

# Zygomorphic flowers have fewer visitors

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**Botanists have long identified angiosperm species with bilaterally symmetrical (zygomorphic) flowers as having more specialized pollination interactions than species with radially symmetrical (actinomorphic) flowers. Zygomorphic flowers facilitate more precise contact with pollinators, guide pollinator behavior, and exclude less effective pollinators. However, to our knowledge, the basic idea that zygomorphic flowers are visited by a smaller subset of available pollinators has not been broadly evaluated. We compiled data on 32,901 plant-pollinator associations in 159 communities around the world and classified the plants' floral symmetry. Globally and within individual communities, we found that plant species with zygomorphic flowers are visited by fewer pollinators. We also found that the structures of pollination networks differ for plants with different floral symmetry, in ways that may arise from differences in pollinator diversity. These results may explain associations between zygomorphy and diversification, and imply that species with zygomorphic flowers face greater risks of extinction due to pollinator loss.**

Pollination | Floral morphology | Specialization | Network structure

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## 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 (2, 3), or to the degree to which a flower manipulates pollinator behavior (5) — or it may refer to association with a subset of all available pollinators (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, 9–11). However, data addressing the third sense in which zygomorphic flowers are specialized — association with a narrower suite of pollinators than are available — 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 (2, 3, 12). Zygomorphy is associated with greater net rates of speciation (13, 14), consistent with the hypothesis that using fewer pollinators creates more opportunities for reproductive isolation (15). Greater specialization based on symmetry might also interact with global patterns of diversity, such as latitudinal gradients (16, 17): recent syntheses find evidence that biotic interactions are stronger in the

tropics (18, 19), though assessments of latitudinal effects on pollination specifically have mixed results (20, 21).

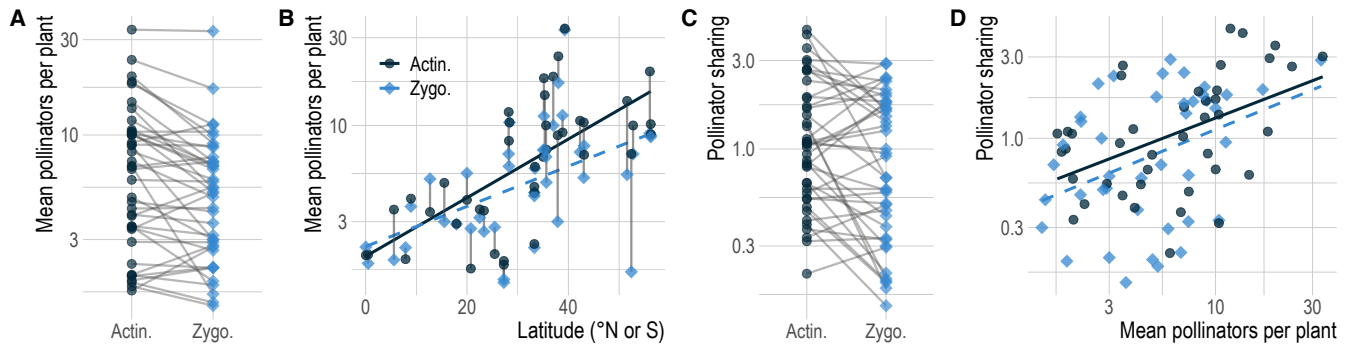
However, to our knowledge, direct documentation that zygomorphic flowers associate with fewer pollinators is restricted to anecdotal observations (e.g. (2, 3, 5)). Broad confirmation of this understanding would illuminate the extensive research linking pollination associations to diversification (2, 14, 15, 22, 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.

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 (20, 21), 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 plant-pollinator 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.

## Results

We compiled 159 plant-pollinator association networks, recording 32,901 observed visits to 2,745 plant species, from online repositories (SI Data Table 1), then classified plant species in this dataset as having either actinomorphic or zygomorphic flowers. Globally, and across individual networks, zygomorphic species were a minority: Out of 2,703 species for which we could identify floral symmetry, 491 (18%) were zygomorphic; only 5 networks had more zygomorphic than actinomorphic species, while 67 lacked any zygomorphic species. In a global network assembled from all observations, the median number of pollinators associated with plants having zygomorphic flowers was significantly smaller than that for plants having actinomorphic flowers (5 pollinators per plant with zygomorphic flowers vs 7 per plant with actinomorphic flowers;  $p < 10^{-5}$  in a one-tailed Wilcoxon signed-rank test).

In 41 networks comprising 2,421 floral visitation records,



**Fig. 1.** (A) Pollinator diversity per plant across paired sub-networks of flowers with actinomorphic (dark circles) or zygomorphic (light diamonds) symmetry (one-sided paired Wilcoxon test,  $p < 0.001$ ). (B) Pollinator diversity versus latitude north or south, with linear regression lines for each symmetry type ( $\rho = 0.43$ ,  $p < 10^{-15}$  for actinomorphic species,  $\rho = 0.42$ ,  $p < 10^{-8}$  for zygomorphic). Gray lines link sub-network pairs. (C) Pollinator sharing for paired sub-networks of flowers with different symmetry (one-sided paired Wilcoxon test,  $p = 0.02$ ). (D) Pollinator diversity versus pollinator sharing in sub-networks with both types of symmetry ( $\rho = 0.49$ ,  $p < 0.01$  for actinomorphic,  $\rho = 0.36$ ,  $p = 0.02$  for zygomorphic).

there were a sufficient number of plant taxa (at least three) 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. Across these paired sub-networks, zygomorphic species consistently had fewer pollinators per plant (one-tailed paired Wilcoxon test on mean pollinators per plant,  $p < 0.001$ ; figure 1A). Pollinator count was also strongly and positively correlated with latitude for species with both types of floral symmetry (Spearman's  $\rho = 0.43$ ,  $p < 10^{-15}$  for actinomorphic species,  $\rho = 0.42$ ,  $p < 10^{-8}$  for zygomorphic; figure 1B).

To determine whether shared history could account for the association between symmetry type and pollinator count, we identified 2,507 species in our dataset represented in a recently published phylogeny of seed plants (28) and used this tree to test for phylogenetic signal in pollinator count and symmetry; we found significant signal for both (Pagel's  $\lambda = 0.07$  and  $0.51$  respectively,  $p < 0.001$  for both). To compare the effect of floral symmetry to those of variation in local pollinator pools, global patterns of biodiversity, and phylogenetic effects, we fitted generalized linear mixed models (GLMMs) with Poisson-distributed error to the pollinator count data; the best-fit model predicted pollinator count with a random effect of network identity; fixed effects of latitude, floral symmetry, and phylogenetic distances among plant species; and an interaction between latitude and symmetry ( $R^2 = 0.76$ ,  $\Delta AICc = 20.4$  for the next-best model, which lacked the interaction).

We also found that multiple metrics of network structure differed with floral symmetry (29, 30). Sub-networks for zygomorphic species had greater connectance (one-tailed paired Wilcoxon test,  $p < 0.001$ ), greater web asymmetry ( $p < 0.001$ ), greater nestedness ( $p < 10^{-7}$ ), greater modularity ( $p < 10^{-4}$ ), and greater codependency ( $p < 10^{-7}$ ; (30)). Zygomorphic sub-networks also had lower pollinator sharing ( $p < 0.02$ ; figure 1C), but did not differ in host sharing by pollinators ( $p = 0.44$ ). We hypothesized that these differences arose from the differences in pollinator count, and indeed for sub-networks with both kinds of floral symmetry we

found significant correlations between the mean number of pollinators per plant and connectance, web asymmetry, and pollinator sharing (Table 1). Pollinator sharing was correlated with latitude for actinomorphic sub-networks ( $\rho = 0.43$ ,  $p < 0.001$ ), but not for zygomorphic sub-networks ( $\rho = 0.19$ ,  $p = 0.23$ ). We compared the fit of GLMs with Gamma-distributed error predicting pollinator sharing with latitude, floral symmetry, and a random effect of network identity; the best-fit model predicted pollinator sharing with floral symmetry and the random effect of network ( $R^2 = 0.11$ ), though it was not a substantially better fit than models incorporating an additive effect of latitude ( $R^2 = 0.10$ ,  $\Delta AICc = 1.1$ ) and an interaction between latitude and floral symmetry ( $R^2 = 0.10$ ,  $\Delta AICc = 0.6$ ).

## 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 pollination 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. Pollinator count is also cor-

**Table 1.** Correlations between metrics of network structure and mean number of pollinators per plant, for sub-networks with actinomorphic or zygomorphic symmetry<sup>1</sup>

Network metric	Correlations with $\bar{N}_{pollinators}$			
	Actinomorphic		Zygomorphic	
	$\rho$	$P(\rho)$	$\rho$	$P(\rho)$
Connectance	<b>-0.48</b>	0.002	<b>-0.59</b>	$< 10^{-4}$
Web asymmetry	<b>0.88</b>	$< 10^{-10}$	<b>0.92</b>	$< 10^{-10}$
Nestedness	-0.29	0.08	<b>-0.44</b>	0.004
Modularity	0.02	0.92	0.06	0.75
Codependency	<b>0.37</b>	0.02	<b>0.29</b>	0.05
Pollinator sharing	<b>0.48</b>	0.001	<b>0.40</b>	0.02
Host sharing	<b>-0.41</b>	0.010	-0.28	0.09

related with latitude north or south (Figure 1B), with plants in communities farther from the equator having more pollinators regardless of their floral symmetry. This is consistent with less specialized pollination interactions at higher latitudes (but see (21)), and it interacts with floral symmetry such that the effect of latitude is somewhat smaller for zygomorphic taxa.

The 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 (2, 5, 13–15). Selective benefits to floral forms that control pollinator access include reduced receipt of heterospecific pollen (2, 15) and more effective transfer of conspecific pollen (5, 31). An ecological association between floral symmetry and pollinator diversity also provides quantified ecological context for documented associations between floral zygomorphy and diversification (13, 14, 32). The causal relationship, however, remains ambiguous. It may be that association with fewer, possibly more dedicated, pollinators creates more opportunities for the evolution of reproductive isolation (2, 15, 32); but it may also be that more specialized pollination associations allow lineages to subdivide other axes of ecological variation more finely (14, 22).

Our result also has 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 (33, 34). Consistent use of fewer pollinators suggests that zygomorphic species should be correspondingly more vulnerable to co-extinction as pollinators decline, and may be more responsible for pollinator co-extinctions in the event of their disappearance. Although this is a coarse pattern, having simple rubrics for triage is critical for conserving the 300,000+ species of angiosperms, most of which will never benefit from an individualized conservation assessment. Perhaps more importantly, our result offers 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 (35).

## Materials and Methods

We compiled floral visitation networks from Web of Life ([www.web-of-life.es](http://www.web-of-life.es)) and the Interaction Web DataBase ([nceas.ucsb.edu/interactionweb](http://nceas.ucsb.edu/interactionweb)), identified unique plant taxa (typically species) across all networks, and classified 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 in Supporting Information.

We conducted analysis in R (v.3.5.3 (36)). We divided networks containing at least 3 plants with each kind of symmetry into paired sub-networks, and summarized network structure for each. We calculated pollinator sharing, nestedness, connectance, and web asymmetry of individual sub-networks using the `networklevel()` function of the `bipartite` package (37), and quantified modularity using a short-random-walks algorithm implemented in the `cluster_walktrap()` function in the `igraph` package (38). Codependency is the exponent  $z$  of a codependent area relationship, estimated by fitting a power law to the number of hosts and affiliates in networks subsampled by hosts (30, 39). We tested for phylogenetic signal using functions in the `phylosignal` package (40). We tested the hypotheses that pollinator count and pollinator sharing differed with respect to floral symmetry by fitting and comparing GLMMs using the `glmer` function of the `lme4` package (41). Competing models explained variation in pollinator count or pollinator sharing with a random effect of source network identity and possible fixed effects of floral symmetry, latitude, and phylogenetic distances (the first two principal components of the distance matrix, which jointly explained 63% of variation), and compared model fit using  $AICc$  (42).

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## Works Cited

1. Charles Darwin. *The Various Contrivances by Which Orchids are Fertilised by Insects*. D. Appleton and Company, New York, 2nd. edition, 1877.
2. A Takhtajan. *Flowering Plants: Origin and Dispersal*. Oliver & Boyd, Edinburgh, 1969.
3. G. Ledyard Stebbins. *Flowering Plants: Evolution Above the Species Level*. Belknap Press, 1974.
4. Peter K. Endress. The Immense Diversity of Floral Monosymmetry and Asymmetry Across Angiosperms. *Botanical Review*, 78(4):345–397, 2012. ISSN 0068101. doi: 10.1007/s12229-012-9106-3.
5. CB Charles B Fenster, W. Scott Armbruster, Michele R Dudash, Paul Wilson, CB Charles B Fenster, and James D Thomson. Pollination syndromes and floral specialization. *Annual Review of Ecology, Evolution, and Systematics*, 35(1):375–403, 2004. ISSN 1543-592X. doi: 10.1146/annurev.ecolsys.34.011802.132347.
6. Timothée Poisot, James D Bever, Adnane Nemri, Peter H Thrall, and Michael E Hochberg. A conceptual framework for the evolution of ecological specialisation. *Ecology Letters*, 14(9):841–851, 2011. ISSN 1461-0248. doi: 10.1111/j.1461-0248.2011.01645.x.
7. Hélène Citerne, Florian Jabbour, Sophie Nadot, and Catherine Damerval. The evolution of floral symmetry. *Advances in Botanical Research*, 54(C):85–137, 2010. ISSN 00652296. doi: 10.1016/S0065-2296(10)54003-5.
8. Hervé Sauquet, Maria von Balthazar, Susana Magallón, James A. Doyle, Peter K. Endress, Emily J. Bailes, Erica Barroso de Moraes, Kester Bull-Hereñu, Laetitia Carrive, Marion Chartier, Guillaume Chomicki, Mario Coiro, Raphaël Cornette, Juliana H. L. El Ottra, Cyril Epicoco, Charles S. P. Foster, Florian Jabbour, Agathe Haevermans, Thomas Haevermans, Rebeca Hernández, Stefan A. Little, Stefan Löfstrand, Javier A. Luna, Julien Massoni, Sophie Nadot, Susanne Pamperl, Charlotte Prieu, Elisabeth Reyes, Patricia dos Santos, Kristel M. Schoonderwoerd, Susanne Sontag, Anaëlle Soulebeau, Yannick Staedler, Georg F. Tschan, Amy Wing-Sze Leung, and Jörg Schönenberger. The ancestral flower of angiosperms and its early diversification. *Nature Communications*, 8(May):16047, 2017. ISSN 2041-1723. doi: 10.1038/ncomms16047.

9. Christine M Kampny. Pollination and flower diversity in the Scrophulariaceae. *The Botanical Review*, 61(4):350–366, 1995.
10. Atushi Ushimaru, Ikumi Dohzono, Yasuoki Takami, and Fujio Hyodo. Flower orientation enhances pollen transfer in bilaterally symmetrical flowers. *Oecologia*, 160(4):667–674, 2009. ISSN 00298549. doi: 10.1007/s00442-009-1334-9.
11. Lazarus Walter Macior. Behavioral aspects of coadaptations between flowers and insect pollinators. *Annals of the Missouri Botanical Garden*, 61(3):760, 2006. ISSN 00266493. doi: 10.2307/2395027.
12. A. Takhtajan. *Evolutionary Trends in Flowering Plants*. Columbia University Press, New York, 1991.
13. Risa D Sargent. Floral symmetry affects speciation rates in angiosperms. *Proceedings of the Royal Society B*, 271(1539):603–608, 2004.
14. Jana C. Vamosi and Steven M. Vamosi. Key innovations within a geographical context in flowering plants: Towards resolving Darwin's abominable mystery. *Ecology Letters*, 13(10): 1270–1279, 2010. ISSN 14610248. doi: 10.1111/j.1461-0248.2010.01521.x.
15. Verne Grant. Pollination systems as isolating mechanisms in angiosperms. *Evolution*, 3(1): 82–97, 1949.
16. Gary G Mittelbach, Douglas W Schemske, Howard V Cornell, Andrew P Allen, Jonathan M Brown, Mark B Bush, Susan P Harrison, Allen H Hurlbert, Nancy Knowlton, Harilaos A Lessios, Christy M McCain, Amy R McCune, Lucinda A McDade, Mark A McPeck, Thomas J Near, Trevor D Price, Robert E Ricklefs, Kaustuv Roy, Dov F Sax, Dolph Schluter, James M Sobel, Michael Turelli, M Jonathan, Mark B Bush, P Susan, Allen H Hurlbert, Nancy Knowlton, A Harilaos, Christy M McCain, R Mccune, and A Lucinda. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, 10(4):315–331, 2007. doi: doi:10.1111/j.1461-0248.2007.01020.x.
17. Roland Jansson and T. Jonathan Davies. Global variation in diversification rates of flowering plants: Energy vs. climate change. *Ecology Letters*, 11(2):173–183, 2008. ISSN 1461023X. doi: 10.1111/j.1461-0248.2007.01138.x.
18. Ryan Briscoe Runquist, Amanda J Gorton, Jeremy B. Yoder, Nicholas J Deacon, Jacob J Grossman, Shan Kothari, Marta Lyons, Seema N Sheth, Peter L Tiffin, and David A Moeller. The relative role of abiotic and biotic environments in local adaptation: A quantitative and qualitative synthesis. *In review*, 2019.
19. Anna L Hargreaves, Rachel M Germain, Megan Bontrager, Joshua Persi, and L Amy. Biotic interactions affect fitness across latitudes, but only drive local. *bioRxiv*, pages 1–41, 2019. doi: 10.1101/575498v1.
20. Jens M. Olesen and Pedro Jordano. Geographic patterns in plant-pollinator mutualistic networks. *Ecology*, 83(9):2416–2424, 2002. ISSN 0012-9658.
21. Jeff Ollerton and Louise Cranmer. Latitudinal trends in plant-pollinator interactions: are tropical plants more specialised? *Oikos*, 98(2):340–350, 2002.
22. W. Scott Armbruster and Nathan Muchhala. Associations between floral specialization and species diversity: Cause, effect, or correlation? *Evolutionary Ecology*, 23(1):159–179, 2009. ISSN 02697653. doi: 10.1007/s10682-008-9259-z.
23. John N. Thompson. *The Geographic Mosaic of Coevolution*. University of Chicago Press, Chicago, 2005.
24. Jens M Olesen, Jordi Bascompte, Yoko L Dupont, and Pedro Jordano. The modularity of pollination networks. *Proceedings of the National Academy of Sciences*, 104(50):19891–19896, 2007.
25. Abhay Krishna, Paulo R Guimara, Pedro Jordano, and Jordi Bascompte. A neutral-niche theory of nestedness in mutualistic networks. *OIKOS*, 117(11):1609–1618, 2008. doi: 10.1111/j.2008.0030-1299.16540.x.
26. Jordi Bascompte, Pedro Jordano, Jens M. Olesen, Carlos J. Melián, and Jens M. Olesen. The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences*, 100(16):9383–9387, 2003. ISSN 0027-8424. doi: 10.1073/pnas.1633576100.
27. Scott L. Nuismer, Bob Week, and Marcelo A. Aizen. Coevolution slows the disassembly of mutualistic networks. *The American Naturalist*, 192(4):490–502, 2018. ISSN 0003-0147. doi: 10.1086/699218.
28. Stephen A. Smith and Joseph W. Brown. Constructing a broadly inclusive seed plant phylogeny. *American Journal of Botany*, 105(3):302–314, mar 2018. ISSN 00029122. doi: 10.1002/ajb2.1019.
29. Eva Delmas, Mathilde Besson, Marie-Hélène Brice, Laura A. Burkle, Giulio V. Dalla Riva, Marie-Josée Fortin, Dominique Gravel, Paulo R. Guimarães, David H. Hembry, Erica A. Newman, Jens M. Olesen, Mathias M. Pires, Justin D. Yeakel, and Timothée Poisot. Analysing ecological networks of species interactions. *Biological Reviews*, 94(1):16–36, feb 2019. ISSN 14647931. doi: 10.1111/brv.12433.
30. Colin J Carlson, Casey M Zipfel, Romain Garnier, and Shweta Bansal. Global estimates of mammalian viral biodiversity accounting for host sharing. *Nature Ecology and Evolution*, 3: 1070–1075, 2019.
31. M. C. Castellanos, P. Wilson, and J. D. Thomson. 'Anti-bee' and 'pro-bird' changes during the evolution of hummingbird pollination in Penstemon flowers. *Journal of Evolutionary Biology*, 17(4):876–885, jul 2004. ISSN 1010-061X. doi: 10.1111/j.1420-9101.2004.00729.x.
32. Kathleen M. Kay and Risa D. Sargent. The role of animal pollination in plant speciation: Integrating ecology, geography, and genetics. *Annual Review of Ecology, Evolution, and Systematics*, 40(637-656):637–656, 2009. ISSN 1543-592X. doi: 10.1146/annurev.ecolsys.110308.120310.
33. Bradford C Lister and Andres Garcia. Climate-driven declines in arthropod abundance restructure a rainforest food web. *Proceedings of the National Academy of Sciences*, 115(44): E10397–E10406, 2018. ISSN 0027-8424. doi: 10.1073/pnas.1722477115.
34. Simon G. Potts, Jacobus C. Biesmeijer, Claire Kremen, Peter Neumann, Oliver Schweiger, and William E. Kunin. Global pollinator declines: Trends, impacts and drivers. *Trends in Ecology and Evolution*, 25(6):345–353, 2010. ISSN 01695347. doi: 10.1016/j.tree.2010.01.007.
35. Sarah A Corbet. Conserving compartments in pollination webs. *Conservation biology*, 14(5):1229–1231, 2000.
36. R Core Team. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria, 2019.
37. C. F. Dormann, J. Frueund, N. Bluthgen, and B. Gruber. Indices, graphs and null models: analyzing bipartite ecological networks. *The Open Ecology Journal*, 2:7–24, 2009.
38. Gabor Csardi and Tamas Nepusz. The igraph software package for complex network research. *InterJournal, Complex Systems*, page 1695, 2006.
39. Colin Carlson. *codependent: Bipartite network rarefaction for affiliate species richness*, 2019. R package version 0.1.1.
40. Francois Keck, Frederic Rimet, Agnes Bouchez, and Alain Franc. phylosignal: an r package to measure, test, and explore the phylogenetic signal. *Ecology and Evolution*, 6(9):2774–2780, 2016. doi: 10.1002/ece3.2051.
41. Douglas Bates, Martin Mächler, Ben Bolker, and Steve Walker. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1):1–48, 2015. doi: 10.18637/jss.v067.i01.
42. Joseph E. Cavanaugh. Unifying the derivations for the Akaike and corrected Akaike information criteria. *Statistics & Probability Letters*, 33(2):201–208, 1997. ISSN 01677152. doi: 10.1016/s0167-7152(96)00128-9.

## Supplementary Information

**SI Data Table 1** — Source studies contributing data to the Web of Life and InteractionWeb Database repositories, which were used in the present analysis; MS Excel spreadsheet

**SI Data Table 2** — Plant taxa, annotated floral symmetry, and pollinator counts; CSV formatted text file