

## Research Article

# Global patterns of species richness of the holarctic alpine herb *Saxifraga*: the role of temperature and habitat heterogeneity

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## Abstract

The effects of contemporary climate, habitat heterogeneity and long-term climate change on species richness are well studied for woody plants in forest ecosystems, but poorly understood for herbaceous plants, especially in alpine–arctic ecosystems. Here, we aim to test if the previously proposed hypothesis based on the richness–environment relationship could explain the variation in richness patterns of the typical alpine–arctic herbaceous genus *Saxifraga*. Using a newly compiled distribution database of 437 *Saxifraga* species, we estimated the species richness patterns for all species, narrow- and wide-ranged species. We used generalized linear models and simultaneous autoregressive models to evaluate the effects of contemporary climate, habitat heterogeneity and historical climate on species richness patterns. Partial regressions were used to determine the independent and shared effects of different variables. Four widely used models were tested to identify their predictive power in explaining patterns of species richness. We found that temperature was negatively correlated with the richness patterns of all and wide-ranged species, and that was the most important environmental factor, indicating a strong conservatism of its ancestral temperate niche. Habitat heterogeneity and long-term climate change were the best predictors of the spatial variation of narrow-ranged species richness. Overall, the combined model containing five predictors can explain ca. 40%–50% of the variation in species richness. We further argued that additional evolutionary and biogeographical processes might have also played an essential role in shaping the *Saxifraga* diversity patterns and should be considered in future studies.

**Keywords** climate change, Last Glacial Maximum, niche conservatism, range size, water–energy dynamics

## 北半球高山和极地虎耳草属物种丰富度的地理格局：温度和生境异质性的作用

**摘要：**现代气候、生境异质性和长期气候变化对森林生态系统中分布的木本植物的物种丰富度格局的影响在以往研究中受到广泛关注，但对高寒-极地生态系统中的草本植物物种丰富度格局及其影响因素的研究仍较少。本研究旨在检验以往研究中基于物种丰富度和环境因子关系提出的假说是否能够解释高寒-极地地区典型草本植物-虎耳草属(*Saxifraga*)的物种丰富度格局。本研究利用全球437种虎耳草属物种分布数据，探讨了全部物种、广域和狭域物种丰富度格局的影响因素。采用广义线性模型和空间自回归模型，评估了现代气候、生境异质性和历史气候对虎耳草属物种丰富度格局的影响。采用偏回归分析了不同变量对物种丰富度的独立解释率和共同解释率，并检验了4种广泛使用的物种丰富度与环境关系模型对物种丰富度格局的解释能力。研究结果表明，温度与虎耳草属所有物种和广域物种的物种丰富度格局呈显著负相关关系，是影响物种丰富度格局最重要的环境因子，这可能反映了虎耳草属对其祖先温带生态位的保守性。生境异质性和末次冰期以来的气候变化是虎耳草属狭域物种丰富度空间变异的最佳预测因子。总体而言，包含5个预测变量的组合模型可以解释大约40%–50%的虎耳草属物种丰富度的空间变异。此外，进化和生物地理过程在虎耳草属物种丰富度格局形成方面可能发挥了重要作用，这有待进一步研究。

**关键词：**气候变化，末次盛冰期，生态位保守，范围大小，水分-能量动态假说

## INTRODUCTION

The arctic–alpine ecosystem, covered by treeless vegetation communities, i.e. shrubland, grassland and tundra, is a widespread ecosystem type ranging from tropical mountaintops to polar regions and occupies about 8% of the global land area (Chapin and Körner 1995). About 4% of all known vascular plant species are found in this cold-dominated ecosystem, including about 1500 arctic species and about 10 000 alpine species including several species-rich genera such as *Saxifraga*, *Ranunculus*, *Aster* and *Gentiana* (Chapin and Körner 1995). In addition, the arctic–alpine ecosystems contain a large carbon and methane pool with a slow turnover rate and play an essential role in maintaining the stability of the earth's climate system (Ernakovich *et al.* 2014; Mod *et al.* 2016). However, these ecosystems are undergoing more pronounced warming than other areas, potentially leading to a higher risk of local species extinction and causing negative effects on ecosystem stability (Jordon-Thaden *et al.* 2013; Liang *et al.* 2018). Hence, understanding the mechanisms and the primary determinants that generate and maintain large-scale species richness patterns in arctic–alpine ecosystems is crucial for biodiversity conservation (Brown *et al.* 2004; Gaston *et al.* 1995).

Several hypotheses related to the contemporary environment have been proposed to explain species richness patterns. The energy hypothesis suggested that higher energy availability could support more

individuals from viable populations and therefore more species in a community (Wright 1983). O'Brien *et al.* (2000) proposed the water–energy dynamics hypothesis, highlighting the importance of the interaction between energy and water in limiting biological activity and ultimately controlling species ranges (O'Brien 1998; O'Brien *et al.* 2000). By incorporating habitat heterogeneity, which promotes species richness by increasing allopatric speciation rates, decreasing extinction rates and offering more ecological niches for species coexistence, O'Brien's model explained over 80% of the variance in tree species richness patterns in Southern Africa (O'Brien *et al.* 2000). More recently, Francis and Currie (2003) supported the water–energy dynamic hypothesis in their study on species richness patterns of flowering plants at a global scale. Similarly, Janzen's hypothesis states that the uniformity in temperature across elevation caused by the lack of seasonality acts as a barrier in species dispersal in tropical mountains (Janzen 1967), indicating the importance of seasonality and topographic relief in determining species richness (Shrestha *et al.* 2018a). However, these hypotheses are not mutually exclusive. Wang *et al.* (2011) proposed a statistical model that combines variables of energy, water, climate seasonality and habitat heterogeneity to represent the range of mechanisms influencing species richness patterns proposed by different hypotheses (combined model). In addition to the contemporary environment, historical climate change could also

influence species richness patterns by affecting species dispersal, extinction and speciation processes. All these hypotheses have been proposed mostly based on woody plants in forest ecosystems and have yet to be tested on herbaceous plants, which have often experienced different evolutionary and climate histories compared with woody plants (Smith and Donoghue 2008).

The species richness models based on all species might not properly identify the important factors for narrow range species because of the disproportionate contribution of the wide-ranged species to the overall richness patterns (Jetz and Rahbek 2002; Lennon *et al.* 2004). With the increase of species range size, the effects of climate on richness tend to increase whereas the effects of habitat heterogeneity decrease. This is because wide-ranged species tend to have higher dispersal ability and reach equilibrium with climate easier than narrow-ranged species. While habitat heterogeneity will likely increase opportunities for speciation in isolated niches and will limit species dispersal, causing a larger effect on narrow-ranged species richness. Although similar results were found for American bats (Tello and Stevens 2010), South American mammals (Ruggiero and Kitzberger 2004) and global Viperidae snakes (Terribile *et al.* 2009), studies on several plant groups have only found partially consistent results (Shrestha *et al.* 2018a). For example, habitat heterogeneity had similar effects on both wide-ranged and narrow-ranged species richness of woody plants (Liu *et al.* 2019; Shrestha *et al.* 2018a), while no effect was found for wide-ranged and narrow-ranged species of the herbaceous family Gesneriaceae in China (Liu *et al.* 2017). These studies also found that narrow-ranged species are more sensitive to long-term climate change, i.e. climate change since the Last Glacial Maximum (LGM), because of their lower genetic diversity and dispersal ability, and smaller population size than wide-ranged species (Liu *et al.* 2017, 2019). These results suggest that range size effects on the relationship between species richness and environmental conditions vary among different groups and life forms and should be considered when evaluating the spatial variation of species richness patterns at a large scale.

As a small herbaceous plant (Fig. 1), *Saxifraga* contains about 450 species globally and exhibits high species richness in arctic–alpine ecosystems across the Northern Hemisphere, with a few species extending their ranges to the alpine regions of the tropical Andes in South America (Ebersbach *et al.* 2017,

2018). Phylogenetic studies suggest that this genus originated in North America ca. 70 ma and dispersed to northern Asia during its early diversification period, colonizing Europe and the Qinghai-Tibetan Plateau (QTP) region in the Late Eocene. Studies on the climatic niche evolution of Saxifragales suggest that the ancestor of *Saxifraga* already adapted to cold areas since 80 mya and that its descendants, including *Saxifraga*, evolved unidirectionally to colder habitats (Folk *et al.* 2019). Most *Saxifraga* species are found on rocky cliffs in high mountains and arctic tundra, where they show higher diversification rates than in other habitats where this genus is present (de Casas *et al.* 2016).

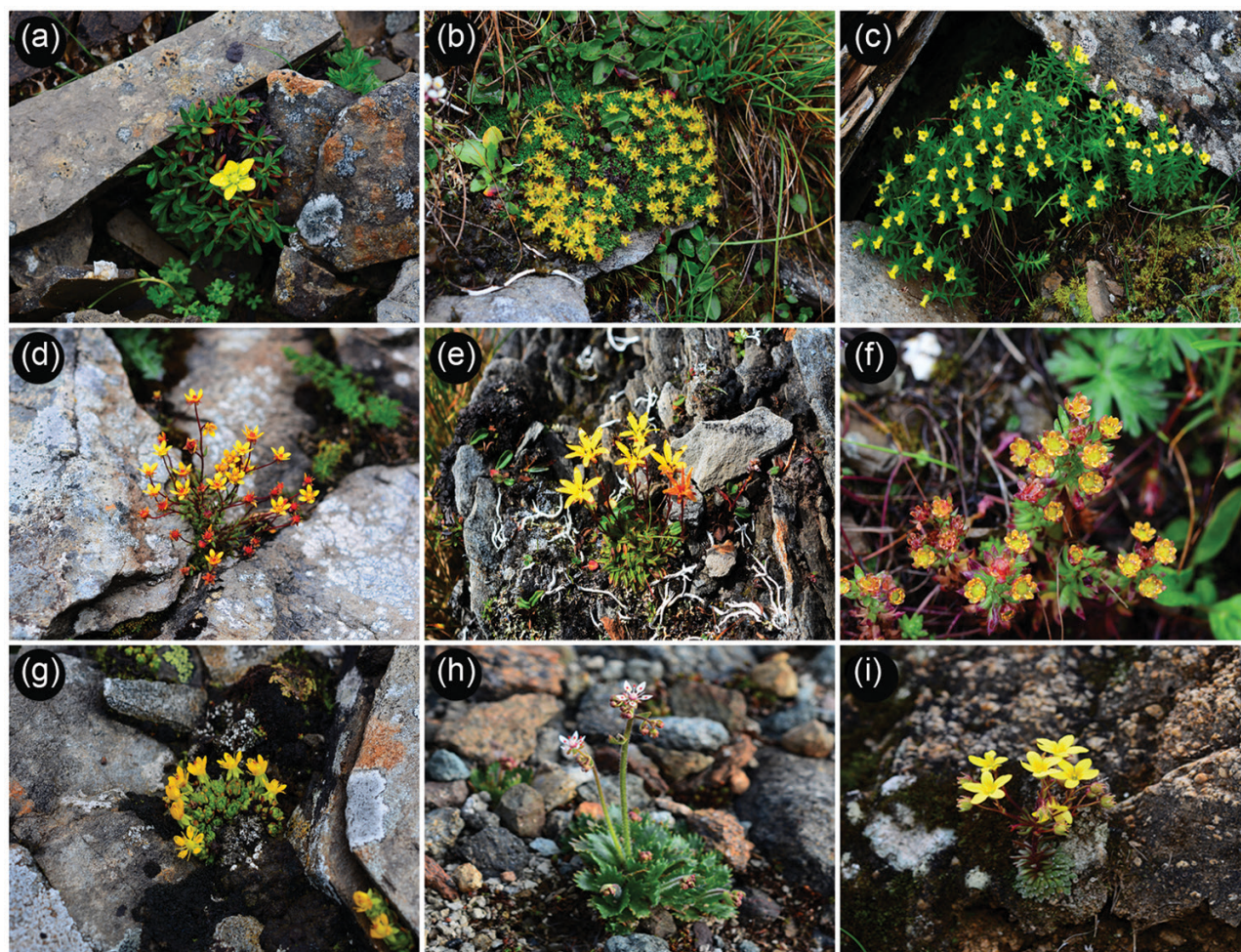
Here, we compiled the distribution of 437 *Saxifraga* species and assessed the primary drivers of its species richness patterns on a global scale. Specifically, we (i) evaluated the relative importance of contemporary climate, habitat heterogeneity and long-term climate change on the species richness patterns of *Saxifraga*; (ii) tested whether previously proposed multiple regression models (i.e. O'Brien *et al.* (2000) water–energy model, Francis and Currie (2003) water–energy model, Janzen (1967) seasonality model and Wang *et al.* (2011) combined model) can also explain species richness of the arctic and alpine group such as *Saxifraga* and (iii) evaluated the variation in the determinants of *Saxifraga* species richness across species with different range sizes (i.e. wide-ranged *vs.* narrow-ranged species).

## MATERIALS AND METHODS

### Species distribution data

The distributions of *Saxifraga* species were compiled from published floras, plant checklists, peer-reviewed articles, online-open databases and herbarium specimens (see Appendix S1). All species names were standardized according to *The Plant List* (TPL, Version 1.1, <http://www.theplantlist.org/>). The unresolved names in TPL were further checked in the *Catalogue of Life* (COL, Annual checklist 2018, <http://www.catalogueoflife.org/annual-checklist/2018/>). If a species name was unresolved in TPL but accepted in COL, we included it in further analysis. Hybrid species in COL or TPL were removed from our database because of the limited available information for compiling their distribution ranges. A recent phylogenetic study suggested that *Saxifraga* is not a monophyletic genus if section *Micranthes* is included (Rawat *et al.* 2019). However, we did not exclude the species from the section *Micranthes* from





**Figure 1:** Representative taxa of *Saxifraga* and their typical habitat. (a) *S. nigroglandulosa* Engl. et Irmsch., (b) *S. glacialis* H. Smith, (c) *S. wardii* W. W. Smith, (d) *S. aurantiaca* Franch., (e) *S. cacuminum* H. Smith, (f) *S. consanguinea* W. W. Smith, (g) *S. stella-aurea* Hook. f. et Thoms., (h) *S. laciniata* Nakai et Takeda, (i) *S. umbellulata* var. *pectinata* (Marquand et Airy-Shaw) J. T. Pan. (a)–(g) were collected from the Balang Mountain (4500 m), Sichuan, China. (h) and (i) were collected from the Changbai Mountain (1700 m), Jilin, China, and the Beishan (3800 m), Xizang, China, respectively. Photographed by Lei Zhang.

our study considering the difficulties in correctly classifying all species of this section, especially in China. Currently, our database includes 437 species covering all *Saxifraga* species from the *Flora of China* (Pan *et al.* 2001), the *Flora of North America* (Flora of North America Editorial Committee 2009), the *Flora of Russia* (Tzvelev 1996) and the *Atlas florae Europaeae* (Jalas and Suominen 1999).

The geographic standard used in the database follows Shrestha *et al.* (2018b), which is an updated version of Xu *et al.* (2016), and islands smaller than 100 000 km<sup>2</sup> in size were excluded. This geographic standard classifies the whole world into 480 geographic units with roughly equal size to account for the area effects on species richness. We standardized and georeferenced the recorded geographical names from different literature sources based on the global geographical names database (GeoNames,

<http://www.geonames.org/>). For Greenland, we downloaded the global consensus land cover at a spatial resolution of 1 km<sup>2</sup> (<https://www.earthenv.org/landcover>) and removed the grids with >50% of the area covered by snow and ice. Finally, the area 215 521 km<sup>2</sup> of Greenland was used for subsequent analysis. For each geographic unit, the number of species was counted. The area of each geographic unit was calculated in ArcGIS (Version 10.4.1) using the Goode homolosine (Land) projection. In total, our database included 3399 distribution records for 437 *Saxifraga* species from 230 geographic units with a mean area of 315 832.6 ± 184 854.6 km<sup>2</sup> (see Supplementary Fig. S1 and Appendix S2). Most geographic units are in the size of 315 833 km<sup>2</sup>. The area was not included in the further analysis because it is not significantly correlated with species richness in our study (Supplementary Fig. S2).



We further divided all species into wide-ranged and narrow-ranged species according to their range sizes. We first calculated the range size of each species as the summed area of all occupied geographical units. Then we ranked all species by descending order of range size and categorized the top 25% (109 of 437) as wide-ranged species and the bottom 50% (219 of 437) as narrow-ranged species (Araújo *et al.* 2008; Liu *et al.* 2017). The wide-ranged and narrow-ranged species accounted for 74% and 12% of the distribution records, respectively. We also used a bottom 25% threshold to define narrow-ranged species following previous studies (Jetz and Rahbek 2002), but narrow-ranged species defined with this threshold accounted for a very low number of distribution records (143 of 3399) and covered very few geographical units (32 of 230). This led to a very low richness of narrow-ranged species, causing high uncertainties in the subsequent statistical analysis. Here, we only report the results based on the bottom 50% as a threshold for narrow-ranged species.

### Environmental variables

To explore the effects of environmental variables on large-scale patterns of *Saxifraga* species richness, we initially included 31 variables in our preliminary analyses, which represented contemporary climate, elevation, past climate and edaphic conditions (see Supplementary Tables S1 and S2). Twenty-one variables with significant effects on *Saxifraga* species richness variation and widely used in previous studies were kept in the subsequent analyses (Francis and Currie 2003; Janzen 1967; Liu *et al.* 2020; O'Brien *et al.* 2000; Wang *et al.* 2011). We classified these variables into five groups describing environmental energy, water availability, habitat heterogeneity, short-term climate change (i.e. climatic seasonality) and long-term climate change (i.e. climate change since LGM) (Table 1).

Contemporary climate variables at a spatial resolution of 30 arc-seconds were downloaded from CHELSA (<http://chelsa-climate.org/>, Version 1.2). Elevation data were downloaded from the Worldclim database ([www.worldclim.org/](http://www.worldclim.org/), Version 1.4) at a spatial resolution of 2.5 arc-minutes. The mean annual temperature and precipitation of the LGM reconstructed by the Community Earth System Model (CCSM4) and the Model for Interdisciplinary Research on Climate Earth System Model (MIROC-ESM) were downloaded from the Worldclim database ([www.worldclim.org/](http://www.worldclim.org/), Version 1.4) at a spatial resolution of 2.5 arc-minutes.

We used the mean values of these two models to account for uncertainties in past climate simulations because Xu *et al.* (2019) found that the mean values showed consistent results with the original values when assessing patterns of oak species richness in the Northern Hemisphere. We used the mean values of each environmental variable within each geographical unit in the following analyses.

Habitat heterogeneity is usually represented by the range values (maximum minus minimum) of elevation, temperature and precipitation, calculated within each geographic unit. In addition to these variables, here we also included coarse fragments volumetric of soil (CFVOL) and the number of soil types to represent habitat heterogeneity. Previous studies showed higher diversification rates of *Saxifraga* in rocky cliffs (de Casas *et al.* 2016). Thus, given the importance of topographic heterogeneity for the overall patterns of *Saxifraga*, and considering that CFVOL is often congruent with such heterogeneity, here we used this variable as an additional (substrate-related) measure of habitat heterogeneity. We used mean values of soil layers at four depths to represent soil properties. The number of soil types within each geographical unit was also counted. Soil properties were downloaded from the global soil geographic database (*SoilGrids*, <https://soilgrids.org/>; Supplementary Table S1). Based on a global compilation of soil profile data and machine learning methods, *SoilGrids* predicts global volumes of coarse fragments of soil at four depths (0, 5, 15 and 30 cm) at 1 km/250 m resolution (Hengl *et al.* 2014, 2017).

We used the 'zonal' statistics tool in ArcGIS (Version 10.4.1) to calculate the mean, range and standard deviation of each variable within a given geographical unit.

### Statistical analyses

We first performed univariate generalized linear models (GLMs) with negative binomial residuals and ordinary least regression models (OLS) to assess the effects of each environmental factor on the spatial variation of *Saxifraga* species richness. GLMs have been widely used to analyse over-dispersed count data like species richness (Ver Hoef and Boveng 2007). We evaluated the goodness of fit for GLMs using pseudo- $R^2$ , which was calculated as (Null Deviance – Residual Deviance)/Null Deviance (Guisan and Zimmermann 2000). Because the spatial autocorrelation in predictors or dependent data will increase the risk of Type I error and may

**Table 1:** The groups of climate, habitat heterogeneity and soil variables, and their abbreviations used in the analyses

Groups	Abbreviations	Environmental variables
Energy	MAT	Annual mean temperature (°C)
	MTWQ	Mean temperature of warmest quarter (°C)
	MTCQ	Mean temperature of coldest quarter (°C)
	PET	Potential evapotranspiration (mm)
	PETmin	Minimum monthly potential evapotranspiration (mm)
Water	MAP	Annual precipitation (mm)
	PWQ	Precipitation of wettest quarter (mm)
	PDQ	Precipitation of driest quarter (mm)
	AET	Annual actual evapotranspiration (mm)
	WD	Water deficit (mm)
	Rainfall	Sum of monthly precipitation values for which mean monthly temperature was above 0 (°C)
Seasonality	TSN	Temperature seasonality
	ART	Temperature annual range (°C)
	PSN	Precipitation seasonality
Habitat heterogeneity	ELER	Elevation range (m)
	MATR	Range of annual mean temperature (°C)
	MAPR	Range of annual precipitation (mm)
	NST	Number of soil types within each geographic unit
	CFVOL	Soil coarse fragments volume (%)
Climate change since LGM	TA	Temperature absolute anomaly (°C)
	PA	Precipitation absolute anomaly (mm)

lead to a false significance level of GLMs, we also built simultaneous autoregressive models with spatial error (SARerr) as recommended by [Kissling and Carl \(2008\)](#). Following [Xu \*et al.\* \(2019\)](#), we set a series of gradient spatial weight matrices at a neighbourhood distance range from 500 to 3000 km with 100 km spacing in the SARerr models. The spatial weights matrix for each neighbourhood distance was calculated by weighting the neighbours with the row standardized coding style. We finally selected one SARerr model that minimized the spatial autocorrelation in the residuals (estimated by Moran's *I*) and the Akaike information criterion (AIC) value as the best model. Due to the collinearity among variables from each environmental group, partial regression was used to estimate the unique and shared effects of each variable on the spatial variation of species richness. For each species group,

the variable from each environmental factor group with explanatory power >10% and significance in SARerr was selected.

We testified to four previously proposed models for the relationships between species richness and climate using GLMs, SARerr and OLS models, respectively. The four models are (i) Richness ~ Rainfall + (PETmin – PETmin<sup>2</sup>) + log (ELER) proposed by [O'Brien \*et al.\* \(2000\)](#), (ii) Richness ~ WD + PET + PET<sup>2</sup> proposed by [Francis and Currie \(2003\)](#), (iii) Richness ~ TSN + ELER proposed by [Janzen \(1967\)](#) and a combined model (iv) Richness ~ Energy + Water + Seasonality + Habitat Heterogeneity + Climate change since LGM. The model proposed by [Wang \*et al.\* \(2011\)](#) only included four variables corresponding to four groups of contemporary environmental factors. Here, we included climate change since LGM to represent the historical climate change effects on species



richness. This model was constructed by selecting one variable from each environmental group, which could reduce collinearity among variables from the same environmental group (Table 1). We made all the possible combinations of variables from the five environmental groups resulting in 900 models for richness patterns of all species, wide-ranged species and narrow-ranged species, respectively. We excluded models including any variable with Variance Inflation Factors (VIF) larger than 3 to account for multicollinearity among variables. Then the model with the lowest AIC was selected as the best model.

We conducted the above analyses for the richness patterns of all species, wide-ranged and narrow-ranged species, separately. In addition, the sensitivity analyses were run by adding the zero-richness data of some geographic units for narrow-ranged species to match the geographical range of wide-ranged species (Supplementary Table S3) and by removing the geographic units of wide-ranged species that lack narrow-ranged species (Supplementary Table S4). All analyses were conducted in R v3.5.3 (R Core Team 2018). GLMs were carried out using the 'glm.nb' function in the R package 'MASS' (Venables and Ripley 2002). Four multiple regression models were also evaluated by the ordinary least squares method with log-transformed richness as dependent variable following O'Brien *et al.* (2000) and Francis and Currie (2003). SARerr models were run with the 'errorsarm' function in R package 'spdep' (Bivand and Wong 2018). The spatial weight matrix of the best SAR model was calculated at a neighbourhood distance of 1100 km for all species, 1200 km for wide-ranged species and 900 km for narrow-ranged species.

## RESULTS

*Saxifraga* species richness is highest in arctic and mountainous regions of the Northern Hemisphere (Fig. 2a). The richness pattern of wide-ranged species is similar to that of all species (Pearson's  $r = 0.80$ ), with the highest number of species in southwestern China followed by regions of middle to high latitude in western North America, mountainous regions in southern Europe and arctic regions (Fig. 2b). The richness of narrow-ranged species is highest in the mountain regions of southwestern China (especially in the Hengduan mountains) and southern Europe (Fig. 2c).

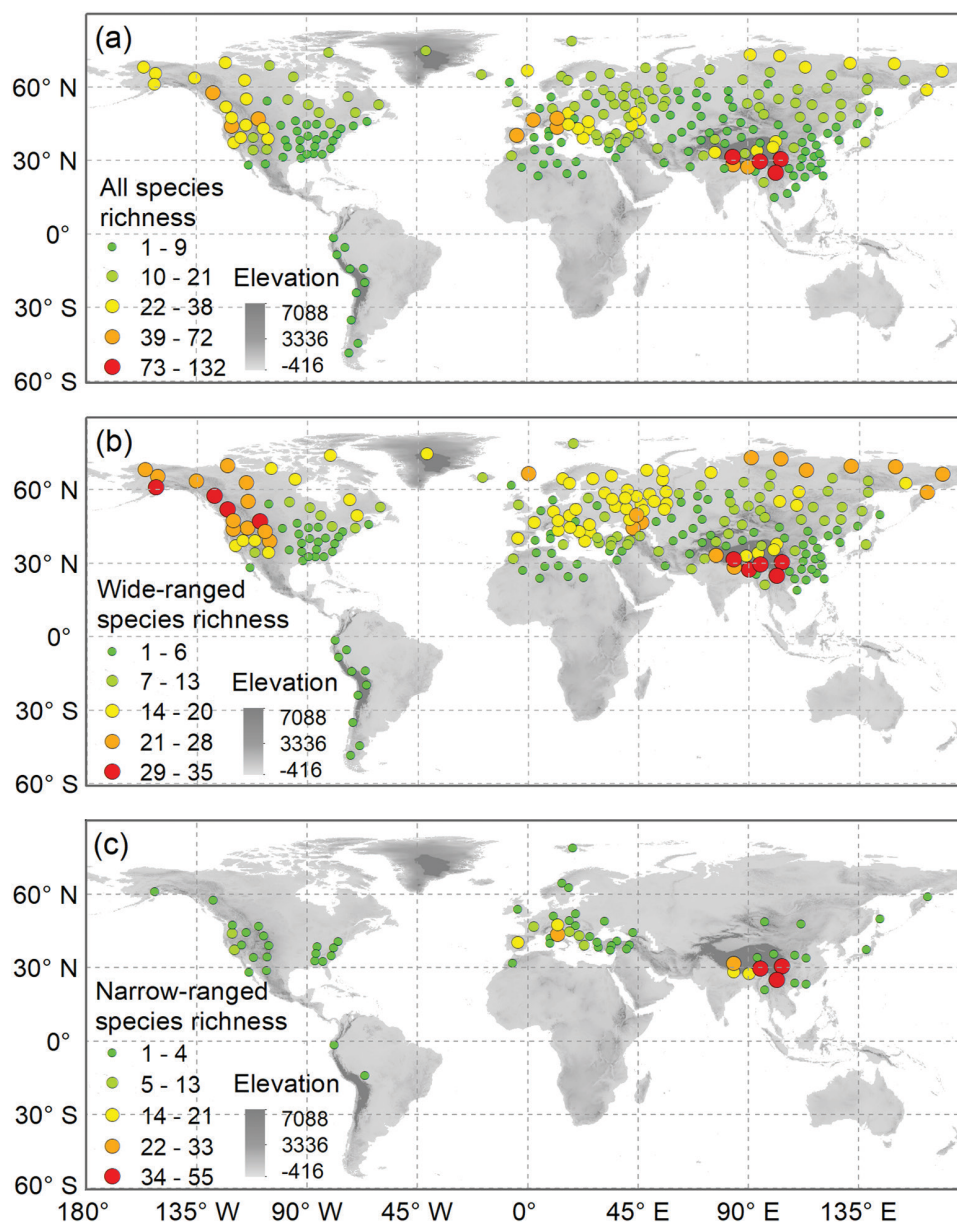
Univariate GLM analysis showed that the effects of environmental factors on the species richness patterns of all species are similar to those of the wide-ranged

species but are different from the narrow-ranged species (Table 2; Fig. 3; Supplementary Tables S5–S7). Environmental energy, habitat heterogeneity and environmental water were the three most important factors explaining the richness patterns of all species. MTWQ (mean temperature of warmest quarter, representing energy availability) was the strongest predictor of variation in *Saxifraga* species richness, being negatively correlated with species richness (pseudo- $R^2 = 20.22\%$ , SAR:  $P < 0.001$ ), followed by ELER (elevation range, pseudo- $R^2 = 14.12\%$ , SAR:  $P < 0.001$ ) and WD (water deficit, pseudo- $R^2 = 8.24\%$ , SAR:  $P < 0.001$ ).

For wide-ranged species, environmental energy, environmental water and climate change since the LGM were the top three important factors in explaining patterns of species richness. Similar to models for all species of *Saxifraga*, MTWQ was negatively correlated with the richness patterns of wide-ranged species and had the highest explanatory power (pseudo- $R^2 = 28.33\%$ , SARerr:  $P < 0.001$ ), followed by WD (pseudo- $R^2 = 10.90\%$ , SARerr:  $P < 0.001$ ) and precipitation anomaly (pseudo- $R^2 = 7.32\%$ , SARerr:  $P < 0.05$ ). Although habitat heterogeneity was positively related to wide-ranged species richness, they had low explanatory power (pseudo- $R^2 < 3\%$ , SARerr:  $P < 0.001$ ).

For narrow-ranged species, habitat heterogeneity and climate change since the LGM showed the highest explanatory power on the patterns of species richness. The explanatory power of ELER on narrow-ranged species richness was 36.15% and was higher than TA (temperature anomaly, pseudo- $R^2 = 28.67\%$ , SAR:  $P < 0.05$ ). Environmental energy, water and temperature seasonality did not show significant effects on the richness patterns of narrow-ranged species after accounting for spatial autocorrelation (SARerr:  $P > 0.1$ ). The results of sensitivity analyses are similar to the univariate GLM analysis (Supplementary Table S3 and S4).

Results of partial regression showed that the joint effects of MTWQ and ELER on the variation of *Saxifraga* species richness was only 2.21% and the independent effects of MTWQ and ELER were 18.01% and 11.90%, respectively. For wide-ranged species, MTWQ independently accounted for 17.92% of the richness variation after the effect of WD was controlled. In contrast, WD explained much less variation (0.49%) after the effect of MTWQ was controlled (Fig. 4). For narrow-ranged species, the independent effect of ELER on richness variation was the largest (12.86%) and long-term climate change (TA) only explained 5.38%



**Figure 2:** Global patterns of species richness of *Saxifraga* L. (a) all species, (b) wide-ranged species and (c) narrow-ranged species. The altitudes are shown in a grey gradient on the map.

independently. Overall, partial regressions results were consistent with the results of univariate GLM, indicating that the variables of environmental energy (i.e. MTWQ) were the most important predictors of *Saxifraga* species richness and wide-ranged species richness, whereas the variables of habitat heterogeneity were the most important predictor of narrow-ranged species. Habitat heterogeneity also had a large independent effect on *Saxifraga* species richness.

The results of multiple regression models using GLM showed that the combined model has the highest explanatory power on the spatial variation of species richness for all *Saxifraga*

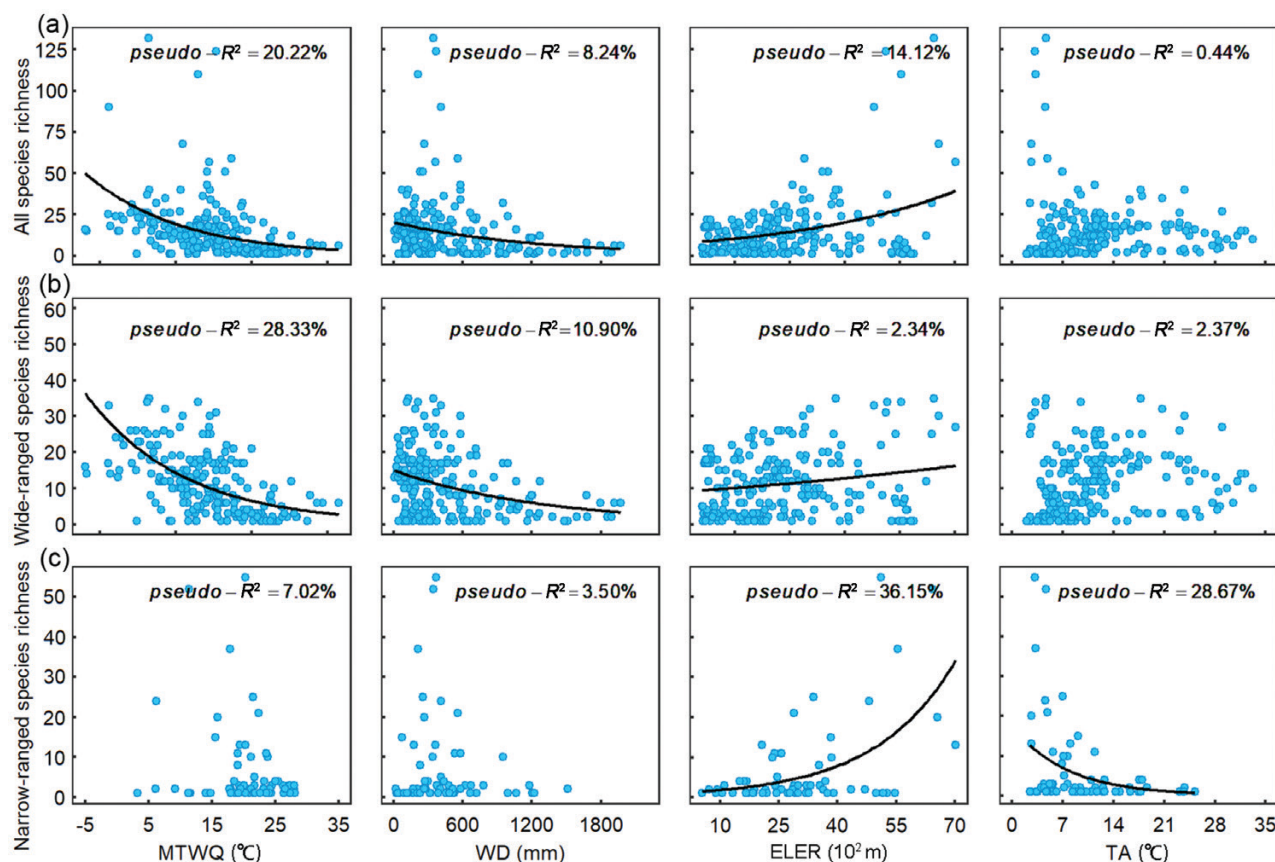
species (pseudo- $R^2 = 42.14\%$ ), wide-ranged species (pseudo- $R^2 = 47.27\%$ ) and narrow-ranged species (pseudo- $R^2 = 54.00\%$ ) compare to other models (Table 3). Stepwise regression selected the same variables for all species and wide-ranged species richness. The second-best model was O'Brien's water–energy dynamic model, which explained 52.89% of the variation in narrow-ranging species richness but only 33.06% and 36.64% of the variation in species richness of all species and wide-ranged species, respectively. Janzen's model explained 41.73% of the variation of narrow-ranged species richness but less than 20% for all species and



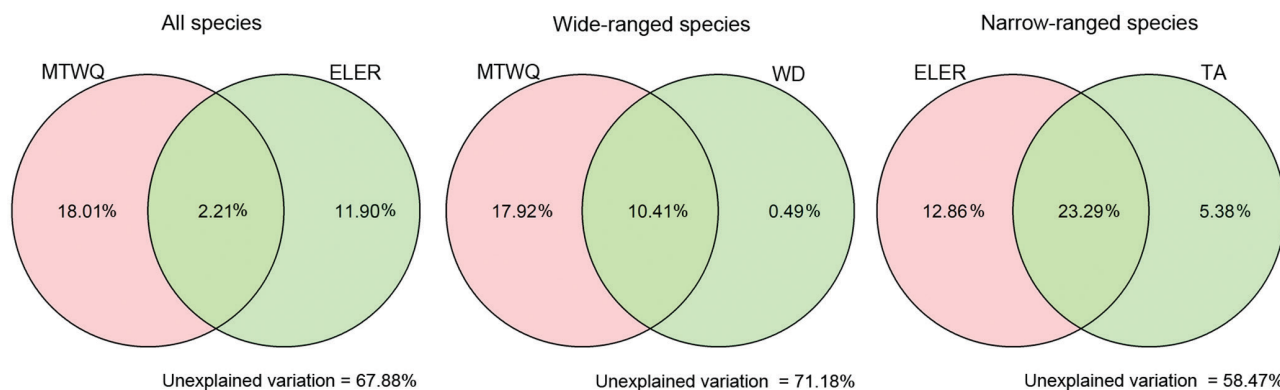
**Table 2:** Pseudo- $R^2$  and the regression coefficients for the predictors of global species richness patterns of *Saxifraga* L. evaluated by negative binomial GLMs

Groups	Predictors	All species		Wide-ranged species		Narrow-ranged species	
		Pseudo- $R^2$ (%)	Coefficients	Pseudo- $R^2$ (%)	Coefficients	Pseudo- $R^2$ (%)	Coefficients
Energy	MAT	8.55	-0.004 (-0.337)***	23.78	-0.005 (-0.453)***	0.20	-0.001 (-0.069)
	MTWQ	20.22	-0.008 (-0.507)***	28.33	-0.008 (-0.491)***	7.02	-0.007 (-0.393)
	MTCQ	2.67	-0.001 (-0.186)***	15.63	-0.003 (-0.371)***	0.81	0.002 (0.145)
	PET	10.66	-0.001 (-0.383)***	25.86	-0.001 (-0.471)***	0.09	<0.001 (-0.054)
	PETmin	4.14	-0.007 (-0.245)***	16.29	-0.011 (-0.382)***	3.43	0.012 (0.319)
Water	MAP	0.17	<0.001 (0.050)	2.47	<0.001 (-0.162)	5.46	0.001 (0.381)
	PWQ	1.58	0.001 (0.133)	0.54	<0.001 (-0.066)	13.69	0.002 (0.567)
	PDQ	2.23	-0.003 (-0.186)	3.31	-0.003 (-0.198)	5.85	-0.004 (-0.332)
	AET	0.42	<0.001 (-0.085)	8.22	-0.001 (-0.324)	3.08	0.001 (0.287)
	WD	8.24	-0.001 (-0.345)***	10.90	-0.001 (-0.320)***	3.50	-0.001 (-0.304)
	Rainfall	0.35	<0.001 (-0.072)	8.82	-0.001 (-0.307)*	2.95	0.001 (0.285)
	TSN	0.40	<0.001 (-0.067)	3.69	<0.001 (0.176)	21.38	<0.001 (-0.805)
Seasonality	ART	1.06	-0.001 (-0.111)	1.83	0.001 (0.127)	17.72	-0.010 (-0.700)
	PSN	0.01	<0.001 (0.012)*	1.29	-0.003 (-0.110)	12.28	0.015 (0.426)
	ELER	14.12	<0.001 (0.360)***	2.34	<0.001 (0.131)***	36.15	<0.001 (0.716)***
Habitat heterogeneity	MATR	13.48	0.004 (0.366)***	2.75	0.001 (0.142)***	32.09	0.009 (0.765)**
	MAPR	8.41	<0.001 (0.307)	1.14	<0.001 (0.095)	19.60	<0.001 (0.681)
	NST	3.41	0.016 (0.189)	0.08	-0.002 (-0.025)	16.09	0.047 (0.549)*
	CFVOL	10.41	0.045 (0.305)***	0.73	0.011 (0.073)*	31.21	0.103 (0.650)***
Climate change since LGM	TA	0.44	-0.009 (-0.069)	2.37	0.019 (0.143)	28.67	-0.131 (-0.759)***
	PA	3.75	0.002 (0.203)**	7.32	0.002 (0.254)***	3.41	0.002 (0.179)

P values were calculated using simultaneous autoregressive models with a spatial error. Numbers in parentheses are standardized coefficients of respective variables. \*\*\*P value <0.01; \*\*P value <0.05; \*P value <0.1. For abbreviations, see Table 1.



**Figure 3:** The relationships between *Saxifraga* species richness and MTWQ, WD, ELER and TA, respectively. Row (a) for all species, row (b) wide-ranged species and row (c) narrow-ranged species. Lines were fitted by GLMs.



**Figure 4:** Variation partitioning analysis to determine how much of the spatial variation in *Saxifraga* species richness across arctic-alpine ecosystems was accounted for by environmental energy, habitat heterogeneity and long-term climate change. Habitat heterogeneity and long-term climate change were represented by elevation range (ELER) and temperature anomaly (TA), respectively.

wide-ranged species. Francis and Currie's model had poor explanatory power (<30%) on the variation of all, wide-ranged and narrow-ranged species richness. Models that included ELER representing habitat heterogeneity could explain a relatively high proportion (>40%) of the variation of narrow-ranged species richness.

OLS and SAR models showed similar results (Supplementary Table S8 and S9).

## DISCUSSION

Using a newly compiled distribution database of *Saxifraga* species, combined with multiple statistic



**Table 3:** The regression coefficients, *P* values and pseudo-*R*<sup>2</sup> of global species richness patterns of *Saxifraga* L. were evaluated by four multiple regression models using negative binomial GLMs

Model type	Predictors	All species			Wide-ranged species			Narrow-ranged species		
		Coefficients	AIC	Pseudo- <i>R</i> <sup>2</sup> (%)	Coefficients	AIC	Pseudo- <i>R</i> <sup>2</sup> (%)	Coefficients	AIC	Pseudo- <i>R</i> <sup>2</sup> (%)
O'Brien <i>et al.</i> (2000)	Rainfall	<0.001 (-0.066)	1625.8	33.06	<0.001 (-0.151)**	1434.8	36.64	<0.001 (0.111)	338.6	52.89
	PETmin	-0.021 (-0.737)***			-0.028 (-0.993)***			0.075 (2.641)**		
	PETmin <sup>2</sup>	<0.001 (0.230)			<0.001 (0.495)**			-0.001 (-3.445)***		
	ELER	<0.001 (0.600)***			<0.001 (0.411)***			<0.001 (0.752)***		
Francis and Currie (2003)	WD	<0.001 (0.076)	1684.4	14.09	0.001 (0.304)***	1460.0	28.8	-0.001 (-0.226)	367.7	21.25
	PET	0.001 (0.404)			-0.001 (-0.406)*			0.010 (3.984)***		
	PET <sup>2</sup>	<0.001 (-0.887)**			<0.001 (-0.343)			<0.001 (-4.036)***		
Janzen (1967)	TSN	<0.001 (0.164)**	1677	15.94	<0.001 (0.290)***	1512.6	10.29	<0.001 (-0.728)**	347.0	41.73
	ELER	<0.001 (0.426)***			<0.001 (0.234)***			<0.001 (0.668)***		
Wang <i>et al.</i> (2011)	Energy	-0.001 (-0.460)***	1593.4	42.14	-0.001 (-0.455)***	1394.7	47.27	-0.014 (-0.395)**	339.2	54.00
	Water	-0.004 (-0.306)***			-0.006 (-0.420)***			0.001 (0.394)***		
	Seasonality	-0.013 (-0.422)***			-0.013 (-0.420)***			-0.016 (-0.464)**		
	Climate change since LGM	<0.001 (0.034)			<0.001 (0.100)**			-0.107 (-0.618)***		
	Habitat heterogeneity	<0.001 (0.601)***			<0.001 (0.358)***			0.151 (0.949)***		

Numbers in parentheses are standardized coefficients of respective variables. \*\*\**P* value <0.01; \*\**P* value <0.05; \**P* value <0.1. For abbreviations, see Table 1. Wang *et al.* (2011) combined model specific: all species richness ~ energy (PET) + water (PDQ) + seasonality (PSN) + climate change since LGM (PA) + habitat heterogeneity (ELER); wide-ranged species richness ~ energy (PET) + water (PDQ) + seasonality (PSN) + climate change since LGM (PA) + habitat heterogeneity (ELER); narrow-ranged species richness ~ energy (PETmin) + water (AET) + seasonality (PSN) + climate change since LGM (TA) + habitat heterogeneity (CFVOL).

models, we find that environmental energy (i.e. MTWQ) is negatively correlated with species richness and that it is the strongest predictor of richness for all *Saxifraga* species and wide-ranged species, while narrow-ranged species are mainly influenced by habitat heterogeneity. These results suggest that the determinants of richness patterns for alpine–arctic groups such as *Saxifraga* might be different from those in groups thriving in other ecosystems. Because current studies on arctic–alpine ecosystems have mostly been conducted at a local scale and confined to specific regions (Graglia *et al.* 2016; Mod *et al.* 2016), more studies at a global scale on species richness patterns and their determinants in these ecosystems are needed.

### Negative effects of environmental energy and water on *Saxifraga* richness

Recent studies suggested that the relationship between species richness and climate might be driven by evolutionary history, i.e. phylogenetic niche conservatism (Pyron and Burbrink 2009; Xu *et al.* 2013, 2019). This hypothesis suggests that lineages tend to retain their ancestral ecological niche over long evolutionary timescales and that colonization of new environments is relatively rare (Wiens *et al.* 2010). For example, plant clades with ancestral climatic niches in arid environments, such as Zygothylaceae (Wang *et al.* 2018), show a strong phylogenetic conservatism to these environments and, thus, a negative relationship between species richness and water availability. In our study, the negative correlation between species richness and energy/water may be linked to the temperate origin and a long history of adaptation and radiation in cold environments of *Saxifraga* (Ebersbach *et al.* 2017). A recent phylogenetic study has found that *Saxifraga* originated in temperate North America around ca. 74 Ma (Ebersbach *et al.* 2017). The ancestor of Saxifragaceae and Grossulariaceae adapted to temperate regions by ca. 81 Ma (Folk *et al.* 2019). Continuous climatic cooling since the Mid-Miocene and the uplift of mountain regions, i.e. Himalaya–Hengduan mountains, leading to a constant expansion of alpine ecosystems, might have provided suitable habitats for *Saxifraga* driving the diversification of *Saxifraga* therein, followed by further diversification of phenotypic and shifts of niches to the extreme cold ecosystems in alpine and arctic regions (Folk *et al.* 2019). For example, *Saxifraga* species with secreting hydathodes and cushion life forms can grow on

limestone rocks and cliff habitats at high altitudes in mountain regions, where they show a relatively high diversification rate (Ebersbach *et al.* 2017).

### Effects of habitat heterogeneity

In our study, habitat heterogeneity is responsible for promoting the high richness of *Saxifraga* in the Himalaya–Hengduan mountains in East Asia and the Alps and Pyrenees in southern Europe through the ecological process (i.e. increasing species coexistence) and historical biogeography processes (i.e. promoting speciation, increasing colonization rates and decreasing local extinction) (Rahbek *et al.* 2019a, 2019b; Stein *et al.* 2014).

First, the increase in habitat heterogeneity will increase species richness because more habitats usually offer more niches and can support more coexisting species (Stein *et al.* 2014). Most *Saxifraga* species are specialized to specific habitats, i.e. forest, shrublands, grassland, tundra or rocky cliffs. The continuous vegetation bands along the elevation gradient in mountain regions provide all habitats for *Saxifraga* species to grow. Topographic heterogeneity, therefore, increases *Saxifraga* species richness.

Second, heterogeneous habitats could also increase species richness by providing refugia during global climatic oscillations (Fjelds  *et al.* 2012). Biogeographic immigration analysis found that *Saxifraga* species have colonized the QTP region and surrounding mountains since the Late Eocene when the global climate started cooling and the colonization rate increased rapidly during the Eocene–Oligocene cooling period (Ebersbach *et al.* 2017; Folk *et al.* 2019). During climatic fluctuations and glaciations in the Quaternary, multiple refugia were identified in the mountainous regions of southern Europe and the Hengduan mountains by population genetic studies of *Saxifraga* (Abbott *et al.* 2000; Grassi *et al.* 2009). This biogeographic evidence suggested that such refugia have led to lower local extinction rates and increased colonization rates for many *Saxifraga* species in the periods of global climate cooling and fluctuation.

Third, with the increasing habitat heterogeneity, allopatric speciation rates also increase due to potential dispersal barriers among different habitats, thereby increasing species richness on a long timescale (Shrestha *et al.* 2018b). Compared with other habitats, i.e. forest and shrublands, *Saxifraga* species diversified faster in the newly emerged tundra and rocky cliffs (de Casas *et al.*

2016). Barriers between mountains impeded the dispersal of *in situ* speciated species to other regions, and further promoted allopatric speciation. These radiation events make the Hengduan mountains the youngest hotspot of *Saxifraga* and other alpine plant groups, i.e. *Gentiana* (Ebersbach *et al.* 2017; Favre *et al.* 2015).

### Richness patterns of species with different range sizes

Previous studies suggested that relationships between species richness and environmental variables vary among species with different range sizes (Tello and Stevens 2010). Wide-ranged species richness, e.g., is mainly influenced by the current climate, while narrow-ranged species richness is controlled primarily by habitat heterogeneity and climate change since the LGM (Jetz and Rahbek 2002). In our study, patterns of *Saxifraga* species richness are reflected in the patterns of wide-ranged species richness because of their exceptionally high contribution to the distributional counts of all *Saxifraga* species combined, thus leading to similar controlling variables for both categories. Our study showed consistent results with previous findings (Jetz and Rahbek 2002).

The hotspots of narrow-ranged species of *Saxifraga*, mainly in high mountain regions with long-term climate stability, are probably caused by the intrinsic properties of these species including low dispersal ability, specialized niche requirements, short time for dispersal and adaptation and extrinsic factors, i.e. existing dispersal barriers as reviewed by Sheth *et al.* (2020). Most narrow-ranged *Saxifraga* species are derived from recent radiation events facilitated by the uplift of mountains. These recently formed species might have had less time to disperse to other regions or to adapt to different habitats compared with older species (Ebersbach *et al.* 2017). The complex topography and soil derived from different types of rocks in the mountains promote the origin of rock-cliff specialized *Saxifraga* species on the one hand and preserve relict species with genotypes controlling specialized adaptation on the other hand (de Casas *et al.* 2016). The *Saxifraga* species that originated or took refuge in mountains during Quaternary climate change became narrow-ranged species (Fjeldså *et al.* 2012) due to strong dispersal barriers in mountain regions. These intrinsic and extrinsic factors controlling species range sizes might determine the primary predictors of the richness patterns of alpine plant species with different range sizes.

### The best model

Compared with the other three models, the combined model including the variables of energy, water, habitat heterogeneity, climate seasonality and climate change since LGM was identified as the best statistical model with the highest explanatory power and lowest AIC values in explaining the richness patterns of all, wide-ranged and narrow-ranged species. A previous study on the species richness patterns of *Quercus* also found that the combined model has a good performance in predicting richness patterns across continents (Nogués-Bravo *et al.* 2007). In our study, the combined models selected the same variables for all and wide-ranged species but not for narrow-ranged species. Such differences in the selected variables among species with different range sizes were also found for *Rhododendron* richness in China (Shrestha *et al.* 2018a). These results suggest that even the multivariate models based on the richness patterns of all species might not predict the richness patterns of narrow-ranged species. For narrow-ranged species, all evaluated models containing ELER had high explanatory power probably because ELER individually contributed to over 30% of the variation in species richness.

The best multivariate models explained 40%–50% of the variation in species richness of *Saxifraga*, which is relatively low compared with findings for other groups and regions (Shrestha *et al.* 2018a). This implies that in addition to the contemporary environment, other biogeographic or evolutionary processes, such as spatial variation in speciation, extinction and dispersal rates, probably have important roles in determining the current richness patterns of *Saxifraga* species. Although the niche evolution and diversification history of *Saxifraga* has been explored in previous studies (Folk *et al.* 2019), their effects on the present richness patterns remain to be investigated in the future.

## CONCLUSIONS

We find a negative relationship between species richness and temperature in *Saxifraga*, which differs from previous results that report a positive correlation in woody plants. Such a negative relationship may be a result of the temperate origin and the history of the cold adaptation of *Saxifraga*. It remains to be explored that whether the clades showing similar evolutionary trajectories with *Saxifraga* are also similar in species richness



patterns and determinants. We also find that habitat heterogeneity is the most important factor in determining richness patterns of narrow-ranged species, which show especially high richness in mountain regions. This suggests that narrow-ranged *Saxifraga* species may be more susceptible to habitat loss than wide-ranged species.

### Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

Appendix S1: Data sources for the distribution compilation of *Saxifraga*.

Appendix S2: The distribution records for *Saxifraga* species.

Table S1: All variables and their abbreviations used in our study.

Table S2: Spearman correlations for selected 31 variables.

Table S3: Pseudo- $R^2$ ,  $P$  values and the regression coefficients for the predictors of global species richness patterns of *Saxifraga* L. evaluated by negative binomial generalized linear models.

Table S4: Pseudo- $R^2$ ,  $P$  values and the regression coefficients for the predictors of global species richness patterns of *Saxifraga* L. evaluated by negative binomial generalized linear models.

Table S5: Pseudo- $R^2$ ,  $P$  value and the regression coefficients evaluated by generalized linear models with negative binomial distributions for the global species richness patterns of *Saxifraga*.

Table S6:  $R^2$ ,  $P$  value and the regression coefficients evaluated by simultaneous autoregressive models with a spatial error for the global species richness patterns of *Saxifraga*.

Table S7: Adjusted- $R^2$ ,  $P$  value and the regression coefficients for the predictors of global species richness patterns of *Saxifraga* L. were evaluated by ordinary least squares regressions.

Table S8: The regression coefficients,  $P$  values and adjusted- $R^2$  of global species richness patterns of *Saxifraga* L. were evaluated by four multiple regression models using ordinary least squares regression models.

Table S9: The coefficients,  $P$  values and  $R^2$  of global species richness patterns of *Saxifraga* L. were evaluated by four multiple regression models using simultaneous autoregressive models with a spatial error.

Figure S1: Histogram of area and relationship between species richness and area.

Figure S2: The geographical units and their numbers used in this study.

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