RESEARCH PAPER

Drivers of large-scale geographical variation in sexual systems of woody plants

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Abstract

Aim: Sexual systems strongly influence angiosperm evolution and play important roles in community assembly and species responses to climate change. However, geographical variation in proportions of different sexual systems (dioecy, monoecy and hermaphroditism) in response to changes in climate, life-history traits and evolutionary age remains poorly understood. Here, we map the geographical variation in proportions of different sexual systems and hypothesize that the prevalence of hermaphrodites increases with aridity owing to their advantages in colonizing harsh environments, whereas dioecy is most successful in humid regions with tall-canopy vegetation and old floras.

Location: China.

Time period: Current.

Major taxa studied: Woody angiosperms.

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

Results: We found contrasting geographical patterns in the proportions of different sexual systems. The proportions of dioecy and monoecy increased with plant height

and were highest in humid regions with older floras, whereas that of hermaphroditism decreased with plant height and was highest in arid regions with younger floras. Plant height was the strongest correlate of sexual system frequency. Climate influenced sexual system frequency both directly and indirectly via its effects on plant height.

Main conclusions: Our study provides the first continuous map of sexual system composition in woody floras over a large spatial scale. Our findings suggest that mature plant height, reflecting plant longevity, dominates geographical variation in sexual systems and that the proportions of different sexual systems in local floras might reflect their correlated evolution with traits in response to climate changes.

KEYWORDS

angiosperms, China, climate change, evolutionary history, geographical pattern, macro evo-devo, plant height, plant reproduction, sexual systems

1 | INTRODUCTION

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

Climate can influence the expression of plant sexual systems by regulating the allocation of resources to female and male function during the flowering period (Zhang, 2003), hence leading to geographical variation in the composition of the sexual systems of local floras (Barrett, 1998; Dorken et al., 2017; Hultine et al., 2016; Jacquemyn et al., 2005; Ricklefs & Wikelski, 2002). For example, recent studies have found that the proportion of outcrossing species decreases with latitude (Moeller et al., 2017), which has been attributed to changes in precipitation, temperature and solar radiation along the latitudinal gradient (Lloyd, 1980). However, previous studies have provided controversial evidence for the effects of climate, especially the effects of water availability, on the biogeographical patterns of plant sexual systems. First, some studies exploring the evolution of sexual systems indicate that drought stress might have contributed to the evolution of dioecy from hermaphroditism

(Ashman, 2006; Yang, Hu, Wang, Zhu, & Meng, 2014), which suggests that the prevalence of dioecy could be associated with arid environments. Second, other studies suggest that the colonization of dry habitats did not require a shift to sexual dimorphism (Sakai, Weller, Wagner, & Soltis, 1997), because spatial separation probably makes dioecious taxa suffer greater challenges of decreased mate assurance (Pannell & Barrett, 1998). Compared with dioecious taxa, hermaphroditic species are likely to have been selected in stressful regions with frequent extinction and re-colonization (Levin, 2012; Obbard, Harris, & Pannell, 2006), because hermaphrodites can provide reproductive assurance via selfing (Barrett, 1998; Elle & Carney, 2003; Harder & Barrett, 1995; Lloyd, 1992). Studies based on field investigations have found that hermaphroditic species from different clades occur widely in dry habitats, whereas dioecious species are more common in humid and tropical regions (Freeman, Harper, & Ostler, 1980; Matallana, Wendt, De Araujo, & Scarano, 2005; Sakai, Wagner, Ferguson, & Herbst, 1995). Although these findings tend to support the second hypothesis, how sexual system composition varies geographically with climate, especially with water availability, remains controversial.

Plants with different life-history traits vary considerably in their sexual systems (Barrett & Eckert, 1990; Moeller et al., 2017; Snell & Aarssen, 2005), which suggests that plant life-history traits are also likely to influence the ecology and evolution of sexual systems (Vamosi, Otto, & Barrett, 2003). Phylogenetic analyses have revealed the association between dioecy and woody growth habits (i.e., the long-lived, perennial growth form; Chazdon, Careaga, Webb, & Vargas, 2003; Vamosi et al., 2003). Likewise, longevity has also been found to be an important trait associated with plant sexual systems (Renner, 2014). Compared with short-lived species, long-lived ones tend to accumulate more genetic load (Klekowski & Godfrey, 1989), to pay a higher fitness cost owing to inbreeding depression and mutation, and to depend more on cross-pollination (Chen, 2003; Klekowski & Godfrey, 1989). Consequently, dioecy has been suggested to be more common in long-lived species than in short-lived ones (Renner, 2014; Renner & Ricklefs, 1995). In contrast, short-lived

species have limited time to find mates, reproduce and complete their life cycle, hence they tend to be selfing (i.e., hermaphroditic and monoecious) species rather than long-lived species (Aarssen, 2000; Morgan, Schoen, & Bataillon, 1997). However, how the composition of sexual systems in local floras changes in association with changes in life-forms and plant longevity remains to be tested.

Evolutionary history has been found to shape the distribution of sexual systems across the phylogeny of seed plants (Lord, Westoby, & Leishman, 1995; Renner & Ricklefs, 1995). For example, significant phylogenetic signals were detected in the sexual systems of 641 species distributed in the Yasuní National Park, Ecuador (Queenborough et al., 2009). Previous evolutionary studies suggest that dioecious species have been derived from hermaphroditism and that dioecious lineages are most often at the tips of angiosperm phylogenies (Barrett, 2013). According to this hypothesis, the prevalence of dioecious and hermaphroditic species in local floras should have opposite correlations with flora age. More specifically, it might be expected that dioecious species are more prevalent in young floras, whereas hermaphroditic species are more prevalent in old floras. However, in contrast to the predictions of this hypothesis, field investigations based on scattered data have found that dioecious species are more common on old than on young islands (Sakai et al., 1995) and in tropical areas (Matallana et al., 2005) dominated by old floras than in temperate areas with young floras. These findings demonstrate that the relationship between the prevalence of a particular sexual system and evolutionary age of floras so far remains inconsistent from an evolutionary and an ecological perspective. Here, we maintain that it is necessary to explore this relationship more comprehensively across larger geographical scales to derive generalities.

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

2 | MATERIALS AND METHODS

2.1 | Sexual systems and distributions of woody plants in China

We compiled a dataset on the sexual systems of all woody plant species in China using published sources: Flora of China (http://foc. eflora.cn/, accessed in April 2018), Flora Republicae Popularis Sinicae (126 issues of 80 volumes), Seeds of Woody Plants in China, eflora

(http://efloras.org/), Tree of Sex (Tree of Sex Consortium, 2014), TRY Plant Trait Database (Kattge et al. 2011), Botanical Information and Ecology Network (BIEN; Maitner et al. 2018) and a journal publication (Goldberg et al., 2017). For species for which the sexual system was reported in multiple sources, those with conflicting reports were checked and corrected or removed. In total, our dataset comprised 10,449 species from 1,082 genera and 157 families and accounted for 93.76% of all woody plants found in China (Supporting Information Table S1). We classified all these species into three categories based on their sexual system, following Cardoso et al. (2018): dioecy (i.e., plant species with separate male and female individuals), monoecy (i.e., plant species with both staminate and pistillate flowers occurring in the same individual but not in the same flower) and hermaphrodites (i.e., plant species with both functional stamens and pistils in the same flower). The category of dioecy includes androdioecious, gynodioecious and polygamodioecious species, whereas monoecy includes monoecious, andromonoecious and gynomonoecious species.

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

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

2.2 | Geographical variation in the proportions of different sexual systems

We first transformed the distribution maps into equal-area grids with a grid cell size of 50 km × 50 km to eliminate the potential bias of unequal area on subsequent analyses (for details, see Wang et al., 2009). Combining the sexual system data and the distribution data of all species, we calculated the proportions of species with each type of sexual system within every grid cell. To ensure the reliability of the calculated proportion for each sexual system, we removed grid cells with less than half of the grid cell area (i.e., grid cells with < 1,250 km^2; for details, see Wang et al., 2009) and grid cells with fewer than 10 woody species. A total of 3,539 of the initial 4,017 grid cells were included in the final analyses.

2.3 | Climatic data

To evaluate the effects of climate on the biogeographical pattern in the composition of sexual systems in different local floras, we used climatic data with a spatial resolution of 1 km × 1 km for the period 1950–2000 obtained from WorldClim (Hijmans, Cameron, Parra,

Jones, & Jarvis, 2005). We obtained the value of every climate variable for each 1 km × 1 km grid cell by calculating the average of all 1 km × 1 km cells within it. Climatic variables were categorized into temperature, precipitation and solar radiation. Temperature variables included mean annual temperature (MAT), mean temperature of coldest quarter (MTCQ) and annual potential evapotranspiration (PET). The PET reflects the amount of evaporation that would occur if sufficient water were available and was calculated following the method of Thornthwaite & Hare, 1955). Precipitation variables included mean annual precipitation (MAP), precipitation seasonality (PSN, the coefficient of variation of mean monthly precipitation) and precipitation of the driest quarter (PDQ). Solar radiation reflects the radiant energy emitted by the sun. The MAP and PDQ were natural logarithm transformed because of their left-skewed distributions. Solar radiation is likely to influence flower coloration through pigmentation, which affects pollination success (Körner, 1999). The average and the full range of values for each climatic variable within each grid cell were estimated with the zonal statistics tool in ArcGIS v.10.0.

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

2.4 | Mature plant height

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

2.5 | Genus age and phylogenetic diversity

Plant genus has been considered to be a more natural unit than other higher taxonomic ranks (Anderson, 1940; Barraclough & Humphreys, 2015). Therefore, average genus age per grid cell has been used widely in large-scale studies to represent the evolutionary age of floras and to test the evolutionary hypotheses of large-scale species diversity patterns (e.g., niche-conservatism

hypothesis, Leopold, Tanentzap, Lee, Heenan, & Fukami, 2015; Lu et al., 2018; Qian, 2014, 2017).

To evaluate the effect of evolutionary age of local floras on the biogeographical pattern of sexual systems (i.e., the per-grid proportions of the three sexual systems), we extracted the genus age from the phylogenetic tree of Chinese vascular plants constructed by Chen et al. (2016) and calculated the average genus age for each grid cell. Moreover, we also evaluated the relationships between the proportions of sexual systems per grid cell and the phylogenetic diversity of local floras. Here, the phylogenetic diversity (PD) was estimated by Faith's PD (Faith, 1992) and the net relatedness index (NRI) of woody species within each grid cell. The results indicated that the proportions of sexual systems per grid cell were not significantly correlated with Faith's PD and the NRI (Supporting Information Figure S1).

2.6 | Statistical analyses

First, spatial linear models (SLMs) were built to evaluate the relative importance of climatic variables (temperature, precipitation and radiation), mature plant height and average genus age per grid cell in determining the biogeographical pattern in sexual systems. Spatial simultaneous autoregressive error models (SARs), allowing the inclusion of residual spatial autocorrelation in data (Kissling & Carl, 2008), were used for the SLMs. Moran's I was used to diagnose the spatial autocorrelation of residuals of SLMs. Using this approach, we could ensure that the spatial autocorrelation had been removed successfully ($p > .05$ in all cases).

To evaluate the effect of phylogenetic conservatism on the distribution of sexual systems of woody plants, we first calculated the proportions of species with different sexual systems for each genus separately. Then, we estimated Blomberg's K (Blomberg et al., 2003) for each sexual system separately at the genus level using the 'phylosignal' function (Kembel et al., 2010) in the R package *picante*. The sexual systems of different species are not phylogenetically independent from each other (Table 1). To account for the influence of phylogenetic dependence of sexual systems on the relationships between the grid-level proportions of the three sexual systems and predictors, we fitted a phylogenetically corrected linear mixed-effects model by maximum likelihood ('lmekin' within the R package *coxme*; Orme, 2012).

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

The above analyses were undertaken with principal component (PC) scores derived from principal components analysis (PCA) using the 'princomp' function in R (Conway & Huffcutt, 2003). One PCA was used to combine the temperature variables (MAT, MTCQ and PET)

TABLE 1 Phylogenetic signal index (Blomberg's *K*) for the within-genus proportions of species with different sexual systems

Sexual system	Phylogenetic signal	*P*-value
Dioecy	0.493	.0001
Monoecy	0.156	.307
Hermaphrodite	0.165	.526

Note: The genus-level phylogenetic tree was extracted from the recently published phylogenetic tree of Chinese vascular plants constructed by Chen et al. (2016).

into a single PC (Temp.PC1) and another was used to combine the precipitation variables (MAP, PSN and PDQ) into a single PC (Prec.PC1) (Supporting Information Table S2). The first PCs accounted for 93.6 and 78.3% of the variations in temperature and precipitation variables, respectively. Pearson correlations among the two PCs and solar radiation, plant height and genus age were < 0.7, indicating a relatively low level of multicollinearity (Dormann et al., 2013). Based on these data explorations, Temp.PC1, Prec.PC1, solar radiation, plant height and genus age were included in the final SLM, lmekin and *SEM* analyses (Table 2).

All analyses were performed in R v.3.3.1 (R Core Team, 2016).

3 | RESULTS

3.1 | Biogeographical patterns in sexual systems

Overall, hermaphroditism is the most common sexual system of woody plants across China: the proportion of hermaphroditic species is ≥ 50% in 96.1% of the grid cells (Figure 1). The proportion of dioecious but not of monoecious species exhibits a strong negative correlation with the proportion of hermaphroditic species (Supporting Information Figure S2). The relative frequency of the three sexual systems varies geographically (Figure 1). The proportion of dioecious species is high in northeast China and in the Qinghai-Tibetan

Plateau, whereas the proportion of monoecious species is high in eastern and southern China. In contrast, the proportion of hermaphrodites is high in northwest China (Figure 1c).

3.2 | Influence of climate on sexual systems

Temperature (Temp.PC1) had weak effects on the composition of sexual systems, either with or without controlling for other explanatory variables in SAR (Table 2; Supporting Information Table S3). In *SEM*, the influence of temperature on the proportions of dioecious and hermaphroditic species was strong in non-humid areas, indicating that correlations between plant height and temperature might have masked the effects of temperature (Figure 3). Precipitation affected the prevalence of particular sexual systems weakly in both non-humid and humid areas (Table 2). Solar radiation also had weak effects on the composition of sexual systems (Table 2). After controlling for the effect of climate on plant height in the SEMs, in the humid area solar radiation had a significant negative effect on dioecy and monoecy and a positive effect on hermaphroditism (Figure 3).

3.3 | Influence of mature plant height as a proxy for longevity on sexual systems

Sexual system composition varied with plant height (Figure 2). The proportions of hermaphroditic species decreased with plant height; that is, shorter plants (e.g., < 5 m) had a disproportionately high proportion of hermaphrodites. In contrast, the proportions of dioecious and monoecious species increased with plant height (Table 2).

Average plant height per grid cell consistently had the highest explanatory power for geographical variation in the composition of sexual systems, either with or without controlling for other predictors (Table 2; Figure 3; Supporting Information Table S4).

TABLE 2 Spatial linear models with simultaneous autoregressive errors for proportions of sexual systems as the dependent variable and climate variables (temperature, precipitation and radiation), mature plant height and genus age as multiple independent variables

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

Note: Moran's *I* showed that there was no spatial autocorrelation in the residuals of the spatial linear models. We show the partial regression coefficients with their standard errors for the explanatory variables. The table shows results from the whole of China, the area with < 800 mm precipitation (non-humid area) and the area with> 800 mm precipitation (humid area). Values in bold are significant at *p* < .05, and three relevant digits were presented for all the values.

Abbreviations: Herma. = hermaphrodite; MHt = mature plant height.
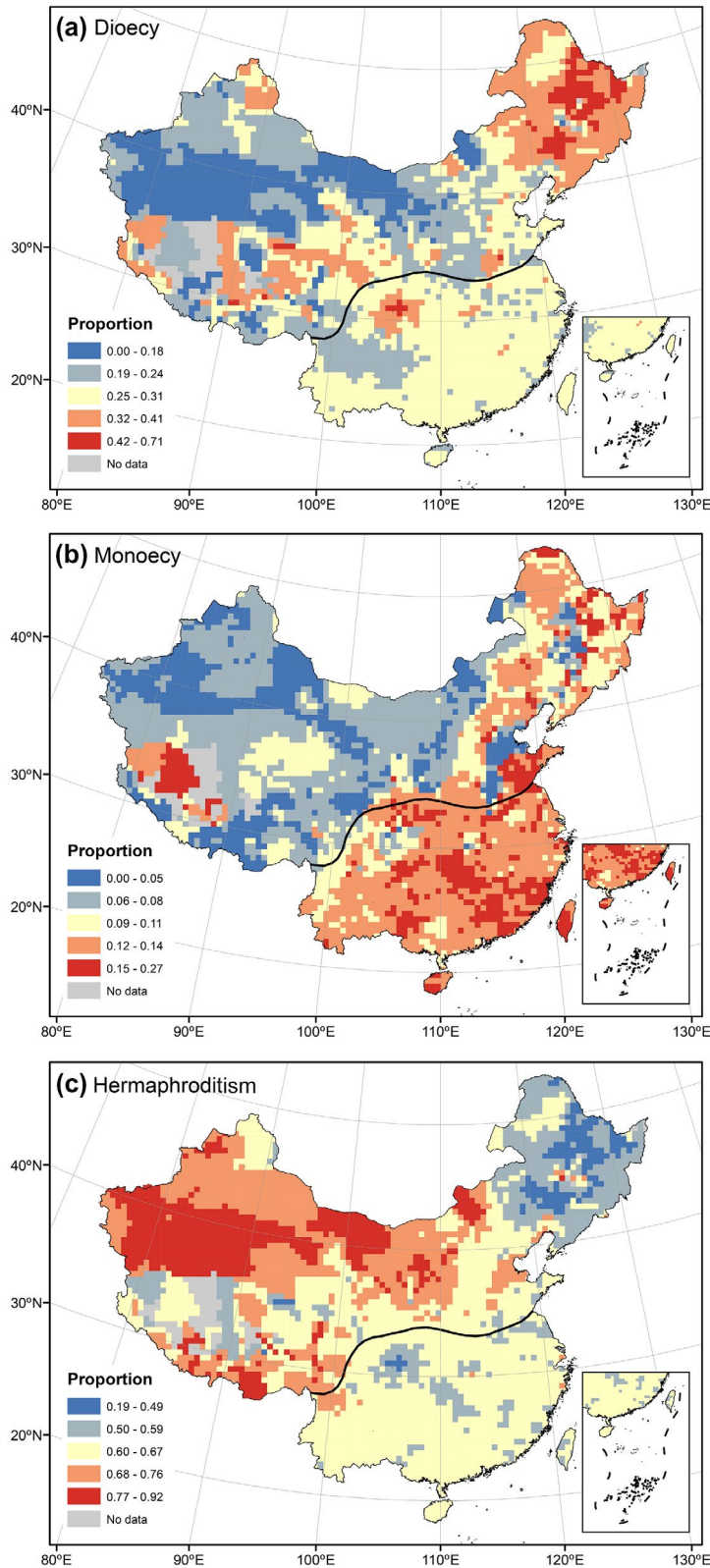
FIGURE 1 Spatial patterns in the proportion of different sexual systems in local floras: (a) dioecy; (b) monoecy; and (c) hermaphroditism. The continuous black line is the isoline of mean annual precipitation of 800 mm, which also closely tracks the isoline of mean annual temperature of 0°C. Grid cells with fewer than 10 woody species are shown in grey [Colour figure can be viewed at wileyonlinelibrary.com]

3.4 | Influence of evolutionary age on sexual systems

Blomberg's K indicated significant phylogenetic signal in the within-genus proportion of dioecious species ($p < .001$), suggesting that dioecy in woody plants is phylogenetically conserved, and closely related genera tend to have similar proportions of dioecy. In contrast, the monoecious and hermaphroditic proportions had no significant phylogenetic signal ($p > .05$; Table 1).

Whether controlling for phylogeny and other predictors or not, average genus age per grid cell was significantly but weakly
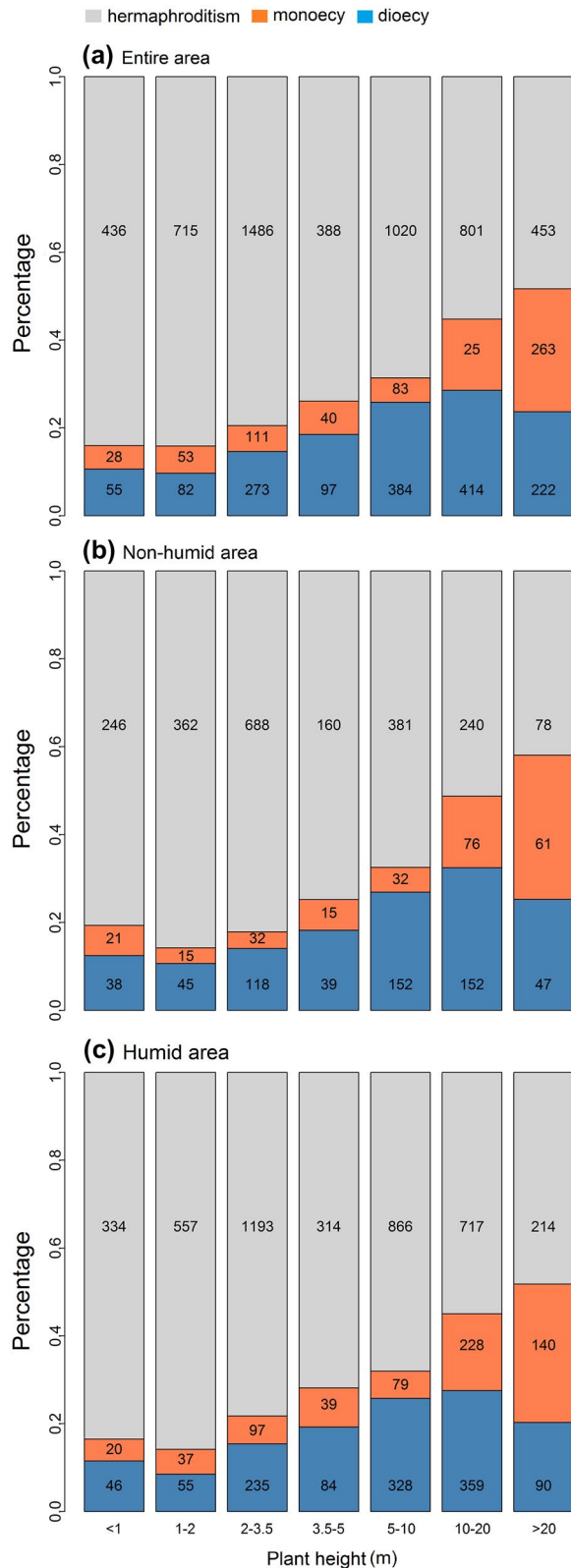
FIGURE 2 Comparison between the proportions of species with different sexual systems across different plant heights. Corresponding plant heights are shown under the x axis. (a) Whole study area. (b) The area with yearly precipitation <800 mm (non-humid area). (c) The area with precipitation >800 mm (humid area) [Colour figure can be viewed at wileyonlinelibrary. com]

correlated with biogeographical patterns of sexual systems in both humid and non-humid areas (Tables 2; Figure 2; Supporting Information Table S3).

4 | DISCUSSION

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

4.1 | Influence of mature plant height on sexual systems

The geographical variation in the proportions of different sexual systems across China are driven predominantly by variations in plant height (see Figure 1; Supporting Information Figure S4). This extends previous findings that the frequency of life forms is correlated with the frequency of mating systems across latitude (Moeller et al., 2017) or that the proportion of dioecious species is higher among trees than among other life forms (e.g., Bawa et al., 1985; Renner & Ricklefs, 1995) and higher in canopy (24.5%) than in understorey species (9.8%) (Kress & Beach, 1994). Theoretical and observational evidence indicates that large plants could allocate more biomass to sexual reproduction (Niklas & Enquist, 2003), leading to a larger flower size and/or a higher number of floral structures (e.g., petals and stamens) than small plants in both herbaceous (Arroyo, Dudley, Jespersen, Pacheco, & Cavieres, 2013; Lambrecht & Dawson, 2007; Schmid, Bazzaz, & Weiner, 1995) and tree-sized species (Hirayama, Nanami, Itoh, & Yamakura, 2008). This might intensify the disadvantages of self-incompatibility and benefit cross-pollination in dioecious species (Harder & Barrett, 1995), especially during mass-flowering events (Eckert, 2000). In contrast, selection pressure might be expected to increase the proportion of selfing hermaphrodites among small plants.

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

Given the well-documented association between plant height and longevity (Marbà et al., 2007; Moles & Leishman, 2008;
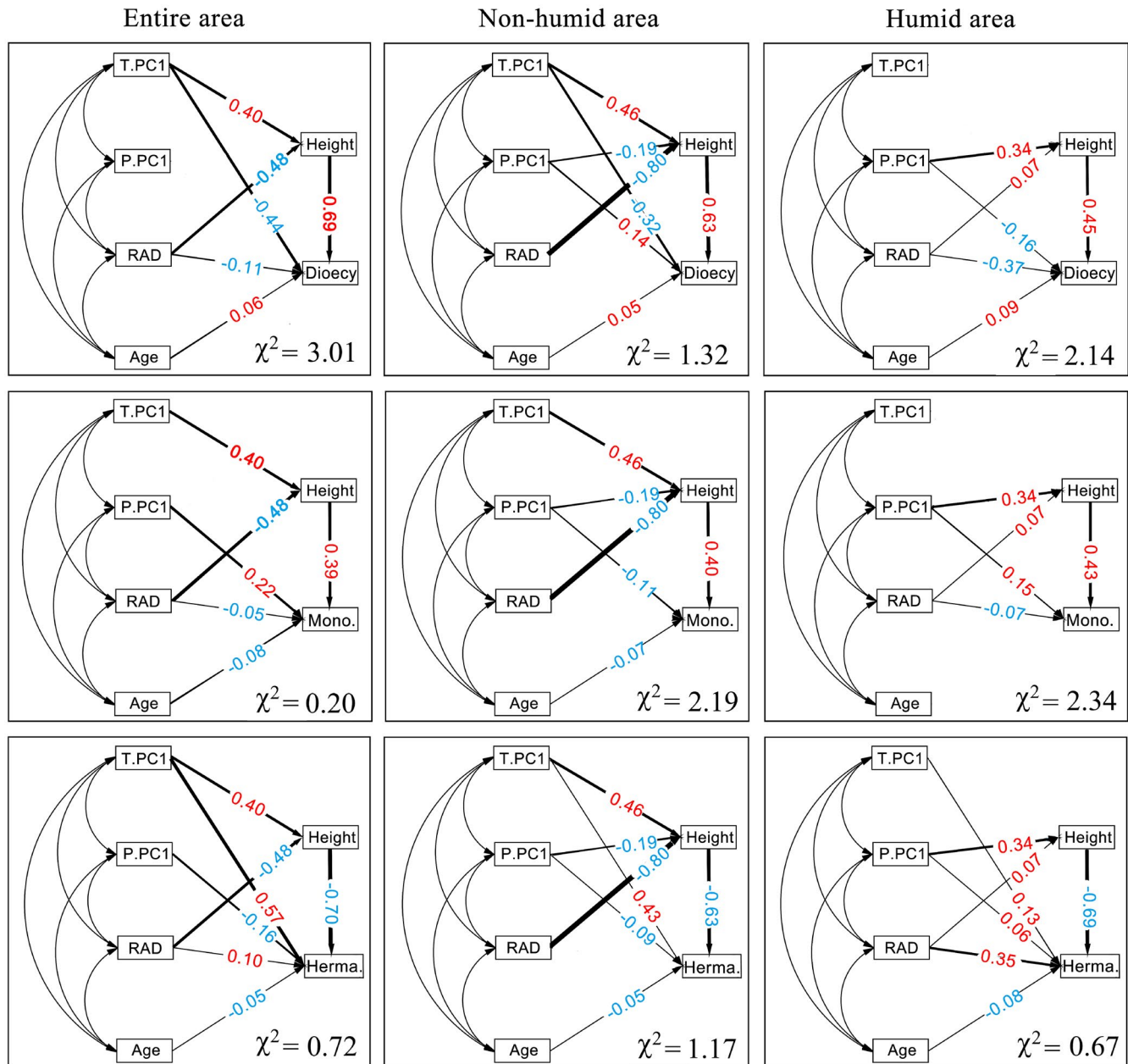
FIGURE 3 Path diagrams showing interactions among climate [the first principal components of temperature (T.PC1), precipitation (P.PC1) and solar radiation (RAD)], mature plant height (Height), genus age (Age) and proportions of sexual systems. The values next to the arrows are standardized path coefficients. Red values indicate positive relationships and blue values negative relationships. The line thickness of path arrows represents the strength of the relationship. Paths with $P > .05$ are not shown. Mono. = monoecy; Herma. = hermaphroditism [Colour figure can be viewed at wileyonlinelibrary.com]

Moles et al., 2009), our results also suggest an association between sexual systems and longevity, in particular increased frequency of dioecy and monoecy with longevity. Our results thus generalize previous findings about a positive association between dioecy and plant longevity at the family level (Renner, 2014) to the species level and to monoecy. In contrast, short-lived species are expected to have a higher frequency of hermaphrodites, which might explain a higher frequency of hermaphrodites in temperate regions compared with sub-tropical and tropical regions (Moeller et al., 2017).

4.2 | Influence of climate on the proportions of sexual systems

Our results are consistent with previous findings that mating strategies of woody plants are sensitive to variations in contemporary climate (reflected by both temperature and precipitation) across space (Chaves, Maroco, & Pereira, 2003; Dorji et al., 2013; Etterson & Mazer, 2016; Waller, 1980). However, the effects of climate on the proportions of different sexual systems tended to be indirect, because we found that climate had weak direct effects on the

biogeographical patterns of sexual systems in both SLMs and SEMs (Table 2; Figure 3). We found that the proportions of hermaphroditic plants were highest in drylands in western China (Figure 1), suggesting that hermaphrodites have better drought tolerance than dioecious and monoecious species (Obbard et al., 2006; Verdú, 2004). Hermaphrodites are often selfers (Moeller et al., 2017; Peng et al., 2014), and selfers have been found to be able to accelerate carbon assimilation rates, flower early and complete their life cycle rapidly (Mazer, Dudley, Hove, Emms, & Verhoeven, 2010), potentially reducing their exposure to drought in drylands (Ivey, Dudley, Hove, Emms, & Mazer, 2016). Solar radiation may affect the relative representation of sexual systems via its influence on flower coloration (Peng et al., 2014). For example, Peng et al. (2014) found that hermaphroditism was significantly associated with showy flower colour in alpine plants. Quantifying the influence of solar radiation on the frequency of different sexual systems via flower coloration deserves further study.

4.3 | Evolutionary history of sexual systems

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

However, genus age was only weakly correlated with the geographical pattern of sexual system composition across China (Table 2; Supporting Information Figure S3). For example, the proportion of hermaphroditic species was highest in northwest China, where woody floras are relatively young (Lu et al., 2018), which supports the idea that hermaphrodites have been favoured in regions with frequent extinction and re-colonization. In contrast, higher proportions of dioecy might have been maintained only in regions with low rates of local extinction and re-colonization, owing to the limitation of mating opportunities (Obbard et al., 2006). This might explain the high proportion of dioecious species in northeast China, where woody floras are relatively old (Lu et al., 2018). The relationship between sexual system composition and clade age in a region may be confounded by the magnitude and velocity of climate change, life-history strategies, local adaptation and generation times (Hultine et al., 2016; Qian, 2014, 2017).

4.4 | Comparison between patterns in the prevalence of different sexual systems

Although previous studies have noted phylogenetic patterns in the distribution of dioecy, monoecy and hermaphroditism, little is known about the association between ecological conditions and the distribution of different sexual systems. We found clear evidence

that dioecious and hermaphroditic species are favoured by opposite ecological conditions: the proportion of dioecy decreased with solar radiation but increased with plant height and genus age, whereas that of hermaphroditism showed the opposite trends (Table 2). This finding suggests that dioecy and hermaphroditism might represent two evolutionary extremes of adaptation to specific selection pressures (e.g., climate) during evolutionary history (Moeller et al., 2017; Snell & Aarssen, 2005).

Biogeographical patterns in the proportion of monoecious species were more complex than those of the other two sexual systems. In Costa Rica, Vamosi and Queenborough (2010) found a comparable reliance of dioecious and monoecious species on insect and wind pollination in a series of forest plots along a local transect. This might be attributable to more common wind dispersal in dry forests, which leads to lower metabolic costs for plants to produce nectar and fleshy fruits, whereas more expensive insect pollination could ensure reproductive success in wet tropical forests (Rech et al., 2016). Here, we found that the proportions of dioecious and monoecious species consistently increased with the average plant height per grid cell. But we also found that the proportion of monoecy responded to climate (precipitation in arid areas and radiation in humid areas) in a similar manner to that of the proportion of hermaphrodites. These results might indicate that monoecy adapts to specific ecological conditions flexibly or that monoecy is an intermediate stage between the other two sexual systems (Goldberg et al., 2017) and thus is not so clearly associated with particular environmental conditions. It is noteworthy that many previous studies about the distribution of sexual systems have pooled monoecious and hermaphroditic species together (e.g., Dorken, Freckleton, & Pannell, 2017; Queenborough et al., 2009; Vamosi, Mazer, & Cornejo, 2008). As a result, the ecological and evolutionary aspects of monoecy have not been well studied compared with those of dioecy and hermaphroditism.

4.5 | Caveat to correlative studies

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

4.6 | Conclusions

Our findings suggest that mature plant height is the strongest predictor of the biogeographical pattern of woody angiosperm sexual

systems across local floras in China and that climate also plays an important role, whereas the evolutionary age of floras has a relatively weak influence. The proportions of dioecy and hermaphrodites in local floras had opposite trends along abiotic and biotic drivers, suggesting that these two sexual systems might represent opposite directions of evolution in adapting to environmental pressures. The flexible response of monoecy to ecological conditions compared with dioecy and hermaphroditism deserves further investigation owing to the intermediate state of monoecy between the other two. Our findings shed light on the ecological drivers of geographical variation in sexual systems of woody plants across China and suggest that environmental adaptation significantly influences the biogeographical pattern of sexual systems. Moreover, our finding that present-day geographical variation in sexual systems is strongly related to contemporary climate variables suggests that the composition of sexual systems in local floras might be sensitive to global climate change, and different responses of different sexual systems to ongoing and future climate change could lead to significant changes in the species composition in local plant communities.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA ACCESSIBILITY

The data supporting the results in are archived in Dryad: https://doi.org/10.5061/dryad.pk0p2nghx.

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REFERENCES

Aarssen, L. W. (2000). Why are most selfers annuals? A new hypothesis for the fitness benefit of selfing. *Oikos*, 89, 606–612. https://doi.org/10.1034/j.1600-0706.2000.890321.x

Anderson, E. (1940). The concept of the genus: II. A survey of modern opinion. *Bulletin of the Torrey Botanical Club*, 67, 363–369. https://doi.org/10.2307/2481069

Arroyo, M. T. K., Dudley, L. S., Jespersen, G., Pacheco, D. A., & Cavieres, L. A. (2013). Temperature-driven flower longevity in a high-alpine species of *Oxalis* influences reproductive assurance. *New Phytologist*, 200, 1260–1268.

Ashman, T. L. (2006). The evolution of separate sexes: A focus on the ecological context. In L. D. Harder & S. C. H. Barrett (Eds.), *Ecology and evolution of flowers* (pp. 204–222). Oxford: Oxford University Press.

Barraclough, T. G., & Humphreys, A. M. (2015). The evolutionary reality of species and higher taxa in plants: A survey of post-modern opinion and evidence. *New Phytologist*, 207, 291–296.

Barrett, S. C. H. (1998). The evolution of mating strategies in flowering plants. *Trends in Plant Sciences*, 3, 335–341. https://doi.org/10.1016/S1360-1385(98)01299-0

Barrett, S. C. H. (2013). The evolution of plant reproductive systems: How often are transitions irreversible? *Proceedings of the Royal Society B: Biolocial Sciences*, 280, 20130913. https://doi.org/10.1098/rspb.2013.0913

Barrett, S. C. H., & Eckert, C. G. (1990). Variation and evolution of mating systems in seed plants. In S. Kawano (Ed.), *Biological approaches and evolutionary trends in plants*. Tokyo: Academic Press.

Barrett, S. C. H., & Harder, L. D. (1996). Ecology and evolution of plant mating. *Trends in Ecology and Evolution*, 11, 73–79. https://doi.org/10.1016/0169-5347(96)81046-9

Barrett, S. C. H., & Harder, L. D. (2017). The ecology of mating and its evolutionary consequences in seed plants. *Annual Review of Ecology, Evolution, and Systematics*, 48, 135–157. https://doi.org/10.1146/annurev-ecolsys-110316-023021

Bawa, K. S., Perry, D. R., & Beach, J. H. (1985). Reproductive biology of tropical lowland rain forest trees. I. Sexual systems and incompatibility mechanisms. *American Journal of Botany.*, 72, 331–345.

Blomberg, S. P., Garland, T., & Ives, A. R. (2003). Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution.*, 57, 717–745.

Burd, M., & Allen, T. F. H. (1988). Sexual allocation strategy in wind-pollinated plants. *Evolution*, 42, 403–407. https://doi.org/10.1111/j.1558-5646.1988.tb04145.x

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

Cardoso, J. C. F., Viana, M. L., Matias, R., Furtado, M. T., Caetano, A. P. D. S., Consolaro, H., & Brito, V. L. G. D. (2018). Towards a unified terminology for angiosperm reproductive systems. *Acta Botanica Brasilica*, 32, 329–348. https://doi.org/10.1590/0102-33062018abb0124

Charlesworth, D. (2006). Evolution of plant breeding systems. *Current Biology*, 16(17), R726–R735. https://doi.org/10.1016/j.cub.2006.07.068

Chaves, M. M., Maroco, J. P., & Pereira, J. S. (2003). Understanding plant responses to drought—From genes to the whole plant. *Functional Plant Biology*, 30, 239–264. https://doi.org/10.1071/FP02076

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

Chen, X. Y. (2003). Breeding system. In D. Y. Zhang (Ed.), *Plant life-history evolution and reproductive ecology* (pp. 269–287). Beijing: Science Press.

Chen, Z.-D., Yang, T., Lin, L., Lu, L.-M., Li, H.-L., Liu, B. … China Phylogeny Consortium. (2016). Tree of life for the genera of Chinese vascular plants. *Journal of Systematics and Evolution*, 54, 273–276.

Conway, J. M., & Huffcutt, A. I. (2003). A review and evaluation of exploratory factor analysis practices in organizational research. *Organizational Research Methods*, 6, 147–168. https://doi.org/10.1177/1094428103251541

Dorji, T., Totland, Ø., Moe, S. R., Hopping, K. A., Pan, J., & Klein, J. A. (2013). Plant functional traits mediate reproductive phenology and success in response to experimental warming and snow addition in Tibet. *Global Change Biology*, 19, 459–472. https://doi.org/10.1111/gcb.12059

Dorken, M. E., Freckleton, R. P., & Pannell, J. R. (2017). Small-scale and regional spatial dynamics of an annual plant with contrasting sexual systems. *Journal of Ecology*, 105, 1044–1057. https://doi.org/10.1111/1365-2745.12719

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., … Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36, 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Eckert, C. G. (2000). Contributions of autogamy and geitonogamy to self-fertilization in a mass-flowering, clonal plant. *Ecology*, 81, 532–542. https://doi.org/10.1890/0012-9658(2000)081[0532:COAAGT]2.0.CO;2

Elle, E., & Carney, R. (2003). Reproductive assurance varies with flower size in Collinsia parviflora(Scrophulariaceae). *American Journal of Botany*, 90(6), 888–896.

Etterson, J. R., & Mazer, S. J. (2016). How climate change affects plants' sex lives: Shifts in plant sex ratios help plant species to expand upslope in a warmer climate. *Science*, 353, 32–33. https://doi.org/10.1126/science.aag1624

Faith, D. (1992). Conservation evaluation and phylogenetic diversity. *Biological Conservation*, 61, 1–10. https://doi.org/10.1016/0006-3207(92)91201-3

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

Freeman, D. C., Harper, K. T., & Ostler, W. K. (1980). Ecology of plant dioecy in the intermountain region of western North America and California. *Oecologia*, 44, 410–417. https://doi.org/10.1007/BF00545246

Goldberg, E. E., Otto, S. P., Vamosi, J. C., Mayrose, I., Sabath, N., Ming, R., & Ashman, T. L. (2017). Macroevolutionary synthesis of flowering plant sexual systems. *Evolution*, 71, 898–912. https://doi.org/10.1111/evo.13181

Harder, L. D., & Barrett, S. C. H. (1995). Mating cost of large floral displays in hermaphrodite plants. *Nature*, 373, 512–515. https://doi.org/10.1038/373512a0

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high-resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25, 1965–1978. https://doi.org/10.1002/joc.1276

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

Hultine, K. R., Grady, K. C., Wood, T. E., Shuster, S. M., Stella, J. C., & Whitham, T. G. (2016). Climate change perils for dioecious plant species. *Nature Plants*, 2, 16109. https://doi.org/10.1038/nplants.2016.109

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

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

Kattge, J., Diaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönisch, G., et al. (2011). TRY–a global database of plant traits. *Global Change Biology*, 17, 2905–2935.

Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P., & Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics.*, 26, 1463–1464.

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

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

Körner, C. (1999). *Alpine plant life: Functional plant ecology of high mountain ecosystems*. Berlin: Springer-Verlag.

Kress, W. J., & Beach, J. H. (1994). Flowering plant reproductive systems. In L. A. McDade, K. S. Bawa, H. Hespenheide, & G. Hartshorn (Eds.), *La Selva: ecology and natural history of a neotropical rain forest* (pp. 161–182). Chicago, IL: University of Chicago Press.

Lambrecht, S. C., & Dawson, T. E. (2007). Correlated variation of floral and leaf traits along a moisture availability gradient. *Oecologia*, 151, 574–583. https://doi.org/10.1007/s00442-006-0617-7

Leopold, D. R., Tanentzap, A. J., Lee, W. G., Heenan, P. B., & Fukami, T. (2015). Evolutionary priority effects in New Zealand alpine plants across environmental gradients. *Journal of Biogeography.*, 42, 729–737.

Levin, D. A. (2012). Mating system shifts on the trailing edge. *Annuals of Botany*, 109, 613–621. https://doi.org/10.1093/aob/mcr159

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

Lloyd, D. G. (1982). Selection of combined versus separate sexes in seed plants. *The American Naturalist*, 120, 571–585. https://doi.org/10.1086/284014

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

Lord, J. M., Westoby, M., & Leishman, M. (1995). Seed size and phylogeny in six temperate floras: Constraints, niche conservatism, and adaptation. *The American Naturalist*, 146, 349–364. https://doi.org/10.1086/285804

Lu, L.-M., Mao, L.-F., Yang, T., Ye, J.-F., Liu, B., Li, H.-L., … Chen, Z.-D. (2018). Evolutionary history of the angiosperm flora of China. *Nature*, 554, 234–238. https://doi.org/10.1038/nature25485

Maitner, B. S., Boyle, B., Casler, N., Condit, R., Donoghue, J., Durán, S. M., … McMahon, S. (2018). The bien r package: A tool to access the Botanical Information and Ecology Network (BIEN) database. *Methods in Ecology and Evolution.*, 9, 373–379.

Marbà, N., Duarte, M. C., & Agustí, S. (2007). Allometric scaling of plant life history. *Proceedings of the National Academy of Sciences USA*, 104, 15777–15780. https://doi.org/10.1073/pnas.0703476104

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

Mazer, S. J., Dudley, L. S., Hove, A. A., Emms, S. K., & Verhoeven, A. S. (2010). Physiological performance in *Clarkia* sister taxa with contrasting mating systems: Do early flowering autogamous taxa avoid water stress relative to their pollinator-dependent counterparts? *International Journal of Plant Science*, 171, 1029–1047.

Moeller, D. A., Briscoe Runquist, R. D., Moe, A. M., Geber, M. A., Goodwillie, C., Cheptou, P. O., … Winn, A. A. (2017). Global biogeography of mating system variation in seed plants. *Ecology Letters*, 20, 375–384. https://doi.org/10.1111/ele.12738

Moles, A. T., & Leishman, M. R. (2008). The seedling as part of a plant's life history strategy. In M. A. Leck, V. T. Parker, & R. L. Simpson (Eds.), *Seedling ecology and evolution* (pp. 217–238). Cambridge, UK: Cambridge University Press.

Moles, A. T., Warton, D. I., Warman, L., Swenson, N. G., Laffan, S. W., Zanne, A. E., … Leishman, M. R. (2009). Global patterns in plant height. *Journal of Ecology*, 97, 923–932. https://doi.org/10.1111/j.1365-2745.2009.01526.x

Morgan, M. T., Schoen, D. J., & Bataillon, T. M. (1997). The evolution of self-fertilization in perennials. *The American Naturalist*, 150, 618–638. https://doi.org/10.1086/286085

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

Obbard, D. J., Harris, S. A., & Pannell, J. R. (2006). Sexual systems and population genetic structure in an annual plant: Testing the metapopulation model. *The American Naturalist*, 167, 354–366. https://doi.org/10.1086/499546

Olson, M. S., Hamrick, J. L., & Moore, R. (2016). Breeding systems, mating systems, and genomics of gender determination in angiosperm trees. In: A. Groover & Q. Cronk (Eds.), *Comparative and evolutionary genomics of angiosperm trees. Plant genetics and genomics: Crops and models* (Vol. 21, pp. 139–158). Cham: Springer.

Orme, D. (2012). *The Caper package: comparative analysis of phylogenetics and evolution in R.* Retrieved from http://cran.r-project.org/web/packages/caper.

Pannell, J., & Barrett, S. C. H. (1998). Baker's law revisited: Reproductive assurance in a metapopulation. *Evolution*, 52, 657–668. https://doi.org/10.1111/j.1558-5646.1998.tb03691.x

Peng, D. L., Ou, X. K., Xu, B., Zhang, Z. Q., Niu, Y., Li, Z. M., & Sun, H. (2014). Plant sexual systems correlated with morphological traits: Reflecting reproductive strategies of alpine plants. *Journal of Systematics and Evolution*, 52, 368–377. https://doi.org/10.1111/jse.12046

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

Qian, H. (2014). Contrasting relationships between clade age and temperature along latitudinal versus elevational gradients for woody angiosperms in forests of South America. *Journal of Vegetation Science*, 25, 1208–1215. https://doi.org/10.1111/jvs.12175

Qian, H. (2017). Relationship between clade age and temperature for angiosperm tree species in forest communities along an elevational gradient in tropical Asia. *Journal of Plant Ecology*, 10, 618–625.

Queenborough, S. A., Mazer, S. J., Vamosi, S. M., Garwood, N. C., Valencia, R., & Freckleton, R. P. (2009). Seed mass, abundance and breeding system among tropical forest species: Do dioecious species exhibit compensatory reproduction or abundances? *Journal of Ecology*, 97, 555–566. https://doi.org/10.1111/j.1365-2745.2009.01485.x

Core Team, R. (2016). *R: A Language and Environment for Statistical Computing.* Vienna: R Foundation for Statistical Computing. https://www.R-project.org/

Rech, A. R., Dalsgaard, B., Sandel, B., Sonne, J., Jens-Christian Svenning, J.-S., Holmes, N., & Ollerton, J. (2016). The macroecology of animal versus wind pollination: Ecological factors are more important than historical climate stability. *Plant Ecology & Diversity*, 9, 253–262. https://doi.org/10.1080/17550874.2016.1207722

Renner, S. S. (2014). The relative and absolute frequencies of angiosperm sexual systems: Dioecy, monoecy, gynodioecy, and an updated online database. *American Journal of Botany*, 101, 1588–1596. https://doi.org/10.3732/ajb.1400196

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

Ricklefs, R. E., & Wikelski, M. (2002). The physiology/life history nexus. *Trends in Ecology and Evolution*, 17, 462–468. https://doi.org/10.1016/S0169-5347(02)02578-8

Sakai, A. K., Wagner, W. L., Ferguson, D. M., & Herbst, D. R. (1995). Biogeographical and ecological correlates of dioecy in the Hawaiian flora. *Ecology*, 76, 2530–2543. https://doi.org/10.2307/2265826

Sakai, A. K., Weller, S. G., Wagner, P. S., & Soltis, D. E. (1997). Adaptive radiation in the endemic Hawaiian genera *Schiedea* and *Alsinidendron* (Caryophyllaceae: Alsinoideae): Phylogenetic insights into the evolution of dioecy. In T. Givnish & K. Sytsma (Eds.), *Molecular evolution and adaptive radiation* (pp. 455–474). New York, NY: Cambridge University Press.

Schmid, B., Bazzaz, F. A., & Weiner, J. (1995). Size dependency of sexual reproduction and of clonal growth in two perennial plants. *Canada Journal of Botany*, 73, 1831–1837. https://doi.org/10.1139/b95-194

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

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

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

Thornthwaite, C. W., & Hare, F. K. (1955). Climatic classification in forest. *Unasylva.*, 9, 51–59.

Tree of Sex Consortium: Ashman, T. L., Bachtrog, D., Blackmon, H., Goldberg, E., Hahn, M., Kirkpatrick, M., … Vamosi, J. (2014). Tree of sex: A database of sexual systems. *Scientific Data*, 1, 140015. https://doi.org/10.1038/sdata.2014.15

Vamosi, J. C., Otto, S. P., & Barrett, S. C. (2003). Phylogenetic analysis of the ecological correlates of dioecy in angiosperms. *Journal of Evolutionary Biology*, 6, 1006–1018. https://doi.org/10.1046/j.1420-9101.2003.00559.x

Vamosi, S. M., Mazer, S. J., & Cornejo, F. (2008). Breeding systems and seed size in a Neotropical flora: Testing evolutionary hypotheses. *Ecology*, 89, 2461–2472. https://doi.org/10.1890/07-0674.1

Vamosi, S. M., & Queenborough, S. A. (2010). Breeding systems and phylogenetic diversity of seed plants along a large-scale elevational gradient. *Journal of Biogeography*, 37, 465–476. https://doi.org/10.1111/j.1365-2699.2009.02214.x

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

Waller, D. M. (1980). Environmental determinants of outcrossing in Impatiens capensis (Balsaminaceae). *Evolution*, 34, 747–761.

Wang, Z.-H., Brown, J. H., Tang, Z.-Y., & Fang, J.-Y. (2009). Temperature dependence, spatial scale, and tree species diversity in eastern Asia and North America. *Proceedings of the National Academy of Sciences USA*, 106, 13388–13392. https://doi.org/10.1073/pnas.0905030106

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

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

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

BIOSKETCH

Yunyun Wang is a lecturer whose research focuses on the patterns of reproductive traits at large spatial scales and the roles of reproductive traits in community assembly.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.