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1 **Global distribution and evolutionary transitions of angiosperm**
2 **sexual systems**

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26

27 **Running title:** Spatiotemporal pattern in plant sexual system

28 **Type of article:** Letters

29 The manuscript contains an abstract (147 words), main text (4995 words), 78 references, 4
30 figures, 1 table and 1 electronic supplementary material.

31 **Data availability.** Angiosperm sexual system and climate data used in this study will all be
32 available in the public Dryad Digital Repository once the manuscript is accepted. Species
33 distribution maps, original environmental data and phylogenies can be obtained directly from
34 the online databases or publications described in the Methods.

35

36 **Abstract**

37 Angiosperm sexual systems are fundamental to the evolution and distribution of plant
38 diversity, yet spatiotemporal patterns in angiosperm sexual systems and their drivers remain
39 poorly known. Using data on sexual systems and distributions of 68453 angiosperm species,
40 we present the first global maps of sexual system frequencies and evaluate sexual system
41 evolution during the Cenozoic. Frequencies of dioecy and monoecy increase with latitude,
42 while hermaphrodites are more frequent in warm and arid regions. Transitions to dioecy from
43 other states were higher than to hermaphroditism, but transitions away from dioecy increased
44 since the Cenozoic, suggesting that dioecy is not an evolutionary end-point. Transitions
45 between hermaphroditism and dioecy increased, while transitions to monoecy decreased with
46 paleo-temperature when paleo-temperature > 0 °C. Our study demonstrates the biogeography
47 of angiosperm sexual systems from a macroecological perspective, and enhances our
48 understanding of plant diversity patterns and their response to climate change.

49

50 **Keywords:** sexual system; dioecy; hermaphroditism; monoecy; macro evo-devo; climate
51 change; temperature; flowering plants

52

53

54 **Introduction**

55 Owing to the strong benefits of genetic diversity resulting from sexual reproduction
56 (Kondrashov 1988), approximately 97.8% of angiosperms genera reproduce sexually in their
57 natural environment (Hojsgaard et al. 2014). Species with different sexual systems often vary
58 in their morphological (Renner & Ricklefs 1995), physiological (Tognetti 2012; Etterson &
59 Mazer 2016), life-history (Moeller et al. 2017) and reproductive traits (Lebel-Hardenack &
60 Grant 1997; Pannell 2017). Life-history trade-offs may have contributed to sex expression
61 instability (Korpelainen 1998; Charlesworth 1999), and the differential establishment and
62 success of alternative sexual systems in response to different ecological, geographical and
63 climatic settings (Fox 1985; Wang et al. 2020a, b). Therefore, sexual systems are frequently
64 considered as a key factor underpinning the evolution of angiosperm diversity (Barrett 2002;
65 Sabath et al. 2016). Their evolution and geographical distribution have intrigued scientists
66 since Darwin (1876).

67 Previous work on the biogeography of sexual systems, particularly dioecy, has yielded
68 contradictory results. For example, it has been reported that the prevalence of dioecy in local
69 floras increases with latitude in both North America and Siberia (Fox 1985; Godin 2017;
70 Kevan & Godglick 2017). In contrast, others suggest that the prevalence of dioecy was the
71 highest in tropical areas, and decreased with latitude (Lloyd 1980; Vamosi et al. 2003;
72 Moeller et al. 2017). Studies at a global scale are needed to resolve geographical patterns in
73 the prevalence of dioecy. In contrast to dioecy, geographical variation in the frequency of
74 monoecy and hermaphroditism (the most common state among angiosperms) across large
75 spatial scales has been largely ignored in previous studies.

76 The drivers of the geographical variation in sexual system prevalence also remain poorly
77 understood. It has been suggested that growth form and climate (especially precipitation and
78 temperature) influence may be determinants of this variation (Etterson & Mazer 2016;
79 Moeller et al. 2017; Wang et al. 2020a). Both ecological and phylogenetic studies indicate
80 that dioecy is widely associated with woody growth forms, whilst hermaphroditism is
81 associated with herbaceous growth habits (Vamosi et al. 2003; Moeller et al. 2017). Climate
82 may significantly influence the prevalence of different sexual systems through its effect on
83 plant fitness. For example, hermaphrodites have greater reproductive assurance than
84 monoecious or dioecious species at low density. This means that they should have higher
85 fitness in habitats with drought stress (Barrett, 1998; Obbard et al. 2006), which predicts that
86 hermaphrodites should prevail in arid areas (Wang et al. 2020b). Warm temperatures could
87 further exaggerate male-biased sex ratios due to sexual dimorphism in resource acquisition
88 and allocation (Hultine et al. 2016; Tognetti 2012), which puts dioecious species at
89 disadvantage in warm regions. Moreover, dioecious species could undergo upslope range
90 expansion when their habitat has become warmer and drier over a long period of time
91 (Etterson & Mazer 2016). Consequently, dioecy may be more prevalent in cool climates.
92 However, despite a great deal of work, the role of climate in the global biogeography of
93 angiosperm sexual systems remains poorly understood.

94 Empirical and theoretical work has shown that evolutionary transitions between
95 hermaphroditism and dioecy in angiosperms are relatively frequent (Barrett 2002; Torices et
96 al. 2011; Käfer et al. 2017). The transition from hermaphroditism, which has been considered
97 as the ancestral state of many clades (Richards 1997; Doyle 1998), to dioecy has been

98 thoroughly explored (Doyle 1998; Endress 2001; Leonard 2018). In contrast, the evolutionary
99 transition from dioecy to hermaphroditism remains poorly studied (Weeks 2012; Käfer et al.
100 2017) although this type of transition has been found in a range of taxonomic groups (Baker
101 1955).

102 Dioecy is typically hypothesized to be an evolutionary end point, because dioecious
103 species are hypothesised to suffer higher extinction and/or lower speciation rates (Heilbut
104 2000; Barrett 2002). However, recent comparative studies have found relatively frequent
105 transitions from dioecy to other sexual systems (Käfer et al. 2014; Sabath et al. 2016). One
106 reason for this is that stressful environments could reduce mating success in low-density
107 dioecious populations, favouring the evolution of hermaphroditism in females of dioecious
108 species, thereby leading to the stochastic loss of males (Barrett 2013). Many environmental
109 factors could influence the transitions between different sexual systems, of which temperature
110 has been found to be particularly important (Etterson & Mazer 2016; Pérez-Escobar et al.
111 2017). However, the transitions among sexual systems during the evolutionary history of
112 angiosperms, and the degree to which these may have been influenced by climate fluctuations,
113 remain unknown.

114 The spatiotemporal dynamics of angiosperm sexual systems remain relatively
115 unexplored owing to the lack of large comparative datasets with sufficiently broad
116 taxonomical and geographical coverage. Here, using newly compiled data on the sexual
117 systems and global distributions of 68 453 angiosperm species, together with a recently
118 published global angiosperm phylogeny , we describe contemporary global patterns in the
119 prevalence of different sexual systems and the temporal variations in sexual system

120 prevalence and transitions during the Cenozoic. We focus on two hypotheses for the
121 biogeography and evolution of angiosperm sexual systems, and unravel the drivers of the
122 spatiotemporal patterns of angiosperm sexual systems at a global scale. Specifically, we
123 evaluate the hypotheses that 1) dioecious species are more frequent in cold areas, while
124 hermaphroditic species have higher proportions in arid areas; 2) dioecy may not be an
125 evolutionary one-way street.

126

127 **Materials and Methods**

128 ***Sexual systems of angiosperms***

129 A global dataset of angiosperm sexual systems was compiled from published floras and trait
130 databases, including *efloras* (<http://efloras.org/>), *Flora of China* (Wu et al. 1994-2013), *Tree*
131 *of Sex* (Ashman et al. 2014), *Plant Trait Database* (TRY 2012), *Botanical Information and*
132 *Ecology Network* (BIEN, Maitner et al. 2018), *Flora Republicae Popularis Sinicae* (126
133 issues of 80 volumes), *Seeds of Woody Plants in China* and others. We also compiled
134 information from recent publications (Machado et al. 2006; Sabath et al. 2016; Goldberg et al.
135 2017; Perini et al. 2019). Species with conflicting records of their sexual systems in different
136 sources were double-checked and corrected. The sexual systems of a few species likely vary
137 (e.g., Schoen et al. 2017) in response to local biotic and abiotic conditions (e.g., climate
138 variables or pollinator densities; Barrett & Harder 2017). To eliminate the potential influences
139 of these species, we excluded them from the following analyses. In total, our dataset contains
140 sexual system information for 68 453 angiosperm species from 5 550 genera and 355 families
141 (Table S1).

142 We divided species into three categories based on their sexual systems according to
143 Cardoso et al. (2018): dioecy (i.e. species with separate male and female individuals),
144 monoecy (i.e. species with separate male and female flowers on the same plant), and
145 hermaphroditism (i.e. species with both functional pistils and stamens within the same flower).
146 Dioecy includes androdioecious, gynodioecious, and polygamodioecious species; similarly,
147 monoecy includes all monoecious, andromonoecious, and gynomonoeious species. Monoecy
148 has been widely included in comparative analyses on angiosperm sexual systems (Renner
149 2014). We therefore included monoecy as a separate type of sexual system in our analyses.

150 We also compiled information on growth form from published floras, online databases
151 and peer-reviewed journal articles (see Table S2). We classified species into “woody” and
152 “herbaceous” growth forms. Woody species included those recorded as trees, shrubs and
153 woody lianas, while herbaceous species included herbs, herbaceous lianas and subshrubs.

154

155 **Geographical patterns in the frequencies of sexual systems**

156 To document the geographical patterns in the frequencies of sexual systems, we compiled the
157 global distributions of the angiosperm species from published floras, checklists, online
158 databases and peer-reviewed papers (see Table S3 for the complete list of data sources) at a
159 spatial resolution of *ca.* 270 000 km² (*ca.* 4 longitude × 4 latitude). The species names from
160 different data sources were standardized following the *Catalogue of Life*
161 (<http://www.catalogueoflife.org/>, accessed in May 2018), which provides accepted Latin
162 names and synonyms for vascular plants and bryophytes.

163 The boundaries of geographical units used for the compilation of species distributions
164 were taken from the *Global Administrative Areas database* (<http://www.gadm.org/>). To
165 reduce the variation in the sizes of the geographical units, we used geopolitical boundaries at
166 different levels (e.g. countries, counties, states, and provinces) for different regions. Small
167 adjacent pollical regions were merged into larger geographical units to make the sizes of
168 geographical unit relatively homogenous across the world. Excluding the Antarctic, we
169 divided the entire land area of the world into 484 geographical units, and the average size of
170 these units was *ca.* 270 000 km². This approach to defining geographical units has been used
171 in several previous studies on patterns of angiosperm diversity (i.e. Xu et al. 2019; Shrestha et
172 al. 2018).

173 In order to ensure the quality of the data, the distribution maps of all species included in
174 this study were carefully examined. Introduced distributions were removed from the database
175 following *Plants of the World Online* (<http://plantsoftheworldonline.org/>). The final
176 distribution database included 942 162 occurrence records for 68 453 angiosperms. Of these,
177 information on sexual systems, growth forms and distributions was available for 66 913
178 species, including 27 748 woody and 39 165 herbaceous species (Table S1).

179 We estimated the proportions of species with each sexual system for each geographic
180 unit. There are well-recognized associations between sexual system and growth forms
181 (Vamosi et al. 2003), as well differences in functional adaptations to environmental
182 conditions between woody and herbaceous growth forms (Petit & Hampe 2006).
183 Consequently, we estimated the proportions of sexual systems for all species combined, as
184 well as for woody and herbaceous species separately.

185

186 **Current Climate**

187 Previous studies have found that climate influences the phenology and resource use of sexual
188 organs during plant reproduction (Tognetti 2012; Hultine et al. 2016). We selected several
189 variables to represent climate in our analyses. These were: mean annual temperature (MAT),
190 mean annual precipitation (MAP), temperature seasonality (TSN, the coefficient of variation
191 of mean monthly temperature), precipitation seasonality (PSN, the coefficient of variation of
192 mean monthly precipitation). These variables have been used in previous studies on sexual
193 systems (Wang et al. 2020a).

194 We used the anomaly of mean annual temperature and mean annual precipitation since
195 the Last Glacial Maximum (LGM, ca 18 000–22 000 yr. BP) (MAT_{ano} and MAP_{ano},
196 respectively) to evaluate the effects of Quaternary climate change on the distribution of
197 angiosperm sexual systems (Araújo et al. 2008). MAT, MAP, TSN, and PSN with a spatial
198 resolution of 1 × 1 km (Hijmans et al. 2005) for the period 1970–2000 were downloaded from
199 the WorldClim website (<http://www.worldclim.org/bioclimate>). The climate variables for each
200 geographical unit (ca. 270 000 km²) were estimated as the average of all 1 × 1 km cells within
201 it. MAT_{ano} and MAP_{ano} were calculated as the difference in MAT and MAP between the
202 LGM and the present (i.e. MAT_{present}-MAT_{LGM}, MAP_{present}-MAP_{LGM}), and were used
203 to represent the change in mean annual temperature and mean annual precipitation since the
204 LGM respectively.

205

206 **Paleo-temperature data**

207 Most extant angiosperm species diversified during the Cenozoic (from 64 Million years age
208 [Mya] to the present), a period that experienced dramatic global climate and tectonic changes
209 (Zachos et al. 2001). Climate change has been found to affect gender-specific resource
210 demand and allocation, and may have further led to shifts among sexual systems (Etterson &
211 Mazer 2016). To evaluate the effects of paleo-temperature fluctuations on the rate of
212 transition between sexual systems during the Cenozoic, we used the global mean temperature
213 (i.e. the global mean temperature over ice-free oceans per Mya estimated from oxygen
214 isotopic abundances in ocean sediment cores since 64 Mya until present, Zachos et al. 2001)
215 as a measure of long-term global temperature change. This dataset of global mean
216 temperature has been widely used in biogeographical and paleoclimate studies (Li et al. 2014;
217 Turk et al. 2020).

218

219 **Angiosperm phylogenies**

220 We used the dated mega phylogeny of angiosperm species (353 185 tips) constructed by
221 Smith & Brown (2018). The backbone of this phylogeny was constructed using molecular
222 data from GenBank on 79 881 taxa. Species lacking sequence data were inserted into the
223 phylogeny as basal polytomies in their families based on current taxonomy (Smith & Brown
224 2018). This phylogeny has been widely used in biogeographic and macroecological studies
225 (Weigelt et al. 2020). To reduce the possible influences of polytomies on the estimation of
226 phylogenetic analyses, we resolved the polytomies along the tips of the phylogeny using a
227 Yule bifurcation process (Kuhn et al. 2011; Roquet et al. 2013). After matching the species

228 names with sexual system information with the phylogeny a total of 61 230 species were
229 retained (Table S1).

230

231 **Statistical analyses**

232 We first used beta regression (Cribari-Neto & Zeileis 2010) to assess the effects of each
233 predictor on the global patterns of sexual system proportions per geographic unit for all
234 species combined, as well as for woody and herbaceous species separately. We used modified
235 *t*-tests that could account for the effect of spatial autocorrelations to test the effects of the
236 climate variables (Clifford et al. 1989).

237 To examine potential biases in estimates of the proportions of each system per
238 geographical unit caused by unequal sampling effort across regions, we first calculated the
239 sampling proportion as the ratio between the richness of species with sexual system data and
240 the total species richness within each geographical unit. We then used beta regression to
241 examine the relationship between the proportion of each sexual system per geographical unit
242 and the proportion of sampled species. A modified *t*-test indicated that these two variables
243 were not correlated with each other (Fig. S1 & S2). This suggests that uneven sampling effort
244 across space did not affect the estimated geographic patterns in proportions of sexual systems.

245 We used the rayDISC function of the R package corHMM (Beaulieu et al. 2013) to
246 reconstruct the ancestral states. The rayDISC function fits a model for the evolution of
247 multi-state categorical traits, allowing for polymorphisms and incompletely resolved trees.
248 For the reconstruction, we fitted three different models that assumed different evolutionary
249 scenarios. The ER model assumes that all transition rates are equal, the SYM model assumes

250 that forward and reverse transitions share the same parameter, and the ARD model assumes
251 that all transition rates are different.

252 It has been suggested that sexual systems may influence speciation in angiosperms (e.g.
253 Heilbuth 2000; but see Goldberg et al. 2017). Therefore, we also estimated ancestral sexual
254 system states using state-dependent speciation and extinction (SSE) models. Specifically, we
255 used stochastic character mapping and HiSSE models (with both three and two hidden states
256 separately, Table S4) in RevBayes (Höhna et al. 2016). The HiSSE model accounts for the
257 impact of possible state-dependent (both the observed and hidden states) diversification rates
258 on ancestral-state reconstructions, does not assume homogenous transition rates across the
259 phylogeny (Beaulieu & O'Meara 2016) and takes into account incomplete taxon sampling. An
260 additional advantage of HiSSE is that it does not suffer from the high sensitivity to model
261 misspecification reported for SSE models that do not consider hidden states (Beaulieu &
262 O'Meara 2016). Each HiSSE analysis consisted of two independent runs each generating 2500
263 stochastic maps, with the first 100 generations used to tune parameters. The results were
264 examined for convergence and effective sample size after discarding 25% of the samples from
265 the posterior as burn-in.

266 Additionally, to assess the proportion of significant character associations that might be
267 recovered by chance (Type I error) based on the number of character states and tips in our tree,
268 we simulated stochastic character histories using the `sim.history` function of the `phytools`
269 package in R (Revell 2012). We ran simulations for 1000 generations under the ER and the
270 ARD models using equal and FitzJohn (FitzJohn et al., 2009) priors for root state frequencies.

271 Based on the ancestral state reconstructions, we counted the proportion of branches
272 reconstructed with each sexual system in every one million year time interval, and estimated
273 temporal changes. We estimated the temporal changes in the transition rates between different
274 sexual systems. The transitions between the three sexual systems were grouped into three
275 categories: 1) from dioecy to monoecy or to hermaphroditism ($D \rightarrow M$ and $D \rightarrow H$,
276 respectively); 2) from hermaphroditism to dioecy or to monoecy ($H \rightarrow D$ and $H \rightarrow M$,
277 respectively); and 3) from monoecy to hermaphroditism or to dioecy ($M \rightarrow H$ and $M \rightarrow D$,
278 respectively). We further evaluated the effect of paleo-temperature on the temporal changes in
279 the frequency of each sexual systems and the frequency of transitions between sexual systems
280 using beta regressions.

281 The ER, SYM, and ARD models yielded consistent results on the temporal changes in
282 the proportions of sexual systems and transitions rates among sexual systems. The ARD
283 model had the lowest Akaike information criterion (AIC) value (AIC values were 18442,
284 17621, and 17000 for ER, SYM, and ARD models, respectively, under both joint and
285 marginal reconstruction). Stochastics maps built using HiSSE models with either two or three
286 hidden states also yielded estimates of the transition rates among sexual systems consistent
287 with the rayDISC ARD model. Simulations based only on root character state prior (either
288 equal state probability or FitzJohn), number of tips and topology produced significantly
289 different patterns compared with analyses based on the actual character dataset (Fig. S3 & S4),
290 which indicates that our results are not an analytical artifact. Therefore, we show the results
291 from ARD model in the main text. For reference, results from all other models were shown in
292 the supplementary information (Fig. S5 & S6).

293 Our full dataset contained 61 230 species, which represent about 25% of the 261 750
294 total species accepted in the Angiosperm Phylogeny Website (Stevens, 2001 onward). In
295 order to assess the reliability of transition estimates given the large fraction of missing taxa,
296 we randomly generated 100 subsamples with the same proportion (i.e. 25%) of the species in
297 our full dataset (n = 15 308) but balanced the proportion of sexual systems (i.e. 77-80% for
298 hermaphroditism and 6-7% for dioecy) following Igea & Tanentzap (2020). We re-ran the
299 transition analyses for each of the 100 subsamples, then calculated mean results and 95%
300 confidence intervals. By comparing the estimates obtained from our full dataset with the
301 estimates generated by this random sampling procedure, we found that the results from both
302 datasets were highly consistent (Fig. S7).

303 All analyses were conducted in R 3.5.3 (The R Core Team, 2019).

304

305 **Results**

306 *Global patterns in sexual system frequency*

307 Mapping the global distribution of sexual systems revealed evidence of considerable spatial
308 variation. Hermaphroditism was most prevalent in the Eurasian steppe, African savanna and
309 along the Mediterranean coasts for all species combined and for herbaceous species, while
310 woody hermaphroditism was most prevalent in African savanna, north India and southeast
311 Australia (Fig. 1). In contrast, dioecy was most prevalent at high northern latitudes for woody
312 and herbaceous species and in humid regions in Southeast Asia for all species combined, but
313 was least prevalent in Africa, southern North American and tropical South America. The
314 proportion of monoecious species was the highest in North America for all species combined

315 and the two growth forms, and was also high in the high latitudes of Eurasia for herbaceous
316 species.

317

318 *Determinants of global patterns in sexual system frequencies*

319 Temperature was the most influential predictor of the geographical patterns in the proportion
320 of sexual systems, but MAT and MATano had contrasting effects in all cases. MATano
321 correlated strongly with the proportions of hermaphroditism and monoecy for all species
322 combined and herbaceous species: hermaphroditic species were positively correlated with
323 MATano, while monoecious species were negatively correlated with MATano ($R^2 = 21.5\% \sim$
324 33.7% , $P < 0.001$). MAT strongly influenced the proportions of both woody hermaphroditism
325 and dioecy and herbaceous dioecy: proportions of woody and herbaceous dioecious species
326 were negatively correlated with MAT, while woody hermaphroditism was positively
327 correlated with MAT ($R^2 = 30.6\% \sim 56.2\%$, $P < 0.001$). Both woody and herbaceous
328 hermaphroditic species decreased with TSN while dioecious species increased ($R^2 = 8.3\% \sim$
329 29.4% , $P < 0.001$).

330 Precipitation has a moderate effect, with the most noticeable pattern being that PSN
331 influenced the prevalence of sexual systems for all species, influencing the distribution of
332 herbaceous sexual systems: the proportion of herbaceous hermaphroditic species increased
333 with PSN, while the proportions of herbaceous dioecious and monoecious species decreased
334 (Fig. 2).

335

336 *Temporal changes in sexual system proportions and transitions*

337 Transition rates away from hermaphroditism to both dioecy and monoecy decreased until ca.
338 20 Mya (Fig. 3b). In contrast, the transition rates from dioecy to hermaphroditism and
339 monoecy increased until 15 Mya, which was mainly driven by the D→M transitions rate (Fig.
340 3c). Transition rates away from monoecy continuously increased, especially from ca. 15 Mya
341 to the present (Fig. 3d). Overall, the transition rates to dioecy were higher than the transition
342 rates to hermaphroditism (Fig. 3 & S5 & S6).

343

344 *Relationship between sexual system transitions and paleo-temperature*

345 Transition rates from hermaphroditism to dioecy (H→D, $R^2 = 0.595$, $P < 0.001$; Fig. 4b,
346 Table S5) and reversal (D→H, $R^2 = 0.567$, $P < 0.001$; Fig. 4c, Table S5) significantly
347 increased with paleo-temperature when paleo-temperature was > 0 °C, but kept relatively
348 stable when paleo-temperature was < 0 °C. This suggests that 0 °C might be a threshold to
349 break the stable transitions between dioecy and hermaphroditism. In contrast, transition rates
350 from both hermaphroditism and dioecy to monoecy (H+D→M) significantly decreased with
351 paleo-temperature, which was mainly attributed to the decline in the D→M transition ($R^2 =$
352 0.321 , $P < 0.001$; Fig. 4d) when paleo-temperature was > 0 °C.

353

354 **DISCUSSION**

355 Based on an extensive dataset on angiosperm distributions and sexual systems, we found that
356 the frequency of dioecy and monoecy increased with latitude and the frequency of
357 hermaphrodites increased with local temperature but decreased with the increase in
358 temperature variation. Of the set of variables examined, environmental temperature had the

359 strongest effect on the global geographical patterns of sexual system frequencies. Although
360 the sexual systems of angiosperms may evolve towards greater sexual differentiation, dioecy
361 is not an evolutionary end point. Our results do not support earlier findings that the frequency
362 of dioecious species decreases with latitude (Lloyd 1980; Moeller et al. 2017) but suggest that
363 environmental temperature may be a dominant factor shaping the spatiotemporal variations in
364 sexual systems of angiosperms. Taken together, our results shed light on the possible future
365 differential responses of of angiosperm sexual systems to climate warming.

366

367 *Contrasting geographical patterns in the frequency of different sexual systems*

368 Our analyses showed that the frequency of dioecy increased from the Southern Hemisphere
369 towards the North Pole for all species combined, and for both woody and herbaceous species
370 independently (see Fig. S8). This result supports and expands previous findings in North
371 America and Siberia (Fox 1985; Godin 2017), but contrasts with the well-documented
372 hypothesis that dioecy should be the most frequent sexual system in tropical floras (Lloyd
373 1980). The frequency of hermaphrodites was the highest in global drylands (including the
374 drylands in southern and northern Africa, central and western Asia) and the eastern Amazon
375 basin in South America (see Fig. 1), although the patterns for woody and herbaceous
376 hermaphrodites were slightly different from each other.

377

378 *Temperature drives the geographical patterns of sexual systems*

379 Our results suggest that temperature was the strongest determinant of the geographical
380 patterns in the frequencies of angiosperm sexual systems. Specifically, the frequency of
381 dioecy in local floras significantly decreased with environmental temperature, which
382 demonstrates that dioecy tends to prevail in cold climates (Godin 2017). This finding does not
383 support the previous hypothesis that dioecy should prevail in tropical floras (Bawa & Opler
384 1975; Sobrevila & Arroyo 1982). Many dioecious species are long-lived perennials with
385 greater longevity and resistance to cold stress than other systems (Lithgow & Kirkwood 1996).
386 Gender-specific differences in water-use efficiency (i.e. males performed better in dry areas)
387 will exacerbate male-biased sex ratio and put dioecious species at high risks in regions with
388 high temperature (Etterson & Mazer 2016).

389 In contrast, the proportions of hermaphrodites significantly increased with contemporary
390 temperature and PSN, suggesting that hermaphrodites tend to prevail in warm and arid
391 climates (Wang et al. 2020b). Hermaphrodites trade-off allocation of resources to flowers in
392 order to optimize the male and female functions in response to climate. Previous studies based
393 on 12 species of the genus *Pedicularis* have found that hermaphrodites tend to be male-biased
394 by investing disproportionately more resources in attractive parts (i.e. corolla, sepals, and
395 anthers) as temperature decreases (Guo et al. 2010). In contrast, hermaphrodites, especially
396 self-fertilizing hermaphrodites, have evolved a series of drought-tolerant attributes that
397 directly benefit both male and female functions in warmer and drier conditions, such as small
398 flowers that facilitate reproductive assurance through self-fertilization, and promote rapid
399 completion of the life cycle (Etterson & Mazer 2016). This avoids mismatch between the

400 timing of flowering and the life-cycles of pollinators caused by rising temperatures (Lloyd &
401 Bawa 1984; Etterson & Mazer 2016).

402 It is noteworthy that previous studies have normally treated monoecy as a special case of
403 hermaphroditism (Renner 2014). However, floral trade-offs differ greatly between
404 monoecious and hermaphroditic plants. Monoecious species balance resources among
405 separate male and female flowers on the same plant, while hermaphrodites allocate resources
406 between male and female functions within a flower. Correspondingly, our results suggest that
407 geographical distributions of the frequency of monoecious species are more similar to those
408 of dioecious species than to those of hermaphrodites.

409 Similarly, the proportions of dioecious and monoecious species consistently decreased
410 with contemporary temperature, but increased with MAT_{ano}. Previous studies also suggest
411 that dioecy and monoecy have similar associations with wind pollination (Renner & Ricklefs
412 1995), small flowers (Vary et al. 2011), and closer kinship at the family level (Renner &
413 Ricklefs 1995). These suggest that the assumption that monoecy is a special case of
414 hermaphroditism is probably justifiable only if monoecious species are self-compatible as
415 frequently as hermaphrodites. Our results suggest that future studies on sexual systems should
416 treat monoecy independently rather than as a special case of hermaphroditism.

417 Additionally, MAT_{ano} was also a significant predictor of sexual system frequencies, and
418 its effect was in contrary to that of MAT in all cases. MAT_{ano} strongly influenced the
419 composition and structure of vegetation, with many modern species migrating northward to
420 survive (Nolan et al. 2018). Previous studies indicate that dioecy is strongly associated with

421 high dispersal ability in trees (Barot & Gignoux 2004), and hence higher recolonization
422 ability compared with hermaphrodites (Renner & Ricklefs 1995).

423

424 *Sexual systems transition towards greater sexual differentiation*

425 Since the Cenozoic, transition rates to dioecy have been higher than to hermaphroditism. A

426 previous study also found that the transition rate from hermaphroditism to dioecy was

427 approximately twice as high as the reverse transition in bryophytes (McDaniel et al. 2012).

428 These results suggest that evolutionary transition may proceed in the direction of greater sex

429 differentiation (Webb 1999), which does not support the recent findings based on a dataset of

430 limited number of genera (Goldberg et al. 2017).

431 We found that average global paleo-temperature significantly promotes the transition

432 from hermaphroditism to sexual differentiation especially when paleo-temperature was over

433 0 °C, suggesting that the evolution of sexual systems may also be an environmentally

434 adaptive strategy to enhance plant fitness (Policansky 1981), similar to the

435 temperature-dependent sex determination in animals (Bókonyi et al. 2019). Temperature

436 increases within a certain range could change the sex allocation between male and female

437 sexual organs. A shift to femaleness could increase seed-set (Blake-Mahmud & Struwe 2019),

438 while a shift to male-biased sex ratio could maintain plant abundance because moderately

439 elevated temperature can help males of dioecious species allocate relatively more biomass to

440 roots, and better meet their higher nitrogen demand for accelerated photosynthetic

441 performances (Tognetti 2012). Nevertheless, the proportions of hermaphrodites and dioecious

442 species did not increase or decrease overall through long-term geological time (see Fig. 4a)

443 because different selective pressures act on different clades (Goldberg et al. 2017), although
444 there is a trend towards greater sexual differentiation. Thus, more population-level empirical
445 studies are necessary to improve our understanding on the evolution and maintenance of the
446 myriad angiosperm sexual systems.

447

448 *Dioecy may not be an evolutionary end point*

449 We found that the transition rate away from dioecy increased continuously during the
450 Cenozoic, which does not support the hypothesis that dioecy is an evolutionary one-way street
451 (Barrett 2002). The potential evolutionary benefits of the transitions away from dioecy to
452 other sexual systems include: 1) avoidance of pollen limitation (Ehlers & Bataillon 2007); 2)
453 the need for reproductive assurance during colonization (Pannell 2000); and 3) sex ratio
454 evolution with hybridization (Barrett et al. 2010). Furthermore, temperature also promoted
455 direct transitions between D and H when paleo-temperature was > 0 °C. It is noteworthy that
456 transition rates from dioecy to the other systems are relatively lower than all the other
457 transitions among the three sexual systems. This possibly suggests that the transitions from
458 dioecy to other systems are likely to be more difficult than other transitions. The evolutionary
459 transition from unisexuality to hermaphroditism requires high genetic variation in sex
460 expression in dioecious populations, or hybridization with other populations (Barrett 2013). In
461 contrast, the reverse transitions, i.e. H→D transition, are easier to achieve. For example, the
462 invasion of a single-sexed mutants into hermaphroditic populations can cause the resource
463 allocation of remaining hermaphrodites to become biased towards the increased presence of

464 single-sex morphs (i.e. monoecy), which may further lead to the evolution of dioecy
465 (Charlesworth & Charlesworth 1978).

466

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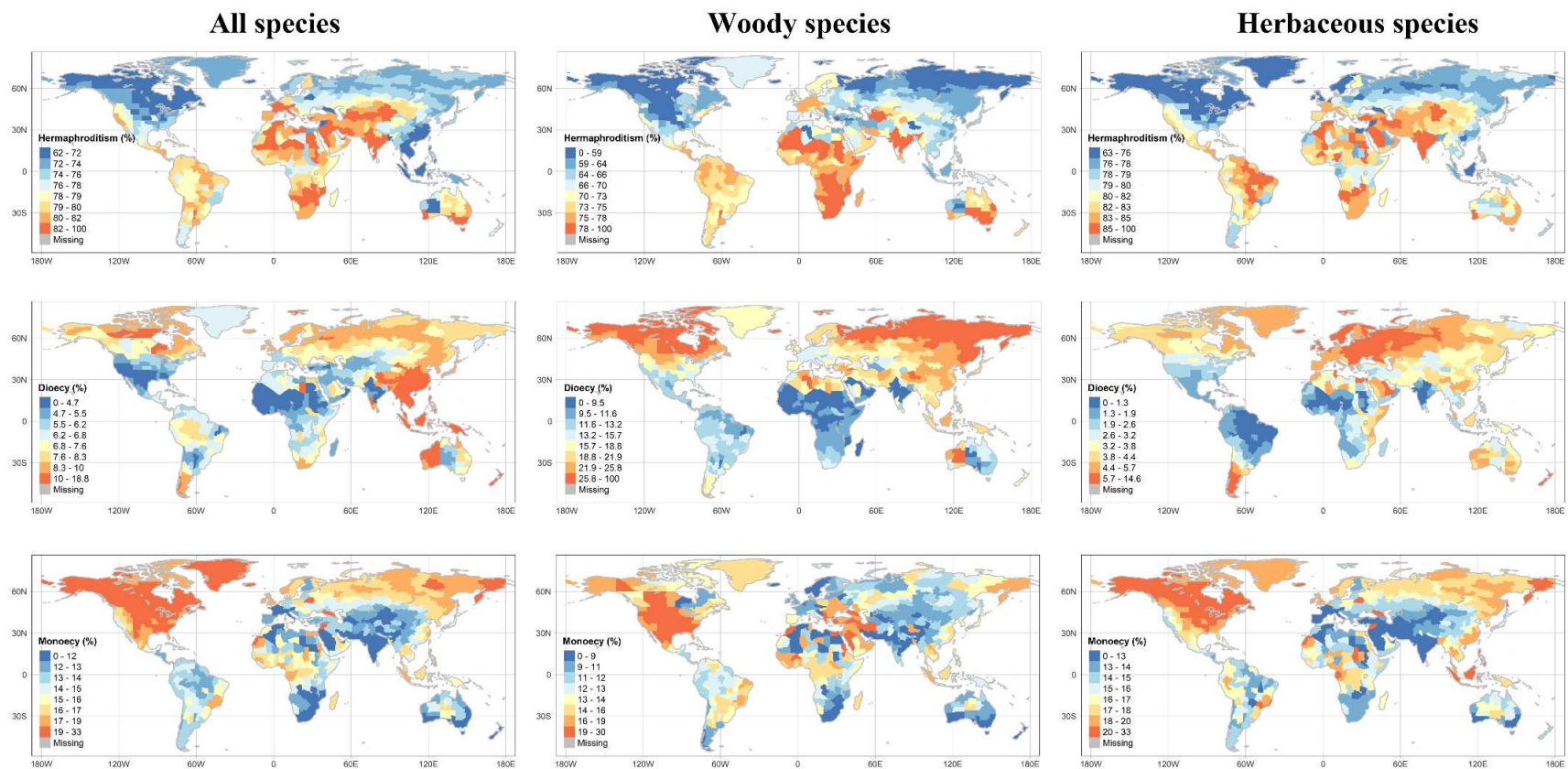
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- 647

648 **Table 1.** The explanatory power (R^2) of each climate variable on the proportions of sexual systems at grid level evaluated using single bivariate
649 beta regression (68,453 species for all species, 27,748 woody species and 39,165 herbaceous species). MAT = Mean Annual Temperature, MAP
650 = Mean Annual Precipitation, TSN = Temperature Seasonality, PSN = Precipitation Seasonality. Significance was estimated using a modified
651 *t*-test (Clifford et al. 1989). Significance codes: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$. Herma. = Hermaphroditism

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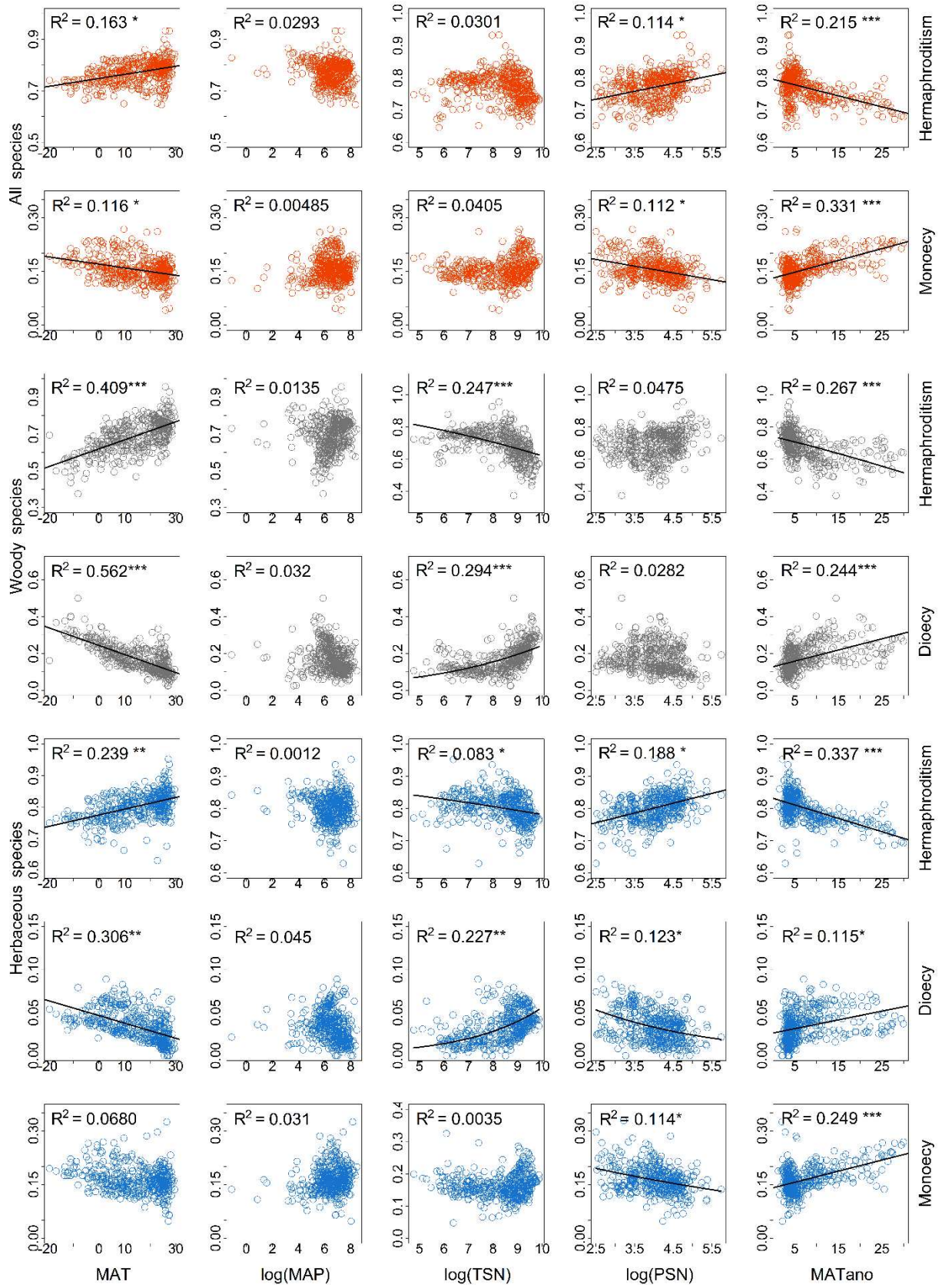
Variable	All species			Woody species			Herbaceous species		
	Herma.	Dioecy	Monoecy	Herma.	Dioecy	Monoecy	Herma.	Dioecy	Monoecy
MAT	0.163*	0.031	0.116*	0.395***	0.555***	-0.0022	0.239***	0.306***	0.0680
MAP(log)	0.0293	0.0361	0.00485	0.0135	0.0320	0.00163	0.0012	0.0445	0.031
TSN(log)	0.0301	-0.0022	0.0405	0.247**	0.294***	0.00276	0.083*	0.227**	0.0035
PSN(log)	0.114*	0.0158	0.112*	0.0475	0.0282	0.00185	0.188*	0.123*	0.114*
MATano	0.215***	0.0057	0.331***	0.267***	0.244***	0.00314	0.337***	0.115*	0.249***
MAPano	0.078	0.059	0.0242	0.0219	0.0612	0.0108	0.0550	0.0191	0.0377

653 **Figure 1.** Global patterns in the prevalence of different sexual systems. From left to right: all species, woody species and herbaceous species.
 654 From top down: hermaphroditism, dioecy and monoecy. Within a site, the prevalence of a sexual system was represented by the proportion of
 655 species with that sexual system. For each group, the proportions of the three sexual systems within each geographical unit sum to one.



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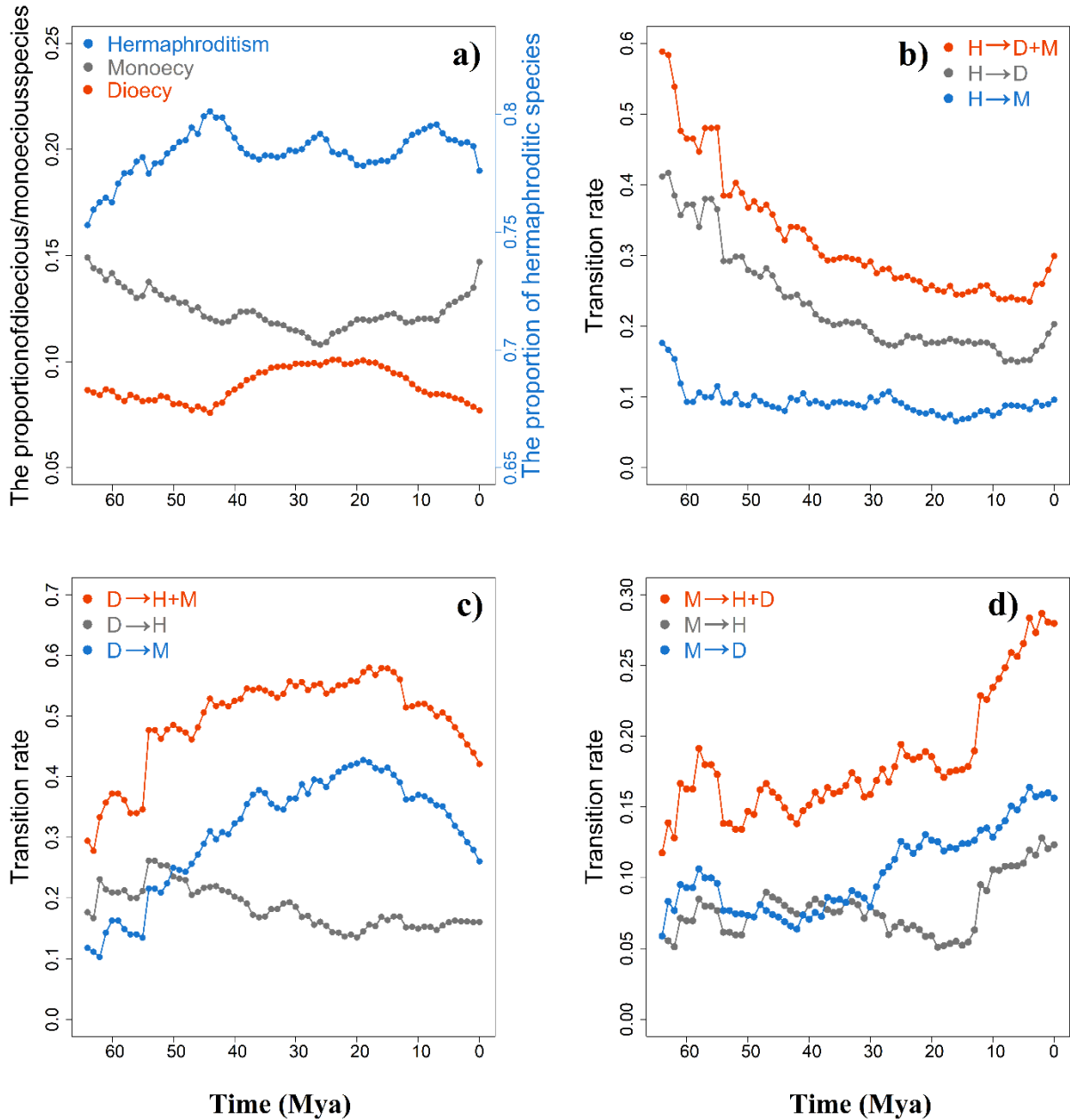
658 **Figure 2.** Relationships between the proportions of angiosperm species with different sexual
659 systems per geographical unit and environment variables (x-axes). From left to right each
660 column represents mean annual temperature [MAT], mean annual precipitation [MAP],
661 log-transformed Precipitation Seasonality [PSN(log)], log-transformed Temperature
662 Seasonality [TSN(log)] and the anomaly of mean annual temperature since the Last Glacial
663 Maximum (ca 18 000–22 000 yr. BP) [MATano] respectively. The y-axes represent the
664 proportion of angiosperm species with different sexual systems within each geographical unit.
665 From top down: hermaphroditism and monoecy of all species, woody hermaphroditism and
666 dioecy, and herbaceous hermaphroditism, dioecy and monoecy. The relationships were
667 assessed by single bivariate beta regressions, and the *P*-values of the regressions were
668 calculated by a modified *t*-test. Regression lines are drawn for significant relationships ($P <$
669 0.05). R^2 values associated with each variable are given in the top left corner of each panel
670 (See the Table 1).



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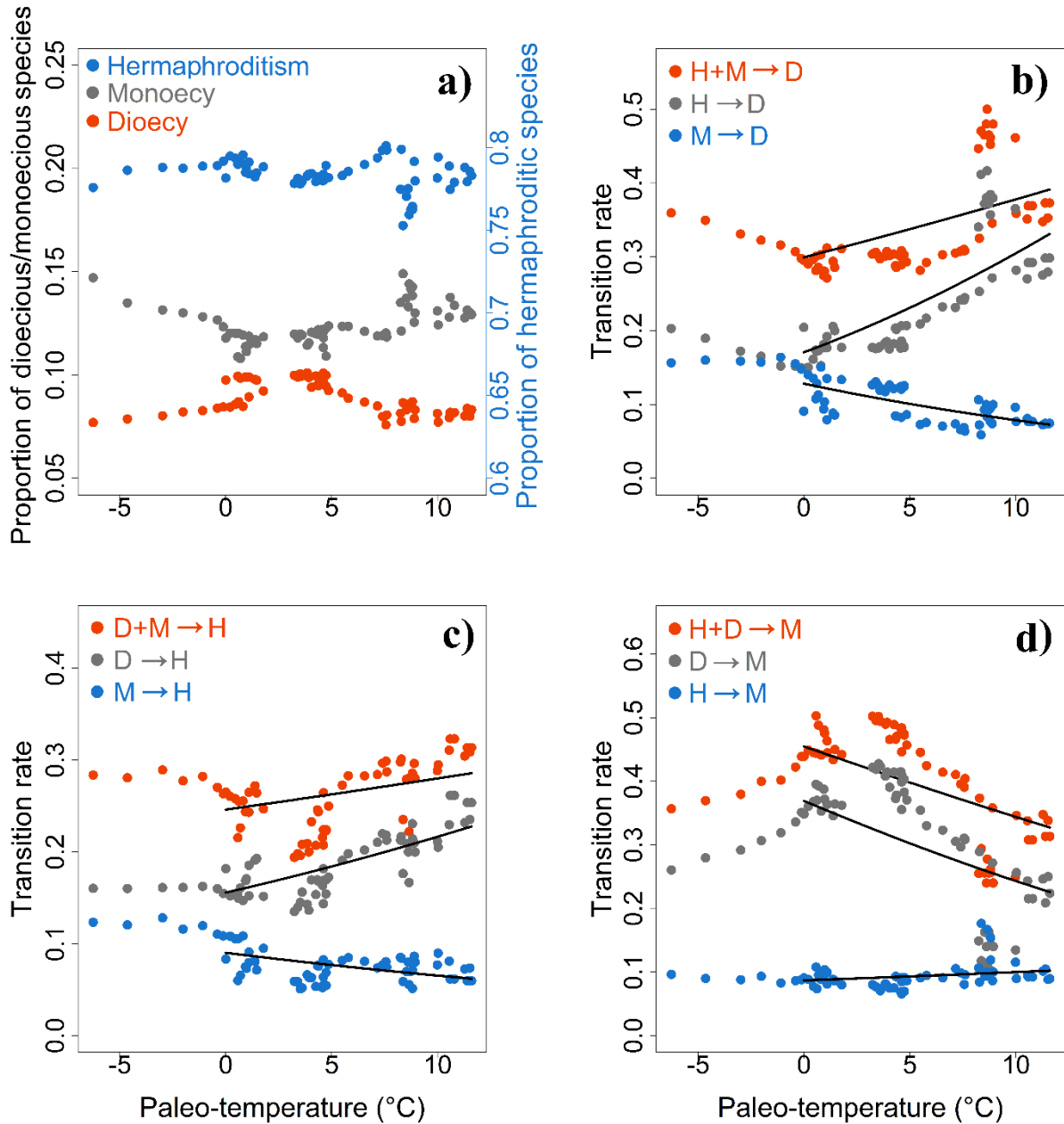
673 **Figure 3.** The temporal changes in the proportions of species with different sexual systems (a)
 674 and the transition rates between different sexual systems (i.e. the ratios of transitions between
 675 two sexual systems to the total number of transitions) (64 – 0 Mya) (b-d). H =
 676 hermaphroditism, D = dioecy, M = monoecy. See Fig. S9 for results for the time period of
 677 135 Mya – 0 Mya.



678

679 **Figure 4** Changes in the proportions of species with different sexual systems (a) and the
 680 transition rates between different sexual systems (i.e. the ratios of transitions between two
 681 sexual systems to the total number of transitions) during the Cenozoic (b–d) as (single,
 682 bivariate beta regression) functions of paleo-temperature. (b), the transitions from dioecy (D);
 683 (c), the transitions from hermaphroditism (H); (d), the transitions from monoecy (M).
 684 Regression lines are drawn for significant relationships in beta regression ($P < 0.05$).

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