

1 **Title: Drivers of large-scale geographical variation in sexual systems of**
2 **woody plants**

3 **Authors:** Yunyun Wang^{1,2}, Tong Lyu^{1,3}, Nawal Shrestha^{1,4}, Lisha Lyu^{1,3}, Yaoqi Li¹, Bernhard
4 Schmid⁵, Robert P Freckleton⁶, Dimitar Dimitrov^{7,8}, Shuguang Liu,² Zhanqing Hao⁹, Zhiheng
5 Wang^{1,*}

6 **Affiliations:**

7 ¹ Institute of Ecology and Key Laboratory for Earth Surface Processes of the Ministry of
8 Education, College of Urban and Environmental Sciences, Peking University, Beijing
9 100871, China

10 ² National Engineering Laboratory for Applied Technology of Forestry & Ecology in South
11 China, Central South University of Forestry and Technology, Changsha 410004, China

12 ³ School of Urban Planning and Design, Shenzhen Graduate School, Peking University,
13 Shenzhen 518055, Shenzhen

14 ⁴ Institute of Innovation Ecology, Lanzhou University, Lanzhou, China

15 ⁵ Department of Geography, University of Zurich, Winterthurerstrasse 190, 8057 Zurich,
16 Switzerland

17 ⁶ Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK

18 ⁷ Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark,
19 University of Copenhagen, Copenhagen, Denmark

20 ⁸ Department of Natural History, University Museum of Bergen, University of Bergen, PO
21 Box 7800, NO-5020 Bergen, Norway

22 ⁹ Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese
23 Academy of Sciences, Shenyang 110016, China

24 * Correspondence should be addressed to: Zhiheng Wang; Tel: +86 10 62760881; Email:
25 zhiheng.wang@pku.edu.cn

26

27 **Running title:** Geographical drivers of plant sexual systems

28

29 **ABSTRACT**

30 **Aim:** Sexual systems strongly influence angiosperm evolution, and play important roles in

31 community assembly and species responses to climate change. However, geographical

32 variation in proportions of different sexual systems (dioecy, monoecy, and hermaphroditism)

33 in response to changes in climate, life-history traits and evolutionary age remains poorly
34 understood. Here, we map the geographical variation in proportions of different sexual
35 systems and hypothesize that the prevalence of hermaphrodites increases with aridity due to
36 their advantages in colonizing harsh environment, whereas dioecy is most successful in humid
37 regions with tall-canopy vegetation and old floras.

38 **Location:** China

39 **Time period:** Current

40 **Major taxa studied:** Woody angiosperms

41 **Methods:** Using data on sexual systems and distributions of 10,449 woody species in China,
42 we estimated the proportions of different sexual systems in local floras (50×50 km grid
43 cells). Spatial linear models, phylogenetic general linear models and structural equation
44 models were used to compare the relative influences of climate, plant height and evolutionary
45 age on geographical variation in proportions of different sexual systems.

46 **Results:** We found contrasting geographical patterns in the proportions of different sexual
47 systems. The proportions of dioecy and monoecy increased with plant height and were highest
48 in humid regions with older floras, while that of hermaphroditism decreased with plant height
49 and was highest in arid regions with younger floras. Plant height was the strongest correlate of
50 sexual system frequency. Climate influenced sexual system frequency both directly and
51 indirectly via its effects on plant height.

52 **Main conclusions:** Our study provides the first continuous map of sexual system composition
53 in woody floras over a large spatial scale. Our findings suggest that mature plant height,

54 reflecting plant longevity, dominates geographical variation in sexual systems and that the
55 proportions of different sexual systems in local floras may reflect their correlated evolution
56 with traits in response to climate changes.

57

58 **Keywords:** angiosperms, China, climate change, evolutionary history, geographical pattern,
59 macro evo-devo, plant height, plant reproduction, sexual systems

60

61 **INTRODUCTION**

62 Plants exhibit remarkable variation in their sexual systems, which act as a major driver of the
63 genetic and evolutionary dynamics of angiosperms (Barrett & Harder, 1996; Charlesworth,
64 2006), as well as having considerable ecological significance (e.g., pathogen resistance,
65 Williams, 2011; herbivore resistance, Campbell & Kessler, 2013). Selective pressures on
66 sexual systems vary with environmental conditions (Barrett, 1998; Ricklefs & Wikelski,
67 2002; Jacquemyn et al., 2005; Dorken, Freckleton, & Pannell, 2017), potentially leading to
68 geographical variation in the composition of sexual systems in local floras. Although a few
69 studies explored changes in sexual systems in different communities using sparse data at
70 restricted spatial scales (Lloyd, 1980; Jacquemyn et al., 2005; Moeller et al., 2017), potential
71 drivers of broad-scale biogeographical patterns in sexual system frequency in local floras
72 have rarely been investigated (Matthew et al., 2016). Contemporary climate, plant life-history
73 traits, and the evolutionary age of floras may all influence the frequency of sexual systems.
74 However, the relative contributions of these drivers remain poorly understood.

75 Climate can influence the expression of plant sexual systems by regulating the allocation
76 of resources to female and male function during the flowering period (Zhang, 2006) and
77 hence can lead to geographical variation in the composition of sexual systems of local floras
78 (Freeman et al. 1976; Barrett, 1998; Ricklefs & Wikelski, 2002; Jacquemyn et al., 2005;
79 Hultine et al., 2016; Dorken, Freckleton, & Pannell, 2017). For example, recent studies found
80 that the proportion of outcrossing species decreased with latitude (Moeller et al. 2017), which
81 has been attributed to changes in precipitation, temperature, and solar radiation along the
82 latitudinal gradient (Lyold, 1980). However, previous studies have provided controversial

83 evidence for the effects of climate, especially the effects of water availability, on the
84 biogeographical patterns of plant sexual systems. First, some studies exploring the evolution
85 of sexual systems indicate that drought stress may have contributed to the evolution of dioecy
86 from hermaphroditism (Webb, 1999; Ashman 2006; Yang et al. 2014), which suggests that the
87 prevalence of dioecy could be associated with arid environment. Second, other studies suggest
88 that the colonization to dry habitats did not require a shift to sex dimorphism (Sakai et al.
89 1997), because spatial separation likely makes dioecious taxa suffer greater challenges of
90 decreased mate assurance (Pannell & Barrett 1998). Compared with dioecious taxa,
91 hermaphroditic species likely have been selected in stressful regions with frequent extinction
92 and re-colonization (Obbard et al. 2006; Levin, 2012), because hermaphrodites can provide
93 reproductive assurance via selfing (Lloyd, 1992; Harder & Barrett 1995; Barrett, 1998; Elle &
94 Carney 2003). Studies based on field investigations find that hermaphroditic species from
95 different clades widely occur in dry habitats while dioecious species are more common in
96 humid and tropical regions (Freeman et al., 1980; Sakai & Wagner, 1995; Matallana et al.
97 2005). Although these findings tend to support the second hypothesis, how sexual system
98 composition varies geographically with climate, especially with water availability, still
99 remains controversial.

100 Plants with different life-history traits vary considerably in their sexual systems (Barrett
101 & Eckert, 1990; Snell & Aarssen, 2005; Moeller et al., 2017), which suggests that plant life-
102 history traits also likely influence the ecology and evolution of sexual systems (Vamosi, Otto,
103 & Barrett, 2003). Phylogenetic analyses have revealed the association between dioecy and
104 woody growth habits (i.e., the long-lived, perennial growth form) (Chazdon et al. 2003;

105 Vamosi, Otto, & Barrett, 2003). Similarly, longevity has also been found to be an important
106 trait associated with plant sexual systems (Renner, 2014). Compared with short-lived species,
107 long-lived ones tend to accumulate more genetic load (Klekowski & Godfrey, 1989), to pay a
108 higher fitness cost due to inbreeding depression and mutation, and to depend more on cross-
109 pollination (Klekowski & Godfrey, 1989; Chen, 2003). Consequently, dioecy has been
110 suggested to be more common in long-lived species than in short-lived ones (Renner &
111 Ricklefs, 1995; Renner 2014). In contrast, short-lived species have limited time to find mates,
112 reproduce, and complete their life cycle, and hence, they tend to contain a larger proportion of
113 selfing species (i.e. hermaphrodite and monoecy) relative to long-lived species (Morgan et al.,
114 1997; Aarssen, 2000). However, how the composition of sexual systems in local floras
115 changes in association with changes in life-forms and plant longevity remain to be tested.

116 Evolutionary history has been found to shape the distribution of sexual systems across
117 the phylogeny of seed plants (Lord et al., 1995; Renner & Ricklefs, 1995). For example,
118 significant phylogenetic signals were detected in the sexual systems of 641 species distributed
119 in the Yasuní National Park, Ecuador (Queenborough et al., 2009). Previous evolutionary
120 studies suggest that dioecious species have been derived from hermaphroditism and that
121 dioecious lineages are most often at the tips of angiosperm phylogenies (Barrett 2013).

122 According to this hypothesis, the prevalence of dioecious and hermaphroditic species in local
123 floras should have opposite correlations with flora age. More specifically, it may be expected
124 that dioecious species are more prevalent in young floras while hermaphroditic species are
125 more prevalent in old floras. However, in contrast to the predictions of this hypothesis, field
126 investigations based on scattered data find that dioecious species are more common on old

127 than on young islands (Sakai et al. 1995) and in tropical areas (Matallana et al. 2005)
128 dominated by old floras than in temperate areas with young floras. These findings
129 demonstrate that the relationship between the prevalence of a particular sexual system and
130 evolutionary age of floras so far remains inconsistent from an evolutionary and an ecological
131 perspective. Here we maintain that it is necessary to explore this relationship more
132 comprehensively across larger geographical scales to derive generalities.

133 With this goal in mind, we compiled data for sexual systems of woody angiosperms
134 spanning a broad environmental gradient in China. By combining these data with high-
135 resolution species distribution maps, we explored the geographical variation in the
136 composition of sexual systems of woody plants in China and their potential abiotic (climatic)
137 and biotic (plant traits and evolutionary age) drivers. Specifically, we aimed to test the
138 following three hypotheses: 1) the proportion of dioecy in floras increases, whereas the
139 proportion of hermaphroditism decreases with humidity. 2) dioecy is positively and
140 hermaphroditism negatively related to longevity across regions. 3) dioecy is most successful
141 in old woody floras, whereas hermaphroditism dominates young ones.

142

143 **MATERIALS AND METHODS**

144 **Sexual systems and distributions of woody plants in China**

145 We compiled a dataset on the sexual system of all woody plant species in China using
146 published sources: Flora of China (Wu, Raven & Hong, 1994-2013), Flora Republicae
147 Popularis Sinicae (126 issues of 80 volumes), Seeds of Woody Plants in China, eflora
148 (<http://efloras.org/>), Tree of Sex (Ashman et al., 2014), Plant Trait Database (TRY, 2012),

149 Botanical Information and Ecology Network (BIEN, Enquist et al., 2016) and journal
150 publication (Goldberg et al., 2017). For species for which the sexual system was reported in
151 multiple sources, those with conflicting reports were checked and corrected or removed. In
152 total, our dataset comprises 10,449 species from 1,082 genera and 157 families, and accounts
153 for 93.76% of all woody plants found in China (Table S1). We classified all these species into
154 three categories based on their sexual system following Cardoso et al. (2018): dioecy (i.e.
155 plant species with separate male and female individuals), monoecy (i.e. plant species with
156 both staminate and pistillate flowers occurring in the same individual but not in the same
157 flower), and hermaphrodites (i.e. plant species with both functional stamens and pistils in the
158 same flower). The category of dioecy includes androdioecious, gynodioecious and
159 polygamodioecious species, while monoecy includes monoecious, andromonoecious and
160 gynomonoecious species.

161 The sexual systems of a few species likely vary (e.g., Schoen, 1982; Dorken, Freckleton,
162 & Pannell, 2017) in response to local abiotic or biotic conditions (e.g., climate variables or
163 pollinator densities; Barrett & Harder, 2017). Such species were excluded from the final
164 dataset used in this study.

165 The distribution data of woody plants across China were taken from the Atlas of Woody
166 Plants in China (Fang et al., 2011), which contains the distribution of all the 11,405 woody
167 species (see Wang et al., 2009, for details). Species distributions were further checked and
168 supplemented using recently published specimen records (see <http://www.nsii.org.cn/>).

169

170 **Geographical variation in the proportions of different sexual systems**

171 We first transformed the distribution maps into equal-area grids with grid cell size of 50×50
172 km to eliminate the potential bias of unequal area on subsequent analyses (see Wang et al.,
173 2009, for details). Combining the sexual-system data and the distribution data of all species,
174 we calculated the proportions of species with each sexual system type within every grid cell.
175 To ensure the reliability of the calculated proportion for each sexual system, we removed grid
176 cells with less than half of the grid cell area (i.e. grid cells with $< 1250 \text{ km}^2$, see Wang et al.,
177 2009, for details), and grid cells with fewer than 10 woody species. A total of 3,539 out of
178 initially 4017 grid cells were finally included in the analyses.

179

180 **Climatic data**

181 To evaluate the effects of climate on the biogeographical pattern in the composition of sexual
182 systems in different local floras we used climatic data with a spatial resolution of 1×1 km for
183 the period 1950–2000 obtained from WorldClim (Hijmans et al., 2005). We obtained the value
184 of every climate variable for each 50×50 km grid cell by calculating the average of all 1×1
185 km cells within it. Climatic variables were categorized into temperature, precipitation and
186 solar radiation. Temperature variables included mean annual temperature (MAT), mean
187 temperature of coldest quarter (MTCQ) and annual potential evapotranspiration (PET). PET
188 reflects the amount of evaporation that would occur if sufficient water were available and was
189 calculated following the method of Thornthwaite (1955). Precipitation variables included
190 mean annual precipitation (MAP), precipitation seasonality (PSN, the coefficient of variation
191 of mean monthly precipitation) and Precipitation of Driest Quarter (PDQ). Solar radiation
192 reflects the radiant energy emitted by the sun. MAP and PDQ were natural-logarithm

193 transformed because of their left-skewed distributions. Solar radiation likely influences flower
194 coloration through pigmentation, which further affects pollination success (Körner, 1999).
195 The average and the full range of values for each climatic variable within each grid cell were
196 estimated with the zonal statistics tool in ArcGIS 10.0.

197 In China, the 800-mm isoline of MAP coincides with the 0 °C isotherm of mean
198 minimum January temperature and is the boundary between non-humid (or semi-humid) areas
199 (including deserts, grasslands and temperate forests) and humid areas (including subtropical
200 and tropical evergreen broad-leaved forests). We used this isoline to evaluate the
201 comprehensive effects of climate on the distributions of sexual systems.

202

203 **Mature plant height**

204 Because height is strongly associated with the longevity of woody plant species (Marbà et al.
205 2007; Moles and Leishman, 2008; Moles et al. 2009), we used the mature plant height as a
206 proxy for longevity to test hypotheses related to longevity. Mature plant height data were
207 extracted from the Flora of China (<http://frps.eflora.cn/>, accessed in November 2013;
208 http://www.efloras.org/flora_page.aspx?flora_id=2, accessed in February 2014). For species
209 with more than one record of the height of mature individuals, we used the average of these
210 records. Species without erect stems (e.g., woody lianas, climbers, scandent shrubs or
211 epiphytes) were excluded from our database following Moles et al. (2009). We then averaged
212 the mature height across all species within each grid cell to examine the effect of plant height
213 on the biogeographic patterns of sexual systems.

214

215 **Genus age and phylogenetic diversity**

216 Plant genus has been considered to be a more natural unit than other higher taxonomic ranks
217 (Anderson, 1940; Barraclough & Humphreys 2015). Therefore, average genus age per grid
218 cell has been widely used in large-scale studies to represent the evolutionary age of floras and
219 to test the evolutionary hypotheses of large-scale species diversity patterns (e.g. niche-
220 conservatism hypothesis, Leopold et al. 2015; Qian 2014, 2017; Qian et al. 2017; Lu et al.
221 2018).

222 To evaluate the effect of evolutionary age of local floras on the biogeographical pattern
223 of sexual systems (i.e. the per-grid proportions of the three sexual systems), we extracted the
224 genus age from the phylogenetic tree of Chinese vascular plants constructed by Chen et al.
225 (2016) and calculated the average genus age for each grid cell. Moreover, we also evaluated
226 the relationships between the proportions of sexual systems per grid cell and phylogenetic
227 diversity of local floras. Here the phylogenetic diversity (PD) was estimated by Faith's PD
228 (Faith, 1992) and net relatedness index (NRI) of woody species within each grid cell. The
229 results indicated that the proportions of sexual systems per grid cell were not significantly
230 correlated with Faith's PD and NRI (Figure S2).

231

232 **Statistical analyses**

233 First, spatial linear models (SLM) were built to evaluate the relative importance of climatic
234 variables (temperature, precipitation and radiation), mature plant height and average genus
235 age per grid cell in determining the biogeographical pattern in sexual systems. Spatial
236 simultaneous autoregressive error models (SARs) allowing the inclusion of residual spatial
237 autocorrelation in data (Kissling & Carl, 2008) were used for the SLMs. Moran's I was used

238 to diagnose the spatial autocorrelation of residuals of SLMs. Using this approach, we could
239 ensure that the spatial autocorrelation had been successfully removed ($P > 0.05$ in all cases).

240 To evaluate the effect of phylogenetic conservatism on the distribution of sexual systems
241 of woody plants, we first calculated the proportions of species with different sexual systems
242 for each genus separately. Then, we estimated Blomberg's K (Blomberg et al., 2003) for each
243 sexual system separately at the genus level using the “phylosignal” function (Keck et al.,
244 2016) in the R package “*picante*”. The sexual systems of different species are not
245 phylogenetically independent from each other (Table 2). To account for the influence of
246 phylogenetic dependence of sexual systems on the relationships between the grid-level
247 proportions of the three sexual systems and predictors, we fitted a phylogenetically corrected
248 linear mixed-effects model by maximum likelihood (“lmeKin” within the R package “*coxme*”;
249 Orme, 2012).

250 To further compare the effects of abiotic (climate) and biotic drivers (plant height and
251 genus age) on the biogeographical pattern in sexual systems, we generated structural equation
252 models (SEM) by assuming that plant height and genus age influence distributions of sexual
253 systems directly, while the climate variables could influence distributions of sexual systems
254 both directly and indirectly via their effects on plant height (Moles et al., 2009).

255 The above analyses were undertaken with principal component scores (PCs) derived
256 from principal component analysis (PCA) using the “princomp” function in R (Conway &
257 Huffcutt, 2003). One PCA was used to combine the temperature variables (MAT, MTCQ and
258 PET) into a single PC (Temp.PC1) and another one was used to combine the precipitation
259 variables (MAP, PSN and PDQ) into a single PC (Prec.PC1) (Table S2). The first principal

260 components accounted for 93.6% and 78.3% of the variations in temperature and precipitation
261 variables, respectively. Pearson correlations among the two PCs and solar radiation, plant
262 height and genus age were lower than 0.7, indicating a relatively low level of multicollinearity
263 (Dormann et al., 2013). Based on these data explorations Temp.PC1, Prec.PC1, solar
264 radiation, plant height and genus age were included in the final SLM, Imekin and SEM
265 analyses (Table1 & Fig. 2).

266 All analyses were performed in R 3.3.1 (R Core team 2016).

267

268 **RESULTS**

269 **Biogeographical patterns in sexual systems**

270 Overall, hermaphroditism is the most common sexual system of woody plants across China:
271 the proportion of hermaphrodite species is $\geq 50\%$ in 96.1% of the grid cells (Fig. 1). The
272 proportion of dioecious but not of monoecious species is strongly negatively correlated with
273 the proportion of hermaphrodite species (Fig. S1). The relative frequency of the three sexual
274 systems varies geographically (Fig. 1). The proportion of dioecious species is high in
275 northeast China and in the Qinghai-Tibetan Plateau whereas the proportion of monoecious
276 species is high in eastern and southern China. In contrast, the proportion of hermaphrodites is
277 high in northwest China (Fig. 1c).

278

279 **Influence of climate on sexual systems**

280 Temperature (Temp.PC1) had weak effects on the composition of sexual systems, both with or
281 without controlling for other explanatory variables in SAR (Table 1 & S3). In SEM, the

282 influence of temperature on proportions of dioecious and hermaphroditic species was strong
283 in non-humid areas, indicating that correlations between plant height and temperature may
284 have masked temperature effects (Fig. 3). Precipitation affected the prevalence of particular
285 sexual systems weakly in both non-humid and humid areas (Table 1). Solar radiation also had
286 weak effects on the composition of sexual systems (Table 1). After controlling for the effect of
287 climate on plant height in the SEMs, in the humid area solar radiation significantly negatively
288 affected dioecy and monoecy and positively affected hermaphroditism (Fig. 3).

289

290 **Influence of mature plant height as a proxy for longevity on sexual systems**

291 Sexual-system composition varied with plant height (Fig. 2). The proportions of
292 hermaphrodite species decreased with plant height, that is, shorter plants (e.g., < 5 m) had a
293 disproportionately high proportion of hermaphrodites. In contrast, the proportions of
294 dioecious and monoecious species increased with plant height (Table 1).

295 Average plant height per grid cell had consistently the highest explanatory power for
296 geographical variation in composition of sexual systems, both with or without controlling for
297 other predictors (Table 1 & S4; Fig. 3).

298

299 **Influence of evolutionary age on sexual systems**

300 Blomberg's K indicated significant phylogenetic signal in the within-genus proportion of
301 dioecious species ($P < 0.001$), suggesting that dioecy in woody plants is phylogenetically
302 conserved, and closely related genera tend to have similar proportions of dioecy. In contrast,
303 the monoecious and hermaphroditic proportions had no significant phylogenetic signal ($P >$

304 0.05, Table 2).

305 Whether controlling for phylogeny and other predictors or not, average genus age per
306 grid cell was significantly but weakly correlated with biogeographical patterns of sexual
307 systems in both humid and non-humid areas (Table 1 & S3; Fig. 2).

308

309 **DISCUSSION**

310 In this study, we investigated the geographical variation of sexual systems of woody plants in
311 China and the mechanisms shaping this variation. We found that climate mainly influenced
312 the biogeographical pattern of sexual systems indirectly by affecting plant height, which we
313 used as a proxy for longevity. Plant height had consistently the highest explanatory power for
314 the proportions of sexual systems across regions. Our findings are thus consistent with the
315 idea that biogeographical patterns in sexual systems reflect longevity (Renner, 2014). Our
316 results also revealed significant contributions of climate and evolutionary age to geographical
317 variation in sexual systems.

318

319 **Influence of mature plant height on sexual systems**

320 The geographical variation in the proportions of different sexual systems across China are
321 predominantly driven by variations in plant height (see Fig. 1 & S4). This extends previous
322 findings that the frequency of life forms correlates with the frequency of mating systems
323 across latitude (Moeller et al., 2017) or that the proportion of dioecious species is higher
324 among trees than among other life forms (e.g. Bawa et al., 1985; Renner & Ricklefs, 1995)
325 and higher in canopy (24.5%) than in understory species (9.8%) (Kress & Beach 1994).

326 Theoretical and observational evidence indicates that large plants could allocate more biomass
327 to sexual reproduction (Niklas & Enquist 2003), leading to larger flower size and/or higher
328 number of floral structures (e.g., petals and stamens) than small plants in both herbaceous
329 (Schmid, Bazzaz, & Weiner, 1995; Lambrecht & Dawson 2007; Arroyo et al. 2013) and tree-
330 sized species (Hirayama et al. 2008; Zhang et al. 2012). This may intensify the disadvantages
331 of self-incompatibility and benefit cross-pollination in dioecious species (Harder & Barrett,
332 1995), especially during mass-flowering events (Eckert et al., 2000). In contrast, selection
333 pressure may be expected to increase the proportion of selfing hermaphrodites among small
334 plants.

335 Being tall can also benefit dioecious species by promoting effective dispersal of pollen
336 and seeds. Since many dioecious species are wind pollinated, being tall can greatly improve
337 pollen dispersal because of the aerodynamics of pollination. Studies indicate that tall
338 individuals of dioecious species can even bypass the flow structures induced by plant
339 morphology (e.g. leaves and branches) to ensure further pollen dispersal and increased mating
340 opportunities (Burd & Allen 1988; Pickup & Barrett 2012; Thomson et al. 2018).

341 Given the well-documented association between plant height and longevity (Marbà et
342 al. 2007; Moles and Leishman, 2008; Moles et al. 2009), our results also suggest an
343 association between sexual systems and longevity, in particular increased frequency of dioecy
344 and monoecy with longevity. Our results thus generalize previous findings about a positive
345 association between dioecy and plant longevity at family level (Renner, 2014) to species level
346 and to monoecy. In contrast, short-lived species are expected to have higher frequency of
347 hermaphrodites, which may explain a higher frequency of hermaphrodites in temperate

348 regions as compared with sub-tropical and tropical regions (Moeller et al., 2017).

349

350 **Influence of climate on the proportions of sexual systems**

351 Our results are consistent with previous findings that mating strategies of woody plants are

352 sensitive to variations in contemporary climate (reflected by both temperature and

353 precipitation) across space (Waller, 1980; Chaves et al., 2003; Dorji et al., 2013; Etterson &

354 Mazer, 2016). However, the effects of climate on the proportions of different sexual systems

355 tended to be indirect since we found that climate had weak direct effects on the

356 biogeographical patterns of sexual systems in both SLMs and SEMs (see Table 1 & Fig. 3).

357 We found that the proportions of hermaphroditic plants were highest in drylands in western

358 China (see Fig. 1), suggesting that hermaphrodites have better drought tolerance than

359 dioecious and monoecious species (Verdú 2004; Obbard et al. 2006). Hermaphrodites are

360 often selfers (Peng et al., 2014, Moeller et al., 2017) and selfers have been found to be able to

361 accelerate carbon assimilation rates, flower early and complete their life cycle rapidly (Mazer

362 et al., 2011. Guerrant, 1989), potentially reducing their exposure to drought in drylands (Ivey

363 et al., 2016). Solar radiation may affect the relative representation of sexual systems via its

364 influence on flower coloration (Peng et al., 2014). For example, Peng et al. (2014) found that

365 hermaphroditism was significantly associated with showy flower color in alpine plants.

366 Quantifying the influence of solar radiation on the frequency of different sexual systems via

367 flower coloration deserves further study.

368

369 **Evolutionary history of sexual systems**

370 We found a significant phylogenetic signal in the genus-level proportions of dioecy,
371 suggesting that the evolution of dioecy has been phylogenetically conserved through
372 evolutionary history (Chazon et al. 2003). In contrast, the genus-level proportions of monoecy
373 and hermaphroditism had very low and non-significant values of Blomberg's K, indicating
374 that monoecious and hermaphroditic species likely have evolved independently many times
375 and possibly for different reasons (Lloyd, 1982).

376 However, genus age correlated only weakly with the geographical pattern of sexual
377 system composition across China (see Table 1 & Fig. S3). For example, the proportion of
378 hermaphroditic species was highest in northwest China where woody floras are relatively
379 young (Lu et al., 2018), which supports the idea that hermaphrodites have been favoured in
380 regions with frequent extinction and re-colonization. In contrast, higher proportions of dioecy
381 may only have been maintained in regions with low rates of local extinction and re-
382 colonization, due to the limitation of mating opportunities (Obbard et al., 2006). This may
383 explain the high proportion of dioecious species in northeast China where woody floras are
384 relatively old (Lu et al., 2018). The relationship between sexual system composition and clade
385 age in a region may be confounded by the magnitude and velocity of climate change, life-
386 history strategies, local adaptation and generation times (Qian 2014, 2017; Hultine et al.,
387 2016).

388

389 **Comparison between patterns in the prevalence of different sexual systems**

390 Although previous studies have noted phylogenetic patterns in the distribution of dioecy,
391 monoecy and hermaphroditism, little has been known about the association between ecological

392 conditions and the distribution of different sexual systems. We found clear evidence that
393 dioecious and hermaphroditic species are favored by opposite ecological conditions: the
394 proportion of dioecy decreased with solar radiation but increased with plant height and genus
395 age, while that of hermaphroditism showed the opposite trends (see Table 1). This finding
396 suggests that dioecy and hermaphroditism may represent two evolutionary extremes of
397 adaptation to specific selection pressures (e.g., climate) during evolutionary history (Snell &
398 Aarssen, 2005; Cannon & Lerdau, 2015; Moller et al., 2017).

399 Biogeographical patterns in the proportion of monoecious species were more complex than
400 those of the other two sexual systems. In Costa Rica, Vamosi & Queenborough (2010) found a
401 comparable reliance of dioecious and monoecious species on insect and wind pollination in a
402 series of forest plots along a local transect. This may be due to more common wind dispersal in
403 dry forests, which lead to lower metabolic costs of plants to produce nectar and fleshy fruits,
404 while more expensive insect pollination could ensure reproductive success in wet tropical
405 forests (Rech et al. 2016). Here we found that the proportions of dioecious and monoecious
406 species consistently increased with the average plant height per grid cell. But we also found
407 that the proportion of monoecy responded to climate (precipitation in arid area and radiation in
408 humid area) in a similar way as the proportion of hermaphrodites did. These results may indicate
409 that monoecy adapts to specific ecological conditions flexibly or that monoecy is an
410 intermediate stage between the other two sexual systems (Goldberg et al., 2017) and thus is not
411 so clearly associated with particular environmental conditions. It is noteworthy that many
412 previous studies about the distribution of sexual systems have pooled monoecious and
413 hermaphroditic species together (e.g. Dorken, Freckleton, & Pannell, 2002; Vamosi, Mazer,

414 Cornejo, 2008; Queenborough et al., 2009). As a result, the ecological and evolutionary aspects
415 of monoecy have not been well studied compare with those of dioecy and hermaphroditism.

416

417 **Caveat to correlative studies**

418 Although correlative studies have the disadvantage that they can only test potential causal
419 relationships, they have the advantage that they can be based on large amounts of data
420 collected under natural conditions. Thus, our analyses offer valuable insights into correlations
421 that can be used to derive causal hypotheses about the potential effects of abiotic (climate)
422 and biotic (plant height, genus age) drivers on geographical variation in the composition of
423 angiosperm sexual systems. Experimental tests of these hypotheses would require large-scale
424 transplantation studies. In addition, species extinctions, together with ongoing and future
425 climate change, may provide unwelcome natural experiments to test these biotic and abiotic
426 hypotheses.

427

428 **CONCLUSIONS**

429 Our findings suggest that mature plant height is the strongest predictor of the biogeographical
430 pattern of woody angiosperm sexual systems across local floras in China and that climate also
431 plays an important role, whereas the evolutionary age of floras has a relatively weak
432 influence. The proportions of dioecy and hermaphrodites in local floras had opposite trends
433 along abiotic and biotic drivers, suggesting that these two sexual systems may represent
434 opposite directions of evolution in adapting to environmental pressures. The flexible response
435 of monoecy to ecological conditions compared with dioecy and hermaphrodite deserves

436 further investigation due to the intermediate state of monoecy between the other two. Our
437 findings shed light on the ecological drivers of geographical variation in sexual systems of
438 woody plants across China and suggest that environmental adaptation significantly influences
439 the biogeographical pattern of sexual systems. Moreover, our finding that present-day
440 geographical variation in sexual systems is strongly related to contemporary climate variables
441 suggests that the composition of sexual systems in local floras may be sensitive to global
442 climate change, and different responses of different sexual systems to ongoing and future
443 climate change could lead to significant changes in the species composition in local plant
444 communities.

445

446 **References**

- 447 Aarssen, L. W. (2000). Why are most selfers annuals? A new hypothesis for the fitness benefit of selfing.
448 *Oikos*, 89(3), 606–612.
- 449 Anderson, E. (1940). The concept of the genus: II. A survey of modern opinion. *Bulletin of the Torrey*
450 *Botanical Club*, 67, 363-369.
- 451 Arroyo, M. T. K., Dudley, L. S., Jespersen, G., Pacheco, D. A., & Cavieres, L. A. (2013). Temperature-
452 driven flower longevity in a high-alpine species of *Oxalis* influences reproductive assurance. *New*
453 *Phytologist*, 200(4), 1260–1268.
- 454 Ashman, T. L. (2006). The evolution of separate sexes: A focus on the ecological context. In L.D. Harder &
455 S.C.H. Barrett (Eds.), *Ecology and Evolution of Flowers*. Oxford, Oxford University Press.
- 456 Ashman, T. L., Bachtrog, D., Blackmon, H., Goldberg, E., Hahn, M., Kirkpatrick, M., Kitano, J., Mank,
457 J., Mayrose, I., Ming, R., Otto, S., Peichel, C., Pennell, M., Perrin, N., Ross, L., Valenzuela, N., &

458 Vamosi, J. (2014). Tree of Sex: A database of sexual systems. The Tree of Sex Consortium. Tree of
459 Sex: A database of sexual systems. *Sci Data*, 1:140015 doi: 10.1038/sdata.2014.15.

460 Barrett, S. C. H., & Eckert, C. G. (1990). Variation and evolution of mating systems in seed plants. In:
461 Biological Approaches and Evolutionary Trends in Plants. Academic Press, Tokyo. Ed. Kawano S.

462 Barrett, S. C. H., & Harder, L. D. (1996). Ecology and evolution of plant mating. *Trends in Ecology and*
463 *Evolution*, 11(2), 73–79.

464 Barrett, S. C. H., & Harder, L. D. (2017). The Ecology of Mating and Its Evolutionary Consequences in
465 Seed Plants. *Annual Review of Ecology, Evolution, and Systematics*, 48, 135–157.

466 Barrett, S. C. H. (2013). The evolution of plant reproductive systems: how often are transitions
467 irreversible? *Proceedings of the Royal Society B: Biological Sciences*, 280(1765), 20130913.

468 Barrett, S. C. H. (1998). The evolution of mating strategies in flowering plants. *Trends in Plant Sciences*,
469 3(9), 335–341.

470 Burd, M., & Allen, T. F. H. (1988). Sexual allocation strategy in wind-pollinated plants. *Evolution*. 42(2),
471 403-407.

472 Campbell, S. A., & Kessler, A. (2013). Plant breeding system transitions drive the macroevolution of
473 defense strategies. *Proceedings of the National Academy of Sciences*, 110(10), 3973–3978.

474 Charlesworth, D. (2006). Evolution of plant breeding systems. *Current Biology*, 16(17), R726–R735.

475 Chazdon, R. L., Careaga, S., Webb, C., & Vargas, O. (2003). Community and phylogenetic structure of
476 reproductive traits of wood species in wet tropical forests. *Ecological Monographs*, 73(3), 331–348.

477 Chen, X. Y. (2003). Breeding system. In Plant life-history evolution and reproductive ecology. Science
478 Press, Beijing, 269–287.

479 Chen, Z, Yang, T., Lin, L., Lu, L. M., Li, H. L., Liu, B., Chen, M., Niu, Y. T., Ye, J. F., Cao, Z. Y., Liu, H.

480 M., Wang, X. M., Wang, W., Zhang, J. B., Meng, Z., Cao, W., Li, J. H., Wu, S. D., Zhao, H. L., Liu,
481 Z. J., Du, Z. Y., Wang, Q. F., Guo, J., Tan, X. X., Su, J. X., Zhang, L. J., Zhang L. J., Yang, L. L.,
482 Liao, Y. Y., Li, M. H., Zhang, G. Q., Chung, S. W., Zhang, J., Xiang, K. L., Li, R. Q., Soltis, D. E.,
483 Soltis, P. S., Zhou, S. L., Ran, J. H., Wang, X. Q., Jin, X. H., Chen, Y. S., Gao, T. G., Li, J. H.,
484 Zhang, S. Z., Lu, A. M. & China Phylogeny Consortium. (2016). Tree of life for the genera of
485 Chinese vascular plants. *Journal of Systematics and Evolution*, 54(4), 273–276.

486 Cardoso, J. C. F., Viana, M. L., Matias, R., Furtado, M. t., Caetano, A. P. S., Consolaro, H., Brito, V. L. G.
487 (2018). Towards a unified terminology for angiosperm reproductive systems. *Acta Botanica*
488 *Brasilica*, 32(3), 329–348.

489 Conway, J. M., & Huffcutt, A. I. (2003). A review and evaluation of exploratory factor analysis practices in
490 organizational research. *Organizational Research Methods*, 6(2), 147–168.

491 Dorji, T., Totland, Ø., Hopping, K. A., Pan, J. B., & Klein, J. A. (2013). Plant functional traits mediate
492 reproductive phenology and success in response to experimental warming and snow addition in
493 Tibet. *Global Change Biology*, 19(2), 459–472.

494 Dorken, M. E., Freckleton, R. P., & Pannell, J. R. (2017) Small-scale and regional spatial dynamics of an
495 annual plant with contrasting sexual systems. *Journal of Ecology*, 105(4), 1044–1057.

496 Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B.,
497 Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder,
498 B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013) Collinearity: a review of methods to deal
499 with it and a simulation study evaluating their performance. *Ecography*, 36(1), 27–46.

500 Eckert, C. G. (2000). Contributions of Autogamy and Geitonogamy to Self-Fertilization in a Mass-
501 Flowering, Clonal Plant. *Ecology*, 81(2), 532–542.

502 Enquist, B. J., Condit, R., Peet, R. K., Schildhauer, M., & Thiers, B. M. (2016). Cyber infrastructure for an
503 integrated botanical information network to investigate the ecological impacts of global climate
504 change on plant biodiversity. *PeerJ Preprints*, 4, e2615v2.

505 Faith, D. (1992). Conservation evaluation and phylogenetic diversity. *Biological Conservation*, 61(1), 1-10.

506 Fang, J., Wang, Z., & Tang, Z. (2011). Atlas of woody plants in China: distribution and climate. Spring,
507 Berlin.

508 Thomson, F. J., Letten, A. D., Tamme, R., Edwards, W., & Moles, A. T. (2018). Can dispersal investment
509 explain why tall plant species achieve longer dispersal distances than short plant species? *New*
510 *Phytologist*. 217(1), 407-415.

511 Freeman, D. C., Harper, K. T., & Ostler, W. K. (1980). Ecology of plant dioecy in the intermountain region
512 of western North America and California. *Oecologia*, 44(3), 410–417.

513 Goldberg, E. E., Otto, S. P., Vamosi, J. C., Mayrose, I., Sabath, N., Ming, R., & Ashman, T. L. (2017).
514 Macroevolutionary synthesis of flowering plant sexual systems. *Evolution*, 71(4), 898–912.

515 Guerrant, E. O. (1988). Heterochrony in plants: the intersection of evolution, ecology, and ontogeny. In M.
516 L. McKinney [ed.], *Heterochrony in evolution*, 111–133. Plenum Press, New York, USA.

517 Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high-resolution
518 interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25, 1965–
519 1978.

520 Hirayama, D., S. Nanami, A. Itoh, and T. Yamakura. 2008. Individual resource allocation to vegetative
521 growth and reproduction in subgenus *Cyclobalanopsis* (*Quercus*, Fagaceae) trees. *Ecological*
522 *Research*, 23: 451-458.

523 Hultine, K. R., Grady, K. C., Wood, T. E., Shuster, S. M., Stella, J. C., & Whitham, T. G. (2016). Climate

524 change perils for dioecious plant species. *Nature plants*, 2, 16109.

525 Ivey, C. T., Dudley, L. S., Hove, A. A., Emms, S. K., & Mazer, S. J. (2016). Outcrossing and photosynthetic
526 rates vary independently within two *Clarkia* species: Implications for the joint evolution of drought
527 escape physiology and mating system. *Annals of Botany*, 118(5), 897–905.

528 Jacquemyn, H., Micheneau, C., Roberts, D. L., & Pailler, T. (2005). Elevational gradients of species
529 diversity, breeding system and floral traits of orchid species on Réunion Island. *Journal of*
530 *Biogeography*, 32(10), 1751–1761.

531 Kissling, W. D., & Carl, G. (2008). Spatial autocorrelation and the selection of simultaneous autoregressive
532 models. *Global Ecology and Biogeography*, 17(1), 59–71.

533 Klekowski, E. J., & Godfrey, P. J. (1989). Aging and mutation in plants. *Nature*, 340, 389–391.

534 Körner, C. (1999). *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems*. Springer-
535 Verlag, Berlin.

536 Lambrecht, S. C., & Dawson, T. E. (2007) Correlated variation of floral and leaf traits along a moisture
537 availability gradient. *Oecologia*. 151, 574–583.

538 Levin, D. A. (2012). Mating system shifts on the trailing edge. *Annals of Botany*, 109(3), 613–621.

539 Lloyd, D. G. (1980). Sexual strategies in plants. I. An hypothesis of serial adjustment of maternal
540 investment during one reproductive session. *New Phytologist*, 86(1), 69–79.

541 Lloyd, D. G. (1982). Selection of combined versus separate sexes in seed plants. *American Naturalist*,
542 120(5), 571–585.

543 Lloyd, D. G. (1992). Self- and cross-fertilization in plants. II. The selection of self-fertilization.
544 *International Journal of Plant Sciences*, 153(3), 370–380.

545 Lord, J. M., Westoby, M., & Leishman, M. (1995). Seed size and phylogeny in six temperate floras:

546 constraints, niche conservatism, and adaptation. *The American Naturalist*, 146(3), 349–364.

547 Lu, L. M., Mao, L. F., Yang, T., Ye, J. F., Liu, B., Li, H. L., Sun, M., Miller, J. T., Mathews, S., Hu, H. H.,
548 Niu, Y. T., Peng, D. X., Chen, Y. H., Smith, S. A., Chen, M., Xiang, K. L., Le, C. T., Dang, V. C., Lu,
549 A. M., Soltis, P. S., Soltis, D. E., Li, J. H., & Chen, Z. D. (2018). Evolutionary history of the
550 angiosperm flora of China. *Nature*, 554, 234–238.

551 Marbà, N., Duarte, M. C., & Agustí, S. (2007). Allometric scaling of plant life history. *Proceedings of the*
552 *National Academy of Sciences*, 104(40), 15777–15780.

553 Matallana, G., Wendt, T., De Araujo, D. S.D., & Scarano, F. R. (2005). High abundance of dioecious plants
554 in a tropical coastal vegetation. *American Journal of Botany* 92(9):1513-1519.

555 Pickup, M., & Barrett, S. H. (2012). Reversal of height dimorphism promotes pollen and seed. *Biology*
556 *Letters*. 8(2), 245-248.

557 Moeller, D. A., Briscoe Runquist, R. D., Moe, A. M., Geber, M. A., Goodwillie, C., Cheptou, P. O., Eckert,
558 C. G., Elle, E., Johnston, M. O., Kalisz, S., Ree, R. H., Sargent, R. D., Vallejo-Marin, M., & Winn,
559 A. A. (2017). Global biogeography of mating system variation in seed plants. *Ecology Letters*, 20(3),
560 375-384.

561 Moles, A. T., & Leishman, M. R. (2008). The seedling as part of a plant's life history strategy. In M. A.
562 Leck, V. T. Parker & R. L. Simpson (Eds.) *Seedling Ecology and Evolution*. Cambridge, Cambridge
563 University Press.

564 Moles, A. T., Warton, D. I., Warman, L., Swenson, N. G., Laffan, S. W., Zanne, A. E., Pitman, A.,
565 Hemmings, F. A., & Leishman, M. R. (2009). Global patterns in plant height. *Journal of Ecology*,
566 97(5), 923–932.

567 Morgan, M.T., Schoen, D. J., & Bataillon, T. M. (1997). The evolution of self-fertilization in perennials.

568 *The American Naturalist*, 150(5), 618–638.

569 Niklas, K., & Enquist, B. (2003). An allometric model for seed plant reproduction. *Evolutionary Ecology*
570 *Research*, 5, 79–88

571 Obbard, D. J., Harris, S. A., & Pannell, J. R. (2006). Sexual systems and population genetic structure in an
572 annual plant: testing the metapopulation model. *The American Naturalist*, 167(3), 354–366.

573 Pannell, J., & Barrett, S. C. H. (1998). Baker’s law revisited: reproductive assurance in a metapopulation.
574 *Evolution*, 52(3), 657–668.

575 Peng, D. L., Ou, X. K., Xu, B., Zhang, Z. Q., Niu, Y., Li, Z. M., & Sun, H. (2014). Plant sexual systems
576 correlated with morphological traits: Reflecting reproductive strategies of alpine plants. *Journal of*
577 *Systematics and Evolution*, 52(3), 368–377.

578 Queenborough, S. A., Mazer, S. J., Vamosi, S. M., Garwood, N. C., Valencia, R., & Freckleton, R. P.
579 (2009). Seed mass, abundance and breeding system among tropical forest species: Do dioecious
580 species exhibit compensatory reproduction or abundances? *Journal of Ecology*, 97(3), 555–566.

581 Renner, S. S., & Ricklefs, R. E. (1995). Dioecy and its correlates in the flowering plants. *American Journal*
582 *of Botany*, 82(5), 596–606.

583 Renner, S. S. (2014). The relative and absolute frequencies of angiosperm sexual systems: dioecy,
584 monoecy, gynodioecy, and an updated online database. *American Journal of Botany*, 101(10), 1588–
585 1596.

586 Ricklefs, R. E., & Wikelski, M. (2002). The physiology/life history nexus. *Trends in Ecology and*
587 *Evolution*, 17(10), 462–468.

588 Sakai, A. K., Wagner, W. L., Ferguson, D. M., & Herbst, D. R. (1995). Biogeographical and ecological
589 correlates of dioecy in the Hawaiian flora. *Ecology*, 76(8), 2530–2543.

590 Sakai, A. K., Weller, S. G., Wagner, P. S., & Soltis, D. E. (1997). Adaptive radiation in the endemic
591 Hawaiian genera *Schiedea* and *Alsinidendron* (Caryophyllaceae: Alsinoideae): phylogenetic insights
592 into the evolution of dioecy. In T. Givnish & K. Sytsma (Eds.), *Molecular evolution and adaptive*
593 *radiation*. New York, Cambridge University Press.

594 Schmid, B., Bazzaz, F.A., & Weiner, J. (1995). Size dependency of sexual reproduction and of clonal
595 growth in two perennial plants. *Canada Journal of Botany*. 73, 1831-1837.

596 Schoen, D. L. (1982). The breeding system of *Gilia achilleifolia*: variation in floral characteristics and
597 outcrossing rate. *Evolution*, 36(2), 352–360.

598 Snell, R., & Aarssen, L. W. (2005). Life history traits in selfing versus outcrossing annuals: exploring the
599 ‘time-limitation’ hypothesis for the fitness benefit of self-pollination. *BMC Ecology*, 5, 2.

600 Thornthwaite, C. W., & Mather, J. R. (1955). *The Water balance*. Centerton, New Jersey.

601 Vamosi, J. C., Otto, S. P., & Barrett, S. C. (2003). Phylogenetic analysis of the ecological correlates of
602 dioecy in angiosperms. *Journal of Evolutionary Biology*, 6(5), 1006–1018.

603 Vamosi, S. M., Mazer, S. J., & Cornejo, F. (2008). Breeding systems and seed size in a Neotropical flora:
604 testing evolutionary hypotheses. *Ecology*, 89(9), 2461–2472.

605 Vamosi, S. M., & Queenborough, S. A. (2010). Breeding systems and phylogenetic diversity of seed plants
606 along a large-scale elevational gradient. *Journal of Biogeography*, 37(3), 465–476.

607 Verdú, M. (2004). Physiological and reproductive differences between hermaphrodites and males in the
608 androdioecious plant *Fraxinus ornus*. *Oikos*, 105(2), 239-246.

609 Wang, Z. H., Brown J. H., Tang, Z. Y., & Fang, J. Y. (2009). Temperature dependence, spatial scale, and
610 tree species diversity in eastern Asia and North America. *Proceedings of the National Academy of*
611 *Sciences of the United States of American*, 106(32), 13388-13392.

612 Williams, A., Antonovics, J., & Rolff, J. (2011). Dioecy, hermaphrodite and pathogen load in plants. *Oikos*,
613 120(5), 657–660.

614 Xiang, Q. B., & Lowry, P. P. (2007). Araliaceae. In Z. Y. Wu, P. H. Raven & D. Y. Hong (Eds.), *Flora of*
615 *China*. (Vol. 13) (Clusiaceae through Araliaceae). Beijing, Science Press and St. Louis, Missouri
616 Botanical Garden Press.

617 Yang, J., Hu, L. J., Wang, Z. K., Zhu, W. L., & Meng, L. H. (2014). Responses to drought stress among sex
618 morphs of *Oxyria sinensis* (Polygonaceae), a subdioecious perennial herb native to the East
619 Himalayas. *Ecology and Evolution*, 4(21), 4033–4040.

620 Zhang, D. Y. (2003). *Plant life-history evolution and reproductive ecology*. Beijing, Science Press.

621

622 **Conflict of interest statement**

623 The authors declare that they have no conflict of interest.

624 **Data accessibility**

625 Should the manuscript be accepted, the data supporting the results in the paper will be
626 archived in Dryad and the data DOI will be included at the end of the article.

TABLES

Table 1 Spatial linear models (SLMs) with simultaneous autoregressive errors (SAR) for proportions of sexual systems as the dependent variable and climate variables (temperature, precipitation and radiation), mature plant height and genus age as multiple independent variables. We show the partial regression coefficients with their standard errors for the explanatory variables. The table shows results from entire China, the area with less than 800 mm precipitation (non-humid area), and the area with over 800 mm precipitation (humid area). Values in bold are significant at $p < 0.05$ and three relevant digits were presented for all the values. MHt - mature plant height; Herma - Hermaphrodite. Moran's I showed that there was no spatial autocorrelation in the residuals of the SLMs.

Variable	Entire area			Non-humid area			Humid area		
	Dioecy	Monoecy	Herma.	Dioecy	Monoecy	Herma.	Dioecy	Monoecy	Herma.
Temp.PC1	-0.00207	0.00509	0.00204	-0.00110	0.00402	-0.00101	0.00091	0.00145	<0.0001
Prec.PC1	<0.0001	-0.00151	0.00145	0.00467	-0.00100	-0.00212	-0.00196	-0.00104	0.00308
Radiation	-0.00146	-0.00579	0.000643	-0.00482	-0.00679	0.00584	-0.00291	0.00171	0.00890
MHt	0.0390	0.0116	-0.0523	0.0381	0.00967	-0.0520	0.00458	0.00817	-0.0189
Genus age	0.00276	0.00406	-0.00687	0.00206	0.00485	-0.00677	0.00476	0.00057	-0.00596
Pseudo- R^2	0.83	0.82	0.89	0.84	0.77	0.89	0.68	0.67	0.79
Moran's I	0.013	0.010	0.010	0.013	0.010	0.010	0.020	<0.001	0.020

Table 2 Phylogenetic signal indice (Blomberg's *K*) for the within-genus proportions of species with different sexual systems. The genus-level phylogenetic tree was extracted from the recently published phylogenetic tree of Chinese vascular plants constructed by Chen et al. (2016).

Sexual system	Phylogenetic Signal	<i>P</i> value
Dioecy	0.493	0.0001
Monoecy	0.156	0.307
Hermaphrodite	0.165	0.526

1 **FIGURES**

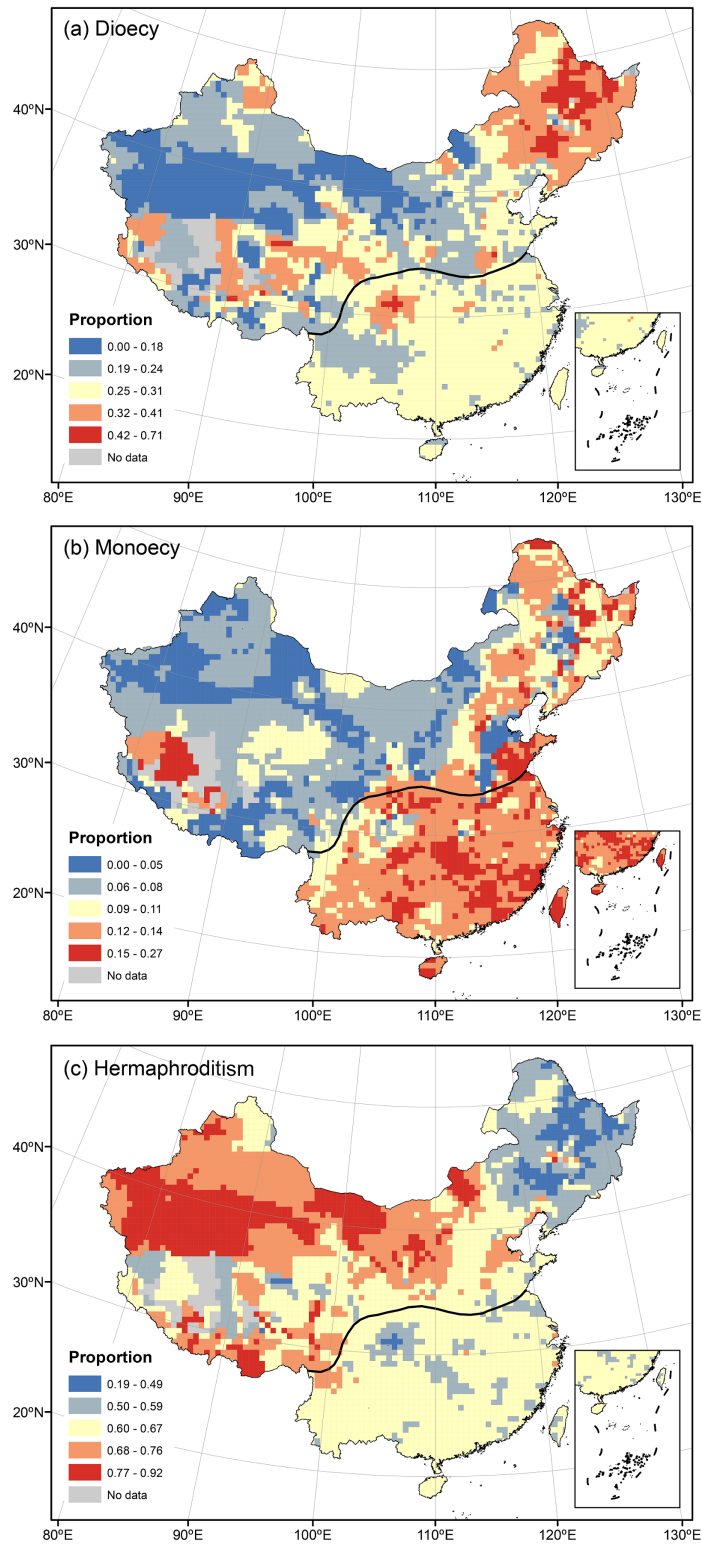
2 **Figure 1.** Spatial patterns in the proportion of different sexual systems in local floras. (a)
3 dioecy; (b) monoecy; (c) hermaphroditism. The solid black line in the figures is the isoline of
4 mean annual precipitation of 800 mm, which also closely tracks to the isoline of mean annual
5 temperature of 0 °C. Grid cells with fewer than 10 woody species are shown in grey.

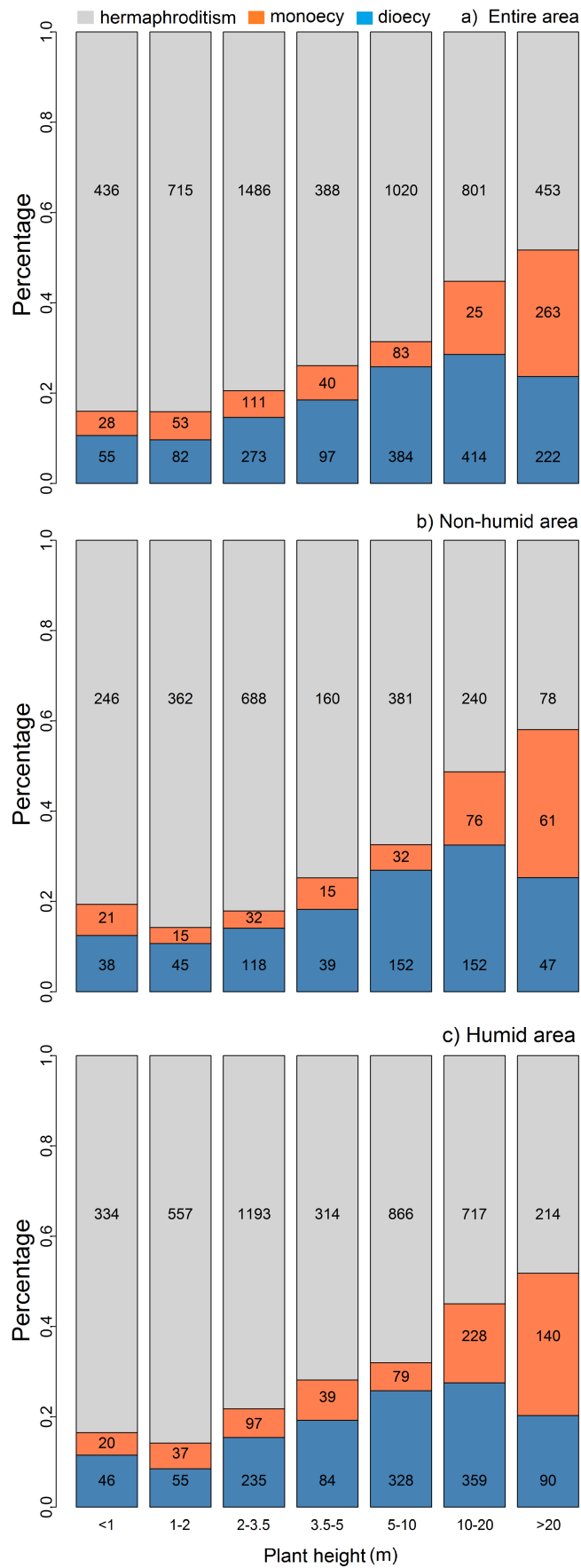
6 **Figure 2** Comparison between the proportions of species with different sexual systems across
7 different plant heights. Corresponding plant heights are shown under the x axis. Panel (a)
8 represents the whole study area, panel (b) represents the area with yearly precipitation < 800
9 mm (non-humid area), and panel (c) represents the area with precipitation > 800 mm (humid
10 area).

11 **Figure 3** Path diagrams showing interactions among climate (the first principal components
12 of temperature [T.PC1] and precipitation [P.PC1] and solar radiation [RAD]), mature plant
13 height (Height), genus age (Age), and proportions of sexual systems. The values next to the
14 arrows are standardized path coefficients. Red values indicate positive relationships and blue
15 values indicate negative relationships. The line thickness of path arrows represents the
16 strength of the relationship. The paths with $p > 0.05$ are not shown. Mono. = Monoecy,
17 Herma. = Hermaphroditism.

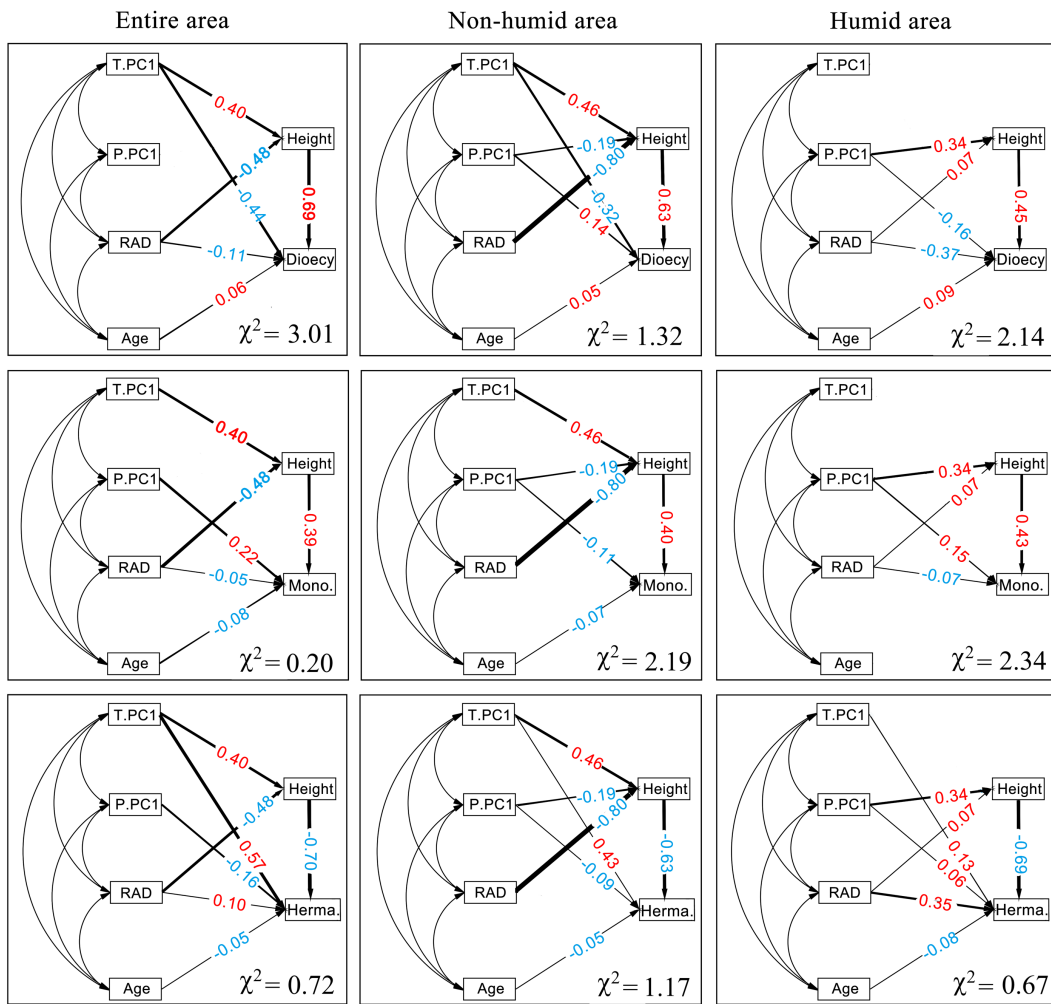
18

19





24 **Figure 3**



25