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

Minhua Zhang[1], Xiaoqing Hu[2], Fangliang He[1,3]*

[1]*ECNU-Alberta Joint Lab for Biodiversity Study, Tiantong Forest Ecosystem National Observation and Research Station, School of Ecological and Environmental Sciences, East China Normal University, Shanghai, China, 200241*

[2]*School of Life Sciences, Sun Yat-sen University, Guangzhou, China, 510275*

[3]*Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada T6G 2H1*

Correspondence: Fangliang He (fhe@ualberta.ca)

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 dioecious, monoecious, and hermaphroditic species count and abundance while incorporating evolutionary history and local climate factors. Our results showed that plants were more likely to be dioecious than hermaphroditic in Oceania and Tropical Asia, but were more likely to be monoecious than dioecious in Europe and North America compared with Tropical Africa. We further found plants were more likely to be monoecious than dioecious in island communities. Plants were more likely to be monoecious than dioecious in areas with high precipitation but were more likely to be dioecious than monoecious in areas with high precipitation of coldest quarter. 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

Plants display varieties of sexual systems, which are known to play important roles in species evolution,

25   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

but also hinders our ability to understand and predict their influence on biodiversity maintenance and

30   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

same individuals), and hermaphroditism (having both male and female parts in the same flower). Although

35   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). The proportion of hermaphroditism could be higher in tropical forests than in temperate forests as

40   precipitation and the proportion of biotic pollination decrease with latitude. These former studies do not agree

on the effects of elevations on the distribution of the three sexual systems. Dioecy and monoecy could both

show high incidence in lowland forest communities and thus hermaphroditism increased towards high elevation

(Baker and Cox, 1984; Queenborough and Vamosi, 2010; but see Arroyo and Squeo, 1990). These geographic

patterns are challenged by subsequent studies with more extended data and phylogenetic analyses (Vamosi et al.,

45   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

distance dispersal (Baker, 1955; Pannell et al., 2015), we would expect regions with different geographic and

50   evolutionary histories could thus have different compositions of plant sexual systems (Ashton, 1967; Rickleffs

and He, 2016; Zhang et al., 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). Supposing abiotic and biotic conditions are equal, dioecious plant species would have lower relative incidence in temperate regions, e.g., Europe and North America than in tropical regions, e.g., Tropical Asia and

55 Oceania, compared with other sexual systems, due to the expected low colonization rates of dioecious plants in temperate regions. In contrast, because dioecy could also be newly evolved from other sexual systems after colonization (Baker and Cox, 1984; Sakai, 1995), areas with younger species age are expected 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

60 history on the incidences of plant sexual systems to 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 hermaphroditism favors 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 dynamics plots 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

80 shaping geographic patterns. We would expect that plants are more likely to be dioecious than hermaphroditic in tropical and adjacent regions, e.g., Tropical Asia and Oceania compared with other regions. We would also

expect plants more likely to be monoecious than dioecious in temperate regions, e.g., Europe and North America compared with other regions. We would also expect that plants in areas with younger species ages and lower precipitation are more likely to be dioecious than hermaphroditic and monoecious.

2 Methods

2.1 Data sources

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/).

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: 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 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 stems, 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

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), an evolutionary factor (mean species age), three plot characteristics (number of species, number of trees, area), and 22 climate factors (MAT, MAP, PET, and 19 bioclimate variables). We also consider the interactive term between mena species age and MAP in the models. In each plot, a species can only be either dioecious, monoecious, or hermaphroditic, leading to $\pi_1 + \pi_2 + \pi_3 = 1$. This is a multinomial logistic regression model where the dependent variable is a nominal with three levels (dioecy, monoecy, and hermaphroditism). The multinomial logistic model has the form:

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

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

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

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 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 the "fitDiscrete" function from R package *geiger* (Pagel, 1999; Pennell et al., 2014). We then compared it with a 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 number of species, number of trees and plot area 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, 2002).

To reduce multicollinearity, we first excluded bioclimate variables with pairwise Pearson correlation coefficients >0.95 and then excluded variables that had a variance inflation factor >10 with other variables and kept variables with the clearest biological meaning (Table S1, S2). Note the "multinom" function in R does not

provide *p*-values for the regression coefficients; *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 hermaphroditism) 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 trees of species (i.e., abundance) that have a given sexual system over the total number of trees 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

3.1 Geographic patterns of plant sexual systems

The spatial distribution of dioecy, monoecy, and hermaphroditism showed considerable variations on the global scale (Fig. 1). The proportions of dioecious species and individuals were negatively associated with latitude (Fig. S1a, b), while the incidence of monoecious species and individuals had a positive association with latitude (Fig. S1c, d). The negative association with latitude was also observed for the proportions of hermaphroditic species incidences and individuals (Fig. S1e, f). However, when the effects of region, plot characteristics, and climate factors were considered, the latitude variable was not retained in the final model, as it was closely correlated with the region and environmental factors (Table 1, S2). The effects of elevation on the proportions of plant sexual systems was not significant either at the species level or individual level when other variables were included (Table 1, S2).

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, S3). Compared to Tropical 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 hermaphroditic than dioecious (Table 1). Plants were more likely to be monoecious than dioecious in island communities compared with mainland communities. We also found plants were more likely to be dioecious in areas of high species richness (Table 1). The model including regional and local factors explained 74.6% of the variance in the incidence of dioecious species and 68.2% of the variance in the incidence of dioecious individuals (Fig. 2; Table 1, S3). For monoecy, the model explained 87.2% of the variance in the incidence of species and 82.3% of the variance in the incidence of

individuals. The model explained 81.0% of the variance in the incidence of hermaphroditic species and 69.6% of the variance in the incidence of hermaphroditic individuals.

3.3 Effects of evolutionary history and climate 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 (https://github.com/Minhua322/plant-sex-system). Plants were more likely to be dioecious in areas with younger species age, while more likely to be monoecious in areas with older species age (Fig. 3). But the effect of mean species age was not significant when including other varibles, while the interactive term between mean species age and mean annual precipitation showed negative effects on the proportion of monoecy (Table 1). Local climate also had significant effects on the proportion of the three sexual systems (Table 1, S1). Plants were significantly more likely to be monoecious than dioecious in areas with high annual potential precipitation (Fig. 4). Plants were more likely to be dioecious than to be monoecious in areas with high precipitation of coldest quarter (Fig. S3).

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, 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 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). As temperate plant communities have been assembled from tropical flora (Qian and Ricklefs 2016), tropical and the nearby regions where dioecy originated are expected to have higher incidences of dioecy 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, S3), which supports the deduction of Baker's law on the dispersal limitation effect on

dioecy. We also found Europe and North America contain a high proportion of monoecious species (Table 1). Monoecious plants are mostly wind pollinated; they also show an increased proportion with latitude (Regal, 1982; Friedman and Barrett, 2009; Rech et al., 2016). Furthermore, we found an island effect on the incidence of plant sexual systems (Table 1), suggesting the disadvantage of dioecy might prevent their colonization on island.

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 Queenborough, 2010; Réjou-Méchain and Cheptou, 2015). Our results also found significant region effects on the proportions of individuals with different sexual systems (Table S3). For example, we found the proportion of dioecious individuals was lower in Europe, while the proportion of monoecious individuals was lower in Oceania. These observations may explain one of the oldest biogeographic patterns that species composition and the dominance of certain plant families vary markedly across different 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 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 plant sexual systems (but see Wang et al., 2020, 2021). Our study showed plants in regions of younger species age are more likely to be dioecious than monoecious (Fig. 3). These results suggested evolutionary processes might dimmish the effect of Baker's law (Baker, 1955; Sakai, 1995; Pannell et al., 2015). However, the effects of age were not significant after including other regional and local factors. The effect of species age on plant sexual systems was different at regional and global scales (Wang et al., 2020), which could be explained by the interactive effects between species age and precipitation across different regions.

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 more likely to be monoecious than dioecious in areas with high annual precipitation, while plants were more likely to be dioecious than monoecious in areas with high precipitation of coldest quarter (Table 1, Fig.4, S3). This result does 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 hermaphroditism and monoecy. Previous studies found that dioecious plants are more likely to flower in the dry season with low temperature than hermaphroditism and monoecy, thus precipitation of coldest quarter could be a limited factor for dioecy but not for monoecy and hermaphroditism (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 determining the distribution of plant sexual systems, 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

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 such as long-distance dispersal, the evolution of sexual systems after colonization, and local climate, e.g., precipitation, together could shape the global distribution 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 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 the paper.

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

Acknowledgements. We thank colleagues of the ForestGEO network for kindly providing us with their plot data. We thank ForestGEO for organizing the 2018 Analytical Workshop in the Czech Republic, from which we received valuable feedback on the present study.

Financial support. This study was funded by the National Natural Science Foundation of China (31901105), the Fundamental Research Funds for the Central Universities, the ECNU-Albert joint lab for Biodiversity Studies, and the NSERC (Canada).

References

265   Ashton, P. S.: Speciation among tropical forest trees: some deductions in the light of recent evidence, Biol. J. Linn. Soc., 1, 155–196, https://doi.org/10.1111/j.1095-8312.1969.tb01818.x, 1969.

Arroyo, M. T. K., and Squeo F. A.: Relationship between plant breeding systems and pollination. In: Biological approaches and evolutionary trends in plants, edited by: S. Kawano. Academic Press, London, 205–227, https://doi.org/10.1016/B978-0-12-402960-6.50004-4, 1990.

270   Ashman, T.: The evolution of separate sexes: a focus on the ecological context. In: Ecology and Evolution of Flowers, edited by: Harder L. D, and S. C. H. Barrett. Oxford University Press, Oxford, 204–222, ISBN 97801985708519780198570868, 2006.

Baker, H. G.: Self-Compatibility and Establishment After 'Long-Distance' Dispersal, Evolution., 9, 347–349, https://doi.org/10.2307/2405656, 1955.

275   Baker, H. G. and Cox, P. A.: Further Thoughts on Dioecism and Islands, Ann. Missouri Bot. Gard., 71, 244, https://doi.org/10.2307/2399068, 1984.

Barrett, S. C. H.: The evolution of plant sexual diversity, Nat. Rev. Genet., 3, 274–284, https://doi.org/10.1038/nrg776, 2002.

Barry Cox, C.: The biogeographic regions reconsidered, J. Biogeogr., 28, 511–523,

280   https://doi.org/10.1046/j.1365-2699.2001.00566.x, 2001.

Bawa, K. S.: Evolution of Dioecy in Flowering Plants, Annu. Rev. Ecol. Syst., 11, 15–39, https://doi.org/10.1146/annurev.es.11.110180.000311, 1980.

Bawa, K. S.: Outcrossing and the Incidence of Dioecism in Island Floras, Am. Nat., 119, 866–871, https://doi.org/10.1086/283960, 1982.

285   Bawa, K. S. and Opler, P. A.: Dioecism in Tropical Forest Trees, Evolution (N. Y)., 29, 167, https://doi.org/10.2307/2407150, 1975.

Cadotte, M. W., and Davies T. J. (Eds.): Phylogenies in ecology: a guide to concepts and methods. Princeton University Press, Princeton, NJ, ISBN 9780691157689, 2016.

Cardoso, J. C. F., Viana, M. L., Matias, R., Furtado, M. T., Caetano, A. P. de S., Consolaro, H., and Brito, V. L.

G. de: Towards a unified terminology for angiosperm reproductive system, Acta Bot. Brasilica, 32, 329–

348, https://doi.org/10.1590/0102-33062018abb0124, 2018.

Charlesworth, D.: Evolution of Plant Breeding Systems, Curr. Biol., 16, R726-35,

https://doi.org/10.1016/j.cub.2006.07.068, 5 September 2006.

Chen, X.-S. and Li, Q.-J.: Patterns of plant sexual systems in subtropical evergreen broad-leaved forests in Ailao

Mountains, SW China, J. Plant Ecol., 1, 179–185, https://doi.org/10.1093/jpe/rtn019, 2008.

Cheptou, P. and Massol, F.: Pollination Fluctuations Drive Evolutionary Syndromes Linking Dispersal and

Mating System, Am. Nat., 174, 46–55, https://doi.org/10.1086/599303, 2009.

Condit, R. S.: Tropical Forest Census Plots-Methods and Results from Barro Colorado Island, Panama and a

Comparison with Other Plots. Springer‐Verlag and R G. Landes Company, Berlin and Georgetown, TX,

ISBN 3540641440, 1998.

Cronk, Q.: The distribution of sexual function in the flowering plant: from monoecy to dioecy, Philos. Trans. R.

Soc. B Biol. Sci., 377, https://doi.org/10.1098/rstb.2021.0486, 2022.

Davies, S. J., Abiem, I., Abu Salim, K., Aguilar, S., Allen, D., Alonso, A., Anderson-Teixeira, K., Andrade, A.,

Arellano, G., Ashton, P. S., Baker, P. J., Baker, M. E., Baltzer, J. L., Basset, Y., Bissiengou, P., Bohlman, S.,

Bourg, N. A., Brockelman, W. Y., Bunyavejchewin, S., Burslem, D. F. R. P., Cao, M., Cárdenas, D., Chang,

L.-W., Chang-Yang, C.-H., Chao, K.-J., Chao, W.-C., Chapman, H., Chen, Y.-Y., Chisholm, R. A., Chu, C.,

Chuyong, G., Clay, K., Comita, L. S., Condit, R., Cordell, S., Dattaraja, H. S., de Oliveira, A. A., den

Ouden, J., Detto, M., Dick, C., Du, X., Duque, Á., Ediriweera, S., Ellis, E. C., Obiang, N. L. E., Esufali, S.,

Ewango, C. E. N., Fernando, E. S., Filip, J., Fischer, G. A., Foster, R., Giambelluca, T., Giardina, C.,

Gilbert, G. S., Gonzalez-Akre, E., Gunatilleke, I. A. U. N., Gunatilleke, C. V. S., Hao, Z., Hau, B. C. H.,

He, F., Ni, H., Howe, R. W., Hubbell, S. P., Huth, A., Inman-Narahari, F., Itoh, A., Janík, D., Jansen, P. A.,

Jiang, M., Johnson, D. J., Jones, F. A., Kanzaki, M., Kenfack, D., Kiratiprayoon, S., Král, K., Krizel, L.,

Lao, S., Larson, A. J., Li, Y., Li, X., Litton, C. M., Liu, Y., Liu, S., Lum, S. K. Y., Luskin, M. S., Lutz, J. A.,

Luu, H. T., Ma, K., Makana, J.-R., Malhi, Y., Martin, A., McCarthy, C., McMahon, S. M., McShea, W. J.,

Memiaghe, H., Mi, X., Mitre, D., Mohamad, M., Monks, L., et al.: ForestGEO: Understanding forest

diversity and dynamics through a global observatory network, Biol. Conserv., 253, 108907,

https://doi.org/10.1016/j.biocon.2020.108907, 2021.

De Jong, T. J., Shmida, A., and Thuijsman, F.: Sex allocation in plants and the evolution of monoecy, Evol. Ecol. Res., 10, 1087–1109, 2008.

320 Etterson, J. R. and Mazer, S. J.: How climate change affects plants' sex lives, https://doi.org/10.1126/science.aag1624, 2016.

Friedman, J. and Barrett, S. C. H.: Wind of change: New insights on the ecology and evolution of pollination and mating in wind-pollinated plants, Ann. Bot., 103, 1515–1527, https://doi.org/10.1093/aob/mcp035, 2009.

325 Gaston K.J.: Global patterns in biodiversity, Nature, 405, 220–227, 2000.

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

Jin, Y. and Qian, H.: V.PhyloMaker: an R package that can generate very large phylogenies for vascular plants, Ecography., 1–7, https://doi.org/10.1111/ecog.04434, 2019.

330 Jin, Y. and Qian, H.: V.PhyloMaker2: An updated and enlarged R package that can generate very large phylogenies for vascular plants, Plant Divers., 44, 335–339, https://doi.org/10.1016/j.pld.2022.05.005, 2022.

Kang, H. and Bawa, K. S.: Effects of successional status, habit, sexual systems, and pollinators on flowering patterns in tropical rain forest trees, Am. J. Bot., 90, 865–876, https://doi.org/10.3732/ajb.90.6.865, 2003.

335 Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P., and Webb, C. O.: Picante: R tools for integrating phylogenies and ecology, Bioinformatics, 26, 1463–1464, https://doi.org/10.1093/bioinformatics/btq166, 2010.

Pagel, M.: Inferring the historical patterns of biological evolution, Nature, 401, 877–884, 1999.

Pannell, J. R., Auld, J. R., Brandvain, Y., Burd, M., Busch, J. W., Cheptou, P. O., Conner, J. K., Goldberg, E. E., 340 Grant, A. G., Grossenbacher, D. L., Hovick, S. M., Igic, B., Kalisz, S., Petanidou, T., Randle, A. M., de Casas, R. R., Pauw, A., Vamosi, J. C., and Winn, A. A.: The scope of Baker's law, New Phytol., 208, 656-667, https://doi.org/10.1111/nph.13539, 2015.

Pennell, M. W., Eastman, J. M., Slater, G. J., Brown, J. W., Uyeda, J. C., Fitzjohn, R. G., Alfaro, M. E., and Harmon, L. J.: Geiger v2.0: An expanded suite of methods for fitting macroevolutionary models to 345 phylogenetic trees, Bioinformatics, 30, 2216–2218, https://doi.org/10.1093/bioinformatics/btu181, 2014.

Qian, H. and Ricklefs, R. E.: Out of the tropical lowlands: latitude versus elevation, Trends Ecol. Evol., 31, 738–741, https://doi.org/10.1016/j.tree.2016.07.012, 2016.

R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, https://www.R-project.org/, 2023.

350   Rech, A. R., Dalsgaard, B., Sandel, B., Sonne, J., Svenning, J. C., Holmes, N., and Ollerton, J.: The macroecology of animal versus wind pollination: ecological factors are more important than historical climate stability, Plant Ecol. Divers., 9, 253–262, https://doi.org/10.1080/17550874.2016.1207722, 2016.

Regal, P. J.: Pollination by wind and animals: ecology of geographic patterns., Annu. Rev. Ecol. Syst. Vol. 13, 497–524, https://doi.org/10.1146/annurev.es.13.110182.002433, 1982.

355   Réjou-Méchain, M. and Cheptou, P. O.: High incidence of dioecy in young successional tropical forests, J. Ecol., 103, 725–732, https://doi.org/10.1111/1365-2745.12393, 2015.

Renner, S. and Ricklefs, R.: Dioecy and its correlates in the flowering plants, Am. J. Bot., 82, 596–606, 1995.

Renner, S. S.: The relative and absolute frequencies of angiosperm sexual systems: Dioecy, monoecy, gynodioecy, and an updated online database, Am. J. Bot., 101, 1588–1596,

360   https://doi.org/10.3732/ajb.1400196, 2014.

Ricklefs, R. E. and He, F.: Region effects influence local tree species diversity, Proc. Natl. Acad. Sci., 113, 674–679, https://doi.org/10.1073/pnas.1523683113, 2016.

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

365   Sakai, A. K., and S. G. Weller: Gender and Sexual Dimorphism in Flowering Plants: A review of Terminology, Biogeographic Patterns, Ecological Correlates, and Phylogenetic Approaches. In: Gender and Sexual Dimorphism in Flowering Plants, edited by: Geber, M. A., T. E. Dawson, and L. F. Delph. Springer-Verlag, Berlin Heidelberg, 1–31, https://link.springer.com/chapter/10.1007/978-3-662-03908-3_1, 1999.

Schluter, D. and Pennell, M. W.: Speciation gradients and the distribution of biodiversity, Nature, 546, 48–55,

370   https://doi.org/10.1038/nature22897, 2017.

Tsuji, K. and Fukami, T.: Sexual Dimorphism and Species Diversity: from Clades to Sites, Trends Ecol. Evol., 35, 105–114, https://doi.org/10.1016/j.tree.2019.09.001, 2020.

Vamosi, J. C., Otto, S. P., and Barrett, S. C. H.: Phylogenetic analysis of the ecological correlates of dioecy in angiosperms., J. Evol. Biol., 16, 1006–18, 2003.

375   Vamosi, S. M.: A Reconsideration of the Reproductive Biology of the Atlantic Forest in the Volta Velha Reserve, Biodivers. Conserv., 15, 1417–1424, https://doi.org/10.1007/s10531-005-0308-4, 2006.

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

380   Venables, W. N., and Ripley B. D.: Modern Applied Statistics with S, 4th ed. Springer, New York, NY, ISBN
978-1-4899-2821-4, 2002.

Wang, Y., Luo, A., Lyu, T., Dimitrov, D., Xu, X., Freckleton, R. P., Li, Y., Su, X., Li, Y., Liu, Y., Sandanov, D.,
Li, Q., Hao, Z., Liu, S., and Wang, Z.: Global distribution and evolutionary transitions of angiosperm
sexual systems, Ecol. Lett., 24, 1835–1847, https://doi.org/10.1111/ele.13815, 2021.

385   Wang, Y., Lyu, T., Shrestha, N., Lyu, L., Li, Y., Schmid, B., Freckleton, R. P., Dimitrov, D., Liu, S., Hao, Z., and
Wang, Z.: Drivers of large-scale geographical variation in sexual systems of woody plants, Glob. Ecol.
Biogeogr., 29, 546–557, https://doi.org/10.1111/geb.13052, 2020.

Willig, M. R., Kaufman, D. M., and Stevens, R. D.: Latitudinal Gradients of Biodiversity: Pattern, Process,
Scale, and Synthesis, Annu. Rev. Ecol. Evol. Syst., 34, 273–309,

390   https://doi.org/10.1146/annurev.ecolsys.34.012103.144032, 2003.

Zhang, J., Nielsen, S. E., Mao, L., Chen, S., and Svenning, J. C.: Regional and historical factors supplement
current climate in shaping global forest canopy height, J. Ecol., 104, 469–478,
https://doi.org/10.1111/1365-2745.12510, 2016.

Zhang, M. and He, F.: Plant sex affects the structure of plant–pollinator networks in a subtropical forest,

395   Oecologia, 185, 269–279, https://doi.org/10.1007/s00442-017-3942-0, 2017.

Zhang, M. and He, F.: Plant breeding systems influence the seasonal dynamics of plant-pollinator networks in a
subtropical forest, Oecologia, 195, 751–758, https://doi.org/10.1007/s00442-021-04863-5, 2021.

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

399   of woody flowering plants. Dioecy was set as the baseline system. M and H represent monoecy and hermaphroditism,

400   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		-0.359 (0.637)	1.711 (0.445)	0.573	**1.23*e*-4**
Region	Europe	1.491 (0.456)	-0.725 (0.456)	**1.07*e*-3**	0.111
	Neotropical	0.390 (0.163)	0.142 (0.110)	**0.017**	0.196
	North America	1.050 (0.246)	-0.554 (0.204)	**2.01*e*-5**	**6.68*e*-3**
	Oceania	0.473 (0.198)	-0.641 (0.140)	**0.017**	**4.40*e*-6**
	Temperate Asia	0.230 (0.163)	-0.409 (0.112)	0.158	**2.58*e*-4**
	Tropical Asia	0.239 (0.148)	-0.361 (0.099)	0.108	**2.45*e*-4**
Island		0.304 (0.125)	-0.041 (0.083)	**0.015**	0.625
Mean species age		1.049 (0.677)	0.440 (0.550)	0.121	0.423
Elevation		-0.128 (0.274)	0.296 (0.199)	0.641	0.137
Number of species		-0.170 (0.091)	-0.139 (0.065)	0.062	**0.032**
Number of trees		0.010 (0.064)	7.52 *e*-3 (0.046)	0.875	0.869
MAP (mean annual precipitation)		0.838 (0.347)	0.261 (0.239)	**0.016**	0.274
Mean species age×MAP		-2.658 (1.493)	-0.927 (1.155)	0.075	0.422
Precipitation of warmest quarter (BIO18)		0.012 (0.354)	0.083 (0.253)	0.973	0.744
Precipitation of coldest quarter (BIO19)		-0.675 (0.217)	-0.106 (0.151)	**1.88*e*-3**	0.482

401
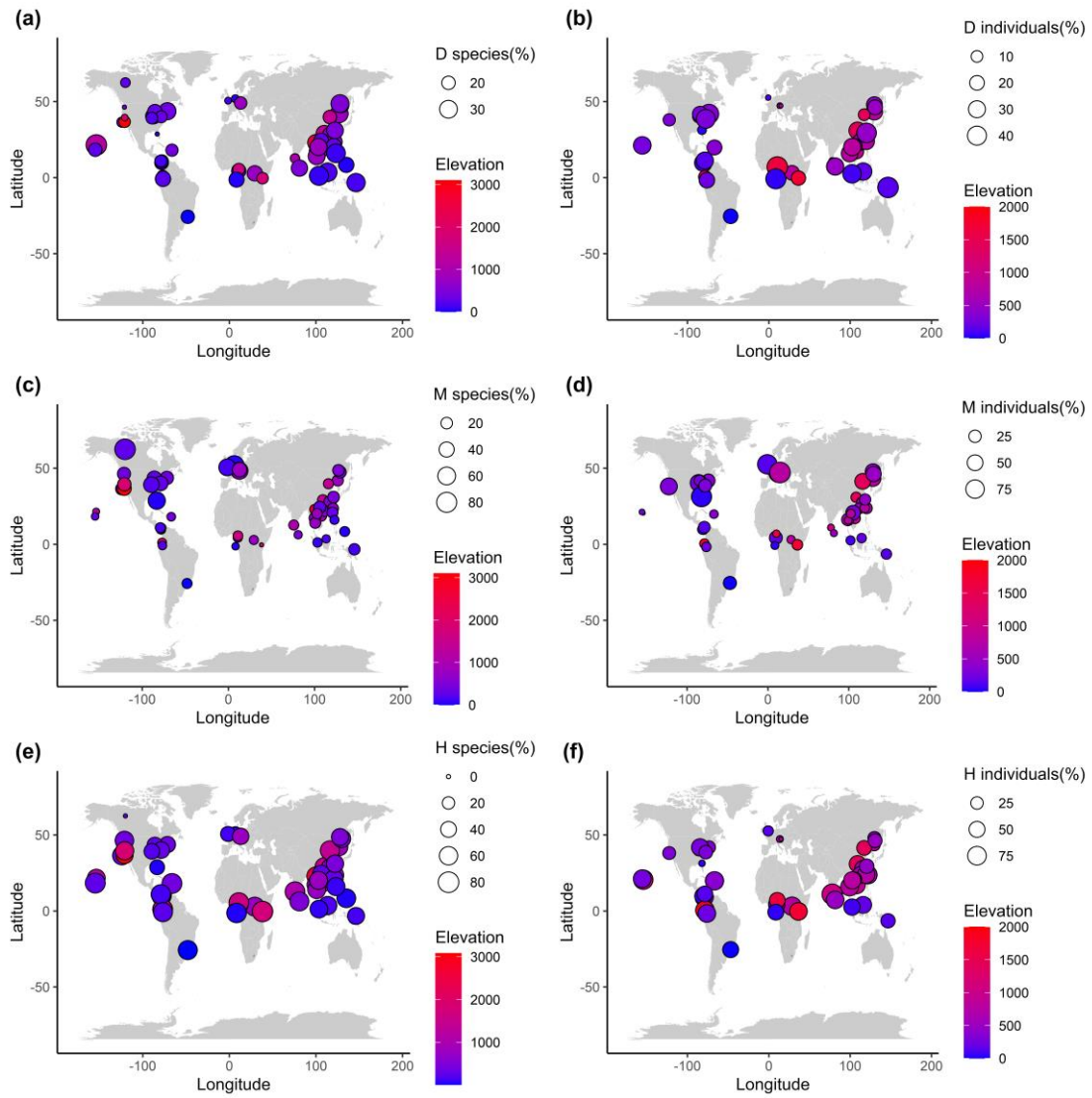
Figure 1. Global distribution of the three sexual systems of woody flowering plants across the study plots.

(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 hermaphroditism,

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).
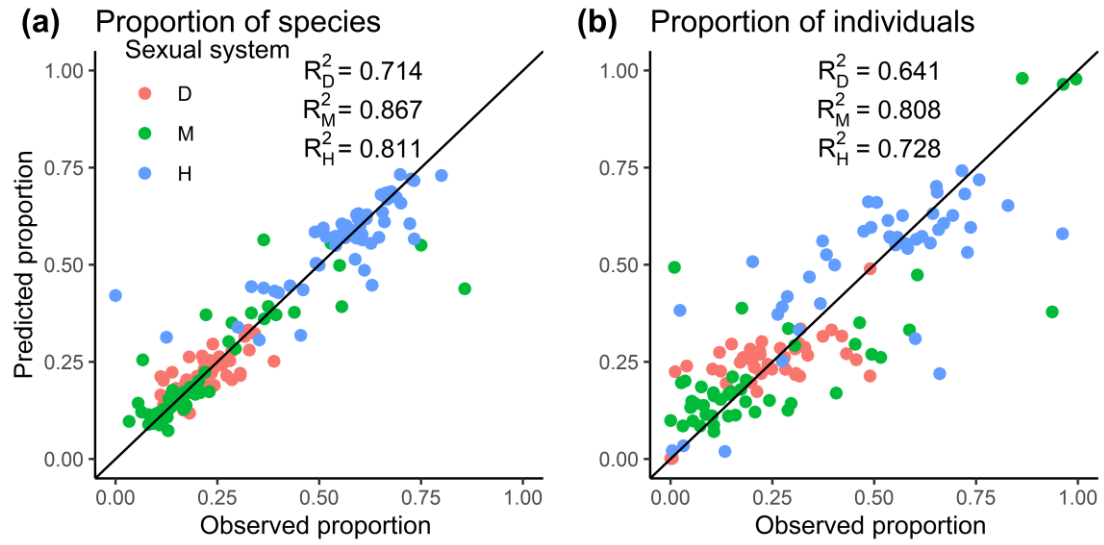
Figure 2. The best selected multinomial logistic models showing the relationships between the observed proportion and the proportion predicted from the best multinomial logistic models for (a) species, and (b) individuals, respectively. D, M, and H represent dioecy, monoecy, and hermaphroditism, respectively. *R²* values for the models are given in each panel.
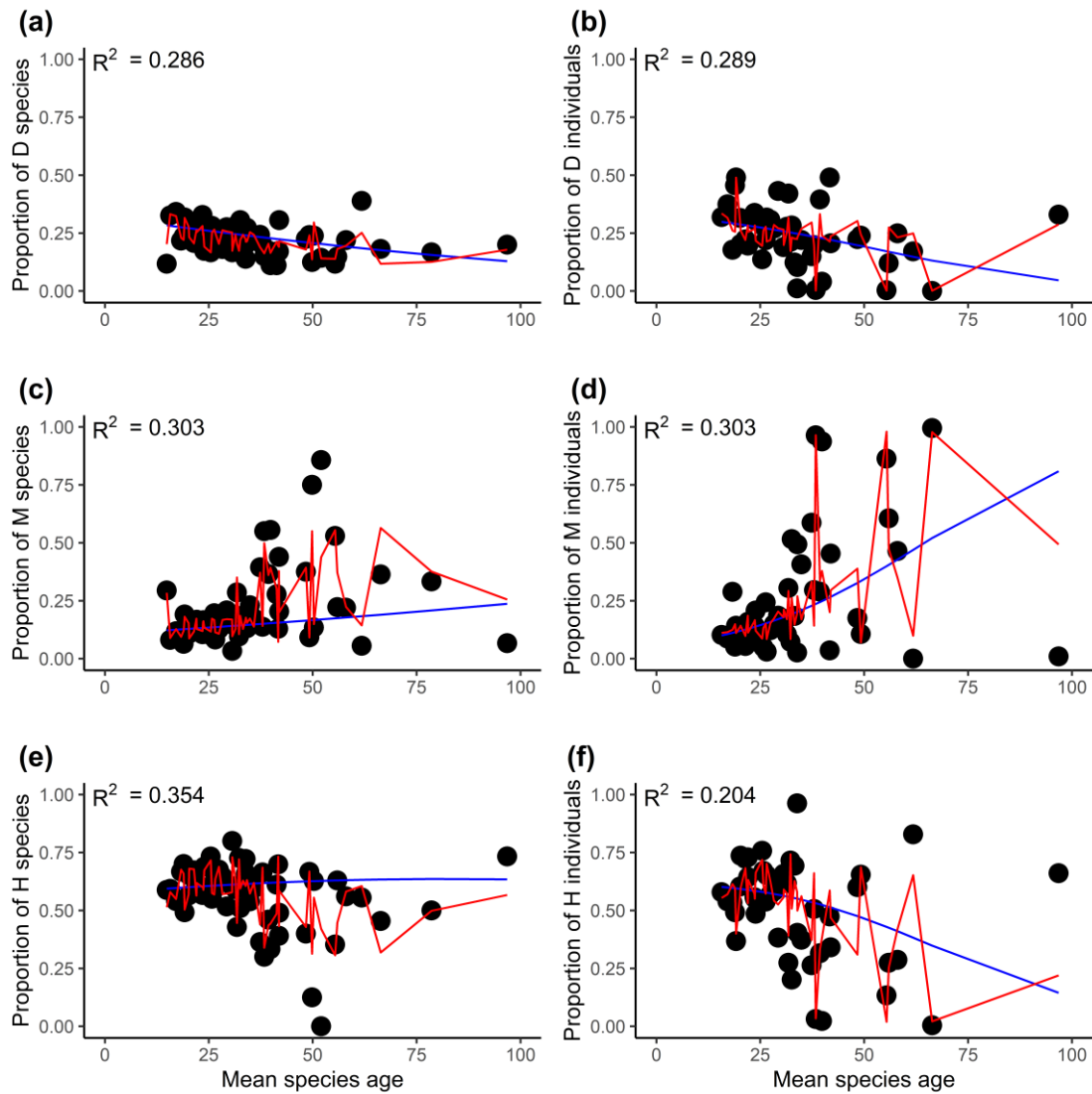
Figure 3. The relationships between the proportion of flowering plants with different sexual systems and mean species age (millions of years). (a), (c) and (e) are for the proportion of species, and (b), (d), and (f) are for the proportion of the individual. D, M, and H represent dioecy, monoecy, and hermaphroditism, 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 S3 for species and individuals, respectively. R^2 values associated with models only including mean species age are given in each panel.
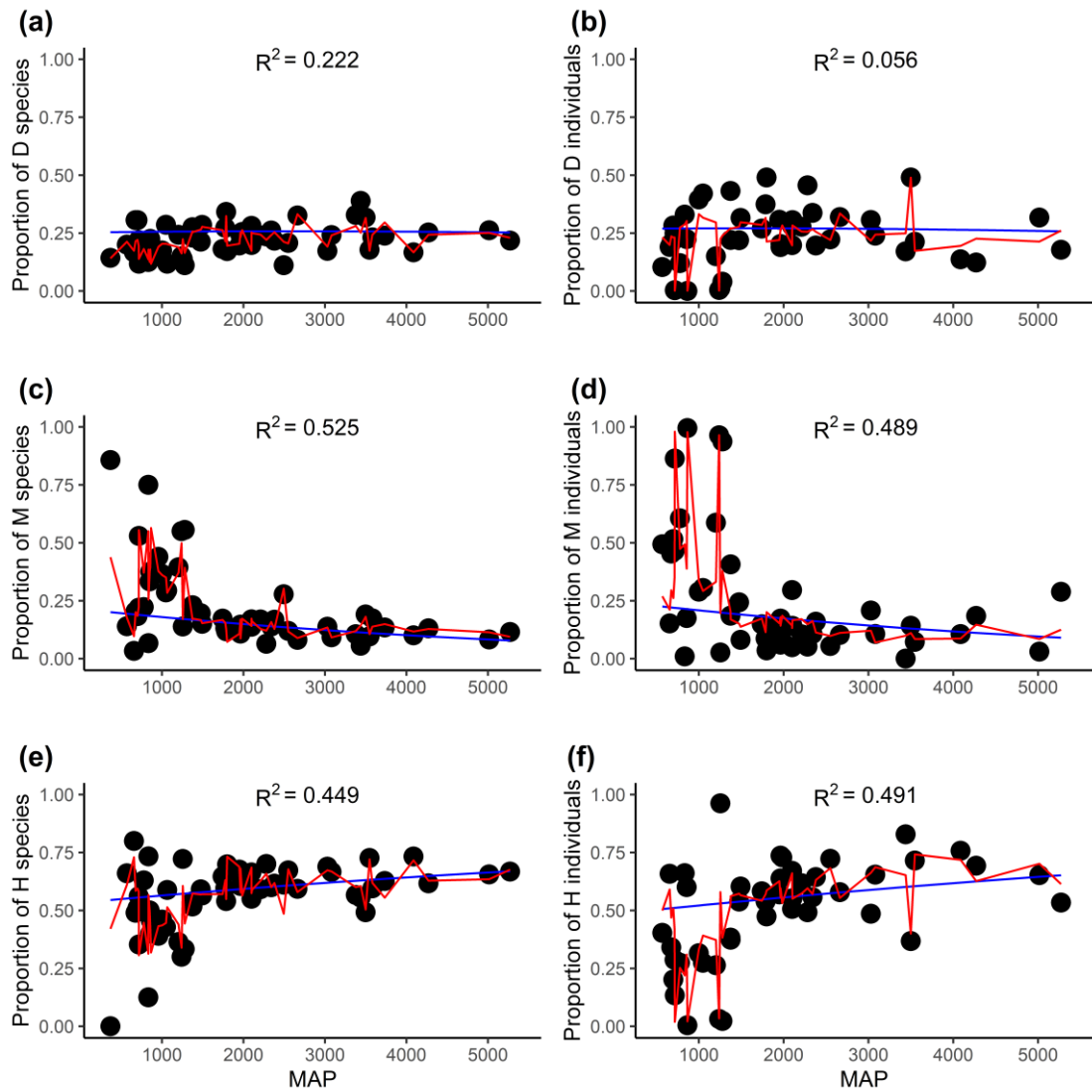
Figure 4. The relationships between the proportion of flowering plants with different sexual systems and mean annual precipitation (MAP). (a), (c) and (e) are for the proportion of species, and (b), (d), and (f) are for the proportion of the individual. D, M, and H represent dioecy, monoecy, and hermaphroditism, respectively. The blue line is the multinomial logistic model that only includes MAP 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 S3 for species and individuals, respectively. R^2 values associated with models only including MAP are given in each panel.