

## HISTORICAL AND CONTEMPORARY CLIMATE LEGACY OF THE LARGE-SCALE DISTRIBUTIONAL PATTERNS OF PLANT RICHNESS ACROSS DIFFERENT TAXONOMIC LEVELS: AN ASSESSMENT OF PROTECTED AREAS IN CHINA

### EL LEGADO CLIMÁTICO HISTÓRICO Y CONTEMPORÁNEO DE LOS PATRONES DE DISTRIBUCIÓN A GRAN ESCALA DE LA RIQUEZA VEGETAL EN DIFERENTES NIVELES TAXONÓMICOS: UNA EVALUACIÓN DE LAS ÁREAS PROTEGIDAS EN CHINA

CHUN-JING WANG<sup>1,2,3,4</sup>, AND JI-ZHONG WAN<sup>1,4\*</sup>

<sup>1</sup>State Key Laboratory of Plateau Ecology and Agriculture, Qinghai University, Xining, China

<sup>2</sup>College of Agriculture and Animal Husbandry, Qinghai University, Xining, China

<sup>3</sup>School of Nature Conservation, Beijing Forestry University, Beijing, China

<sup>4</sup>Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago, Chile

\* Corresponding author: wan1276@163.com

#### Abstract

**Background:** Historical and contemporary climates may shape the distributional patterns of plant species richness across different scales. However, few studies have focused on the effects of historical and contemporary climate changes on the distributional patterns of plant richness in Chinese protected areas across different taxonomic levels.

**Hypotheses:** Historical and contemporary climates can have an important legacy effect on the large-scale distributional patterns of plant richness across different taxonomic levels.

**Studied species:** Vascular plants.

**Study site:** China.

**Method:** We used data on plant richness at the family, genus, and species levels from Chinese protected areas and applied regression modeling to explore the relationships between climate change and plant richness among vascular, fern, seed, gymnosperm, and angiosperm plants based on paleoclimate (Last Glacial Maximum; LGM, ca. 22,000 years ago) and contemporary climate data.

**Results:** The large-scale distributional patterns of plant richness could be predicted across different taxonomic levels on the basis of paleoclimate and contemporary climate data. Specifically, historical and contemporary climate variables were found to better correlate with fern plant richness than seed plant richness. For seed plants, the explanatory power of historical and contemporary climate variables was found to be stronger for the richness of gymnosperms than for the richness of angiosperms.

**Conclusions:** The distributional pattern of plant richness could be predicted across different taxonomic levels after including paleoclimate (LGM, ca. 22,000 years ago) and contemporary climate data from China. Our study could support the effectiveness of the management of protected areas in China.

**Key words:** China, climate legacy, conservation, paleoclimate, plant diversity, taxonomic level, vascular plants.

#### Resumen

**Antecedentes:** Los climas históricos y contemporáneos contribuyen a conformar el patrón de la distribución de la riqueza de especies de plantas a diferentes escalas. Sin embargo, muy pocos estudios se han concentrado en entender los efectos de los cambios históricos y contemporáneos del clima en el patrón de la distribución de la riqueza de plantas en diferentes niveles taxonómicos en China.

**Hipótesis:** Los climas históricos y contemporáneos pueden tener un importante efecto de legado en los patrones de distribución a gran escala de la riqueza de plantas a diferentes niveles taxonómicos.

**Especies de estudio:** Plantas vasculares.

**Sitio de estudio:** China.

**Métodos:** Empleando datos de reservas naturales chinas y modelado de Regresión Ponderada Geográficamente aplicada junto con el método de Mínimos Cuadrados Ordinarios, utilizamos la información de riqueza de plantas a nivel de familia, género y especies para explorar las relaciones entre el cambio climático histórico y contemporáneo, y la riqueza de plantas a nivel de familia, género y especie entre diferentes grupos de plantas vasculares, helechos, semillas, gimnospermas y angiospermas.

**Resultados:** En comparación con las plantas de semilla, los climas históricos y contemporáneos predicen mejor la riqueza de helechos. Para las plantas con semillas, los poderes explicativos de los climas históricos y contemporáneos son más fuertes para la riqueza de gimnospermas que para la de angiospermas.

**Conclusiones:** El patrón de distribución de la riqueza de plantas se pueden predecir a diferentes niveles taxonómicos utilizando datos paleoclimáticos y de clima contemporáneo en China.

**Palabras clave:** China, diversidad vegetal, legado climático, nivel taxonómico, paleoclima, plantas vasculares.

Plant richness can deeply affect ecosystem structure and function (Tilman *et al.* 1997). Both the historical and contemporary climate can influence the large-scale geographic patterns of plant richness (Kreft & Jetz 2007, Normand *et al.* 2011, Sandel *et al.* 2011, Svenning *et al.* 2015, Liu *et al.* 2018). Time lags in the legacy effects of historical climates on biodiversity may vary widely across different plant species (Normand *et al.* 2011, Svenning *et al.* 2015, Shrestha *et al.* 2018). These time lags may influence the response of the distributional and richness patterns of plant species to climate change via several mechanisms (*e.g.*, diversification, lineage adaptation, range shifts, population buildup, and physiological responses; Svenning *et al.* 2015). Contemporary plant richness is to some degree the product of diversification within the Cenozoic (Colinvaux & De Oliveira 2001, Svenning *et al.* 2015), and in this way, paleoclimates may influence the diversification of plants and shape the current distribution of plant richness at large scales (Svenning *et al.* 2015).

Different studies (*e.g.*, Svenning 2003, Svenning & Skov 2007, Fang *et al.* 2012, Svenning *et al.* 2015, Liu *et al.* 2018) have shown that contemporary climates are the main predictors of large-scale distributional patterns of plant richness. For example, the mean annual temperature (MAT) and mean annual precipitation (MAP) in recent years have been shown to influence the contemporary distributional patterns of plant richness in China (Wang *et al.* 2010, 2012, Yang *et al.* 2014, Wang *et al.* 2017). European plant richness is one of the best-known examples in which regional distributions of plant richness are strongly affected by contemporary temperature and precipitation as well as by late Quaternary glacial-interglacial climates (Kreft & Jetz 2007, Svenning & Skov 2007, Fang *et al.* 2012, Svenning *et al.* 2015). The physiological responses of plant species to historical climates may be delayed, and contemporary climates may also affect the distribution of plant richness (Svenning & Skov 2007, Svenning *et al.* 2015).

The understanding of the effects of historical and contemporary climate on plant richness can provide new insights into the evolution of plant species at large scales. Previous studies (*e.g.*, Svenning 2003, Wang *et al.* 2010, 2012, Yang *et al.* 2014, Svenning *et al.* 2015, Liu *et al.* 2018) have evaluated the effects of historical and contemporary climates on plant richness at the species level. However, to fully understand these effects, it is important to evaluate them in terms of large-scale distributional patterns of plant richness at different taxonomic levels, from family to species, and from ferns to angiosperms.

The evaluation of biodiversity at the family and genus levels can indicate the evolutionary distinctiveness of a given set of species and provide more information on the evolutionary processes affecting plant species richness across different spatial and temporal scales than studies only focusing on the species level (O'Brien *et al.* 1998, Pimm & Joppa

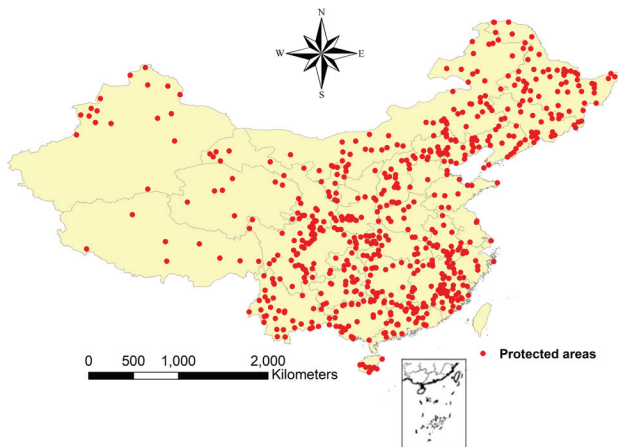
2015, Qian & Ricklefs 2007, Huang *et al.* 2016). In addition, phylogenetic endemism and biogeography may indicate the evolutionary distinctiveness of plants at large scales (Prinzinger 2001, Huang *et al.* 2016). The large-scale patterns of biodiversity at the family and genus levels can be accurately used to identify instances of phylogenetic endemism and geographical concentrations related to the evolutionary history of plants (O'Brien *et al.* 1998, Qian & Ricklefs 2007, Huang *et al.* 2016, Millar *et al.* 2017).

The climatic niche development of higher plants across different taxonomic levels (*i.e.*, species, family, and genus) differs considerably at large scales (O'Brien *et al.* 1998, Pimm & Joppa 2015). Hence, dissimilarity in the large-scale distributional patterns of plant richness may exist across different taxonomic levels. Furthermore, previous studies have identified different legacy effects of climate on the large-scale distributional patterns of plant richness in non-seed and seed plants (Peppe *et al.* 2014, Boyce & Lee 2017, Xu *et al.* 2018). Non-seed plants may be more sensitive to the velocity of climate change than seed plants due to their different reproduction and dispersal characteristics (Peppe *et al.* 2014, Xu *et al.* 2018). Lu *et al.* (2018) explored the evolutionary history of the angiosperm flora of China at the species, family, and genus levels and identified areas of high species richness and phylogenetic diversity. However, we need to explore the differences in the effects of historical and contemporary climates on the large-scale distributional patterns of plant richness across different taxonomic levels.

Here, we tested the following hypotheses: 1) historical and contemporary climates can affect the large-scale distributional patterns of plant richness and 2) the effects of historical and contemporary climates on plant richness vary across different plant groups and taxonomic levels. To test the abovementioned hypotheses, we used data on plant richness from Chinese protected areas at the family, genus, and species levels and explored the relationships between historical and contemporary climate and plant richness based on different groups of vascular, fern, seed, gymnosperm, and angiosperm plants. The testing of these two hypotheses will allow our study to contribute to the development of effective strategies for the conservation of plant diversity in protected areas in China.

## Materials and methods

**Plant richness data.** Data on plant richness, including that of ferns (non-seed) and seed plants, including gymnosperms and angiosperms, were collected and organized across different taxonomic levels (*i.e.*, the total number of families, genera, and species) from published records regarding natural reserves in China. The list of published records was provided by the study by Wang *et al.* (2017, Figure 1). Based on the published records, we extracted data on the plant



**Figure 1.** Distribution of the protected areas in China used in our analysis.

taxon richness found in core areas of protected areas. In China, the goal of core zones of protected areas is to protect relatively undisturbed natural vegetation, which has a long, uninterrupted history in this region, and the associated data thus represent an ideal dataset of plant richness (Tang *et al.* 2010, Zhang *et al.* 2017).

Based on previous studies (*e.g.*, Huang *et al.* 2016, Feng *et al.* 2017, Zhang *et al.* 2017, Liu *et al.* 2018), we transposed the plant richness data from the core zones of the protected areas into grid data at a spatial resolution of 10 arc minutes (*c.*  $16 \times 16$  km). Different groups of vascular plants (fern, gymnosperm, and angiosperm plants) were analysed in our study, as vascular plants include non-seed plants (ferns) and seed plants (gymnosperms and angiosperms). For the accurate nomenclature of scientific names, we followed the Plant List ([www.theplantlist.org](http://www.theplantlist.org)) and compared the lists of families, genera, and species based on The Plant List (<http://www.theplantlist.org>) and the Flora of China (<http://frps.iplant.cn/>) to identify the plant groups in our study. We deleted the wrong data on plant richness of protected areas. We found that the effect of the area of a nature preserve on plant richness could be excluded from further analyses because there was no significant relationship between reserve size and plant richness across the different taxonomic levels (*i.e.*, the total number of families, genera, and species) based on linear regression modelling ( $P > 0.05$ ). Finally, data from protected areas were obtained (detailed information in the Supplemental data and Figure 1).

**Climate data.** The MAT and MAP were used to assess the legacy effects of climate on the large-scale distributional pattern of plant richness (*e.g.*, Svenning *et al.* 2015, Feng *et al.* 2017, Blonder *et al.* 2018). Feng *et al.* (2017) showed that historical and contemporary MAT and MAP could influence plant endemism in China. We downloaded the grid maps of historical and contemporary MAT and MAP at a spatial resolution of 10 arc minutes (*ca.*  $16 \times 16$  km) from

the WorldClim database (<http://www.worldclim.org/>). The extremely dry and cold climate during the Last Glacial Maximum (LGM; approximately 22,000 years ago) excluded tropical forests from China and caused other strong vegetational changes (Wang *et al.* 2012, Feng *et al.* 2017). Paleoclimate (*i.e.*, the LGM) has been shown to be the main driver of plant richness at large scales (*e.g.*, Kreft & Jetz 2007, Svenning & Skov 2007, Fang *et al.* 2012, Svenning *et al.* 2015). The Holocene has not been long enough to have allowed speciation in most cases (Lister 2004, Svenning *et al.* 2015); hence, we used average climate data from 1950–2000 AD to represent the contemporary scenario and paleoclimate data (*i.e.*, the LGM) for the historical scenario. Paleoclimate data in regard to MAT and MAP were obtained from the CCSM4 general circulation model (<http://www.cesm.ucar.edu/models/ccsm4.0/>). The CCSM4 model consists of a coupled atmospheric, oceanic, and sea ice model with noninteractive vegetation and an atmospheric resolution of 10.0 arc minutes. The model is driven by variations in orbital configuration, greenhouse, ice-sheet topography, and coincident sea level changes and bathymetry for paleoclimates (Lawrence & Oleson 2012). The paleoclimate data have the same coordinate system and resolution as the contemporary climate data. A paired-sample *t*-test coupled with a Bonferroni adjustment was used to evaluate the differences between the paleoclimate data and contemporary climate data across all the protected areas. The paired-sample *t*-test was conducted in JMP version 11.0 (SAS Institute Inc., Cary NC).

**Data analysis.** Spatial autocorrelation in ecological data can inflate Type I errors in statistical analyses (Diniz-Filho *et al.* 2003). Hence, we used Moran's I coefficient calculated on the basis of a distance matrix to assess the spatial autocorrelation in plant richness across the different taxonomic levels (*i.e.*, the total number of families, genera, and species) (Diniz-Filho *et al.* 2003). The default settings were used in SAM 4.0 (Rangel *et al.* 2010), and the default number of distance classes was 17 with an equal number of pairs between different protected areas according to the available plant richness data (Rangel *et al.* 2010). Pearson correlation coefficients were used to assess the correlations in plant richness between the different groups (*i.e.*, vascular, fern, seed, gymnosperm, and angiosperm) and taxonomic levels (*i.e.*, family, genus, and species) across the protected areas. The analysis of Pearson correlation coefficients was conducted in JMP version 11.0 (SAS Institute Inc., Cary NC).

Then, we used geographically weighted regression (GWR) coupled with the ordinary least squares (OLS) method to evaluate both the historical and contemporary climates and identify the large-scale distributional patterns of plant richness (Brunsdon *et al.* 1996, Mellin *et al.* 2014, Xu *et al.* 2016). GWR is a local form of linear regression that is used to spatially model varying relationships based on the assessment of nonstationarity and the effects of spatial scale on ecological data (Brunsdon *et al.* 1996, Mellin *et al.* 2014). Previous studies (*e.g.*, Foody 2004, Eiserhardt *et al.* 2011, Mellin *et al.* 2014) have shown that GWR is useful in the investigation of spatially varying biodiversity-environment

relationships because spatial autocorrelation and heterogeneity exist in ecological data. The variables pertaining to the historical and contemporary climates (including MAT and MAP) were regarded as explanatory variables, and plant richness was regarded as the dependent variable across the different groups of vascular, fern, seed, gymnosperm, and angiosperm plants. The specific settings for the GWRs were as follows: 1) the spatial function of the GWR was Gaussian; 2) the adaptive kernel was 10 % neighbours; and 3) optimization to minimize the AICc (corrected Akaike information criterion) was used for all bandwidths (Brunsdon *et al.* 1996, Eiserhardt *et al.* 2011, Xu *et al.* 2016). The GWR analysis was conducted with SAM 4.0 (Rangel *et al.* 2010).

The correlation coefficients ( $r$ ) and  $P$ -values from the GWR and OLS analyses were used to assess the associations between the historical and contemporary climates (including MAT and MAP) and plant richness. We used the adjusted  $R^2_{adj}$  (%) from the GWR to determine the explanatory power of the historical and contemporary climate in regard to the large-scale distributional pattern of plant richness (Blonder *et al.* 2018, Liu *et al.* 2018). Meanwhile, the  $R^2_{adj}$  (%) of the OLS analysis was used to test the relationships between the historical and contemporary climates and plant richness. Then, we compared the correlation coefficient ( $r$ ) and  $R^2_{adj}$  (%) of the GWR with the OLS analysis to test whether the GWR performed better than the OLS method (Brunsdon *et al.* 1996).

Finally, we used OLS to determine the best predictors of the large-scale distributional patterns of plant richness at different taxonomic levels (*i.e.*, the total number of species, families, and genera) across the vascular, fern, seed, gymnosperm, and angiosperm plant groups in independent analyses (Nagelkerke 1991, Liu *et al.* 2018). The adjusted  $R^2_{adj}$  (%) from the OLS analysis was used to determine the explanatory power of climate in regard to the large-scale distributional patterns of plant richness. We conducted the OLS analysis in JMP 10.0 (SAS Institute Inc., Cary, NC).

## Results

The ranges of vascular plant richness were 11-257, 30-1372, and 45-4543 at the family, genus, and species levels, respectively (Table 1). The average vascular plant richness was 132, 506, and 1117 from the family to species level (Table 1). Specifically, the average fern species richness was 20, 40, and 87 at the family, genus, and species levels, respectively, and the average seed plant species richness was 112, 467, and 1027 at the family, genus, and species levels, respectively (Table 1). The average family, genus, and species richness values were 4 (ranging from 1 to 10), 8 (ranging from 1 to 33) and 14 (ranging from 1 to 102) for gymnosperms and 108 (ranging from 22 to 203), 460 (ranging from 52 to 1,244) and 1,024 (ranging from 65 to 3,931) for angiosperm plants, respectively (Table 1).

The MAP and MAT in the contemporary climate were significantly higher than those in the paleoclimate (paired-sample  $t$ -test;  $P < 0.05$ ). Specifically, the average historical MAT was 5.1 °C (ranging from -14.8 °C to 21.9 °C), and

**Table 1.** Basic description of plant richness in protected areas in China

	Mean	SD	Max.	Min.
Vascular plant family	132	58.0	257	11
Vascular plant genus	506	267.4	1372	30
Vascular plant species	1117	773.2	4543	45
Fern family	20	13.4	50	1
Fern genus	40	31.8	127	1
Fern species	87	92.0	594	1
Seed plant family	112	44.9	210	22
Seed plant genus	467	234.1	1251	53
Seed plant species	1027	689.2	3949	43
Gymnosperm family	4	2.4	10	1
Gymnosperm genus	8	5.9	33	1
Gymnosperm species	14	12.0	102	1
Angiosperm family	108	42.6	203	22
Angiosperm genus	460	229.0	1244	52
Angiosperm species	1024	672.2	3931	65

the contemporary MAT was 10.1 °C (ranging from -8.9 °C to 25.5 °C; Table 2). The average historical MAP was 830.7 mm (ranging from 17 mm to 2232 mm), and the contemporary MAP was 952.4 mm (ranging from 26 mm to 2,262 mm; Table 2).

Based on the Moran's  $I$  coefficients, the spatial autocorrelation in the plant richness data was low across the different taxonomic levels (most Moran's  $I$  coefficients were  $< 0.200$  or  $> -0.200$ ; Figure 2). We found that there were significant correlations in plant richness among the different taxonomic levels (*i.e.*, families, genera, and species;  $P < 0.05$ ; Table 3). Additionally, a significant relationship of plant richness among the different vascular, fern, seed, gymnosperm, and angiosperm plant groups could be detected ( $P < 0.05$ ; Table 3). The correlation coefficients were the largest (0.9979;  $P < 0.05$ ) between seed and gymnosperm plants at the family level, between vascular and seed plants at the genus level (0.9979;  $P < 0.05$ ), and between seed and angiosperm plants (0.9979;  $P < 0.05$ ) at the species level (Table 3).

All the correlation coefficients in the GWR between the historical and contemporary climate variables (including MAT and MAP) and plant richness were higher than 0.49 ( $P < 0.001$ ), and those in the OLS analysis were higher than 0.20 across the different taxonomic levels ( $P < 0.001$ ; Table 4). Values of  $R^2_{adj}$  (%) represent the adjusted  $R^2_{adj}$  (%) values obtained from the GWR and OLS analyses conducted to determine the explanatory power of historical and contemporary climate variables on the large-scale distributional pattern of plant richness. Based on  $R^2_{adj}$ , the GWR showed better modelling performance than the OLS analysis, indicating that both historical and contemporary climate coupled with spatial autocorrelation can explain the distributional patterns of plant richness at large scales (Table 4).



**Table 2.** Basic description of mean annual temperature (MAT; °C) and mean annual precipitation (MAP; mm) in protected areas in China

	Mean	SD	Max.	Min.
Historical MAT	5.3	8.2	21.9	-14.8
Historical MAP	842.0	534.7	2232	17
Contemporary MAT	10.3	7.1	25.5	-8.9
Contemporary MAP	962.6	520.7	2262	26

The following results regarding the  $R^2_{adj}$  value were obtained from the GWR. The combination of historical and contemporary climate could explain the richness of vascular plant families, genera, and species ( $R^2_{adj} = 25.8\%$ ,  $26.1\%$ , and  $26.4\%$ , respectively;  $P < 0.001$ ; Table 4), and both historical and contemporary climate had the strongest explanatory power in regard to the richness of fern genera and species ( $R^2_{adj} = 34.6\%$  and  $37.6\%$ , respectively;  $P < 0.001$ ; Table 4). The historical and contemporary MAT and MAP had the strongest explanatory power in regard to richness at the family level ( $P < 0.001$ ; Table 4) but the smallest explanatory power in regard to species richness based on the  $R^2_{adj}$  (%) from the OLS analysis ( $P < 0.001$ ; Table 4).

Historical MAT explained plant richness at different taxonomic levels in a better way than contemporary MAT, and this explanatory power of the MAP was opposite to that of the MAT across the different taxonomic levels (Figure 3). Furthermore, the explanatory power of the contemporary MAP was the strongest for plant richness at the family, genus, and species levels (Figure 3). With the exception of historical and contemporary MAT, historical and contemporary climate variables better explained fern richness than seed plant richness across all the taxonomic levels (Figure 3). Regarding gymnosperm and angiosperm plants, the explanatory power of historical and contemporary climates was stronger for gymnosperm plant richness than angiosperm plant richness across all taxonomic levels (Figure 4). Furthermore, the

historical and contemporary MAP had the strongest explanatory power in regarding to angiosperm plant richness at the family level ( $R^2_{adj} > 60.0\%$ ;  $P < 0.001$ ; Figure 4).

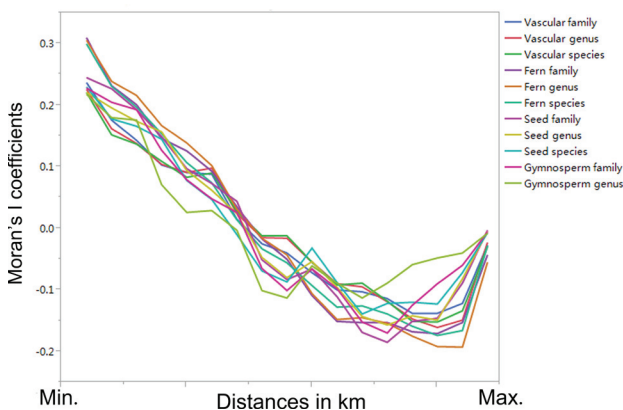
## Discussion

Our results showing that the average vascular plant richness was 132 (ranging from 11 to 257), 506 (ranging from 30 to 1,372), and 1,117 (ranging from 45 to 4,543) at the family, genus, and species levels, respectively, and that the plant richness was also high for fern, seed, gymnosperm, and angiosperm plants in protected areas of China (detailed information in Table 1) indicate that the protected area network in China has rich plant resources. In particular, Chinese protected areas have a high richness of angiosperm plants (Table 1). Hence, the ability of protected areas to conserve plant richness is strong in China.

We found that the contemporary climate variables (*i.e.*, MAP and MAT) were significantly higher than those for the paleoclimate (paired-sample *t*-test;  $P < 0.05$ ; Table 2), and previous studies (*e.g.*, Araújo *et al.* 2011, Keppel *et al.* 2015, Wan *et al.* 2018) have shown that climate change has a high potential to threaten the effectiveness of protected areas in terms of conserving plant diversity at large scales. The exploration of the legacy effects of climate on the large-scale distributional patterns of plant richness is key for plant diversity conservation in protected areas in China. Based on the database of plant richness data from Chinese protected areas (with low spatial autocorrelation in plant richness data across different taxonomic levels; Figure 2), we examined the legacy effects of historical and contemporary climate on the large-scale distributional patterns of plant richness across different taxonomic levels.

The results of our GWR for both the historical and contemporary climate show significant explanatory power in terms of plant richness in China across various taxonomic levels (Table 4; Figures 3, 4), which hints that historical and contemporary climate affect the large-scale distributional patterns of plant richness across various taxonomic levels. Interestingly, the MAT was more important in the historical climate scenario than the present day scenario; however, the opposite was true of MAP according to the results of the explanatory power analysis (Figures 3, 4). The explanatory power of the historical and contemporary climate variables was higher at the family and genus levels and decreased at the species level based on the results regarding  $R^2$  (Figures 3, 4). O'Brien *et al.* (1998) showed that the realized distributional limits of families and genera (unlike species) could be constrained by year-round or seasonally high ambient energy and by seasonally low ambient energy regardless of the water regime. Therefore, the historical and contemporary climate can better explain family and genus richness than species richness. Furthermore, historical and contemporary climate variables (including MAT and MAP) were found to better explain the richness of fern (non-seed) plants than that of seed plants (Figures 3, 4).

Some studies (*e.g.*, Wang *et al.* 2012, Svenning & Sandel 2013, Svenning *et al.* 2015) have found that both the

**Figure 2.** Moran's I coefficients across different taxonomic levels (*i.e.*, families, genera, and species) and groups (*i.e.*, vascular, fern, seed, gymnosperm, and angiosperm plants).

**Table 3.** Pearson correlation coefficients for plant richness between different taxonomic levels (*i.e.*, families, genera, and species) and groups (*i.e.*, vascular, fern, seed, gymnosperm, and angiosperm plants) based on protected area data

	Vascular			Fern			Seed			Gymnosperm			Angiosperm		
	Family	Genus	Species	Family	Genus	Species	Family	Genus	Species	Family	Genus	Species	Family	Genus	Species
Vascular	Family	1.0000	0.9301	0.8308	0.9439	0.9188	0.8119	0.9913	0.9170	0.8010	0.6713	0.5321	0.9896	0.9247	0.8000
	Genus	0.9301	1.0000	0.9409	0.8791	0.8912	0.8374	0.926	0.9979	0.9222	0.6828	0.5762	0.9252	0.9932	0.9178
	Species	0.8308	0.9409	1.0000	0.7810	0.8131	0.8346	0.8218	0.9431	0.9910	0.6615	0.5499	0.8149	0.9375	0.9865
Fern	Family	0.9439	0.8791	0.781	1.0000	0.9594	0.8608	0.9126	0.858	0.7518	0.6516	0.5319	0.9198	0.8849	0.7720
	Genus	0.9188	0.8912	0.8131	0.9594	1.0000	0.9261	0.8890	0.8668	0.7799	0.645	0.5396	0.8969	0.8987	0.8136
	Species	0.8119	0.8374	0.8346	0.8608	0.9261	1.0000	0.7832	0.8156	0.7918	0.6346	0.5165	0.7798	0.8415	0.8315
Seed	Family	0.9913	0.9260	0.8218	0.9126	0.889	0.7832	1.0000	0.9246	0.8154	0.6667	0.5271	0.9979	0.9259	0.8071
	Genus	0.9170	0.9979	0.9431	0.8580	0.8668	0.8156	0.9246	1.0000	0.9378	0.6751	0.5881	0.9256	0.9947	0.9329
	Species	0.8010	0.9222	0.991	0.7518	0.7799	0.7918	0.8154	0.9378	1.0000	0.6469	0.5657	0.8046	0.9309	0.9954
Gymnosperm	Family	0.8220	0.7681	0.7000	0.7844	0.7673	0.6869	0.8106	0.7585	0.6816	1.0000	0.8609	0.7143	0.7575	0.6843
	Genus	0.6713	0.6828	0.6615	0.6516	0.6450	0.6346	0.6667	0.6751	0.6469	0.8609	0.9007	0.6614	0.6842	0.6606
	Species	0.5321	0.5762	0.5499	0.5319	0.5396	0.5165	0.5271	0.5881	0.5657	0.7143	1.0000	0.5249	0.6023	0.6466
Angiosperm	Family	0.9896	0.9252	0.8149	0.9198	0.8969	0.7798	0.9979	0.9256	0.8046	0.7958	0.6614	1.0000	0.9284	0.8105
	Genus	0.9247	0.9932	0.9375	0.8849	0.8987	0.8415	0.9259	0.9947	0.9309	0.7575	0.6842	0.9284	1.0000	0.9376
	Species	0.8000	0.9178	0.9865	0.7720	0.8136	0.8315	0.8071	0.9329	0.9954	0.6606	0.6466	0.8105	0.9376	1.0000

**Table 4.** Results of geographically weighted regression (GWR) and ordinary least squares (OLS) analysis of the effects of both historical and contemporary climate on plant richness

	GWR			OLS		
	<i>r</i>	<i>R</i> <sup>2</sup> adj (%)	<i>P</i> -value	<i>r</i>	<i>R</i> <sup>2</sup> adj (%)	<i>P</i> -value
Vascular plant family	0.560	25.8	< 0.001	0.491	23.8	< 0.001
Vascular plant genus	0.563	26.1	< 0.001	0.474	22.1	< 0.001
Vascular plant species	0.566	26.4	< 0.001	0.461	20.9	< 0.001
Fern family	0.624	33.9	< 0.001	0.552	30.1	< 0.001
Fern genus	0.629	34.6	< 0.001	0.544	29.3	< 0.001
Fern species	0.613	37.6	< 0.001	0.499	24.5	< 0.001
Seed plant family	0.611	32.2	< 0.001	0.536	28.4	< 0.001
Seed plant genus	0.629	34.6	< 0.001	0.521	26.8	< 0.001
Seed plant species	0.636	35.6	< 0.001	0.508	25.5	< 0.001
Gymnosperm family	0.586	28.9	< 0.001	0.512	25.9	< 0.001
Gymnosperm genus	0.566	26.5	< 0.001	0.438	18.8	< 0.001
Gymnosperm species	0.521	21.2	< 0.001	0.361	12.7	< 0.001
Angiosperm family	0.543	23.7	< 0.001	0.454	20.3	< 0.001
Angiosperm genus	0.567	26.6	< 0.001	0.453	20.2	< 0.001
Angiosperm species	0.576	27.6	< 0.001	0.444	19.3	< 0.001

This table shows the correlation coefficients (*r*) and *P*-values of GWR and OLS analysis of the associations between historical and contemporary climate variables (including MAT and MAP) and plant richness across different taxonomic levels (*i.e.*, family, genus, and species) based on the vascular, fern, seed, gymnosperm, and angiosperm plant groups.

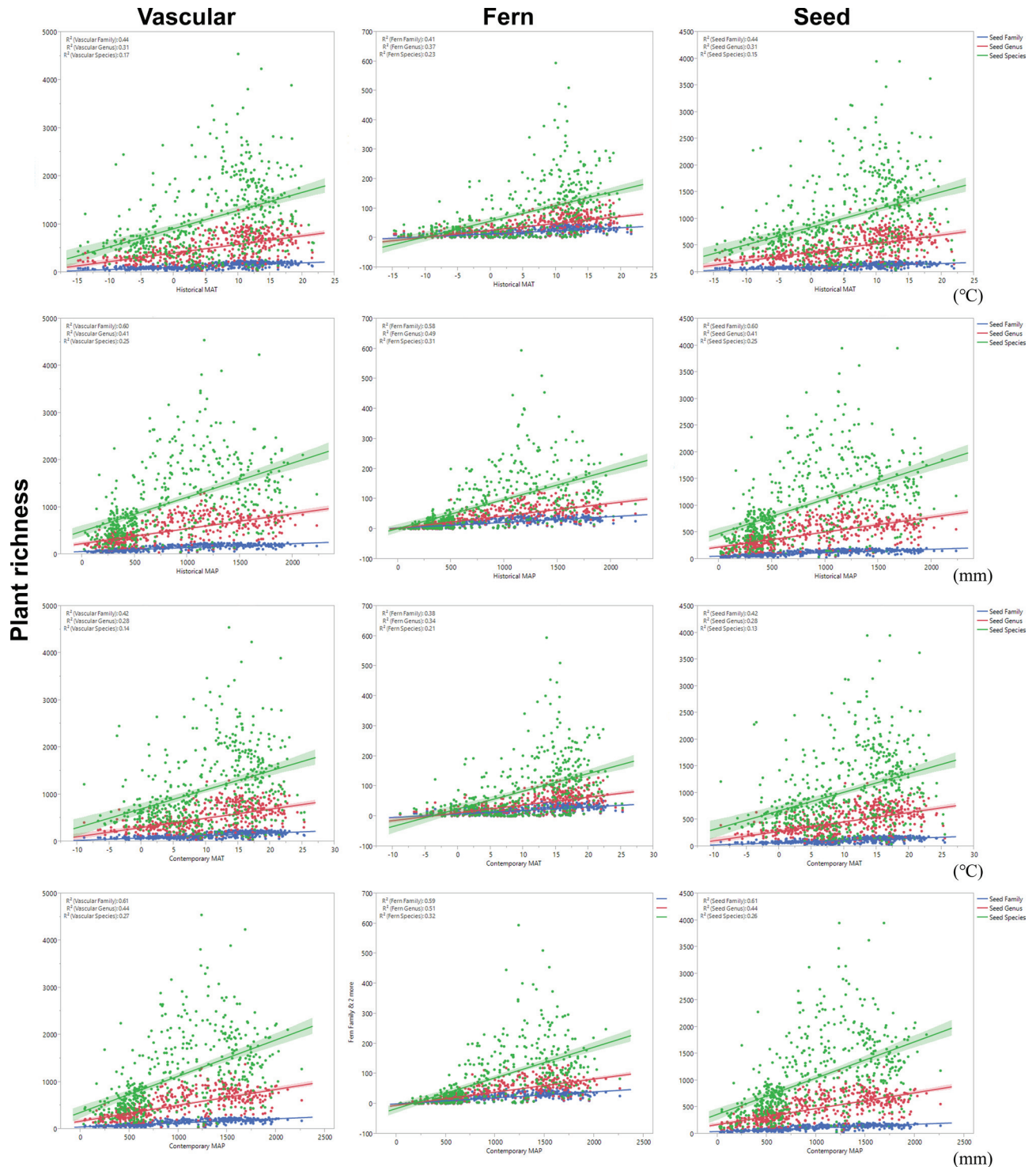
historical and contemporary climate can explain large-scale distributional patterns of plant richness. However, these effects may change across different taxonomic levels depending on the MAT and MAP (Figures 3, 4). There is ample evidence showing that Quaternary climatic change shaped the current patterns of plant richness and endemism across different regions of the world (*e.g.*, North America, Europe, and Africa; Svenning & Skov 2007, Normand *et al.* 2011, Svenning *et al.* 2015, Barnosky *et al.* 2016, Cotton *et al.* 2016). The dynamics of plant richness may not follow the climatic equilibrium (Svenning & Sandel 2013, Svenning *et al.* 2015). In addition, a shift to a new climatic equilibrium can cause time lags (Svenning & Sandel 2013, Svenning *et al.* 2015). Plant species may experience a slower response to changes in temperature than to those of precipitation, and in many places, the migration of these species has shown a time lag in response to temperature changes (Svenning & Sandel 2013, Normand *et al.* 2011, Svenning *et al.* 2015).

Plant community structure is strongly influenced by water under environmental change, and plant richness is strongly correlated with current water availability on a large scale (O'Brien 1998, O'Brien *et al.* 1998, Yang *et al.* 2011). For example, the distributional pattern of plant richness is an important link to late Cenozoic precipitation trends, and a positive correlation between the mean annual rainfall and woody plant richness can be observed in southern Africa (O'Brien 1998, O'Brien *et al.* 1998). Therefore, the response lags of plant richness to historical temperature and the ef-

fects of current precipitation on plant richness may drive the distributional pattern of plant richness at a large scale.

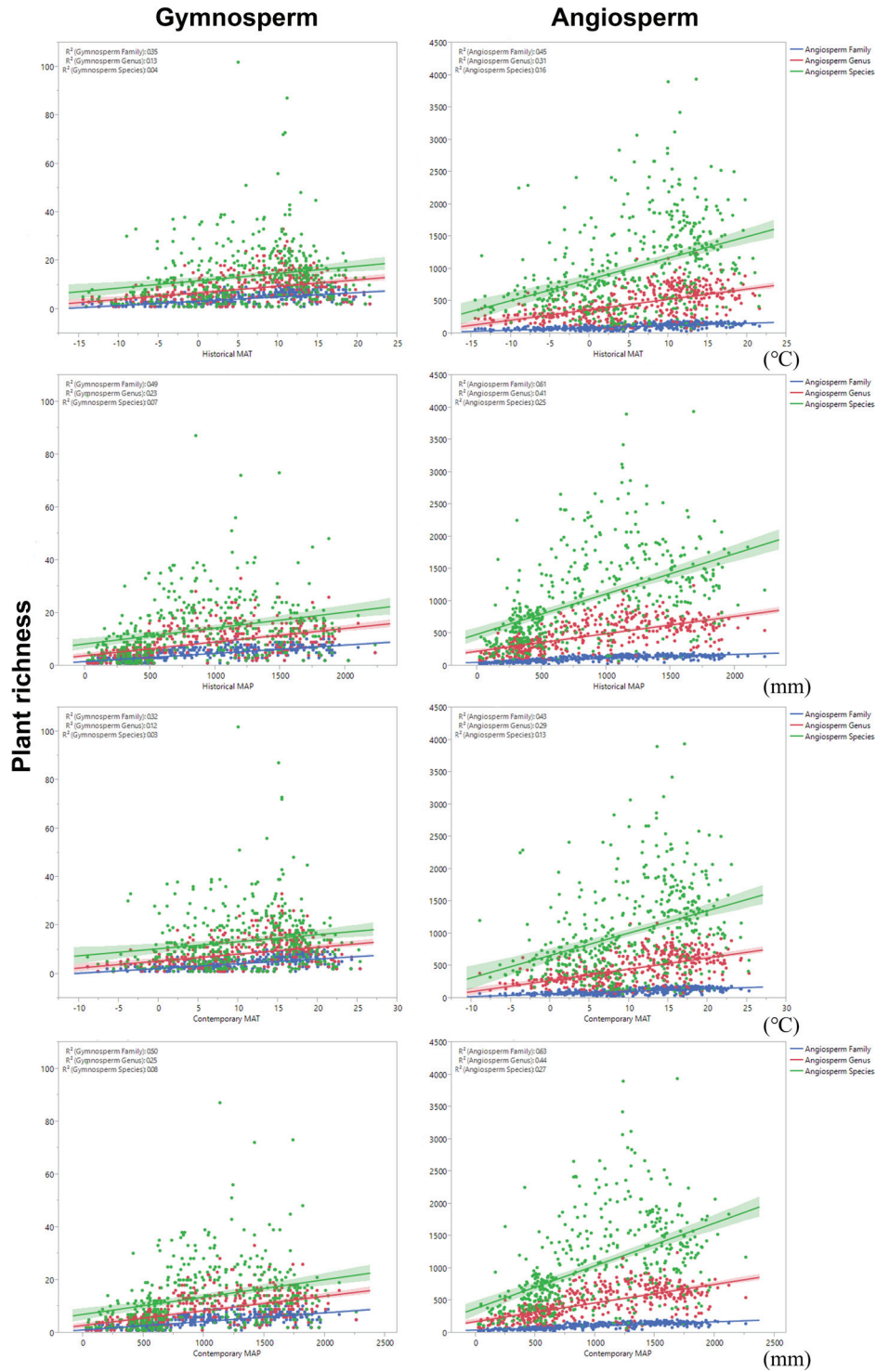
Blonder *et al.* (2018) found that paleoclimate (*i.e.*, MAT and MAP) is a better predictor of the spatial pattern of contemporary functional plant composition than contemporary climate predictors. The spatial pattern of contemporary functional plant composition is related to the distribution of plant richness at large scales (Petchey & Gaston 2002, Thompson *et al.* 2005, White *et al.* 2018). Furthermore, plant species diversity may change more than functional-trait diversity because high levels of trait-based redundancy imply that the loss of a particular species should not affect ecosystem functions because of the maintenance of other species with similar traits (Díaz & Cabido 2001, Petchey & Gaston 2006). Relationships between functional-trait diversity and plant richness can still exist at various spatial and temporal scales (Petchey & Gaston 2002, 2006, Kraft *et al.* 2015). Hence, historical MAT may have greater effects than contemporary MAT on the distributional pattern of plant richness, and contemporary MAP could also strongly affect the plant richness pattern.

The explanatory power of the historical and contemporary climate variables in regard to plant richness varied across the different taxonomic levels (Table 4; Figures 3, 4). Specifically, the historical and contemporary climate had the strongest explanatory power in terms of the family richness and the smallest explanatory power in regard to the species richness (Table 4; Figures 3, 4). The family taxonomic level can define the collective evolutionary distinctiveness of a set



**Figure 3.** Changes in the large-scale richness of vascular, fern, and seed plants as a function of historical and contemporary climate across different taxonomic levels. The lines associated with the points in each panel indicate the relationships between historical and contemporary climate and plant richness across different taxonomic levels (*i.e.*, family, genus, and species). Shaded areas over the dashed regression lines represent the 95 % confidence interval of the fitted values for each evaluated order. Values of  $R^2$  represent the adjusted  $R^2_{adj}$  (%) values from the OLS analysis, which indicate the explanatory power of historical and contemporary climate variables in regard to the large-scale distributional pattern of plant richness. We transferred the values of  $R^2_{adj}$  to Figure 3 based on the unit “%”. Plant richness represents the number of families, genera, and species. All the  $R^2_{adj}$  (%) values obtained from the OLS analysis were significant ( $P < 0.05$ ).





**Figure 4.** Changes in the large-scale richness of gymnosperm and angiosperm plants as a function of historical and contemporary climate across different taxonomic levels. The lines associated with the points in each panel indicate the relationships between historical and contemporary climate and plant richness across different taxonomic levels (i.e., family, genus, and species). Shaded areas over the dashed regression lines represent the 95 % confidence intervals of the fitted values for each evaluated order. Values of  $R^2$  represent the adjusted  $R^2_{adj}$  (%) values obtained from the OLS analysis, which indicate the explanatory power of historical and contemporary climates in regard to the large-scale distributional pattern of plant richness. We transferred the values of  $R^2_{adj}$  to Figure 4 based on the unit “%”. Plant richness represents the number of families, genera, and species. All the  $R^2_{adj}$  (%) values obtained from the OLS analysis were significant ( $P < 0.05$ ).

of species (Qian & Ricklefs 2007, Huang *et al.* 2016). Furthermore, species' abilities to thrive in an environment, resist and solve physiological problems, interact with other species and influence various ecosystem processes are determined by their functional traits (Díaz & Cabido 2001, Fonseca & Ganade 2001, Rosenfeld 2002, Kuebbing *et al.* 2018). In other words, while some species exhibit uncommon traits (functionally unique species), other species are functionally similar (*i.e.*, represent redundant species) within one specific family (Naeem 1998, Rosenfeld 2002). Hence, the effects of historical and contemporary climate on the large-scale distributional pattern of plant richness were found to be significant at the family level.

Furthermore, other recent environmental variables (*e.g.*, human influences and usage of land) may influence the distributional patterns of plant species richness at large scales (Kier *et al.* 2005, Gerstner *et al.* 2014). Such effects may escalate with increases in habitat areas and ranges (Lundholm 2009). The habitat areas and distributional ranges of plants are generally wider at the family level than at the species level (O'Brien *et al.* 1998, Huang *et al.* 2016). Therefore, the explanatory power of the historical and contemporary climate in regard to plant richness may rely on changes in taxonomic level (*i.e.*, family, genus, and species) due to changes in habitat areas and distributional ranges.

Our results indicate that the influence of climate on plant richness at large scales differs between non-seed and seed plants (Table 4 and Figure 3). Fossil plant records (*e.g.*, Dubiel 1987, Collinson 2001, 2002, Watkins & Cardelús 2012, Naugolnykh *et al.* 2016) indicate that paleoclimates have affected the large-scale distributional pattern of ferns, while current bioclimatic variables, mainly those related to humidity (as water is an essential medium for fern reproduction), are closely associated with the variation in fern community composition. The physiological requirements and relative habitat restrictions of fern plants make them more sensitive to climate change than seed plants, and the effects of climate on plant richness may therefore differ between fern and seed plants (Schneider *et al.* 2004, Peppe *et al.* 2014).

We found that the explanatory power of the historical and contemporary climate variables was higher for gymnosperm plant richness than for angiosperm richness (Table 4 and Figure 4). Such variation in explanatory power may be the result of evolutionary history and physiological adaptations to historical and contemporary climate (Wang *et al.* 2010, Yang *et al.* 2014, Lu *et al.* 2018, Xu *et al.* 2018). For instance, Lu *et al.* (2018) found that herbaceous plants usually have higher molecular substitution rates than woody plants, partly due to their shorter generation times, apparently enabling herbaceous species in China to adapt quickly in response to climate change through increased genetic divergence and higher speciation rates.

Environmental heterogeneity and precipitation are the most important predictors of the diversity patterns of gymnosperms, followed by historical temperatures (Lü *et al.* 2018). A number of gymnosperm plants are distributed mainly in western China (Lü *et al.* 2018), and there is a large difference in historical temperature and contemporary precipitation be-

tween eastern and western China (Qin *et al.* 2015, Lu *et al.* 2018, Lü *et al.* 2018). Furthermore, the temperature sensitivity of spring tree growth, water use, and successional strategies vary dramatically between the dominant angiosperm and gymnosperm plants (Bond 1989, Ma *et al.* 2016, Wan *et al.* 2017, Trugman *et al.* 2018). The differences in the variables correlated with plant richness between gymnosperm and angiosperm plants may be related to their evolutionary histories and physiological adaptations to historical temperature and contemporary precipitation (Lu *et al.* 2018, Lü *et al.* 2018). Hence, historical and contemporary climate influence the large-scale distributional patterns of gymnosperm and angiosperm plant richness to different extents.

Our study used protected area data to explore the effects of historical and contemporary climate on the large-scale distributional patterns of plant richness across different taxonomic levels, contributing to the conservation of plant diversity in China. China is the country/territory on Earth experiencing the greatest degree of land transformation (Liu *et al.* 2003, López-Pujol *et al.* 2006, Zhang *et al.* 2017). Based on our results that the historical climate can shape the large-scale distributional pattern of plant richness, we predict that it will take a long time for the plant diversity in China to recover if the plant richness is damaged. Furthermore, it will be necessary to use large-scale data from protected areas to assess the effects of climate change on plant diversity in protected areas around the world (Araújo *et al.* 2011, Wan *et al.* 2014, Keppel *et al.* 2015, Wan *et al.* 2018). Thus, plant diversity data from protected areas could be beneficial not only for scientists but also for decision makers and practitioners in other fields (Araújo *et al.* 2011, Wan *et al.* 2016, Zhang *et al.* 2017). Hence, future studies should pay attention to the strategic value of different protected areas in the context of the plant diversity they protect, especially considering the current trends of land transformation around the world.

In conclusion, the distributional patterns of plant richness at large scales could be predicted across different taxonomic levels after the assessment of paleoclimate and contemporary climate data. Pleistocene temperature and current precipitation effects were studied to understand plant richness patterns, and such effects were found to be most important at the family level. In particular, the historical and contemporary climate data were better correlated with fern plant richness than with seed plant richness. Understanding the effects of historical and contemporary climate on the large-scale distributional patterns of plant richness across various taxonomic levels may help guide predictions of future plant diversity and facilitate the conservation of plant diversity under climate change.

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## Supplementary material

Data on plant richness, mean annual temperature (MAT; °C) and mean annual precipitation (MAP; mm). The data on plant richness refer to different taxonomic levels (*i.e.*, family, genus, and species) based on the vascular, fern, seed, gymnosperm, and angiosperm plant groups.