

1 **Phylogeny and climate explain contrasting hydraulic traits in different life forms**
2 **of 150 woody Fabaceae species**

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41

42 Author contributions

43 Hui Liu and Qing Ye designed the study. Hui Liu, Xiaorong Liu, Qi Luo, Yixue Lin,
44 Nan Ye collected data. Hui Liu performed the analyses. Hui Liu and Qing Ye drafted
45 the manuscript and Marjorie R. Lundgren, Sophie N. R. Young, Guangyou Hao
46 contributed substantially to subsequent versions.

47

48 Conflict of interest

49 The authors declare no conflict of interest.

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51 Data accessibility statement

52 The data that support the findings of this study are available on the Dryad Digital
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54

55 It is not open yet, the Reviewer sharing link is:

56 https://datadryad.org/stash/share/t06NBJWT8n1doHeZ55YFtPzMmgi1U5E4RmK_w
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58

59

60 **Abstract**

- 61 1. The contrasting hydraulic traits observed among different plant life forms are
62 shaped by entangled environmental and evolutionary processes. However, we lack
63 understanding of the relative importance of life form, climate and phylogeny in
64 explaining the variance of hydraulic traits.
- 65 2. We analyzed seven hydraulic traits and eleven climatic variables of 150 Fabaceae
66 species representing three life forms from 62 sites worldwide, using phylogenetic
67 comparative analyses and variance partitioning.
- 68 3. The phylogenetic signal found in most traits disappeared after considering life form,
69 indicating that phylogenetic conservatism in traits originated from the divergence
70 among life forms. The trait-climate relationships were also phylogenetically
71 dependent, implying that trait responses are driven by climate and phylogeny
72 together. Variance partitioning showed that phylogeny and climate explained
73 greater trait variation than life form did.
- 74 4. *Synthesis.* The climate-driven hydraulic trait responses in Fabaceae still existed
75 with phylogeny being considered, suggesting that this large family may be
76 particularly sensitive to climate change. Our results emphasize the need to include
77 phylogeny in plant hydraulic adaptation studies under future climate change.

78

79 **Key words:** climatic niche, embolism vulnerability, leaf to stem area ratio,
80 photosynthetic rate, phylogenetic generalized least square, plant life form, sapwood
81 density, specific leaf area, xylem hydraulic conductivity, variance partitioning.

82

83

84 摘要

85 1. 植物的水力性状在不同的植物生活型中差异显著，且是复杂的环境适应和演
86 化过程形成的结果。然而，我们对植物生活型、气候变量和系统发育在解释
87 植物水力性状差异的相对重要性方面仍缺乏了解。

88 2. 我们构建了一个来自全球 62 个样点、乔灌藤三种生活型的 150 个豆科物种
89 共 7 个水力性状和 11 个气候变量的数据库，用系统发育比较分析和方差分解
90 的方法解析了上述问题。

91 3. 考虑植物生活型后，大多数水力性状和气候变量中发现的系统发育信号消失
92 了，这表明这些参数的系统发育保守性源于植物生活型之间的分化。水力性
93 状与气候变量的关系也具有系统发育依赖性，这意味着性状变异是由气候和
94 系统发育共同驱动的。方差分解的结果表明系统发育和气候变量比植物生活
95 型解释了更多的水力性状变异。

96 4. 即使考虑了系统发育的影响，豆科植物中气候驱动的水力性状响应仍然存
97 在，表明这个世界广布的大科可能对气候变化特别敏感。我们的结果强调了
98 将系统发育纳入未来气候变化下植物水分适应机理研究中的重要性。

99

100 **Introduction**

101 The hydraulic system is crucial to the survival and growth of plants (W. R. L. Anderegg
102 et al., 2016; Choat et al., 2018; Hammond et al., 2022). Across global biomes, plants
103 have developed distinct hydraulic strategies to adapt to environmental water status. To
104 quantify these differing strategies, several key hydraulic traits have been widely
105 measured. In particular, stem xylem hydraulic conductivity (K_S) and the water potential
106 at which 50% of maximal conductivity is lost (P50) have long been used to assess plant
107 hydraulic efficiency and xylem safety, respectively (Sperry et al., 1988). At the global
108 scale, K_S and P50 show weak trade-offs, representing strategies from high hydraulic
109 efficiency (*i.e.* high K_S) to robust drought tolerance (*i.e.* more negative P50) (Gleason
110 et al., 2016). These two key hydraulic traits are related to wood density and the diameter
111 of stem vessels (Chave et al., 2009). As for leaf traits, turgor loss point (Ψ_{tlp}) is an
112 indicator of leaf drought tolerance (Bartlett et al., 2016), while photosynthetic rate per
113 leaf area (A_{area}) and specific leaf area (SLA) are components of the classic leaf
114 economics spectrum (LES) that link the LES to hydraulic traits (Wright et al., 2004).
115 Leaf to stem area ratio (A_L/A_S) is another widely used trait that relates to whole plant
116 economics and hydraulics, and reflects the water balance between leaf-level water
117 consumption and stem-level water supply (Mencuccini et al., 2019). Some plant
118 hydraulic traits are particularly sensitive to climatic conditions across species and
119 regions. For instance, K_S increases with growth season temperature and precipitation
120 on a global scale (He et al., 2020), while Ψ_{tlp} and P50 become less negative from arid
121 to humid regions (Peters et al., 2021). Therefore, identifying different plant hydraulic
122 strategies and how hydraulic traits are related to climate is crucial for understanding
123 plant responses to increasing global drought events (W. R. L. Anderegg et al., 2019;
124 Brodribb et al., 2020).

125 Phylogenetic niche conservatism (PNC) in hydraulic traits has been reported in
126 diverse plant families (Ávila-Lovera et al., 2023; Liu et al., 2015; Sanchez-Martinez et
127 al., 2020), indicating that closely related species are more likely to show similar water
128 use strategies. Previous phylogenetic studies have shown that it is easier to detect PNC
129 in functional traits at large spatial scales or across families than within a single family

130 (Cavender-Bares et al., 2006; Graham et al., 2018; Losos, 2008). However, identifying
131 PNC within a single family can be more ecologically meaningful, and reveal
132 phylogenetic effects in great details, such as the divergent evolution of hydraulic traits
133 detected across different life forms in Magnoliaceae (Liu et al., 2015). Meanwhile, how
134 phylogeny is further related to species adaptations to climate remains unclear, as many
135 studies on trait-climate relationships do not consider phylogeny (Pinho et al., 2021;
136 Skelton et al., 2021). Of those few studies that have tested the role of phylogeny in trait-
137 climate relationships, one detected phylogenetic signals in the relationships of height
138 and leaf size with mean growth season temperature and precipitation (Liu, Osborne, et
139 al., 2019), another detected phylogenetic signals in the relationships between five
140 hydraulic traits and the global water availability gradient (Sanchez-Martinez et al.,
141 2020). These findings suggest that phylogenetic analyses on traits and trait-climate
142 relationships are meaningful, and more are needed to reveal the mechanisms underlying
143 plant responses to climate (L. D. L. Anderegg, 2023).

144 In addition to phylogeny, life form (growth form) is also a crucial factor that
145 influences plant traits and their responses to climate. Life form is determined by both
146 short-term environmental adaptation and long-term evolution processes. As such,
147 different life forms are restricted to specific climatic and geographic ranges (Xu et al.,
148 2018). Indeed, different climate niches and anatomical structures among tree, shrub and
149 liana life forms have long been recognized (Baas & Schweingruber, 1987; Du Rietz,
150 1931; Schnitzer, 2002). For example, shrubs typically exist in more arid areas, and have
151 more drought tolerant traits than coexisting trees (David. D Ackerly & DD, 2004).
152 Meanwhile, lianas have large vessels and little wood for mechanical support (Rosell &
153 Olson, 2014), which results in high water transport efficiency (*i.e.* high K_S), but
154 increased vulnerability to drought-induced cavitation relative to trees: an example of
155 the hydraulic tradeoff between efficiency and safety (Chen et al., 2015; Willson et al.,
156 2022; Zhu & Cao, 2009). However, another study found that hydraulic efficiency was
157 decoupled from safety in tropical lianas (van der Sande et al., 2019). These direct
158 comparison studies between life forms, however, may be confounded by phylogeny,
159 *i.e.*, species from different families are intrinsically different, or life form itself is related

160 with phylogenetic background. Nevertheless, direct comparisons between life forms
161 against a phylogenetic background within a single family are still lacking.

162 As the third largest family of angiosperms, Fabaceae has ~770 genera and over
163 19,500 species (Azani et al., 2017). Many species in Fabaceae are cosmopolitan,
164 showing particular diversity and abundance in seasonal dry tropical forests and
165 temperate shrub lands, thus making the family a longtime focus of ecological studies
166 (Gagnon et al., 2019; Lewis et al., 2005; Rundel, 1989; Yahara et al., 2013). Life forms
167 in Fabaceae range from herbs and lianas, to shrubs and trees, which are each adapted to
168 diverse environments (Lewis et al., 2005). An inventory of 42 Neotropical forests found
169 that the abundance of species in Fabaceae was twice as high in dry (drought deciduous)
170 versus wet (evergreen) secondary forests (Gei et al., 2018). The authors attributed the
171 success of the dry-forest Fabaceae species to their small leaflets, which facilitate leaf
172 temperature regulation and their ability to fix nitrogen, which in turn confers a
173 photosynthetic advantage. However, these explanations do not account for hydraulic
174 traits, which are directly linked with plant drought tolerance, and are crucial both in
175 explaining the distribution of species in Fabaceae, and in predicting their responses to
176 future climate change.

177 Overall, linking hydraulic traits to life form, phylogeny and climatic conditions
178 could help us understand how hydraulic strategies facilitate the high diversity and
179 global distribution of Fabaceae. Here, we perform phylogenetic analyses on seven
180 hydraulic traits and eleven climatic variables of 150 Fabaceae species representing three
181 woody life forms (lianas, trees and shrubs) from 62 sites worldwide (Fig. 1) to address
182 the following questions: (1) Are phylogenetic signals present in hydraulic traits of
183 Fabaceae species? Given that PNC has already been found in hydraulic traits within
184 two single families (Liu et al., 2015; Liu & Osborne, 2015), we expect to find similar
185 phylogenetic signals in hydraulic traits here. However, the phylogenetic signals may be
186 weak because the contrasting traits among life forms may confound the results, as
187 detected for trees versus shrubs in Magnoliaceae (Liu et al., 2015). (2) How are
188 hydraulic trait-climate relationships affected by phylogeny in Fabaceae? Previous
189 attempts to answer this question in other families have either showed no phylogenetic

190 effects (Liu & Osborne, 2015) or significant phylogenetic effects on diverse trait-
191 climate relationships (Liu, Osborne, et al., 2019), thus more investigation is needed. (3)
192 What are the relative contributions of climate, phylogeny and life form in explaining
193 the variance in hydraulic traits in Fabaceae? We expect that a large proportion of trait
194 variance may be attributed to phylogeny because phylogeny reflects intrinsic
195 interspecific differences (Losos, 2008), which form the basis for climatic selection and
196 plant adaptations.

197

198 **Materials and Methods**

199 **Hydraulic data**

200 We compiled a by far the largest dataset of hydraulic traits for woody species in
201 Fabaceae. We did not include herbaceous species as their stem trait measurements are
202 different from woody ones and thus, are not directly comparable with woody species.
203 This dataset was composed of data gathered from the literature (detailed references are
204 provided in [Table S1](#)), and data of eleven woody Fabaceae species measured by this
205 study (detailed measurement methods are provided in [Notes S1](#), we did not need
206 permission for fieldwork). For inclusion in our dataset, data were required to meet the
207 following criteria: (1) all the stem traits were measured on small terminal branches
208 (0.4~1.0 cm in diameter, because these branches were most commonly reported in
209 literature), and all the leaf traits were measured on sun exposed mature leaves; (2) all
210 the individuals were from natural field experiments rather than greenhouse experiments,
211 in order to correspond to natural climate data. In total, we had seven hydraulic traits in
212 the dataset: sapwood specific hydraulic conductivity (K_S), the water potential at which
213 50% of maximal conductivity is lost (P50), wood density (WD), stem vessel diameter
214 (V_{dia}), photosynthetic rate per leaf area (A_{area}), specific leaf area (SLA), and leaf to
215 stem area ratio (A_L/A_S). Furthermore, we distinguished life form for each species based
216 on their maximum height and/or qualitative descriptors from floras: trees are tall
217 perennial woody plants that are greater than five meters, shrubs are short perennial
218 woody plants that are less than five meters, and lianas are clearly described as woody
219 vines without a specified height. The final dataset included 150 Fabaceae species (34

220 lianas, 82 trees and 34 shrubs) from 62 sites worldwide (Table S1).

221

222 **Climate data**

223 For all the 62 georeferenced sites in the hydraulic traits database, we extracted climatic
224 data from the WorldClim2 database (Fick & Hijmans, 2017) using the *extract* function
225 in the R 3.5.1 (R Core Team, 2018) package *raster* (Hijmans et al., 2022). Next we
226 extracted values for the aridity index (AI = MAP/PET; ratio of mean annual
227 precipitation to potential evapotranspiration) from the Global-Aridity dataset
228 (<http://www.cgiar-csi.org>). Higher AI values are indicative of a wetter climate. Both
229 the WorldClim2 and Global-Aridity datasets are based on average values from 1950–
230 2000 from weather station data at 0.5×0.5 degree resolution. In total, we included
231 eleven climatic variables: aridity index (AI), mean annual temperature (MAT),
232 seasonality of temperature (Ts; standard deviation across monthly measurements ×
233 100), the highest and lowest temperatures of the year (Tmax, Tmin), mean annual
234 precipitation (MAP), seasonality of precipitation (Ps; coefficient of variation across
235 monthly measurements × 100), the highest and lowest monthly precipitation of the
236 year (Pmax, Pmin), vapor pressure deficit (VPD) and solar radiation (SR). We extracted
237 water vapor (VP) and SR values for 12 months at each site from WorldClim2, then
238 calculated VPD as the difference between VP and VP at saturation (VPsat - VP). We
239 calculated monthly VP_{sat} based on monthly air temperature (T) as $a \times \exp[b \times T / (c + T)]$,
240 where *a*, *b*, and *c* are constants of 0.611 kPa, 17.502 (unitless), and 240.97 °C,
241 respectively (Campbell & Norman, 1998). VPD was an indicator of the evaporative
242 potential of the atmosphere, and SR indicated solar energy received. Mean values of 12
243 months' VPD and SR were used in the analyses. These variables reflect the mean and
244 extreme values of climatic conditions for each site, as well as the degree to which they
245 fluctuate, all of which may affect plant adaptations through hydraulic traits.

246

247 **Phylogenetic tree**

248 We constructed a phylogenetic tree of the 150 Fabaceae species using the R package
249 *V.PhyloMaker2* (Jin & Qian, 2022). The mega-tree *GBOTB.extended.tre* in this

250 package includes 74,531 species of 479 families, the largest dated plant phylogeny
251 derived from two famous mega-trees, based on molecular data from NCBI GenBank,
252 phylogenetic data from the Open Tree of Life, and fossil records (Smith & Brown, 2018;
253 Amy E. Zanne et al., 2014). Twelve of our Fabaceae species were missing from the
254 mega-tree. For these species, we selected Scenario 3 in *V.PhyloMaker2* to manually
255 attach them to their close relatives in the mega-tree using the branch length adjuster
256 (BLADJ) method. The rule that BLADJ binds the tip for a new species to the half-way
257 point of the genus branch originated from Phylocom (Webb et al., 2008). We adjusted
258 the positions of two species according to published phylogenies because they were
259 arranged incorrectly as outliers; namely *Parapiptadenia rigida* (Sulaiman et al., 2003)
260 and *Syrmatium glabrum* (Degtjareva et al., 2006). These efforts yielded a 150-species
261 time-calibrated tree that we used in subsequent analyses (Fig. 1).

262

263 **Data analyses**

264 All analyses and figures were done in R 4.1.1 (R Core Team, 2018). For each trait, we
265 first calculated mean values for multiple measures on the same species from the same
266 site. Next, for the 20 species that occurred in more than one site, we averaged their trait
267 values across sites for each species, as the phylogenetic models can only accommodate
268 one value per species. All the data were ln-transformed to fulfil the requirement of
269 normal distribution in the following analyses and, if the original values were negative
270 (e.g., P50), absolute values were used.

271 To test how hydraulic traits differed among life forms (lianas, trees and shrubs),
272 we used ANOVA and multiple comparisons. We checked the residuals-versus-fits plot
273 for each ANOVA to ensure the homogeneity of variance of each model using the
274 Levene's test from the *leveneTest* function in the R package *car* (Hector et al., 2010).
275 Then we used Scheffé's *S* test for multiple comparisons to handle different sample sizes
276 in each life form, because this test is conservative and entirely coherent with ANOVA
277 results (Midway et al., 2020). Scheffé's *S* test was done with the function *scheffe.test*
278 in the R package *agricolae*, and values and multiple comparison results of plant traits
279 and climatic variables were reported in Table S2 and Notes S2.

280 To examine phylogenetic signals (the first question in our study), we first
281 employed δ to measure the phylogenetic signal for categorical traits (*i.e.*, life form).
282 The δ statistic is based on the concept of Shannon entropy, where higher δ values
283 indicate stronger phylogenetic signals. This approach calculates 1000 simulated δ by
284 randomly sampling the categorical trait 1000 times. P values are estimated by
285 comparing true and simulated δ , and $P < 0.05$ means a significant phylogenetic signal
286 (Borges et al., 2019). Next we estimated Pagel's λ for quantitative traits (*i.e.*, hydraulic
287 and climate data). Pagel's λ indicates the degree to which the residual variation of a trait
288 correlates with phylogeny, using maximum likelihood (Pagel, 1999). It gives λ values
289 between zero and one, for which $\lambda = 0$ indicates no phylogenetic signal, whereas $\lambda = 1$
290 implies that the distribution of trait values across the phylogeny is as expected under
291 Brownian motion. We constructed phylogenetic generalized least square (PGLS)
292 models using the *pgls* function in the R package *caper* (Orme et al., 2018). For each
293 trait y , we used the model *pgls*($y \sim 1$) to investigate phylogenetic signal in trait y and
294 *pgls*($y \sim$ life form) to test the influence of life form, and found that all the models had
295 normally or near normally distributed residuals. Strong phylogenetic signals indicate
296 that species have retained their ancestral traits, while weak phylogenetic signals
297 indicate that traits among species were more labile.

298 To explore how trait-climate relationships are affected by phylogeny (the second
299 question in our study), we first reduced the number of dimensions in our hydraulic traits
300 and climatic variables dataset using phylogenetic principal component analysis (PPCA).
301 We carried out the PPCA using the *phyl.pca* function in the R package *phytools* (Revell,
302 2012). We used PPCA rather than conventional PCA, because PPCA accounts for
303 phylogenetic non-independence among species, and we theorized that life form and
304 phylogeny act in concert to shape the ecology of Fabaceae (Fig. 1). We did not do
305 pairwise relationships for each climatic variable because those variables are unlikely to
306 influence traits individually (Chave et al., 2009). As missing data markedly reduced
307 sample size in PPCA, we limited the PPCA to four hydraulic traits (K_S , P50, WD,
308 A_L/A_S). These traits had sufficiently large sample sizes and also when taken together
309 represented both hydraulic efficiency (K_S , WD, A_L/A_S) and safety (P50). We carried out

310 the PPCA on the hydraulic traits and climatic variables separately, and extracted their
311 first and second phylogenetic principal components (PPC1 and PPC2). We noticed that
312 in climate PPCA, precipitation of driest month (Pmin) and precipitation seasonality (Ps)
313 were the first two variables of PPC3, which may also affect hydraulic traits (Liu et al.,
314 2021), but the total variance explained by PPC3 was only 11.1%, therefore we only
315 used PPC1 and PPC2 in the subsequent analyses because they accounted for the highest
316 percentage of total variance (75.3%) compared to other components. We then estimated
317 Pagel's λ for PPC1 and PPC2 (as done previously for the individual traits), and tested
318 the relationships between traits and climate PPC1 and PPC2 using PGLS models
319 *pgls*($y \sim \text{PPC1}$) and *pgls*($y \sim \text{PPC2}$). Furthermore, conventional trait-climate relationships
320 that did not control for phylogeny were modeled as *lm*($y \sim \text{PPCs}$) and *sma*($y \sim \text{PPCs}$),
321 using general linear models (LM), and standardized major axis (SMA) regressions in
322 the R package *smatr* (Warton et al., 2012), in order to compare relationships when
323 phylogeny is accounted for and when it is not.

324 To calculate the relative importance of climate, phylogeny and life form in
325 explaining the variance of each hydraulic trait and trait PPC1 and PPC2 (the third
326 question in our study), we used the phylogenetic eigenvector regression (PVR) to
327 partition the total variance (Desdevises et al., 2003). Although PGLS can detect
328 differences between phylogenetic and conventional models, it cannot assign a value to
329 the proportion of variance explained by phylogeny. PVR used multiple linear regression
330 models of a dependent variable (trait y) based on two factors: phylogenetic and
331 ecological components. The variance of y could be partitioned as $[a]+[b]+[c]+[d]$,
332 where $[a]$ is the pure ecological effect, $[b]$ is the interaction between ecology and
333 phylogeny, $[c]$ is the pure phylogenetic effect, and $[d]$ is the unexplained variance. In
334 this study, we accounted for ecological effects as either climate or life form, and
335 phylogenetic effect as phylogenetic principal coordinates (*i.e.*, species scores along
336 eigenvectors) calculated from a distance matrix. Then we calculated R^2 from multiple
337 regression models, including Model E ($y \sim \text{climate or life form}$; $R^2_{\text{E}}=[a]+[b]$), Model P
338 ($y \sim \text{phylogenetic principal coordinates}$; $R^2_{\text{P}}=[b]+[c]$), and Model PE ($y \sim \text{both}$
339 $\text{phylogenetic and ecological variables}$; $R^2_{\text{PE}}=[a]+[b]+[c]$). Therefore, the individual

340 values of [a], [b] and [c] are calculated as: $[a]=R^2_{PE}-R^2_P$; $[b]=R^2_P+R^2_E-R^2_{PE}$; $[c]=R^2_{PE}-$
341 R^2_E , leaving the residual $[d]=1-[a]-[b]-[c]$. Notably, although Model E or Model P
342 includes only ecological or phylogenetic factors, the variance of the model still contains
343 the overlap part between ecology and phylogeny, due to their inseparable nature (Table
344 S5). Only variables that significantly contribute to each multiple regression model will
345 be retained based on a stepwise variable selection. Akaike Information Criterion (AIC)
346 values were used to select the most parsimonious models (Burnham et al., 2011). All
347 the principal coordinates were used in the full phylogenetic model, in order to extract
348 as many phylogenetic effects as possible, while Model PE used the combined variables
349 from Model E and P (Desvignes et al., 2003). We built three models to partition
350 variance, namely Climate+Phylogeny (Model CP), Lifeform+Phylogeny (Model LP)
351 and Lifeform+Climate (Model LC).

352

353 Results

354 Sampling patterns and trait differences among life forms

355 Across the phylogenetic tree, life form showed a significant phylogenetic signal
356 ($\delta=2.11$, mean of random $\delta=0.51$, $P<0.001$), with lianas clustered in Cercidoideae and
357 shrubs in Papilionoideae (Fig. 1a). The 150 sampled species across Fabaceae showed
358 no phylogenetic signal ($\delta=4.72$, mean of random $\delta=25.34$, $P=1.000$), indicating that
359 they were randomly distributed across the whole family (Fig. 1b). Furthermore, the
360 distribution of sites and the number of species from each life form across the global
361 map showed that sites were widely distributed in both dry and wet environments (Fig.
362 1c,d,e), thus climatic niche differences across life forms were caused by species
363 preference rather than sampling bias (Table S2).

364 Hydraulic traits and climatic niches differed significantly among life forms in
365 Fabaceae (detailed results in Notes S2, Fig. S1 and Table S2). Briefly, lianas exhibit
366 riskier hydraulic strategies (*i.e.*, high K_s and P50, low WD, wide V_{dia} , high A_L/A_s and
367 SLA), whereas shrubs are more conservative. Lianas live in wet habitats while shrubs
368 are found in drier and cooler places (*i.e.*, lowest mean annual precipitation and
369 temperature, strongest seasonality *etc.*). Trees show intermediate hydraulic traits and

370 climatic variables between lianas and shrubs (Fig. S1; Table S2).

371

372 **Phylogenetic Principal Components Analyses**

373 The first two components of PPCA on the four hydraulic traits explained 78.8% of the
374 total variation (PPC1, 52.3%; PPC2, 26.4%; Fig. 2a; Table S3a). K_S and A_L/A_S had
375 positive loadings on PPC1, while WD had a negative loading on PPC1, indicating an
376 axis of hydraulic efficiency along PPC1. P50 was associated with PPC2, reflecting an
377 axis of hydraulic safety. PPCA distinguished the three life forms along PPC1 but not
378 PPC2. Lianas fell more positively than shrubs along PPC1, while trees were
379 intermediate between the two (Fig. 2a).

380 PPC1 and PPC2 based on the eleven climatic variables explained 46.3% and 29.0%
381 of the total variation, respectively (Fig. 2b; Table S3b). MAT, Pmax, Tmin and MAP
382 were the first four positive loadings on PPC1, while Ts was the only negative loading.
383 AI was positively, and VPD negatively correlated with PPC2. Similar to the hydraulic
384 PPCA, the climatic PPCA distinguished shrubs from trees and lianas through PPC1 but
385 not PPC2 (Fig. 2b). Higher values of PPC1 indicated hotter (MAT and Tmin), wetter
386 (MAP and Pmax) and less seasonal (Ts) climatic conditions, and higher values of PPC2
387 indicated more precipitation (higher AI) and wetter air (VPD) environment.

388

389 **Phylogenetic signal in hydraulic traits and climatic variables**

390 All seven hydraulic traits, except A_{area} , showed significant phylogenetic signal ($\lambda=0.33$ –
391 0.73 , $P<0.05$ for $\lambda=0$; Table 2a). However, adding the factor *life form* into the models
392 eliminated the phylogenetic signal in all traits (all $P>0.05$ for $\lambda=0$; Table 2a). PPC1 of
393 those traits showed phylogenetic signal but lost it when *life form* was added, while
394 PPC2 had no phylogenetic signals with or without life form (Table 2a).

395 All eleven climatic variables, except SR, exhibited strong phylogenetic signals
396 ($\lambda=0.14$ – 0.90 , $P<0.05$ for $\lambda=0$; Table 2b). Adding *life form* into PGLS lead to four
397 invalid models ($P>0.05$, R^2 values as low as 0.01 – 0.03), eliminated phylogenetic
398 signals for five variables, and maintained phylogenetic signals in only MAT and Ts
399 ($\lambda=0.43$ and 0.61 , respectively; Table 2b). Both climate PPC1 and PPC2 showed

400 phylogenetic signals, but the signals also lost after considering *life form* (Table 2b).

401

402 **Phylogenetic influences on the trait-climate relationships**

403 We found significant positive relationships between climate PPC1 and K_S , V_{dia} , A_L/A_S
404 and SLA, and negative relationships between climate PPC1 and P50 and WD (Fig. 3).

405 After accounting for phylogeny in PGLS models, the slopes of all the relationships
406 became flatter compared to LM and SMA models though the overall trend remained
407 the same (red lines in Fig. 3; Table S4a). This indicated that Fabaceae species (*esp.*
408 shrubs) have lower K_S and P50, narrower vessels and more dense wood and leaves,
409 support less leaf areas per stem area in cooler and drier habitats. R^2 of PGLS ($R^2=0.08$ –
410 0.17) was slightly lower than R^2 of LM and SMA ($R^2=0.09$ – 0.20) (Table S4a).
411 Meanwhile, phylogenetic signals in all the relationships also became weaker ($\lambda=0.14$ –
412 0.52 ; Table S4a) than in the single traits ($\lambda=0.33$ – 0.73 ; Table 1a).

413 Climate PPC1 did not show a correlation with A_{area} , but PPC2 showed a negative
414 relationship with A_{area} (Fig. S2; Table S4b). Similarly, the PGLS slopes of trait-climate
415 relationships based on PPC2 were flatter than slopes of LM and SMA models, R^2 values
416 of PGLS were also slightly lower, phylogenetic signals in the relationships were weaker
417 than in the single traits (Fig. S2; Table S4b).

418

419 **Variance partitioning of different hydraulic traits**

420 For K_S , Climate+Phylogeny (Model CP) and Lifeform+Phylogeny (Model LP) fitted
421 better than Lifeform+Climate (Model LC) ($R^2=0.829$, 0.819 and 0.638 , respectively;
422 Table S5). In Model CP, joint contribution of climate and phylogeny accounted for the
423 largest proportion of the total variance (44%; Fig. 4a), while in Model LP, phylogeny
424 showed the largest proportion (43%; Fig. 4b), and in Model LC, the proportion of the
425 residual was the largest, indicating that neither life form nor climate influenced much
426 (36%; Fig. 4c). Overall, K_S was best explained by phylogeny (both single and joint
427 effects $R^2=0.772$, hereafter as joint R^2), followed by climate (joint $R^2=0.499$) and life
428 form (joint $R^2=0.389$; Table S5).

429 For P50, Model CP and Model LP also fitted better than Model LC, and in the

430 three models, phylogeny (46%), phylogeny (60%) and residual (62%) explained the
431 largest proportion of variance, respectively. P50 was best explained by phylogeny (joint
432 $R^2=0.677$), then climate (0.329) and life form (0.103; Fig. 4; Table S5). Similarly for
433 WD, Model CP and LP fitted better than LC, with phylogeny (41%), phylogeny (37%)
434 and residual (53%) as the largest proportion of explained variance, respectively. WD
435 was best explained by phylogeny (joint $R^2=0.682$), then life form (0.356) and climate
436 (0.312; Fig. 4; Table S5). For Vdia, Model CP, LP and LC showed similar fitness,
437 corresponding to the largest proportion as joint effect of climate and phylogeny (49%),
438 residual (40%) and residual (37%), respectively. Vdia was nearly evenly explained by
439 phylogeny (joint $R^2=0.583$), climate (0.547), and life form (0.315; Fig. 4; Table S5).

440 For A_{area} , climate (40%), residual (75%) and climate (60%) were the largest
441 proportion of explained variance for Model CP, LP and LC, respectively. A_{area} was
442 explained by the order climate (joint $R^2=0.602$), phylogeny (0.245) and life form
443 (0.009). For A_L/A_S , the largest explanatory factors in Model CP, LP and LC were joint
444 effect of climate and phylogeny (39%), residual (48%) and climate (57%), respectively.
445 A_L/A_S was explained by climate (joint $R^2=0.732$), phylogeny (0.481) and life form
446 (0.208). For SLA, the largest explanatory factors in Model CP, LP and LC were climate
447 and phylogeny joint effect (53%), phylogeny (47%) and residual (37%), respectively.
448 SLA was explained by the order phylogeny, climate and life form (joint $R^2=0.740$,
449 0.606 and 0.305, respectively; Fig. 4; Table S5). Analyses on trait PPC1 and PPC2
450 showed similar variance partitioning patterns as for K_S and P50 (the largest loadings on
451 each axis), respectively, except that the proportion of explained variance of life form
452 for PPC2 was smaller than that for P50 (0.028 versus 0.103, Fig. 4; Table S5).

453

454 Discussion

455 This study clarified how hydraulic strategies differed among three woody life forms of
456 Fabaceae species, and disentangled the effects of life form, phylogeny and climate on
457 hydraulic traits of Fabaceae species across a broad taxonomic and geographical range.
458 Phylogenetic signal existed in most plant traits and climatic variables, but disappeared
459 when life form was considered, implying that phylogenetic niche conservatism in

460 Fabaceae may originate from the divergence among life forms. Meanwhile, the
461 phylogeny-based trait-climate relationships became flatter than those conventional
462 models, showing that trait responses were influenced by both evolution and
463 environment, thus will be very sensitive to future climate change. Variance partitioning
464 further indicated that most traits were explained mainly by phylogeny or climate, and
465 by life form to a lesser extent. This study thoroughly examine the ecological and
466 evolutionary drivers beyond hydraulic adaptation of Fabaceae, provide evidence that
467 phylogeny acts as the cornerstone and climate as a strong selective pressure on the
468 contrasting hydraulic strategies between lianas and shrubs (Willson et al., 2022). Our
469 study therefore emphasizes the need to consider phylogeny in evaluating hydraulic
470 susceptibility of Fabaceae species to more frequent future heat and drought events
471 (Hammond et al., 2022).

472

473 **Different hydraulic adaptive strategies among life forms**

474 Contrasting hydraulic traits among the three life forms of Fabaceae reflect their
475 adaptive strategies, which are consistent with previous studies across diverse plant
476 families (Baas & Schweingruber, 1987; Liu, Gleason, et al., 2019; Rosell & Olson,
477 2014; Schnitzer, 2002). In general, corresponding to the climate niches, Fabaceae lianas
478 and shrubs fall at two ends of the “hydraulic spectrum” from luxurious to conservative
479 water use strategies (Oliveira et al., 2021), with trees in the middle. On one hand, lianas
480 live in wet habitats and have extremely high hydraulic conductivity (K_S), which may be
481 caused by highly variable vessel diameter (V_{dia}) as reported before (Dias et al., 2019)
482 and by greater water demand from higher leaf area per stem area (A_L/A_S) (Fig. S1). Such
483 highly variable V_{dia} may further enable lianas to break the constraint of hydraulic
484 efficiency and safety trade-off (Fig. S4) (van der Sande et al., 2019). Indeed, lianas did
485 not significantly differ from trees in hydraulic safety (P50) (Fig. S1), such that they can
486 tolerate drought stress similarly to coexisting trees by employing other compensatory
487 strategies, such as leaf shedding, stem water storage or deep roots to avoid hydraulic
488 cavitation (Chen et al., 2015; Dias et al., 2019). On the other hand, the low hydraulic
489 conductivity of shrubs were due to more sections of vessels, which results from more

490 branch internodes than trees (David. D Ackerly & DD, 2004; A E Zanne et al., 2006).
491 Thus, arid climate niches, lower specific leaf area (SLA) and high drought tolerances
492 of shrubs may also explain the doubled abundance of Fabaceae species in open dry
493 compared with dense wet Neotropical forests (Gei et al., 2018).

494

495 **Life form based phylogenetic niche conservatism in Fabaceae**

496 Our finding of phylogenetic signals in all the plant traits, except A_{area} , is consistent with
497 previous studies (Ávila-Lovera et al., 2023; Liu et al., 2015; Sanchez-Martinez et al.,
498 2020). Strong phylogenetic signals indicate that species have retained their ancestral
499 traits through restricted genetic variation (Prinzing et al., 2001) or stabilizing selection
500 (D. D. Ackerly, 2009), while the lack of phylogenetic dependence (*e.g.*, in A_{area})
501 indicates that species are more labile during adaptation to novel environments.
502 Moreover, λ values in K_S , P50 and A_L/A_S in our study were slightly smaller than in other
503 studies across families (Ávila-Lovera et al., 2023; Sanchez-Martinez et al., 2020). This
504 can be explained because it is harder to detect phylogenetic signals within a single
505 family due to stronger phylogenetic niche conservatism (PNC) across families (Graham
506 et al., 2018; Losos, 2008).

507 However, phylogenetic signals disappeared once life form was considered in the
508 models is likely because the three life forms in Fabaceae are phylogenetically
509 dependent ($\delta=2.11$, $P<0.001$; **Fig. 1**), thus adding it to the models weakened
510 phylogenetic influences. Such a pattern has been reported before, when Liu *et al.*, (2012)
511 found that adding a phylogenetic dependent factor “subfamily”, strongly reduced λ
512 values of plant morphological traits. The two exceptions (*i.e.*, MAT and Ts) that
513 maintained their phylogenetic signals after adding life form, were likely caused by
514 larger climate differences among clades than among life forms. We thus identified the
515 divergent evolution of life forms within Fabaceae (**Fig. 1**), such that species in some
516 clades may have a greater probability of evolving into a particular life form, such as
517 shrubs clustered in Papilionoideae.

518

519 **Phylogeny matters in the trait-climate relationships**

520 The tight associations between trait and climate were not surprising, as many studies
521 had already found such adaptations. For example, at the global scale, K_S (He et al.,
522 2020), vessel diameter (Hacke et al., 2017) and SLA (Wright et al., 2004) increase with
523 mean annual temperature and precipitation separately, while wood density shows the
524 opposite pattern (Chave et al., 2009). Our novel contribution here is to confirm that the
525 trait-climate relationships still exist after considering phylogeny (Fig. 3; Table S4).
526 Thus such relationships were not only driven by divergence within deep nodes in the
527 phylogenetic tree (*e.g.*, along the splits between subfamilies) (Freckleton et al., 2002),
528 but also by other ecological processes that lead to the phylogenetic independent
529 covariance of trait-climate relationships (Pinho et al., 2021). This is true in Fabaceae,
530 for instance, woody-lianas in the Caesalpinia (*i.e.*, a clade in Caesalpinioideae that
531 comprises mainly trees) occurred in rainforest in Southeast Asia during the Eocene
532 (Gagnon et al., 2019), suggesting that clades in wet habitats with less exposure to
533 drought stress lack selection pressure to increase their xylem resistance to embolism,
534 but instead select for highly conductive sapwood (Liu et al., 2021). Later, at least six
535 woody-shrub clades in phaseoloid (*i.e.*, the largest group in Papilionoideae) diverged
536 rapidly from herbaceous clades in response to the Late Oligocene aridity and warming
537 (Li et al., 2013), corresponding to drought tolerant traits in shrubs. Our results also
538 confirmed the widely reported weak trait-climate relationships, due to the combination
539 of evolutionary and ecological effects, they became even weaker against the
540 phylogenetic background (L. D. L. Anderegg, 2023).

541

542 **Phylogeny and climate explained more variance of hydraulic traits**

543 Our hypothesis that phylogeny may explain a larger proportion of variance in Fabaceae
544 hydraulic traits was partly supported: K_S , P50, WD and SLA, as well as trait PPC1 and
545 PPC2 were mainly explained by phylogeny, A_{area} and A_L/A_S by climate, and V_{dia} by
546 both (Fig. 4; Table S5). The four phylogeny driven traits were reasonable, because they
547 also showed strong phylogenetic signals in our data and the literature (Ávila-Lovera et
548 al., 2023). However, there were large proportions of joint effects of phylogeny and
549 climate, sometime even larger than the pure phylogeny effect (*e.g.*, K_S and SLA). These

550 traits, along with the phylogeny+climate driven V_{dia} , supported the classic viewpoint
551 that plant traits are shaped by both evolutionary and ecological factors (Desdevises et
552 al., 2003; Westoby et al., 1995). As for the two climate driven traits, both were highly
553 labile and respond quickly to environmental fluctuations, such as A_{area} to temperature
554 (Wright et al., 2004) and A_L/A_S to water (Mencuccini et al., 2019). The smaller effects
555 of life form in the partitioning models indicate a weaker factor relative to phylogeny
556 and climate, but not that life form is unimportant (*e.g.*, note the contrasting traits among
557 life forms in Fig. S1). Many studies aimed to find simple drivers that affect plant
558 adaptations, but instead identify multiple factors, within which phylogeny is always the
559 cornerstone (Liu, Taylor, et al., 2019; Skelton et al., 2021). Therefore, incorporating
560 phylogeny into hydraulic trait-climate relationships can provide more insight into the
561 potential responses of species or vegetation to climatic changes (Sanchez-Martinez et
562 al., 2020; Xu et al., 2018).

563 We also acknowledge some caveats in our study. First, although the unbalanced
564 samplings of some traits among life forms was statistically handled here, a paucity of
565 hydraulic trait data for Fabaceae species highlights a clear need for extensive hydraulic
566 measurements in this family in the future, especially for lianas, which are very
567 vulnerable under drought (Willson et al., 2022). Second, compared with case studies,
568 compiled datasets may obscure relationships due to larger trait variation, but the
569 relationships can still be found. Third, current classification of life form lacks
570 herbaceous species due to different structures, which might limit the generality of our
571 results. Finally, both evolution and phenotypic plasticity account for plant responses to
572 climatic change (Münzbergová et al., 2017), such that plasticity in hydraulic traits might
573 obscure our results. According to previous studies, many hydraulic traits showed some
574 degree of plasticity, such as high plasticity in leaf to stem area ratio, low plasticity of
575 P_{50} and wood density, inconsistent patterns in leaf turgor loss point and xylem
576 hydraulic conductivity (L. D. L. Anderegg et al., 2021; Pritzkow et al., 2020), thus the
577 degree of plasticity for even the same trait differed across species and varied with
578 environmental change magnitudes (Binks et al., 2016). However, we focused on
579 interspecific rather than intraspecific differences at the global scale, and the

580 dramatically distinct climatic conditions and contrasting adaptive traits in this study
581 were sufficient to detect phylogenetic and ecological patterns.

582

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873

874 **Supporting Information**

875 **Notes S1.** Plant functional traits measurement methods.

876 **Notes S2.** Hydraulic traits and climatic variables differ among life forms.

877

878 **Table S1.** Full dataset in this study. (Provided in a separate excel file)

879 **Table S2.** Comparisons of plant functional traits and climatic variables across life forms
880 of studied Fabaceae species.

881 **Table S3.** Phylogenetic principal component (PPC) loadings based on functional traits
882 and climatic variables of studied Fabaceae species.

883 **Table S4.** Results of general Linear Model (LM), Standardized Major Axis (SMA) and
884 Phylogenetic Generalized Least Square (PGLS) models on functional traits and the first
885 two climate phylogenetic principal components (PPCs) of studied Fabaceae species.

886 **Table S5.** Relative contributions to total variance in functional traits of studied
887 Fabaceae species based on two-factor models.

888

889 **Figure S1.** Plant functional traits across three woody life forms of studied Fabaceae
890 species.

891 **Figure S2.** Relationships between functional traits and the second phylogenetic
892 principal component (PPC2) of climatic niches of studied Fabaceae species.

893 **Figure S3.** Hydraulic efficiency–safety trade-off across three woody life forms of
894 studied Fabaceae species.

895

Table 1 Summary of variables included in this study.

Trait	Units	Description
(a) Plant functional traits		
<i>Stem traits</i>		
K_s	$\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$	Xylem conductivity per unit of cross-sectional sapwood area, indicates stem hydraulic efficiency
P50	MPa	Water potential at which 50% of the maximum conductivity is lost, indicates stem hydraulic safety
WD	g cm^{-3}	Wood density
Vdia	μm	Diameter of stem vessels
<i>Leaf traits</i>		
A_{area}	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Photosynthetic rate per leaf area
A_L/A_S	$\text{cm}^2 \text{m}^{-2}$	Leaf to stem area ratio
SLA	$\text{cm}^2 \text{g}^{-1}$	Specific leaf area
(b) Climatic niche		
<i>Temperature related variables</i>		
MAT	$^{\circ}\text{C}$	Mean Annual Temperature
Ts	unitless	Temperature seasonality; the standard deviation of monthly temperature
Tmax	$^{\circ}\text{C}$	Maximum temperature of warmest month
Tmin	$^{\circ}\text{C}$	Minimum temperature of coldest month
<i>Precipitation related variables</i>		
MAP	mm	Mean Annual Precipitation
Ps	unitless	Precipitation seasonality; the standard deviation/ mean of 12 months
Pmax	mm	Precipitation of wettest month
Pmin	mm	Precipitation of driest month
AI	unitless	Aridity Index = MAP/PET; potential evapotranspiration (PET)
VPD	kPa	Vapor Pressure Deficit
SR	$\text{kJ m}^{-2} \text{day}^{-1}$	Solar Radiation

898 **Table 2** Results of Phylogenetic Generalized Least Square (PGLS) model on functional
 899 traits, climatic niches and phylogenetic principal components (PPCs) of Fabaceae
 900 species. The effects of life form on (a) plant functional traits and their PPCs, (b) climatic
 901 niches and their PPCs. Models used ln-transformed values (absolute values were input
 902 for originally negative values) except for PPC1 and PPC2. Sampling size (n), Pagel's
 903 λ , P values for $\lambda=0$ of each model, R^2 , F , P of the whole model are listed. Life form:
 904 liana, tree, and shrub. – indicates that $P_{(\lambda=0)}$ value is not credible when the whole model
 905 is invalid ($P>0.05$).

	$y \sim 1$			$y \sim \text{life form}$				
	n	λ	$P_{(\lambda=0)}$	λ	$P_{(\lambda=0)}$	R^2	F	P
(a) Plant functional traits								
<i>Stem traits</i>								
K_S	126	0.47	***	0.00	ns	0.39	39.83	***
P50	83	0.38	*	0.14	ns	0.08	3.85	*
WD	113	0.54	***	0.27	ns	0.29	21.94	***
Vdia	63	0.73	**	0.30	ns	0.29	12.58	***
<i>Leaf traits</i>								
A_{area}	75	0.04	ns	0.04	-	0.01	0.34	ns
A_L/A_S	95	0.33	*	0.00	ns	0.21	12.12	***
SLA	87	0.53	***	0.16	ns	0.24	13.55	***
<i>PPCA on plant functional traits</i>								
PPC1	51	0.97	**	0.25	ns	0.45	14.82	***
PPC2	51	0.00	ns	0.00	-	0.03	0.56	ns
(b) Climatic niche								
<i>Temperature related niche</i>								
MAT	150	0.61	***	0.43	***	0.13	11.24	***
Ts	150	0.64	***	0.61	***	0.08	6.68	**
Tmax	150	0.41	***	0.09	ns	0.11	9.81	***
Tmin	150	0.62	**	0.00	ns	0.14	12.49	***

Precipitation related niche

MAP	150	0.61	***	0.10	ns	0.29	31.45	***
Ps	150	0.56	***	0.46	-	0.02	1.50	ns
Pmax	150	0.59	***	0.00	ns	0.35	41.50	***
Pmin	150	0.90	***	0.91	-	0.02	1.59	ns
AI	150	0.14	*	0.03	ns	0.15	13.13	***
VPD	149	0.22	***	0.22	-	0.02	1.89	ns
SR	149	0.12	ns	0.14	-	0.01	0.63	ns

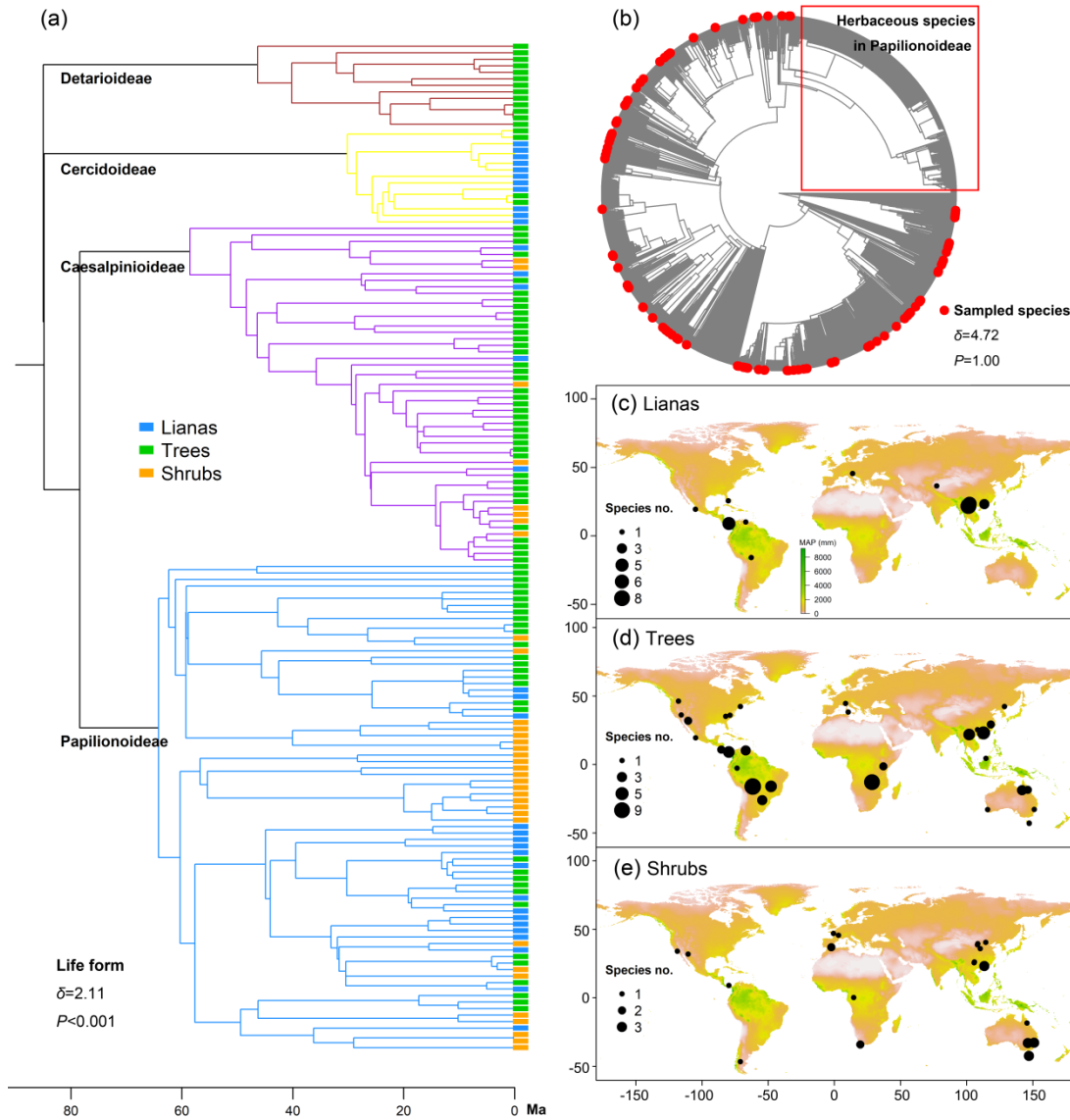
PPCA on climatic niches

PPC1	149	0.70	***	0.17	ns	0.26	26.75	***
PPC2	149	0.20	*	0.09	-	0.05	0.24	ns

906

907

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910

911 **Figure 1** Phylogenetic trees of Fabaceae species and sampling status in this study. (a)

912 The 150 species with subfamily and life form labelled. (b) The 150 species sampled

913 across the whole Fabaceae tree from Smith & Brown (2018), with gaps mainly in

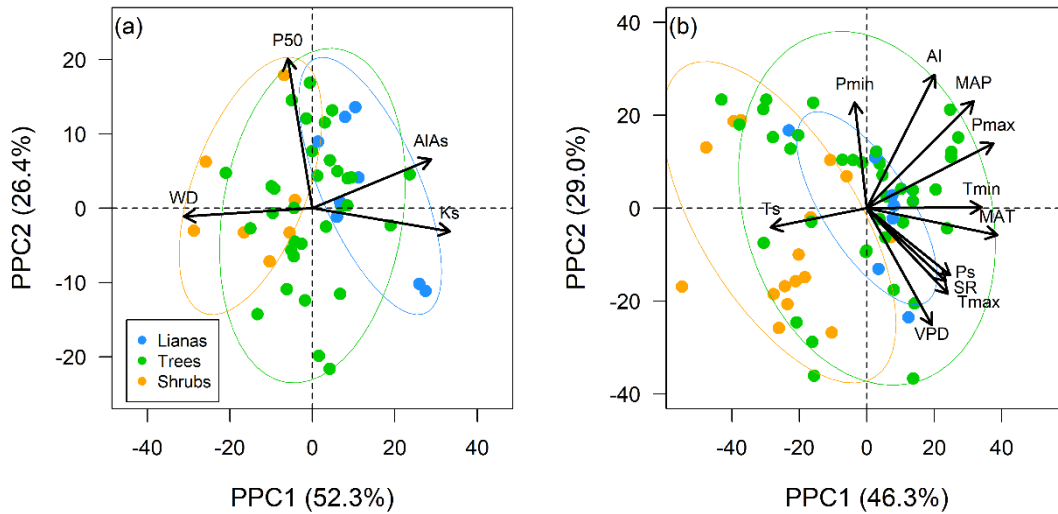
914 herbaceous clades; δ statistic is used to detect phylogenetic signal in categorical factors,915 $P<0.001$ indicates significant phylogenetic signal (please see details in the Methods).

916 (c, d, e) The distribution of sampling sites and the number of species for lianas, trees

917 and shrubs in this study, respectively. The background of the map is mean annual

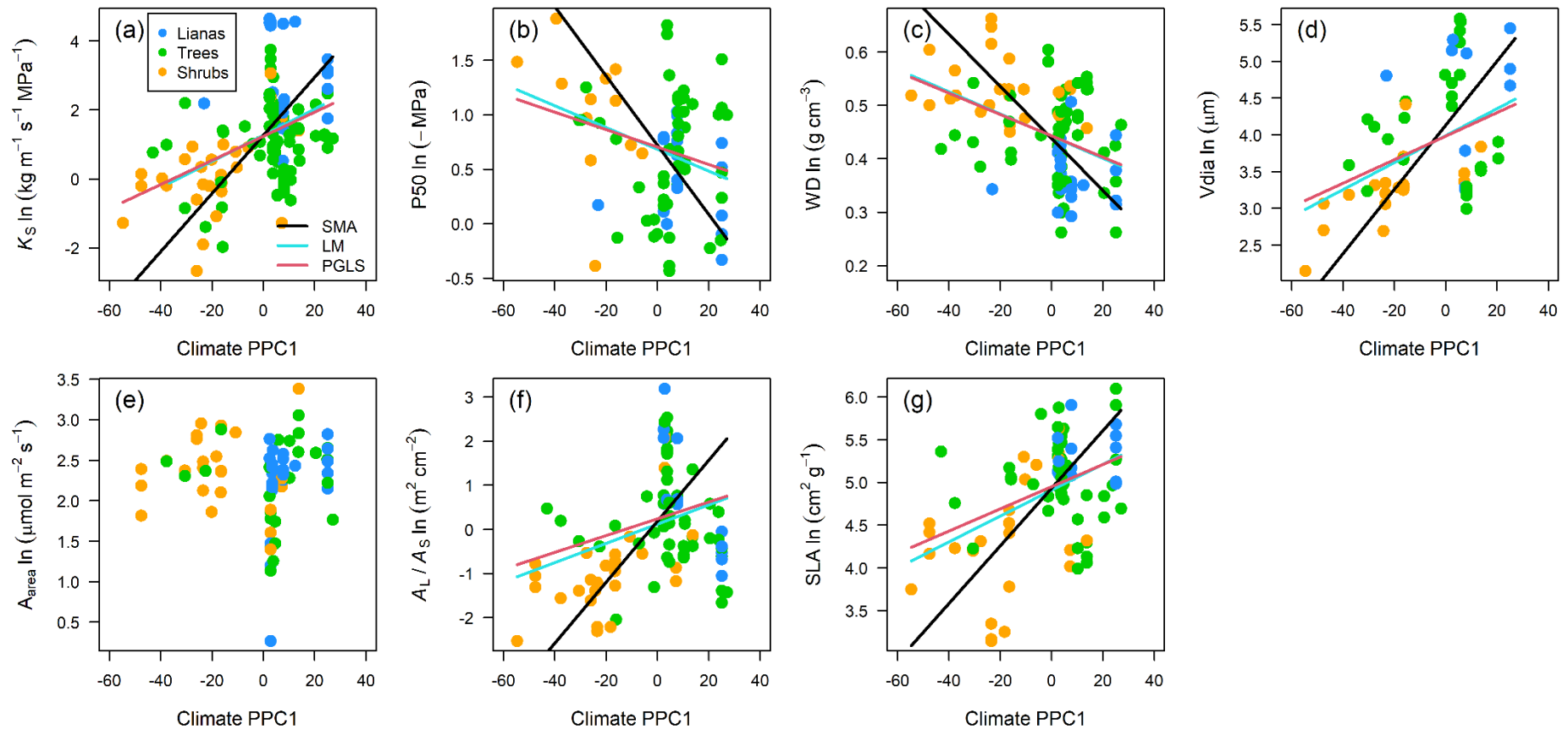
918 precipitation (MAP).

919



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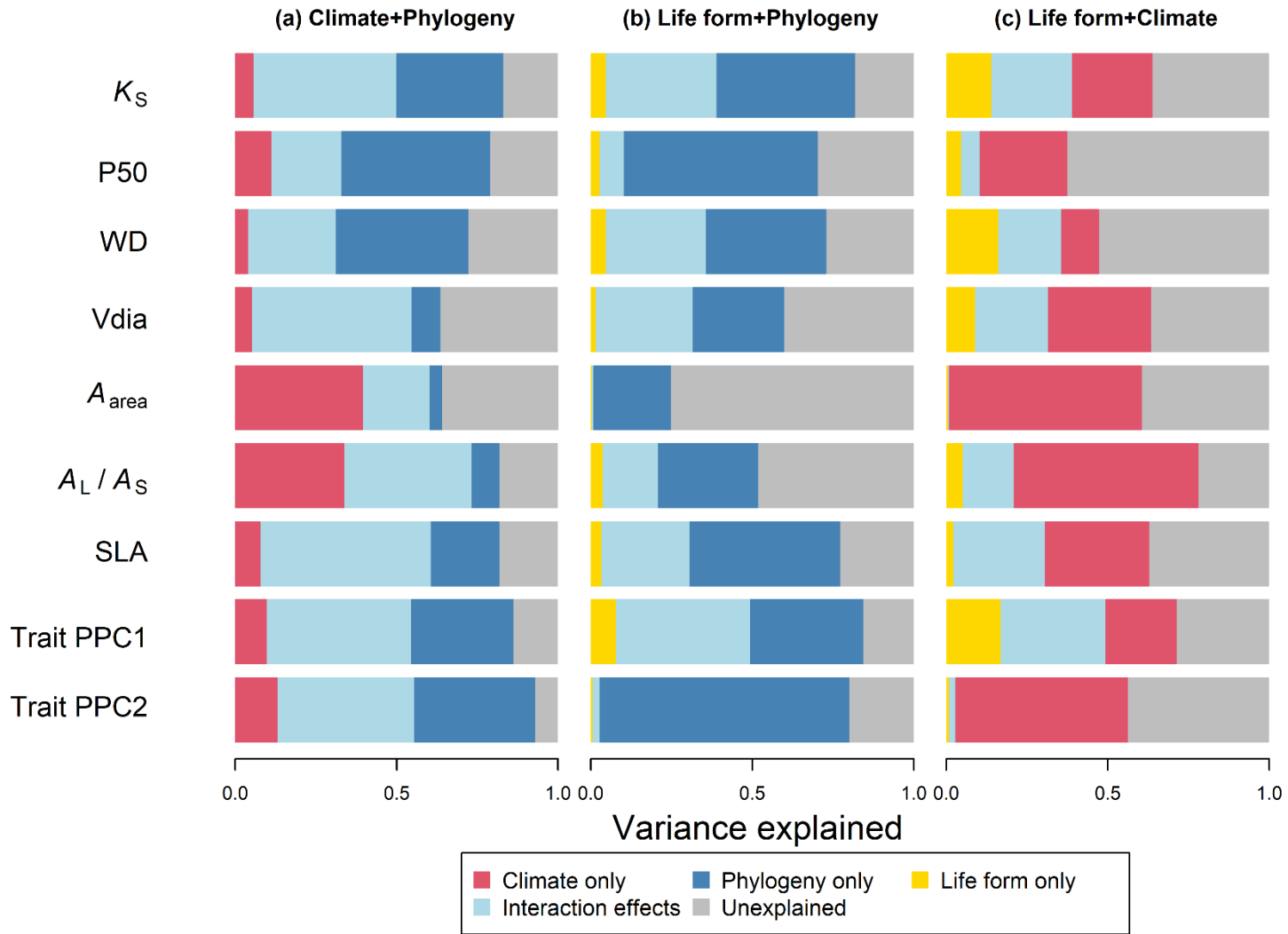
921 **Figure 2** Phylogenetic principal component analysis (PPCA) on (a) four hydraulic
 922 traits and (b) eleven climatic variables of studied Fabaceae species. Both phylogenetic
 923 principal component (PPC) loadings and species of different life forms (lianas, *blue*;
 924 trees, *green*; and shrubs, *orange*) are shown. Percentage of variance explained by each
 925 PPC is shown in the axis labels. Abbreviations are in [Table 1](#); loadings are reported in
 926 [Table S3](#).



928

929 **Figure 3** Relationships between functional traits and the first phylogenetic principal component (PPC1) of climatic niches on studied Fabaceae
 930 species. Phylogenetic generalized least square (PGLS, red line) models account for relatedness across species, whilst general linear models (LM,
 931 cyan line) and standardized major axis (SMA, black line) models do not. Only significant models are plotted, with detailed parameters in [Table](#)

932 **S4.** Data are coloured by life forms (lianas, *blue*; trees, *green*; and shrubs, *orange*). More positive PPC1 indicates wetter and less seasonal
933 climatic conditions. Relationships between hydraulic traits and climate PPC2 are in **Figure S3** and **Table S4**.
934



936 **Figure 4** Relative contributions to total variance in plant functional traits of studied Fabaceae species. Models are based on (a) Climate and
937 phylogeny, (b) Life form and phylogeny, and (c) Life form and climate. Different colors indicate variance explained by pure climate (red), pure
938 phylogeny (blue), pure life form (yellow), the interaction effects from two factors (light blue), and the unexplained variance (grey).
939 Abbreviations are in [Table 1](#), detailed model coefficients are in [Table S5](#).
940