

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

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26 **Abstract**

27 **Aims** The effects of contemporary climate, habitat heterogeneity, and long-term
28 climate change on species richness are well studied for woody plants in forest
29 ecosystems, but poorly understood for herbaceous plants, especially in alpine-arctic
30 ecosystems. Here, we aim to test if the previously proposed hypothesis based on the
31 richness-environment relationship could explain the variation of richness patterns of
32 the typical alpine-arctic herbaceous genus *Saxifraga*.

33 **Methods** Using a newly compiled distribution database of 437 *Saxifraga* species, we
34 estimated the species richness patterns for all species, narrow- and wide-ranged
35 species. We used generalised linear models and simultaneous autoregressive models
36 to evaluate the effects of contemporary climate, habitat heterogeneity, and historical
37 climate on species richness patterns. Partial regressions were used to determine the
38 independent and shared effects of different variables. Four widely used models were
39 tested to identify their predictive power in explaining patterns of species richness.

40 **Important Findings** We found that temperature is negatively correlated with the
41 richness patterns of all and wide-ranged species and is the most important
42 environmental factor, indicating a strong conservatism of its ancestral temperate
43 niche. Habitat heterogeneity and long-term climate change are the best predictors of
44 the spatial variation of narrow-ranged species richness. Overall, the combined model
45 containing five predictors can explain ca. 40~50% of the variation in species richness.
46 We further argue that additional evolutionary and biogeographical processes might
47 have also played an essential role in shaping the *Saxifraga* diversity patterns and
48 should be considered in future studies.

49 **Keywords**

50 Climate change, last glacial maximum, niche conservatism, range size, water-energy
51 dynamics

52

53 INTRODUCTION

54 The arctic-alpine ecosystem, covered by treeless vegetation communities, i.e.,
55 shrubland, grassland, and tundra, is a widespread ecosystem type ranging from
56 tropical mountaintops to polar regions and occupies about 8% of the global land area
57 (Chapin and Körner 1995). About 4% of all known vascular plant species are found in
58 this cold-dominated ecosystem, including about 1, 500 arctic species and about 10,
59 000 alpine species including several species-rich genera such as *Saxifraga*,
60 *Ranunculus*, *Aster*, and *Gentiana*, etc. (Chapin and Körner 1995). In addition, the
61 arctic-alpine ecosystems contain a large carbon and methane pool with a slow
62 turnover rate and play an essential role in maintaining the stability of the earth's
63 climate system (Ernakovich *et al.* 2014; Mod *et al.* 2016). However, these ecosystems
64 are undergoing more pronounced warming than other areas, potentially leading to a
65 higher risk of local species extinction and causing negative effects on ecosystem
66 stability (Jordon-Thaden *et al.* 2013; Liang *et al.* 2018). Hence, understanding the
67 mechanisms and the primary determinants that generate and maintain large-scale
68 species richness patterns in arctic-alpine ecosystems is crucial for biodiversity
69 conservation (Brown *et al.* 2004; Gaston *et al.* 1995).

70 Several hypotheses related to the contemporary environment have been proposed
71 to explain species richness patterns. The energy hypothesis suggested that higher
72 energy availability could support more individuals from viable populations and
73 therefore more species in a community (Wright 1983). O'Brien *et al.* (2000) proposed
74 the water-energy dynamics hypothesis, highlighting the importance of the interaction
75 between energy and water in limiting biological activity and ultimately controlling
76 species ranges (O'Brien 1998; O'Brien *et al.* 2000). By incorporating habitat
77 heterogeneity, which promotes species richness by increasing allopatric speciation
78 rates, decreasing extinction rates, and offering more ecological niches for species
79 coexistence, O'Brien's model explained over 80% of the variance in tree species
80 richness patterns in Southern Africa (O'Brien *et al.* 2000). More recently, Francis and
81 Currie (2003) supported the water-energy dynamic hypothesis in their study on

82 species richness patterns of flowering plants at a global scale. Similarly, Janzen's
83 hypothesis states that the uniformity in temperature across elevation caused by the
84 lack of seasonality acts as a barrier in species dispersal in tropical mountains (Janzen
85 1967), indicating the importance of seasonality and topographic relief in determining
86 species richness (Shrestha *et al.* 2018a). However, these hypotheses are not mutually
87 exclusive. Wang *et al.* (2011) proposed a statistical model that combines variables of
88 energy, water, climate seasonality, and habitat heterogeneity to represent the range of
89 mechanisms influencing species richness patterns proposed by different hypotheses
90 (Combined model). In addition to the contemporary environment, historical climate
91 change could also influence species richness patterns by affecting species dispersal,
92 extinction, and speciation processes. All these hypotheses have been proposed mostly
93 based on woody plants in forest ecosystems and have yet to be tested on herbaceous
94 plants, which have often experienced different evolutionary and climate histories
95 compared to woody plants (Smith and Donoghue 2008).

96 The species richness models based on all species might not properly identify the
97 important factors for narrow range species because of the disproportionate
98 contribution of the wide-ranged species to the overall richness patterns (Jetz and
99 Rahbek 2002; Lennon *et al.* 2004). With the increase of species range size, the effects
100 of climate on richness tend to increase whereas the effects of habitat heterogeneity
101 decrease. This is because wide-ranged species tend to have higher dispersal ability
102 and reach equilibrium with climate easier than narrow-ranged species. While habitat
103 heterogeneity will likely increase opportunities for speciation in isolated niches and
104 will limit species dispersal, causing a larger effect on narrow-ranged species richness
105 Although similar results were found for American bats (Tello and Stevens 2010),
106 South American mammals (Ruggiero and Kitzberger 2004), and global Viperidae
107 snakes (Terribile *et al.* 2009), studies on several plant groups have only found
108 partially consistent results (Shrestha *et al.* 2018a). For example, habitat heterogeneity
109 had similar effects on both wide-ranged and narrow-ranged species richness of woody
110 plants (Liu *et al.* 2019; Shrestha *et al.* 2018a), while no effect was found for wide-

111 ranged and narrow-ranged species of the herbaceous family Gesneriaceae in China
112 (Liu *et al.* 2017). These studies also found that narrow-ranged species are more
113 sensitive to long-term climate change, i.e., climate change since the Last Glacial
114 Maximum (LGM), because of their lower genetic diversity and dispersal ability, and
115 smaller population size than wide-ranged species (Liu *et al.* 2017; Liu *et al.* 2019).
116 These results suggest that range size effects on the relationship between species
117 richness and environmental conditions vary among different groups and life forms
118 and should be considered when evaluating the spatial variation of species richness
119 patterns at a large scale.

120 As a small herbaceous plant (Figure 1), *Saxifraga* contains about 450 species
121 globally and exhibits high species richness in arctic-alpine ecosystems across the
122 Northern Hemisphere, with a few species extending their ranges to the alpine regions
123 of the tropical Andes in South America (Ebersbach *et al.* 2017; Ebersbach *et al.*
124 2018). Phylogenetic studies suggest that this genus originated in North America ca. 70
125 Ma and dispersed to northern Asia during its early diversification period, colonizing
126 Europe and the Qinghai-Tibetan Plateau (QTP) region in the Late Eocene. Studies on
127 the climatic niche evolution of Saxifragales suggest that the ancestor of *Saxifraga*
128 already adapted to cold areas since 80 mya and that its descendants, including
129 *Saxifraga*, evolved unidirectionally to colder habitats (Folk *et al.* 2019). Most
130 *Saxifraga* species are found on rocky cliffs in high mountains and arctic tundra, where
131 they show higher diversification rates than in other habitats where this genus is
132 present (de Casas *et al.* 2016).

133 Here, we compiled the distribution of 437 *Saxifraga* species and assessed the
134 primary drivers of its species richness patterns on a global scale. Specifically, we 1)
135 evaluated the relative importance of contemporary climate, habitat heterogeneity, and
136 long-term climate change on the species richness patterns of *Saxifraga*; 2) tested
137 whether previously proposed multiple regression models (i.e., O'Brien *et al.* (2000)
138 water-energy model, Francis and Currie (2003) water-energy model, Janzen (1967)
139 seasonality model and Wang *et al.* (2011) combined model) can also explain species

140 richness of the arctic and alpine group such as *Saxifraga*, and 3) evaluated the
141 variation in the determinants of *Saxifraga* species richness across species with
142 different range sizes (i.e., wide-ranged vs. narrow-ranged species).

143 MATERIALS AND METHODS

144 Species distribution data

145 The distributions of *Saxifraga* species were compiled from published floras, plant
146 checklists, peer-reviewed articles, online-open databases, and herbarium specimens
147 (see Appendix S1). All species names were standardised according to *The Plant List*
148 (TPL, Version 1.1, <http://www.theplantlist.org/>, Access date: 2017/09). The
149 unresolved names in TPL were further checked in the *Catalogue of Life* (COL,
150 Annual checklist 2018, <http://www.catalogueoflife.org/annual-checklist/2018/>). If a
151 species name was unresolved in TPL but accepted in COL, we included it in further
152 analysis. Hybrid species in COL or TPL were removed from our database because of
153 the limited available information for compiling their distribution ranges. A recent
154 phylogenetic study suggested that *Saxifraga* is not a monophyletic genus if section
155 *Micranthes* is included (Rawat *et al.* 2019). However, we did not exclude the species
156 from the section *Micranthes* from our study considering the difficulties in correctly
157 classifying all species of this section, especially in China. Currently, our database
158 includes 437 species covering all *Saxifraga* species from the *Flora of China* (Pan *et*
159 *al.* 2001), the *Flora of North America* (Flora of North America Editorial Committee
160 1993), the *Flora of Russia* (Tzvelev 1996), and the *Atlas florae Europaeae* (Jalas *et*
161 *al.* 1999).

162 The geographic standard used in the database follows Shrestha *et al.* (2018b),
163 which is an updated version of Xu *et al.* (2016), and islands smaller than 100, 000
164 km² in size were excluded. This geographic standard classifies the whole world into
165 480 geographic units with roughly equal size to account for the area effects on species
166 richness. We standardised and georeferenced the recorded geographical names from
167 different literature sources based on the global geographical names database

168 (GeoNames, <http://www.geonames.org/>). For Greenland, we downloaded the global
169 consensus land cover at a spatial resolution of 1 km²
170 (<https://www.earthenv.org/landcover>, access 03-2019) and removed the grids
171 with >50% of the area covered by snow and ice. Finally, the area 215, 521 km² of
172 Greenland was used for subsequent analysis. For each geographic unit, the number of
173 species was counted. The area of each geographic unit was calculated in ArcGIS
174 (Version 10.4.1) using the Goode homolosine (Land) projection. In total, our database
175 included 3,399 distribution records for 437 *Saxifraga* species from 230 geographic
176 units with a mean area of 315, 832.6 km² ± 184, 854.6 km² (see Appendix S2). Most
177 geographic units are in the size of 315, 833 km². The area was not included in the
178 further analysis because it is not significantly correlated with species richness in our
179 study (Figure S1 in Appendix S1).

180 We further divided all species into wide-ranged and narrow-ranged species
181 according to their range sizes. We first calculated the range size of each species as the
182 summed area of all occupied geographical units. Then we ranked all species by
183 descending order of range size and categorized the top 25% (109 of 437) as wide-
184 ranged species and the bottom 50% (219 of 437) as narrow-ranged species (Araújo *et*
185 *al.* 2008; Liu *et al.* 2017). The wide-ranged and narrow-ranged species accounted for
186 74% and 12% of the distribution records, respectively. We also used a bottom 25%
187 threshold to define narrow-ranged species following previous studies (Jetz and
188 Rahbek 2002), but narrow-ranged species defined with this threshold accounted for a
189 very low number of distribution records (143 of 3399) and covered very few
190 geographical units (32 of 230). This led to a very low richness of narrow-ranged
191 species, causing high uncertainties in the subsequent statistical analysis. Here, we
192 only report the results based on the bottom 50% as a threshold for narrow-ranged
193 species.

194

195 **Environmental variables**

196 To explore the effects of environmental variables on large-scale patterns of *Saxifraga*
197 species richness, we initially included 31 variables in our preliminary analyses, which
198 represented contemporary climate, elevation, past climate, and edaphic conditions
199 (see Tables S1 and S2 in Appendix S3). Twenty-one variables with significant effects
200 on *Saxifraga* species richness variation and widely used in previous studies were kept
201 in the subsequent analyses (O'Brien et al. 2000; Francis and Currie 2003; Janzen,
202 1967; Wang *et al.* 2011; Liu *et al.* 2020). We classified these variables into five
203 groups describing environmental energy, water availability, habitat heterogeneity,
204 short-term climate change (i.e., climatic seasonality), long-term climate change (i.e.,
205 climate change since LGM) (Table 1).

206 Contemporary climate variables at a spatial resolution of 30 arc-seconds were
207 downloaded from CHELSA (<http://chelsa-climate.org/>, version 1.2). Elevation data
208 was downloaded from the Worldclim database (www.worldclim.org/, version 1.4,
209 access 08-2012) at a spatial resolution of 2.5 arc minutes. The mean annual
210 temperature and precipitation of the LGM reconstructed by the Community Earth
211 System Model (CCSM4) and the Model for Interdisciplinary Research on Climate
212 Earth System Model (MIROC-ESM) were downloaded from the Worldclim database
213 (www.worldclim.org/, version 1.4, access 08-2016) at a spatial resolution of 2.5 arc
214 minutes. We used the mean values of these two models to account for uncertainties in
215 past climate simulations because Xu *et al.* (2019) found that the mean values showed
216 consistent results with the original values when assessing patterns of oak species
217 richness in the northern hemisphere. We used the mean values of each environmental
218 variable within each geographical unit in the following analyses.

219 Habitat heterogeneity is usually represented by the range values (maximum
220 minus minimum) of elevation, temperature, and precipitation, calculated within each
221 geographic unit. In addition to these variables, here we also included coarse fragments
222 volumetric of soil (CFVOL) and the number of soil types to represent habitat
223 heterogeneity. Previous studies showed higher diversification rates of *Saxifraga* in
224 rocky cliffs (de Casas *et al.* 2016). Thus, given the importance of topographic

225 heterogeneity for the overall patterns of *Saxifraga*, and considering that CFVOL is
226 often congruent with such heterogeneity, here we used this variable as an additional
227 (substrate-related) measure of habitat heterogeneity. We used mean values of soil
228 layers at four depths to represent soil properties. The number of soil types within each
229 geographical unit was also counted. Soil properties were downloaded from the global
230 soil geographic database (*SoilGrids*, <https://soilgrids.org/>, access date: 2018/04)
231 (Table S1 in Appendix S3). Based on a global compilation of soil profile data and
232 machine learning methods, *SoilGrids* predicts global volumes of coarse fragments of
233 soil at four depths (0cm, 5cm, 15 cm, and 30cm) at 1km/250m resolution (Hengl *et al.*
234 2014; Hengl *et al.* 2017).

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

237

238 **Statistical analyses**

239 We first performed univariate generalised linear models (GLMs) with negative
240 binomial residuals and ordinary least regression models (OLS) to assess the effects of
241 each environmental factor on the spatial variation of *Saxifraga* species richness.

242 GLMs have been widely used to analyze over-dispersed count data like species
243 richness (Ver Hoef and Boveng 2007). We evaluated the goodness of fit for GLMs
244 using *pseudo-R*², which was calculated as (Null Deviance-Residual Deviance)/Null
245 Deviance (Guisan and Zimmermann 2000). Because the spatial autocorrelation in
246 predictors or dependent data will increase the risk of Type I error and may lead to a
247 false significance level of GLMs, we also built simultaneous autoregressive models
248 with spatial error (SARerr) as recommended by Kissling and Carl (2008). Following
249 Xu *et al.* (2019), we set a series of gradient spatial weight matrices at a
250 neighbourhood distance range from 500 km to 3000 km with 100 km spacing in the
251 SARerr models. The spatial weights matrix for each neighbourhood distance was
252 calculated by weighting the neighbours with the row standardized coding style. We

253 finally selected one SARerr model that minimized the spatial autocorrelation in the
254 residuals (estimated by Moran's I) and the Akaike information criterion (AIC) value
255 as the best model. Due to the collinearity among variables from each environmental
256 group, partial regression was used to estimate the unique and shared effects of each
257 variable on the spatial variation of species richness. For each species group, the
258 variable from each environmental factor group with explanatory power >10% and
259 significance in SARerr was selected.

260 We testified four previously proposed models for the relationships between
261 species richness and climate using GLMs, SARerr, and OLS models, respectively.
262 The four models are (a) Richness \sim Rainfall + (PETmin - PETmin²) + log (ELER)
263 proposed by O'Brien *et al.* (2000), (b) Richness \sim WD + PET + PET² proposed by
264 Francis and Currie (2003), (c) Richness \sim TSN + ELER proposed by Janzen (1967),
265 and a combined model (d) Richness \sim Energy + Water + Seasonality + Habitat
266 Heterogeneity + Climate change since LGM. The model proposed by Wang *et al.*
267 (2011) only included four variables corresponding to four groups of contemporary
268 environmental factors. Here we included climate change since LGM to represent the
269 historical climate change effects on species richness. This model was constructed by
270 selecting one variable from each environmental group, which could reduce
271 collinearity among variables from the same environmental group (Table 1). We made
272 all the possible combinations of variables from the five environmental groups
273 resulting in 900 models for richness patterns of all species, wide-ranged species, and
274 narrow-ranged species, respectively. We excluded models including any variable with
275 variance inflation factors (VIF) larger than 3 to account for multicollinearity among
276 variables. Then the model with the lowest Akaike information criterion (AIC) was
277 selected as the best model.

278 We conducted the above analyses for the richness patterns of all species, wide-
279 ranged and narrow-ranged species, separately. All analyses were conducted in R
280 v3.5.3 (R Core Team, 2018). GLMs were carried out using the 'glm.nb' function in the
281 R package 'MASS' (Venables and Ripley 2002). Four multiple regression models

282 were also evaluated by the ordinary least squares method with log-transformed
283 richness as dependent variable following O'Brien *et al.* (2000) and Francis and Currie
284 (2003). SARerr models were run with the 'errorsarlm' function in R package 'spdep'
285 (Bivand and Wong 2018). The spatial weight matrix of the best SAR model was
286 calculated at a neighbourhood distance of 1100 km for all species, 1200 km for wide-
287 ranged species, and 900 km for narrow-ranged species.

288

289 RESULTS

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

297 Univariate GLM analysis showed that the effects of environmental factors on the
298 species richness patterns of all species are similar to those of the wide-ranged species
299 but are different from the narrow-ranged species (Table 2, Figure 3, Tables S3, S4 and
300 S5 in Appendix S3). Environmental energy, habitat heterogeneity, and environmental
301 water were the three most important factors explaining the richness patterns of all
302 species. MTWQ (mean temperature of warmest quarter, representing energy
303 availability) was the strongest predictor of variation in *Saxifraga* species richness,
304 being negatively correlated with species richness ($pseudo-R^2 = 20.22\%$, SAR: P
305 < 0.001), followed by ELER (elevation range, $pseudo-R^2 = 14.12\%$, SAR: $P < 0.001$)
306 and WD (water deficit, $pseudo-R^2 = 8.24\%$, SAR: $P < 0.001$).

307 For wide-ranged species, environmental energy, environmental water, and climate
308 change since the LGM were the top three important factors in explaining patterns of
309 species richness. Similar to models for all species of *Saxifraga*, MTWQ was

310 negatively correlated with the richness patterns of wide-ranged species and had the
311 highest explanatory power ($pseudo-R^2 = 28.33\%$, SARerr: $P < 0.001$), followed by
312 WD ($pseudo-R^2 = 10.90\%$, SARerr: $P < 0.001$) and precipitation anomaly ($pseudo-R^2$
313 $= 7.32\%$, SARerr: $P < 0.05$). Although habitat heterogeneity was positively related to
314 wide-ranged species richness, they had low explanatory power ($pseudo-R^2 < 3\%$,
315 SARerr: $P < 0.001$).

316 For narrow-ranged species, habitat heterogeneity and climate change since the
317 LGM showed the highest explanatory power on the patterns of species richness. The
318 explanatory power of ELER on narrow-ranged species richness was 36.15% and was
319 higher than TA (temperature anomaly, $pseudo-R^2 = 28.67\%$, SAR: $P < 0.05$).
320 Environmental energy, water, and temperature seasonality did not show significant
321 effects on the richness patterns of narrow-ranged species after accounting for spatial
322 autocorrelation (SARerr: $P > 0.1$).

323 Results of partial regression showed that the joint effects of MTWQ and ELER on
324 the variation of *Saxifraga* species richness was only 2.21% and the independent
325 effects of MTWQ and ELER were 18.01% and 11.90%, respectively. For wide-
326 ranged species, MTWQ independently accounted for 17.92% of the richness variation
327 after the effect of WD was controlled. In contrast, WD explained much less variation
328 (0.49%) after the effect of MTWQ was controlled (Figure 4). For narrow-ranged
329 species, the independent effect of ELER on richness variation was the largest
330 (12.86%) and long-term climate change (TA) only explained 5.38% independently.
331 Overall, partial regressions results were consistent with the results of univariate GLM,
332 indicating that the variables of environmental energy (i.e., MTWQ) were the most
333 important predictors of *Saxifraga* species richness and wide-ranged species richness,
334 whereas the variables of habitat heterogeneity were the most important predictor of
335 narrow-ranged species. Habitat heterogeneity also had a large independent effect on
336 *Saxifraga* species richness.

337 The results of multiple regression models using GLM showed that the combined
338 model has the highest explanatory power on the spatial variation of species richness

339 for all *Saxifraga* species ($pseudo-R^2 = 42.14\%$), wide-ranged species ($pseudo-R^2 =$
340 47.27%), and narrow-ranged species ($pseudo-R^2 = 54.00\%$) compare to other models
341 (Table 3). Stepwise regression selected the same variables for all species and wide-
342 ranged species richness. The second-best model was O'Brien's water-energy dynamic
343 model, which explained 52.89% of the variation in narrow-ranging species richness
344 but only 33.06% and 36.64% of the variation in species richness of all species and
345 wide-ranged species, respectively. Jazen's model explained 41.73% of the variation of
346 narrow-ranged species richness but less than 20% for all species and wide-ranged
347 species. Francis and Currie's model had poor explanatory power ($< 30\%$) on the
348 variation of all, wide-ranged and narrow-ranged species richness. Models that
349 included ELER representing habitat heterogeneity could explain a relatively high
350 proportion ($>40\%$) of the variation of narrow-ranged species richness.

351 SAR and OLS models showed similar results (Tables S6 and S7 in Appendix S3).

352

353 **DISCUSSION**

354 Using a newly compiled distribution database of *Saxifraga* species, combined with
355 multiple statistic models, we find that environmental energy (i.e. MTWQ, mean
356 temperature of warmest quarter) is negatively correlated with species richness and
357 that it is the strongest predictor of richness for all *Saxifraga* species and wide-ranged
358 species, while narrow-ranged species are mainly influenced by habitat heterogeneity.
359 These results suggest that the determinants of richness patterns for alpine-arctic
360 groups such as *Saxifraga* might be different from those in groups thriving in other
361 ecosystems. Because current studies on arctic-alpine ecosystems have mostly been
362 conducted at a local scale and confined to specific regions (Graglia *et al.* 2016; Mod
363 *et al.* 2016), more studies at a global scale on species richness patterns and their
364 determinants in these ecosystems are needed.

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

366 Recent studies suggested that the relationship between species richness and climate
367 might be driven by evolutionary history, i.e., phylogenetic niche conservatism (Pyrøn
368 and Burbrink 2009; Xu *et al.* 2019; Xu *et al.* 2013). This hypothesis suggests that
369 lineages tend to retain their ancestral ecological niche over long evolutionary
370 timescales and that colonization of new environments is relatively rare (Wiens *et al.*
371 2010). For example, plant clades with ancestral climatic niches in arid environments,
372 such as Zygophyllaceae (Wang *et al.* 2018), show a strong phylogenetic conservatism
373 to these environments and, thus, a negative relationship between species richness and
374 water availability. In our study, the negative correlation between species richness and
375 energy/water may be linked to the temperate origin and a long history of adaptation
376 and radiation in cold environments of *Saxifraga* (Ebersbach *et al.* 2017). A recent
377 phylogenetic study has found that *Saxifraga* originated in temperate North America
378 around ca. 74 Ma (Ebersbach *et al.* 2017). The ancestor of Saxifragaceae and
379 Grossulariaceae adapted to temperate regions by ca. 81 Ma (Folk *et al.* 2019).
380 Continuous climatic cooling since the Mid-Miocene and the uplift of mountain
381 regions, i.e., Himalaya-Hengduan mountains, leading to a constant expansion of
382 alpine ecosystems, might have provided suitable habitats for *Saxifraga* driving the
383 diversification of *Saxifraga* therein, followed by further diversification of phenotypic
384 and shifts of niches to the extreme cold ecosystems in alpine and arctic regions (Folk
385 *et al.* 2019). For example, *Saxifraga* species with secreting hydathodes and cushion
386 life forms can grow on limestone rocks and cliff habitats at high altitudes in mountain
387 regions, where they show a relatively high diversification rate (Ebersbach *et al.* 2017).

388

389 **Effects of habitat heterogeneity**

390 In our study, habitat heterogeneity is responsible for promoting the high richness of
391 *Saxifraga* in the Himalaya-Henduan mountains in East Asia and the Alps and
392 Pyrenees in southern Europe through the ecological process (i.e., increasing species
393 coexistence) and historical biogeography processes (i.e., promoting speciation,

394 increasing colonization rates and decreasing local extinction) (Rahbek *et al.* 2019a;
395 Rahbek *et al.* 2019b; Stein *et al.* 2014).

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

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

415 **Third**, with the increasing habitat heterogeneity, allopatric speciation rates also
416 increase due to potential dispersal barriers among different habitats, thereby
417 increasing species richness on a long timescale (Shrestha *et al.* 2018b). Compared to
418 other habitats, i.e., forest and shrublands, *Saxifraga* species diversified faster in the
419 newly emerged tundra and rocky cliffs (de Casas *et al.* 2016). Barriers between
420 mountains impeded the dispersal of *in-situ* speciated species to other regions, and
421 further promoted allopatric speciation. These radiation events make the Hengduan

422 mountains the youngest hotspot of *Saxifraga* and other alpine plant groups, i.e.,
423 *Gentiana* (Ebersbach *et al.* 2017; Favre *et al.* 2015).

424

425 **Richness patterns of species with different range sizes**

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

436 The hotspots of narrow-ranged species of *Saxifraga*, mainly in high Mountain
437 regions with long-term climate stability, are probably caused by the intrinsic properties
438 of these species including low dispersal ability, specialized niche requirements, short
439 time for dispersal and adaptation, and extrinsic factors, i.e., existing dispersal barriers
440 as reviewed by Sheth *et al.* (2020). Most narrow-ranged *Saxifraga* species are derived
441 from recent radiation events facilitated by the uplift of mountains. These recently
442 formed species might have had less time to disperse to other regions or to adapt to
443 different habitats compared to older species (Ebersbach *et al.* 2017). The complex
444 topography and soil derived from different types of rocks in the mountains promote the
445 origin of rock-cliff specialized *Saxifraga* species on one hand and preserve relict species
446 with genotypes controlling specialized adaptation on the other hand (de Casas *et al.*
447 2016). The *Saxifraga* species that originated or took refuge in mountains during
448 Quaternary climate change became narrow-ranged species (Fjeldså *et al.* 2012) due to
449 strong dispersal barriers in mountain regions. These intrinsic and extrinsic factors

450 controlling species range sizes might determine the primary predictors of the richness
451 patterns of alpine plant species with different range sizes.

452

453 **The best model**

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

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

478

479 **Conclusion**

480 We find a negative relationship between species richness and temperature in
481 *Saxifraga*, which differs from previous results that report a positive correlation in
482 woody plants. Such a negative relationship may be a result of the temperate origin and
483 the history of cold adaptation of *Saxifraga*. It remains to be explored that whether the
484 clades showing similar evolutionary trajectories with *Saxifraga* are also similar in
485 species richness patterns and determinants. We also find that habitat heterogeneity is
486 the most important factor in determining richness patterns of narrow-ranged species,
487 which show especially high richness in mountain regions. This suggests that narrow-
488 ranged *Saxifraga* species may be more susceptible to habitat loss than wide-ranged
489 species.

490

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500

501

502

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668

669 ***Supplementary data***

670 All data necessary to reproduce the analyses presented in this study are included in the
671 Supporting Information (Appendix 1 to 3).

672 Appendix S1 – Data sources for the distribution compilation of *Saxifraga*

673 Appendix S2 – The distribution records for *Saxifraga* species

675 **Tables**

676 **Table 1** The groups of climate, habitat heterogeneity, and soil variables, and their
 677 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)

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680

681 **Table 2** *Pseudo-R*² and the regression coefficients for the predictors of global species richness patterns of *Saxifraga* L. evaluated by negative binomial generalised
 682 linear models. *P-values* were calculated using simultaneous autoregressive models with a spatial error. Numbers in parentheses are standardised coefficients of
 683 respective variables. ***, *p-value* < 0.01; **, *p-value* < 0.05; *, *p-value* < 0.1. For abbreviations, see Table 1.

684

Groups	Predictors	All species		Wide-ranged species		Narrow-ranged species	
		<i>Pseudo-R</i> ² (%)	Coefficients	<i>Pseudo-R</i> ² (%)	Coefficients	<i>Pseudo-R</i> 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)
Seasonality	TSN	0.40	<0.001(-0.067)	3.69	<0.001(0.176)	21.38	<0.001(-0.805)
	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)
Habitat heterogeneity	ELER	14.12	<0.001(0.360) ***	2.34	<0.001(0.131) ***	36.15	<0.001(0.716) ***
	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)

685 **Table 3** The regression coefficients, p - values, and $pseudo-R^2$ of global species richness patterns of *Saxifraga* L. were evaluated by four multiple
 686 regression models using negative binomial generalised linear models. Numbers in parentheses are standardised coefficients of respective variables.
 687 ***, p -value < 0.01; **, p -value < 0.05; *, p -value < 0.1. For abbreviations, see Table 1.

Model type	Predictors	All species			Wide-ranged species			Narrow-ranged species		
		Coefficients	AIC	$Pseudo-R^2(\%)$	Coefficients	AIC	$Pseudo-R^2(\%)$	Coefficients	AIC	$Pseudo-R^2(\%)$
O'Brien et al. (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 ²	<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 ²	<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 et al. (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) ***		

688 Note: Wang *et al.* (2011) combined model specific: all species richness ~ energy (PET) + water (PDQ) + seasonality (PSN) + climate change since LGM
 689 (PA) + habitat heterogeneity (ELER); Wide-ranged species richness ~ energy (PET) + water (PDQ) + seasonality (PSN) + climate change since LGM (PA) +
 690 habitat heterogeneity (ELER); Narrow-ranged species richness ~ energy (PETmin) + water (AET) + seasonality (PSN) + climate change since LGM (TA) +
 691 habitat heterogeneity (CFVOL).

692 **Figures**

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

701

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

705

706 **Figure 3** The relationships between *Saxifraga* species richness and mean temperature of
707 warmest quarter (MTWQ), water deficit (WD), elevation range (ELER), and
708 temperature absolute anomaly (TA), respectively. Row (a) for all species, row (b) wide-
709 ranged species, and row (c) narrow-ranged species. Lines were fitted by generalised
710 linear models.

711

712 **Figure 4** The unique and shared variance of environmental energy, habitat
713 heterogeneity, and long-term climate change on the richness patterns of all species,
714 wide-ranged species, and narrow-ranged species using the variance partitioning
715 analysis. Habitat heterogeneity and long-term climate change were represented by
716 elevation range (ELER) and temperature absolute anomaly (TA), respectively.

1 **Tables**

2 **Table 1** The groups of climate, habitat heterogeneity, and soil variables, and their
 3 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)

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6

7 **Table 2** *Pseudo-R*² and the regression coefficients for the predictors of global species richness patterns of *Saxifraga* L. evaluated by negative binomial generalised
 8 linear models. *P-values* were calculated using simultaneous autoregressive models with a spatial error. Numbers in parentheses are standardised coefficients of
 9 respective variables. ***, *p-value* < 0.01; **, *p-value* < 0.05; *, *p-value* < 0.1. For abbreviations, see Table 1.

Groups	Predictors	All species		Wide-ranged species		Narrow-ranged species	
		<i>pseudo-R</i> ² (%)	Coefficients	<i>pseudo-R</i> ² (%)	Coefficients	<i>pseudo-R</i> 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(-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(0.05)	2.47	0(-0.162)	5.46	0.001(0.381)
	PWQ	1.58	0.001(0.133)	0.54	0(-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(-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(-0.32) ***	3.50	-0.001(-0.304)
	Rainfall	0.35	0(-0.072)	8.82	-0.001(-0.307) *	2.95	0.001(0.285)
Seasonality	TSN	0.40	0(-0.067)	3.69	0(0.176)	21.38	0(-0.805)
	ART	1.06	-0.001(-0.111)	1.83	0.001(0.127)	17.72	-0.01(-0.7)
	PSN	0.01	0(0.012) *	1.29	-0.003(-0.11)	12.28	0.015(0.426)
Habitat heterogeneity	ELER	14.12	0(0.36) ***	2.34	0(0.131) ***	36.15	0(0.716) ***
	MATR	13.48	0.004(0.366) ***	2.75	0.001(0.142) ***	32.09	0.009(0.765) **
	MAPR	8.41	0(0.307)	1.14	0(0.095)	19.60	0(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(0.65) ***
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)

11 **Table 3** The regression coefficients, *p* - values, and *pseudo-R*² of global species richness patterns of *Saxifraga* L. were evaluated by four multiple
 12 regression models using negative binomial generalised linear models. Numbers in parentheses are standardised coefficients of respective variables.
 13 ***, *p*-value < 0.01; **, *p*-value < 0.05; *, *p*-value < 0.1. For abbreviations, see Table 1.

Model type	Predictors	All species			Wide-ranged species			Narrow-ranged species		
		Coefficients	AIC	<i>Pseudo-R</i> ² (%)	Coefficients	AIC	<i>Pseudo-R</i> ² (%)	Coefficients	AIC	<i>Pseudo-R</i> ² (%)
O'Brien et al. (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 ²	<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 ²	<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 et al. (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) ***		

14 Note: Stepwise regression models specific: all species richness ~ energy (PET) + water (PDQ) + seasonality (PSN) + climate change since LGM (PA) +
 15 habitat heterogeneity (ELER); Wide-ranged species richness ~ energy (PET) + water (PDQ) + seasonality (PSN) + climate change since LGM (PA) + habitat
 16 heterogeneity (ELER); Narrow-ranged species richness ~ energy (PETmin) + water (AET) + seasonality (PSN) + climate change since LGM (TA) + habitat
 17 heterogeneity (CFVOL).

Figures

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., (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 (1700m), Jilin, China, and the Beishan (3800m), Xizang, China, respectively. — Photographed by Lei Zhang.



Figure 2 Global patterns of species richness of *Saxifraga* L. (a) all species, (b) wide-ranged species, and (c) narrow-ranged species.

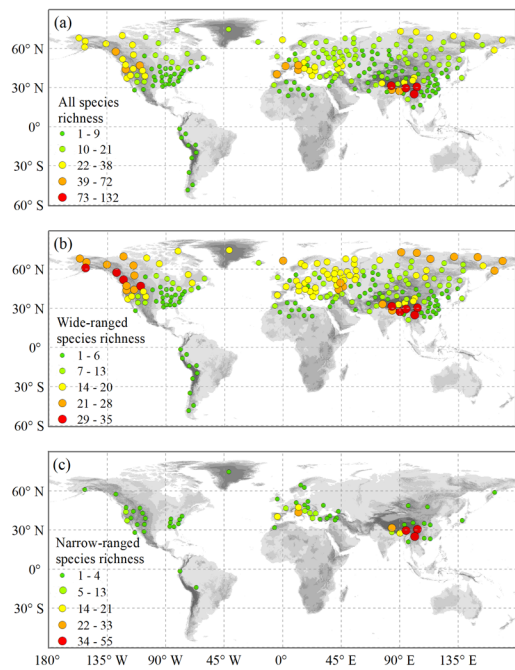


Figure 3 The relationships between *Saxifraga* species richness and mean temperature of the warmest quarter (MTWQ), water deficit (WD), elevation range (ELER), and temperature absolute anomaly (TA), respectively. Row (a) for all species, row (b) wide-ranged species, and row (c) narrow-ranged species. Lines were fitted by generalised linear models.

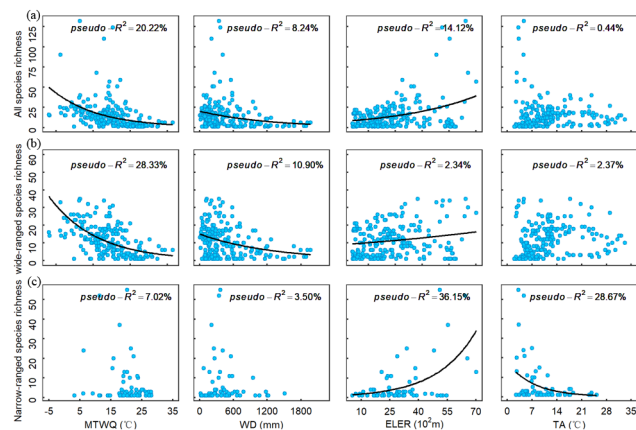


Figure 4 The unique and shared variance of environmental energy, habitat heterogeneity, and long-term climate change on the richness patterns of all species, wide-ranged species, and narrow-ranged species using the variance partitioning analysis. Habitat heterogeneity and long-term climate change were represented by elevation range (ELER) and temperature absolute anomaly (TA), respectively.

