



Determinants of richness patterns differ between rare and common species: implications for Gesneriaceae conservation in China

Yunpeng Liu , Zehao Shen, Qinggang Wang, Xiangyan Su, Wanjun Zhang, Nawal Shrestha, Xiaoting Xu  and Zhiheng Wang*

Department of Ecology, College of Urban and Environmental Sciences, Key Laboratory of Earth Surface Processes of Ministry of Education, Peking University, Beijing 100871, China

ABSTRACT

Aim Whether richness patterns and determinants are consistent between common and rare species remains controversial, and the answer is fundamental for the conservation of species in vulnerable habitats. Although effects of climate and geological history on species richness have been widely explored, their relative contribution among common and rare species is poorly understood. Here, using a valuable ornamental plant family Gesneriaceae, we evaluated how contemporary climate, habitat heterogeneity and long-term climate change affect the distribution of rare and common species. Additionally, we identified hotspots of Gesneriaceae diversity and evaluated its protection gap in China.

Location China.

Methods Distribution of Gesneriaceae was compiled at a spatial resolution of 50×50 km. Species were grouped as rare and common based on the number of grid cells they occupied, and their richness patterns and hotspots were estimated separately. Generalized linear models and Random Forest were used to compare effects of different factors on species richness.

Results Richness of Gesneriaceae peaked in south-western China. The Yunnan–Guizhou Plateau and Hengduan Mountains were identified as hotspots for overall and common species, while only the former was hotspot for rare species. Temperature seasonality, winter coldness and temperature change since the Last Glacial Maximum (LGM) dominated species richness patterns, but their relative effects differed between species range size. Temperature seasonality had strongest effects on richness of common species, whereas temperature change since the LGM was strongest for rare species. Neither current nor past precipitation affects richness patterns significantly.

Main conclusions Gesneriaceae species richness is strongly influenced by temperature changes. Specifically, rare and common species are primarily dominated by long- and short-term temperature changes, respectively. These findings suggest that most Gesneriaceae species may face high risk under future climate changes, and hence, more conservation efforts are urgently needed, especially in Yunnan–Guizhou Plateau, which is hotspot of rare species.

Keywords

biodiversity hotspots, biogeography, climate change, diversity pattern, endemism, Last Glacial Maximum, range size, winter coldness.

*Correspondence: Zhiheng Wang, Department of Ecology, College of Urban and Environmental Sciences, Key Laboratory of Earth Surface Processes of Ministry of Education, Peking University, Beijing 100871, China.
E-mail: zhiheng.wang@pku.edu.cn

INTRODUCTION

The large-scale pattern of species richness has intrigued ecologists and biogeographers since the time of Darwin (Huston, 1994). Studying the mechanisms of large-scale species richness patterns not only improves our understanding of the evolution of species but also enhances biodiversity conservation under global changes (Brown, 1999; Pennisi, 2005; Kreft & Jetz, 2007). It is generally accepted that contemporary climate (e.g. environmental energy, water condition and climate fluctuation) has strong explanatory power on patterns of species richness (Currie & Paquin, 1987; Currie, 1991; Svenning & Skov, 2007). Meanwhile, recent studies suggest that species richness patterns, especially those of rare species with low dispersal abilities and narrow distribution ranges, may be jointly influenced by the interaction between modern climate and long-term climate change (Svenning & Skov, 2007). However, the relative importance of contemporary and long-term climate change on species richness patterns is still controversial (Currie & Paquin, 1987; Currie, 1991; Svenning & Skov, 2007; Araújo *et al.*, 2008).

Geographic range size of species can significantly influence the patterns of species richness. Previous studies have shown that species richness patterns are generally determined by relatively few common species (i.e. wide-ranging species) (Jetz & Rahbek, 2002; Lennon *et al.*, 2004). Meanwhile, range size can also influence the relative importance of climatic heterogeneity at different temporal scales (Svenning & Skov, 2007), because species with different range size differ in their environmental requirements (Magurran & Henderson, 2003) and functional traits (Cornwell & Ackerly, 2010). However, some other studies have shown that both common and rare species are affected by the same environmental factors (Currie & Paquin, 1987; Siqueira *et al.*, 2012). This issue has been well studied on many vertebrate groups (Siqueira *et al.*, 2012; Katayama *et al.*, 2014), especially birds (Jetz & Rahbek, 2002; Lennon *et al.*, 2004). However, there are fewer studies on ornamentally valuable and threatened plant species with narrow climatic adaption in vulnerable habitats.

Gesneriaceae is a family originated in late Palaeocene/Eocene (Clark *et al.*, 2013), comprising perennial herbs, shrubs and small trees, and mainly distributed in tropical areas. The origination time and current distribution of Gesneriaceae suggests that the pattern of species richness of this family may be primarily determined by temperature. This family contains two subfamilies, Cyrtandroideae (ca. 1900 species) and Gesnerioideae (> 1000 species) (Perret *et al.*, 2013). Their habitats are mountain forests of mid-elevation regions with rocks or calcified soil (Li, 1996; Perret *et al.*, 2013). In China, the family Gesneriaceae is represented by a single subfamily Cyrtandroideae containing 525 species in 52 genera (Wei *et al.*, 2004). Flowers of Gesneriaceae are highly diversified and beautiful, so there are many ornamentals in this family (Wen & Li, 2006). However, floristic investigation

has shown that the Gesneriaceae species in China exhibit typical local endemism. Many species in this family are physiologically and morphologically specialized (Burt & Bokhari, 1973; Chautems, 2004; Herat & Theobald, 2008) and therefore occupy specific and narrower niches (Wei *et al.*, 2004; Kolehmainen & Mutikainen, 2007). Consequently, these species have very small population size (Wen & Li, 2006) and are likely to become endangered due to habitat destruction or overexploitation (Dai & Luo, 2009). Current ecological studies on this family have mainly focused on evaluation of potential endangerment and population dynamics of certain genera or species (Wen & Li, 2006), while few studies have explored the diversity pattern and its underlying mechanisms in the level of whole China (Zhang, 2012). Therefore, it is crucial to study the diversity pattern of this family, which will be conducive to the protection of this family in future (Li, 1996; Wei *et al.*, 2004; Wen & Li, 2006; Dai & Luo, 2009).

In this study, we aimed to (1) estimate species richness patterns and identify diversity hotspots of Gesneriaceae in China, (2) evaluate the relative effects of contemporary climate and past climate change on Gesneriaceae diversity, and (3) compare the primary determinants of species richness for rare and common species.

METHODS

Distribution of Gesneriaceae in China

County-level occurrence for the 525 species of Gesneriaceae in China was collected from several sources, including *Plants of Gesneriaceae in China* (Li & Wang, 2005), *Atlas of Woody Plants in China* (Fang *et al.*, 2011), the National Specimen Information Infrastructure (NSII, <http://www.nsii.org.cn/>, accessed in July 2015) and *Flora of China* volume 18 (Wang *et al.*, 1998). The nomenclature followed the *Flora of China*. The distribution records at only county level were compiled from these sources and were merged into a single database. To further improve the quality of the distribution data, the distribution map of each species was generated and examined carefully. The records of cultivation were removed from the database. The county-level distribution maps were then transferred into gridded distributions with a spatial resolution of 50 × 50 km. Grid cells with less than half of their area being inside China along the country border or being terrestrial along the coast were omitted. In total, 3794 distribution grid cells were used in our analyses.

The range size of species, defined as the number of grid cells occupied by a species, ranged from 1 to 755. The frequency distribution of species range size was strongly right-skewed (see Appendix Figure S2.4 in Supporting Information). In other words, most Gesneriaceae species have very narrow distribution ranges, while only a few have large ranges. The mean and median of species range size were 32 and 11 grid cells, respectively. To explore the differences in the richness patterns of rare and common species,

we ranked all species into an ascending order of range size. We then categorized the upper 50% and the lower 25% species as rare and common species, respectively, following previous studies (Araújo *et al.*, 2008). Based on this classification, we identified 251 species as rare species and 131 as common species. All rare species have range sizes smaller than 11 grid cells and represented 7.5% of the total records (1245 of 16,686 records), while common species have range sizes > 28 grid cells and represented 77.8% of the total records (12,987 of 16,686 records). In preliminary analysis, we initially selected 25% threshold for rare species, but it yielded very low number of records (405 of 16,686), which led to very low richness of rare species and might induce high uncertainties in the following statistical analysis. Moreover, we also used 50% and 50% as thresholds for rare and common species, and the results were all consistent with those based on 50% and 25% as thresholds for rare and common species (See supplementary materials Table S1.2). Therefore, we reported the results based on 50% and 25% as thresholds for rare and common species in the manuscript to facilitate comparison with previous findings.

Environmental factors

Habitat heterogeneity was measured by elevation range (Elev) and Shannon–Wiener index of vegetation diversity (VEGE). Elev measured the elevation range inside the grid cell. It was calculated from GTOPO30 digital elevation model (resolution: 3", resampled to 100 m × 100 m; available at http://eros.usgs.gov/#/Find_Data/Products_and_Data_Available/gtopo30_info). VEGE was calculated as: $VEGE = \sum [pi \times \ln(pi)]$, where pi represents the area proportion of the vegetation type i in area per grid cell. The vegetation map of China was extracted from Vegetation Atlas of China (1:1,000,000), in which the vegetation in China is classified into 573 formations (China Vegetation Map Editing Committee, 2001).

Mean annual temperature (MAT) and mean temperature of the coldest quarter (MTCQ) represented environmental energy. Annual precipitation (MAP), actual evapotranspiration (AET) and moisture index (MI) represented water availability. Annual range of temperature (ART) and precipitation seasonality (PSN) represented climate seasonality. Climate data were obtained from the WorldClim website (<http://www.worldclim.org>) at the spatial resolution of 1 arc-min, which were then transformed into a resolution of 50 × 50 km in ARCGIS 10.0 by calculating average of all data points within each grid cell. MI and AET were calculated using the method of Thornthwaite & Hare (1955).

The MAT and MAP in the Last Glacial Maximum (LGM) reconstructed by MIROC-ESM model (Watanabe *et al.*, 2011) were also obtained from the WorldClim website (<http://www.worldclim.org>). The data were similarly transformed to a resolution of 50 × 50 km in ARCGIS 10.0. We calculated the absolute values of the difference in MAT and MAP between the LGM and the present (i.e. $|MAT_{LGM} - MAT_{present}|$ and $|MAP_{LGM} - MAP_{present}|$) to

represent long-term climate change (T_{Ano} and P_{Ano}) since the Last Glacial Maximum, following previous studies (Sandel *et al.*, 2011). The velocity of MAT and MAP since the LGM (T_{Vel} and P_{Vel}) was also calculated following the method of Loarie *et al.* (2009), which measured the spatial distance that species must migrate to track climate change (Loarie *et al.*, 2009).

Data analyses

Species richness was estimated as the total number of species in each grid cell. Then, the complementary algorithm (Dobson *et al.*, 1997; Zhang *et al.*, 2015) was applied to identify the species richness hotspots of Gesneriaceae in China. Specifically, the algorithm first selects grid cells with the highest species richness. Then, it searches for grid cells with the next highest number of species that are not found in the selected ones. This process is repeated until all species are included. Following previous studies (Zhang *et al.*, 2015), the grid cells covering 90% of all species are finally identified as species richness hotspots.

The frequency distribution of species richness within grid cells (Fig. 3) is Poissonian, which is consistent with previous studies (Faraway, 2006; Wang *et al.*, 2012). Therefore, generalized linear models (GLMs) were used to analyse the relationships between species richness and environmental variables. Compared with GLM with Poissonian errors, GLM with quasi-Poissonian errors could compensate for the overdispersion in data (Crawley, 2007). Therefore, we used GLMs with quasi-Poissonian residuals to evaluate the richness–environment relationship. For each environmental factor, we developed a GLM and the explanatory power of the factor was estimated by the adjusted R^2_{adj} (%), which is calculated as follows: $R^2_{adj} (\%) = 100 \times (1 - (\text{residuals deviance} / \text{model DF}) / (\text{species richness deviance} / \text{residuals DF}))$.

To eliminate the effects of spatial autocorrelation in significance testing, we used modified t -test (Clifford *et al.*, 1989) to test the difference between the real and GLM-predicted richness patterns. The test creates an effective sample size that takes into account the spatial structure by introducing the estimated covariance matrixes for the distance classes (Dutilleul *et al.*, 1993; Dale & Fortin, 2009) and then corrects the correlation coefficient between the real and GLM-predicted richness. The GLM was considered as significant when the P value of the modified t -test was < 0.1. For comparison with the GLM analysis, we also used Random Forest containing all environmental predictors to evaluate the relative importance (represented by increase in node purity) of environmental predictors in explaining the patterns of species richness. Random Forest is not sensitive to spatial autocorrelation (Marmion *et al.*, 2009) and could also deal with nonlinear relationships between species richness and predictors (Breiman, 2001; Feng *et al.*, 2015).

All statistical analyses were carried out in R version 3.0 (<http://www.r-project.org/>).

RESULTS

The richness of Gesneriaceae species in China was higher in southern China than in northern China (Fig. 1a), where water and energy are limited. Complementary algorithm identified the Yunnan–Guizhou Plateau (23°–27° N; 100°–110° E) and Hengduan Mountains (22°–32°5′ N; 97°–103° E) as the two hotspots for overall and common species, which contained more than 90% of the Chinese Gesneriaceae species (Figs 2a,b & 3a,b). However, the hotspots for rare species were only located in the Yunnan–Guizhou Plateau (Figs 2c & 3c).

Generalized linear models showed that for overall species, temperature-related variables had stronger explanatory power than water-related variables. Specifically, ART was the strongest predictor and explained 42.78% ($P = 0.014$) of the variance, followed by MTCQ ($R^2 = 27.9\%$, $P = 0.053$), T_{Ano} ($R^2 = 25.71\%$, $P = 0.074$) and T_{Vel} ($R^2 = 23.46\%$, $P = 0.056$). The effects of elevation range and water availability were relatively lower than temperature-related variables (Table 1). Results based on Random Forest were consistent with those of GLMs: the four most important variables for the richness of overall species were ART, T_{Vel} , T_{Ano} and MTCQ (Fig. 3).

Common species contributed more to the spatial structure of species richness patterns than rare species as has been previously observed in other studies (Jetz & Rahbek, 2002; Lennon *et al.*, 2004). The best and second best predictors for the diversity pattern of common species remained ART ($R^2 = 39.71\%$, $P = 0.022$) and MTCQ ($R^2 = 25.74\%$, $P = 0.072$), followed by T_{Vel} ($R^2 = 23.60\%$, $P = 0.047$), which is consistent with the results for overall species (Table 1). However, the effect of T_{Ano} ($R^2 = 22.81\%$, $P = 0.115$) was not significant according to the modified *t*-test (Table 1). In contrast to overall and common species, both GLM and Random Forest analyses showed that T_{Ano} ($R^2 = 20.22\%$, $P = 0.026$) was the best predictor for the diversity patterns of rare species, followed by ART ($R^2 = 12.04\%$, $P = 0.035$) and MTCQ ($R^2 = 10.54\%$, $P = 0.044$). T_{Vel} , elevation range and water availability did not significantly explain the diversity patterns of rare species (Table 1). Results for rare species based on Random Forest were generally consistent with those of GLMs (Fig. 3).

DISCUSSION

Effects of long-term climate change and climate seasonality

According to climate stability hypothesis, climate fluctuation is a threat to species, and thus, stable climate tends to increase species richness of a region (Stevens, 1989). ART representing seasonal variation in temperature is one of the major factors for short-term climate stability and is strongly correlated with the species richness patterns of Gesneriaceae (Table 1). According to Stevens (1989), the ability of

environmental tolerances is lower in low latitudes than in high latitudes, because the temperature seasonality and daily change in low-latitude regions are not as high as they are in high-latitude regions. Stable climate also promotes the survival of species with narrow niches that tend to have narrow range size (Stevens, 1989). Similarly, Klopfer *et al.* suggest that smaller annual range of climatic condition reduces niche overlap and supports species with narrower niches (Klopfer, 1959; Klopfer & MacArthur, 1960, 1961). Meanwhile, the high temperature in low-latitude region may shorten generation time and accelerate speciation, leading to more new species (Rohde, 1992; Allen *et al.*, 2006). These findings explain why most of the rare species were constrained in southern China where annual range of temperature is low.

We found that temperature anomaly (T_{Ano}) can be an important factor for overall species and is even the best predictor for rare species (Fig. 3 and Table 1). Meanwhile, temperature velocity (T_{Vel}) has significant effects on the richness of overall and common species (Table 1). According to Milankovitch cycles, glacial cycle forced by astronomical cycles affects climate (especially temperature) on a time-scale of 20–100 ka and leads to large changes in species' geographic distributions and evolution (Bennett, 1990; Webb & Bartlein, 1992). The time-scale of Milankovitch cycles (10–100 ka) is much shorter than most species' age (1–30 Ma) (Dynesius & Jansson, 2000). Consequently, Milankovitch cycles provide strong environmental filtering effect during the species evolutionary process (Bennett, 1990; Dynesius & Jansson, 2000; Mittelbach *et al.*, 2007). During the LGM (25–15 ka), the glaciers covered the largest land area and sea level was much lower than the present. The temperature change from this period to the present is one of the strongest climate changes in the history of the Quaternary, which has significantly affected modern plant diversity patterns (Sandel *et al.*, 2011). The adaptation to this long-term climate shifts is mainly driven by Darwinian natural selection (Bennett, 1990), and regions with high temperature fluctuation will select species with strong dispersal ability or 'generalists' (Sandel *et al.*, 2011). Species with low climatic tolerances or those that are not able to timely rearrange themselves geographically in response to climatic fluctuation (e.g. most rare species) will be filtered out when they spread into areas with high climate fluctuation (Svenning & Skov, 2007).

Our analysis revealed that the LGM-to-present temperature change (T_{Ano}) exhibits marked geographic variation. The two hotspots of Gesneriaceae, that is the Yunnan–Guizhou Plateau and Hengduan Mountains, have low level of temperature anomaly (see Figure S2.1). Therefore, it is possible that many Gesneriaceae species (especially the rare and endemic ones) surviving in these regions did not face extreme environmental stress due to stable climate condition, which largely prevented their immigration as well as change in adaptive strategies.

Recent studies suggest that dispersal via range shift (Parmesan & Yohe, 2003) is one of the most important ways that species respond to climatic changes (Hof *et al.*,

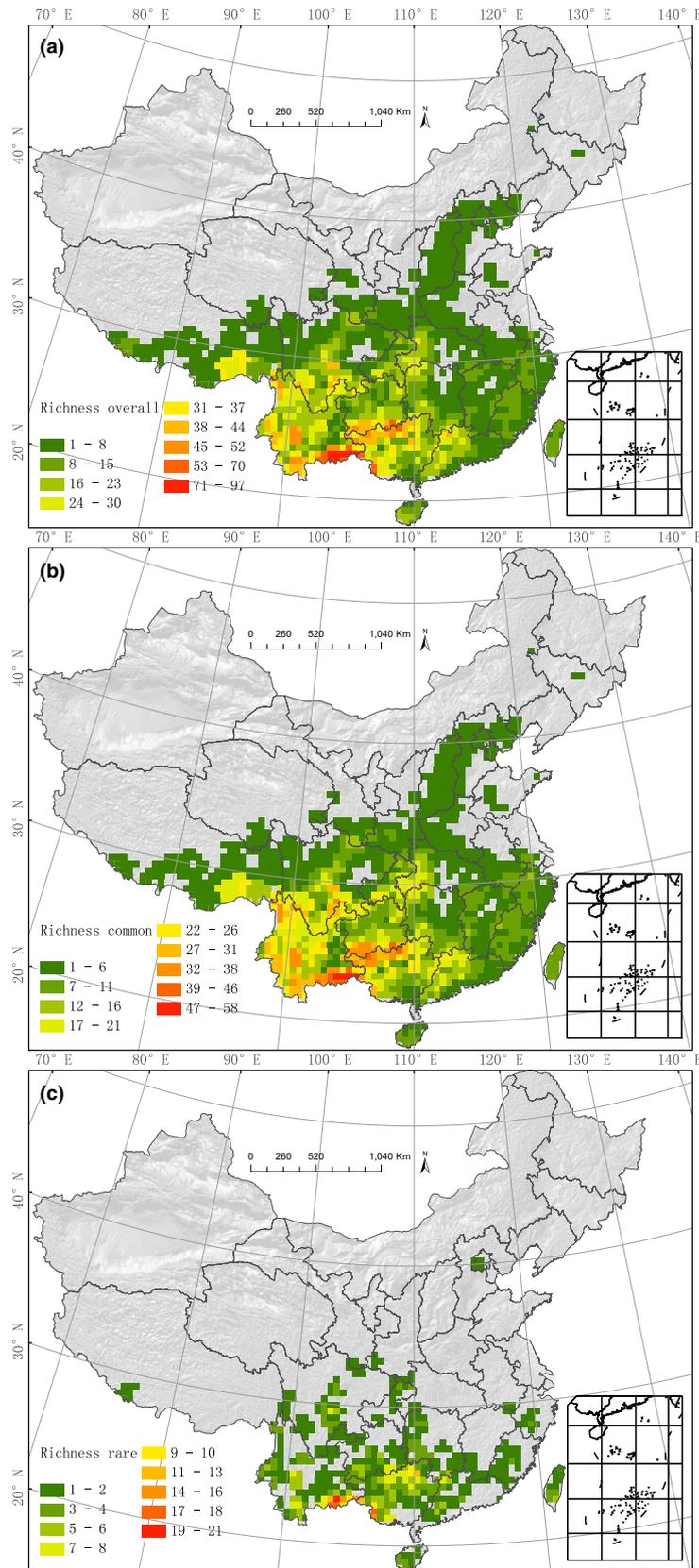


Figure 1 Gesneriaceae diversity in China: (a) all Gesneriaceae species, (b) common species, (c) rare species. All of the distribution maps were compiled with equal area projection (Asia North Albers cubic equal area projection) in ARCGIS 10.0 (ESRI, Inc.). [Colour figure can be viewed at wileyonlinelibrary.com]

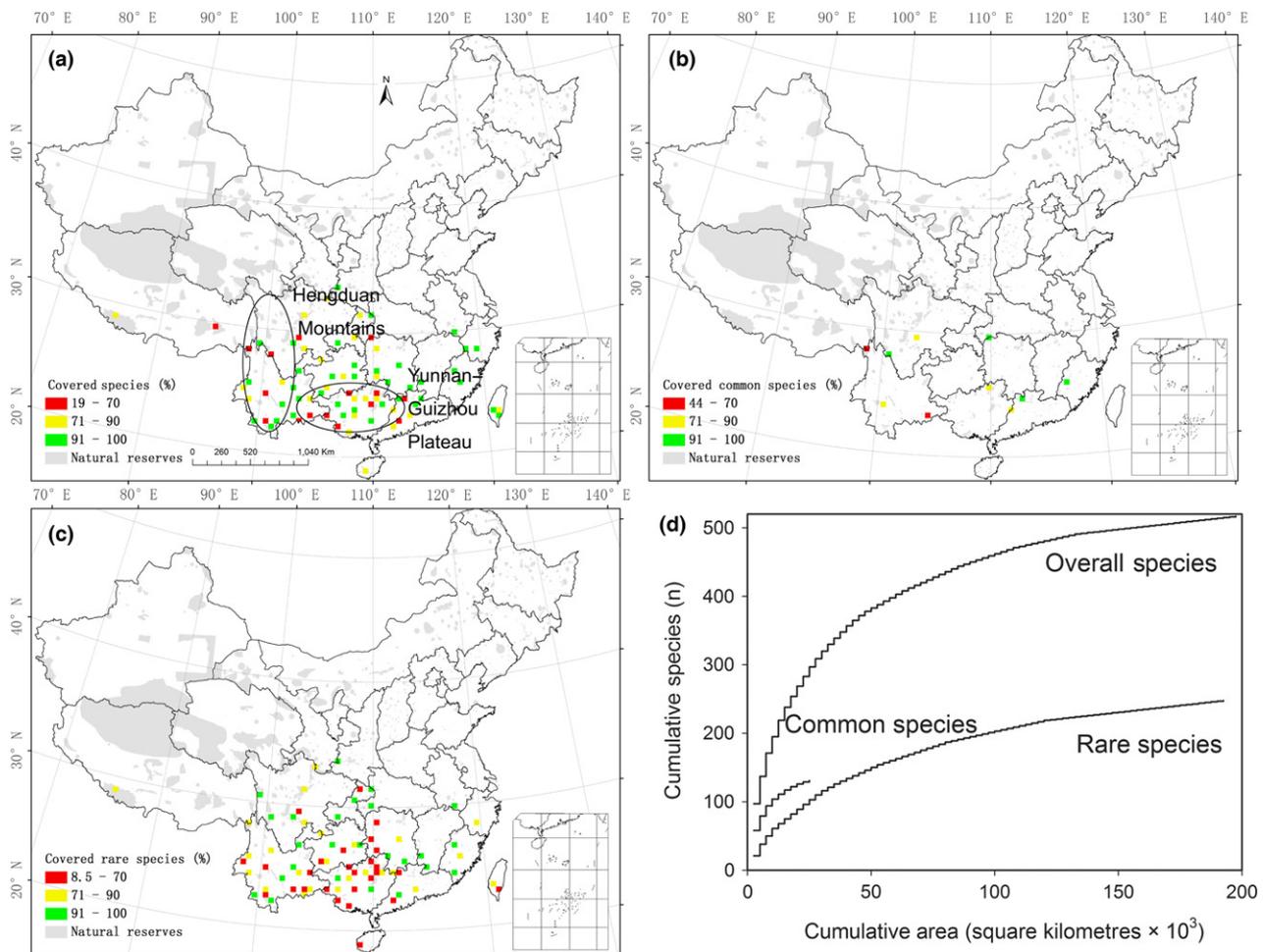


Figure 2 Hotspots of Gesneriaceae richness among different geographic range sizes based on the complementary algorithm. (a) Overall species, (b) common species, (c) rare species. The colour gradients indicate the proportion of species selected by the complementary algorithm, and regions with red and yellow spot are identified as hotspots. The grey shade represents the current nature reserves in China. (d) The relationship between the cumulative area of land sampled and the cumulative number of species that are included. All of the distribution maps were compiled with equal area projection (Asia North Albers cubic equal area projection) in ARCGIS 10.0 (ESRI, Inc.). [Colour figure can be viewed at wileyonlinelibrary.com]

2011). However, most of Gesneriaceae species are rare (Appendix Fig. S1.4) and have very small population sizes (Wen & Li, 2006) and narrow niches (Welander, 1984; Ren *et al.*, 2003; Wang & Cronk, 2003; Wei *et al.*, 2004). Moreover, the habitats of most Gesneriaceae species are highly associated with special bedrock (e.g. limestone soil matrix) and isolated. These ecological characteristics limit their range expansion and thus lower their ability to track both past and future climate changes via dispersal. It is noteworthy that current global warming is the fastest in the last 50 Ma as suggested by previous studies (Solomon, 2007), which is 10 times faster than that since the Last Glacial Maximum (IPCC, 2007). Moreover, the greatly modified landscapes by human activity will also inhibit dispersal for many species, requiring them to detour around human-created barriers and land use change. These previous findings together with our results suggest that Gesneriaceae species face severe challenges under future global changes.

Effects of winter coldness on species diversity

Our results indicated that winter coldness (represented by MTCQ) was the second best predictor in explaining species richness patterns. Winter temperature in northern China is comparatively low (usually below 0 °C), and mean annual temperature is 8–15 °C. This will likely discourage Gesneriaceae to spread northwards. Freezing tolerance hypothesis (also called tropical niche conservatism hypothesis) suggests that species richness–climate relationship is rooted in their ancestral niche (Romdal *et al.*, 2013). This hypothesis predicts that winter coldness plays more important roles in the dispersal of tropical species than temperate species (Wang *et al.*, 2011). The origination of Gesneriaceae can be dated back to late Palaeocene/Eocene (Clark *et al.*, 2013). This period represents one of the warmest periods in the earth's history in the last 100 Ma. Therefore, the origin environment may likely force the evolution of a tropical lineage

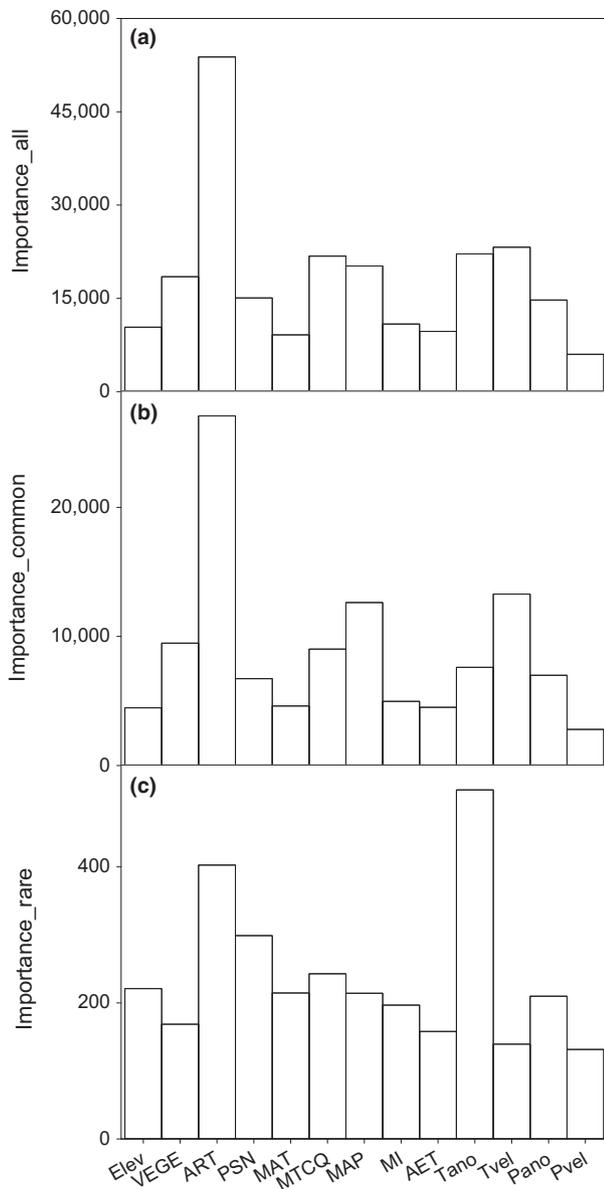


Figure 3 Results of Random Forest models. Importance values (y -axis) are represented by the increase in node purity. Abbreviations of variables: Elev, elevation range; VEGE, Shannon–Wiener index of vegetation diversity; ART, annual range of temperature; PSN, precipitation seasonality (coefficient of variation); MAT, mean annual temperature; MTCQ, mean temperature of the coldest quarter; MAP, mean annual precipitation; MI= moisture index based on the method of Thornthwaite & Hare (1955); AET, actual evapotranspiration; T_{Ano} , MAT anomaly; T_{Vel} , MAT velocity; P_{Ano} , MAP anomaly; P_{Vel} , MAP velocity.

with low tolerance for coldness, which plays an important role in determining the richness pattern of Gesnerioideae. Meanwhile, based on fossil flora of the Northern Hemisphere, Chaney (1940) suggested that during Eocene, the northern boundary of tropical and subtropical plants in the Northern Hemisphere advanced northwards (Chaney, 1940). At present, many Gesneriaceae species (including all 25

endemic genera in China) are located in the Eocene tropics (Li, 1996), and this also suggests that the ancestors of this group were well adapted to tropical climate, but not temperate climate. Winter coldness therefore significantly limits the northward distribution of this group because of their tropical niche conservatism.

These findings are consistent with previous studies on the physiology of Gesneriaceae species. For example, previous physiological study on genus *Titanotrichum* (Gesneriaceae) has shown that the flowering inflorescences do not predominate over bulbil inflorescences (i.e. vegetative growth) until temperature is increased to 23 °C, and seed propagation capacity of plants is inhibited by low temperature (Wang & Cronk, 2003). Similarly, another study on genus *Aeschynanthus* (Gesneriaceae) found that low temperature delayed the time of the first flower and eventually decreased the proportion of flowering plants of this genus in the local floras (Welander, 1984). These studies suggest that Gesneriaceae species have difficulties to colonize regions with low winter temperature due to the effects of winter temperature on reproduction.

Effects of geographic range size on species richness patterns

Notably, the relative importance of long-term climate change and climate seasonality is different. Existing studies have shown that geographic patterns in species richness are mainly contributed by common (wide-ranging) species (Jetz & Rahbek, 2002; Lennon *et al.*, 2004) because the larger number of distribution records of common species has a disproportionate contribution to the species richness counts. Our study showed similar results that overall and common species share similar patterns of species richness and their most important explanatory variables are contemporary climate, including ART and MTCQ. In contrast, temperature anomaly is the strongest predictor for the diversity of rare species, and this is a major and important deviation from common species.

Long-term climate stability is able to preserve more genotypes that control specialized adaptation. These genotypes usually indicate species with low vagility (low dispersal ability and propensity) (Jansson, 2003), and therefore, such species are more likely to have small range sizes (Dynesius & Jansson, 2000; Jansson, 2003). Using distribution data of 55 tree species in the non-glaciated parts of Europe, Svenning & Skov (2007) found that trees with restricted distributions failed to fully occupy climatically suitable areas during the post-LGM range expansions due to lack of dispersal abilities (Svenning & Skov, 2007; Sandel *et al.*, 2011). Thus, it is hard for rare species to spread out of their hotspots, even in the presence of appropriate habitats elsewhere (Dynesius & Jansson, 2000; Svenning, 2003), and this can particularly explain the reduced correlation between modern climate gradients and species richness patterns. Most rare species in Gesneriaceae exhibit local endemism (Ren *et al.*, 2003; Wei *et al.*, 2004). Hence, compared

Table 1 The coefficients of determination (R^2_{adj} , %) of the generalized linear models (GLMs) between species richness of Gesneriaceae and selected climatic variables. Modified *t*-test (Dutilleul *et al.*, 1993) was used to examine the significance for all variables. * $P < 0.1$; ** $P < 0.05$. Species richness was log10-transformed prior to analyses. The coefficients of determination (R^2_{adj}) have been adjusted for the number of variables in each model to make them comparable.

No. of species	Overall			Common			Rare		
	R^2_{adj}	Slope	SE	R^2_{adj}	Slope	SE	R^2_{adj}	Slope	SE
<i>Heterogeneity</i>									
Elev (m)	4.96	0.0002	1.00E-05	5.17	0.0002	1.00E-05	0.57	-0.0001	3.00E-05
VEGE	11.31**	0.6761	1.59E-02	11.77**	0.6377	1.81E-02	0.11	0.0618	6.50E-02
<i>Climatic seasonality</i>									
ART (°C)	42.78**	-0.1236	1.55E-03	39.71**	-0.1091	1.74E-03	12.04**	-0.0735	7.37E-03
PSN (mm)	1.08	-0.0048	3.70E-04	1.53	-0.0053	4.20E-04	0.34	0.0028	1.65E-03
<i>Environmental energy</i>									
MAT (°C)	15	0.0658	1.43E-03	13.73	0.0575	1.58E-03	8.29*	0.0535	6.87E-03
MTCQ (°C)	27.90*	0.077	1.21E-03	25.74*	0.0677	1.35E-03	10.54**	0.0517	5.75E-03
<i>Water availability</i>									
MAP (mm)	12.01	0.0007	2.00E-05	10.92	0.0006	2.00E-05	1.98	0.0003	7.00E-05
MI (unitless)	8.4	0.006	1.50E-04	8.62	0.0057	1.70E-04	0.12	-0.0007	7.50E-04
AET (mm)	10.47	0.0014	3.00E-05	8.85	0.0012	4.00E-05	6.44	0.0011	1.50E-04
<i>Historic climate change</i>									
T_{Ano} (°C)	25.71*	0.4052	6.36E-03	22.81	0.35	7.13E-03	20.22**	0.3756	3.00E-02
T_{Vel} (m yr ⁻¹)	23.46*	-0.0024	5.00E-05	23.6**	-0.0021	6.00E-05	1.82	-0.0008	2.30E-04
P_{Ano} (mm)	0.47	0.0002	3.00E-05	2.05	0.0004	3.00E-05	6.38	-0.0005	7.00E-05
P_{Vel} (m yr ⁻¹)	3.38	-0.0065	3.20E-04	3.14	-0.0055	3.50E-04	0.25	-0.0023	1.67E-03

Elev, elevation range; VEGE, Shannon–Wiener index of vegetation diversity; ART, annual range of temperature; PSN, precipitation seasonality (coefficient of variation); MAT, mean annual temperature; MTCQ, mean temperature of the coldest quarter; MAP, mean annual precipitation; MI, moisture index based on the method of Thornthwaite & Hare (1955); AET, actual evapotranspiration; T_{Ano} , MAT anomaly; T_{Vel} , MAT velocity; P_{Ano} , MAP anomaly; P_{Vel} , MAP velocity.

to ART, T_{Ano} was a superior explanatory factor for rare species, which means there might be a low range filling in rare species of Gesneriaceae. The different effects of T_{Ano} and T_{Vel} on rare and common species richness may also suggest that rare Gesneriaceae species may not be able to track climate changes due to their low dispersal ability and their special requirement for limestone soil matrix (Welder, 1984; Ren *et al.*, 2003; Wang & Cronk, 2003; Wei *et al.*, 2004). Similarly, previous studies found that the distributions of rare species of European reptiles and amphibians (Araújo *et al.*, 2008), plants (Normand *et al.*, 2011), insects (Hortal *et al.*, 2011) and Chinese woody plants (Wang *et al.*, 2012) have not tracked the climate changes since the LGM due to dispersal limitation. Together, these findings suggest that rare species may face higher extinction risks induced by climate change than common species. Meanwhile, a recent study on the community-level thermal tolerance of ocean fish and invertebrate species found that the sea surface temperature exceeds the current community temperature index (CTI) in tropical/subtropical oceans and future warming may lead to elevated environmental temperature relative to CTI (Stuart-Smith *et al.*, 2015). Due to the difficulties in tracking climate changes and lower thermal breadth, rare species may therefore suffer more from the increase in environmental temperature.

Effects of elevation range and water availability

In our study, explanatory power of elevation range was very low for all range size categories, especially for rare species, suggesting that elevation range may not be a critical driving factor of Gesneriaceae species richness (Table 1). As MTCQ was the limiting factor, it indicates that Gesneriaceae species mostly prefer comparatively warmer habitats, and hence, high-elevation region with cool climate is probably not favourable for the distribution of this group. Therefore, our results did not show a significant effect of elevation range on diversity of Gesneriaceae species.

Effects of water availability and precipitation seasonality on diversity patterns were relatively weak compared to energy. A possible reason might be that the demand for water shows obvious differences among species in this family. For example, some species need high moisture for growth, while others can be highly resistant to drought (Wei *et al.*, 2004). These differences in water utilization strategy among various species could be attributed to their distribution in variable habitats.

Geological differences between two hotspots of Gesneriaceae

We found two distribution centres for common species, both located in south-west China (Fig. 2b,c, also see Fig. 1b,c).

The first diversity centre was located in the Yunnan–Guizhou Plateau and the second in Hengduan Mountains. However, the diversity of rare species only peaked in the former. These hotspots contained most grid cells with over 40 species per grid cell and covered about 90% of the total species richness.

The elevation range is higher in Hengduan Mountains than in the Yunnan–Guizhou Plateau (see Appendix Figure S2.1). However, this difference in elevation range seems to have no effect in the diversity patterns of common and rare species (Table 1). The differences in geological history between these two regions could possibly be the reason for uneven accumulation of species with variable range sizes.

Ancestral range analyses and molecular dating indicate that the ancestors of Gesneriaceae diverged from its sister clade during the Late Cretaceous (Perret *et al.*, 2013). The Yunnan–Guizhou Plateau might be an important diversification centre for Gesneriaceae and many other groups of angiosperms in the Northern Hemisphere during this period (Wu & Wang, 1957). Hence, it is possible that strong evolutionary radiation of Gesneriaceae might have taken place in the Yunnan–Guizhou Plateau, while Hengduan Mountains suffered strong Himalayan orogeny and experienced more glaciation than the Yunnan–Guizhou Plateau (Wu, 1988; Li & Li, 1993). Therefore, higher concentration of rare species in the Yunnan–Guizhou Plateau can be linked to a long-term climate stability considering the fact that rare species are highly sensitive to climate change events.

Gesneriaceae family contains many very rare and valuable ornamental species. However, in the recent days, most species of this family are facing high risk of extinction due to overexploitation. The two hotspots of species diversity identified here therefore could serve as conservation priorities for the future conservation of Gesneriaceae species. More importantly, our analysis suggested that the hotspots of Gesneriaceae diversity differ between range sizes. Both Yunnan–Guizhou Plateau and Hengduan Mountains are hotspots for the common species and the whole family, while rare species are only located in the former (Fig. 2b,c, also see Fig. 1b,c). This discrepancy in hotspots of varying range sizes may be related to different geological history of the two regions and is vital for conservation for this family.

It is noteworthy that the planning of the existing network of nature reserves in China is mainly based on total species diversity, and rarely considers the difference in the hotspots of rare vs. common species. For example, Hengduan Mountains harbours a larger number of plant species than the Yunnan–Guizhou Plateau, leading to more nature reserves in the former (see Appendix Figure S2.3 and Table S1.3). However, many highly specialized Gesneriaceae species are restricted to the karst habitat in the Yunnan–Guizhou Plateau, which suggests that there is a serious protection gap for this family in this area. Therefore, more conservation effort in the karst habitat in the Yunnan–Guizhou Plateau is needed in future.

CONCLUSIONS

The south-western China harbours most species of Gesneriaceae and the Yunnan–Guizhou Plateau and Hengduan Mountains are two hotspots of this family, which can serve as conservation priorities for future conservation planning. Climatic stability, winter coldness and long-term climate change were the most important determinants for the diversity patterns of this group, while the relative importance of contemporary climate and long-term climate change on species diversity varies across species with different range size. The importance of LGM-to-present climate change on species diversity is greater for rare species than for common species, indicating that rare species are probably still associated with their glacial refugia.

Our study indicated that Gesneriaceae species are sensitive to climatic fluctuation at both short- and long-term scales. With rapid economic proliferation and urbanization, intense exploration on mountains and constant land use change in south-west China, the habitats of Gesneriaceae and other rare species are continuously being destructed. Global climate change in future is also likely to expose Gesneriaceae species to high extinction risk due to their difficulties to track climate changes and their special requirement for limestone soil matrix. Although the Yunnan–Guizhou Plateau harbours more rare species than the Hengduan Mountains, there are less nature reserves in the former, which indicates that more conservation effort is urgently needed in the Yunnan–Guizhou Plateau. Studies such as this are very crucial to understanding the mechanism driving diversity of rare species and hence creating action plans to sustainably conserve the depleting resources.

ACKNOWLEDGEMENTS

We thank Franz Essl and two referees for their constructive comments. This work was supported by the National Natural Science Foundation of China (#31522012, #31470564, #31321061), Chinese Academy of Sciences-Peking University Pioneer Collaboration Team and the Thousand Young Talents Program and The Recruitment Program of Global Youth Experts.

REFERENCES

- Allen, A.P., Gillooly, J.F., Savage, V.M. & Brown, J.H. (2006) Kinetic effects of temperature on rates of genetic divergence and speciation. *Proceedings of the National Academy of Sciences USA*, **103**, 9130–9135.
- Araújo, M.B., Nogués-Bravo, D., Diniz-Filho, J.A.F., Haywood, A.M., Valdes, P.J. & Rahbek, C. (2008) Quaternary climate changes explain diversity among reptiles and amphibians. *Ecography*, **31**, 8–15.
- Bennett, K.D. (1990) Milankovitch cycles and their effects on species in ecological and evolutionary time. *Paleobiology*, **16**, 11–21.

- Breiman, L. (2001) Random forests. *Machine Learning*, **45**, 5–32.
- Brown, J.H. (1999) Macroecology: progress and prospect. *Oikos*, **87**, 3–14.
- Burtt, B.L. & Bokhari, M.H. (1973) Studies in the Gesneriaceae of the Old World. xXXVI. foliar sclereids in New Guinea and Pacific Cymandra. *Notes from the Royal Botanic Garden Edinburgh*.
- Chaney, R.W. (1940) Tertiary forests and continental history. *Geological Society of America Bulletin*, **51**, 469–488.
- Chautems, A. (2004) Gesneriaceae. *Illustrated handbook of succulent plants dicotyledons* (ed. by U. Eggli), pp. 272–285. Springer, Berlin, Germany.
- China Vegetation Map Editing Committee (2001) *Vegetation atlas of China*. Science Press, Beijing.
- Clark, J.L., Weber, A. & Möller, M. (2013) A new formal classification of Gesneriaceae. *Selbyana*, **21**, 68–94.
- Clifford, P., Richardson, S. & Hémon, D. (1989) Assessing the significance of the correlation between two spatial processes. *Biometrics*, **45**, 123–134.
- Cornwell, W.K. & Ackerly, D.D. (2010) A link between plant traits and abundance: evidence from coastal California woody plants. *Journal of Ecology*, **98**, 814–821.
- Crawley, M.J. (2007) *The R book*. Wiley Publishing, London, UK.
- Currie, D.J. (1991) Energy and large-scale patterns of animal- and plant-species richness. *The American Naturalist*, **137**, 27–49.
- Currie, D.J. & Paquin, V. (1987) Large-scale biogeographical patterns of species richness of trees. *Nature*, **329**, 326–327.
- Dai, Z.-F. & Luo, G.-Y. (2009) Resources of wild Gesneriaceae ornamental plants in tropical region of China. *Guizhou Agricultural Sciences*, **1**, 13–15.
- Dale, M.R.T. & Fortin, M.J. (2009) Spatial autocorrelation and statistical tests: some solutions. *Journal of Agricultural Biological & Environmental Statistics*, **14**, 188–206.
- Dobson, A.P., Rodriguez, J.P., Roberts, W.M. & Wilcove, D.S. (1997) Geographic distribution of endangered species in the United States. *Science*, **275**, 550–553.
- Dutilleul, P., Clifford, P., Hémon, D. & Richardson, S. (1993) Modifying the t test for assessing the correlation between two spatial processes. *Biometrics*, **49**, 305–314.
- Dynesius, M. & Jansson, R. (2000) Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. *Proceedings of the National Academy of Sciences USA*, **97**, 9115–9120.
- Fang, J., Wang, Z. & Tang, Z. (2011) *Atlas of woody plants in China: distribution and climate*. Higher Education Press, Springer, Berlin & Beijing.
- Faraway, J.J. (2006) *Extending the linear model with R: generalized linear, mixed effects and nonparametric regression models*. CRC Press, Boca Raton.
- Feng, G., Mao, L., Sandel, B., Swenson, N.G. & Svenning, J.C. (2015) High plant endemism in China is partially linked to reduced glacial-interglacial climate change. *Journal of Biogeography*, **43**, 145–154.
- Herat, R.M. & Theobald, W.L. (2008) Comparative studies of vegetative anatomy and morphology of the Gesneriaceae of Sri Lanka. *Botanical Journal of the Linnean Society*, **78**, 285–298.
- Hof, C., Levinsky, I., Araújo, M.B. & Rahbek, C. (2011) Rethinking species' ability to cope with rapid climate change. *Global Change Biology*, **17**, 2987–2990.
- Hortal, J., Diniz-Filho, J.A.F., Bini, L.M., Rodríguez, M.Á., Baselga, A., Nogués-Bravo, D., Rangel, T.F., Hawkins, B.A. & Lobo, J.M. (2011) Ice age climate, evolutionary constraints and diversity patterns of European dung beetles. *Ecology Letters*, **14**, 741–748.
- Huston, M.A. (1994) *Biological diversity: the coexistence of species on changing landscapes*. Cambridge University Press, Cambridge, UK.
- IPCC. (2007) *Climate change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.
- Jansson, R. (2003) Global patterns in endemism explained by past climatic change. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 583–590.
- Jetz, W. & Rahbek, C. (2002) Geographic range size and determinants of avian species richness. *Science*, **297**, 1548–1551.
- Katayama, N., Amano, T., Naoe, S., Yamakita, T., Komatsu, I., Takagawa, S., Sato, N., Ueta, M. & Miyashita, T. (2014) Landscape heterogeneity-biodiversity relationship: effect of range size. *PLoS ONE*, **9**, e93359.
- Klopfer, P.H. (1959) Environmental determinants of faunal diversity. *The American Naturalist*, **93**, 337–342.
- Klopfer, P.H. & MacArthur, R.H. (1960) Niche size and faunal diversity. *The American Naturalist*, **94**, 293–300.
- Klopfer, P.H. & MacArthur, R.H. (1961) On the causes of tropical species diversity: niche overlap. *The American Naturalist*, **95**, 223–226.
- Kolehmainen, J. & Mutikainen, P. (2007) Population stage structure, survival and recruitment in the endangered East African forest herb *Saintpaulia*. *Plant Ecology*, **192**, 85–95.
- Kreft, H. & Jetz, W. (2007) Global patterns and determinants of vascular plant diversity. *Proceedings of the National Academy of Sciences USA*, **104**, 5925–5930.
- Lennon, J.J., Koleff, P., Greenwood, J.J.D. & Gaston, K.J. (2004) Contribution of rarity and commonness to patterns of species richness. *Ecology Letters*, **7**, 81–87.
- Li, Z. (1996) The geographical distribution of the subfamily Cyrtandroideae. *endl. emend. burtt* (Gesneriaceae). *Acta Phytotaxonomica Sinica*, **4**, 341–360.
- Li, X.-W. & Li, J. (1993) A preliminary floristic study on the seed plants from the region of Hengduan Mountain. *Acta Botanica Yunnanica*, **15**, 217–231.
- Li, Z. & Wang, W. (2005) *Plants of Gesneriaceae in China*. Henan Science and Technology Publ, Zhengzhou, China.

- Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B. & Ackerly, D.D. (2009) The velocity of climate change. *Nature*, **462**, 1052–1055.
- Magurran, A.E. & Henderson, P.A. (2003) Explaining the excess of rare species in natural species abundance distributions. *Nature*, **422**, 714–716.
- Marmion, M., Luoto, M., Heikkinen, R.K. & Thuiller, W. (2009) The performance of state-of-the-art modelling techniques depends on geographical distribution of species. *Ecological Modelling*, **220**, 3512–3520.
- Mittelbach, G.G., Schemske, D.W., Cornell, H.V., Allen, A.P., Brown, J.M., Bush, M.B., Harrison, S.P., Hurlbert, A.H., Knowlton, N. & Lessios, H.A. (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, **10**, 315–331.
- Normand, S., Ricklefs, R.E., Skov, F., Bladt, J., Tackenberg, O. & Svenning, J.C. (2011) Postglacial migration supplements climate in determining plant species ranges in Europe. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 3644–3653.
- Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.
- Pennisi, E. (2005) What determines species diversity? *Science*, **309**, 90.
- Perret, M., Chautems, A., Araujo, A.O.D. & Salamin, N. (2013) Temporal and spatial origin of Gesneriaceae in the New World inferred from plastid DNA sequences. *Botanical Journal of the Linnean Society*, **171**, 61–79.
- Ren, H., Peng, S.L., Zhang, D.X., Jian, S.G., Wei, Q., Zhang, Q.M., Liu, N., Shi Jin, L.I., Chen, W.B. & Zhuang, Y.Z. (2003) The ecological and biological characteristics of an endangered plant, *Primulina tabacum* Hance. *Acta Ecologica Sinica*, **23**, 1012–1017.
- Rohde, K. (1992) Latitudinal gradients in species diversity: the search for the primary cause. *Oikos*, **65**, 514–527.
- Romdal, T.S., Araújo, M.B. & Rahbek, C. (2013) Life on a tropical planet: niche conservatism and the global diversity gradient. *Global Ecology and Biogeography*, **22**, 344–350.
- Sandel, B., Arge, L., Dalsgaard, B., Davies, R.G., Gaston, K.J., Sutherland, W.J. & Svenning, J.-C. (2011) The influence of Late Quaternary climate-change velocity on species endemism. *Science*, **334**, 660–664.
- Siqueira, T., Bini, L.M., Roque, F.O., Couceiro, S.R.M., Trivinho-Strixino, S. & Cottenie, K. (2012) Common and rare species respond to similar niche processes in macroinvertebrate metacommunities. *Ecography*, **35**, 183–192.
- Solomon, S. (2007) *Climate change 2007: the physical science basis. contribution of working group I to the fourth 16 assessment report of the intergovernmental panel on climate change*. Cambridge university Press, Cambridge, UK.
- Stevens, G.C. (1989) The latitudinal gradient in geographical range: how so many species coexist in the tropics. *The American Naturalist*, **113**, 240–256.
- Stuart-Smith, R.D., Edgar, G.J., Barrett, N.S., Kininmonth, S.J. & Bates, A.E. (2015) Thermal biases and vulnerability to warming in the world's marine fauna. *Nature*, **528**, 88–92.
- Svenning, J.C. (2003) Deterministic Plio-Pleistocene extinctions in the European cool-temperate tree flora. *Ecology Letters*, **6**, 646–653.
- Svenning, J.C. & Skov, F. (2007) Ice age legacies in the geographical distribution of tree species richness in Europe. *Global Ecology and Biogeography*, **16**, 234–245.
- Thorntwaite, C. & Hare, F.K. (1955) Climatic classification in forestry. *Unasylva*, **9**, 51–59.
- Wang, C.-N. & Cronk, Q.C. (2003) Meristem fate and bulbil formation in *Titanotrichum* (Gesneriaceae). *American Journal of Botany*, **90**, 1696–1707.
- Wang, W., Pan, K., Li, Z., Weitzman, A. & Skog, L. (1998) *Gesneriaceae. Flora of China*, **18**, 244–401.
- Wang, Y.Z., Mao, R.B., Liu, Y., Li, J.M., Dong, Y., Li, Z.Y. & Smith, J.F. (2011) Phylogenetic reconstruction of *Chirita* and allies (Gesneriaceae) with taxonomic treatments. *Journal of Systematics and Evolution*, **49**, 50–64.
- Wang, Z., Rahbek, C. & Fang, J. (2012) Effects of geographical extent on the determinants of woody plant diversity. *Ecography*, **35**, 1160–1167.
- Watanabe, S., Hajima, T., Sudo, K., Nagashima, T., Takemura, T., Okajima, H., Nozawa, T., Kawase, H., Abe, M. & Yokohata, T. (2011) MIROC-ESM 2010: model description and basic results of CMIP5-20c3 m experiments. *Geoscientific Model Development*, **4**, 845–872.
- Webb, T. & Bartlein, P. (1992) Global changes during the last 3 million years: climatic controls and biotic responses. *Annual Review of Ecology and Systematics*, **23**, 141–173.
- Wei, Y.-G., Zhong, S.-H. & Wen, H.-Q. (2004) Studies of the flora and ecology Gesneriaceae in Guangxi province. *Acta Botanica Yunnanica*, **26**, 173–182.
- Welander, N.T. (1984) Influence of temperature and day-length on flowering in *Aeschynanthus speciosus*. *Scientia Horticulturae*, **22**, 157–161.
- Wen, F. & Li, Z. (2006) Research advance on Gesneriaceae plant. *Chinese Wild Plant Resources*, **25**, 1–6.
- Wu, Z. (1988) Hengduan mountain flora and her significance. *Journal of Japanese Botany*, **63**, 297–311.
- Wu, Z.-Y. & Wang, W.-T. (1957) Preliminary report on the study of plant flora in the tropical and subtropical regions of Yunnan I. *Journal of Systematics & Evolution*, **6**, 183–254.
- Zhang, W.-J. (2012) *Geographical patterns and explanations of Gesneriaceae species richness in China*. Peking University, Beijing, China.
- Zhang, Z., Yan, Y., Tian, Y., Li, J., He, J.S. & Tang, Z. (2015) Distribution and conservation of orchid species richness in China. *Biological Conservation*, **181**, 64–72.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Supplementary tables.

Appendix S2 Supplementary figures.

Table S1.1 Table S2 Correlation coefficients between different predictors.

Table S1.2 The coefficients of determination (R^2_{adj} , %) of the generalized linear models (GLMs) between species richness of Gesneriaceae and selected climatic variables.

Table S1.3 Nature reserves located in the two hotspots of Gesneriaceae in China.

Figure S2.1 Patterns of environmental factors in China.

Figure S2.2 Correlations between environmental factors and species richness with different range size.

Figure S2.3 Comparison of the number and area of nature reserves in the two hotspots of Gesneriaceae in China.

Figure S2.4 Frequency distribution histogram showing number of records for each species.

BIOSKETCH

Yunpeng Liu is a master student whose research focuses on patterns of plant diversity and underlying mechanisms at large spatial scales. The macroecology research group conducting this article is interested in the mechanisms underlying large-scale patterns of plant diversity and species conservation.

Author contributions: Y.L., Z.S. and Z.W. conceived the idea; Y.L. and Z.W. collected the data; Y.L., Q.W., X.S., W.Z. and Z.W. conducted the analysis; Y.L. and Z.W. led the writing, and all authors contributed to the writing.

Editor: Franz Essl