

Attachment 2

THE SCALING UP OF COEVOLUTION IN POLLINATION NETWORKS BEYOND SPECIES PAIRS

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Abstract

On a macroevolutionary scale, processes such as coevolution can play a large role in determining who interacts with whom in ecological networks. However, it is unclear whether or how these phenomena are actually detectable in observed assemblages. Here, we aim to bridge this gap by using cophylogenetic analysis to scale up coevolution in 54 empirical pollination networks from the species pair to: (i) the entire interaction network and (ii) the modular structure of those networks. Our results suggest that the interaction and phylogenetic structures of pollination networks cannot be considered independent with 70% of networks showing significant cophylogeny. These significant patterns of cophylogeny suggest that macroscopic coevolution, as opposed to chance or vicariance, is responsible for the structure of pollination assemblages. At the intermediate scale—modules of tightly interacting groups of species—the patterns expected of macroscopic coevolution are not universally observed. Contrary to previous hypotheses, this suggests that topological modules as we understand them do not represent a fundamental macroscopic unit of coevolution and are more likely determined by multiple eco-evolutionary factors.

• **Keywords:** compartmentalization, diffuse coevolution, ecological networks, guild coevolution, modularity, mutualism, mutualistic networks, cophylogeny

1. Introduction

Species do not exist in isolation, but are instead constantly interacting with other species in the community. Each of these interactions can impact the fitness of individuals and lead to selection for amplification or avoidance of future interactions [1, 2]. When two species interact over enough time, reciprocal selection can lead to concurrent evolutionary change in both species [1]. This process is generally referred to as coevolution, and it often leads to the evolutionary trajectory of pairs of species, and potentially their descendants, becoming deeply intertwined [1]. The coevolution of species can have multiple outcomes, although these most simply can be generalised into two categories: microscopic and macroscopic. Akin to marcoecology—the study of large-scale ecological patterns—macroscopic coevolution can be considered the pattern of coupled divergence of interacting clades that implies a large degree of trait complementarity between interaction partners [3, 4, 5]. Conversely, microscopic coevolution—otherwise coadaptation or pairwise coevolution—is the reciprocal trait evolution of interacting species [1, 6].

At the microscopic level of species pairs, coevolution has been widely studied [1, 2], from corals and their zooxanthellae to symbiotic organelles in eukaryotes. Comparatively, the degree to which macroscopic coevolution is responsible for the structure and functioning of entire communities is poorly understood at the scale of taxonomically rich interacting clades [1, 7]. Among the ecological systems in which one might expect to observe coevolution at a community scale, the mutualistic assemblages of flowering plants and their pollinators are a logical candidate [8, 9]. This is because the positive feedback of mutualisms [9] and myriad examples of extreme pollination-driven coevolution (such as between figs and fig wasps) should make macroscopic coevolutionary signal particularly observable in pollination networks. Furthermore, the notion of diffuse coevolution tenets that, as most species interact with several partners, coevolution should manifest itself above specific pairs of plants and pollinators [1, 6, 10, 11].

Assessing the coevolution of communities is a long-standing question in evolutionary biology [1, 3, 7], and the ultimate solution requires consideration of both microscopic and macroscopic coevolutionary

40 processes [1, 12]. Nevertheless, important initial insights can be obtained with the quantification of the
41 macroscopic coevolutionary processes observable in the patterns of species interaction and evolutionary
42 history [3, 13]. Furthermore, extant interactions—that are typically only possible with trait complemen-
43 tarity [1, 5]—can indicate a certain level of codependent trait evolution at the scale of species' pairs or
44 taxonomically higher [3, 13].

45 Cophylogenetic analysis is one common approach that provides insight to the community-wide pat-
46 terns of interaction and evolutionary history between species—the same patterns expected of macroscopic
47 coevolution [3, 14]. At its backbone is the pattern of cospeciation which measures the degree to which
48 two phylogenies match in their speciation and divergence events [13, 15]. However, this pattern alone
49 can arise from several processes including vicariance, chance, and coevolution [1, 12, 13]. Thus, the
50 second aspect of a cophylogenetic pattern that must be present alongside cospeciation is phylogenetic
51 congruence of interactions—that the interactions observed occur between evolutionarily coupled clades
52 [14, 16]. Cophylogeny is therefore more than just phylogenetic signal of interactions for both interacting
53 groups as it simultaneously considers both phylogenies alongside the extant interactions.

54 Though it is a tantalizing possibility, a signal of macroscopic coevolution such as cophylogeny may
55 not extend across an entire pollination network to the same extent that other ecological or evolutionary
56 processes, such as the direct and indirect propagation of disturbance in food webs [17], traverse interaction
57 networks. Nonetheless, it is widely accepted that diffuse coevolutionary processes may still be manifest
58 in pollination networks at the level of subsets of the community [1, 7, 8]. At the same time, it has been
59 observed that closely interacting groups of species, or modules, are a ubiquitous structural feature of
60 ecological communities including pollination networks [8, 18]. Given that coevolution is assumed to act
61 above the level of species pairs [1, 10], it has therefore been hypothesized that modules are an, if not *the*,
62 ecologically relevant product of coevolution [8, 19].

63 Despite theory that provides tentative support for this hypothesis [11], a more directed test of empiri-
64 cal network structure is needed to confirm such results. As with community-wide cophylogeny, multiple

constraints must be satisfied for empirically observed modules to show cophylogeny or be considered a product of macroscopic coevolution (Fig. 1). First, they should reflect the cospeciation of the network such that closely related species tend to be found in the same module. This consistency between modules and phylogenies, however, does not take into account the fact that some interactions, and implied trait complementarity, can be considered more consistent with the cophylogenetic narrative than others when they occur between closely coupled clades [5, 13, 14, 16]. Therefore secondly, if modules reflect cophylogenetic patterns, they should also be comprised of these phylogenetically congruent interactions, with the less congruent interactions falling between modules.

Here, we study 54 pollination networks from around the world to quantify the degree to which these networks show a significant cophylogenetic pattern. In particular, we search for evidence of cophylogeny at two specific scales: *(i)* network cophylogeny—where any observable cospeciation should be embodied by the interactions of the entire network—and *(ii)* modular cophylogeny—where the modules of a network should tend to contain closely related plant species, closely related pollinator species, and the most congruent interactions between them. Addressing patterns of cophylogeny at these two macroscopic scales represents an important step towards a robust, quantitative integration of coevolutionary processes with the modern theory underpinning community ecology.

2. Material and methods

(a) Empirical data and phylogeny construction

We analyzed a dataset comprised of 54 plant-pollinator mutualistic networks from a wide range of locations around the globe and with diverse species assemblages [20, Table S1]. In each of the networks, the presence or absence of interactions is based on observed visitation of flowering plants by their animal pollinators. In total, these networks include 1,388 species of flowering plants, 2,930 species of flower-visiting animals, and over 15,000 interactions. Studying the cophylogenetic patterns between two sets of interacting species, such as plants and pollinators, requires an understanding of the evolutionary history of

89 both groups. Central to the accuracy and robustness of our method were rigorously resolved phylogenies
90 of flowering plants and their pollinators, and we followed several steps to generate these. First, to ensure
91 all species identifications were up-to-date, we verified all species' names in the original interaction ma-
92 trices. Plant names were checked and corrected with the NCBI database (<http://www.ncbi.nlm.nih.gov/>)
93 whereas we corrected animal names with the `gnr_resolve` function in the R package `taxize`, which ac-
94 cessed a range of taxonomic databases [21]. Second, we constructed dated phylogenies for both groups
95 with the verified species' names. To do so, we started with a taxonomic tree given by the classification
96 function in `taxize` with preferential acceptance of classifications returned by the NCBI database [21]. We
97 compiled estimated divergence times of the flowering plants and insect pollinators from accepted phylo-
98 genies [22, 23]. We then used the `bladj` function from `phylocom` [24] to obtain branch length estimates
99 for any clades missing from these two studies. Although some of the divergence times we use should be
100 treated as an approximation [25], the accurate dating of even a subset of phylogenetic tips, which we have
101 achieved with two accepted phylogenies [22, 23] can improve the performance of comparative methods
102 such as ours [26].

103 **(b) Measuring whole-network cophylogeny**

104 To conduct an indirect assessment of macroscopic coevolution in each of our pollination networks, we
105 implemented a recently developed Procrustean method to directly assess cophylogeny in those networks
106 [14]. This approach, referred to as PACo, approaches the cophylogeny problem by optimizing the fit of
107 the phylogeny-interaction graphs of each network [14, 27]. PACo provides a quantification of the global
108 fit of the phylogenetic objects—a measure of cophylogeny and a proxy for macroscopic coevolution—
109 using the sums of squares residual distance between phylogenetic-interaction graphs [14, 27]. The smaller
110 the residual distance, the better the fit of the two graphs (*i.e.* phylogenies) and thus a higher degree of
111 cophylogeny reflected in the extant interactions. Similarly, the phylogenetic congruence of each individ-
112 ual interaction is equal to the residual distance between the two corresponding points on the phylogenetic

113 graphs. PACo offers several analysis options including a choice of whether to superimpose the raw
114 phylogenetic graphs (asymmetric) or to normalize both graphs to the same dimensionality before a super-
115 imposition is done (symmetric) [14]. The order of superimposition can also be specified (*i.e.* plants on
116 pollinators and vice versa), a decision based on the evolutionary assumptions of the system [14]. In this
117 study, we have focused on the results of the symmetric method where the normalized pollinator graph
118 is superimposed on the normalized plant graph. Nonetheless, our results do not differ qualitatively nor
119 quantitatively when selecting alternative configurations (Fig. S1).

120 We determined the significance of cophylogeny at the network level as captured by PACo by compar-
121 ing the sum of squared residuals of the Procrustean superimposition of plant and pollinator phylogenies
122 with the same from an ensemble of 1,000 randomizations of the network of interactions between plants
123 and pollinators. In each randomization, we conserved the number of interactions for each species as
124 well as the total number of interactions [28]. A conservative null model such as this does not rely on
125 an evolutionary assumption about which group is driving the cophylogenetic pattern allowing us to test
126 the hypothesis that both the plant and pollinator phylogenetic histories are constrained by the other via
127 their interactions. However, there are several alternate null models (the results for which do not differ
128 qualitatively from the model we present) and selection depends on the evolutionary assumptions made.
129 For example, in host-parasite systems it is perhaps more appropriate to assume that host speciation drives
130 parasite speciation and implement a less constrained null model [14].

131 **(c) Identifying network modules**

132 To test whether cophylogeny was consistent with modularity, we first needed to identify modules in the
133 interaction networks—compartments in which species are more likely to interact with each other than the
134 rest of the network [18]—given the observed interactions. In order to identify such modules in each of the
135 different networks, we followed the approach proposed by Barber [29] and implemented in MODULAR
136 [30], which partitions nodes with a stochastic optimization procedure. While there are several such

137 methods to assess modularity, the method employed here has been demonstrated to perform as well or
138 better than other contemporary module detection algorithms in bipartite networks [31].

139 To determine whether the observed network structure was significantly modular we implemented the
140 same null model used to assess network-wide cophylogeny and compared observed modularity to an
141 ensemble of 1000 randomisations of each network that maintained the degree distribution. This null
142 model has been widely used to assess the significance of modularity in ecological networks [8, 28], while
143 at the same time it allows for comparison of our results for network cophylogeny and modularity.

144 **(d) Measuring modular cophylogeny**

145 The first step we took to quantify the cophylogeny and infer the degree of macroscopic coevolution in
146 modules was to quantify how modules related to the evolutionary histories of both groups of species.
147 To do so, we fitted a likelihood model for discrete character evolution, using a continuous-time Markov
148 model of trait evolution [32]. Our assessment compared the degree to which the phylogeny predicts
149 covariance among module assignment of species [33], or in other words, the degree to which closely
150 related species tend to share the same module.

151 We determined the significance of the phylogenetic signal of modules by comparing our results to
152 those that would be obtained after randomly assigning module participants. First, we compared the
153 likelihood that the observed species-module assignment was the product of an evolutionary process versus
154 the corresponding likelihood from 1,000 randomized assignments. Therefore, a significant phylogenetic
155 signal of pollination modules implies that the observed modules are more consistent with this evolutionary
156 process than expected at random.

157 While the degree to which networks as a whole show cophylogeny can be established with PACo
158 [14, 27], an assessment of the extent to which cophylogenetic processes characterize topological modules
159 requires subsequent analysis. As noted earlier, the phylogenetic congruence of an interaction is given
160 by the residual of two points in the Procrustean superimposition of the phylogenetic-interaction graphs;

161 therefore, an interaction can be considered more congruent when its contribution to the overall residual
162 of the Procrustean analysis is small [14]. Thus, if modules are the product of cophylogeny, we expected
163 interactions within modules to have a higher degree of congruence (*i.e.* to have smaller residuals on aver-
164 age) than interactions between species in different modules. We tested this assumption using one-factor
165 analysis of variance (ANOVA) of the log-transformed Procrustean partial residuals of each interaction,
166 where the decision to log-transform the data was made to improve the normality but also did not qualita-
167 tively affect our results or conclusions.

168 We determined the significance of the within-module cophylogeny by comparing our results to those
169 that would be obtained after randomly assigning module participants. We compared the Akaike's In-
170 formation Criterion (AIC) of the ANOVA that contrasts the degree of cophylogeny within and between
171 observed modules against an ensemble of 1000 AIC values of the same with the randomized module as-
172 signments. We randomized the species' module assignments using two approaches. In the first approach,
173 we allowed for an arbitrary number of species in each module and an arbitrary number of modules. In the
174 second, more conservative approach we maintained the observed number of modules and the number of
175 species within each of them. Differences between approaches are not substantial and do not qualitatively
176 affect our results or conclusions, therefore we presented the results of the second, more conservative
177 approach. Results for the first approach can be found in the *Supplementary Material* (Fig. S1).

178 **3. Results**

179 Across our dataset, we found that a large proportion of pollination networks (38 out of 54 networks)
180 could be considered cophylogenetic assemblages (Monte Carlo test, $p < 0.05$; Fig. 2A). The observation
181 of high levels of cophylogeny at a network scale, such as this, therefore provided the necessary baseline
182 from which we could assess how cophylogeny was manifest at the modular scale. Implementing the
183 bipartite modularity optimization of Barber [29] and a conservative null model (*Materials and Methods*)
184 we observed that 57% (31 out of 54) of networks in our dataset were significantly modular (Monte Carlo

185 test, $p < 0.05$; Fig. 2B). Furthermore, of the significantly modular networks, 74% also showed significant
186 cophylogeny (Fig. 3).

187 On the surface, these high levels of cophylogeny and modularity would appear to support the hy-
188 pothesis that macroscopic coevolution acts at a modular scale. However, as described earlier, this still
189 amounts to circumstantial evidence and a deeper investigation of the relationships between each interac-
190 tion and the respective phylogenies is required. Specifically, if module participation is the natural result
191 of cophylogeny, we expected that modules based on who tends to interact with whom are consistent with
192 the evolutionary histories of both plants and pollinators—that is, they show cospeciation. Here we in-
193 stead found that the modules of a network are consistent with the plant and pollinator phylogenies in only
194 26% and 54% of networks, respectively (Monte Carlo test, $p < 0.05$; Figs. 2C, 2D, and 4). However,
195 when considering only the 31 significantly modular networks, the proportion of networks that exhibit
196 phylogenetic signal of module assignment increases to 35% and 58%, respectively (Fig. 3).

197 Our second consideration to assess cophylogeny in modules is the degree of phylogenetic congruence
198 of their constituent interactions. In general, we expected that within-module interactions would tend
199 to be more congruent than between-module interactions if modules represented a cophylogenetic unit
200 (Fig. 5). We found that observed modules were significantly better than random at explaining interaction
201 congruence in only 26% of the empirical networks (Monte Carlo test, $p < 0.05$; Figs. 2E, 4). Again,
202 this proportion increases slightly to 29% when considering exclusively networks that were significantly
203 modular (Fig. 3).

204 In total, we have assessed three complementary measures—conservation of the plant phylogeny,
205 conservation of the pollinator phylogeny, and within-module cophylogeny—to quantify whether cophy-
206 logeny is manifest in the modules of pollination networks. Across the 54 networks, varying proportions of
207 networks' modules satisfy these cophylogenetic constraints at a modular scale (Fig. 2 C-E). Though each
208 of these were observed at a greater frequency than would be expected at random ($p < 0.001$ in all cases;
209 [34]) just four networks appear to satisfy constraints for cophylogeny at the modular scale (Fig. 4). As

210 such, fulfilling one constraint for cophylogeny does not necessarily facilitate fulfilment of others (Chi-
211 squared tests; both phylogenies conserved, $p < 0.001$; plant phylogeny conserved and within-module
212 interaction cophylogeny, $p = 0.201$; pollinator phylogeny conserved and within-module interaction co-
213 phylogeny, $p = 0.002$; all three constraints, $p = 0.532$; Figs. 2C-E and 3). When put together, our results
214 indicate that there is limited evidence at best that modules reflect cophylogenetic patterns or represent a
215 definitive unit of macroscopic coevolution (Figs. 3 and S1).

216 4. Discussion

217 Coevolution has long been hypothesized to manifest itself in ecological assemblages above the level of
218 species pairs [1, 6, 7, 8, 10]. Here, we address this hypothesis with a formal quantification of cophyloge-
219 netic patterns in pollination networks. We have demonstrated that a strong signal is present in pollination
220 networks, with 70% of the networks analyzed exhibiting significant levels of whole-network cophylogeny.
221 Despite current thinking that suggests cophylogeny cannot provide evidence for coevolution [1, 12], our
222 results in taxonomically rich and globally sourced networks provide a potential counter argument. Many
223 previous studies of cophylogeny address these patterns in specific genera and clades rather than across en-
224 tire trophic groups such as the flowering plants and pollinators that we focus on here [35, 36, 37, 38, 39].
225 As such, ours is perhaps the first study of cophylogeny in large assemblages of interacting species and the
226 high levels of significantly cophylogenetic networks we observe suggest that this pattern can still arise
227 quite consistently when scaled up.

228 Furthermore, for patterns of cophylogeny to be this ubiquitous across such distinct systems, Occam's
229 razor would indicate that it arises from a common process. On the one hand, these patterns can arise due to
230 both biogeographical [1, 40] and coevolutionary processes [1, 41]. On the other, multiple previous studies
231 have indicated that phylogenetic congruence in pollination systems is most parsimoniously explained by
232 coevolution [39, 41]. Furthermore, the taxonomically diverse and global nature of our dataset makes it
233 unlikely that vicariance alone can account for the high levels of network cophylogeny we observed here.

Likewise, traits are such a strong predictor of interactions in mutualistic networks [42, 43] that strong interaction congruence, like that observed here, is rather unlikely—albeit not impossible—to observe in the complete absence of coupled trait evolution between taxa that maintained trait complementarity across the trees. Our results therefore support the idea that coevolution is indeed an influential process in shaping pollination networks and that many of these communities can be considered macroscopically coevolved assemblages [1]. Our results further suggest that an imprint of coevolution can at times be observed in the topological modules of pollination networks. Having said that, it cannot be considered the pervasive structural force that some have suggested [1, 7, 8, 10, 19].

The link between traits and interactions in ecological communities [43, 44] also offers at least two potential explanations as to why we did not universally see macroscopic coevolution in topological modules. First, in the networks we have studied, closely related pollinators tend to co-occur in modules more than twice as often as closely related plants. This result may be a consequence of convergence in pollination networks via pollination syndromes, whereby plants are thought to converge on traits selected for by pollinator functional groups [45]. As functional groups of pollinators are often considered to be broad clades that tend to be more closely related than the plants they visit [45], pollination syndromes may explain why we see such a disparity in terms of phylogenetic conservation of modules. Second, it has been suggested that free-living mutualists tend to converge on traits as opposed to species [1]. If traits rather than species converge in pollination networks, future inquiry that incorporates specific trait histories and microscopic coevolutionary dynamics *alongside* phylogenetic and interaction data may perhaps expose a more vivid signal of coevolution [5].

Beyond macroscopic coevolution, modularity in ecological networks is also thought to be influenced by several ecological processes including species' abundance [46], body mass [47] and species richness [48]. The collective action of these processes and others may act to effectively layer over the products of coevolution, resulting in the weak signal we tend to observe in network modules. Our results also show variation in the extent to which coevolution within modules is quantifiable—for example, the pollinator

259 phylogeny is conserved by the modular structure in roughly half the networks we assess—suggesting
260 that the contribution of ecological processes to modular structure may differ on both spatial and temporal
261 scales [7]. Therefore, attempts to tease apart the contributions of ecological, evolutionary, and coevolu-
262 tionary processes to the modular structure of ecological networks may be as important as attempts that
263 aim to tease apart the ecological mechanisms alone [49, 50].

264 Conversely, it is also possible that a modular structure will always fail to serve as a definitive unit of
265 macroscopic coevolution in pollination networks when examined at the whole-network scale. For exam-
266 ple, it is entirely plausible, and perhaps even likely, that the role of macroscopic coevolution in contribut-
267 ing to module structure differs between the modules observed in a network. Variation in the strength of
268 macroscopic coevolution observable at a module scale may arise from differences in the period of shared
269 evolutionary history of participant species [19], infiltration of modules by exotic species [51], or merely
270 the aforementioned suite of ecological determinants. Furthermore, the balance of pollinator species to
271 plant species in a module may also indicate the extent to which coevolution has shaped the assemblage,
272 with suggestions that balanced, or symmetrical, modules are more likely the product of coevolution and
273 predisposed to reciprocal selection whereas asymmetrical modules are more likely driven by abundance
274 [52, 53]. Thus, a description of coevolution at a modular scale in ecological networks requires not only
275 a consideration of the multiple determinants of ecological modularity, but also an explicit focus on indi-
276 vidual modules and their constituent species.

277

278 **Data accessibility:** All interaction networks can be found on the Web of Life database ([http://www.web-](http://www.web-of-life.es)
279 [of-life.es](http://www.web-of-life.es)). Summaries of the datasets used in this article can also be found as part of the supplemen-
280 tary material. Both plant and pollinator phylogenies for each interaction network are available through
281 GitHub: <http://github.com/stoufferlab/to-be-added-upon-publication/>

282

283 **Authors' contributions:** M. C. H. and E. F. C. contributed equally to the work; M. C. H. and D. B. S.

284 designed research; M. C. H. and E. F. C. performed research; E. F. C. analyzed data; M. C. H. led the
285 writing; and E. F. C. and D. B. S. contributed substantially to the writing.

286

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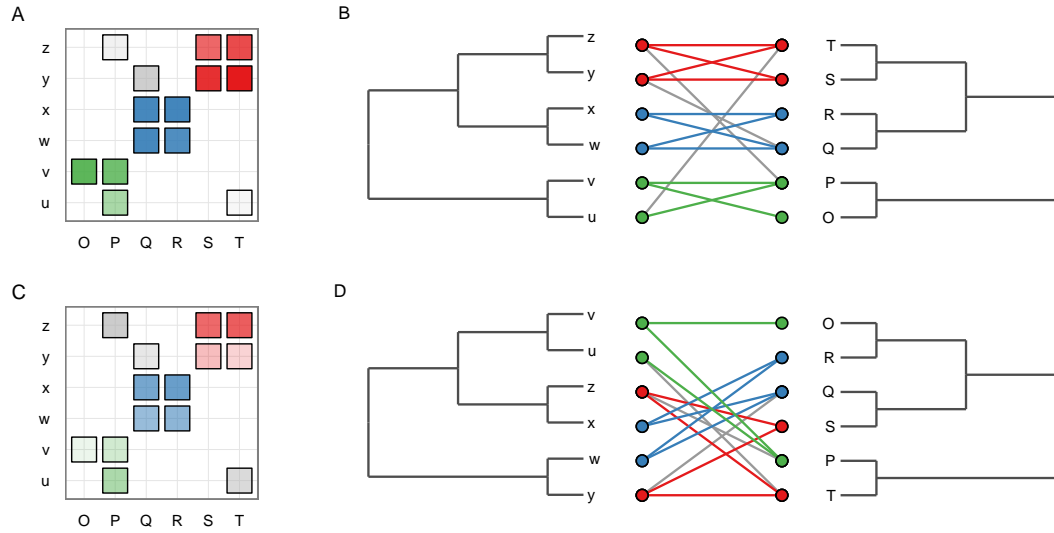


Figure 1: Graphical representation of our key hypotheses for modular cophylogeny in pollination networks. (A) We show a significantly modular network composed of three modules of tightly interacting species as indicated by the different colors (e.g., the green module containing species u, v, O, and P). This matrix format is one way to represent a binary bipartite ecological network; the pollinator species are on the x-axis (O–T), the plants on the y-axis (u–z), and a solid square at their intersection indicates the presence of an interaction between those species. (B) The modules in this network are highly cophylogenetic since they are made up of closely related species in both phylogenies and the evolutionary histories of these interacting species mirror each other strongly. (C and D), Despite the fact that this network is significantly modular, there is no evidence for modular cophylogeny since there is no tendency of its three modules to be composed of closely related species nor for species in extant interactions to exhibit comparable evolutionary histories. In both (A) and (C), the shading of the interactions is indicative of that interactions' cophylogenetic signal where the darker the shade the higher the signal (*Materials and Methods*).

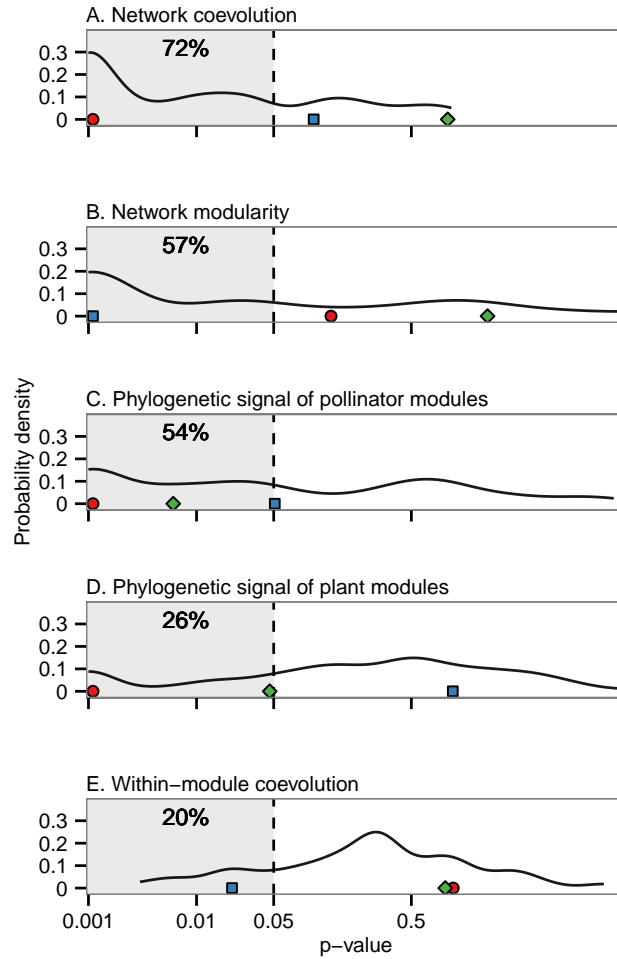


Figure 2: The structure of empirical pollination networks provides varying degrees of support for the different constraints for whole-network and modular copyloeny. (A)-(E) We show the probability densities of the p-values associated with our hypothesis testing of each criteria: (A) network copyloeny, (B) network modularity, (C) phylogenetic signal of pollinator modules, (D) phylogenetic signal of plant modules, and (E) within-module copyloeny. In each panel, we indicate the the proportion of networks that are significant for each measure compared to the corresponding null hypothesis (*Materials and Methods*). The red circle, blue square, and green diamond on each plot show the values for three representative networks to indicate the variability within as well as across individual networks.



Figure 3: Graphical summary of the results of our analysis of cophylogeny in empirical pollination networks. Each column is for a different empirical network and the rows show the outcome of different statistical tests. In all rows a dark blue cell indicates a significant result for the network whereas light blue indicates the result was non-significant. Row 1 shows the proportion of significantly modular networks. Row 2 shows the proportion of significantly cophylogenetic networks. Rows 3 & 4 show the proportion of networks with phylogenetic signal of the pollinator and plant modules, respectively. Row 5 shows the support for within-module cophylogeny of the networks.

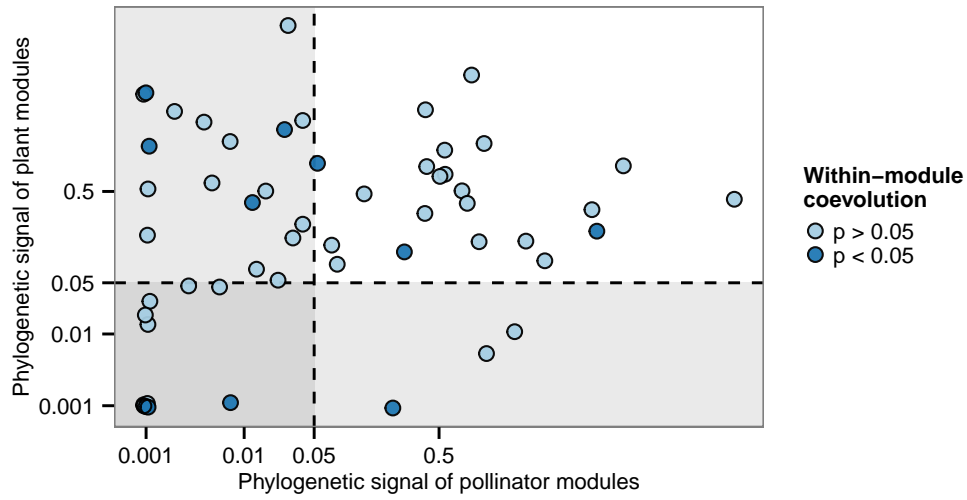


Figure 4: Few empirical pollination networks simultaneously support the hypothesis of substantial modular cophylogeny. For each of the 54 empirical networks, we plot the phylogenetic signal of pollinator modules (on the x-axis) versus the phylogenetic signal of the plant modules (on the y-axis). Networks to the left of the vertical dashed line and below the horizontal dashed line exhibit significant phylogenetic signal for pollinators and plants, respectively. The color of symbol indicates whether the networks' modular structure significantly explained the variation of interaction-level cophylogeny; dark blue indicates those networks whose modules have a significant tendency to contain the most congruent interactions whereas light blue indicates the opposite. Only four of the empirical networks fulfil all three constraints.

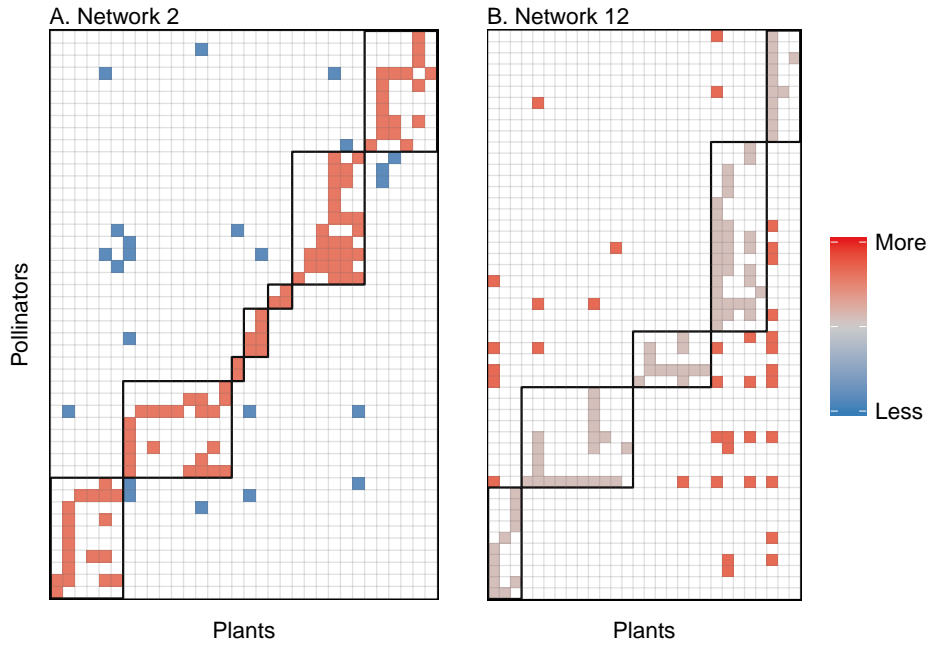


Figure 5: There is substantial variation in the extent to which the modular structure of a network captures macroscopic cophylogeny. We show here how two representative networks fit the constraint that within-module interactions should be more congruent than between-module interactions. The color of the within- and between-module interactions in each network is given by the mean cophylogenetic signal of all interactions in that group. (A) The constraint for within-module cophylogeny is fulfilled by Network 2 since the interactions within modules tend to show significantly more cophylogeny than those falling between modules. (B) In contrast, the constraint for within-module cophylogeny is not fulfilled by Network 12 since within-module interactions tend to show less cophylogeny than the between-module counterparts. In cases like this—which are the norm of our study—the whole network provides stronger support for cophylogeny than do topological modules.

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