Zygomorphic flowers have fewer visitors

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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 floral visitation records in 159 communities around the world and classified the plants' floral symmetry. Globally and within individual communities, plant species with zygomorphic flowers are indeed visited by fewer pollinator species. 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

A textbook axiom of pollination ecology is that flowers with bilateral symmetry are more specialized than flowers with radial symmetry [1–4]. What this means, however, varies 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 particular set of pollinators (i.e., pollination syndromes; [6,7]) — or, finally, it may refer to association with a smaller set of available pollinators than seen for other comparable plant species [8]. Zygomorphic flowers are derived within the angiosperms [9,10], and extensive research examines how floral structure attracts, guides, or excludes pollinators [5,6,11–14]. However, data addressing the fourth 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 [1,3,15]. Zygomorphy is associated with greater net rates of speciation [16,17], consistent with the hypothesis that using fewer or more constant pollinators creates more opportunities for reproductive isolation [18]. Greater pollination specialization might also interact with global patterns of diversity, such as latitudinal gradients [19,20]: recent syntheses find evidence that biotic interactions are stronger in the tropics [21,22], though assessments of latitudinal effects on pollination specifically have mixed results [23,24].

Floral symmetry has been broadly considered as an element of pollination syndromes [6,7], but to our knowledge, direct documentation that zygomorphic flowers associate with fewer pollinators is restricted to anecdotal observations (e.g. [1,3,5]). Broad confirmation of this understanding would illuminate the extensive research linking pollination to diversification [1,15,17,18,25]. 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.

If floral symmetry creates systematic differences in pollinator associations, these differences should manifest in plant-pollinator visitation networks. Plant-pollinator associations have been prominent case studies in the development of ecological network theory, including network structure and assembly [26–28], global patterns of biodiversity [23,24], and evolutionary stability against species losses [29]. Association networks provide community-level perspective on the diversity of animals visiting flowers with particular traits, and public databases of plant-visitor association compiled for studies of network structure have global coverage to examine visitor diversity and sharing among co-occurring angiosperm species. Here, we test the hypothesis that zygomorphic flowers have fewer pollinators 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 Interaction Web DataBase (www.nceas.ucsb.edu/interactionweb), identified unique plant 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 species from the working dataset if we were unable to find authoritative descriptions or images, or if they were wind-pollinated. Data and scripts have been posted to Github, at github.com/JBYoderLab/floral_symmetry_visitation.

We conducted analysis in R v. 3.6.2 [30]. For each plant species in the dataset, we totalled the 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 examined the structure of complete networks, and of the sub-networks of visitors to plants with each type of floral symmetry in each community, calculating connectance, web asymmetry, and coextinction curves [31] using the `networklevel()` and `second.extinct()` functions in the `bipartite` package [32].

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 [33], using the `congeneric.merge()` function from the package `pez` [34] to add species to the tree if they were not already included. We tested for phylogenetic signal using the `phylosignal` package [35], estimating Blomberg's K and K* [36], Abouheif's C_{mean} [37], Moran's I [38], and Pagel's λ [39] statistics. We performed principal

component analysis of the phylogenetic distance matrix for all plant taxa and used phylogenetic distance principal components as covariates in 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 Bayesian multilevel regression models using the `brms` package [40,41]. Competing models explained visitor count and sharing with a group effect of source network identity and possible population effects of floral symmetry, latitude, and the first two principal components of the phylogenetic distance matrix (which jointly explained 61% of variation). We compared model fit in terms of the expected log pointwise predictive density (ELPD) using leave-one-out cross-validation, implemented in `brms` with the `LOO()` function [42].

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 the floral symmetry of plant species in all networks. Globally, and across individual networks, zygomorphic flowers were a minority: Of 2,715 species for which we could identify floral symmetry, 498 (18%) were zygomorphic; only five networks had more zygomorphic than actinomorphic species, while 70 lacked any (Figure 1B). Across all observed visits, the number of visitors to zygomorphic flowers was significantly smaller than that for actinomorphic flowers (median 4 pollinators per species with zygomorphic flowers versus 5 per species with actinomorphic flowers; $p = 0.003$, one-tailed Wilcoxon test; Figure 1C). At the same time, zygomorphic flowers shared a somewhat higher proportion of their visitors with other species in

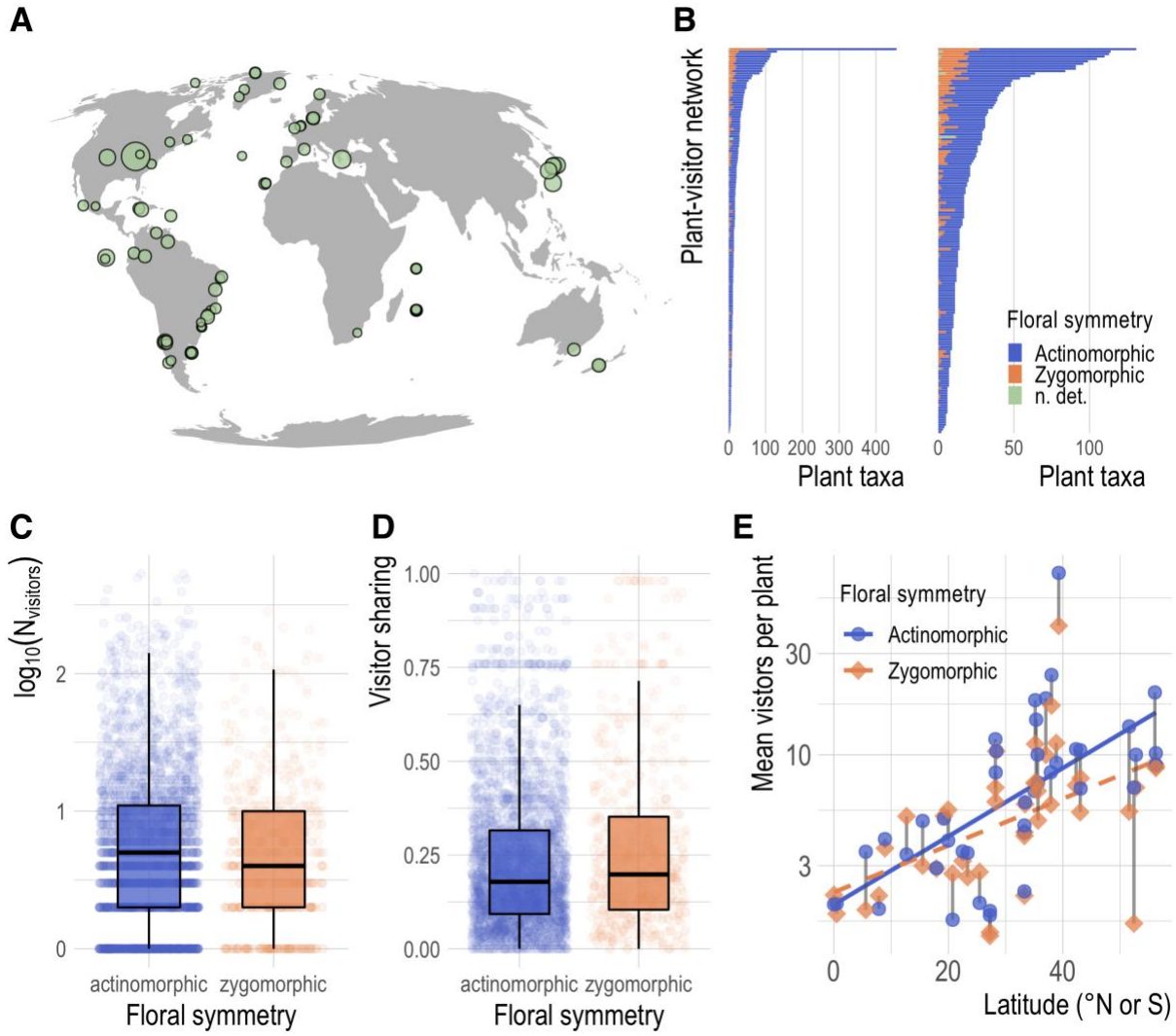

Figure 1. The global plant visitation dataset. (A) Global distribution of the plant-visitor networks in our compiled dataset, with points scaled to indicate relative size, in terms of plant taxa. (B) Bar plots giving the number of plant taxa for each network, coloured according to floral symmetry annotation (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.

the same community (median 0.20 for zygomorphic versus 0.18 for actinomorphic, $p = 0.003$; Figure 1D). We found significant phylogenetic signal for floral symmetry ($C_{mean} = 0.85$, Moran's

$I = 0.10$, $K = 0.20$, $K^* = 0.22$, and $\lambda = 0.89$; $p < 0.001$ for all); visitor count significantly deviated from the null models for C_{mean}, I, and λ ($p < 0.001$ for each) but not for K and K*.

Thirty-nine networks comprising 46,026 visitation records included enough plant species of each symmetry type (at least five) to compare sub-networks based on symmetry — that is, to compare visitation networks for plants with different symmetry having access to the same pool of possible pollinators. Zygomorphic sub-networks had significantly fewer mean visitors per plant (one-tailed paired Wilcoxon test, $p < 0.001$; Figure 2A), 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 ($p < 0.001$), 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 species, a higher 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 or plant coextinction robustness.

The best-fit Bayesian regression model explaining visitor count 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 ($R^2 = 0.28$; $\Delta ELPD \geq 3.8$ versus all other models; Supplementary Tables 2, 3). For

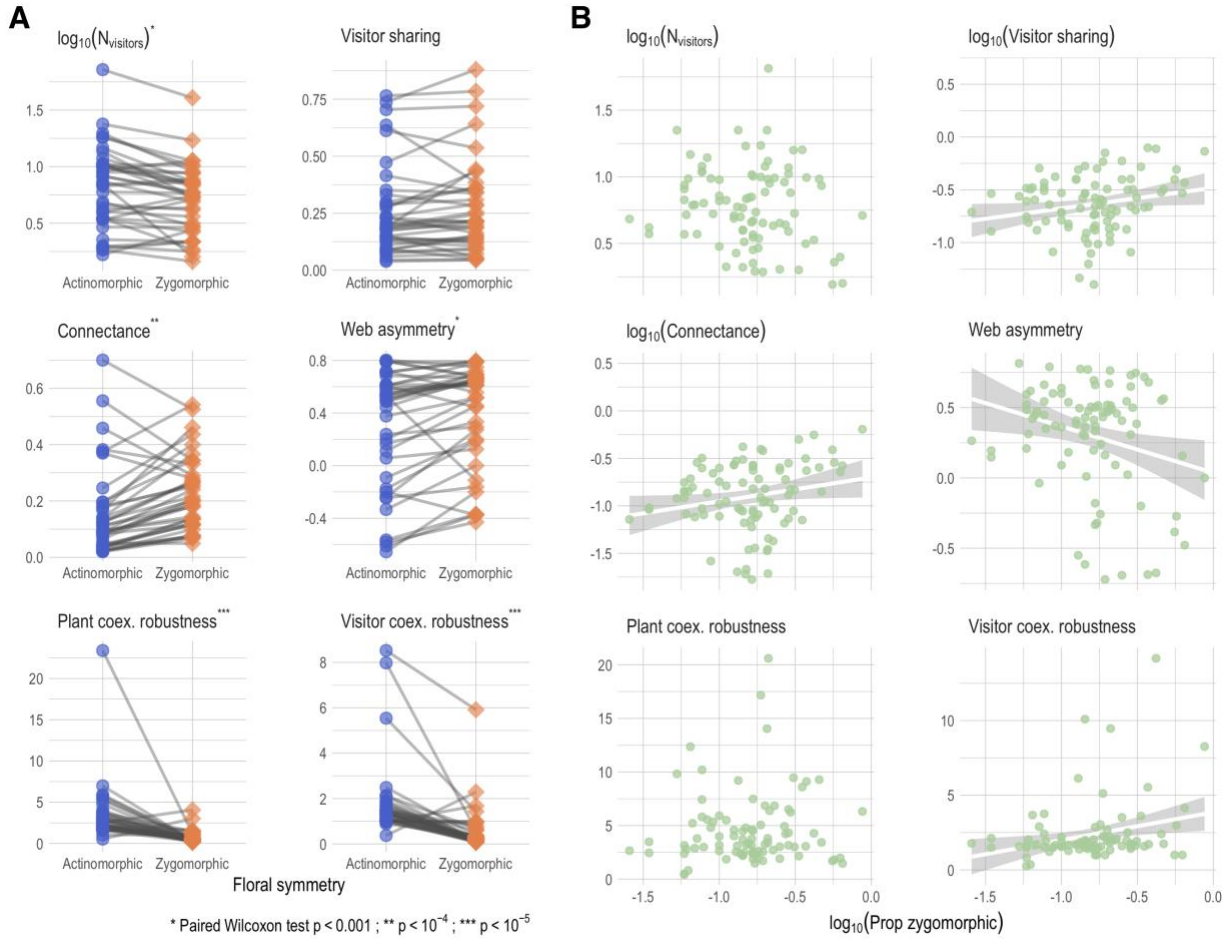

Figure 2. Floral symmetry and plant-visitor network structure. (A) Comparisons of subnetworks created based on floral symmetry, for mean number of visitors per plant, visitor sharing, connectance, web asymmetry, nestedness, modularity, and coextinction robustness from the perspectives of both plants 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 $p \leq 0.05$.

visitor sharing, the best-fit model also included all terms; but all simpler that included an effect of floral symmetry had $\Delta ELPD \leq 0.6$ ($R_2 = 0.66$ for all such models; Supplementary Tables 4, 5).

DISCUSSION

The classic hypothesis of floral symmetry is that zygomorphic flowers have more specialized pollination — which could mean that they are visited by fewer pollinator species. We find that, globally and at the level of individual visitation 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 these differences in visitor diversity (Figure 1C,D; Figure 2). Sub-networks of plants with zygomorphic flowers show significantly greater connectance, greater web asymmetry, and lower coextinction robustness for both plants and visitors (Figure 2A); and full visitation networks with more zygomorphic flowers show broadly parallel patterns (Figure 2B). Floral symmetry and visitor count 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. Bayesian multilevel regression that accounts for these potential confounding effects nevertheless finds significant effects of floral symmetry on visitor count and sharing.

The visitation network data we examine here have notable limitations for assessing pollination specialization. Many of the individual datasets do not evaluate visitors' pollen transfer, and often treat interactions 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. However, we think it unlikely that data restricted to effective pollinators would reverse the qualitative pattern we see in our analysis — unless there

is some way in which observations of visitation is systematically biased based on floral symmetry.

Visitor sharing, as calculated from this data, may similarly 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 a foraging trip, a key concept in the theory of plant-pollinator specialization [1,18]. 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 [28], 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 visitor 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 consistently 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 [1,5,16–18]. Selective benefits to floral forms that control pollinator access include reduced receipt of heterospecific pollen [1,18] and more effective transfer of conspecific pollen [5,43]. An ecological association between floral symmetry

and pollinator diversity also provides context for documented associations between floral zygomorphy and diversification [16,17,44]. The direction of the causal relationship, however, remains ambiguous. It may be that association with a smaller set of pollinators creates more opportunities for to evolve reproductive isolation [1,18,44]; but it may also be that more specialized pollination associations allow lineages to subdivide other axes of ecological variation more finely [17,25].

Our results also have important implications for conservation. Despite significant uncertainty surrounding the magnitude of global insect defaunation, pollinators are widely known to be in rapid decline due to pesticide use, habitat degradation, and emerging infections [45,46]. As we find, zygomorphic species may be more vulnerable to coextinction with pollinators and may be responsible for more pollinator co-extinctions if they themselves are lost (Figure 2A). The patterns we find are coarse, but 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 support 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 [47].

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DATA, CODE, AND MATERIALS

Data including floral symmetry annotations, visitor counts and sharing, and network structure statistics are available with scripts in a Github repository, github.com/JBYoderLab/floral_symmetry_visitation

COMPETING INTERESTS

The authors declare no competing interests.

AUTHORS' CONTRIBUTIONS

JBY and CJC conceived and designed the study; GG annotated 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 gave final approval for publication and agree to be held accountable for the work performed.

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