Zygomorphic flowers are visited by fewer species

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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 pollinator species 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, plants with zygomorphic flowers are indeed visited by fewer species. At the same time, zygomorphic flowers share a somewhat larger proportion of their visitor species with other co-occurring plant species, and have particularly high sharing with co-occurring plants that also have zygomorphic flowers. The structures of visitation sub-networks for plants with different floral symmetry also differ in ways that may arise from differences in visitor diversity, with sub-networks of zygomorphic species showing greater connectance, greater asymmetry, and lower coextinction robustness of both plants and visitor species. 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]. “Specialized,” however, has multiple meanings in evolution and ecology, and more than one may apply in any particular case. 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 pollinator species 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 may be 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 more effective pollination [1,3,15]. Zygomorphy is associated with greater net rates of speciation [16–18], consistent with the hypothesis that using fewer or more constant pollinators creates more opportunities for reproductive isolation [19]. Greater pollination specialization might also interact with global patterns of diversity, such as latitudinal gradients [20,21]: recent syntheses find evidence that biotic interactions are stronger in the tropics [22,23], though assessments of latitudinal effects on pollination specifically have mixed results [24,25].

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 pollinator species is restricted to anecdotal observations (e.g. [1,3,5]). Broad confirmation of this understanding would illuminate the extensive research linking pollination to diversification [1,15,17,19,26]. Ecologically, the use of fewer pollinators by zygomorphic flowers may have implications for factors ranging from species' geographic extents and their risks of local extinction due to pollinator loss.

If floral symmetry creates systematic differences in pollinator associations, these differences should manifest in floral visitation networks. Plant-pollinator associations have been prominent case studies in studies of investigations of ecological networks' structure and assembly [27–29], geographic variation [24,25], and evolutionary stability [30]. Public databases of floral visitation networks have global coverage, making it possible to examine visitor diversity and sharing among co-occurring angiosperm species across a variety of contexts. Here, we compile a global dataset of floral visitation records to test the hypothesis that zygomorphic flowers have fewer visitor species, and examine how this effect of floral symmetry may shape plant-pollinator networks.

METHODS

We compiled floral visitation networks from the Web of Life (www.web-of-life.es) and Interaction Web DataBase (www.nceas.ucsb.edu/interactionweb). Networks varied widely in size, attributable to heterogeneity in the time periods over which they were studied, the standards by which visits were recorded, and the geographic range of communities represented (Figure 1).

We accounted for this heterogeneity in subsequent analyses by simplifying visitation into a binary state, and by examining contrasts within individual networks or treating network identity as a random effect (see below).

We identified unique plant taxa (hereafter 'species'; identification of both plants and visitors varied in taxonomic resolution, but 95% of records had plants identified to species), 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. We determined symmetry based on the perianth, but in ambiguous cases also considered symmetry of the androecium or gynoecium; for example, a flower with a very nearly radially symmetric corolla, but stamens arrayed in a bilaterally symmetric manner, would be coded as zygomorphic. 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 (designated "n. det." in Figure 1B). Data and scripts have been posted to Github, at github.com/JBYoderLab/floral_symmetry_visitation.

We conducted analysis in R v. 4.0 [31]. For each plant species in the dataset, we totalled the visitor species recorded, and calculated an index of visitor species sharing, the proportion of visitor species to each plant species that also visit each other co-occurring plant species, averaged across the co-occurring plant species:

$$\frac{\sum_{j=1}^{n} p_{ij}}{n} \qquad \text{Eq. 1}$$

Where p_{ij} is the proportion of visitors to focal plant *i* that also visit co-occurring plant *j* in a group of *n* co-occurring plant species. We calculated sharing with all plants in the same network, and sharing with plants in the same network having each type of floral symmetry. 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 (the realized proportion of possible plant-visitor links [32]), web asymmetry (the degree to which visitor species outnumber plants or vice-versa), and coextinction curves (the relationship between species losses in one trophic level and species losses in another [33]) using the `networklevel()` and `second.extinct()` functions in the `bipartite` package [34].

To test for phylogenetic signal in floral symmetry, visitor species counts, and visitor species sharing, and to control for phylogeny in subsequent analysis, we mapped taxa in our dataset to a recently published time-calibrated supertree of the seed plants [35], using the `congeneric.merge()` function from the package `pez` [36] to add species to the tree if they were not already included. We tested for phylogenetic signal using the `phylosignal` package [37], estimating Blomberg's K and K* [38], Abouheif's C_{mean} [39], Moran's I [40], and Pagel's λ [41] 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 species count and visitor species sharing differed with respect to floral symmetry by fitting Bayesian multilevel regression models using the `brms` package [42,43]. Competing models explained visitor count and sharing with a group effect

(analogous to a random effect in a ML framework) of source network identity and possible population (i.e., fixed) effects of floral symmetry, latitude, and the first two principal components of phylogenetic distance (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 [44].

RESULTS

We compiled 159 plant-visitor networks, recording 53,609 observed visits to 2,700 angiosperm species (Figure 1A; Supplementary Table 1). We were able to classify floral symmetry for 2,685 plant species, and were able to place 2,582 of these in the time-calibrated supertree [35]. Globally, and in individual networks, zygomorphic flowers were a minority: Overall, 498 species (18%) were zygomorphic; only five networks had more zygomorphic than actinomorphic species, while 70 lacked any (Figure 1B). Across all networks, the number of visitor species 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). 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 species number significantly deviated from the null models for C_{mean}, I, and λ ($p < 0.001$ for each) but not for K and K*.

At the same time, zygomorphic flowers shared a somewhat higher proportion of their visitor species with co-occurring plants (median 0.20 for zygomorphic versus 0.18 for actinomorphic, $p = 0.003$; Figure 1D). Plants also had greater sharing with co-occurring plants of the same floral

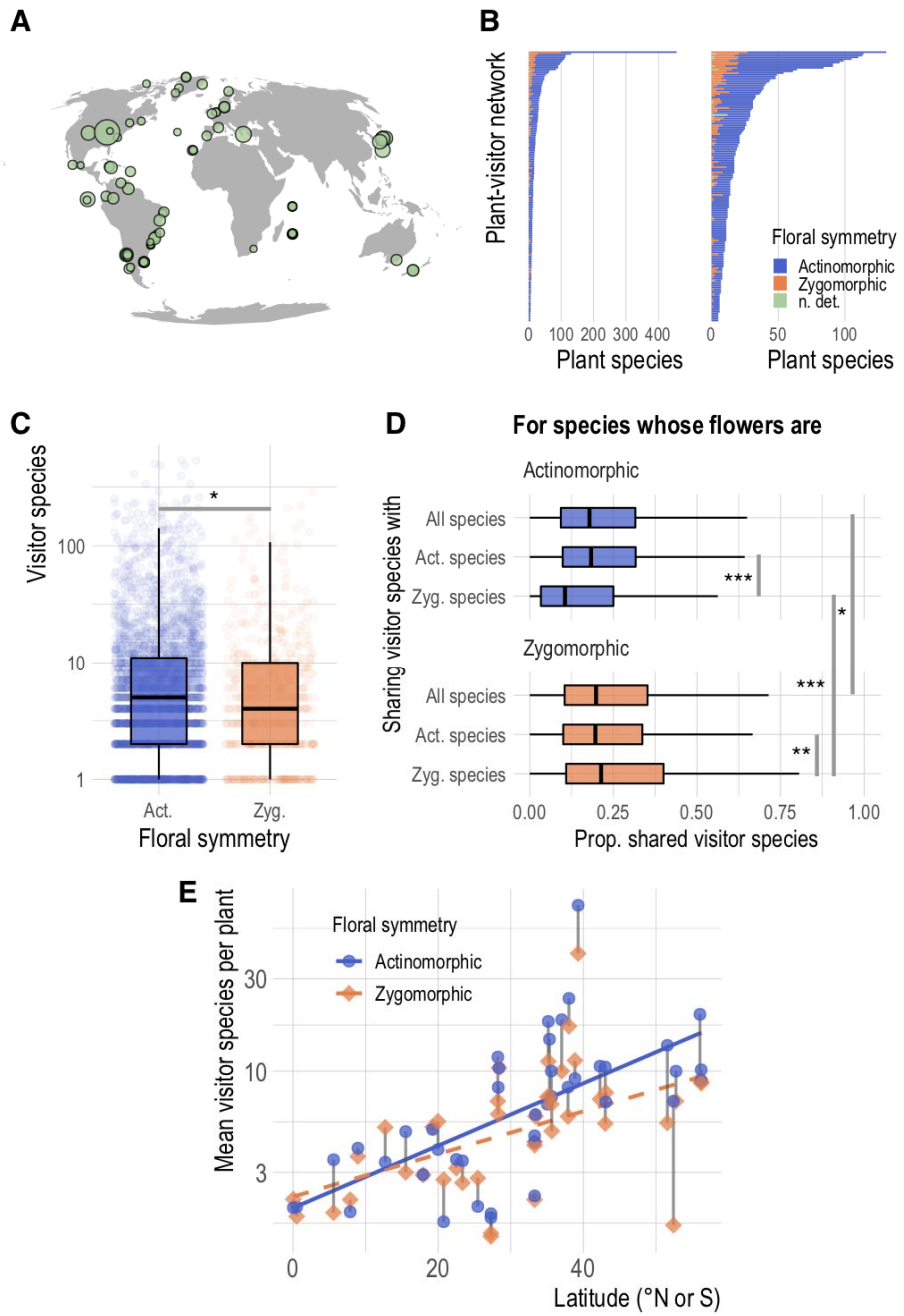

Figure 1. The global plant visitation dataset. (A) Global distribution of the plant-visitor networks, with points scaled to indicate numbers of plant taxa. (B) Bar plots giving the number of plant taxa for each network, coloured according to floral symmetry (left, full dataset, right, all networks except for the largest, to provide better visibility. (C) Visitor species per plant, grouped by floral symmetry. (D) Sharing of visitor species with all co-occurring plant species, and co-occurring species with each type of floral symmetry. (E) Mean visitor species per plant in sub-networks for plants with differing symmetries, with grey lines linking points for zygomorphic and actinomorphic taxa from the same network, plotted against latitude of the network location. In (C) and (D), asterisks indicate significant differences in one-tailed Wilcoxon tests: * $p < 0.01$, ** $p < 10^{-4}$, *** $p < 10^{-5}$.

symmetry (actinomorphic species, median sharing of 0.24 with actinomorphic species versus 0.19 with zygomorphic species, $p = 0.003$; zygomorphic species, median sharing of 0.30 with zygomorphic species versus 0.27 with actinomorphic species; $p < 10^{-5}$; Figure 1D). This meant that zygomorphic species and actinomorphic species did not significantly differ in their sharing with actinomorphic species (median of 0.24 versus 0.27; $p = 0.08$) but zygomorphic species had substantially higher sharing with zygomorphic species than actinomorphic species (0.30 versus 0.19; $p < 10^{-5}$).

Thirty-nine networks comprising 46,026 visitation records included enough plants 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 visitor species. Zygomorphic sub-networks had significantly fewer mean visitor species per plant (one-tailed paired Wilcoxon test, $p < 0.001$; Figure 2A), but only marginally greater visitor sharing ($p = 0.06$). Zygomorphic sub-networks had 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 that included at least one zygomorphic plant, a higher proportion of zygomorphic plants was significantly associated with greater visitor sharing (Figure 2B; product moment correlation on log-transformed values = 0.22, $p = 0.04$) and greater connectance (cor = 0.21, $p = 0.04$), paralleling the sub-network results. However, networks with more zygomorphic flowers also had lower web asymmetry (cor = -0.26, $p = 0.01$), and greater visitor coextinction robustness (cor = 0.27, $p = 0.01$), the opposite of patterns seen in symmetry-based sub-networks. The proportion of zygomorphic flowers was not correlated with the mean number of visitors per

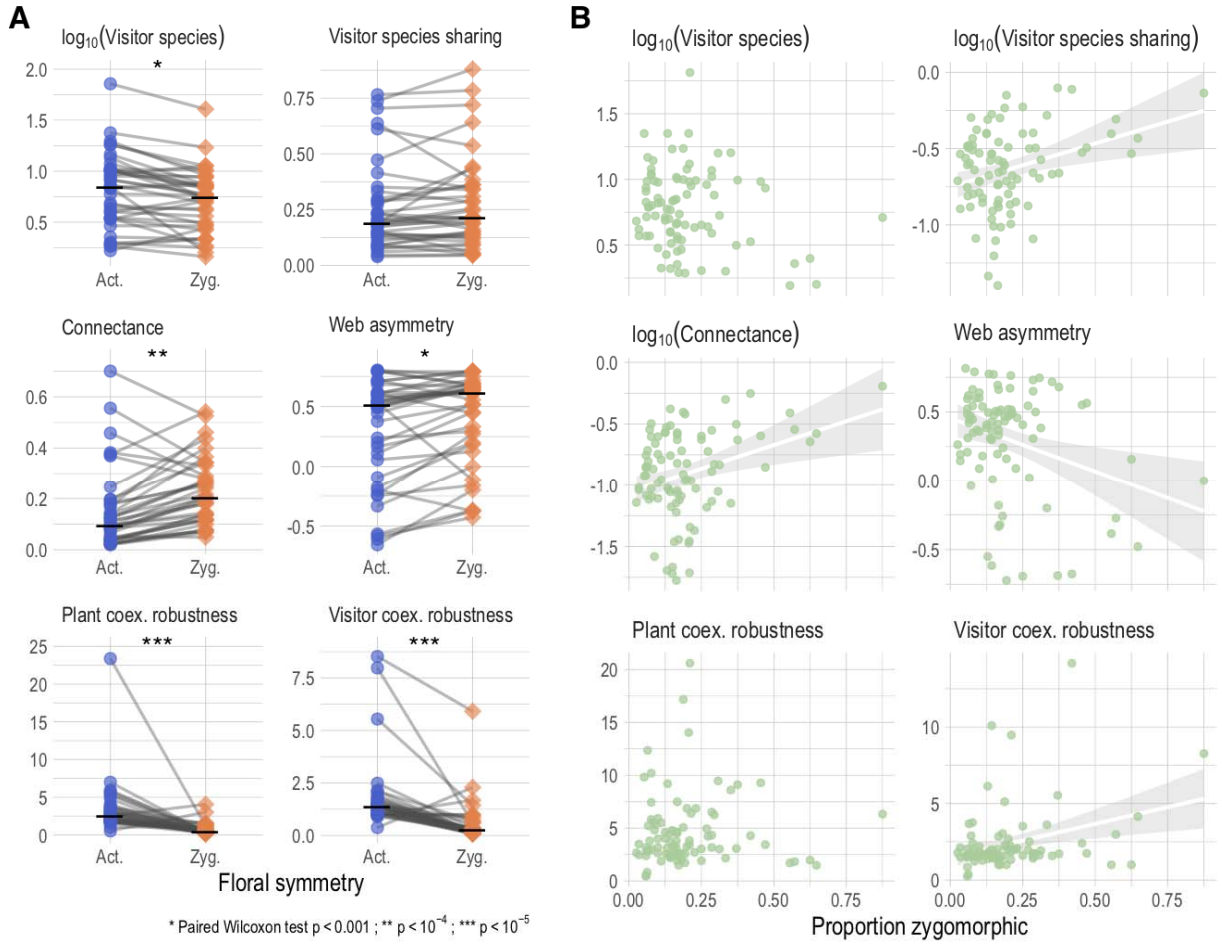

Figure 2. Floral symmetry and plant-visitor network structure. (A) Network descriptive statistics for sub-networks based on floral symmetry. Grey lines link points representing zygomorphic and actinomorphic sub-networks from the same source network, horizontal black bars mark the median value within each floral symmetry type, and asterisks mark significant differences in one-tailed paired Wilcoxon tests. (B) Scatterplots of 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 95% CI) are given when the correlation is significant with $p \leq 0.05$.

plant or plant coextinction robustness.

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

sharing, the best-fit model also included all terms; but all simpler models 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

Zygomorphic flowers have long been considered to 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 communities, plant species with zygomorphic flowers do indeed have fewer visitor species, and that the visitation networks of plants with zygomorphic symmetry may be structured by this difference (Figure 1C,D; Figure 2A). Sub-networks of plants with zygomorphic flowers show greater connectance, greater web asymmetry, and lower coextinction robustness for both plants and visitors (Figure 2A); however, these patterns do not necessarily translate to whole visitation networks (Figure 2B). Visitor species count is correlated with latitude north or south (Figure 1E), and both floral symmetry and visitor count show significant phylogenetic structure. Bayesian multilevel regression that accounts for these potential confounding effects nevertheless finds significant effects of floral symmetry on visitor count and sharing.

The visitation records we examine have limitations for assessing pollination specialization. Many of the original studies do not evaluate visitors' pollen transfer, and often record interactions as a binary, while in reality floral visitors vary considerably in visitation frequency and effectiveness as pollinators. Thus, the effective pollinators of the plants in our dataset are likely a subset of recorded visitors. However, we think it unlikely that data restricted to effective pollinators would

reverse the qualitative pattern we see, because a reversal would require systematic bias based on floral symmetry in recording of visits.

Our findings that zygomorphic flowers share more of their visitor species make sense given the nature of our data and other aspects of pollinator specialization associated with zygomorphy. Arithmetically, a plant with fewer visitors can more easily share a high proportion of them even if the absolute number of visitors shared is low. Higher sharing by zygomorphic species probably also reflects network structure. Plant-visitation networks are generally nested [29], so the fact that zygomorphic species tend to have fewer visitor species means that their visitors are more likely to interact with many other plant taxa. Zygomorphic flowers, which often manipulate pollinator behaviour, apply pollen to specific parts of pollinators' bodies, or attract pollinators that show greater constancy over a single foraging trip, may be better able to tolerate the elevated risk of receiving heterospecific pollen arising from higher visitor sharing [1,19]. The fact that the highest rate of sharing we see in our data is between zygomorphic flowers and other co-occurring zygomorphic species is consistent with this hypothesis.

In our compiled dataset, plants with both types of floral symmetry had more visitor species in communities farther from the equator (Figure 1E). This could reflect bias in the resolution of species in more tropical communities, as there are more undescribed species in the tropics, and in the Global South [45]. We do find that networks farther from the equator have more plant and visitor species recorded (cor = 0.54 for plants, cor = 0.65 for visitors, $p < 10^{-5}$ for both; see Figure 1A). However, the correlation weakens or disappears if the comparison is with latitude rather than distance from the equator (i.e., treating distance south of the equator as different from

distance north: cor = 0.3, p = 0.69 for plants; cor = 0.16, p = 0.05 for visitors), suggesting this is not simply an issue of better taxonomy in the Global North. Moreover, if plant and visitor species numbers show similar correlations with distance from the equator, we might expect that the number of visitors *per* plant would be constant across latitudes, contrary to what we find. An alternative biological explanation is that floral visitation is more specialized in the tropics, independent of floral symmetry. Testing this hypothesis with greater rigor is beyond the scope of our data, but it would be consistent with recent syntheses finding stronger effects of biological interactions in the tropics [22,23].

An ecological association between floral symmetry and pollinator diversity provides context for evolutionary associations between floral zygomorphy and diversification [16,17,47]. The direction of the causal relationship, however, remains ambiguous. It may be that association with fewer pollinators creates more opportunities to evolve reproductive isolation [1,19,47] or increases the number of plant species that can be supported by a given community of pollinators [17]; or it may be that more specialized pollination associations evolve in response to greater diversity as co-occurring species must subdivide available pollinators more finely [26].

Our results also have important implications for conservation. Most directly, we find lower coextinction robustness for sub-networks of plants with zygomorphic flowers, which may be explained by higher connectance and asymmetry in the same sub-networks (Figure 2A) and higher visitor species sharing among zygomorphic plant species (Figure 1D). These patterns are not necessarily borne out at the level of whole plant communities (Figure 2B), suggesting that larger communities may be robust to disturbances that endanger their most specialized members.

Nevertheless, our examination of sub-networks defined by floral symmetry does suggest that plant taxa with zygomorphic flowers are at greater risk of extinction due to pollinator loss. Despite significant uncertainty in the magnitude of global insect defaunation, pollinators are widely known to be in rapid decline due to pesticide use, habitat degradation, and emerging infections [48,49]. The patterns we find are coarse, but simple rubrics for triage are critical for conserving the more than 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 [50].

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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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