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**Growing-season temperature and precipitation are independent drivers of global variation in xylem hydraulic conductivity**

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Keywords:	biome, climate, functional types, hydraulic diversity, species distribution, water transport
Abstract:	<p>Stem xylem-specific hydraulic conductivity (KS) represents the potential for plant water transport per unit xylem cross-section, length, and driving force. Variation in KS has implications for plant transpiration and photosynthesis, growth and survival, and also the geographic distribution of species. Clarifying the global-scale patterns of KS and its major drivers are needed for a better understanding of how plants adapt water transport to different environmental conditions, particularly under global climate change scenarios. Here, we compiled a xylem hydraulics dataset with 1315 species-at-site combinations (975 woody species representing 146 families, from 199 sites worldwide), and investigated how KS varied with climatic variables, plant functional types and biomes. Growing-season temperature (Tgs) and growing-season precipitation (Pgs) drove global variation in KS independently with Tgs and Pgs explaining 23%</p>

	<p>and 15% of the variation in KS, respectively. Both the mean and variations of KS were highest in the warm and wet tropical region, and lowest in the cold or dry regions, such as tundra and desert biomes. Our results suggest that future warming and redistribution of seasonal precipitation may have significant impact on species functional diversity or community species composition, depending on whether the sensitivities of KS to Tgs or Pgs are predominantly influenced by genotypic or phenotypic variations, particularly at high latitudes where it is projected that wet areas will get wetter and dry regions will become drier. Our results also highlight an important role for KS in predicting changes in plant hydraulic diversity and community species composition under global climate change.</p>

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Manuscripts

1 **Growing-season temperature and precipitation are independent**  
2 **drivers of global variation in xylem hydraulic conductivity**

3

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39

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52 Y.S., X.M. and G.H. contributed to the data collection. P.H. and Q.Y. wrote the initial  
53 manuscript. I.J.W., S.G., E.W., H.L., S.Z., M.L., G.H, P.B.R. Y.P.W. and D.S.E.  
54 contributed to improving the manuscript.

55

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57 supporting these results will be archived in a public repository (Dryad) and the DOI  
58 for these data will be included at the end of the article.

59

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**66 Abstract**

67 Stem xylem-specific hydraulic conductivity ( $K_S$ ) represents the potential for plant  
68 water transport per unit xylem cross-section, length, and driving force. Variation in  $K_S$   
69 has implications for plant transpiration and photosynthesis, growth and survival, and  
70 also the geographic distribution of species. Clarifying the global-scale patterns of  $K_S$   
71 and its major drivers are needed for a better understanding of how plants adapt water  
72 transport to different environmental conditions, particularly under global climate  
73 change scenarios. Here, we compiled a xylem hydraulics dataset with 1315  
74 species-at-site combinations (975 woody species representing 146 families, from 199  
75 sites worldwide), and investigated how  $K_S$  varied with climatic variables, plant  
76 functional types and biomes. Growing-season temperature ( $T_{gs}$ ) and growing-season  
77 precipitation ( $P_{gs}$ ) drove global variation in  $K_S$  independently with  $T_{gs}$  and  $P_{gs}$   
78 explaining 23% and 15% of the variation in  $K_S$ , respectively. Both the mean and  
79 variations of  $K_S$  were highest in the warm and wet tropical region, and lowest in the  
80 cold or dry regions, such as tundra and desert biomes. Our results suggest that future  
81 warming and redistribution of seasonal precipitation may have significant impact on  
82 species functional diversity or community species composition, depending on whether  
83 the sensitivities of  $K_S$  to  $T_{gs}$  or  $P_{gs}$  are predominantly influenced by genotypic or  
84 phenotypic variations, particularly at high latitudes where it is projected that wet areas  
85 will get wetter and dry regions will become drier. Our results also highlight an  
86 important role for  $K_S$  in predicting changes in plant hydraulic diversity and  
87 community species composition under global climate change.

## 88 INTRODUCTION

89 Earth's precipitation belts will be likely redistributed because of global warming,  
90 influencing water availability for many inhabitants on the planet (Pachauri et al., 2014;  
91 Putnam & Broecker, 2017). It is possible that shifts in temperature and rainfall  
92 patterns may lead to widespread forest decline in regions where droughts are  
93 predicted to increase in duration and severity (Allen et al., 2010; Klein & Hartmann,  
94 2018). Quantifying physiological traits associated with water supply and drought  
95 survival (e.g., hydraulic conductivity and water potential at hydraulic dysfunction) has  
96 great potential for improving predictions of shifts in community composition (Li et al.,  
97 2015), species' distribution (Anderegg, 2015; Fei et al., 2017), and ecosystem  
98 function (Myers-Smith, Thomas, Bjorkman, 2019).

99 Hydraulic conductivity,  $K_S$ , represents the water transport potential for the xylem  
100 tissue. It is expressed as the rate of water transport through a given area and length of  
101 sapwood across a given pressure gradient (Sperry, Donnelly, Tyree, 1988).  
102 Transporting water from soil to the canopy requires an intact water column in the  
103 xylem from roots to shoots (Gleason, Butler, Ziemińska, Waryszak, Westoby, 2012),  
104 and  $K_S$  plays a critical role in regulating whole plant water budget and physiological  
105 processes by influencing plant transpiration (Manzoni et al., 2013), photosynthesis  
106 (Santiago et al., 2004; Zhu, Song, Li, Ye, 2013; Ávila-Lovera, Zerpa, Santiago, 2017),  
107 growth (Poorter et al., 2010; Fan, Zhang, Hao, Ferry Slik, Cao, 2012; Liu et al., 2019),  
108 and survival (Anderegg et al., 2012, 2016). The interaction between water availability  
109 and hydraulic conductivity can also strongly influence the geographic distribution of

110 plant species (Pockman & Sperry, 2000; Nardini & Luglio, 2014).

111 A number of studies have examined the covariation among xylem structure,  
112 hydraulic vulnerability, xylem hydraulic efficiency, and safety from embolism (Zanne  
113 et al., 2010; Jacobsen, Pratt, Tobin, Hacke, Ewers, 2012; Méndez-Alonzo, Paz,  
114 Zuluaga, Rosell, Olson, 2012), and also the correlations between these hydraulic traits  
115 and climatic variables. For instance, Zhang et al. (2013) studied 316 angiosperm tree  
116 species in south-west China, and found that xylem conduit diameter was positively  
117 correlated with mean annual temperature (MAT) and precipitation (MAP). Similarly,  
118 at the global scale, Morris et al. (2018) found that mean vessel diameter was  
119 positively correlated with mean annual temperature and precipitation across 2332  
120 woody angiosperm species. Furthermore, xylem safety ( $P_{50}$ ; xylem water potential  
121 resulting in 50% loss of hydraulic conductivity) in stems and leaves has been found to  
122 correlate negatively with precipitation (Choat et al., 2012; Blackman et al., 2014; Li et  
123 al., 2018). Considering that  $K_S$  and its primary component, vessel diameter, are  
124 positively correlated with precipitation, and that safety is negatively correlated with  
125 precipitation, we might then reasonably expect an inverse correlation between  $K_S$  and  
126  $P_{50}$  across species and habitats, i.e., that an efficiency-safety trade-off exists for  
127 vascular plants. Although such a trade-off is often implied (e.g., Choat et al., 2012),  
128 the empirical support for it is not always strong, or even inconsistent (Zhu, Song, Li,  
129 Ye, 2013; Gleason et al., 2016).

130 Two contradictory syntheses have been conducted previously to understand  
131 regional patterns of  $K_S$ . Maherali et al. (2004) investigated  $K_S$  among 167 woody



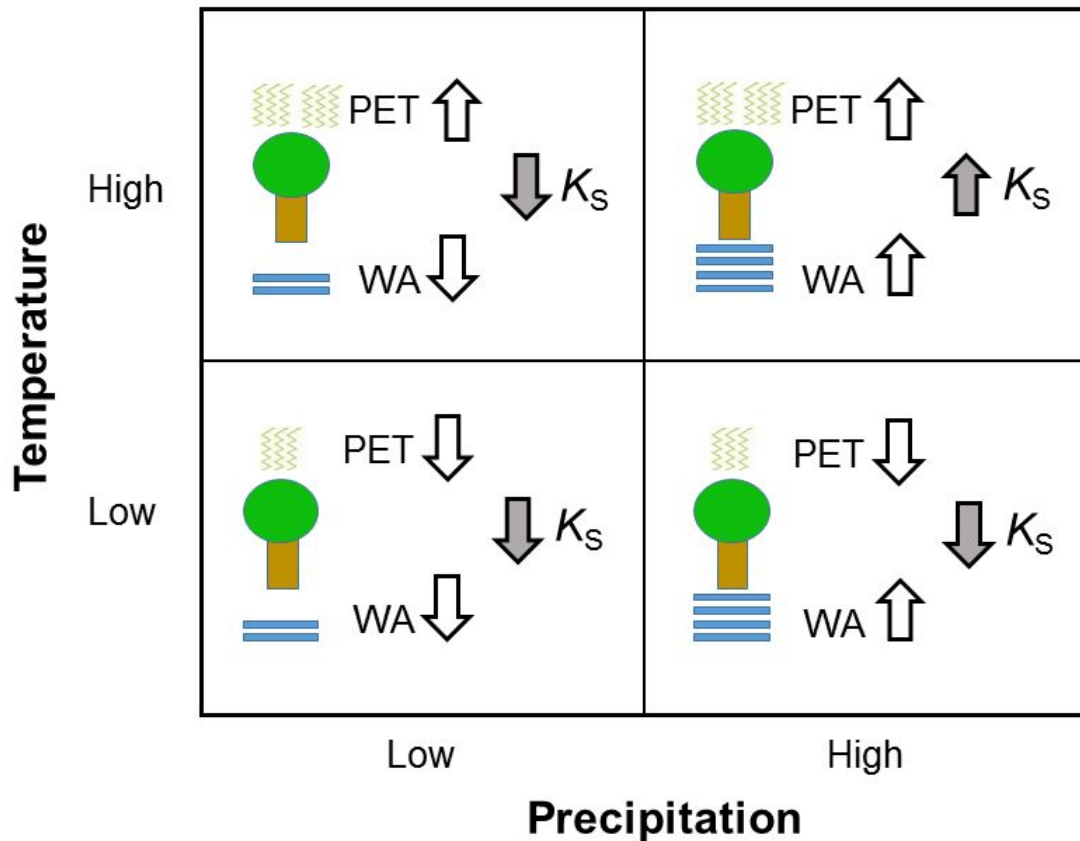
132 species in North Carolina and Texas, USA, and reported that  $K_S$  was higher at drier  
133 sites (lower MAP). They gave two possible reasons for this result. First, high  $K_S$   
134 might facilitate the increased transpiration under dry conditions without increasing the  
135 water potential gradient, and thus without increasing embolization risk (Maherali &  
136 DeLucia, 2001; Mencuccini, 2003). This, could be adaptive for plants in arid  
137 environments with high evaporative demand. Second, in that study most species from  
138 arid regions were deciduous with short leaf lifespan, and thus were able to avoid  
139 xylem embolization by dropping their leaves during drought, yet also maintain high  
140  $K_S$  during times of sufficient water availability (Reich et al., 1999). More recently,  
141 Gleason et al. (2013) studied 120 angiosperm species from eight sites across a broad  
142 range of climates in eastern Australia. They found that  $K_S$  was strongly and positively  
143 correlated with summer precipitation. They suggested that natural selection in wet and  
144 high radiation habitats should favor the evolution of highly conductive xylem to  
145 achieve high levels of water transport and therefore photosynthetic income, whereas  
146 natural selection in arid habitats should favor shorter stature and lower leaf surface  
147 area to sapwood cross-sectional area ratio ( $A_L/A_S$ ) to maintain water balance, whilst at  
148 the same time, avoiding hydraulic failure.

149 Despite these regional studies have revealed certain relationship between  
150 precipitation and  $K_S$  (yet to some extent, the results are contradictory), our  
151 understanding remains limited about how  $K_S$  varies across plant functional types and  
152 biomes, and which climatic factors drive the variations in  $K_S$  at the global scale.

153  $K_S$  is one of the key traits that significantly influence how water and carbon are

154 coupled and the success of different water use strategies in different environment  
155 (Santiago et al., 2004; Poorter et al., 2010; Anderegg et al., 2012; Fan, Zhang, Hao,  
156 Ferry Slik, Cao, 2012; Manzoni et al., 2013; Zhu, Song, Li, Ye, 2013; Anderegg,  
157 2015; Ávila-Lovera, Zerpa, Santiago, 2017). In areas with warmer temperatures and  
158 abundant soil moisture,  $K_S$  can be high in part because species must compete, so in  
159 order to pre-emptively use available soil moisture, fast water transport and high water  
160 use are likely selected for (Gleason, Butler, Waryszak, 2013; Morris et al., 2018). In  
161 cool, but moist places, PET (potential evapotranspiration) and other climate drivers  
162 are rarely high, so there is no selective advantage in having higher  $K_S$ . But in places  
163 with climate between those previous two conditions or sometimes are dry, low  $K_S$   
164 may be selected for to enhance survival (Anderegg et al., 2016; Petit, Anfodillo,  
165 Carraro, Grani, Carrer, 2011; possible conditions were shown in Figure 1). Here from  
166 unpublished data and the literature, we compiled a dataset of  $K_S$  measurements for  
167 975 woody species sampled from 199 sites worldwide (1315 species-at-site  
168 combinations, in total) (Figure S1a in Supporting Information). These species and  
169 sites represent a wide range of plant functional types (PFTs) and biomes (Figure S1b).  
170 Climate data for each site were derived from the source publications of  $K_S$  data or  
171 from global climate datasets (see Data file S1).

172



173

174 **Figure 1 Conceptual framework for xylem-specific hydraulic conductivity ( $K_S$ )**175 **under different environmental scenes.** PET indicates potential evapotranspiration,176 WA indicates water availability.  $K_S$  is selected for helping plants exchange water and177 carbon and grow fast. At warm and wet sites,  $K_S$  can be high because species must

178 compete, fast and high water transport and use is selected for. At cold sites, PET is

179 not high, there is no selective advantage in having higher  $K_S$ , despite precipitation is180 high. At dry sites, low  $K_S$  is selected for survival.

182 We sought to quantify, at the global scale:

183 (1)  $K_S$  variation in relation to climatic variables, in doing so identifying key  
184 factors underpinning  $K_S$  variation. As xylogenesis is often limited by low  
185 temperatures and precipitation (Petit, Anfodillo, Carraro, Grani, Carrer, 2011; Zhang,  
186 Gou, Manzanedo, Zhang, Pederson, 2018), we hypothesize that growing-season  
187 temperature and precipitation [i.e., monthly mean temperature  $\geq 5$  °C and monthly  
188 precipitation / PET  $\geq 0.05$ ; (Wright et al., 2017)] strongly and positively affect  $K_S$ .

189 (2) How does  $K_S$  vary across plant functional types and biomes which are both  
190 highly influenced by climate such as temperature and precipitation? Presumably lianas  
191 have high photosynthetic rates, enabled by the high  $K_S$ , conferring a competitive  
192 advantage over other woody species in closed canopy forests (Chen et al., 2015, 2017;  
193 Apgaua et al., 2017; van der Sande, Poorter, Schnitzer, Engelbrecht, Markesteijn,  
194 2019). By contrast, the conducting tissue in conifers is made up of narrow,  
195 close-ended tracheids (Bond, 1989; Sperry, Hacke, Pittermann, 2006; Field & Wilson,  
196 2012), thus facilitating low  $K_S$ . In regions where both the temperature and  
197 precipitation are high (e.g., tropical rainforest), high  $K_S$  is necessary to support high  
198 evapotranspiration (Yuan et al., 2010); whereas species in dry or cold regions, the risk  
199 of embolism is high from drought or freeze-thaw cycles (Choat et al., 2012; Anderegg  
200 & HilleRisLambers, 2016; Niu, Meinzer, Hao, 2017).

201 (3) Are  $K_S$  variations higher in lianas and tropical rainforest species but lower in  
202 conifers and tundra or desert species? Presumably tropical rainforest occupies a wide  
203 heterogeneity of environment such as precipitation and light, a long evolutionary time

204 and intense competitive interactions, diverse species with varies of  $K_S$  could coexist in  
205 these areas (Denslow, 1987; Wing et al., 2009; Ma et al., 2018). By contrast, species  
206 in desert or tundra biomes with low  $K_S$  values can rapidly respond to severe  
207 environment such as cold or dry (Woodward, Lomas, Kelly, 2004; Maire et al., 2012).  
208 We hypothesize that liana species and tropical rainforest species have the highest  
209 variation in  $K_S$ , while conifers and tundra or desert species have the lowest variation  
210 in  $K_S$ .

211

## 212 **MATERIALS AND METHODS**

### 213 **Data collection**

214 We compiled datasets of  $K_S$  based on published and unpublished data (Data file S1).  
215 Almost half of the data came from the previously published Xylem Functional Traits  
216 Database (XFT; Gleason et al., 2016), which could be accessed from the TRY Plant  
217 Traits Database (<https://www.try-db.org/TryWeb/Home.php>; Kattge et al., 2011). We  
218 also conducted searches on Web of Science, Google Scholar and China National  
219 Knowledge Infrastructure (<http://www.cnki.net>) using the keywords “xylem hydraulic  
220 conductivity”, “branch/stem hydraulic conductivity”, “water conductivity” and  
221 “hydraulic traits”. To minimize ontogenetic and methodological variation, we  
222 included data that met the following criteria: i) wild plants growing in natural  
223 ecosystems, excluding greenhouse and common garden experiments; ii) xylem  
224 hydraulic conductivity measured on terminal stem or branch segments (commonly  
225 3–10 mm in diameter and 10–30 cm in length), i.e., measurements on root or leaf

226 tissues were not included; iii) measurements were made on adult plants or saplings,  
227 but not on seedlings; iv)  $K_S$  was measured (e.g., Sperry, Donnelly, Tyree, 1988), not  
228 estimated from vessel measurements (e.g., Hagen–Poiseuille equation); and v) only  
229 maximum hydraulic conductivity was used, not so-called “native” hydraulic  
230 conductivity. After we collected the data, we checked the dataset and deleted the  
231 overlap values of the same species at the same site.

232       Based on information in source publications and online floras (e.g.,  
233 <http://frps.eflora.cn/>), species were coded into the following plant functional types  
234 (PFTs): liana, conifer, evergreen angiosperm tree, deciduous angiosperm tree,  
235 evergreen angiosperm shrub and deciduous angiosperm shrub. Sites were assigned to  
236 biomes: tropical rainforest, tropical savanna, tropical deciduous forest, subtropical  
237 monsoon forest, temperate deciduous forest, semi-arid woodland plus shrubland,  
238 boreal tundra, and desert.

239       Climate data were taken from the original reports, where available, otherwise  
240 variables such as mean annual and monthly precipitation, temperature, solar radiation,  
241 wind speed were extracted from the WorldClim version 2  
242 (<http://worldclim.org/version2>) (Fick & Hijmans, 2017). When elevation data from  
243 the WorldClim database did not match elevations from published reports, temperature  
244 was scaled to match published elevations using a lapse rate of  $6.0\text{ }^{\circ}\text{C km}^{-1}$  increase in  
245 elevation. The data of annual and monthly potential evapotranspiration were extracted  
246 from the CGIAR-CSI consortium (<http://www.cgiar-csi.org/data>) (Zomer, Trabucco,  
247 Bossio, Verchot, 2008). Aridity index (whether monthly or annual) is the ratio of

248 precipitation to PET. Variation of aridity index is calculated using coefficient of  
249 variation of the annual aridity index of recent 50 years (1966-2015) extracted from the  
250 SPEI data (<http://spei.csic.es/database.html>) (Beguería, Vicente-Serrano, Reig,  
251 Latorre, 2014). The data of monthly vapor pressure deficit (VPD) was extracted from  
252 the TerraClimate dataset (<http://www.climatologylab.org/terraclimate.html>)  
253 (Abatzoglou, Dobrowski, Parks, Hegewisch, 2018). We defined the growing season  
254 as being the set of consecutive months that satisfied the conditions (Wright et al.,  
255 2017): (i) Monthly mean temperature  $\geq 5$  °C, and (ii) Monthly precipitation / PET  $\geq$   
256 0.05.

257

## 258 **Data analysis**

259 Relationships between  $K_S$  and environmental variables were characterized using  
260 Pearson correlation and linear regression. One-way ANOVA with least significant  
261 difference was used to test for differences in mean  $K_S$  for species grouped into PFTs  
262 and biomes. Levene's test was used to compare variance in  $K_S$  among different PFTs  
263 and biomes. Multiple regression and stepwise regression analyses were conducted to  
264 estimate predictive equations for  $K_S$ . Quadratic regression were used to evaluate  
265 relationship between  $K_S$  and latitude. All analyses were run in R software (version  
266 3.5.0).

267

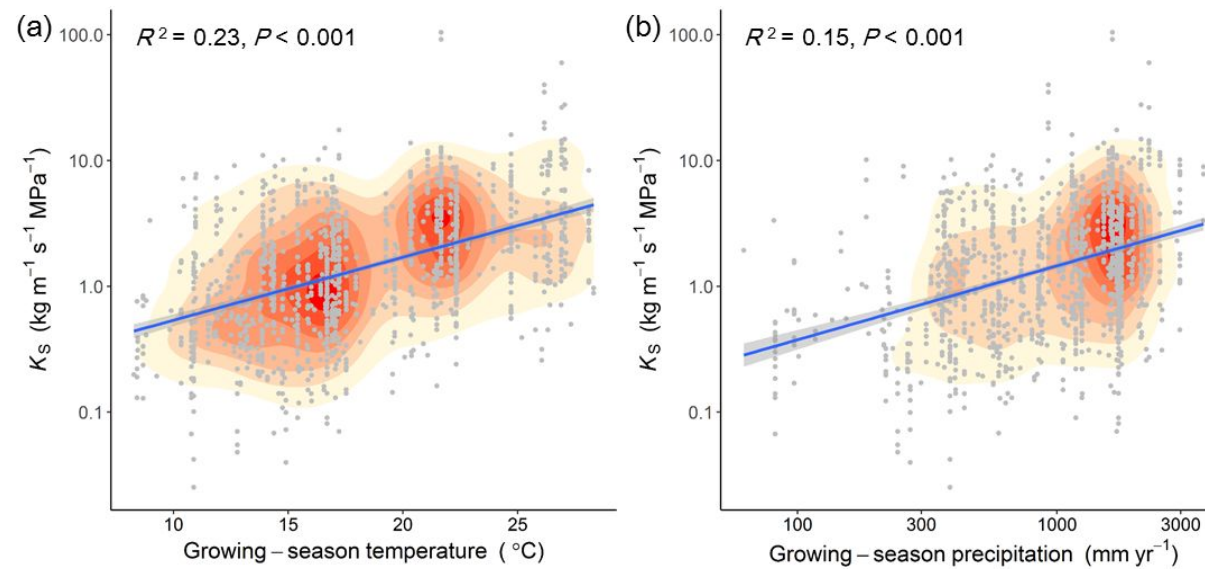
## 268 **RESULTS**

269 Our synthesis of  $K_S$  from 199 sites around the world showed that growing-season

270 temperature ( $T_{gs}$ , Figure 2a) and precipitation ( $P_{gs}$ , Figure 2b) explained 23% and  
271 15% of the global variation in  $K_S$ , respectively, e.g., higher  $K_S$  at warmer and/or  
272 wetter sites (Figure S1c, Figure S2). Several other climatic variables such as solar  
273 radiation and aridity index explained relatively smaller portions of variation in  $K_S$   
274 than  $T_{gs}$  or  $P_{gs}$  (Figure S3).

For Review Only





275

276 **Figure 2 Global variation in stem xylem-specific hydraulic conductivity ( $K_S$ ) in relation to climate:** global variation in stem xylem

277 specific-hydraulic conductivity in relation to site growing-season temperature (a), and site growing-season precipitation (b).  $R^2$  and  $P$  values are

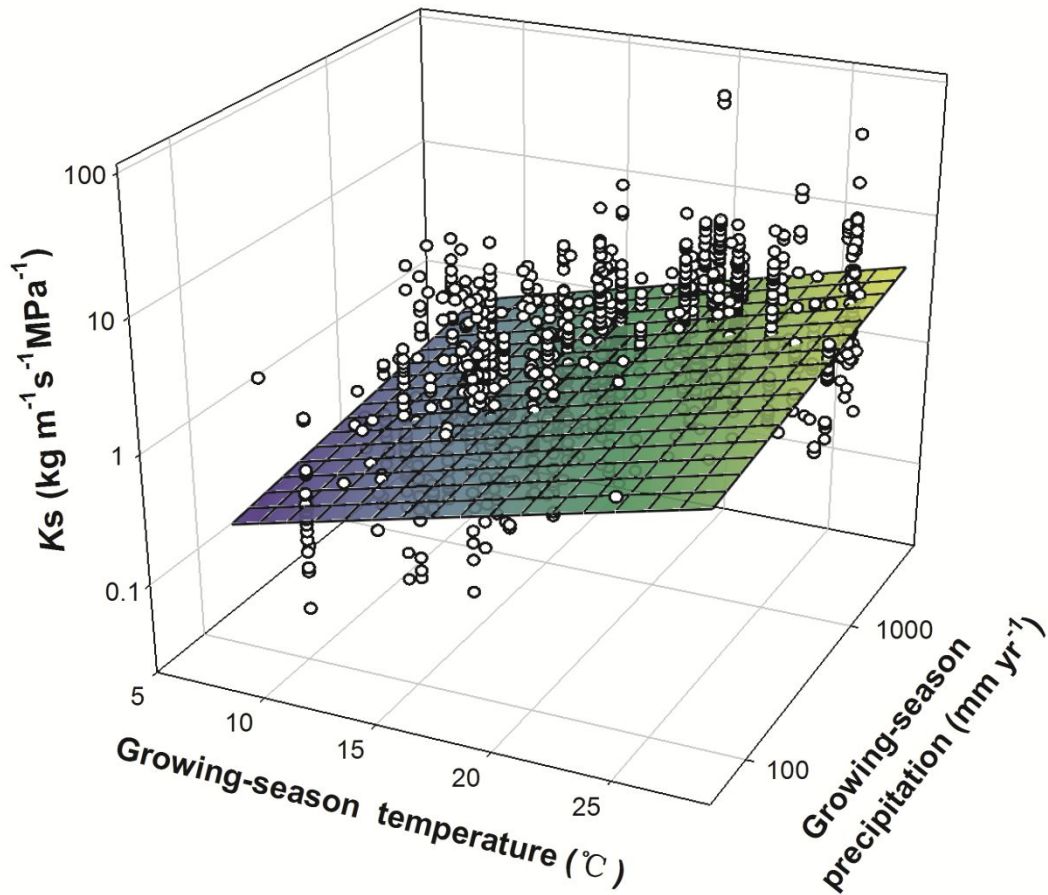
278 reported. Colours indicate the density of points from highest density (red) to lowest (yellow). Solid lines represent fitted ordinary least squares

279 (OLS) regression models with 95th confidence intervals.

280 We also quantified the explanatory power of combinations of climate variables,  
281 including testing for possible interactions.  $K_S$  increased independently with Tgs and  
282 Pgs ( $R^2 = 0.24$ ; Figure 3;  $P$  value for interaction between Tgs and Pgs was  $0.847 >$   
283  $0.1$ ). Regression models using all climate variables, or a subset identified in a  
284 step-wise process, explained up to 31% variation in  $K_S$ , and regression models using  
285 all climatic variables, plant functional types and biomes explained up to 40%  
286 variation in  $K_S$  (Table S1).

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289

290 **Figure 3 Global variation in stem xylem specific-hydraulic conductivity in**

291 **relation to site growing-season temperature and site growing-season**

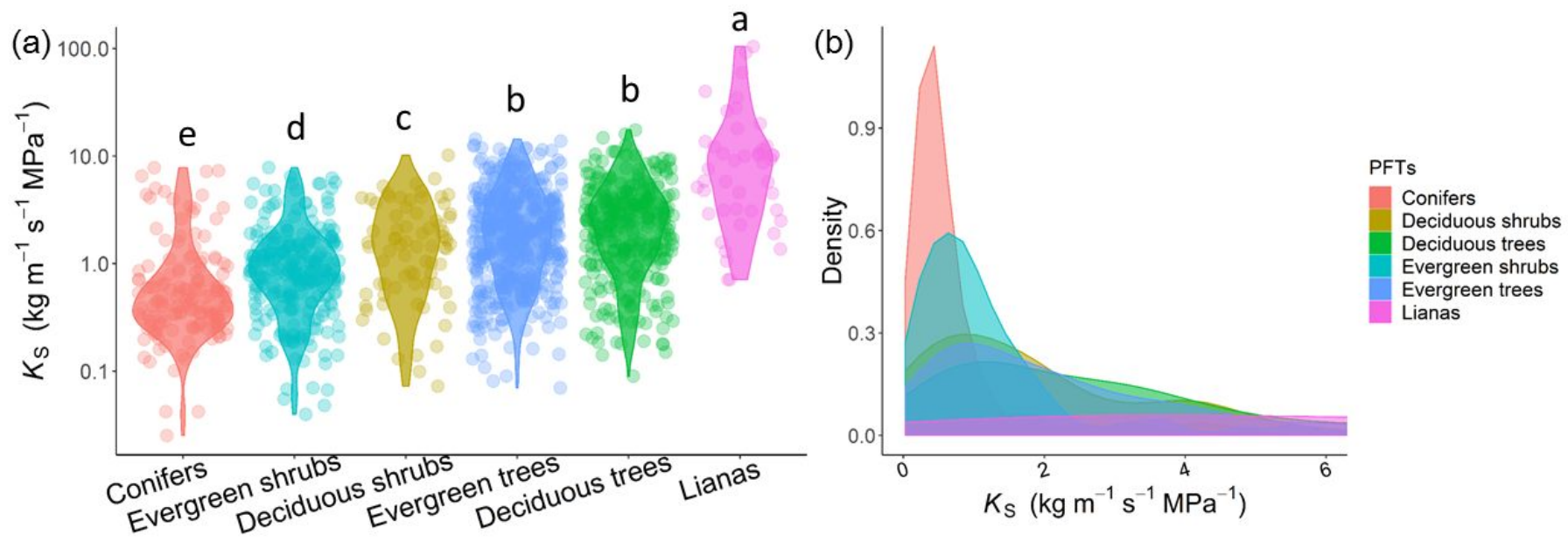
292 **precipitation.** The best-fit function estimated by multiple linear regression was  $\log K_S$

293  $= 0.19 \log P_{gs} + 0.04 T_{gs} - 1.19$  (all parameters  $P < 0.001$ ;  $R^2 = 0.24$ ).  $K_S$ , stem xylem

294 specific-hydraulic conductivity ( $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ );  $P_{gs}$ , growing-season precipitation

295 (mm);  $T_{gs}$ , growing-season temperature ( $^{\circ}\text{C}$ ).

297 Considering plant functional types, on average lianas had 4.7-15.2 times higher  
298  $K_S$  ( $14.43 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$ ) than other PFTs (Figure 4a; Table S2). Deciduous trees  
299 and evergreen trees had similar mean values of  $K_S$  ( $3.06 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$  and  $2.71 \text{ kg}$   
300  $\text{m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$ , respectively; Table S2). Evergreen shrubs had lower  $K_S$  than deciduous  
301 shrubs. Conifers had the lowest mean value of  $K_S$  ( $0.95 \text{ kg m}^{-1} \text{ s}^{-1} \text{ MPa}^{-1}$ ). Additionally,  
302 the variance in  $K_S$  was lowest in conifers and evergreen shrubs, but highest in lianas  
303 (Figure 4b, Figure S4, Levene's test, Table. S3).



304

305 **Figure 4 Patterns of stem xylem-specific hydraulic conductivity ( $K_s$ ) across plant functional types:** (a) Differences of stem xylem-specific  
 306 hydraulic conductivity among plant functional types (PFTs). Significant differences ( $P < 0.05$ ) among PFTs are indicated by different lowercase  
 307 letters (a-e). (b) Density distribution of stem xylem-specific hydraulic conductivity among plant functional types (PFTs).

308

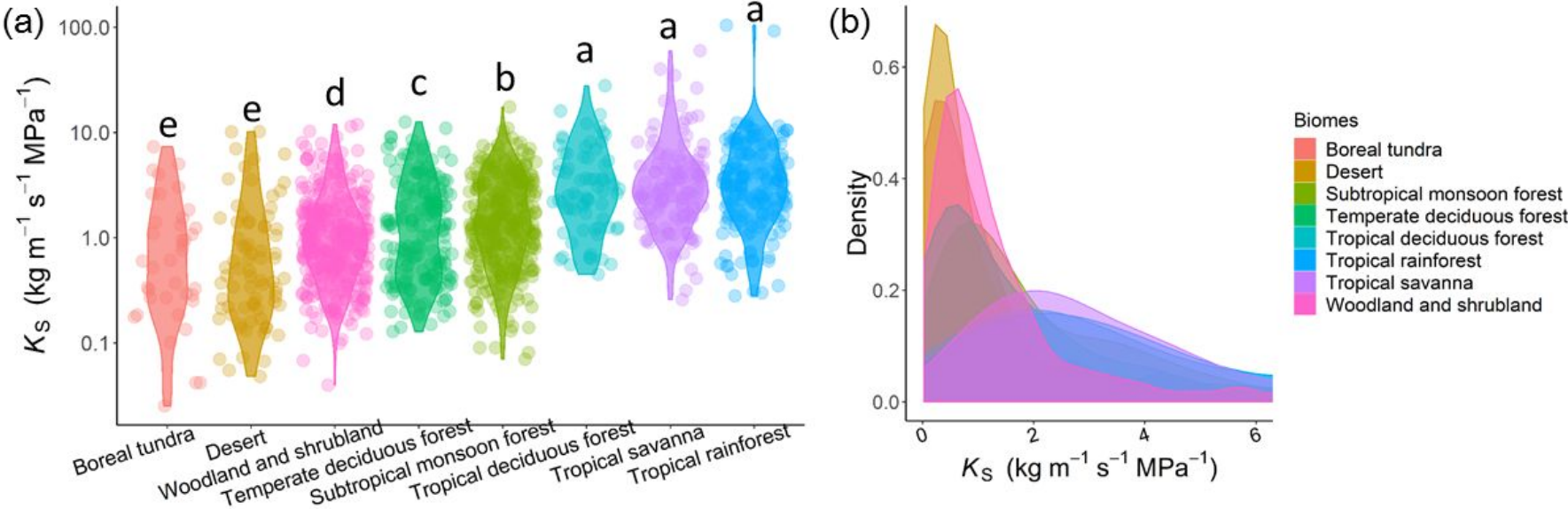
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311

312        Considering plant biomes, tropical rainforest species had the highest  $K_S$  (5.29 kg  
313  $\text{m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ ) (Figure 5a; Table S4), and boreal tundra and desert species had the  
314 lowest (1.25  $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$  and 1.28  $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ , respectively). Interestingly, the  
315 variance in  $K_S$  increased from biomes with low temperature (for example, boreal  
316 tundra) or low precipitation (for example, desert) to biomes with high temperature and  
317 high precipitation (for example, tropical rainforests) (Figure 5b, Figure S5, Levene's  
318 test, Table S5).

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320 **Figure 5 Patterns of stem xylem-specific hydraulic conductivity ( $K_s$ ) across biomes:** (a) Differences of stem xylem-specific hydraulic

321 conductivity among plant biomes. Significant differences ( $P < 0.05$ ) among biomes are indicated by different lowercase letters (a-e). (b) Density

322 distribution of stem xylem-specific hydraulic conductivity among plant biomes.

## 323 **DISCUSSION**

324 In this study, we analyzed the global patterns of plant xylem hydraulic conductivity  
325 ( $K_S$ ), including how this trait differs among plant functional types and biomes, and its  
326 coordination with climatic variables, thus providing new insights into how climate  
327 affects plant water use and the evolution of plant water use strategies.

328 Our results showed that air temperature was a more significant explanatory  
329 variable than precipitation, but both were influential. Moreover, species such as lianas  
330 from warm regions (e.g., tropical rainforests and tropical savannas) had relatively  
331 high  $K_S$ , whereas species such as conifers in cold regions (e.g., boreal tundra and  
332 woodland plus shrubland) had relatively low  $K_S$ . There are three possible  
333 interpretations for these results: first, the most obvious explanation for the observed  
334 temperature effect is that plants in warm habitats need high transpiration rates,  
335 supported by high  $K_S$ , to avoid overheating during warm periods (Wright et al., 2017).  
336 That said, in regions such as tropical and subtropical forests where temperature is high,  
337 species generally have wood tissue with wide xylem vessels (Morris et al., 2018), and  
338 high xylem hydraulic conductivity in order to support high evapotranspiration (Yuan  
339 et al., 2010). Moreover, this argument could also apply to warm deserts, but in that  
340 biome  $K_S$  values were substantially lower than in tropical and subtropical forests. By  
341 contrast, in cold sites such as tundra and woodland plus shrubland, PET is never high,  
342 so there is no selective advantage in having higher  $K_S$ , no matter if the sites are moist  
343 or not. Second, there is a benefit of small conduits for resistance to freezing  
344 embolisms (Field & Brodribb, 2001; Pittermann & Sperry, 2003), and small conduits



345 may only achieve low  $K_S$  (Morris et al., 2018). By contrast, high  $K_S$  with wide  
346 conduits has risk of embolism from freeze-thaw cycles (Niu, Meinzer, Hao, 2017).  
347 Third, species at warm sites need to compete for light and thus grow fast, and require  
348 high photosynthesis, and associated high water transport capacity (Fan, Zhang, Hao,  
349 Ferry Slik, Cao, 2012; Chen et al., 2015; Apgaua et al., 2017).

350 We found  $K_S$  was high at high rainfall sites, which is consistent with Gleason et  
351 al. (2013), suggesting that differences in  $K_S$  between wet and dry climates reflect the  
352 competing requirements among water transport, embolism and maintenance cost per  
353 unit water transported on the water transport system. A plant's hydraulic architecture  
354 influences the rate at which water can be transported from the roots to the canopy  
355 (Liang et al., 2019), but it also represents a risk (i.e., hydraulic failure) and a  
356 significant carbon cost for construction and maintenance processes. As such, we  
357 might expect evolutionary advantages to high  $K_S$  in habitats with low risk of  
358 embolism and high potential for CO<sub>2</sub> assimilation, and advantages to minimizing the  
359 risk of hydraulic failure as well as minimizing xylem construction and maintenance  
360 costs in shaded and/or arid environments. Although this idea may account for the  
361 evolution of highly conductive xylem in high-rainfall habitats, it does not provide a  
362 satisfying explanation for why low  $K_S$  should arise in arid habitats. This is because,  
363 even in these habitats, higher  $K_S$  should confer either greater water transport per unit  
364 cross-sectional investment, or confer less cross-sectional investment per unit water  
365 transport (i.e., thinner stems or less living sapwood). Only in the case where higher  $K_S$   
366 results in compromised mechanical stability (Zanne et al., 2010), increased

367 susceptibility to drought or cold weather injury, or a significant carbon expenditure  
368 that would be amortised by survival over a long time period, should natural selection  
369 favor the evolution of low  $K_S$ .

370       Compared to mean annual temperature and precipitation, we found that mean  
371 temperature and precipitation over the growing-season alone explained more variance  
372 of the observed  $K_S$  (Figure 2; Figures S3a and b), indicating the important role of  
373 growing season in mediating the variation in  $K_S$ . One possible interpretation is that  
374 xylogenesis takes place mainly in growing season. Excessive cold or dry conditions  
375 during growing season can adversely affect xylem growth, therefore limit the total  
376 number and size of xylem elements at the stem apex, which will prevent the  
377 construction of an efficient transport system (Petit, Anfodillo, Carraro, Grani, Carrer,  
378 2011; Zhang, Gou, Manzanedo, Zhang, Pederson, 2018).

379       This work represents an important step towards a better understanding of  
380 geographic variation in plant hydraulic strategies, and builds towards a more reliable  
381 conceptual model of global vegetation functioning and its risks with climate change.  
382 Nevertheless, it should be noted that our results are based on observations of plants at  
383 biome or PFT scale under present climate conditions. Whether the observed  
384 sensitivities to temperature and precipitation are strongly influenced by phenotypical  
385 variation within the same species or genotypic variations among different species can  
386 have significant implications on future climate impact on community species  
387 composition (Anderegg, 2015; Pfautsch et al., 2016; Anderegg et al., 2018; Osnas et  
388 al., 2018). If phenotypical variation dominates, the impact of climate change will be

389 not as great as the case with genotypic variation being dominant. This warrants further  
390 investigation in the future.

391 In summary, our results highlight the important and independent roles of  
392 growing-season temperature and precipitation in mediating  $K_S$  throughout the world.  
393 Our data support the continued development and improvement of processes-based  
394 global vegetation models that explicitly link  $K_S$  to performance, such as plant growth,  
395 death and dispersal (Prentice et al., 2007; Zhou, Duursma, Medlyn, Kelly, Prentice,  
396 2013). We suggest that the continued measurement and inclusion of important plant  
397 hydraulic traits in these modelling efforts will improve our understanding of  
398 species-climate linkages as well as our ability to predict demographic shifts in the  
399 face of climate change.

400

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