

1 **Zygomorphic flowers have fewer potential pollinator species**

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15 **ABSTRACT**

16 Botanists have long identified bilaterally symmetrical (zygomorphic) flowers with more
17 specialized pollination interactions than radially symmetrical (actinomorphic) flowers.
18 Zygomorphic flowers facilitate more precise contact with pollinators, guide pollinator behaviour,
19 and exclude less effective pollinators. However, whether zygomorphic flowers are actually
20 visited by a smaller subset of available pollinator species has not been broadly evaluated. We
21 compiled 53,609 floral visitation records in 159 communities and classified the plants' floral
22 symmetry. Globally and within individual communities, plants with zygomorphic flowers are
23 indeed visited by fewer species. At the same time, zygomorphic flowers share a somewhat larger
24 proportion of their visitor species with other co-occurring plants, and have particularly high
25 sharing with co-occurring plants that also have zygomorphic flowers. Visitation sub-networks for
26 zygomorphic species also show differences that may arise from reduced visitor diversity,
27 including greater connectance, greater web asymmetry, and lower coextinction robustness of
28 both plants and visitor species — but these changes do not necessarily translate to whole plant-
29 visitor communities. These results provide context for widely documented associations between
30 zygomorphy and diversification and imply that species with zygomorphic flowers may face
31 greater risk of extinction due to pollinator loss.

32

33 INTRODUCTION

34 An axiom of pollination ecology is that flowers with bilateral symmetry are more specialized
35 than flowers with radial symmetry [1–4]. “Specialized,” however, has multiple meanings in
36 evolution and ecology, which are not mutually exclusive. Specialization may refer to a derived
37 character state in a phylogenetic context [1,3], or the degree to which a flower manipulates
38 pollinator behaviour [5], or it may refer to association with a particular set of pollinators (i.e.,
39 pollination syndromes; [6,7]) — or, finally, it may refer to association with fewer available
40 pollinator species than seen for comparable plant species [8]. Zygomorphic flowers are derived
41 within the angiosperms [9–11], and extensive research examines how floral structure attracts,
42 guides, or excludes pollinators [5,6,12–15]. However, data addressing the fourth sense in which
43 zygomorphic flowers may be specialized — association with fewer pollinators than otherwise
44 expected — are surprisingly sparse.

45
46 Floral symmetry has been recognized as an important feature of angiosperm diversity since at
47 least the 18th Century [4]. Modern treatments identified zygomorphy as derived, and
48 hypothesized that zygomorphic forms facilitate more effective pollination [1,3,16]. Zygomorphy
49 is associated with greater diversification rates [17–19], consistent with the hypothesis that using
50 fewer or more constant pollinators creates more opportunities for reproductive isolation [20].
51 Greater pollination specialization might also interact with global patterns of diversity, such as
52 latitudinal gradients [21,22]: recent syntheses find evidence that biotic interactions are stronger
53 in the tropics [23,24], though assessments of latitudinal effects on pollination specifically have
54 mixed results [25,26].

55

56 Floral symmetry has been considered as an element of pollination syndromes [6,7], but to our
57 knowledge, documentation that zygomorphic flowers associate with fewer pollinator species is
58 restricted to anecdotal observations (e.g. [1,3,5]). Broad confirmation of this understanding
59 would illuminate the research linking pollination to diversification [1,16,18,20,27]. Ecologically,
60 the use of fewer pollinators by zygomorphic flowers may have implications for factors ranging
61 from species' geographic extents to risks of extinction due to pollinator loss.

62
63 If floral symmetry creates systematic differences in pollinator associations, these differences
64 should manifest in floral visitation networks. Plant-pollinator associations have been prominent
65 case studies in investigations of ecological networks' structure and assembly [28–30], geographic
66 variation [25,26], and evolutionary stability [31]. Databases of floral visitation networks have
67 global coverage, recording visitor diversity and sharing among co-occurring angiosperm species
68 across a variety of contexts. Here, we compile a global dataset of floral visitation records to test
69 the hypothesis that zygomorphic flowers have fewer visitor species, and examine how this effect
70 may shape plant-pollinator networks.

71

72 **METHODS**

73 We compiled floral visitation networks from the Web of Life (www.web-of-life.es) and
74 Interaction Web DataBase (www.nceas.ucsb.edu/interactionweb). Networks varied widely in
75 size, attributable to heterogeneity in the time periods over which they were studied, their
76 observation protocols, and the geographic ranges of communities represented (Figure 1). We
77 accounted for this in subsequent analyses by simplifying visitation into a binary state (the most

78 common recording mode), and by examining contrasts within individual networks or treating
79 network identity as a random effect (see below).

80

81 We identified unique plant taxa across all networks (hereafter ‘species’; identification of plants
82 and visitors varied in resolution, but 95% of records had plants identified to species), and
83 classified their floral symmetry based on taxonomic knowledge, formal descriptions of species or
84 higher taxa, and, when necessary, inspecting images of herbarium sheets or reliably identified
85 fresh flowers. We determined symmetry based on the perianth, but in ambiguous cases also
86 considered symmetry of the androecium or gynoecium; for example, a flower with a very nearly
87 radially symmetric corolla, but stamens arrayed in a bilaterally symmetric manner, would be
88 coded as zygomorphic. In some cases, we classified symmetry not based on individual flowers
89 but on flowering heads (e.g., we considered species in the Asteraceae actinomorphic). We
90 removed species from the working dataset if we were unable to find authoritative descriptions or
91 images, or if they were wind-pollinated (“n. det.”, Figure 1B). Data and scripts are posted to
92 Dryad, at <https://datadryad.org/10.5061/dryad.gxd2547j3>

93

94 We conducted analysis in R v. 4.0 [32]. For each plant species in the dataset, we totalled the
95 visitor species recorded, and calculated an index of visitor species sharing, the proportion of
96 visitor species to each plant species that also visit each other co-occurring plant species,
97 averaged across the co-occurring plant species. We calculated sharing with all plants in the same
98 network, and sharing with plants in the same network having each type of floral symmetry. We
99 examined the structure of complete networks, and of the sub-networks of visitors to plants with
100 each type of floral symmetry in each community, calculating connectance (the realized

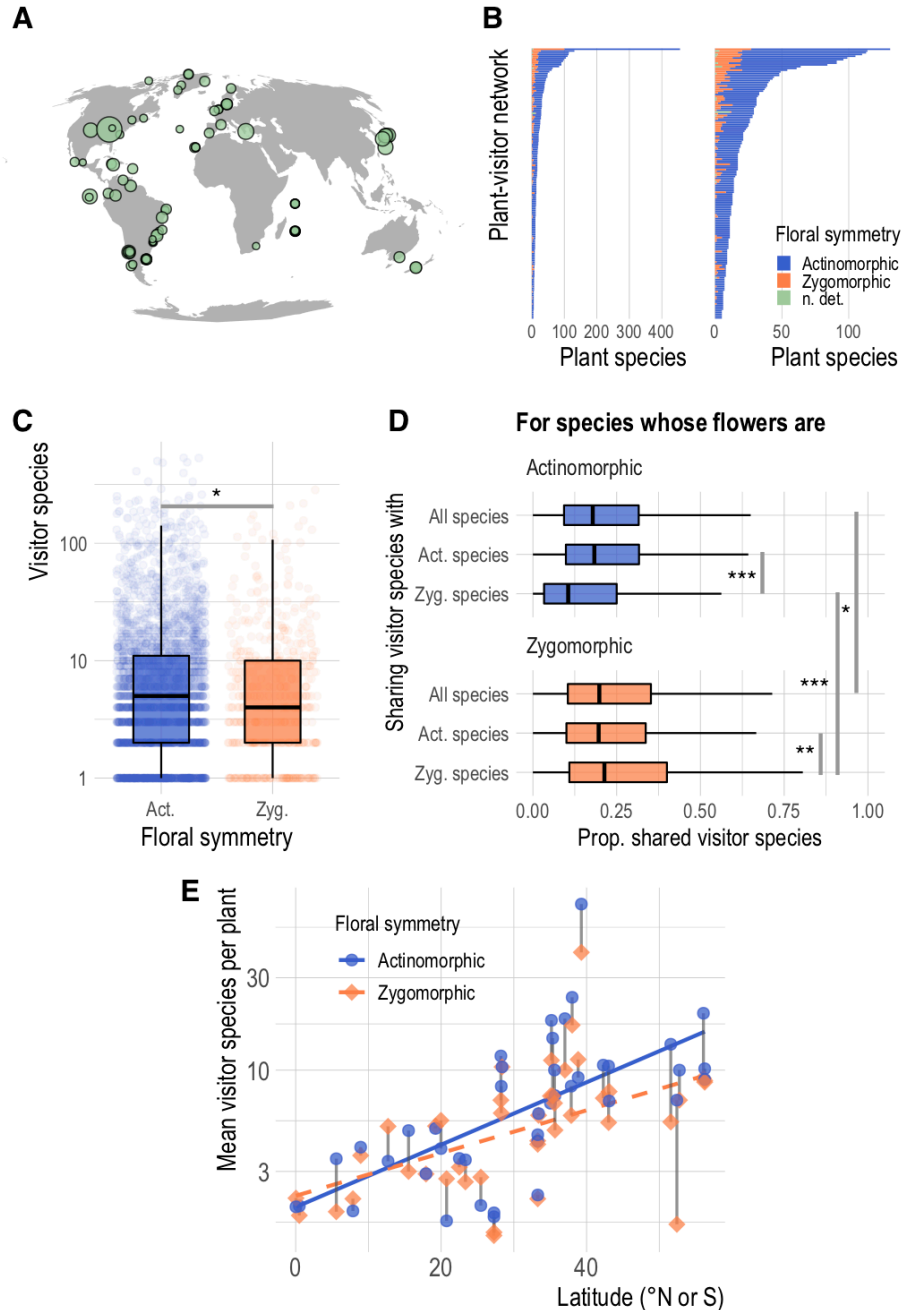
101 proportion of possible plant-visitor links [33]), web asymmetry (the degree to which visitor
102 species outnumber plant species or vice-versa), and coextinction curves (the relationship between
103 species losses in one trophic level and species losses in another [34]) using the
104 `networklevel()` and `second.extinct()` functions in the `bipartite` package [35].

105

106 To test for phylogenetic signal in floral symmetry, visitor species count, and visitor species
107 sharing, and to control for phylogeny in subsequent analysis, we mapped taxa in our dataset to a
108 recently published time-calibrated supertree of the seed plants (the “ALLMB” supertree of [36]),
109 using the `congeneric.merge()` function from the package `pez` [37] to add species to the
110 tree if they were not already included. We tested for phylogenetic signal using the
111 `phylosignal` package [38], estimating Blomberg’s K and K^* [39], Abouheif’s C_{mean} [40],
112 Moran’s I [41], and Pagel’s λ [42] statistics. We performed principal component analysis of the
113 phylogenetic distance matrix for all plant taxa and used phylogenetic distance principal
114 components as covariates in models fitted to explain variation in visitor count and sharing.

115

116 We tested the hypotheses that visitor species count and visitor species sharing differed with
117 respect to floral symmetry by fitting Bayesian multilevel regression models using the `brms`
118 package [43,44]. Competing models explained visitor count and sharing with a group effect
119 (analogous to a random effect in a ML framework) of source network identity and possible
120 population (i.e., fixed) effects of floral symmetry, latitude, and the first two principal components
121 of phylogenetic distance (which jointly explained 61% of variation). We compared model fit in
122 terms of expected log pointwise predictive density (ELPD) using leave-one-out cross-validation,
123 implemented in `brms` with the `LOO()` function [45].

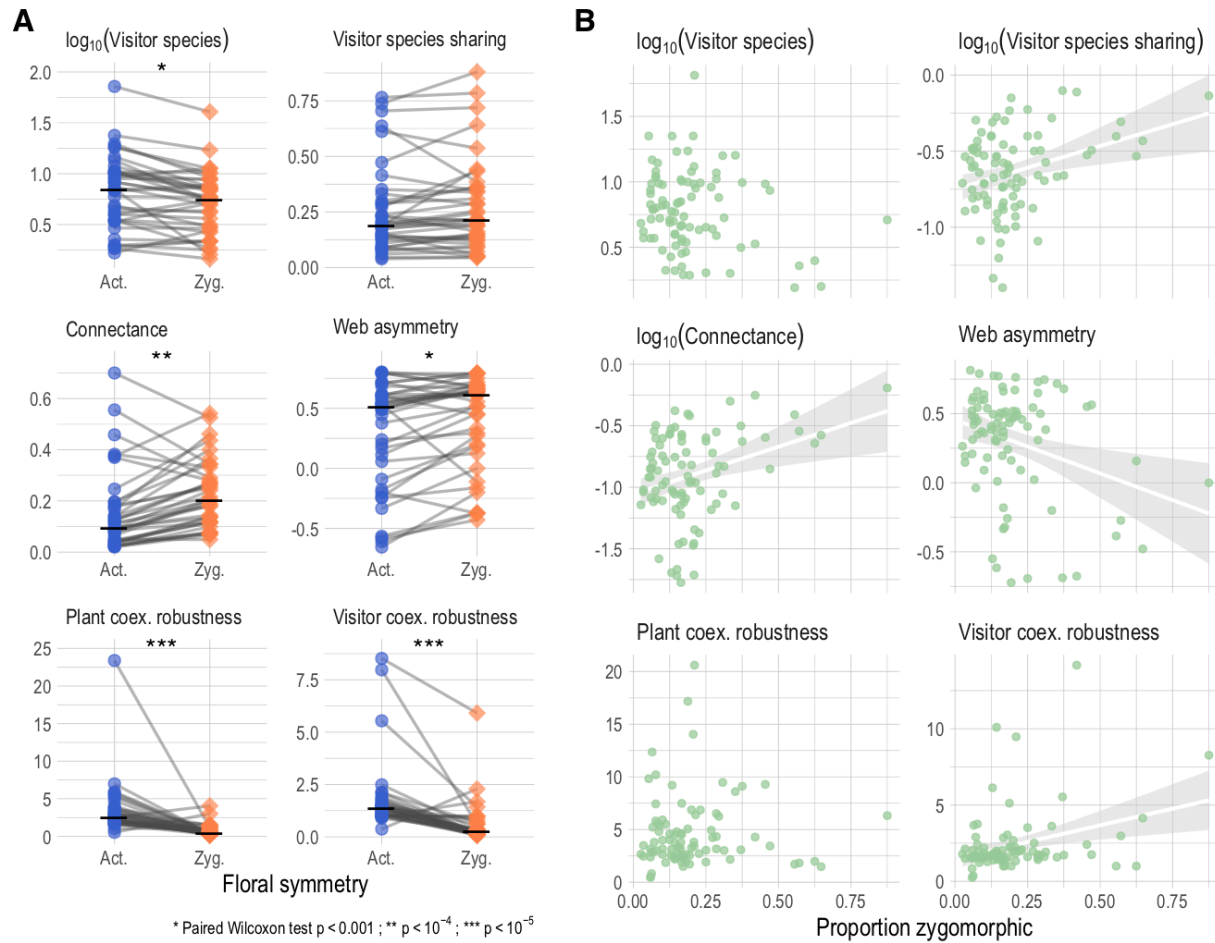


124
 125 **Figure 1. The global plant visitation dataset.** (A) Global distribution of the plant-visitor
 126 networks, with points scaled to indicate numbers of plant taxa. (B) Bar plots giving the number
 127 of plant taxa for each network, coloured according to floral symmetry (left, full dataset, right, all
 128 networks except for the largest, to provide better visibility). (C) Visitor species per plant, grouped
 129 by floral symmetry. (D) Sharing of visitor species with all co-occurring plant species, and co-
 130 occurring species with each type of floral symmetry. (E) Mean visitor species per plant in sub-
 131 networks for plants with differing symmetries, with grey lines linking points for zygomorphic
 132 and actinomorphic taxa from the same network, plotted against latitude of the network location.
 133 In (C) and (D), asterisks indicate significant differences in one-tailed Wilcoxon tests: * $p < 0.01$,
 134 ** $p < 10^{-4}$, *** $p < 10^{-5}$.

135 RESULTS

136 We compiled 159 networks, recording 53,609 observed visits to 2,700 angiosperm species
137 (Figure 1A; Supplementary Table 1). We were able to classify floral symmetry for 2,685 plant
138 species, and were able to place 2,582 of these in the time-calibrated supertree [36]. Globally, and
139 in individual networks, zygomorphic flowers were a minority: 498 species (18%) were
140 zygomorphic; only five networks had more zygomorphic than actinomorphic species, while 70
141 lacked any (Figure 1B). Globally, the number of visitor species to zygomorphic flowers was
142 significantly smaller than that for actinomorphic flowers (median 4 pollinators per zygomorphic
143 species with zygomorphic flowers versus 5 per actinomorphic species; $p = 0.003$, one-tailed
144 Wilcoxon test; Figure 1C). We found significant phylogenetic signal for floral symmetry ($C_{\text{mean}} =$
145 0.85 , Moran's $I = 0.10$, $K = 0.20$, $K^* = 0.22$, and $\lambda = 0.89$; $p < 0.001$ for all); visitor species
146 count deviated from the null models for C_{mean} , I , and λ ($p < 0.001$ for each) but not for K and K^* .
147
148 At the same time, zygomorphic flowers shared a higher proportion of their visitor species with
149 co-occurring plants (median 0.20 for zygomorphic versus 0.18 for actinomorphic, $p = 0.003$;
150 Figure 1D). Plants also had greater sharing with co-occurring plants of the same floral symmetry
151 (actinomorphic species, median sharing of 0.24 with actinomorphic species versus 0.19 with
152 zygomorphic species, $p = 0.003$; zygomorphic species, median sharing of 0.30 with zygomorphic
153 species versus 0.27 with actinomorphic species; $p < 10^{-5}$; Figure 1D).

154
155 Thirty-nine networks comprising 46,026 visitation records included enough plants of each
156 symmetry type (at least five) to compare sub-networks based on symmetry — that is, to compare
157 networks for plants with different symmetry having access to the same pool of possible visitor



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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 $p \leq 0.05$.

168 species. Zygomorphic sub-networks had significantly fewer mean visitor species per plant (one-
169 tailed paired Wilcoxon test, $p < 0.001$; Figure 2A), but only marginally greater visitor sharing
170 ($p = 0.06$). Zygomorphic sub-networks had significantly greater connectance ($p < 10^{-4}$), greater
171 asymmetry ($p < 0.001$), and lower coextinction robustness, as measured by the exponent of the
172 coextinction curve, for both plants ($p < 10^{-5}$) and visitors ($p < 10^{-5}$). Among 89 complete

173 networks that included at least one zygomorphic plant, a higher proportion of zygomorphic
174 plants was associated with greater visitor sharing (Figure 2B; product-moment correlation on
175 log-transformed values = 0.22, $p = 0.04$) and greater connectance ($\text{cor} = 0.21$, $p = 0.04$),
176 paralleling the sub-network patterns. However, networks with more zygomorphic flowers also
177 had lower asymmetry ($\text{cor} = -0.26$, $p = 0.01$), and greater visitor coextinction robustness ($\text{cor} =$
178 0.27 , $p = 0.01$), the opposite of patterns in symmetry-based sub-networks. The proportion of
179 zygomorphic flowers was not correlated with the mean number of visitors per plant or plant
180 coextinction robustness.

181
182 The best-fit model explaining visitor count included floral symmetry, latitude, an interaction
183 between symmetry and latitude, and phylogeny in addition to the group effect of network identity
184 ($R^2 = 0.28$; $\Delta\text{ELPD} \geq 3.8$ versus all other models; Supplementary Tables 2, 3). For visitor
185 sharing, the best-fit model also included all terms; but all simpler models that included an effect
186 of symmetry had $\Delta\text{ELPD} \leq 0.6$ ($R^2 = 0.66$ for all such models; Supplementary Tables 4, 5).

187

188 **DISCUSSION**

189 Zygomorphic flowers have long been considered to be more specialized, which could mean that
190 they are visited by fewer pollinator species. We find that, globally and at the level of individual
191 communities, plants with zygomorphic flowers do indeed have fewer visitor species, and that the
192 visitation networks of plants with zygomorphic symmetry may be structured by this difference
193 (Figure 1C,D; Figure 2A). Sub-networks of plants with zygomorphic flowers show greater
194 connectance, greater asymmetry, and lower coextinction robustness for both plants and visitors
195 (Figure 2A); however, these patterns do not necessarily translate to whole networks (Figure 2B).

196 Visitor species count is correlated with latitude north or south (Figure 1E), and both floral
197 symmetry and visitor count show significant phylogenetic structure. Bayesian multilevel
198 regressions accounting for these confounding effects nevertheless find significant effects of floral
199 symmetry on visitor species count and sharing.

200

201 The visitation records we examine have limitations for assessing pollination specialization. Many
202 of the original studies do not evaluate visitors' pollen transfer, and often record visits as a binary,
203 while in reality floral visitors vary considerably in visitation frequency and effectiveness as
204 pollinators. Thus, the effective pollinators of the plants in our dataset are likely a subset of
205 recorded visitors. However, we think it unlikely that data restricted to effective pollinators would
206 reverse the qualitative patterns we see, because a reversal would require systematic bias based on
207 floral symmetry in recording visits.

208

209 Our findings that zygomorphic flowers share more visitor species make sense given the other
210 aspects of pollinator specialization associated with zygomorphy. Arithmetically, a plant with
211 fewer visitors can more easily share a high proportion of them even if the absolute number of
212 visitors shared is low, but higher sharing by zygomorphic species probably also reflects network
213 structure. Plant-visitation networks are generally nested [30], so the fact that zygomorphic
214 species tend to have fewer visitor species means that their visitors are more likely to interact with
215 many other plant taxa. Zygomorphic flowers, which often manipulate pollinator behaviour, apply
216 pollen to specific parts of pollinators' bodies, or attract pollinators that show greater constancy
217 over a single foraging trip, may be better able to tolerate elevated risk of receiving heterospecific
218 pollen due to higher visitor sharing [1,20]. The fact that the highest rate of sharing we see in our

219 data is between zygomorphic flowers and other co-occurring zygomorphic species is consistent
220 with this hypothesis.

221

222 In our compiled dataset, plants with both types of floral symmetry had more visitor species in
223 communities farther from the equator (Figure 1E). This could reflect bias in the resolution of
224 species in more tropical communities, as there are more undescribed species in the tropics, and in
225 the Global South [46]. Networks farther from the equator do have more plant and visitor species
226 recorded (cor = 0.54 for plants, cor = 0.65 for visitors, $p < 10^{-5}$ for both; see Figure 1A).

227 However, the correlation weakens or disappears if the comparison is with latitude rather than
228 distance from the equator (i.e., treating distance south of the equator as different from distance
229 north: cor = 0.3, $p = 0.69$ for plants; cor = 0.16, $p = 0.05$ for visitors), suggesting this is not
230 simply an issue of better taxonomy in the Global North. Moreover, if plant and visitor species
231 numbers show similar correlations with distance from the equator, we might expect that the
232 number of visitors *per* plant would be constant across latitudes. An alternative explanation is that
233 floral visitation is more specialized in the tropics, independent of floral symmetry. Testing this
234 hypothesis with greater rigor is beyond the scope of our data, but it would be consistent with
235 recent syntheses finding stronger effects of biological interactions in the tropics [23,24].

236

237 An ecological association between floral symmetry and pollinator diversity may explain
238 evolutionary associations, across the angiosperms, between floral zygomorphy and
239 diversification [17,18,47]. The direction of the causal relationship, however, remains ambiguous.
240 It may be that association with fewer pollinators creates more opportunities to evolve
241 reproductive isolation [1,20,47] or increases the number of plant species that can be supported by

242 a given community of pollinators [18]; or it may be that more specialized pollination evolves in
243 response to greater diversity as co-occurring species must subdivide available pollinators more
244 finely [27].

245

246 Finally, our results have important implications for conservation. We find lower coextinction
247 robustness for sub-networks of plants with zygomorphic flowers, which may be explained by
248 higher connectance and asymmetry of these sub-networks (Figure 2A) and higher visitor sharing
249 among zygomorphic flowers (Figure 1D). These patterns are not necessarily borne out at the
250 level of whole communities (Figure 2B), suggesting that larger communities may be robust to
251 disturbances that endanger their most specialized members. Nevertheless, our analysis does
252 imply that plant taxa with zygomorphic flowers are at greater risk of extinction due to pollinator
253 loss. Despite significant uncertainty in the magnitude of losses, pollinators are widely known to
254 be in rapid decline due to pesticide use, habitat degradation, and emerging infections [48,49].
255 The patterns we find are coarse, but simple rubrics for triage are critical for conserving the more
256 than 300,000 species of angiosperms, most of which will never benefit from individualized
257 conservation assessment. Perhaps more importantly, our results support the idea that
258 “compartments” of the global plant-pollinator network must be targets for holistic conservation,
259 focused on preserving interactions and functionality where the network is most fragile [50].

260

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265 an adventure.

266

267 **DATA, CODE, AND MATERIALS**

268 Data including floral symmetry annotations, visitor counts and sharing, and network structure
269 statistics are available with scripts on Dryad, <https://datadryad.org/10.5061/dryad.gxd2547j3>

270

271 **COMPETING INTERESTS**

272 The authors declare no competing interests.

273

274 **AUTHORS' CONTRIBUTIONS**

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

279

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