Global distribution and evolutionary transitions of angiosperm sexual systems

Yunyun Wang¹,²#, Ao Luo²#, Tong Lyu², Dimitar Dimitrov³, Xiaoting Xu⁴, Robert P Freckleton³, Yaoqi Li², Xiangyan Su², Yichao Li², Yunpeng Liu², Denis Sandanov⁶, Qingjun Li⁷, Shuguang Liu¹, Zhiheng Wang⁵,*

¹ National Engineering Laboratory for Applied Technology of Forestry & Ecology in Southern China, and College of Life Science and Technology, Central South University of Forest and Technology, Changsha 410004, China
² Institute of Ecology and Key Laboratory for Earth Surface Processes of the Ministry of Education, College of Urban and Environmental Sciences, Peking University, Beijing 100871, China
³ Department of Natural History, University Museum of Bergen, University of Bergen, P.O. Box 7800, 5020 Bergen, Norway
⁴ Key Laboratory of Bio-Resource and Eco-Environment of Ministry of Education, College of Life Sciences, Sichuan University, Chengdu 610065, Sichuan, China
⁵ Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK
⁶ Institute of General and Experimental Biology, Siberian Branch of Russian Academy of Science, Ulan-Ude 670047, Russia
⁷ Laboratory of Ecology and Evolutionary Biology, State Key Laboratory for Conservation and Utilization of Bio-Resources in Yunnan, Yunnan University, Kunming, Yunnan 650091, China.

# These authors contribute equally

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

Running title: Spatiotemporal pattern in plant sexual system

Type of article: Letters

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

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.
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.

Keywords: sexual system; dioecy; hermaphroditism; monoecy; macro evo-devo; climate change; temperature; flowering plants
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
monoecy and hermaphroditism (the most common state among angiosperms) across large spatial scales has been largely ignored in previous studies.

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

Empirical and theoretical work has shown that evolutionary transitions between hermaphroditism and dioecy in angiosperms are relatively frequent (Barrett 2002; Torices et
The transition from hermaphroditism, which has been considered as the ancestral state of many clades (Richards 1997; Doyle 1998), to dioecy has been thoroughly explored (Doyle 1998; Endress 2001; Leonard 2018). In contrast, the evolutionary transition from dioecy to hermaphroditism remains poorly studied (Weeks 2012; Käfer et al. 2017) although this type of transition has been found in a range of taxonomic groups (Baker 1955).

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

The spatiotemporal dynamics of angiosperm sexual systems remain relatively unexplored owing to the lack of large comparative datasets with sufficiently broad taxonomical and geographical coverage. Here, using newly compiled data on the sexual systems and global distributions of 68 453 angiosperm species, together with a recently
published global angiosperm phylogeny, we describe contemporary global patterns in the prevalence of different sexual systems and the temporal variations in sexual system prevalence and transitions during the Cenozoic. We focus on two hypotheses for the biogeography and evolution of angiosperm sexual systems, and unravel the drivers of the spatiotemporal patterns of angiosperm sexual systems at a global scale. Specifically, we evaluate the hypotheses that 1) dioecious species are more frequent in cold areas, while hermaphroditic species have higher proportions in arid areas; 2) dioecy may not be an evolutionary one-way street.

Materials and Methods

Sexual systems of angiosperms

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

We divided species into three categories based on their sexual systems according to Cardoso et al. (2018): dioecy (i.e. species with separate male and female individuals), monoecy (i.e. species with separate male and female flowers on the same plant), and hermaphroditism (i.e. species with both functional pistils and stamens within the same flower).

Dioecy includes androdioecious, gynodioecious, and polygamodioecious species; similarly, monoecy includes all monoecious, andromonoecious, and gynomonoecious species. Monoecy has been widely included in comparative analyses on angiosperm sexual systems (Renner 2014). We therefore included monoecy as a separate type of sexual system in our analyses.

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

Geographical patterns in the frequencies of sexual systems

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

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

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

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

**Current Climate**

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

We used the anomaly of mean annual temperature and mean annual precipitation since the Last Glacial Maximum (LGM, ca 18,000–22,000 yr. BP) (MATano and MAPano, respectively) to evaluate the effects of Quaternary climate change on the distribution of angiosperm sexual systems (Araújo et al. 2008). MAT, MAP, TSN, and PSN with a spatial resolution of 1 × 1 km (Hijmans et al. 2005) for the period 1970–2000 were downloaded from the WorldClim website ([http://www.worldclim.org/bioclim](http://www.worldclim.org/bioclim)). The climate variables for each geographical unit (ca. 270,000 km²) were estimated as the average of all 1 × 1 km cells within it. MATano and MAPano were calculated as the difference in MAT and MAP between the LGM and the present (i.e. MATpresent-MATLGM, MAPpresent-MAPLGM), and were used to represent the change in mean annual temperature and mean annual precipitation since the LGM respectively.
Most extant angiosperm species diversified during the Cenozoic (from 64 Million years age [Mya] to the present), a period that experienced dramatic global climate and tectonic changes (Zachos et al. 2001). Climate change has been found to affect gender-specific resource demand and allocation, and may have further led to shifts among sexual systems (Etterson & Mazer 2016). To evaluate the effects of paleo-temperature fluctuations on the rate of transition between sexual systems during the Cenozoic, we used the global mean temperature (i.e. the global mean temperature over ice-free oceans per Mya estimated from oxygen isotopic abundances in ocean sediment cores since 64 Mya until present, Zachos et al. 2001) as a measure of long-term global temperature change. This dataset of global mean temperature has been widely used in biogeographical and paleoclimate studies (Li et al. 2014; Turk et al. 2020).

Angiosperm phylogenies

We used the dated mega phylogeny of angiosperm species (353 185 tips) constructed by Smith & Brown (2018). The backbone of this phylogeny was constructed using molecular data from GenBank on 79 881 taxa. Species lacking sequence data were inserted into the phylogeny as basal polytomies in their families based on current taxonomy (Smith & Brown 2018). This phylogeny has been widely used in biogeographic and macroecological studies (Weigelt et al. 2020). To reduce the possible influences of polytomies on the estimation of phylogenetic analyses, we resolved the polytomies along the tips of the phylogeny using a
Yule bifurcation process (Kuhn et al. 2011; Roquet et al. 2013). After matching the species names with sexual system information with the phylogeny a total of 61 230 species were retained (Table S1).

**Statistical analyses**

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

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

We used the rayDISC function of the R package corHMM (Beaulieu et al. 2013) to reconstruct the ancestral states. The rayDISC function fits a model for the evolution of multi-state categorical traits, allowing for polymorphisms and incompletely resolved trees.

For the reconstruction, we fitted three different models that assumed different evolutionary
scenarios. The ER model assumes that all transition rates are equal, the SYM model assumes that forward and reverse transitions share the same parameter, and the ARD model assumes that all transition rates are different.

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

Additionally, to assess the proportion of significant character associations that might be recovered by chance (Type I error) based on the number of character states and tips in our tree, we simulated stochastic character histories using the sim.history function of the phytools package in R (Revell 2012). We ran simulations for 1000 generations under the ER and the ARD models using equal and FitzJohn (FitzJohn et al., 2009) priors for root state frequencies.
Based on the ancestral state reconstructions, we counted the proportion of branches reconstructed with each sexual system in every one-million-year time interval, and estimated temporal changes. We estimated the temporal changes in the transition rates between different sexual systems. The transitions between the three sexual systems were grouped into three categories: 1) from dioecy to monoecy or to hermaphroditism (D→M and D→H, respectively); 2) from hermaphroditism to dioecy or to monoecy (H→D and H→M, respectively); and 3) from monoecy to hermaphroditism or to dioecy (M→H and M→D, respectively). We further evaluated the effect of paleo-temperature on the temporal changes in the frequency of each sexual system and the frequency of transitions between sexual systems using beta regressions.

The ER, SYM, and ARD models yielded consistent results on the temporal changes in the proportions of sexual systems and transitions rates among sexual systems. The ARD model had the lowest Akaike information criterion (AIC) value (AIC values were 18442, 17621, and 17000 for ER, SYM, and ARD models, respectively, under both joint and marginal reconstruction). Stochastics maps built using HisSE models with either two or three hidden states also yielded estimates of the transition rates among sexual systems consistent with the rayDISC ARD model. Simulations based only on root character state prior (either equal state probability or FitzJohn), number of tips and topology produced significantly different patterns compared with analyses based on the actual character dataset (Fig. S3 & S4), which indicates that our results are not an analytical artifact. Therefore, we show the results from ARD model in the main text. For reference, results from all other models were shown in the supplementary information (Fig. S5 & S6).
Our full dataset contained 61,230 species, which represent about 25% of the 261,750 total species accepted in the Angiosperm Phylogeny Website (Stevens, 2001 onward). In order to assess the reliability of transition estimates given the large fraction of missing taxa, we randomly generated 100 subsamples with the same proportion (i.e. 25%) of the species in our full dataset (n = 15,308) but balanced the proportion of sexual systems (i.e. 77-80% for hermaphroditism and 6-7% for dioecy) following Igea & Tanentzap (2020). We re-ran the transition analyses for each of the 100 subsamples, then calculated mean results and 95% confidence intervals. By comparing the estimates obtained from our full dataset with the estimates generated by this random sampling procedure, we found that the results from both datasets were highly consistent (Fig. S7).

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

**Results**

**Global patterns in sexual system frequency**

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

Determinants of global patterns in sexual system frequencies

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

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

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

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

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

**DISCUSSION**

Based on an extensive dataset on angiosperm distributions and sexual systems, we found that the frequency of dioecy and monoecy increased with latitude and the frequency of hermaphrodites increased with local temperature but decreased with the increase in temperature variation. Of the set of variables examined, environmental temperature had the
strongest effect on the global geographical patterns of sexual system frequencies. Although the sexual systems of angiosperms may evolve towards greater sexual differentiation, dioecy is not an evolutionary end point. Our results do not support earlier findings that the frequency of dioecious species decreases with latitude (Lloyd 1980; Moeller et al. 2017) but suggest that environmental temperature may be a dominant factor shaping the spatiotemporal variations in sexual systems of angiosperms. Taken together, our results shed light on the possible future differential responses of angiosperm sexual systems to climate warming.

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

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

**Temperature drives the geographical patterns of sexual systems**
Our results suggest that temperature was the strongest determinant of the geographical patterns in the frequencies of angiosperm sexual systems. Specifically, the frequency of dioecy in local floras significantly decreased with environmental temperature, which demonstrates that dioecy tends to prevail in cold climates (Godin 2017). This finding does not support the previous hypothesis that dioecy should prevail in tropical floras (Bawa & Opler 1975; Sobrevila & Arroyo 1982). Many dioecious species are long-lived perennials with greater longevity and resistance to cold stress than other systems (Lithgow & Kirkwood 1996).

Gender-specific differences in water-use efficiency (i.e. males performed better in dry areas) will exacerbate male-biased sex ratio and put dioecious species at high risks in regions with high temperature (Etterson & Mazer 2016).

In contrast, the proportions of hermaphrodites significantly increased with contemporary temperature and PSN, suggesting that hermaphrodites tend to prevail in warm and arid climates (Wang et al. 2020b). Hermaphrodites trade-off allocation of resources to flowers in order to optimize the male and female functions in response to climate. Previous studies based on 12 species of the genus Pedicularis have found that hermaphrodites tend to be male-biased by investing disproportionally more resources in attractive parts (i.e. corolla, sepals, and anthers) as temperature decreases (Guo et al. 2010). In contrast, hermaphrodites, especially self-fertilizing hermaphrodites, have evolved a series of drought-tolerant attributes that directly benefit both male and female functions in warmer and drier conditions, such as small flowers that facilitate reproductive assurance through self-fertilization, and promote rapid completion of the life cycle (Etterson & Mazer 2016). This avoids mismatch between the
timing of flowering and the life-cycles of pollinators caused by rising temperatures (Lloyd & Bawa 1984; Etterson & Mazer 2016).

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

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

Additionally, MATano was also a significant predictor of sexual system frequencies, and its effect was in contrary to that of MAT in all cases. MATano strongly influenced the composition and structure of vegetation, with many modern species migrating northward to survive (Nolan et al. 2018). Previous studies indicate that dioecy is strongly associated with
high dispersal ability in trees (Barot & Gignoux 2004), and hence higher recolonization ability compared with hermaphrodites (Renner & Ricklefs 1995).

**Sexual systems transition towards greater sexual differentiation**

Since the Cenozoic, transition rates to dioecy have been higher than to hermaphroditism. A previous study also found that the transition rate from hermaphroditism to dioecy was approximately twice as high as the reverse transition in bryophytes (McDaniel et al. 2012). These results suggest that evolutionary transition may proceed in the direction of greater sex differentiation (Webb 1999), which does not support the recent findings based on a dataset of limited number of genera (Goldberg et al. 2017).

We found that average global paleo-temperature significantly promotes the transition from hermaphroditism to sexual differentiation especially when paleo-temperature was over 0 °C, suggesting that the evolution of sexual systems may also be an environmentally adaptive strategy to enhance plant fitness (Policansky 1981), similar to the temperature-dependent sex determination in animals (Bókony et al. 2019). Temperature increases within a certain range could change the sex allocation between male and female sexual organs at population level. A shift to femaleness could increase seed-set (Blake-Mahmud & Struve 2019), while a shift to male-biased sex ratio could maintain plant abundance because moderately elevated temperature can help males of dioecious species allocate relatively more biomass to roots, and better meet their higher nitrogen demand for accelerated photosynthetic performances (Tognetti 2012). Nevertheless, the proportions of hermaphrodites and dioecious species did not increase or decrease overall through long-term
geological time (see Fig. 4a) because different selective pressures act on different clades (Goldberg et al. 2017), although there is a trend towards greater sexual differentiation. Thus, more population-level empirical studies are necessary to improve our understanding on the evolution and maintenance of the myriad angiosperm sexual systems.

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

We found that the transition rate away from dioecy increased continuously during the Cenozoic, which does not support the hypothesis that dioecy is an evolutionary one-way street (Barrett 2002). The potential evolutionary benefits of the transitions away from dioecy to other sexual systems include: 1) avoidance of pollen limitation (Ehlers & Bataillon 2007); 2) the need for reproductive assurance during colonization (Pannell 2000); and 3) sex ratio evolution with hybridization (Barrett et al. 2010). Furthermore, temperature also promoted direct transitions between D and H when paleo-temperature was $> 0 \, ^\circ\text{C}$. It is noteworthy that transition rates from dioecy to the other systems are relatively lower than all the other transitions among the three sexual systems. This possibly suggests that the transitions from dioecy to other systems are likely to be more difficult than other transitions. The evolutionary transition from unisexuality to hermaphroditism requires high genetic variation in sex expression in dioecious populations, or hybridization with other populations (Barrett 2013). In contrast, the reverse transitions, i.e. H→D transition, are easier to achieve. For example, the invasion of a single-sexed mutants into hermaphroditic populations can cause the resource allocation of remaining hermaphrodites to become biased towards the increased presence of
single-sex morphs (i.e. monoecy), which may further lead to the evolution of dioecy (Charlesworth & Charlesworth 1978).

ACKNOWLEDGEMENTS

This work was supported by the Strategic Priority Research Program of Chinese Academy of Sciences (#XDB31000000), the National Key Research Development Program of China (#2017YFA0605101), National Natural Science Foundation of China (#31901216; #31988102) and Natural Science Foundation of Hunan Province (#2020JJ5977), D.D. received additional support by the Norwegian Metacenter for Computational Science (NOTUR; project NN9601K). D.S. D.S. studies supported by the federal budget (project 121030900138-8).
References


Maitner B.S., Boyle B., Casler N., Condit R., Donoghue J., Durán S.M., Guadarrama D., Hinchliff

C.E., Jørgensen P.M., Kraft N.J.B., McGill B., Merow C., Morueta-Holme N., Peet R.K., Sandel B.,


(2018). The bien r package: A tool to access the Botanical Information and Ecology Network


67, 567-572.


B.M., Cheddadi, R., Djamali, M., Dodson J., Edwards M.E., Gosling W.D., Haberle S., Hotchkiss


K.-B., Liu Y., Lozhkin A.V., McGlone M.S., Marchant R.A., Momohara A., Moreno P.I., Müller S.,

Otto-Bliensner B.L., Shen C., Stevenson J., Takahara H., Tarasov P.E., Tipton J., Vincens A., Weng


Floresta e Ambient., 26, e20180384.


Syst.*, 37, 187-214.


Renner S.S. (2014). The relative and absolute frequencies of angiosperm sexual systems: dioecy, monoecy,

gynodioecy, and an updated online database. *Am. J. Bot.*, 101, 1588-1596.


596-606.


Roquet C., Thuiller W. & Lavergne S. (2013). Building megaphylogenies for macroecology: taking up the


Sabath N., Goldberg E.E., Glick L., Einhorn N., Ashman T.-L., Ming R., Otto S.P., Vamosi J.C. & Mayrose

I. (2016). Dioecy does not consistently accelerate or slow lineage diversification across multiple


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

<table>
<thead>
<tr>
<th>Variable</th>
<th>All species</th>
<th>Woody species</th>
<th>Herbaceous species</th>
</tr>
</thead>
<tbody>
<tr>
<td>MAT</td>
<td>0.163*</td>
<td>0.031</td>
<td>0.116*</td>
</tr>
<tr>
<td>MAP(log)</td>
<td>0.0293</td>
<td>0.0361</td>
<td>0.00485</td>
</tr>
<tr>
<td>TSN(log)</td>
<td>0.0301</td>
<td>-0.0022</td>
<td>0.0405</td>
</tr>
<tr>
<td>PSN(log)</td>
<td>0.114*</td>
<td>0.0158</td>
<td>0.112*</td>
</tr>
<tr>
<td>MATano</td>
<td><strong>0.215</strong>*</td>
<td>0.0057</td>
<td><strong>0.331</strong>*</td>
</tr>
<tr>
<td>MAPano</td>
<td>0.078</td>
<td>0.059</td>
<td>0.0242</td>
</tr>
</tbody>
</table>
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.
Figure 2. Relationships between the proportions of angiosperm species with different sexual systems per geographical unit and environment variables (x-axes). From left to right each column represents mean annual temperature [MAT], mean annual precipitation [MAP], log-transformed Precipitation Seasonality [PSN(log)], log-transformed Temperature Seasonality [TSN(log)] and the anomaly of mean annual temperature since the Last Glacial Maximum (ca 18 000–22 000 yr. BP) [MATano] respectively. The y-axes represent the proportion of angiosperm species with different sexual systems within each geographical unit. From top down: hermaphroditism and monoecy of all species, woody hermaphroditism and dioecy, and herbaceous hermaphroditism, dioecy and monoecy. The relationships were assessed by single bivariate beta regressions, and the $P$-values of the regressions were calculated by a modified $t$-test. Regression lines are drawn for significant relationships ($P < 0.05$). $R^2$ values associated with each variable are given in the top left corner of each panel (See the Table 1).
Figure 3. The temporal 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) (64 – 0 Mya) (b-d). H = hermaphroditism, D = dioecy, M = monoecy. See Fig. S9 for results for the time period of 135 Mya – 0 Mya.
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 ($P < 0.05$).