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 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,

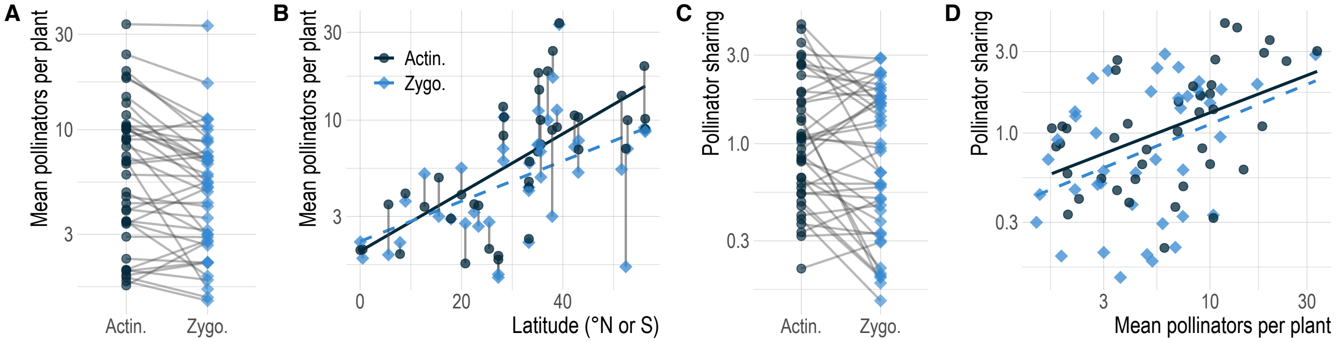

Fig. 1. (A) Pollinator diversity per plant across paired sub-networks of flowers with actinomorphic (dark circles) or zygomorphic (light diamonds) symmetry (one-sided paired Wilcoxon test, $p < 0.001$). (B) Pollinator diversity versus latitude north or south, with linear regression lines for each symmetry 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[1]

	Correlations with $\bar{N}_{pollinators}$			
	Actinomorphic		Zygomorphic	
Network metric	ρ	$P(\rho)$	ρ	$P(\rho)$
Connectance	$\mathbf{-0.48}$	0.002	$\mathbf{-0.59}$	$< 10^{-4}$
Web asymmetry	$\mathbf{0.88}$	$< 10^{-10}$	$\mathbf{0.92}$	$< 10^{-10}$
Nestedness	-0.29	0.08	$\mathbf{-0.44}$	0.004
Modularity	0.02	0.92	0.06	0.75
Codependency	$\mathbf{0.37}$	0.02	$\mathbf{0.29}$	0.05
Pollinator sharing	$\mathbf{0.48}$	0.001	$\mathbf{0.40}$	0.02
Host sharing	$\mathbf{-0.41}$	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) and the Interaction Web DataBase (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).

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.

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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