spectral diversity indices from Landsat images in 1990 and 2000, modeled them to climate variables and made prediction, consequently to identify the key ones.

Methods

Study areas

Grassland reserves were selected from the World Database on Protected Areas (WDPA) (UNEP-WCMC, <https://www.protectedplanet.net>). Overall, data sets were collated for 10 large-scale grassland dynamic areas distributed worldwide (Fig. 1), with a median size of 1000 km², within which plant species richness and β -diversity patterns were extracted (see below section, the code indicates corresponding nature reserve). Areas of this size are sufficiently large to include adequate samples of species richness and their typical distribution patterns but generally sufficiently small to avoid substantial heterogeneity in climate, geological parent materials, and topography within them (Ricklefs and He 2016). We assembled a set of local plot characteristics and climate data for each reserve and used stepwise linear regression models to characterize the relationship between vascular plant richness in WDPA grasslands and local climatic variables to statistically test potential links between climatic variables and local species richness as a basis for models exploring future climate change effects. Detailed descriptions of the 10 grassland areas selected from the WDPA are given in online Appendix Table A.

Plot conditions

In this study, we generated 1120 plots (30 m × 30 m) with an even distribution, in each grassland nature reserve based on WDPA map through spatial technique using ArcGIS software (ESRI, Redlands, CA, USA). The sampling initiative further covered a wide range of environmental variables representing the underlying environmental gradients present in the data due to the wide spatial coverage. The 10 nature reserves were also broadly

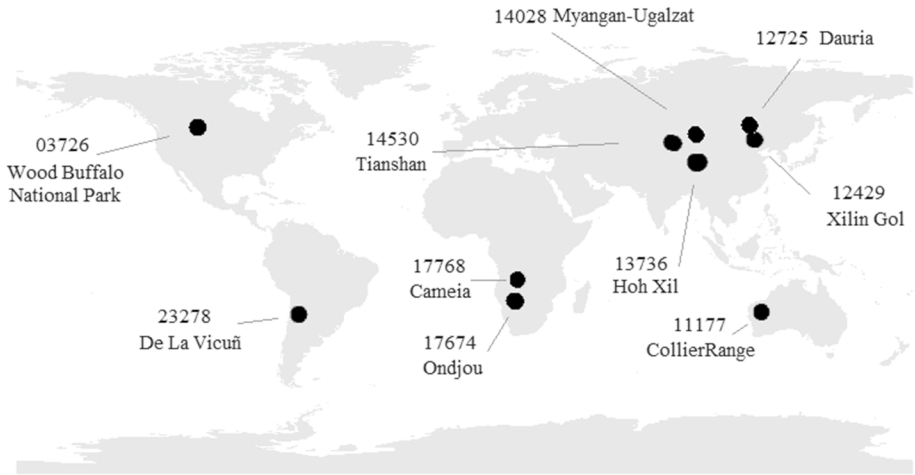


Fig. 1 Geographical distribution of 10 grassland nature reserves (NRs) in six continents. Numbers beside the nature reserve names indicate the number of paths and rows in the Landsat routes and consequently as the code of that NR. Geospatial data for the map in all figures are from the WorldClim project (<http://www.worldclim.org>) and the World Database on Protected Areas (<http://www.wdpa.org>). Nature reserve belongs to the following climate type: 03726: Arid cold steppe with dry summer; 17674: hot arid steppe; 11177: arid steppe, hot arid; 14028, 14530, 23278: Cold arid desert; 17768: warm temperate steppe with dry winter; 12429: cold desert with hot summer; 12725: cold desert with warm summer; 13736: polar tundra

classified according to their main climate, precipitation, and temperature (<https://www.mapsofworld.com/world-maps/world-climate-map.html>). Type B climates include a tropical and subtropical desert climate (Bwh and part of Bwk), tropical and subtropical steppe climate (Bsh), and mid-latitude steppe and desert climate (Bsk and part of Bwk); Type C climates include humid subtropical climates (Cfa and Cwa), Mediterranean climates (Csa and Csb), and marine west coast climates (Cfb and Cfc); Type D climates include humid continental climates (Dfa, Dfb, Dwa, and Dwb) and continental subarctic climate (Dfc, Dfd, Dwc, and Dwd); Type E climates include a tundra climate (ET) and snow and ice climate (EF); and Type H climates include the different climates in the highlands of the world with local variations. The world climate map based on Köppen classification is therefore the most comprehensive, detailed, and yet easily understood representation of the various climatic types worldwide.

Plant richness derived from landsat images

In this study, we used the plant species richness (SR) in each plot (30 m × 30 m) to represent the plant alpha (α)-diversity. The variation in plant richness across plots within 10 km² was used to indicate β -diversity. To acquire plant α - and β -diversity data in the 10 grassland nature reserves from 1970 to 2000 across the world, we used Landsat TM (hereafter, Landsat) data. Cloud-free Landsat satellite images with a spatial resolution of 30 m were downloaded from the Global Land Cover Facility site hosted by the University of Maryland (glcap.umiaccs.umd.edu). All satellite images were radiometrically and atmospherically corrected following Chavez (1996) in IDRISI GIS. We corrected the images for shading effects caused by the topography using a digital elevation model. Vegetation indices were

calculated based on band ratios that further compensated for some of the topographical effects (Riano et al. 2003). All images are from the growing season [the highest normalized differenced vegetation index (NDVI)], allowing for the direct extraction of diversity information in the grasslands. All image processing was performed using ERDAS Imagine processing software. The modified soil-adjusted vegetation index (MSAVI) and spectral coefficient of variance (CV) were selected as indicators for plant diversity in the current study.

The MSAVI was calculated using the following formula:

$$\text{MSAVI} = \left\{ [2 \times \text{NIR} + 1] - \text{sqrt}[\text{sq}(2 \times \text{NIR} + 1) - 8 \times (\text{NIR} - R)] \right\} / 2, \quad (1)$$

where R and NIR represent the reflectance at the red (0.6–0.7 μm) and near-infrared (NIR) wavelengths (0.7–1.1 μm), respectively. Since the study grasslands ranged from closed to open sparse coverages, soil reflectance patterns can considerably affect spectral signals across sites. MSAVI can reduce the effects of soil background (Qi et al. 1994), demonstrating a very strong performance in estimating plant richness (Castillo-Riffart et al. 2017).

Spectral CV was another indicator generally used, indicating plant richness within a plot or plant β -diversity across plots within a spatial extent.

$$\text{CV} = \left(\sqrt{\frac{\sum_{i=1}^n (R_i - R)^2}{n}} \right) / R \quad (2)$$

For plot-level diversity, R_i and R are the reflectance at wave band i and the mean reflectance from band 1 to band n (where n is the total number of bands used), respectively. For Landsat, only bands 1–5 and 7 are used, so that $n=6$. For β -diversity across plots, R_i and R are the reflectance at waveband i and the mean reflectance at waveband i of all n study plots within each 10 km matrix, respectively.

CV is particularly suitable for estimating Simpson's biodiversity (Wang et al. 2018a) and also significantly related to plant species richness (Gholizadeh et al. 2018). In a prairie grassland, CV showed a higher relationship with Shannon's index, Simpson's index, and species richness (Wang et al. 2018a, b).

Climatic data

Climate variables with 1 square kilometer were extracted from the WorldClim 1.4 database (<http://www.worldclim.org/>). We specifically considered the 19 bioclimatic variables, BIO1–BIO19, which describe the average temperature and precipitation and seasonal variation in temperature and precipitation (see details in the note in Table 1), has been widely used in ecological niche modeling (Hijmans and Graham 2006; Elith and Leathwick 2009; Ricklefs and He 2016). These bioclimatic variables were available for all plots and provided an adequate description of the local climate. We used these 19 climatic variables in the period 1970–2000 to establish models of plant diversity, and 19 climatic variables in 2050 and 2070 (from WorldClim 1.4 database) to predict plant diversity based on the established models.

Models

The spectral and climatic variables were divided into two subsets: training datasets and validating datasets, occupied by 70% and 30% of the total datasets for each nature reserve,

Table 1 Stepwise forward-selecting multiple linear regression models for plant diversity using the significant variables from 19 climatic variables across the different grasslands in the world

| Climatic variables | | MSAVI | | | | | | | | | | | CV | | | | | | | | | | |
|-------------------------|-----|-------|-------|-------|-------|-------|-------|--------|-------|-------|-------|-------|-------|-------|--------|-------|-------|-------|-------|-------|-------|--|--|
| | | Bsk | Bsh | BSh | BWk | BWL | BWk | Cwb | Dwb | Dwa | PT | Bsk | Bsh | BSh | BWk | BWL | BWk | Cwb | Dwb | Dwa | PT | | |
| BIO1 | R | 0.190 | | | | | | | | | | | | | | | | | | | | | |
| | VIF | 1.000 | | | | | | | | | | | | | | | | | | | | | |
| BIO2 | R | | | | | | | | | | | | | | | | | | | | | | |
| | VIF | | | | | | | | | | | | | | | | | | | | | | |
| BIO3 | R | | -0.15 | | 0.125 | 0.063 | 0.265 | | | | | | | | | | | | | | | | |
| | VIF | | 1.441 | | 3.936 | 1.142 | 1.346 | | | | | | | | | | | | | | | | |
| BIO4 | R | | | | | | | | | | | | | | | | | | | | | | |
| | VIF | | | | | | | | | | | | | | | | | | | | | | |
| BIO5 | R | | | | | | | | | | | | | | | | | | | | | | |
| | VIF | | | | | | | | | | | | | | | | | | | | | | |
| BIO6 | R | | | | | | | | | | | | | | | | | | | | | | |
| | VIF | | | | | | | | | | | | | | | | | | | | | | |
| BIO7 | R | | | | | | | | | | | | | | | | | | | | | | |
| | VIF | | | | | | | | | | | | | | | | | | | | | | |
| BIO8 | R | | | | | | | | | | | | | | | | | | | | | | |
| | VIF | | | | | | | | | | | | | | | | | | | | | | |
| BIO9 | R | | | | | | | | | | | | | | | | | | | | | | |
| | VIF | | | | | | | | | | | | | | | | | | | | | | |
| BIO10 | R | | | | | | | | | | | | | | | | | | | | | | |
| | VIF | | | | | | | | | | | | | | | | | | | | | | |
| BIO11 | R | | | | | | | | | | | | | | | | | | | | | | |
| | VIF | | | | | | | | | | | | | | | | | | | | | | |
| BIO12 | r | | | | | | | | | | | | | | | | | | | | | | |
| | VIF | | | | | | | | | | | | | | | | | | | | | | |
| BIO13 | r | | | | | | | | | | | | | | | | | | | | | | |
| | VIF | | | | | | | | | | | | | | | | | | | | | | |
| BIO14 | r | | | | | | | | | | | | | | | | | | | | | | |
| | VIF | | | | | | | | | | | | | | | | | | | | | | |
| BIO15 | r | | | | | | | | | | | | | | | | | | | | | | |
| | VIF | | | | | | | | | | | | | | | | | | | | | | |
| BIO16 | r | | | | | | | | | | | | | | | | | | | | | | |
| | VIF | | | | | | | | | | | | | | | | | | | | | | |
| BIO17 | r | | | | | | | | | | | | | | | | | | | | | | |
| | VIF | | | | | | | | | | | | | | | | | | | | | | |
| BIO18 | r | | | | | | | | | | | | | | | | | | | | | | |
| | VIF | | | | | | | | | | | | | | | | | | | | | | |
| BIO19 | r | | | | | | | | | | | | | | | | | | | | | | |
| | VIF | | | | | | | | | | | | | | | | | | | | | | |
| Adjusted R ² | | 0.071 | 0.154 | 0.198 | 0.383 | 0.080 | 0.475 | -0.122 | 0.278 | 0.448 | 0.491 | 0.061 | 0.159 | 0.365 | -0.344 | 0.198 | 0.396 | 0.084 | 0.096 | 0.689 | 0.341 | | |
| MSE | | 0.005 | 0.001 | 0.001 | 0.006 | 0.013 | 0.002 | -0.003 | 0.004 | 0.002 | 0.005 | 0.001 | 0.000 | 0.000 | 0.001 | 0.001 | 0.000 | 0.000 | 0.001 | 0.000 | 0.000 | | |

Bsk: Arid cold steppe with dry summer, Bsh: hot arid steppe, BSh: arid steppe, hot arid, BWk: Cold arid desert, Cwb: warm temperate steppe with dry winter, Dwa: cold desert with hot summer, Dwb cold desert with warm summer, PT polar tundra, BIO1-19 climate variables 1–19; r related coefficient, VIF variance inflation factor, MSE Mean Squared Error. BIO1 = Annual Mean Temperature; BIO2 = Mean Diurnal Range (Mean of monthly (max temp—min temp)); BIO3 = Isothermality (BIO2/BIO7) (* 100); BIO4 = Temperature Seasonality (standard deviation × 100); BIO5 = Max Temperature of Warmest Month; BIO6 = Min Temperature of Coldest Month; BIO7 = Temperature Annual Range (BIO5-BIO6); BIO8 = Mean Temperature of Wettest Quarter; BIO9 = Mean Temperature of Driest Quarter; BIO10 = Mean Temperature of Warmest Quarter; BIO11 = Mean Temperature of Coldest Quarter; BIO12 = Annual Precipitation; BIO13 = Precipitation of Wettest Month; BIO14 = Precipitation of Driest Month; BIO15 = Precipitation Seasonality (Coefficient of Variation); BIO16 = Precipitation of Wettest Quarter; BIO17 = Precipitation of Driest Quarter; BIO18 = Precipitation of Warmest Quarter; BIO19 = Precipitation of Coldest Quarter

respectively. The training datasets were used to develop climate-based models for estimating spectral diversity indices. The developed models were validated by validating the datasets for accuracy and consistency. Only models that passed the validating test were used for the prediction of spectral indices based on the climatic variables of 2050 and 2070. The process includes the following three steps. First, the linear relationship between spectral diversity indices and 19 climatic variables was assessed by obtaining bivariate correlations for each nature reserve. To undergo a reduction for each response variable (spectral plant richness: MSAVI, CV), explanatory variables with correlations $|r| \leq 0.1$ were excluded because of their weak explanatory power. In the second step, collinearity was addressed by testing correlations for each possible pair of explanatory variables. If $|r| > 0.7$, the explanatory variable strongly correlated with the response variable was included. The ones weakly

correlated with spectral diversity indices will be excluded. This resulted in a unique set of climatic variables for each response variable (see Table 1). A concern when analyzing spatial data with regression models is spatial auto-correlation, that is, the data are auto-correlated in space and thus are not independent. Spectral diversity indices and climatic variables were checked for autocorrelation using Durbin–Watson statistics. If no auto-correlation was detected, we performed regressions. When autocorrelation was detected, however, the autoregressive parameters were removed until all remaining parameters were statistically significant. In step three, a stepwise selection procedure was used for model selection based on the adjusted R^2 , p -value, MSE, VIF, and DW values (Ricklefs and He 2016). The models with high R^2 , $p < 0.01$, low MSE, $VIF < 10$, and $DW \approx 2$ (R^2 , calculated as the squared Pearson's correlation coefficient; p -value, significance level; MSE, mean square error; VIF, variance inflation factor; DW, Durbin–Watson values), were selected as proposed models and then validated using validated datasets. The performance of the proposed models in the validating test was assessed using four evaluation parameters obtained in the validated datasets: R^2 , MSE, and the significance level (p) between the predicted and observed spectral richness values. Models with the highest adjusted R^2 and the lowest MSE with a $p < 0.01$ are considered qualified models (Thenkabail et al. 2000; Lucas and Carter 2008; Fassnacht et al. 2014), and were used for the prediction of spectral richness in 2050 and 2070.

In the last step, the selected models were used to predict the spectral diversity indices in 2050 and 2070 based on projected climate variables. Variables for future climate projections were based on the IPCC Fifth Assessment Report, from which we selected 11 global climate models (BCC-CSM1-1, CCSM4, GISS-E2-R, HadGEM2-AO, HadGEM2-ES, IPSL-CM5A-LR, MIROC5, MRI-CGCM3, MIROC-ESM-CHEM, MIROC-ESM, and NorESM1-M) and three contrasting representative concentration pathways (RCP4.5, RCP6.0, and RCP8.5) for the years 2050 (average for 2041–2060) and 2070 (average for 2061–2080). These climate data were also extracted from the WorldClim 1.4 database. The climatic and spectral data were processed using Microsoft Excel 2017, and the Statistical Package for the Social Sciences 25 (SPSS 25; Chicago, Illinois, USA) was used for correlation coefficient, regression, and other statistical analyses.

Results

Key climatic variables

While all of the grassland ecosystems investigated showed highly significant links to some of the bioclimatic predictors, the actual predictors included in the predictive models varied greatly. Our variable selection analysis selected the corresponding climatic variables as predictors of spectral indices (Table 1). For arid steppes (03726, 11177, 17674), the influencing climatic variables were completely different. For cold arid deserts (14028, 14530, 23278), isothermality (BIO3) was positively related to MSAVI, and the annual mean temperature (BIO1) was negatively related to the both MSAVI and CV. Both BIO3 and the mean temperature of the wettest quarter (BIO8) were positively significantly related to both spectral indices for protecting the area of 14,530. The precipitation of the driest month (BIO14) was negatively related to both MSAVI and CV for the protected area 14,028. The coefficient of variation in precipitation seasonality (BIO15) was negatively related to both MSAVI and CV for protecting area 23,278.

BIO1, BIO14, and BIO17 (precipitation of the driest quarter) were significantly related to the spectral indices of warm-summer desert 12,725. For the hot-summer desert, 12,429, BIO2 [mean monthly temp (max temp—min temp)] was significantly negatively related to the spectral indices. For the polar tundra 13,736, BIO3 was negatively related to the spectral indices. Spectral meta-learner for regression (SMLR) models, which demonstrated high statistical significance and low square mean error, were used for further validation.

Spectral model validation

Linear regression models clearly indicate that the selected spectral indices to model grassland species richness and turnover provided reliable estimates across the global grassland regions (Fig. 2). Overall, the models perform better in tropical and subtropical grasslands than in more temperate grasslands and polar tundra. With regard to species richness, MSAVI performed well, while CV also showed a strong performance across the different grasslands, with the exception of the 17,768 grassland, where a discernible prediction bias was observed, with the measured spectral CV being significantly lower than expected based on the 19 climatic variables.

The changing trends in plot-level plant richness (MSAVI, CV) and variation among plots (CV-MSAVI, CV-CV) for the 10 grasslands differed between the current climatic conditions and future scenarios, with both increase or decrease tendency in plot-level plant richness, and a clear decreased tendency in β -diversity in the future (Fig. S1). In most cases, we observed a decreasing tendency for plot-level plant richness. For grasslands 03,726 and 14,530, characterized by an arid steppe or dry winter and warm summer, the plant richness has an increasing trend. An obvious decreased trend was projected for beta-diversity: CV-MSAVI or CV-CV. A significant decrease in CV-MSAVI in all grasslands under 11 climatic scenarios indicated a clear tendency of homogenization in species composition. CV-CV also demonstrated a decreasing tendency in future climate scenarios; exceptions were grasslands of 14,028 and 17,768 in which CV-CV increased or both. These two grasslands were characterized by the climatic features of the cold desert, dry winter, and warm summer.

Discussion

Change trends

Using spectral diversity indices extracted from Landsat remote sensing imageries, we predicted plant richness would decrease in most grasslands except of arid steppes, and plant spectral β -diversity would significantly decrease in the next decades, indicating a strong bio-homogenization tendency. Numerous previous studies (Smith et al. 2015) have suggested that increases in species richness in central Asian grasslands occur almost synchronously with climate warming, as demonstrated by the high synchrony of species richness and interannual temperature and precipitation fluctuations. The results in the current study indicated that only the Tianshan grassland (14,530), characterized by a cold arid desert climate, was expected to increase in plant richness in the next few decades, whereas findings from other sites (Xilin Gol, Myangan-Ugalzat) indicated a declining trend (12,429,

14,028), or inconsistency between MSAVI and CV (Dauria, Hoh Xil: 12,725, 13,736). The dominant species in central Asian grasslands are annual and perennial plants, and their proportion is not significantly related to climate fluctuation (Dullinger et al. 2012; Hülber et al. 2016). Annual plants react very strongly to short-term weather fluctuations, making their appearance dependent on stochastic events (Fischer et al. 2020). Perennial plants perhaps respond even more so than annual plants in some cases, given the range of germination strategies in annuals. Other reasons are the shallower rooting structure and seasonality/phenology of these herbaceous vegetation types. These may partially explain why high fluctuations existed among the results in predicting future plant richness changes.

Biotic homogenization has been found to be a general issue under climatic change in many studies (Hewitt et al. 2010; Poniowski et al. 2018). The expected biotic homogenization in plant species in the next few decades in all types of grasslands under future climate change scenarios were also observed in our study. We can infer this change demonstrates that generalist species will dominate grasslands under future climate conditions. Contrary to generalists (which have high adaptation to climatic warming), climate (especially temperature and rainfall seasonality) mainly drives endemism, which is connected to ecological speciation and specialization to local conditions (Irl et al. 2015). Under climatic warming, only endemic species resistant to high temperatures can survive. Consequently, communities with various species having diverse functions were gradually replaced by communities with functional groups suitable to reduced precipitation and increased temperature, and the β -diversity consequently declined. Fischer et al. (2020) show that drought events can lead to the expansion of ruderal species.

Climate variable performance

We used climate variables to predict plant spectral diversity, since climate variables are strong predictors of plant diversity. Short-term variations in weather conditions can explain up to 63% of the interannual variability in plant species richness and diversity in four American grasslands (Jonas et al. 2015). Another study in North America also found that plant richness correlated strongly with current temperature and was weakly correlated with the historical climate (Vazquez-Rivera and Currie 2015). Although the spatial distribution of plant species diversity is also determined by several other factors, including dispersal and human land use (Mazziotta et al. 2015), the current climate is typically by far the strongest predictor of plant diversity (Vazquez-Rivera and Currie 2015). The variability in climatic conditions (i.e., their isolation in a spatial context) might affect the pattern of diversity and endemism by restricting immigration and enabling speciation (Steinbauer et al. 2012), promoting adaptive differentiation processes in plant communities (Nosil 2012). This is the theoretic base for predicting spectral plant diversity using 19 climatic variables.

In accordance with our expectations, climate variables performed differently regarding spectral plant diversity indices. The climatic variable BIO3 [mean diurnal range—mean of monthly (max temp—min temp)] divided by the temperature annual range (max temperature of warmest month—min temperature of coldest month) is positively related to plant richness, and is forecasted to increase plant richness in the next few decades. However, this enhanced effect is weakened by the annual mean temperature, which is negatively related to the plant richness. This joint effect was expected to reduce plant richness over the next few decades in the cold arid desert grasslands in our study regions (14,028, 14,530, and 23,278). The key climatic variables influencing

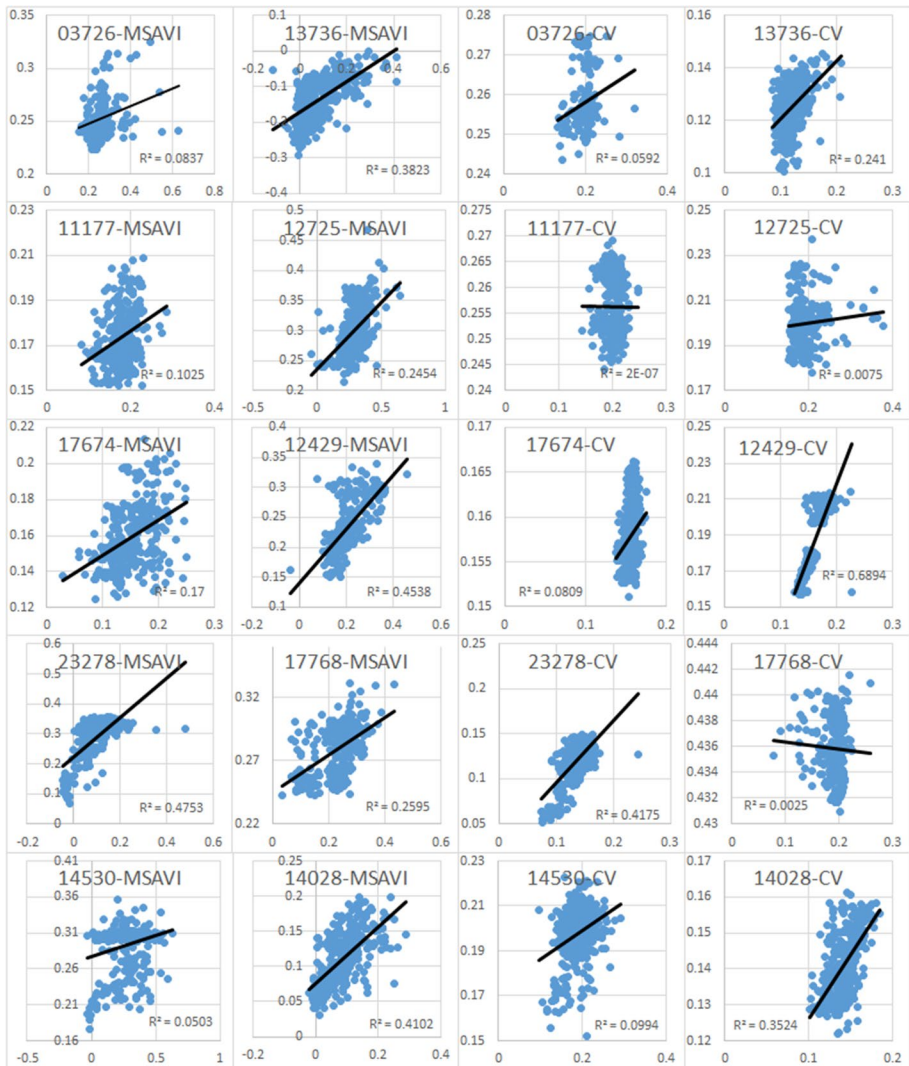


Fig. 2 Measured (x-axis) vs. predicted spectral diversity indices (y-axis) from our selected spectral meta-learner for regression (SMLR) models for each grassland nature reserve

plant diversity are different since the dominant climates are different from one site to another. In Northern America, climate change was found to cause species loss at all experimental sites across the three temperate grasslands (White et al. 2014). For arid steppes (03,726, 11,177, and 17,674), the influencing climatic variables were completely different. Both BIO3 and BIO8 (mean temperature of the wettest quarter) were positively significantly related to spectral indices for the Tianshan nature reserve (14,530). BIO14 (precipitation of the driest month) was negatively related to both the MSAVI and CV for Myangan-Ugalzat nature reserve (14,028). BIO15 (coefficient of variation in precipitation seasonality) was negatively related to both the MSAVI and

CV for De La Vicuña nature reserve (23,278). BIO1, BIO14, and BIO17 (precipitation of the driest quarter) were significantly related to the spectral indices of area Dauria (12,725), since they belonged to warm-summer desert grasslands. For hot-summer desert grassland Xilin Gol (12,429), BIO2 (mean of monthly [max temp—min temp]) was significantly negatively related to spectral indices. For the polar tundra in Hoh Xil (13,736), BIO3 was negatively related to the spectral indices.

Limitations

We only used climatic variables as independent variables to predict spectral diversity; this study excluded the impacts of human disturbance because study areas are nature reserves. Human disturbances can reduce species richness at a local scale, although habitat fragmentation or shifts can reduce endemic species richness (Hanski et al. 2013; Burrows et al. 2014; Aronson et al. 2014; Newbold et al. 2015) or increase plant richness through the spread of exotic species (Bruno et al. 2004; McKinney 2008; Elahi et al. 2015). The elected nature reserves as study areas can improve the precision of predicted models, since the strong effects of human activities are excluded. Uncertainty still exists in the prediction of global plant richness owing to incomplete sampling and differences in the force drivers of plant diversity across grasslands on Earth (Regnier et al. 2015). The time lag effect exists because the impact of force drivers and the response of plant richness did not occur concurrently (Alexander et al. 2018). This effect weakens the accuracy of the predicted model (Gilbert and Levine 2013; Essl et al. 2015). Other factors influencing grassland diversity include grazing, nitrogen deposition, and unusual weather events. These complexities in influencing factors may induce diverse effects on plant richness responses to climate change in various types of grasslands worldwide, depending on the particular nature of the climate, environmental conditions, and the potential for dispersal (Pauli et al., 2012; Vellend et al., 2013). In Tianshan (14,530), the main environmental factors affecting the distribution patterns in plant diversity were elevation, soil water, total nitrogen, available nitrogen, organic matter, and total salt (Liu 2017). These factors (elevation, soil water, and chemical components) were kept unchanged in the periods of 1990–2000 and 2050–2070 in our study, since we compared the changes in the same plots during these periods.

Conclusions

Using spectral plant diversity indices extracted from Landsat remote sensing imagery as indicators of plant α - and β -diversity, we predicted the changes in plant diversity of 10 grassland nature reserves across the Earth in 2050 and 2070, based on stepwise linear regression models between spectral diversity indices and 19 climatic variables during 1990 and 2000. In most cases, spectral plant richness demonstrated a declining trend, while an increasing trend was observed in arid steppes. Generally, spectral β -diversity demonstrated a significant declining trend in the next few decades for all studied grasslands (from tropical to tundra) under 11 climatic scenarios, indicating a clear tendency of homogenization in species composition. Our study provides the basis for using remote sensing techniques to predict the changes in plant diversity caused by climate warming at a large scale across different ecosystems. Such an approach can be widely used in studies regarding biome

responses to climate change since the remote sensing techniques have the advantages of multiple spatial and temporal scales and can be repeatedly observed across different sites by the same standards.

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Author contributions YP devised the project. YP, WS and JA developed the research questions and study design. YP processed and analyzed data. All authors contributed to the manuscript writing and editing.

Data availability The data that support the findings of this study are available from the corresponding authors.

Declarations

Conflict of interest The authors declare no conflict of interest.

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Authors and Affiliations

Yu Peng¹  · Jinchao Feng¹ · Weiguo Sang¹ · Jan Christoph Axmacher²

✉ Yu Peng
yuu.peng@muc.edu.cn

✉ Weiguo Sang
swg@muc.edu.cn

¹ College of Life and Environmental Sciences, Minzu University of China, Beijing 100081, China

² UCL Department of Geography, University College London, Pearson Building, Gower Street, London, UK