Zygomorphic flowers have fewer visitors

Jeremy B. Yoder[1,3], Giancarlo Gomez[1], and Colin J. Carlson[2]

[1] Department of Biology, California State University Northridge, Los Angeles, CA, 91330, USA

[2] Department of Biology, Georgetown University, Washington, D.C. 20057, USA

[3] *To whom correspondence should be addressed:* jeremy.yoder@csun.edu

Keywords: Pollination, floral morphology, ecological specialization, interaction networks

3,838 words, 2 figures, no tables

ABSTRACT

Botanists have long identified bilaterally symmetrical (zygomorphic) flowers as having more specialized pollination interactions than radially symmetrical (actinomorphic) flowers. Zygomorphic flowers facilitate more precise contact with pollinators, guide pollinator behaviour, and exclude less effective pollinators. However, to our knowledge, whether zygomorphic flowers are actually visited by a smaller subset of available pollinators has not been broadly evaluated. We compiled 53,609 plant visitation records in 159 communities around the world and classified the plants' floral symmetry. Globally and within individual communities, plant species with zygomorphic flowers do indeed have fewer visitors. Likely as a consequence of this difference, however, zygomorphic flowers share a somewhat larger proportion of their visitors with other taxa in the same community. The structures of visitation sub-networks for plants with different floral symmetry, and full networks with varying proportions of zygomorphic flowers, also differ in ways that may arise from differences in visitor diversity. These results provide context for widely documented associations between zygomorphy and diversification and imply that species with zygomorphic flowers may face greater risk of extinction due to pollinator loss.

INTRODUCTION

One of the textbook axioms of pollination ecology is that flowers with bilateral symmetry are more specialized than flowers with radial symmetry [1–4]. What this means, however, can vary widely with context. “Specialization” may refer to a derived character state in a phylogenetic context [1,3], or to the degree to which a flower manipulates pollinator behaviour [5] — or it may refer to association with a smaller set of available pollinators than seen for other comparable plant taxa [6]. It is well established that zygomorphic flowers are derived within the angiosperms [7,8], and extensive research examines how floral structure attracts, guides, or excludes pollinators [5,9–12]. However, data addressing the third sense in which zygomorphic flowers are specialized — association with fewer pollinators than otherwise expected — are surprisingly sparse.

Floral symmetry has been recognized as an important feature of angiosperm diversity since at least the 18th Century [4]. Modern treatments identified zygomorphy as derived, and hypothesized that zygomorphic forms facilitate greater consistency of pollinator visitation, and thus more effective pollination [1,3,13]. Zygomorphy is associated with greater net rates of speciation [14,15], consistent with the hypothesis that using fewer pollinators creates more opportunities for reproductive isolation [16]. Greater specialization based on symmetry might also interact with global patterns of diversity, such as latitudinal gradients [17,18]: recent syntheses find evidence that biotic interactions are stronger in the tropics [19,20], though assessments of latitudinal effects on pollination specifically have mixed results [21,22].

However, to our knowledge, direct documentation that zygomorphic flowers associate with fewer pollinators is restricted to anecdotal observations (e.g. Takhtajan 1969; Stebbins 1974; Fenster et al. 2004). Broad confirmation of this understanding would illuminate the extensive research linking pollination associations to diversification [1,13,15,16,23]. Ecologically, greater pollinator specificity for species with zygomorphic flowers implies that they should have smaller geographic ranges and be more prone to local extinction due to pollinator loss. But this is all conjecture without data showing that zygomorphic flowers do actually tend to have fewer pollinators.

If floral symmetry creates systematic differences in pollinator associations, these differences could be expected to manifest in the structure of plant-pollinator visitation networks. Plant-pollinator associations have been prominent case studies in the development of ecological network theory, including network structure and assembly [24–26], global patterns of biodiversity [21,22], and evolutionary stability against species losses [27]. The structures of association networks provide community-level perspective on the diversity of pollinators visiting flowers with particular traits, and public databases of plant-pollinator association compiled for studies of network structure have global coverage to examine pollinator number and sharing among co-occurring angiosperm taxa. Here, we test the hypothesis that zygomorphic flowers have more specialized pollination in a global dataset of floral visitation networks, comparing the number of floral visitors and examining differences in the structure of association networks for plant taxa with actinomorphic or zygomorphic floral symmetry.

METHODS

We compiled floral visitation networks from Web of Life (www.web-of-life.es) and the Interaction Web DataBase (www.nceas.ucsb.edu/interactionweb) repositories, identified unique plant taxa (typically species) across all networks, and classified their floral symmetry based on taxonomic knowledge, formal descriptions of species or higher taxa, and, when necessary, inspecting images of herbarium sheets or reliably identified fresh flowers. In some cases, we classified symmetry not based on individual flowers but on whole flowering heads (e.g., we considered species in the Asteraceae actinomorphic). We removed taxa from the working dataset if we were unable to find authoritative descriptions or images, or if they were wind-pollinated. Data and sources are provided in the Dryad archive (Dryad DOI here).

We conducted analysis in R v. 3.6.2 [28]. For each plant species in the dataset, we totalled the number of unique visitors observed for each, and calculated visitor sharing as

$$\frac{\sum_{j=1}^{n} s_{ij}}{(n-1)}$$

Where s_{ij} is the proportion of visitors to plant i that also visit plant j, $i \neq j$, in a community of n plants. We calculated network structure metrics for complete communities, and for the sub-networks of visitors to plants in each community with each type of floral symmetry. We calculated nestedness, connectance, web asymmetry, and coextinction curves [29] for full networks and sub-networks using the `networklevel()` function of the `bipartite` package [30], and quantified modularity using a short-random-walks algorithm implemented in the `cluster_walktrap()` function in the `igraph` package [31].

To test for phylogenetic signal in floral symmetry, visitor counts, and visitor sharing, and to control for phylogeny in subsequent analysis, we mapped taxa in our dataset to a recently published supertree of the seed plants [32]. We tested for phylogenetic signal using the `phylosignal` package [33], estimating Blomberg's K and K* [34], Abouheif's C_{mean} [35], Moran's I [36], and Pagel's λ [37] statistics. We performed principal component analysis of the phylogenetic distance matrix for all plant taxa and used phylogenetic distance principal components as covariates in Bayesian regression models fitted to explain variation in visitor count and sharing.

We tested the hypotheses that visitor count and visitor sharing differed with respect to floral symmetry by fitting and comparing Bayesian multilevel regression models using the `brms` package [38,39]. Competing models explained variation in pollinator count, pollinator sharing, or network structure metrics with a group effect of source network identity and possible population effects of floral symmetry and latitude. For regressions fitted to pollinator count and sharing metrics of individual taxa, we also included the first two principal components of the phylogenetic distance matrix (which jointly explained 65% of variation) as population effects alongside network identity, latitude, and floral symmetry. We estimated model fit in terms of the expected log pointwise predictive density (ELPD) using the leave-one-out cross-validation method implemented in `brms` with the `LOO()` function [40].

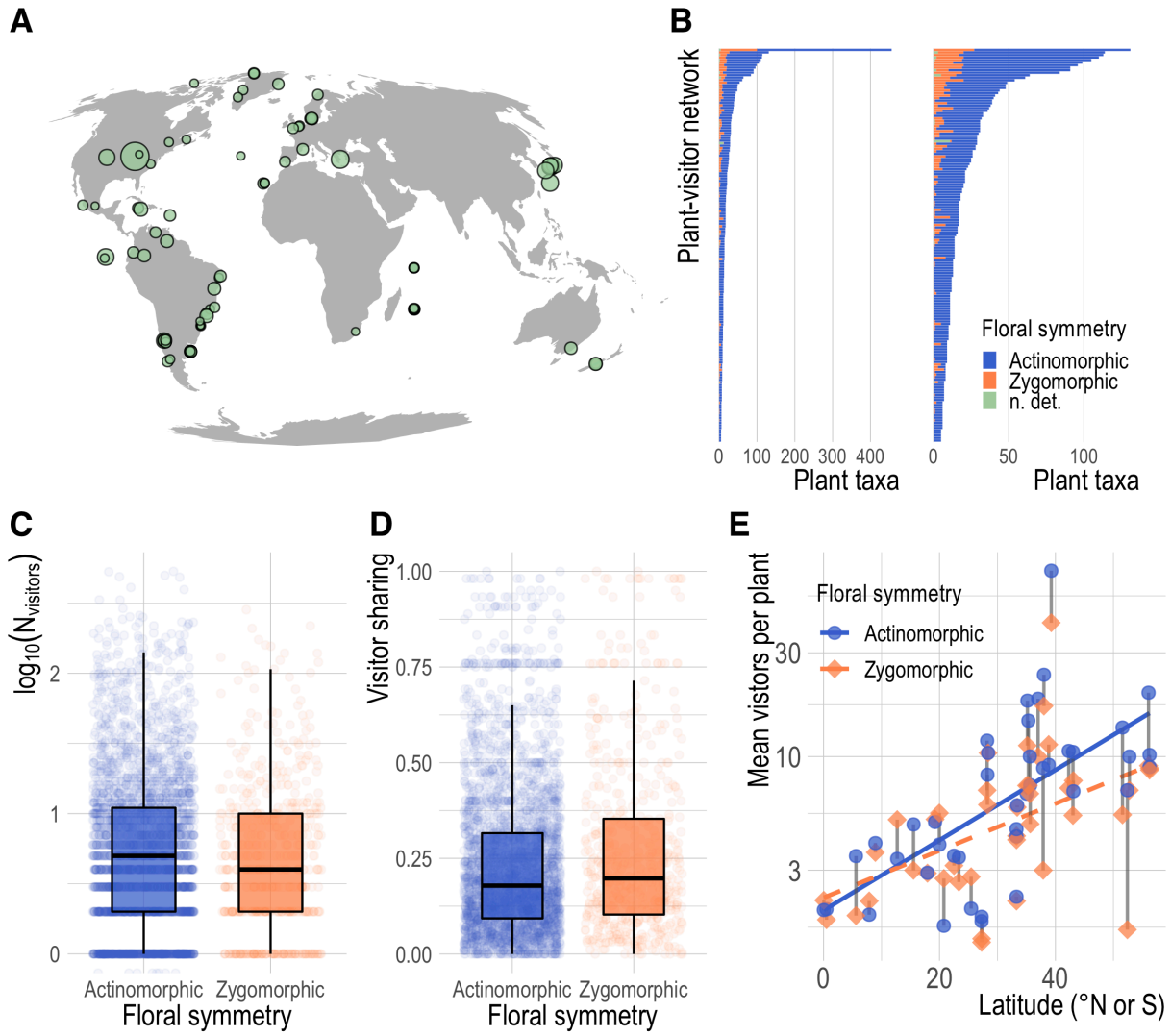

Figure 1. The global plant visitation dataset. (A) Global distribution of the plant-visitor networks in our compiled dataset, with points scaled to indicate relative size, in terms of plant taxa. (B) Bar plots giving the number of plant taxa for each network, coloured according to floral symmetry annotation (left, full dataset, right, all networks except for the largest, to provide better visibility. (C) Visitors per plant across the whole dataset, grouped by floral symmetry (one-tailed Wilcoxon test, $p = 0.002$). (D) Visitor sharing for each plant across the whole dataset, grouped by floral symmetry (one-tailed Wilcoxon test, $p = 0.004$). (E) Visitors per plant, averaged within sub-networks for plants with differing symmetries, versus the latitude of the network location; grey lines link points for actinomorphic and zygomorphic taxa from the same network.

RESULTS

We compiled 159 plant-visitor networks, recording 53,609 observed visits to 2,734 angiosperm taxa, from online repositories (Figure 1A; Supplementary Table 1), then classified plant taxa in

this dataset as having either actinomorphic or zygomorphic flowers. Globally, and across individual networks, zygomorphic species were a minority: Out of 2,668 species for which we could identify floral symmetry, 488 (18%) were zygomorphic; only five networks had more zygomorphic than actinomorphic species, while 70 lacked any zygomorphic species (Figure 1B). Across all observed visits in the dataset, the number visitors to plants having zygomorphic flowers was significantly smaller than that for plants having actinomorphic flowers (median 4 pollinators per plant with zygomorphic flowers versus 5 per plant with actinomorphic flowers; $p = 0.002$ in a one-tailed Wilcoxon signed-rank test; Figure 1C). At the same time, taxa with zygomorphic flowers shared a somewhat higher proportion of their visitors with other taxa in the same community (median 0.20 for zygomorphic versus 0.18 for actinomorphic, $p = 0.004$; Figure 1D). We found significant phylogenetic signal for floral symmetry across all statistics ($C_{mean} = 0.33$, Moran's $I = 0.02$, $K = 0.05$, $K^* = 0.05$, and $\lambda = 0.50$; $p < 0.001$ for all); but pollinator count metrics only showed significant deviations from the null models for C_{mean} and λ ($p < 0.001$ for each; $p \geq 0.05$ for all others).

In 39 networks comprising 46,026 floral visitation records, there were a sufficient number of plant taxa (at least five) with each type of symmetry to compare sub-networks for flowers with different symmetry — that is, to compare the diversity of floral visitors for plants with different symmetry having access to the same pool of possible pollinators, and the structure of networks for plants with differing symmetry. Zygomorphic sub-networks had significantly fewer mean visitors per plant (one-tailed paired Wilcoxon test, $p < 0.001$; Figure 2), but only marginally greater visitor sharing ($p = 0.06$). Zygomorphic sub-networks differed from actinomorphic sub-networks in a variety of structural metrics (Figure 2), having significantly greater connectance

($p < 10^{-4}$), greater web asymmetry ($p < 0.001$), greater nestedness ($p < 10^{-5}$), and greater modularity ($p < 0.001$), and lower coextinction robustness, as measured by the exponent of the coextinction curve, for both plants ($p < 10^{-5}$) and visitors ($p < 10^{-5}$). Among 89 complete networks including at least one zygomorphic plant taxon, a greater proportion of zygomorphic plants was significantly associated with greater visitor sharing (Figure 2B; Pearson's product moment correlation on log-transformed values = 0.22, $p = 0.04$), greater connectance (cor = 0.21, $p = 0.04$), lower web asymmetry (cor = -0.26, $p = 0.01$), and greater visitor coextinction robustness (cor = 0.27, $p = 0.01$); but the proportion of zygomorphic flowers was not correlated with the mean number of visitors per plant, networks' nestedness, modularity, or plant coextinction robustness.

The best-fit Bayesian regression model explaining variation in the number of visitors to each plant included floral symmetry, latitude, an interaction between symmetry and latitude, and phylogeny in addition to the group effect of network identity, estimating a significant negative main effect of zygomorphic symmetry ($R^2 = 0.28$; $\Delta ELPD \geq 5.4$ versus all other models; Supplementary Tables 2, 3). The best-fit model explaining variation in visitor sharing included floral symmetry, phylogeny, and the group effect of network identity, and was a significantly better fit to the data than any model including an effect of latitude; this model had a significant positive effect of zygomorphic symmetry ($R^2 = 0.66$; $\Delta ELPD > 6$ versus all other models; Supplementary Tables 4, 5).

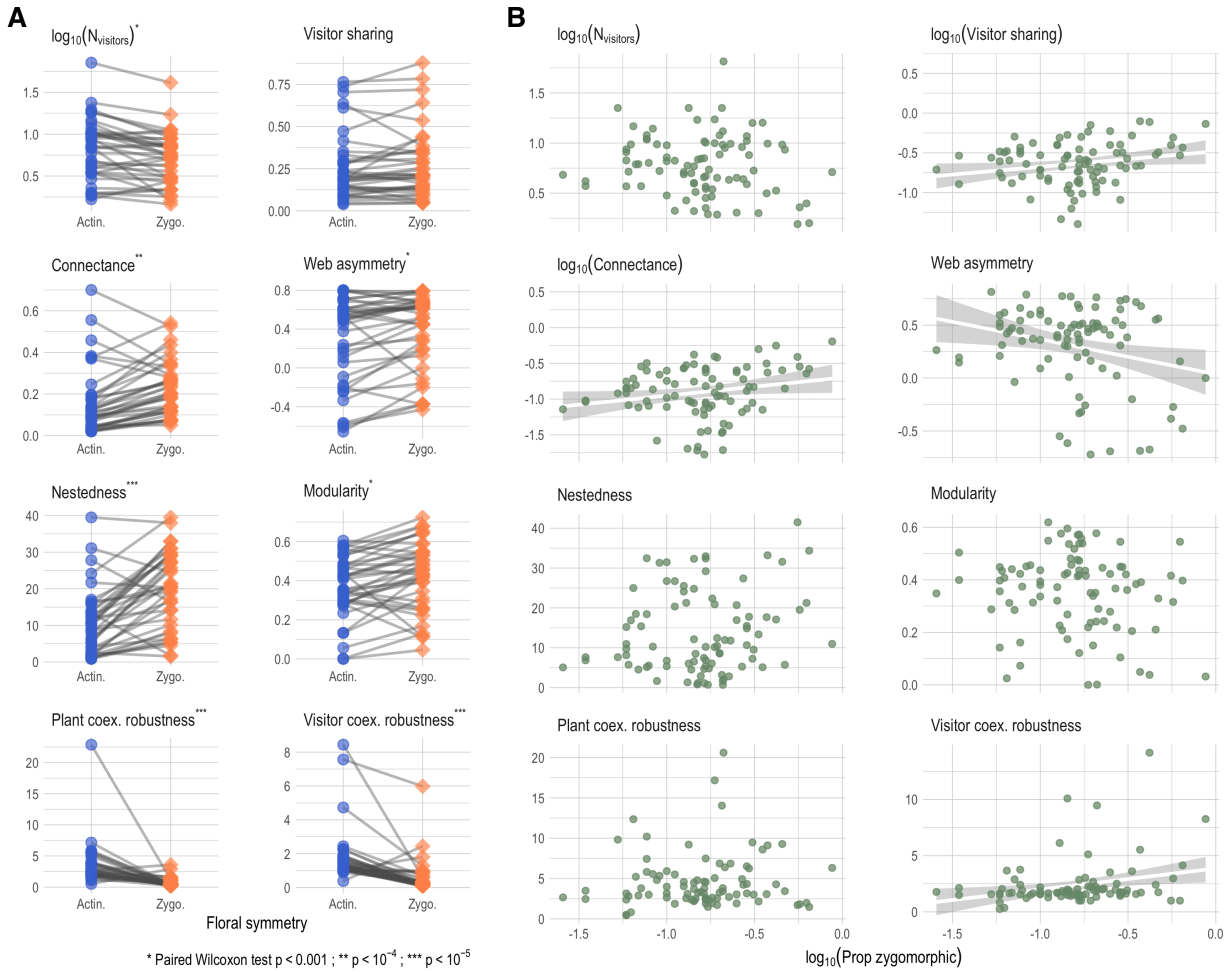

Figure 2. Floral symmetry and plant-visitor network structure. (A) Comparisons of subnetworks created based on floral symmetry, for mean number of visitors per plant, visitor sharing, connectance, web asymmetry, nestedness, modularity, and coextinction robustness from the perspectives of both plants and visitors, with indications sub-networks differ significantly based on one-tailed paired Wilcoxon tests. Gary lines link points representing zygomorphic and actinomorphic sub-networks from the same source network. (B) Scatterplots of the relationships between the proportion of zygomorphic flowers in a network and the set of network structure metrics in A; linear regression lines (white with grey shading indicating 95% CI) are given for all cases in which the correlation is significant with $p \leq 0.05$.

DISCUSSION

The classic hypothesis of floral symmetry is that zygomorphic flowers have more specialized pollination, meaning that they are visited by fewer pollinator species. We find that, globally and at the level of individual association networks, plants with zygomorphic flowers do indeed have

fewer visitors, and that the visitation networks of plants with zygomorphic symmetry differ from the networks of plants with actinomorphic symmetry in ways that may arise from this difference in pollinator diversity (Figure 1C,D; Figure 2). In particular, sub-networks of plants with zygomorphic flowers show significantly greater connectance, greater web asymmetry, greater nestedness, greater modularity, and lower coextinction robustness for both plants and visitors (Figure 2A); and full visitation networks in which more plant taxa have zygomorphic flowers show broadly parallel patterns, with the exception of a positive correlation between proportion of zygomorphic flowers and visitor coextinction robustness (Figure 2B). Floral symmetry, visitor count, and visitor sharing show significant phylogenetic structure; and visitor count is correlated with latitude north or south (Figure 1E), such that plants in communities farther from the equator have more visitors regardless of their floral symmetry, though the correlation with latitude is somewhat smaller for zygomorphic taxa. Bayesian multilevel regression modelling that accounts for these potential confounding effects nevertheless finds significant effects of floral symmetry on visitor count and visitor sharing.

The visitation network data we examine here have notable limitations for assessing pollination specialization, because they treat visitation as a binary, while in reality floral visitors vary considerably in their effectiveness as pollinators. Thus, the effective pollinators of the plant species in our dataset are likely a subset of the recorded visitors. Our metric of visitor sharing, similarly, may not reflect the relative “constancy” of associations between effective pollinators and plants — that is, the degree to which pollinators continue to visit flowers of a particular species over multiple visits in a foraging trip, a key concept in the theory of plant-pollinator specialization and pollinator-mediated reproductive isolation [1,16]. This may explain why our

visitor sharing metric is higher for zygomorphic flowers. Rather than capturing constancy in the sense of pollinator foraging behaviour, visitor sharing is inherently limited by the number of visitors to a plant species: species with fewer visitors likely share a larger proportion of them simply because, arithmetically, fewer visitors represent a given proportion of sharing. The positive association between visitor sharing and zygomorphy is also likely a reflection of network structure; like other mutualistic networks, plant-visitation networks are generally nested [26], so the fact that zygomorphic species tend to have fewer visitors means that their visitors are more likely to be relatively generalized, visiting many other plant taxa.

An association between floral symmetry and pollinator count is partly attributable to shared history, but this does not exclude the possibility of correlated evolution — phylogenetic correlations should arise if the evolution of zygomorphy is accompanied by a reduction in pollinator number. Possible evolutionary causes for this pattern are the subject of an extensive literature on angiosperms' coevolution with animal pollinators [1,5,14–16]. Selective benefits to floral forms that control pollinator access include reduced receipt of heterospecific pollen [1,16] and more effective transfer of conspecific pollen [5,41]. An ecological association between floral symmetry and pollinator diversity also provides quantified ecological context for documented associations between floral zygomorphy and diversification [14,15,42]. The causal relationship, however, remains ambiguous. It may be that association with a smaller set of pollinators creates more opportunities for the evolution of reproductive isolation [1,16,42]; but it may also be that more specialized pollination associations allow lineages to subdivide other axes of ecological variation more finely [15,23].

Our results also have important implications for conservation work. Despite significant uncertainty surrounding the current magnitude of global insect defaunation, pollinators are widely known to be in rapid decline due to pesticide use, habitat degradation, and emerging infections [43,44]. As we find, zygomorphic species may be more vulnerable to coextinction as pollinators decline and may be more responsible for pollinator co-extinctions if they themselves are lost (Figure 2A). Although the patterns we find are coarse and variable at the community level, simple rubrics for triage are critical for conserving the 300,000+ species of angiosperms, most of which will never benefit from individualized conservation assessment. Perhaps more importantly, our results offer support for the idea that "compartments" of the global plant-pollinator network must be targets for holistic conservation, focused on preserving interactions and functionality where the network is most fragile [45].

ACKNOWLEDGEMENTS

JBY was supported by start-up funds from California State University Northridge, and CJC by a postdoctoral fellowship from the Georgetown Environment Initiative. We thank Shweta Bansal for helpful conversations and Stephen Sondheim for teaching us that a faboid legume can begin an adventure.

DATA, CODE, AND MATERIALS

Floral symmetry annotations, visitor counts and sharing, and network structure statistics have been uploaded to the Dryad repository, DOI 10.5061/dryad.3j9kd51df

COMPETING INTERESTS

The authors declare no competing interests.

AUTHORS' CONTRIBUTIONS

JBY and CJC conceived and designed the study; GG annotated plants' floral symmetry with supervision from JBY, and JBY and GG conducted analysis with code provided by CJC; JBY drafted the paper in consultation with CJC and GG. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

REFERENCES

1. Takhtajan A. 1969 *Flowering Plants: Origin and Dispersal*. Edinburgh: Oliver & Boyd.
2. Darwin C. 1877 *The Various Contrivances by Which Orchids are Fertilised by Insects*. 2nd. New York: D. Appleton and Company.
3. Stebbins GL. 1974 *Flowering Plants: Evolution Above the Species Level*. Belknap Press, Harvard.
4. Endress PK. 2012 The Immense Diversity of Floral Monosymmetry and Asymmetry Across Angiosperms. *Bot. Rev.* **78**, 345–397. (doi:10.1007/s12229-012-9106-3)
5. Fenster CCB, Armbruster WS, Dudash MR, Wilson P, Fenster CCB, Thomson JD. 2004 Pollination syndromes and floral specialization. *Annu. Rev. Ecol. Evol. Syst.* **35**, 375–403.

(doi:10.1146/annurev.ecolsys.34.011802.132347)

6. Poisot T, Bever JD, Nemri A, Thrall PH, Hochberg ME. 2011 A conceptual framework for the evolution of ecological specialisation. *Ecol. Lett.* **14**, 841–851. (doi:10.1111/j.1461-0248.2011.01645.x)

7. Citerne H, Jabbour F, Nadot S, Damerval C. 2010 The evolution of floral symmetry. *Adv. Bot. Res.* **54**, 85–137. (doi:10.1016/S0065-2296(10)54003-5)

8. Sauquet H *et al.* 2017 The ancestral flower of angiosperms and its early diversification. *Nat. Commun.* **8**, 16047. (doi:10.1038/ncomms16047)

9. Charles B. Fenster, W. Scott Armbruster, Michele R. Dudash. 2009 Specialization of flowers: is floral orientation an overlooked first step? *New Phytol.* **183**, 502–506.

10. Kampny CM. 1995 Pollination and flower diversity in the Scrophulariaceae. *Bot. Rev.* **61**, 350–366.

11. Ushimaru A, Dohzono I, Takami Y, Hyodo F. 2009 Flower orientation enhances pollen transfer in bilaterally symmetrical flowers. *Oecologia* **160**, 667–674. (doi:10.1007/s00442-009-1334-9)

12. Macior LW. 2006 Behavioral aspects of coadaptations between flowers and insect pollinators. *Ann. Missouri Bot. Gard.* **61**, 760. (doi:10.2307/2395027)

13. Takhtajan A. 1991 *Evolutionary Trends in Flowering Plants*. New York: Columbia University Press.

14. Sargent RD. 2004 Floral symmetry affects speciation rates in angiosperms. *Proc. R. Soc. B* **271**, 603–608.

15. Vamosi JC, Vamosi SM. 2010 Key innovations within a geographical context in flowering plants: Towards resolving Darwin's abominable mystery. *Ecol. Lett.* **13**, 1270–1279.

(doi:10.1111/j.1461-0248.2010.01521.x)

16. Grant V. 1949 Pollination systems as isolating mechanisms in angiosperms. *Evolution (N. Y).* **3**, 82–97.

17. Mittelbach GG *et al.* 2007 Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecol. Lett.* **10**, 315–331. (doi:doi:10.1111/j.1461-0248.2007.01020.x)

18. Jansson R, Davies TJ. 2008 Global variation in diversification rates of flowering plants: Energy vs. climate change. *Ecol. Lett.* **11**, 173–183. (doi:10.1111/j.1461-0248.2007.01138.x)

19. Briscoe Runquist R *et al.* 2020 The relative role of abiotic and biotic environments in local adaptation: A quantitative and qualitative synthesis. *Am. Nat.* (doi:10.1086/707322)

20. Hargreaves AL, Germain RM, Bontrager M, Persi J, Amy L. 2020 Local adaptation to biotic interactions: A meta-analysis across latitudes. *Am. Nat.* (doi:10.1086/707323)

21. Olesen JM, Jordano P. 2002 Geographic patterns in plant-pollinator mutualistic networks. *Ecology* **83**, 2416–2424.

22. Ollerton J, Cranmer L. 2002 Latitudinal trends in plant-pollinator interactions: are tropical plants more specialised? *Oikos* **98**, 340–350.

23. Armbruster WS, Muchhala N. 2009 Associations between floral specialization and species diversity: Cause, effect, or correlation? *Evol. Ecol.* **23**, 159–179. (doi:10.1007/s10682-008-9259-z)

24. Olesen JM, Bascompte J, Dupont YL, Jordano P. 2007 The modularity of pollination networks. *Proc. Natl. Acad. Sci.* **104**, 19891–19896.

25. Krishna A, Guimarães Jr PR, Jordano P, Bascompte J. 2008 A neutral-niche theory of nestedness in mutualistic networks. *OIKOS*

26. Bascompte J, Jordano P, Olesen JM, Melián CJ, Olesen JM. 2003 The nested assembly of plant–animal mutualistic networks. *Proc. Natl. Acad. Sci.* **100**, 9383–9387. (doi:10.1073/pnas.1633576100)

27. Nuismer SL, Week B, Aizen MA. 2018 Coevolution Slows the Disassembly of Mutualistic Networks. *Am. Nat.* **192**, 490–502. (doi:10.1086/699218)

28. R Core Team. 2019 R: A language and environment for statistical computing.

29. Memmott J, Waser N, Price M. 2004 Tolerance of pollination networks to species extinctions. *Proc. R. Soc. B Biol. Sci.* **271**, 2605–2611.

30. Dormann CF, Gruber B, Fründ J. 2008 Introducing the bipartite Package : Analysing Ecological Networks. **8**, 8–11.

31. Csardi G, Nepusz T. 2006 The igraph software package for complex network research. *InterJournal* **Complex Sy**, 1695.

32. Smith SA, Brown JW. 2018 Constructing a broadly inclusive seed plant phylogeny. *Am. J. Bot.* **105**, 302–314. (doi:10.1002/ajb2.1019)

33. Keck F, Rimet F, Bouchez A, Franc A. 2016 Phylosignal: An R package to measure, test, and explore the phylogenetic signal. *Ecol. Evol.* **6**, 2774–2780. (doi:10.1002/ece3.2051)

34. Blomberg SP, Garland T, Ives AR. 2003 Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution (N. Y).* **57**, 717–745. (doi:10.1111/j.0014-3820.2003.tb00285.x)

35. Abouheif E. 1999 A method for testing the assumption of phylogenetic independence in comparative data. *Evol. Ecol. Res.* **1**, 895–909.

36. Gittleman JL, Kot M. 1990 Adaptation: Statistics and a null model for estimating phylogenetic effects. *Syst. Zool.* **39**, 227. (doi:10.2307/2992183)

37. Pagel M. 1999 Inferring the historical patterns of biological evolution. *Nature* **401**, 877–884. (doi:10.1038/44766)

38. Bürkner P-C. 2017 brms: An R package for Bayesian multilevel models using Stan. *J. Stat. Softw.* **80**, 1–28. (doi:10.18637/jss.v080.i01)

39. Bürkner P-C. 2018 Advanced Bayesian multilevel modeling with the R package brms. *R J.* **10**, 395. (doi:10.32614/RJ-2018-017)

40. Vehtari A, Gelman A, Gabry J. 2017 Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Stat. Comput.* **27**, 1413–1432. (doi:10.1007/s11222-016-9696-4)

41. Castellanos MC, Wilson P, Thomson JD. 2004 'Anti-bee' and 'pro-bird' changes during the evolution of hummingbird pollination in Penstemon flowers. *J. Evol. Biol.* **17**, 876–885. (doi:10.1111/j.1420-9101.2004.00729.x)

42. Kay KM, Sargent RD. 2009 The role of animal pollination in plant speciation: Integrating ecology, geography, and genetics. *Annu. Rev. Ecol. Evol. Syst.* **40**, 637–656. (doi:10.1146/annurev.ecolsys.110308.120310)

43. Lister BC, Garcia A. 2018 Climate-driven declines in arthropod abundance restructure a rainforest food web. *Proc. Natl. Acad. Sci.* **115**, E10397–E10406. (doi:10.1073/pnas.1722477115)

44. Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE. 2010 Global pollinator declines: Trends, impacts and drivers. *Trends Ecol. Evol.* **25**, 345–353. (doi:10.1016/j.tree.2010.01.007)

45. Corbet SA. 2000 Conserving compartments in pollination webs. *Conserv. Biol.* **14**, 1229–1231. (doi:10.1046/j.1523-1739.2000.00014.x)