Global distribution and evolutionary transitions of angiosperm sexual systems

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

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Abstract

Angiosperm sexual systems are fundamental to the evolution and distribution of plant

diversity, yet spatiotemporal patterns in angiosperm sexual systems and their drivers remain

poorly known. Using data on sexual systems and distributions of 68453 angiosperm species,

we present the first global maps of sexual system frequencies and evaluate sexual system

evolution during the Cenozoic. Frequencies of dioecy and monoecy increase with latitude,

while hermaphrodites are more frequent in warm and arid regions. Transitions to dioecy from

other states were higher than to hermaphroditism, but transitions away from dioecy increased

since the Cenozoic, suggesting that dioecy is not an evolutionary end-point. Transitions

between hermaphroditism and dioecy increased, while transitions to monoecy decreased with

paleo-temperature when paleo-temperature > 0 °C. Our study demonstrates the biogeography

of angiosperm sexual systems from a macroecological perspective, and enhances our

understanding of plant diversity patterns and their response to climate change.

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Introduction

Owing to the strong benefits of genetic diversity resulting from sexual reproduction

(Kondrashov 1988), approximately 97.8% of angiosperms genera reproduce sexually in their

natural environment (Hojsgaard et al. 2014). Species with different sexual systems often vary

in their morphological (Renner & Ricklefs 1995), physiological (Tognetti 2012; Etterson &

Mazer 2016), life-history (Moeller et al. 2017) and reproductive traits (Lebel-Hardenack &

Grant 1997; Pannell 2017). Life-history trade-offs may have contributed to sex expression

instability (Korpelainen 1998; Charlesworth 1999), and the differential establishment and

success of alternative sexual systems in response to different ecological, geographical and

climatic settings (Fox 1985; Wang et al. 2020a, b). Therefore, sexual systems are frequently

considered as a key factor underpinning the evolution of angiosperm diversity (Barrett 2002;

Sabath et al. 2016). Their evolution and geographical distribution have intrigued scientists

since Darwin (1876).

Previous work on the biogeography of sexual systems, particularly dioecy, has yielded

contradictory results. For example, it has been reported that the prevalence of dioecy in local

floras increases with latitude in both North America and Siberia (Fox 1985; Godin 2017;

Kevan & Godglick 2017). In contrast, others suggest that the prevalence of dioecy was the

highest in tropical areas, and decreased with latitude (Lloyd 1980; Vamosi et al. 2003;

Moeller et al. 2017). Studies at a global scale are needed to resolve geographical patterns in

the prevalence of dioecy. In contrast to dioecy, geographical variation in the frequency of

77 monoecy and hermaphroditism (the most common state among angiosperms) across large

78 spatial scales has been largely ignored in previous studies.

79 The drivers of the geographical variation in sexual system prevalence also remain poorly

80 understood. It has been suggested that growth form and climate (especially precipitation and

81 temperature) may be determinants of this variation (Etterson & Mazer 2016; Moeller et al.

82 2017; Wang et al. 2020a). Both ecological and phylogenetic studies indicate that dioecy is

83 widely associated with woody growth forms, whilst hermaphroditism is associated with

84 herbaceous growth habits (Vamosi et al. 2003; Moeller et al. 2017). Climate may significantly

85 influence the prevalence of different sexual systems through its effect on plant fitness. For

86 example, hermaphrodites have greater reproductive assurance than monoecious or dioecious

87 species at low density. This means that they should have higher fitness in habitats with

88 drought stress (Barrett, 1998; Obbard et al. 2006), which predicts that hermaphrodites should

89 prevail in arid areas (Wang et al. 2020b). Warm temperatures could further exaggerate

90 male-biased sex ratios due to sexual dimorphism in resource acquisition and allocation

91 (Hultine et al. 2016; Tognetti 2012), which puts dioecious species at disadvantage in warm

92 regions. Moreover, dioecious species could undergo upslope range expansion when their

93 habitat has become warmer and drier over a long period of time (Etterson & Mazer 2016).

94 Consequently, dioecy may be more prevalent in cool climates. However, despite a great deal

95 of work, the role of climate in the global biogeography of angiosperm sexual systems remains

96 poorly understood.

97 Empirical and theoretical work has shown that evolutionary transitions between

98 hermaphroditism and dioecy in angiosperms are relatively frequent (Barrett 2002; Torices et

99   al. 2011; Käfer et al. 2017). The transition from hermaphroditism, which has been considered

100   as the ancestral state of many clades (Richards 1997; Doyle 1998), to dioecy has been

101   thoroughly explored (Doyle 1998; Endress 2001; Leonard 2018). In contrast, the evolutionary

102   transition from dioecy to hermaphroditism remains poorly studied (Weeks 2012; Käfer et al.

103   2017) although this type of transition has been found in a range of taxonomic groups (Baker

104   1955).

105   Dioecy is typically hypothesized to be an evolutionary end point, because dioecious

106   species are hypothesised to suffer higher extinction and/or lower speciation rates (Heilbuth

107   2000; Barrett 2002). However, recent comparative studies have found relatively frequent

108   transitions from dioecy to other sexual systems (Käfer et al. 2014; Sabath et al. 2016). One

109   reason for this is that stressful environments could reduce mating success in low-density

110   dioecious populations, favouring the evolution of hermaphroditism in females of dioecious

111   species, thereby leading to the stochastic loss of males (Barrett 2013). Many environmental

112   factors could influence the transitions between different sexual systems, of which temperature

113   has been found to be particularly important (Etterson & Mazer 2016; Pérez-Escobar et al.

114   2017). However, the transitions among sexual systems during the evolutionary history of

115   angiosperms, and the degree to which may have been influenced by climate fluctuations,

116   remain unknown.

117   The spatiotemporal dynamics of angiosperm sexual systems remain relatively

118   unexplored owing to the lack of large comparative datasets with sufficiently broad

119   taxonomical and geographical coverage. Here, using newly compiled data on the sexual

120   systems and global distributions of 68 453 angiosperm species, together with a recently

121   published global angiosperm phylogeny , we describe contemporary global patterns in the

122   prevalence of different sexual systems and the temporal variations in sexual system

123   prevalence and transitions during the Cenozoic. We focus on two hypotheses for the

124   biogeography and evolution of angiosperm sexual systems, and unravel the drivers of the

125   spatiotemporal patterns of angiosperm sexual systems at a global scale. Specifically, we

126   evaluate the hypotheses that 1) dioecious species are more frequent in cold areas, while

127   hermaphroditic species have higher proportions in arid areas; 2) dioecy may not be an

128   evolutionary one-way street.

129

130   **Materials and Methods**

131   ***Sexual systems of angiosperms***

132   A global dataset of angiosperm sexual systems was compiled from published floras and trait

133   databases, including *efloras* (*http://efloras.org/*), *Flora of China* (Wu et al. 1994-2013), *Tree*

134   *of Sex* (Ashman et al. 2014), *Plant Trait Database* (TRY 2012), *Botanical Information and*

135   *Ecology Network* (BIEN, Maitner et al. 2018), *Flora Republicae Popularis Sinicae* (126

136   issues of 80 volumes), *Seeds of Woody Plants in China* and others. We also compiled

137   information from recent publications (Machado et al. 2006; Sabath et al. 2016; Goldberg et al.

138   2017; Perini et al. 2019). Species with conflicting records of their sexual systems in different

139   sources were double-checked and corrected. The sexual systems of a few species likely vary

140   (e.g., Schoen et al. 2017) in response to local biotic and abiotic conditions (e.g., climate

141   variables or pollinator densities; Barrett & Harder 2017). To eliminate the potential influences

142   of these species, we excluded them from the following analyses. In total, our dataset contains

143   sexual system information for 68 453 angiosperm species from 5 550 genera and 355 families

144   (Table S1).

145   We divided species into three categories based on their sexual systems according to

146   Cardoso et al. (2018): dioecy (i.e. species with separate male and female individuals),

147   monoecy (i.e. species with separate male and female flowers on the same plant), and

148   hermaphroditism (i.e. species with both functional pistils and stamens within the same flower).

149   Dioecy includes androdioecious, gynodioecious, and polygamodioecious species; similarly,

150   monoecy includes all monoecious, andromonoecious, and gynomonoecious species. Monoecy

151   has been widely included in comparative analyses on angiosperm sexual systems (Renner

152   2014). We therefore included monoecy as a separate type of sexual system in our analyses.

153   We also compiled information on growth form from published floras, online databases

154   and peer-reviewed journal articles (see Table S2). We classified species into "woody" and

155   "herbaceous" growth forms. Woody species included those recorded as trees, shrubs and

156   woody lianas, while herbaceous species included herbs, herbaceous lianas and subshrubs.

157

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

159   To document the geographical patterns in the frequencies of sexual systems, we compiled the

160   global distributions of the angiosperm species from published floras, checklists, online

161   databases and peer-reviewed papers (see Table S3 for the complete list of data sources) at a

162   spatial resolution of *ca.* 270 000 km^2 (*ca.* 4 longitude × 4 latitude). The species names from

163   different data sources were standardized following the *Catalogue of Life*

164 (*http://www.catalogueoflife.org/*, accessed in May 2018), which provides accepted Latin

165 names and synonyms for vascular plants and bryophytes.

166   The boundaries of geographical units used for the compilation of species distributions

167 were taken from the *Global Administrative Areas database* (*http://www.gadm.org/*). To

168 reduce the variation in the sizes of the geographical units, we used geopolitical boundaries at

169 different levels (e.g. countries, counties, states, and provinces) for different regions. Small

170 adjacent pollical regions were merged into larger geographical units to make the sizes of

171 geographical unit relatively homogenous across the world. Excluding the Antarctic, we

172 divided the entire land area of the world into 484 geographical units, and the average size of

173 these units was *ca.* 270 000 km^2. This approach to defining geographical units has been used

174 in several previous studies on patterns of angiosperm diversity (i.e. Xu et al. 2019; Shrestha et

175 al. 2018).

176   In order to ensure the quality of the data, the distribution maps of all species included in

177 this study were carefully examined. Introduced distributions were removed from the database

178 following *Plants of the World Online* (http://plantsoftheworldonline.org/). The final

179 distribution database included 942 162 occurrence records for 68 453 angiosperms. Of these,

180 information on sexual systems, growth forms and distributions was available for 66 913

181 species, including 27 748 woody and 39 165 herbaceous species (Table S1).

182   We estimated the proportions of species with each sexual system for each geographic

183 unit. There are well-recognized associations between sexual system and growth forms

184 (Vamosi et al. 2003), as well differences in functional adaptations to environmental

185 conditions between woody and herbaceous growth forms (Petit & Hampe 2006).

186 Consequently. we estimated the proportions of sexual systems for all species combined, as

187 well as for woody and herbaceous species separately.

188

189 **Current Climate**

190 Previous studies have found that climate influences the phenology and resource use of sexual

191 organs during plant reproduction (Tognetti 2012; Hultine et al. 2016). We selected several

192 variables to represent climate in our analyses. These were: mean annual temperature (MAT),

193 mean annual precipitation (MAP), temperature seasonality (TSN, the coefficient of variation

194 of mean monthly temperature), precipitation seasonality (PSN, the coefficient of variation of

195 mean monthly precipitation). These variables have been used in previous studies on sexual

196 systems (Wang et al. 2020a).

197   We used the anomaly of mean annual temperature and mean annual precipitation since

198 the Last Glacial Maximum (LGM, ca 18 000–22 000 yr. BP) (MATano and MAPano,

199 respectively) to evaluate the effects of Quaternary climate change on the distribution of

200 angiosperm sexual systems (Araújo et al. 2008). MAT, MAP, TSN, and PSN with a spatial

201 resolution of 1×1 km (Hijmans et al. 2005) for the period 1970–2000 were downloaded from

202 the WorldClim website (*http://www.worldclim.org/bioclim*). The climate variables for each

203 geographical unit (*ca.* 270 000 km^2) were estimated as the average of all 1×1 km cells within

204 it. MATano and MAPano were calculated as the difference in MAT and MAP between the

205 LGM and the present (i.e. MATpresent-MATLGM, MAPpresent-MAPLGM), and were used

206 to represent the change in mean annual temperature and mean annual precipitation since the

207 LGM respectively.

208

Paleo-temperature data

210   Most extant angiosperm species diversified during the Cenozoic (from 64 Million years age

211   [Mya] to the present), a period that experienced dramatic global climate and tectonic changes

212   (Zachos et al. 2001). Climate change has been found to affect gender-specific resource

213   demand and allocation, and may have further led to shifts among sexual systems (Etterson &

214   Mazer 2016). To evaluate the effects of paleo-temperature fluctuations on the rate of

215   transition between sexual systems during the Cenozoic, we used the global mean temperature

216   (i.e. the global mean temperature over ice-free oceans per Mya estimated from oxygen

217   isotopic abundances in ocean sediment cores since 64 Mya until present, Zachos et al. 2001)

218   as a measure of long-term global temperature change. This dataset of global mean

219   temperature has been widely used in biogeographical and paleoclimate studies (Li et al. 2014;

220   Turk et al. 2020).

221

Angiosperm phylogenies

223   We used the dated mega phylogeny of angiosperm species (353 185 tips) constructed by

224   Smith & Brown (2018). The backbone of this phylogeny was constructed using molecular

225   data from GenBank on 79 881 taxa. Species lacking sequence data were inserted into the

226   phylogeny as basal polytomies in their families based on current taxonomy (Smith & Brown

227   2018). This phylogeny has been widely used in biogeographic and macroecological studies

228   (Weigelt et al. 2020). To reduce the possible influences of polytomies on the estimation of

229   phylogenetic analyses, we resolved the polytomies along the tips of the phylogeny using a

230   Yule bifurcation process (Kuhn et al. 2011; Roquet et al. 2013). After matching the species

231   names with sexual system information with the phylogeny a total of 61 230 species were

232   retained (Table S1).

233

234   **Statistical analyses**

235   We first used beta regression (Cribari-Neto & Zeileis 2010) to assess the effects of each

236   predictor on the global patterns of sexual system proportions per geographic unit for all

237   species combined, as well as for woody and herbaceous species separately. We used modified

238   t-tests that could account for the effect of spatial autocorrelations to test the effects of the

239   climate variables (Clifford et al. 1989).

240   To examine potential biases in estimates of the proportions of each system per

241   geographical unit caused by unequal sampling effort across regions, we first calculated the

242   sampling proportion as the ratio between the richness of species with sexual system data and

243   the total species richness within each geographical unit. We then used beta regression to

244   examine the relationship between the proportion of each sexual system per geographical unit

245   and the proportion of sampled species. A modified t-test indicated that these two variables

246   were not correlated with each other (Fig. S1 & S2). This suggests that uneven sampling effort

247   across space did not affect the estimated geographic pattens in proportions of sexual systems.

248   We used the rayDISC function of the R package corHMM (Beaulieu et al. 2013) to

249   reconstruct the ancestral states. The rayDISC function fits a model for the evolution of

250   multi-state categorical traits, allowing for polymorphisms and incompletely resolved trees.

251   For the reconstruction, we fitted three different models that assumed different evolutionary

252 scenarios. The ER model assumes that all transition rates are equal, the SYM model assumes

253 that forward and reverse transitions share the same parameter, and the ARD model assumes

254 that all transition rates are different.

255   It has been suggested that sexual systems may influence speciation in angiosperms (e.g.

256 Heilbuth 2000; but see Goldberg et al. 2017). Therefore, we also estimated ancestral sexual

257 system states using state-dependent speciation and extinction (SSE) models. Specifically, we

258 used stochastic character mapping and HiSSE models (with both three and two hidden states

259 separately, Table S4) in RevBayes (Höhna et al. 2016). The HiSSE model accounts for the

260 impact of possible state-dependent (both the observed and hidden states) diversification rates

261 on ancestral-state reconstructions, does not assume homogenous transition rates across the

262 phylogeny (Beaulieu & O'Meara 2016) and takes into account incomplete taxon sampling. An

263 additional advantage of HiSSE is that it does not suffer from the high sensitivity to model

264 misspecification reported for SSE models that do not consider hidden states (Beaulieu &

265 O'Meara 2016). Each HiSSE analysis consisted of two independent runs each generating 2500

266 stochastic maps, with the first 100 generations used to tune parameters. The results were

267 examined for convergence and effective sample size after discarding 25% of the samples from

268 the posterior as burn-in.

269   Additionally, to assess the proportion of significant character associations that might be

270 recovered by chance (Type I error) based on the number of character states and tips in our tree,

271 we simulated stochastic character histories using the sim.history function of the phytools

272 package in R (Revell 2012). We ran simulations for 1000 generations under the ER and the

273 ARD models using equal and FitzJohn (FitzJohn et al., 2009) priors for root state frequencies.

274   Based on the ancestral state reconstructions, we counted the proportion of branches

275   reconstructed with each sexual system in every one-million-year time interval, and estimated

276   temporal changes. We estimated the temporal changes in the transition rates between different

277   sexual systems. The transitions between the three sexual systems were grouped into three

278   categories: 1) from dioecy to monoecy or to hermaphroditism (D→M and D→H,

279   respectively); 2) from hermaphroditism to dioecy or to monoecy (H→D and H→M,

280   respectively); and 3) from monoecy to hermaphroditism or to dioecy (M→H and M→D,

281   respectively). We further evaluated the effect of paleo-temperature on the temporal changes in

282   the frequency of each sexual system and the frequency of transitions between sexual systems

283   using beta regressions.

284   The ER, SYM, and ARD models yielded consistent results on the temporal changes in

285   the proportions of sexual systems and transitions rates among sexual systems. The ARD

286   model had the lowest Akaike information criterion (AIC) value (AIC values were 18442,

287   17621, and 17000 for ER, SYM, and ARD models, respectively, under both joint and

288   marginal reconstruction). Stochastics maps built using HiSSE models with either two or three

289   hidden states also yielded estimates of the transition rates among sexual systems consistent

290   with the rayDISC ARD model. Simulations based only on root character state prior (either

291   equal state probability or FitzJohn), number of tips and topology produced significantly

292   different patterns compared with analyses based on the actual character dataset (Fig. S3 & S4),

293   which indicates that our results are not an analytical artifact. Therefore, we show the results

294   from ARD model in the main text. For reference, results from all other models were shown in

295   the supplementary information (Fig. S5 & S6).

296   Our full dataset contained 61 230 species, which represent about 25% of the 261 750

297   total species accepted in the Angiosperm Phylogeny Website (Stevens, 2001 onward). In

298   order to assess the reliability of transition estimates given the large fraction of missing taxa,

299   we randomly generated 100 subsamples with the same proportion (i.e. 25%) of the species in

300   our full dataset (n = 15 308) but balanced the proportion of sexual systems (i.e. 77-80% for

301   hermaphroditism and 6-7% for dioecy) following Igea & Tanentzap (2020). We re-ran the

302   transition analyses for each of the 100 subsamples, then calculated mean results and 95%

303   confidence intervals. By comparing the estimates obtained from our full dataset with the

304   estimates generated by this random sampling procedure, we found that the results from both

305   datasets were highly consistent (Fig. S7).

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

307

308   **Results**

309   ***Global patterns in sexual system frequency***

310   Mapping the global distribution of sexual systems revealed evidence of considerable spatial

311   variation. Hermaphroditism was most prevalent in the Eurasian steppe, African savanna and

312   along the Mediterranean coasts for all species combined and for herbaceous species, while

313   woody hermaphroditism was most prevalent in African savanna, north India and southeast

314   Australia (Fig. 1). In contrast, dioecy was most prevalent at high northern latitudes for woody

315   and herbaceous species and in humid regions in Southeast Asia for all species combined, but

316   was least prevalent in Africa, southern North American and tropical South America. The

317   proportion of monoecious species was the highest in North America for all species combined

318   and the two growth forms, and was also high in the high latitudes of Eurasia for herbaceous

319   species.

320

321   ***Determinants of global patterns in sexual system frequencies***

322   Temperature was the most influential predictor of the geographical patterns in the proportion

323   of sexual systems, but MAT and MATano had contrasting effects in all cases. MATano

324   correlated strongly with the proportions of hermaphroditism and monoecy for all species

325   combined and herbaceous species: hermaphroditic species were positively correlated with

326   MATano, while monoecious species were negatively correlated with MATano ($R^2 = 21.5\% \sim$

327   33.7%, $P < 0.001$). MAT strongly influenced the proportions of both woody hermaphroditism

328   and dioecy and herbaceous dioecy: proportions of woody and herbaceous dioecious species

329   were negatively correlated with MAT, while woody hermaphroditism was positively

330   correlated with MAT ($R^2 = 30.6\% \sim 56.2\%$, $P < 0.001$). Both woody and herbaceous

331   hermaphroditic species decreased with TSN while dioecious species increased ($R^2 = 8.3\% \sim$

332   29.4%, $P < 0.001$).

333   Precipitation has a moderate effect, with the most noticeable pattern being that PSN

334   influenced the prevalence of sexual systems for all species, influencing the distribution of

335   herbaceous sexual systems: the proportion of herbaceous hermaphroditic species increased

336   with PSN, while the proportions of herbaceous dioecious and monoecious species decreased

337   (Fig. 2).

338

339   ***Temporal changes in sexual system proportions and transitions***

340   Transition rates away from hermaphroditism to both dioecy and monoecy decreased until ca.

341   20 Mya (Fig. 3b). In contrast, the transition rates from dioecy to hermaphroditism and

342   monoecy increased until 15 Mya, which was mainly driven by the D→M transitions rate (Fig.

343   3c). Transition rates away from monoecy continuously increased, especially from ca. 15 Mya

344   to the present (Fig. 3d). Overall, the transition rates to dioecy were higher than the transition

345   rates to hermaphroditism (Fig. 3 & S5 & S6).

346

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

348   Transition rates from hermaphroditism to dioecy (H→D, R^2 = 0.595, P < 0.001; Fig. 4b,

349   Table S5) and reversal (D→H, R^2 = 0.567, P < 0.001; Fig. 4c, Table S5) significantly

350   increased with paleo-temperature when paleo-temperature was > 0 °C, but kept relatively

351   stable when paleo-temperature was < 0 °C. This suggests that 0 °C might be a threshold to

352   break the stable transitions between dioecy and hermaphroditism. In contrast, transition rates

353   from both hermaphroditism and dioecy to monoecy (H+D→M) significantly decreased with

354   paleo-temperature, which was mainly attributed to the decline in the D→M transition (R^2 =

355   0.321, P < 0.001; Fig. 4d) when paleo-temperature was > 0 °C.

356

357   **DISCUSSION**

358   Based on an extensive dataset on angiosperm distributions and sexual systems, we found that

359   the frequency of dioecy and monoecy increased with latitude and the frequency of

360   hermaphrodites increased with local temperature but decreased with the increase in

361   temperature variation. Of the set of variables examined, environmental temperature had the

362   strongest effect on the global geographical patterns of sexual system frequencies. Although

363   the sexual systems of angiosperms may evolve towards greater sexual differentiation, dioecy

364   is not an evolutionary end point. Our results do not support earlier findings that the frequency

365   of dioecious species decreases with latitude (Lloyd 1980; Moeller et al. 2017) but suggest that

366   environmental temperature may be a dominant factor shaping the spatiotemporal variations in

367   sexual systems of angiosperms. Taken together, our results shed light on the possible future

368   differential responses of angiosperm sexual systems to climate warming.

369

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

371   Our analyses showed that the frequency of dioecy increased from the Southern Hemisphere

372   towards the North Pole for all species combined, and for both woody and herbaceous species

373   independently (see Fig. S8). This result supports and expands previous findings in North

374   America and Siberia (Fox 1985; Godin 2017), but contrasts with the well-documented

375   hypothesis that dioecy should be the most frequent sexual system in tropical floras (Lloyd

376   1980). The frequency of hermaphrodites was the highest in global drylands (including the

377   drylands in southern and northern Africa, central and western Asia) and the eastern Amazon

378   basin in South America (see Fig. 1), although the patterns for woody and herbaceous

379   hermaphrodites were slightly different from each other.

380

381   ***Temperature drives the geographical patterns of sexual systems***

382   Our results suggest that temperature was the strongest determinant of the geographical

383   patterns in the frequencies of angiosperm sexual systems. Specifically, the frequency of

384   dioecy in local floras significantly decreased with environmental temperature, which

385   demonstrates that dioecy tends to prevail in cold climates (Godin 2017). This finding does not

386   support the previous hypothesis that dioecy should prevail in tropical floras (Bawa & Opler

387   1975; Sobrevila & Arroyo 1982). Many dioecious species are long-lived perennials with

388   greater longevity and resistance to cold stress than other systems (Lithgow & Kirkwood 1996).

389   Gender-specific differences in water-use efficiency (i.e. males performed better in dry areas)

390   will exacerbate male-biased sex ratio and put dioecious species at high risks in regions with

391   high temperature (Etterson & Mazer 2016).

392   In contrast, the proportions of hermaphrodites significantly increased with contemporary

393   temperature and PSN, suggesting that hermaphrodites tend to prevail in warm and arid

394   climates (Wang et al. 2020b). Hermaphrodites trade-off allocation of resources to flowers in

395   order to optimize the male and female functions in response to climate. Previous studies based

396   on 12 species of the genus *Pedicularis* have found that hermaphrodites tend to be male-biased

397   by investing disproportionally more resources in attractive parts (i.e. corolla, sepals, and

398   anthers) as temperature decreases (Guo et al. 2010). In contrast, hermaphrodites, especially

399   self-fertilizing hermaphrodites, have evolved a series of drought-tolerant attributes that

400   directly benefit both male and female functions in warmer and drier conditions, such as small

401   flowers that facilitate reproductive assurance through self-fertilization, and promote rapid

402   completion of the life cycle (Etterson & Mazer 2016). This avoids mismatch between the

403   timing of flowering and the life-cycles of pollinators caused by rising temperatures (Lloyd &

404   Bawa 1984; Etterson & Mazer 2016).

405   It is noteworthy that previous studies have normally treated monoecy as a special case of

406   hermaphroditism (Renner 2014). However, floral trade-offs differ greatly between

407   monoecious and hermaphroditic plants. Monoecious species balance resources among

408   separate male and female flowers on the same plant, while hermaphrodites allocate resources

409   between male and female functions within a flower. Correspondingly, our results suggest that

410   geographical distributions of the frequency of monoecious species are more similar to those

411   of dioecious species than to those of hermaphrodites.

412   Similarly, the proportions of dioecious and monoecious species consistently decreased

413   with contemporary temperature, but increased with MATano. Previous studies also suggest

414   that dioecy and monoecy have similar associations with wind pollination (Renner & Ricklefs

415   1995), small flowers (Vary et al. 2011), and closer kinship at the family level (Renner &

416   Ricklefs 1995). These suggest that the assumption that monoecy is a special case of

417   hermaphroditism is probably justifiable only if monoecious species are self-compatible as

418   frequently as hermaphrodites. Our results suggest that future studies on sexual systems should

419   treat monoecy independently rather than as a special case of hermaphroditism.

420   Additionally, MATano was also a significant predictor of sexual system frequencies, and

421   its effect was in contrary to that of MAT in all cases. MATano strongly influenced the

422   composition and structure of vegetation, with many modern species migrating northward to

423   survive (Nolan et al. 2018). Previous studies indicate that dioecy is strongly associated with

424   high dispersal ability in trees (Barot & Gignoux 2004), and hence higher recolonization

425   ability compared with hermaphrodites (Renner & Ricklefs 1995).

426

427   ***Sexual systems transition towards greater sexual differentiation***

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

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

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

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

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

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

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

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

436   0 °C, suggesting that the evolution of sexual systems may also be an environmentally

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

438   temperature-dependent sex determination in animals (Bókony et al. 2019). Temperature

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

440   sexual organs at population level. A shift to femaleness could increase seed-set

441   (Blake-Mahmud & Struwe 2019), while a shift to male-biased sex ratio could maintain plant

442   abundance because moderately elevated temperature can help males of dioecious species

443   allocate relatively more biomass to roots, and better meet their higher nitrogen demand for

444   accelerated photosynthetic performances (Tognetti 2012). Nevertheless, the proportions of

445   hermaphrodites and dioecious species did not increase or decrease overall through long-term

446   geological time (see Fig. 4a) because different selective pressures act on different clades

447   (Goldberg et al. 2017), although there is a trend towards greater sexual differentiation. Thus,

448   more population-level empirical studies are necessary to improve our understanding on the

449   evolution and maintenance of the myriad angiosperm sexual systems.

450

451   ***Dioecy may not be an evolutionary end point***

452   We found that the transition rate away from dioecy increased continuously during the

453   Cenozoic, which does not support the hypothesis that dioecy is an evolutionary one-way street

454   (Barrett 2002). The potential evolutionary benefits of the transitions away from dioecy to

455   other sexual systems include: 1) avoidance of pollen limitation (Ehlers & Bataillon 2007); 2)

456   the need for reproductive assurance during colonization (Pannell 2000); and 3) sex ratio

457   evolution with hybridization (Barrett et al. 2010). Furthermore, temperature also promoted

458   direct transitions between D and H when paleo-temperature was > 0 °C. It is noteworthy that

459   transition rates from dioecy to the other systems are relatively lower than all the other

460   transitions among the three sexual systems. This possibly suggests that the transitions from

461   dioecy to other systems are likely to be more difficult than other transitions. The evolutionary

462   transition from unisexuality to hermaphroditism requires high genetic variation in sex

463   expression in dioecious populations, or hybridization with other populations (Barrett 2013). In

464   contrast, the reverse transitions, i.e. H→D transition, are easier to achieve. For example, the

465   invasion of a single-sexed mutants into hermaphroditic populations can cause the resource

466   allocation of remaining hermaphrodites to become biased towards the increased presence of

467 single-sex morphs (i.e. monoecy), which may further lead to the evolution of dioecy

468 (Charlesworth & Charlesworth 1978).

469

477

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

| 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

Figure 1. Global patterns in the prevalence of different sexual systems. From left to right: all species, woody species and herbaceous species.
From top down: hermaphroditism, dioecy and monoecy. Within a site, the prevalence of a sexual system was represented by the proportion of
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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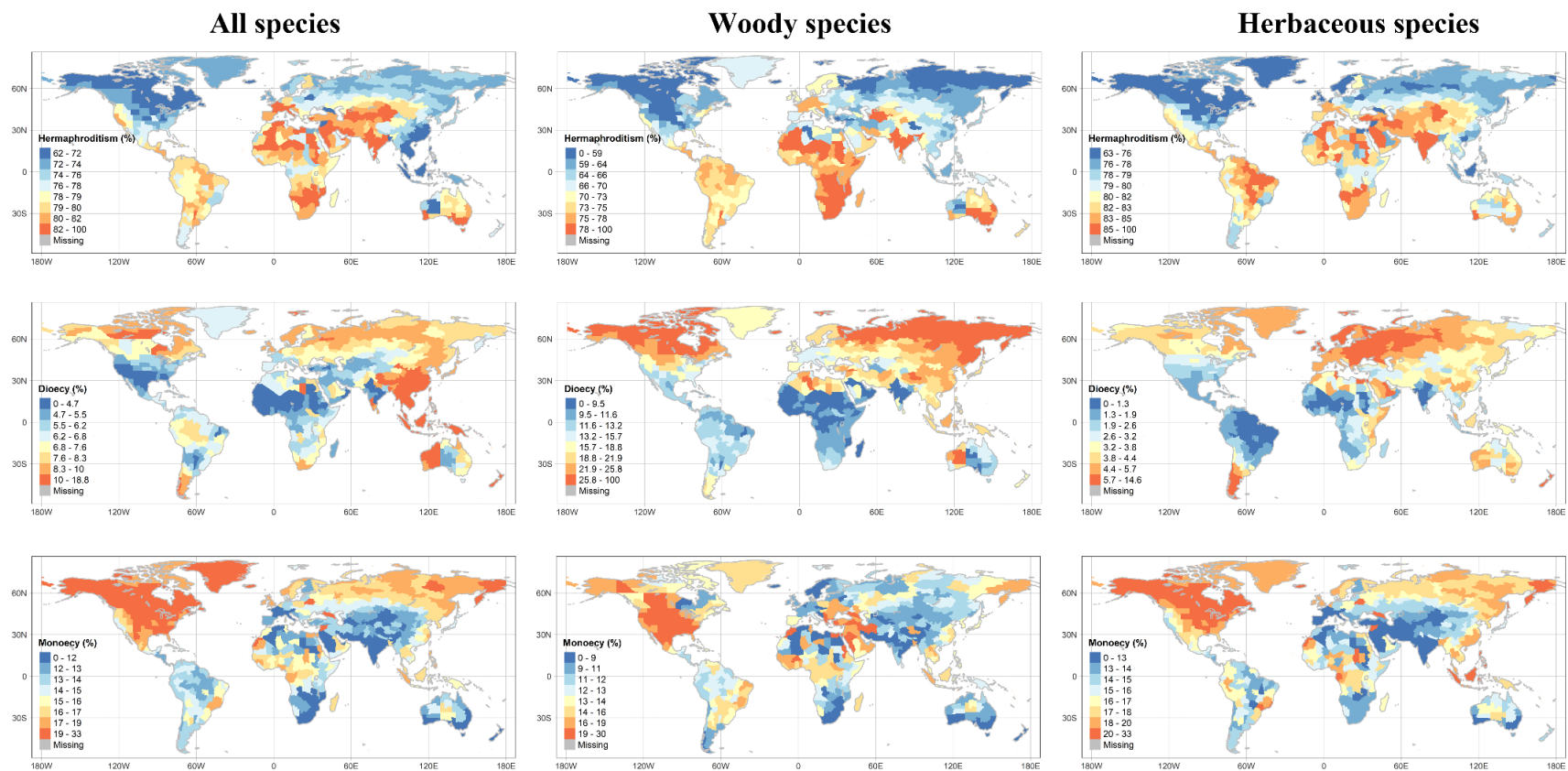
663 **Figure 2.** Relationships between the proportions of angiosperm species with different sexual
664 systems per geographical unit and environment variables (x-axes). From left to right each
665 column represents mean annual temperature [MAT], mean annual precipitation [MAP],
666 log-transformed Precipitation Seasonality [PSN(log)], log-transformed Temperature
667 Seasonality [TSN(log)] and the anomaly of mean annual temperature since the Last Glacial
668 Maximum (ca 18 000–22 000 yr. BP) [MATano] respectively. The y-axes represent the
669 proportion of angiosperm species with different sexual systems within each geographical unit.
670 From top down: hermaphroditism and monoecy of all species, woody hermaphroditism and
671 dioecy, and herbaceous hermaphroditism, dioecy and monoecy. The relationships were
672 assessed by single bivariate beta regressions, and the *P*-values of the regressions were
673 calculated by a modified *t*-test. Regression lines are drawn for significant relationships (P <
674 0.05). R^2 values associated with each variable are given in the top left corner of each panel
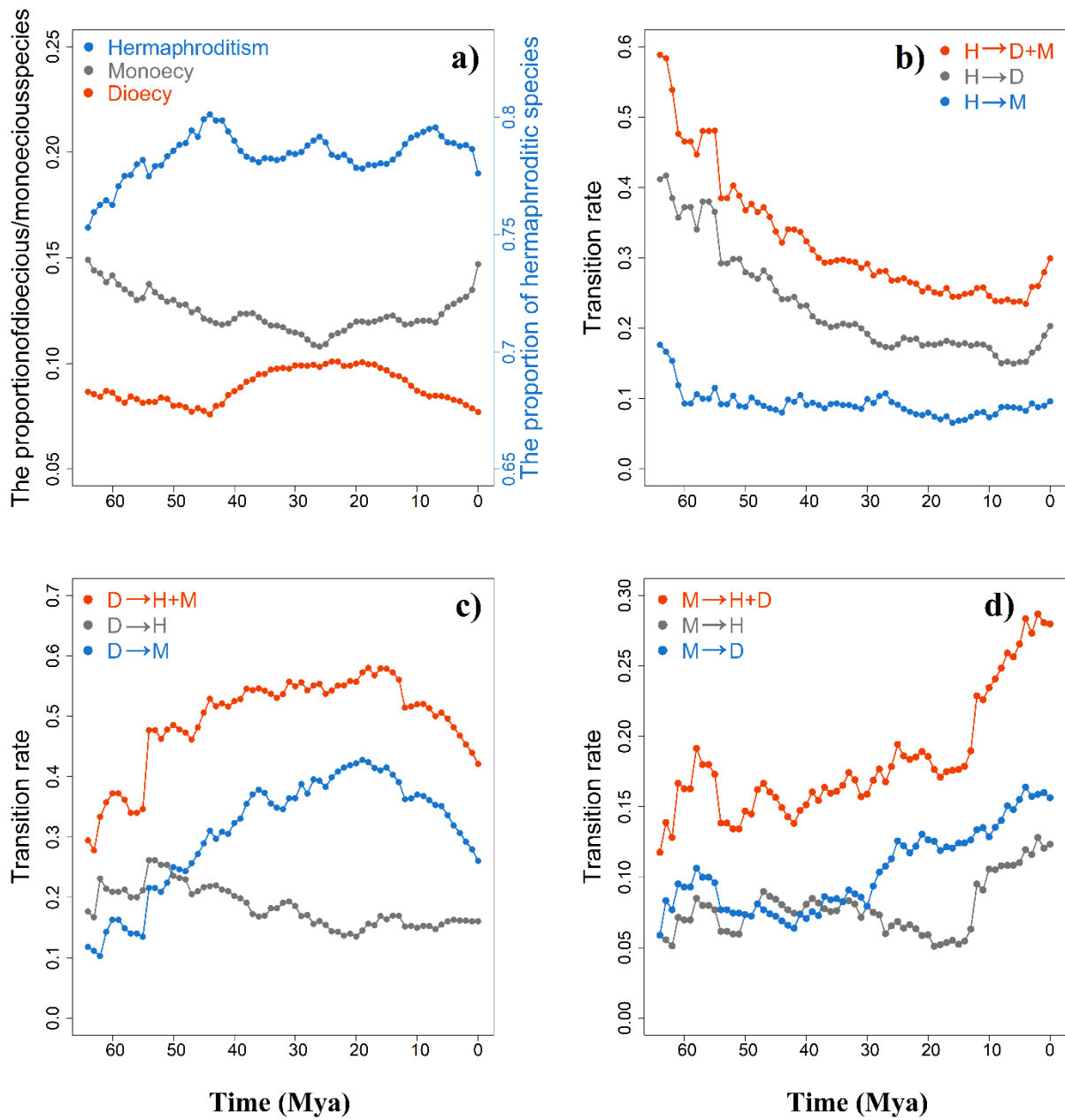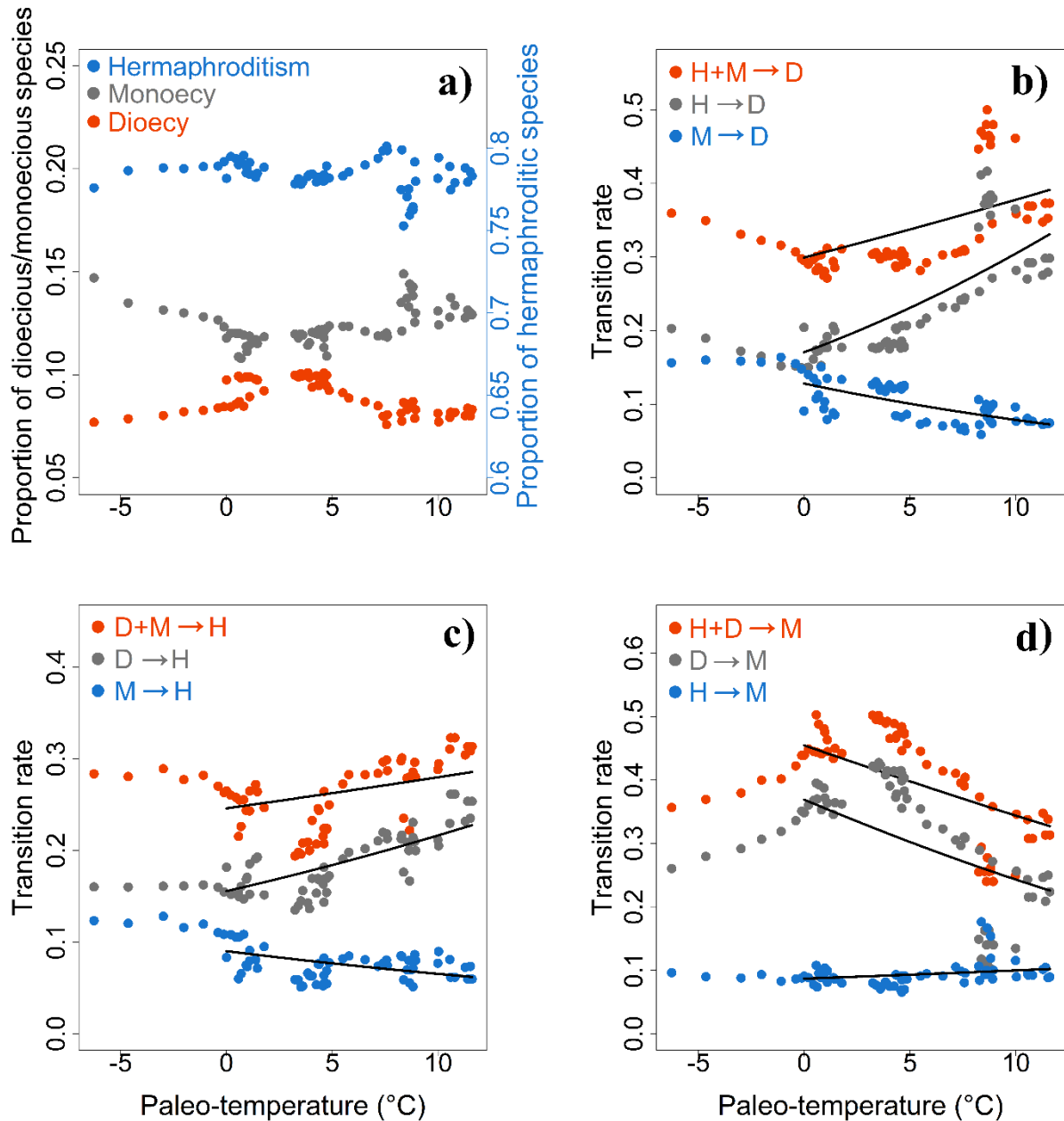675 (See the Table 1).
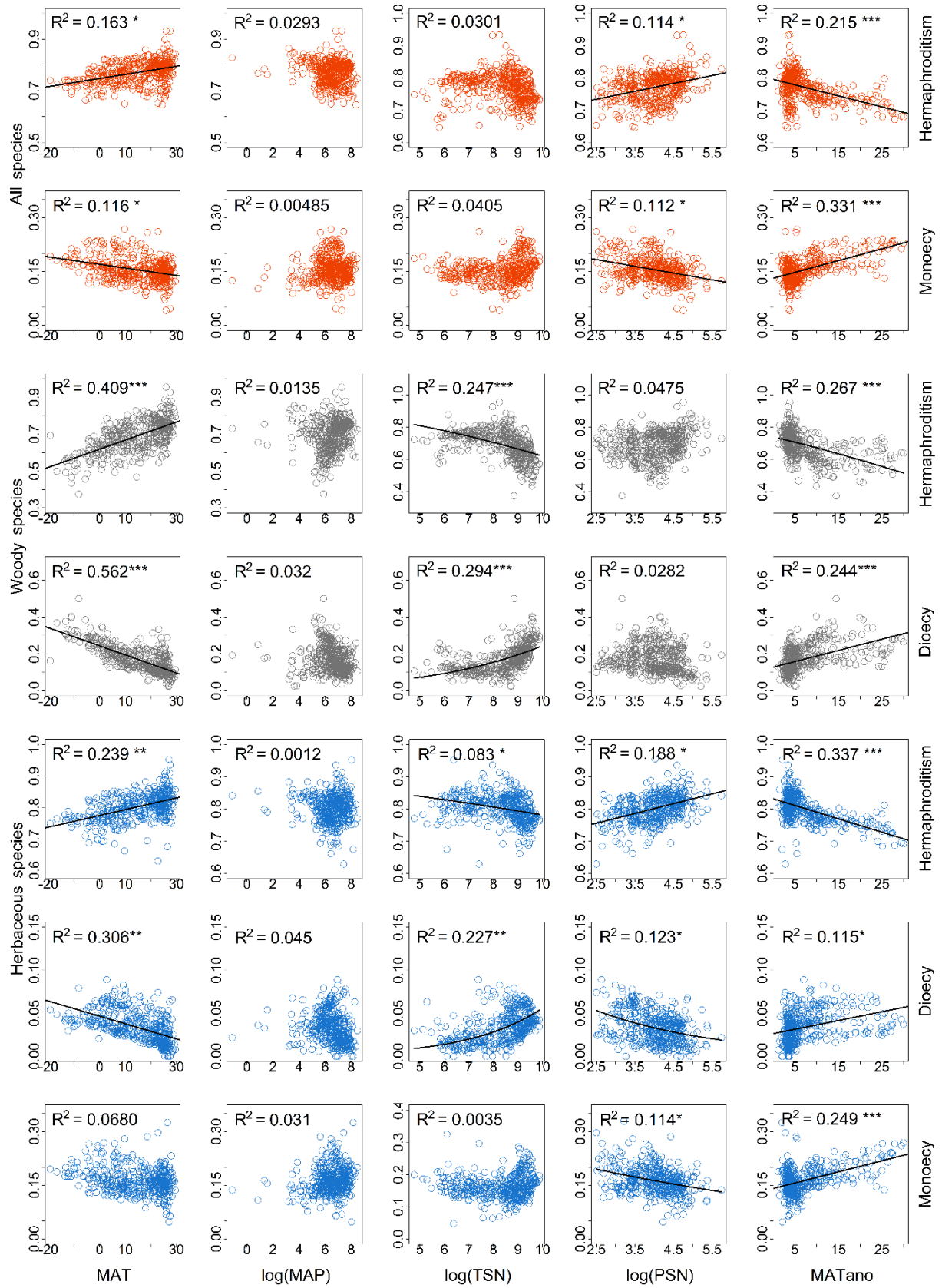
678

679　**Figure 3**. The temporal changes in the proportions of species with different sexual systems (a)

680　and the transition rates between different sexual systems (i.e. the ratios of transitions between

681　two sexual systems to the total number of transitions) (64 – 0 Mya) (b-d). H =

682　hermaphroditism, D = dioecy, M = monoecy. See Fig. S9 for results for the time period of

683　135 Mya – 0 Mya.

684

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