Region effects and local climate jointly shape the global distribution of sexual systems in woody flowering plants

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10   **Abstract.** Understanding the evolution and maintenance of plant sexual diversity needs to incorporate both

regional processes and local climate factors across large geographic scales. Using data of woody flowering

plants from a global set of large-scale forest plots and multinomial logistic regression, we quantified region

effects on the proportion of dioecy, monoecy, and hermaphrodite species count and abundance while

incorporating evolutionary history and local climate factors. We demonstrated that plants were more likely to be

15   dioecy than monoecy in tropical regions than in temperate regions, supporting the role of colonization processes

suggested by Baker's law in structuring the geographic patterns of plant sexual systems. We further found plants

were more likely to be dioecious than monoecious in areas with younger mean species age. Plants were more

likely to be hermaphrodite than dioecious in areas with high annual potential evapotranspiration and

precipitation seasonality but were more likely to be dioecious than monoecious in areas with high precipitation

20   of driest month. Our results suggest that both regional processes and local climate factors play important roles in

shaping the geographic distribution of plant sexual systems, providing a baseline for predicting future changes

in forest communities under global change.

Keywords. Plant sexual systems, Geographic pattern, Region effects, Evolutionary history, Climate effects.

1 Introduction

25 Plants display varieties of sexual systems, which are known to play important roles in species evolution, colonization, and community assembly (Barrett, 2002; Vamosi, 2006; Pannell et al., 2015; Réjou-Méchain and Cheptou, 2015). Despite these advances, the geographic patterns of plant sexual systems and their ecological drivers are not well understood (Vamosi and Queenborough, 2010; Wang et al., 2021). This lack of knowledge does not only prevent us from understanding the selective pressures on plant sexual systems at the global scale

30 but also hinders our ability to understand and predict their influence on biodiversity maintenance and community dynamics at the local scale (Charlesworth, 2006; Etterson and Mazer, 2016; Hultine et al., 2016; Tusiji and Fukami, 2020; Cronk, 2022).

Plant sexual systems can be mainly classified into three types (Barrett, 2002; Cardoso et al., 2018): dioecy (having male and female flowers in different individuals), monoecy (having male and female flowers in the

35 same individuals), and hermaphrodite (having both male and female parts in the same flower). Although dioecy is mostly rare, previous studies show a high incidence of dioecy in tropical forest and island communities, especially for woody species (Bawa and Opler, 1975; Baker and Cox, 1984; Renner and Ricklefs, 1995; Sakai and Weller, 1999; Chen and Li, 2008). In contrast, the incidence of monoecy is high in temperate forests because they are mostly wind pollinated (Regal, 1982; De jong et al., 2008; Fridman and Barrett, 2009; Cronk, 2022). As

40 monoecy takes a higher proportion towards high latitudes forest communities, the proportion of hermaphroditism might be higher in tropical forests than in temperate forests. These former studies do not agree on the effects of elevations on the distribution of the three sexual systems. Dioecy and monoecy could both showed high incidence in lowland forest communities and thus hermaphrodite increased towards high elevation (Baker and Cox, 1984; Queenborough and Vamosi, 2010; but see Arroyo and Squeo, 1990). These geographic

45 patterns are challenged by subsequent studies with more extended data and phylogenetic analyses (Vamosi et al., 2003; Wang et al., 2020, 2021). Thus, more inclusive studies are needed to explore the geographic patterns of plant sexual systems and to determine the ecological drivers underlying these patterns.

Regional processes have been proposed to explain the distribution of plant sexual systems. As the Baker law suggests colonization is less likely for plants that are unable to uniparental reproduction, especially for long

50 distance dispersal (Baker, 1955; Pannell et al., 2015), we would expect regions with different geographic and evolutionary histories could thus have different compositions of plant sexual systems (Ashton, 1967; Rickleffs

and He, 2016; Tusiji and Fukami, 2020). Previous studies found a large clade of dioecious plants in tropical flora, which suggests dioecy might originate in the tropical region (Bawa, 1980; Renner, 2014). As dioecy could have lower colonization rates than other sexual systems, we would expect a higher incidence of dioecious

55   species and individuals in tropical regions than in temporal regions. Furthermore, since dioecy could also be newly evolved from other sexual systems after colonization (Baker and Cox, 1984; Sakai, 1995), we would expect areas with younger species age to have a higher incidence of dioecy. However, some studies suggest a higher incidence of dioecy is associated with older flora (Renner and Ricklefss, 1995; Wang et al., 2020). There is a need to test the effects of region and evolutionary history on the incidences of plant sexual systems to

60   resolve these contrasting results.

Local climate and habitat conditions have also been shown to affect the geographic patterns of plant sexual systems (Sakai and Weller, 1999; Vamosi and Queenborough, 2010; Wang et al., 2020, 2021). Studies have found dioecy to be more likely associated with dry or poor resource habitats (Sakai and Weller, 1999; Ashman, 2006). As predicted by sex allocation theory, plants may not be able to maintain both sexes in a

65   resource-poor environment (Ashman, 2006). This suggests the incidence of dioecy might be high while that of hermaphroditism and monoecy be low in cold and dry areas. Recent studies find high temperatures are a disadvantage to dioecy and monoecy, while hermaphrodites favor warm and arid regions (Hultine et al., 2016; Wang et al., 2021). There is thus a lack of consensus on the climate factors that drive the patterns of different sexual systems. A possible source of the controversy could be that these studies do not simultaneously

70   incorporate the regional processes and local factors in studying biogeographic patterns of sexual systems (Sakai and Weller, 1999; Vamosi and Queenborough, 2010; Wang et al., 2021). In addition, most of these studies use occurrence data based on museum records that might have sampling bias. We intend to reveal region effects on the incidence of plant sexual systems of woody flowering plants by incorporating both regional and local factors based on a global network of forest plots that do not only accurately record the occurrence but also abundance of

75   each species.

In this study, we compiled a species list with information on sexual systems and abundance from 55 forest sites from the ForestGEO global plot network (http://www.forestgeo.si.edu/) to investigate the ecological and evolutionary drivers of geographic patterns of sexual systems. We aimed to explore the geographic variation in plant sexual systems and test the effects of region, evolutionary history, and climate in shaping geographic

80   patterns. We would expect that plants are more likely to be dioecious than monoecy in tropical and adjacent regions with younger species ages. We would also expect that plants in areas with high PET and lower

precipitation are more likely to be dioecy than hermaphrodites.

2 Methods

2.1 Data sources

85   Our study was based on 55 forest dynamic plots from the ForestGEO network (Figure 1) with plot sizes varying

from 4 to 60 ha. The 55 plots were established according to a standardized tree census protocol allowing

comparison across sites, with each stem ≥ 1 cm diameter at breast height (DBH) being mapped and identified to

species (Condit, 1998). We first checked the species name via the Taxonomic Name Resolution Service (TNRS)

online tool to remove synonyms (https://tnrs.biendata.org/).

90   Identification of species' sexual system was referred to databases of eFloras (http://www.efloras.org/),

Plants of the World Online (http://powo.science.kew.org/), and the World Flora Online

(http://www.worldfloraonline.org/), and the Global Plants (https://plants.jstor.org/). We also referred to literature

that provided explicit information for the identification of species or genus' sexual systems (e.g., Renner, 2014;

Wang et al., 2021). In this study, we divided species into three categories based on their sexual systems:

95   hermaphroditism, dioecy, and monoecy according to Queenboraough and Vamosi (2010), Cardoso et al. (2018)

and Wang et al. (2021). We define hermaphroditism as a species having both male and female parts in the same

flower, monoecy as a species that has separate male and female flowers on the same plant (thus including

andromonoecy, gynomonoecy, polygamous-monoecy), and dioecy as a species with different sexual phenotypes

(thus including androdioecy, gynodioecy, and polygamous-dioecy). Species unidentified, species identified to a

100   genus or family that have an uncertain sexual system, or species whose sexual system is unknown were

excluded from our analysis. Those species account for a small portion (<1%) of the species. In total, our data

contain 8018 flowering plant species. We did not consider ferns, gymnosperms, and herbaceous plants, because

our interest was the sexual systems of woody flowering plants.

      We collected plot information including latitude, longitude, region, isolation, area, the number of trees,

105   elevation, mean annual temperature (MAT), and mean annual precipitation (MAP) of the 55 forest plots from

recent studies (Ricklefs and He, 2016; Davies et al., 2021). We collected other 17 bioclimate factors (excluding

BIO1 and BIO12) from WorldClim 2.0 (https://worldclim.org). Annual potential evapotranspiration (PET) was

collected from Global Aridity and PET Database v2 (https://cgiarcsi.community/).

2.2 Data analysis

110 We modeled the proportions of the three sexual systems (π_1, π_2, π_3) in relation to explanatory variables

including five geographic factors (region, isolation, latitude, longitude, elevation), two evolutionary factors

(mean species age and phylogenetic signal), two plot characters (area, number of trees), and 20 climate factors

(MAT, MAP, PET, and 17 bioclimate variables). In each plot, a species can only be either dioecy, monoecy, or

hermaphroditism, leading to $\pi_1 + \pi_2 + \pi_3 = 1$. This is a multinomial logistic regression model where the

115 dependent variable is a nominal with three levels (dioecy, monoecy, and hermaphroditism). The multinomial

logistic model has the form:

$$\pi_1 = \frac{1}{1+\exp(\boldsymbol{\beta_2 x})+\exp(\boldsymbol{\beta_3 x})} \text{ (incidence probability of Dioecious species)}$$

$$\pi_2 = \frac{\exp(\boldsymbol{\beta_2 x})}{1+\exp(\boldsymbol{\beta_2 x})+\exp(\boldsymbol{\beta_3 x})} \text{ (incidence probability of Monoecious species)}$$

$$\pi_3 = \frac{\exp(\boldsymbol{\beta_3 x})}{1+\exp(\boldsymbol{\beta_2 x})+\exp(\boldsymbol{\beta_3 x})} \text{ (incidence probability of Hermaphrodite species)}$$

120 where $\boldsymbol{x}$ is a set of explanatory variables.

Because the effect of region could be confounded with other variables, we developed a full model that

included all geographic factors, plot characteristics, and climatic variables, together with the evolutionary

factors. "region" was a character variable including seven regions (Tropical Africa, Europe, Neotropics, North

America, Oceania, Temperate Asia, and Tropical Asia). "island" was a binary variable with 12 plots being on

125 island and 43 plots on mainland. Absolute latitude was used (4 plots were from south hemisphere). To evaluate

the effect of evolutionary history on the incidence of sexual systems across the study plots, we constructed a

phylogenetic tree including all the species of each plot using R package "V.PhyloMaker2" based on the updated

big tree (Jin and Qian, 2019, 2022). We tested phylogenetic signals for plant sexual systems using lambda using

fit.discrete function from R package "geiger" (Pagel, 1999; Pennell et al., 2014). We then compared it with a

130 null model based on lambda = 0 (for star tree) using the likelihood ratio test in R package "picante" (Kembel et

al., 2010). We extracted species ages by taking the pendant branch length from the phylogeny and calculated the

mean species age for each plot (Cadotte and Davies, 2016). The plot area and the number of trees were log-

transformed, while other numeric variables were standardized to the 0-1 range by $(x - x_{\min})/(x_{\max} - x_{\min})$. The

multinomial logistic model was estimated using "multinom" function of R package nnet (Venables and Ripley,

135 2002).

To reduce multicollinearity, we excluded variables that had a variance inflation factor >10 with other

variables and kept variables with the clearest biological meaning. Model selection was conducted using

backward selection procedure by removing terms that were not significant (p-value > 0.05) based on a

likelihood ratio test. Note the multinom function in R does not provide p-values for the regression coefficients;

140   p-values were calculated using the Wald tests (here z-tests). We performed the above analyses for the proportion

of the three sexual systems at species and individual levels, respectively. "species level" means that the

proportion of each sexual system (dioecy, monoecy, or hermaphrodite) was calculated from the incidence of

species having a given sexual system over the total incidence of the three sexual systems, while "individual

level" means the proportion was calculated from the number of stems of species (i.e., abundance) that have a

145   given sexual system over the total number of stems in a plot. The latter requires species abundance data and 45

of our 55 plots had such data.

     All the analyses were conducted using R 4.2.2 (R core team, 2023) and related packages as mentioned

above.

3 Results

150   **3.1 Geographic patterns of plant sexual systems**

The spatial distribution of dioecy, monoecy, and hermaphrodite showed considerable variations on the global

scale (Fig. 1). The proportions of dioecious species and individuals were negatively associated with latitude

(Fig. 2a, b), while the incidence of monoecious species and individuals had a positive association with latitude

(Fig. 2c, d). The negative association with latitude was also observed for the proportions of hermaphroditic

155   species incidences and individuals (Fig. 2e, f). However, when the effects of evolutionary history, plot

characteristics, and local climate were considered, the latitude became unimportant in explaining the variation of

plant sexual systems, as it had high correlations with the region and environmental factors (Table 1, S1). We

found the proportions of dioecious and monoecious species and individuals decreased with elevation, while the

proportions of hermaphroditism increased with elevation both at species and individual levels (Table 1, Fig. 1).

160   **3.2 Region effects on the incidence of plant sexual systems**

The effects of region on the proportion of the three sexual systems were strong even when the effects of

evolutionary history, plot characteristics, and local climate were considered (Table 1, S1). Compared to Africa,

plants were more likely to be monoecious than dioecious, especially in Europe and North America, while in

Oceania and tropical Asia, plants were less likely to be hermaphrodite than dioecious (Table 1). The model

165   including regions, mean species age, elevation, and precipitation of driest month explained 76.9% of the

variance in the incidence of dioecious species and 67.1% of the variance in the incidence of dioecious

individuals (Fig. 3). For monoecy, the model explained 84.3% of the variance in the incidence of species and

87.5% of the variance in the incidence of individuals. The model explained 81.7% of the variance in the

incidence of hermaphroditic species and 80.4% of the variance in the incidence of hermaphroditic individuals.

170   **3.3 Effects of evolutionary history on the incidence of plant sexual systems**

Evolutionary history had significant effects on the proportion of the three sexual systems (Table 1, S1). In most

plots, plants showed significant phylogenetic signals (with lambda significantly>0) in sexual systems. The

phylogenetic signal was also correlated with the proportion of three plant sexual systems (Fig. S2, S3).

However, lambda was not included in the final model as it had high correlations with other factors (Table 1;

175   Table S1). Plants were more like to be dioecy in areas with younger species age, while plants were more likely

to be monoecy in areas with older species age (Table 1; Fig. 4).

3.4 Effects of climate on the incidence of plant sexual systems

Local climate also had significant effects on the proportion of the three sexual systems (Table 1, S1). Plants

were significantly more likely to hermaphrodite than dioecious in areas with high annual potential

180   evapotranspiration and high precipitation seasonality (Fig. 5, S4). Plants were more likely to be dioecious than

monoecious in areas with high precipitation of driest month (Fig. S5).

4 Discussion

Geographic patterns of sexual systems have attracted much interest from evolutionary ecologists because of

their importance in driving patterns of biodiversity and phenotypic variations (Barrett, 2002; Tusiji and Fukami,

185   2020). Based on 55 forest dynamic plots, we documented the biogeographic patterns of sexual systems of

woody flowering plants and tested region and climate effects on the proportion of three sexual systems on a

global scale. We found a significant geographic pattern in the proportion of sexual systems with latitude and

elevation and revealed the importance of region, evolutionary history, and climate effects in determining the

global distribution of sexual systems in woody flowering plants (Bawa, 1980; Arroyo, 1990; Renner and

190   Ricklefs, 1995; Sakai and Weller, 1999; Vamosi and Queenborough, 2010; Wang et al., 2021).

4.1 Region effects on the proportions of plant sexual systems

As stated by Baker's law, dioecy could hinder long-distance colonization because of their disadvantage in reproduction with limited mate partners, while monoecy and hermaphroditism might facilitate their long-distance colonization by self-pollination (Baker, 1955; Pannell et al., 2015). Thus, tropical regions are expected

195   to have higher incidences of dioecy where dioecious plants were likely originated than temperate regions (Bawa 1980; Renner and Ricklefs, 1995; Sakai and Weller, 1999; Renner, 2014). Our study found a high proportion of dioecy in Oceania and tropical Asia (Table 1, S1), which supports the deduction of Baker's law as they are near the possible origin center of dioecy. However, we did not find island effect on the incidence of plant sexual systems (Table 1), which suggests the disadvantage of dioecy might not prevent their colonization on island

200   (Bawa, 1982; Cheptou and Massol, 2009). We also found Europe and North America contain a high proportion of monoecious species (Table 1). Monoecious plants are mostly wind pollinated, which also shows an increased proportion with latitude (Regal, 1982; Friedman and Barrett, 2009; Rech et al., 2016).

As the incidence of plant sexual systems changed with regions, the population density of each sexual system could also change and thus affects the assembly of forest plant communities (Vamosi, 2006; Vamosi and

205   Queenborough, 2010; Réjou-Méchain and Cheptou, 2015). Our results also found significant region and island effects on the proportions of individuals with different sexual systems (Table S1). For example, we found the proportion of dioecious individuals was lower in Europe, while the proportion of monoecious individuals was lower in Oceania and tropical Asia. These observations may explain one of the oldest biogeographic patterns that species composition and the dominance of certain plant families vary markedly across different

210   biogeographic regions (van Humboldt 1816 cited in Cox, 2001). The regions with higher dioecy contain a high proportion of species from Phyllanthaceae, Euphorbiaceae, and Ebenaceae, which are mostly animal pollinated (Aston, 1969; Bawa, 1980; Chen and Li, 2008; Renner, 2014; Zhang and He, 2017). The regions with a high incidence of monoecy in Europe, temperate Asia, and North America contain a high proportion of species from Fagaceae, Betulaceae, and Sapindaceae. Our results suggest that the effect of sexual systems on colonization

215   possibly drives forest community assembly.

4.2 Effects of evolutionary history on the proportion of plant sexual systems

Although documenting and understanding the effects of evolutionary history on geographic patterns of

species diversity (e.g., latitudinal gradient of species diversity) is a major undertaking in ecology (Gaston, 2000; Willig et al., 2003; Schluter and Pennell, 2017), little is known about their role in the geographic distribution of

220   plant sexual systems (but see Wang et al., 2020, 2021). Our study showed plants in regions with younger species age are more likely to be dioecious than monoecy (Table 1; Fig. 4). These results further support Baker's law, which suggests plants are more likely to be dioecy with young species age (Baker, 1955; Sakai, 1995; Pannell et al., 2015). However, these results do not support a recent study that suggests woody flowering plants in China are more likely to be dioecy in areas with old flora (Wang et al., 2020). One possible reason is the effect of age

225   on plant sexual systems could be confounded with other regional processes and climate factors, which Wang et al. (2020) didn't consider.

4.3 Climate effects on the proportion of plant sexual systems

The effects of local climate on sexual systems have been found in several studies (Sakai and Weller, 1999; Ashman, 2006; Wang et al., 2021). We found that plants were less likely to be hermaphrodite than dioecious in

230   areas with high annual potential evapotranspiration and high precipitation seasonality, while plants were more likely to be dioecious than monoecious in areas with high precipitation of driest month (Table 1, Fig. 5, S4, S5). This result does not support that dioecy survives better in a drier environment as sexual function separates (Sakai and Weller 1999; Ashman 2006; Wang et al. 2021). As dioecious plants are disadvantageous in colonization, we thus expect that they could shift in the flowering phenology rather than habitat from

235   hermaphrodite and monoecy. Previous studies found that dioecious plants are more likely to flower in the dry season than hermaphrodite and monoecy, thus precipitation of driest month could be a limited factor for dioecy but not for hermaphrodite and monoecy (Kang and Bawa, 2003; Zhang and He, 2021). For monoecious plants, they may favor low precipitation when they are flowering in the dry season because most of them are wind pollinated (Regal, 1982; De jong et al., 2008; Rech et al., 2016). Our results highlight the role of precipitation in

240   determining the distribution of plant sexual systems. Precipitation (BIO14 and BIO15) could also affect the proportion of individuals with different sexual systems (Fig. 4; Table S1), through their effects on pollination and physiological processes, thus affecting the assembly of forest community (Regal, 1982; Friedman and Barrett, 2009; Zhang and He, 2021).

5 Conclusions

245   In summary, our study showed significant effects of region, evolutionary history, and climate on the geographic patterns of sexual systems in woody flowering plants on a global scale. Regional processes and local climate must be considered together for understanding the geographic pattern of plant sexual systems. We see the need to collect more extensive data on plant sexual systems that include information on pollination modes and flowering phenology to further disentangle the mechanisms in determining the geographic patterns of sexual

250   systems and their influence on the assembly and dynamics of forest plant communities.

Data availability. Data on the species information and sexual systems, the plot information, and the climate variables for the 55 ForestGEO plots that support the findings of this study are available on GitHub (https://github.com/Minhua322/plant-sex-system).

Author contributions. F.H. designed the study. M.Z. and X.H. collected and analyzed data. M.Z. and F.H. wrote

255   the paper.

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

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392 **Table 1** The results of multinomial logistic model for the proportion of dioecious, monoecious, and hermaphrodite species of

393 woody flowering plants. Dioecy was set as the baseline system. M and H represent monoecy and hermaphrodite,

394 respectively. The region effects were coded in reference to Tropical Africa. *P* values indicate the significance of the z test.

Explanatory variables		Coefficient (SE)		$P(>|z|)$ value	
		M (β_2)	H (β_3)	M	H
Intercept		-0.815 (0.257)	0.450 (0.188)	**1.52e-3**	**0.017**
Region	Europe	2.058 (0.456)	0.021 (0.454)	**6.43e-6**	0.963
	Neotropical	0.362 (0.152)	0.054 (0.103)	**0.017**	0.599
	North America	1.402 (0.230)	-0.150 (0.194)	**1.05e-9**	0.439
	Oceania	0.681 (0.171)	-0.574 (0.120)	**6.97e-5**	**1.79e-6**
	Temperate Asia	0.415 (0.141)	-0.296 (0.097)	**3.24e-3**	**2.29e-3**
	Tropical Asia	0.264 (0.137)	-0.504 (0.093)	0.053	**5.34e-8**
Mean species age		0.779 (0.346)	0.276 (0.262)	**0.024**	0.292
Elevation		-0.066 (0.253)	0.471 (0.183)	0.795	**0.010**
PET		0.126 (0.255)	0.552 (0.183)	0.622	**2.55e-3**
Precipitation of driest month (BIO14)		-0.946 (0.235)	0.134 (0.167)	**5.68e-5**	0.422
Precipitation seasonality (BIO15)		-0.026 (0.326)	0.526 (0.243)	0.938	**0.030**

395
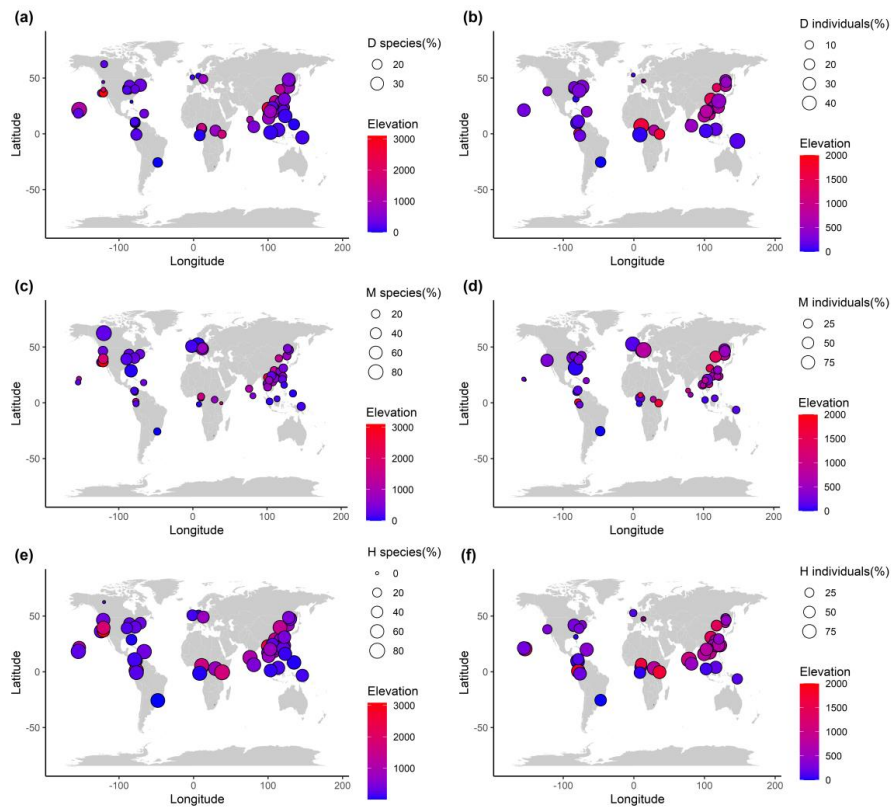
Figure 1. Global distribution of the three sexual systems of woody flowering plants across the study plots.

(a), (c) and (e) are for the proportions of the sexual systems at the species level, and (b), (d), and (f) are for

the proportion at the individual level. D, M, and H represent dioecy, monoecy, and hermaphrodite,

respectively. Note data on the incidence of species sexual systems were available for all 55 plots (i.e., the

species level), while only 45 of the plots had data on species abundance (i.e., the individual level).
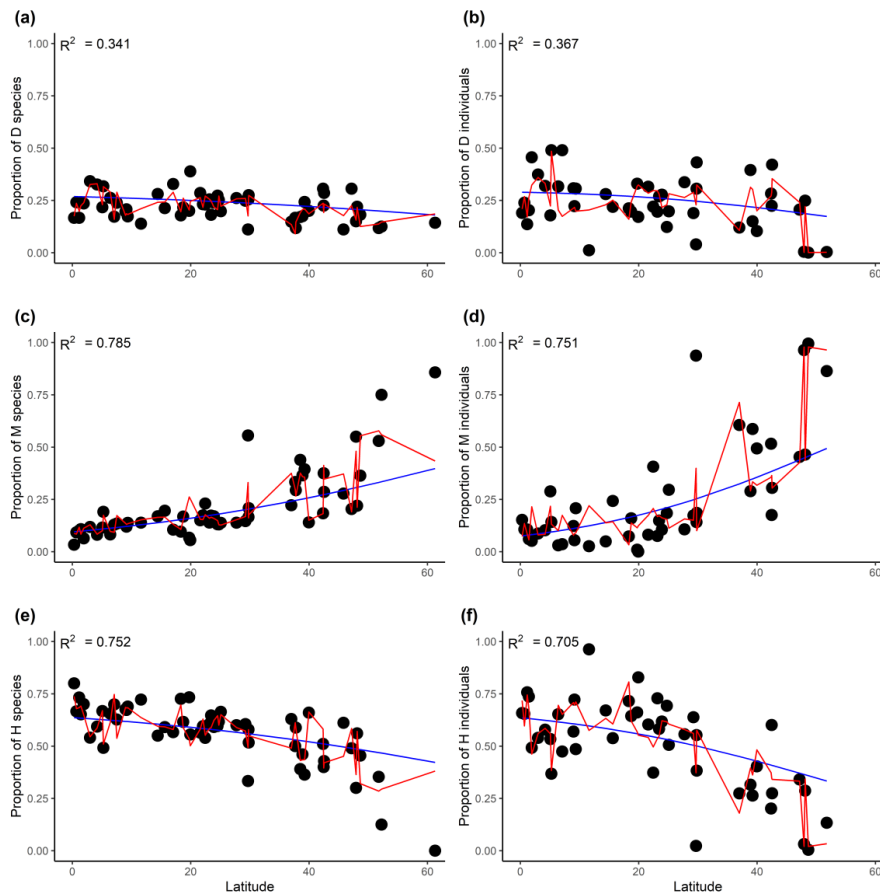
Figure 2. The relationships between the proportion of flowering plants with different sexual systems and latitude. (a), (c) and (e) are for the proportions of species of different sexual systems, and (b), (d), and (f) are for the proportion of the individuals of different sexual systems. D, M, and H represent dioecy, monoecy, and hermaphrodite, respectively. The smooth blue lines are the multinomial logistic model that only included latitude as the explanatory variable (no other variables were included). The red curves are the fitted proportions of the best selected model (i.e., the model presented in Table 1 and S3 for species and individuals, respectively). R^2 values for the model only including latitude are given in each panel.
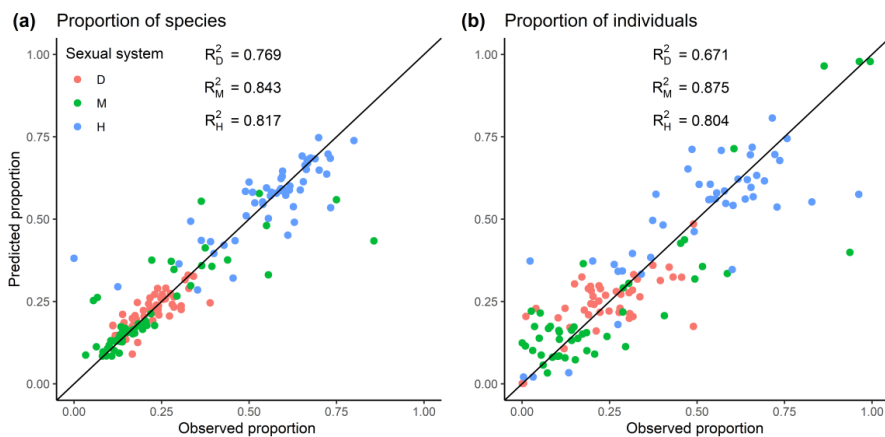
Figure 3. The best selected multinomial logistic models showing the relationships between the observed proportion and the proportion predicted from the best multinomial logistic models for (a) species, and (b) individuals, respectively. D, M, and H represent dioecy, monoecy, and hermaphrodite, respectively. R^2 values for the models are given in each panel.
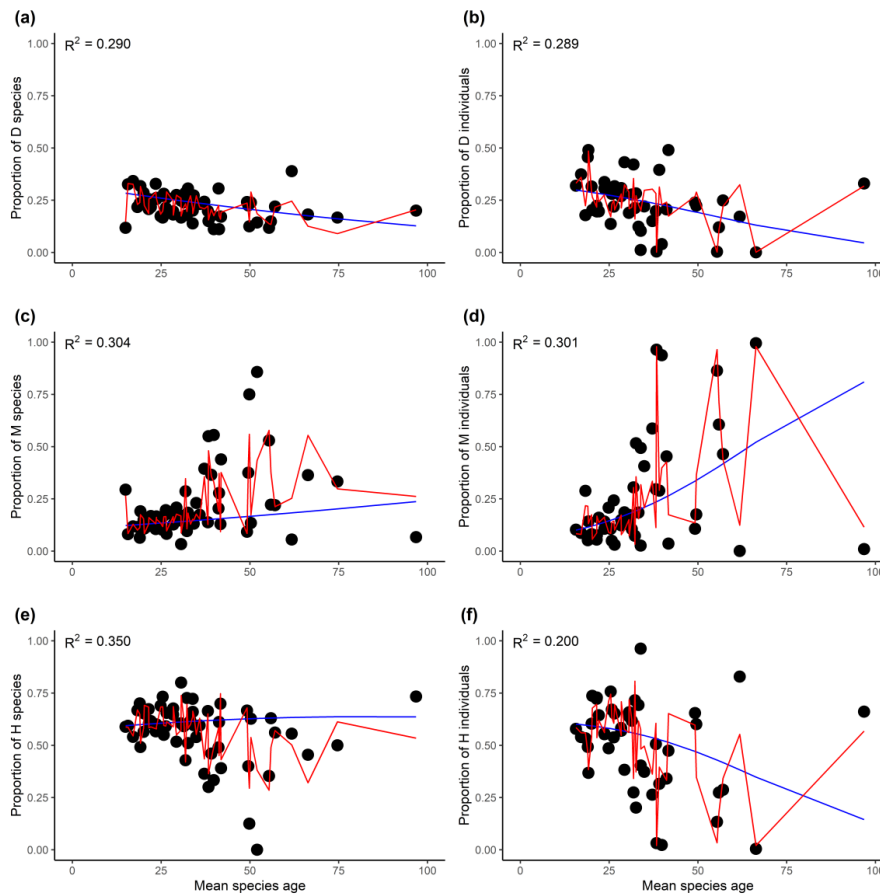
Figure 4. The relationships between the proportion of flowering plants with different sexual systems and mean species age (millions of years). (a), (c) and (e) are for the proportion of species, and (b), (d), and (f) are for the proportion of the individual. D, M, and H represent dioecy, monoecy, and hermaphrodite, respectively. The blue line is the multinomial logistic model that only includes mean species age as the explanatory variable (no other variables are included). The red curves are the fitted proportions based on the best selected model, i.e., the model presented in Table 1 and S1 for species and individuals, respectively. R^2 values associated with models only including mean species age are given in each panel.
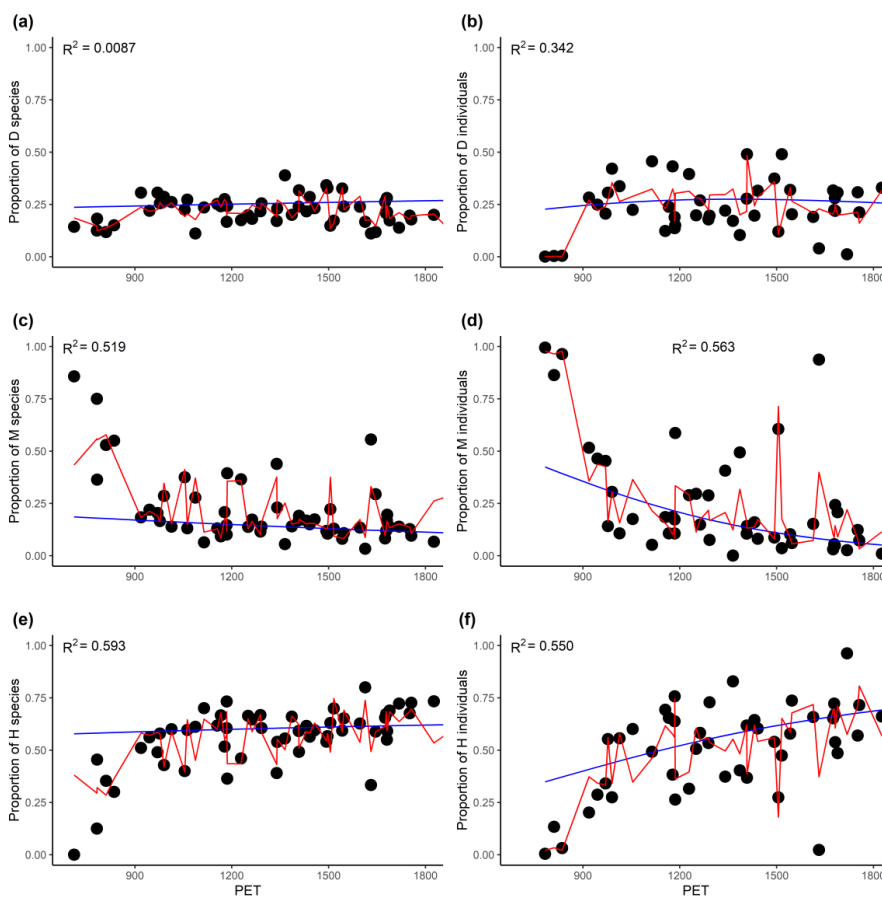
Figure 5. The relationships between the proportion of flowering plants with different sexual systems and annual potential evapotranspiration (PET). (a), (c) and (e) are for the proportion of species, and (b), (d), and (f) are for the proportion of the individual. D, M, and H represent dioecy, monoecy, and hermaphrodite, respectively. The blue line is the multinomial logistic model that only includes PET as the explanatory variable (no other variables are included). The red curves are the fitted proportions based on the best selected model, i.e., the model presented in Table 1 and S1 for species and individuals, respectively. R^2 values associated with models only including PET are given in each panel.