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Related plants tend to share pollinators and herbivores, but strength of phylogenetic signal varies among plant families

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Summary

- Related plants are often hypothesised to interact with similar sets of pollinators and herbivores, but this idea has only mixed empirical support. This may be because plant families vary in their tendency to share interaction partners.
- We quantify overlap of interaction partners for all pairs of plants in 59 pollination and 11 herbivory networks based on the numbers of shared and unshared interaction partners (thereby capturing both proportional and absolute overlap). We test 1) for relationships between phylogenetic distance and partner overlap within each network, 2) whether these relationships varied with the composition of the plant community, and 3) whether well-represented plant families showed different relationships.
- Across all networks, more closely-related plants tended to have greater overlap. The strength of this relationship within a network was unrelated to the composition of the network's plant component, but, when considered separately, different plant families showed different relationships between phylogenetic distance and overlap of interaction partners.
- The variety of relationships between phylogenetic distance and partner overlap in different plant families likely reflects a comparable variety of ecological and evolutionary processes. Considering factors affecting particular species-rich groups within a community may be the key to understanding the distribution of interactions at the network level.

Keywords

ecological networks, herbivory, niche overlap, phylogenetic signal, pollination, specialisation

Introduction

1 Interactions with animals affect plants' life cycles in several critical ways (Mayr, 2001).
2 On one hand, pollination and other mutualistic interactions contribute to the reproductive
3 success of many angiosperms (Ollerton *et al.*, 2011). On the other, herbivores consume
4 plant tissues (McCall & Irwin, 2006) which costs plants energy and likely lowers their
5 fitness (Strauss *et al.*, 2002). In both cases, these interactions do not occur randomly
6 but are strongly influenced by plants' phenotypes (Fontaine & Thébault, 2015). For
7 example, plants that produce abundant or high-quality nectar may receive more visits
8 from pollinators (Robertson *et al.*, 1999) whereas plants that produce noxious secondary
9 metabolites may have fewer herbivores (Johnson *et al.*, 2014). Plant traits are also likely
10 to determine *which* specific pollinators and herbivores interact with a particular plant.
11 Plants with different defences (e.g., thorns vs. chemical defences) may deter different
12 groups of herbivores (Ehrlich & Raven, 1964; Johnson *et al.*, 2014), and pollinators with
13 similar traits are often expected to attract similar sets of pollinators (Waser *et al.*, 1996;
14 Fenster *et al.*, 2004; Ollerton *et al.*, 2009).

15 If attractive and/or defensive traits are heritable, then we can reasonably expect that
16 related plants will have similar patterns of interactions with animals, especially if there is
17 some selection in either group to avoid competition or the number of potential partners
18 is limited (Schemske & Bradshaw, 1999; Ponisio *et al.*, 2017). That is, there may be *phy-*
19 *logenetic signal* in plants' interactions such that closely-related plants may tend to have
20 similar interaction partners. Recent studies that have investigated this question at the
21 level of whole communities, however, have yielded mixed results. In particular, significant
22 phylogenetic signal in plants' sets of interaction partners tends to be rare in empirical
23 networks (Rezende *et al.*, 2007b; Lind *et al.*, 2015; Ibanez *et al.*, 2016; but see Elias *et al.*,
24 2013; Fontaine & Thébault, 2015; Hutchinson *et al.*, 2017). Moreover, statistically sig-
25 nificant degrees of phylogenetic signal or coevolution may only result in small differences
26 in network structure, adding to the difficulty of understanding patterns in species' in-

27 teraction partners (Ponisio *et al.*, 2017). Further, the plant and animal components of
28 networks can show different degrees of phylogenetic conservation of interaction partners.
29 In mutualistic networks, animals often show a stronger phylogenetic signal in their part-
30 ners than do plants (Rezende *et al.*, 2007b; Chamberlain *et al.*, 2014; Rohr *et al.*, 2014;
31 Vamosi *et al.*, 2014; Lind *et al.*, 2015; Fontaine & Thébault, 2015) (but see Rafferty &
32 Ives (2013) for a counterexample). In antagonistic networks, however, actively-foraging
33 consumers tend to show less phylogenetic signal than their prey (Ives & Godfray, 2006;
34 Cagnolo *et al.*, 2011; Naisbit *et al.*, 2011; Fontaine & Thébault, 2015). In part, this
35 may be related to different degrees of interaction intimacy (dependence of one partner
36 on another), which appears to contribute to network structure in mutualistic, but not
37 antagonistic, networks (Guimarães *et al.*, 2007; Ponisio *et al.*, 2017). In any case, it is not
38 straightforward to assume that interactions will always be similar among related species.

39 There are several mechanisms that might weaken the conservation of interaction part-
40 ners. Pollination and herbivory may be affected by a wide variety of traits, and not all of
41 these are likely to be phylogenetically conserved (Rezende *et al.*, 2007a; Kursar *et al.*, 2009;
42 Ibanez *et al.*, 2016). If, for example, floral displays are strongly affected by environmental
43 conditions (Canto *et al.*, 2004), then plant phylogeny may not strongly predict pollination.
44 Even if the traits affecting pollination and herbivory are heritable, plants may experience
45 conflicting selection pressures that weaken the overall association between plant phylogeny
46 and interaction partners (Armbruster, 1997; Lankau, 2007; Siepielski *et al.*, 2010; Wise
47 & Rausher, 2013; Kariñho-Betancourt *et al.*, 2015). For instance, floral traits that are
48 attractive to pollinators can also increase herbivory (Strauss *et al.*, 2002; Adler & Bron-
49 stein, 2004; Strauss & Whittall, 2006; Theis, 2006). Conversely, herbivory can reduce
50 pollination by inducing chemical defences (Adler *et al.*, 2006) or altering floral display or
51 nectar availability (Strauss, 1997). There may also be trade-offs between chemical and
52 physical defences, or defences at different life stages, that weaken the overall heritability
53 of plants' sets of herbivores (Kariñho-Betancourt *et al.*, 2015; Endara *et al.*, 2017). A

54 plant's set of interaction partners therefore reflects a mixture of different environmental
55 effects and different selection pressures, as well as shared phylogenetic history. If these
56 factors affect closely-related plants differently, then closely-related species may not have
57 more similar interaction partners than distantly-related species.

58 This variety of different pressures makes it likely that the relationship between plants'
59 relatedness and the similarity of their interaction partners is not constant across plant
60 clades. Closely-related plants in one clade might be under strong selection to favour
61 dissimilar sets of pollinators to avoid exchanging pollen with other species (Levin & An-
62 derson, 1970; Bell *et al.*, 2005; Mitchell *et al.*, 2009), while plants in other clades may be
63 under strong pressure to continue interacting with a common set of partners. Similarly,
64 plants may experience disruptive selection on defences against herbivores if congeners
65 tend to grow in the same places such that herbivore able to consume one species could
66 easily spread to close relatives (Kursar *et al.*, 2009; Yguel *et al.*, 2014). On the other
67 hand, unrelated plants might converge upon similar phenotypes which attract particu-
68 larly efficient or abundant pollinators (Ollerton, 1996; Wilson *et al.*, 2007; Ollerton *et al.*,
69 2009; Ibanez *et al.*, 2016). Likewise, unrelated plants may converge upon similar defences,
70 leading them to share those herbivores which can overcome these defences (Pichersky &
71 Gang, 2000). In either case, dissimilarity of interactions among related species or simi-
72 larity of interactions among unrelated species could result in weaker phylogenetic signal
73 across an entire plant community. Moreover, all of the aforementioned hypotheses are
74 non-exclusive; different processes likely affect different clades, and these processes might
75 be associated with different pressures imposed by pollination and herbivory (Fontaine &
76 Thébault, 2015).

77 Here we investigate how overlap in interaction partners between pairs of plants (hence-
78 forth "niche overlap") varies over phylogenetic distance. Whereas previous studies have
79 focused on the presence or absence of phylogenetic signal across entire networks, we take
80 a pairwise perspective in order to obtain a more detailed picture of how plant phylogeny

81 relates to network structure. As different plant families (which represent tractable clades
82 for analysis) may have experienced different degrees of coevolution, convergence, etc.,
83 we also complement analyses with entire networks with comparisons among plants in the
84 same family within a network. This novel perspective allows us to investigate the relation-
85 ship between phylogenetic distance and partner overlap at different scales. Specifically,
86 we test 1) whether niche overlap decreases over increasing phylogenetic distance in a large
87 dataset of pollination and herbivory networks, 2) whether the plant family composition
88 of a community affects the relationship between niche overlap and phylogenetic distance
89 in that community, and 3) whether the relationship between niche overlap and phylo-
90 genetic distance differs systematically across plant families. This fine-grained approach
91 gives more detailed information than previous studies.

92 **Materials and Methods**

93 **Network data**

94 We tested for phylogenetic signal in niche overlap within a set of 59 pollination and 11
95 herbivory networks. These networks span a range of biomes (desert to grassland to tundra)
96 and countries (Sweden to New Zealand). The herbivory networks included a variety of
97 types of herbivores but were dominated by leaf-chewing insects. Leaf-chewing and other
98 types of herbivory might be affected by different plant traits and cannot be expected to
99 show the same trends with respect to phylogeny. We therefore restricted our networks to
100 leaf-chewing insects by removing any non-leaf chewing insects and any plants which had
101 no interaction partners after removing other types of herbivores. The adjusted networks
102 range in size between 19 and 997 total species (mean=162, median=97) with between 8
103 and 132 plant species (mean=39.1, median=29.5). See *Table S1, Notes S1* for details on
104 the original sources of all networks. All networks were qualitative and did not include
105 interaction strengths.

106 **Phylogenetic data**

107 In order to fit the plant species in all networks to a common phylogeny, we first compared
108 all species and genus names with the National Center for Biotechnology Information and
109 Taxonomic Name Resolution Service databases to ensure correctness. This was done
110 using the function ‘get_tsn’ in the R (R Core Team, 2016) package *taxize* (Chamberlain
111 & Szocs, 2013; Chamberlain *et al.*, 2019). Species which could not be assigned to an
112 accepted taxonomic name (e.g., ‘Unknown Forb’) were discarded, as were those with
113 binomial names that could not be definitively linked to higher taxa (e.g., ‘*Salpiglossus*
114 *sp.*’). We were left with 2341 unique species in 1027 genera and 195 families. On average,
115 11.43% of plants were removed from each network (median 4.60%, range 0-55.10%).

116 We then estimated phylogenetic distances between the remaining species. To ac-
117 complish this, we constructed a phylogenetic tree based on a dated ‘mega-tree’ of an-
118 giosperms (Zanne *et al.*, 2014). Some species in our dataset were not included in the
119 angiosperm mega-tree. For angiosperms, a sister taxon was identified using Stevens (2001
120 onwards) and the species added manually. Ferns, tree ferns, and a single club moss were
121 added to the base of the tree. This means that closely-related non-angiosperm species
122 appear to have very long phylogenetic distances between them. We therefore excluded
123 comparisons between pairs of non-angiosperms from our analyses. As only two networks
124 (both herbivory networks) included more than one such species and non-angiosperms were
125 always a small minority of any network, we do not believe that omitting these comparisons
126 has greatly affected our results. To obtain trees for each network, we pruned the dated
127 mega-tree to include only species in that network.

128 **Calculating niche overlap**

129 We calculated niche overlap for each pair of plants i and j based on the number of shared
130 and unshared interaction partners (M_{ij} , U_{ij} , respectively). The number of unshared
131 interaction partners gives valuable information about cases where, for example, closely-

132 related plants may have experienced disruptive selection, leading to weaker phylogenetic
133 signal. The sum $M_{ij} + U_{ij}$ indicates the amount of information provided by each pair
134 of plants: a pair of generalists which share most of their interaction partners gives a
135 stronger indication of phylogenetic signal than a pair of extreme specialists with one
136 common interaction partner.

137 Together, M_{ij} and U_{ij} give a Jaccard index (J_{ij}) describing the proportion of shared
138 interactions. J_{ij} is defined:

$$J_{ij} = \frac{M_{ij}}{U_{ij} + M_{ij}}, \quad (1)$$

139 where M_{ij} is the set of *mutual* (shared) interaction partners and U_{ij} the set of unshared
140 interaction partners for plants i and j . In our statistical analyses (see below), we used the
141 tuple (M_{ij}, U_{ij}) as the dependent variable rather than the single value J_{ij} . This allows
142 us to preserve information about the amount of information provided by each pair of
143 plants and weight the observations accordingly. Note that species sharing a large *number*
144 of interaction partners may not share a large *proportion* of interaction partners if the
145 number of interaction partners that are not shared is also large.

146 **Testing conservation of niche overlap within networks**

147 We modelled the relationship between niche overlap and phylogenetic distance using a
148 logistic regression. We used the numbers of shared (M_{ij}) and non-shared (U_{ij}) partners as
149 dependent variables and centred, scaled phylogenetic distance as the independent variable.
150 This approach is conceptually similar to modelling successes and failures in a binomial-
151 distributed process. Accordingly, we assumed a binomially-distributed error structure and
152 used a logit link function to model the dissimilarity in interaction partners J_{ij} of plants i
153 and j . Regressions of niche overlap and phylogenetic distance within each network were
154 fit using the R (R Core Team, 2016) base function “glm” and took the form

$$\text{logit}(J_{ij}) \propto \beta_{\text{distance}} \delta_{ij}, \quad (2)$$

155 where δ_{ij} is the phylogenetic distance between plants i and j and J_{ij} is defined by the
156 tuple (M_{ij}, U_{ij}) (see *Notes S2* for R implementation). The fixed effect of distance in this
157 regression, $\beta_{distance}$, can be understood as the change in log odds of sharing an interaction
158 partner per million-year change in phylogenetic distance.

159 These separate regressions avoid the potential for confounding the effects of differ-
160 ent relationships in different networks. As we also wished to evaluate the overall trend
161 across networks, we fit an additional regression of niche overlap and phylogenetic dis-
162 tance across all network types. As well as the fixed effect of phylogenetic distance, this
163 regression included fixed effects of network type (pollination or herbivory) and the inter-
164 action between phylogenetic network type and random intercepts and slopes per network.
165 This expanded regression was fit using the R (R Core Team, 2016) function ‘glmer’ from
166 package *lme4* (Bates *et al.*, 2015) and took the form

$$\text{logit}(J_{ij}) \propto \beta_{distance}\delta_{ij} + \beta_{pollination}I_{ij} + \beta_{distance:pollination}\delta_{ij}I_{ij}, \quad (3)$$

167 where $I_{ij} = 1$ when plants i and j are drawn from a pollination network and $I_{ij} = 0$ when
168 i and j are drawn from a herbivory network, and all other symbols are as above. Note
169 that we only compared pairs of plants taken from the same network. The fixed effects
170 $\beta_{pollination}$ and $\beta_{distance:pollination}$ are the change in intercept and slope of the log odds of
171 sharing an interaction partner, respectively, relative to the baseline of herbivory networks.

172 To demonstrate the power of defining J_{ij} as a tuple of M_{ij} and U_{ij} rather than a
173 single value, we repeated the above analyses using a Jaccard index based only on the
174 proportion of interaction partners that are shared (i.e., $J_{ij} = M_{ij}/[M_{ij} + U_{ij}]$). Note that
175 while the proportion of shared interaction partners is the same in both cases, the tuple
176 formulation gives more weight to plants with many interaction partners as these provide
177 more information. When comparing the two approaches we observed similar trends but,
178 notably, the tuple definition of J_{ij} had greater power to detect weak relationships (*Notes*
179 *S3*). We therefore show only the results when defining J_{ij} as a tuple in the main text.

180 To test whether the relationship between phylogenetic distance and niche overlap
181 depended on network size, we fit a general linear model for the slope of this relationship
182 inferred from the glm models against the number of plant pairs for which distances could
183 be calculated (hereafter “network size”), network type (again using herbivory networks
184 as a baseline), and their interaction:

$$\beta_{distance} \propto \beta_{size}\eta_N + \beta_{pollination}I_N + \beta_{size:pollination}\eta_N I_N, \quad (4)$$

185 where η_N is the number of plant pairs in network N for which distances could be calcu-
186 lated, I_N is an indicator equal to 1 if network N is a pollination network and 0 otherwise.

187 As the interaction between network type and network size was strong and opposite to
188 the direction of the main effect of network size, we fit an additional general linear model
189 using only data from pollination networks and including only the effect of network size
190 (herbivory networks were the baseline in the full glm). Both models were fit using the
191 R (R Core Team, 2016) base function “glm”. A similar model relating the strength of the
192 relationship between phylogenetic distance and niche overlap to connectance showed no
193 significant trends (*Notes S4*).

194 **Accounting for non-independence**

195 Note that pairs of plants are not independent: the same plant will appear in many pairs,
196 and interactions may be influenced by the overall structure of the community. This vio-
197 lates the assumptions used when calculating the significance of logistic regressions within
198 the R (R Core Team, 2016) base package or the package *lme4* (Bates *et al.*, 2015). To
199 fairly estimate the significance of our regressions, it was therefore necessary to compare
200 the observed relationships to those in a suite of appropriately permuted networks. To
201 create these networks, we shuffled interactions among species while preserving row and
202 column totals. Each species retained the same number of interaction partners as in the
203 observed network but the exact set of partners (and therefore niche overlaps with all

204 other species) varied across permuted networks. We preserved the observed phylogenetic
205 relationships between species in all cases. For each observed network, we created 999 such
206 permuted networks and calculated the relationship between niche overlap and phyloge-
207 netic distance. This gave us a null distribution for each observed network with which to
208 determine the significance of the observed relationship.

209 This permutation approach also allows us to estimate type I and type II error for
210 our analysis. Because the permuted networks should not demonstrate any particular
211 relationship between phylogenetic distance and partner overlap, these slopes should be
212 similar to those obtained after permuting these networks a second time. To estimate type
213 I and type II errors, we created 500 permutations of each permuted network and, again
214 keeping the observed phylogenetic distances between plant species, repeated our analyses.
215 We then determined the number of permuted networks which appear to have significant
216 overlap-phylogenetic distance relationships relative to the permutations of these permuted
217 networks (type I error). Type II error can be determined from the distribution of p -
218 values obtained when comparing the permuted networks to permutations of the permuted
219 networks. Although calculating the exact type II error requires a specific alternative
220 hypothesis, the uniform distribution of p -values we obtained after permuting the permuted
221 networks means that the type II error would increase linearly as the alternative hypothesis
222 was set farther from zero (*Notes S5*).

223 **Linking network-level trends and community composition**

224 Next, we examined the connection between our network-level observations and the num-
225 ber of species in each plant family present in each community. Specifically, we tested the
226 hypothesis that varying relationships between phylogenetic distance and pairwise niche
227 overlap are due to the different distributions of families across networks. We defined
228 the relationship between phylogenetic distance and niche overlap as the change in log
229 odds of two plants in a given network sharing an interaction partner per million years

230 of divergence (i.e., the slope $\beta_{distance}$ from the regression of niche overlap against phylo-
231 genetic distance within a single network). We then related differences in this relation-
232 ship to differences in Bray-Curtis dissimilarity in the family-wise composition of the two
233 plant communities using a non-parametric permutational multi-variate analysis of vari-
234 ance (PERMANOVA; Anderson, 2001). Bray-Curtis dissimilarity considers only those
235 plant families which appear in at least one of a pair of networks (Anderson, 2001; Cirtwill
236 & Stouffer, 2015), ensuring that the shared absence of rare plant families will not make
237 two networks appear more similar than they actually are.

238 Note that a PERMANOVA does not assume that the data are normally distributed,
239 but rather compares the pseudo- F statistic calculated from the observed data to a null
240 distribution obtained by permuting the raw data. As pollination and herbivory networks
241 might have different community composition, we stratified these permutations by network
242 type. That is, the response variable of change in log odds for a pollination network could
243 only be exchanged for that of another pollination network. This stratification procedure
244 ensures that the null distribution used to calculate the P -value is not biased by including
245 combinations of changes in log odds and community composition that would not occur
246 because of inherent differences in the two network types (e.g., *Pinaceae* only appeared in
247 herbivory networks and should not be assigned to pollination networks). We used 9999
248 such stratified permutations to obtain the null distribution and obtain a P -value.

249 **Calculating niche overlap within families**

250 Finally, we compared the breakdown of niche overlap in different plant families. Within-
251 family genetic and trait diversity can be high due to adaptive radiations, heterogeneous
252 selection, and other influences on different species. Plant families offer a reasonable bal-
253 ance between collecting enough species to identify meaningful trends and maintaining a
254 tractable number of analyses. They are therefore the best taxonomic level to investigate
255 phylogenetic conservation in more detail across our large dataset. To test whether dif-

256 ferent families show different conservation of interactions, we used the same definitions
257 of overlap and phylogenetic distance as in the within-network analysis but restricted our
258 regressions to pairs of plants from the same family and the same network. Unlike in our
259 previous analysis, we analysed data from pollination and herbivory networks separately
260 as most well-represented plant families appeared in only one network type. For those
261 families which appeared in both network types, we ran separate analyses on each subset
262 of data.

263 For each plant family, within each network type, we fit one of two similar sets of
264 models. If family f was found in several networks of the same type (e.g., several pollination
265 networks), we fit a mixed-effects logistic regression relating niche overlap to a fixed effect
266 of phylogenetic distance and a random effect for each network using the R (R Core Team,
267 2016) function “glmer” from package *lme4* (Bates *et al.*, 2015). If family f was found in
268 only one network, we omitted the network-level random effect and fit a logistic regression
269 using the R (R Core Team, 2016) base function “glm”. These equations took the same
270 form as equation 2.

271 Models for two families did not converge. In the *Lauraceae*, (represented by four
272 species in one pollination network) and the *Sapindaceae* (represented by five species in
273 one herbivory network and five species in two pollination networks), only one pair of
274 species per network type shared any interaction partners while all other pairs did not
275 share any interaction partners.

276 By considering each family separately, we do risk obtaining some significant results
277 purely by chance. The standard technique for addressing this type of multiple hypothesis
278 testing, the Bonferroni correction, tends to be over-zealous and lead to a failure to reject
279 the null hypothesis even when a large number of significant results before the correction
280 supports the alternative hypothesis (Moran, 2003). To account for multiple testing while
281 also allowing the number of families showing significant trends to carry some weight, we
282 use the correlated Bonferroni test introduced in Drezner & Drezner (2016) (*Notes S6*).

Results

Within-network conservation of niche overlap

Across all networks, more distantly-related plants were less likely to share interaction partners ($\beta_{distance}=-6.82$, $p<0.001$). Plants in pollination networks tended to share fewer interaction partners overall, and the decrease in overlap with increasing phylogenetic distance was steeper ($\beta_{pollination}=-1.44$, $p<0.001$ and $\beta_{distance:pollination}=-18.5$, $p<0.001$, respectively). That is, a pair of plants in the same genus was more likely to share interaction partners than a pair of plants in the same family in both types of networks, but a pair of congeners would be less likely to share pollinators than to share herbivores. Note that, as our networks are qualitative, these results refer only to the number of shared interaction partners rather than to the quantitative strength of competition.

As an illustration, a pair of plants which diverged 10mya would have a probability of 0.202 of sharing a given herbivore and 0.094 of sharing a given pollinator, while a pair of plants which diverged 750mya would have a probability of 0.121 of sharing a given herbivore or 0.011 of sharing a given pollinator. These trends may be related to the numbers of extreme specialists in each network. In our dataset, an average of 48% (+/- 14) of pollinators in a given web were extreme specialists (i.e., visited only one plant species) compared to 29% (+/- 29) of herbivores ($z=5.62$, $df=68$, $P<0.001$ for a binomial regression of specialists and generalists over network type).

Despite these general trends, there was substantial variation between pollination networks, with overlap of interaction partners decreasing with increasing phylogenetic distance in some networks and increasing in others (Fig. 1). Overlap of interaction partners decreased significantly with increasing phylogenetic distance in 7/11 herbivory networks and 33/59 pollination networks. In the remaining four herbivory networks and 25 of the 26 remaining pollination networks, overlap of interaction partners was not related to phylogenetic distance. Overlap of interaction partners increased with increasing phylogenetic

309 distance in only a single pollination network.

310 The slope of the relationship between phylogenetic distance and overlap of interaction
311 partners was related to the number of plant pairs in herbivory, but not pollination, net-
312 works. Larger herbivory networks had higher values of $\beta_{distance}$ ($\beta_{size}=2.58\times 10^{-4}$, $p=0.011$
313 for the full glm; herbivory networks are the baseline). Pollination networks had higher
314 (less negative) slopes overall ($\beta_{pollinator}=0.306$, $p<0.001$ compared to the intercept value
315 of -0.434 for herbivory networks). Pollination networks moreover showed a much weaker
316 relationship between network size and the strength of the overlap-distance relationship
317 ($\beta_{pollination:size}=-2.64\times 10^{-4}$, $p=0.009$). After refitting the glm to the pollination networks
318 alone, there was no significant relationship between network size and the slope of the
319 overlap-distance relationship ($\beta_{size}=-5.91\times 10^{-6}$, $p=0.572$).

320 Comparing the results in the observed networks to those obtained after permuting
321 interactions, the observed slope of the relationship between phylogenetic distance and
322 interaction partner overlap was always more extreme (i.e., always more negative or always
323 more positive) than that obtained in the permuted networks (Fig. 2). Observed networks
324 with a negative relationship between phylogenetic distance and overlap always had a more
325 negative slope than that obtained from the permuted networks, while the 10 networks with
326 positive relationships between phylogenetic distance and overlap always had more positive
327 relationships than the permuted networks. This indicates that even in the networks
328 with non-significant relationships, the association between niche overlap and phylogenetic
329 distance was not random and confirms that the significant results we observe are not
330 due to non-independence of plants within a network. When the slopes of the permuted
331 networks were compared to those obtained from permutations of the permuted networks,
332 there was no relationship, which speaks to the robustness of our methodology (*Notes S5*).

333 **Linking network-level trends and community composition**

334 We were interested in whether the slope of the relationship between phylogenetic distance
335 and niche overlap varied with community composition. In a PERMANOVA of slope
336 against community composition, stratified by network type, we did not find a significant
337 relationship between slope and community composition ($F_{1,68}=1.06$, $p=0.493$). Of the
338 200 families in our dataset, only 29 were represented by more than 20 species. Lumping
339 all other families into an “other” category and repeating the PERMANOVA, we still did
340 not find a significant relationship between slope and community composition ($F_{1,68}=1.12$,
341 $p=0.409$).

342 **Within-family conservation of niche overlap**

343 Taking all families together, the probability of species in the same family sharing in-
344 teraction partners was not significantly related to phylogenetic distance ($\beta_{distance}=-6.48$,
345 $p=0.087$). Pollination networks did not show a significantly different slope from the her-
346 bivory networks ($\beta_{distance:pollination}=1.73$, $p=0.681$). Plants in pollination networks did,
347 however, have a lower intercept probability of sharing interaction partners ($\beta_{pollination}=-$
348 0.776 , $p=0.007$), similar to our within-network results above.

349 Considering each family separately, the relationship between within-family niche over-
350 lap and phylogenetic distance varied widely in both pollination and herbivory networks.
351 In pollination networks, overlap decreased significantly with increasing phylogenetic dis-
352 tance in 14 of the 48 well-represented families (Table 1; Fig. 3). If we apply the correlated
353 Bonferroni correction to account for multiple testing (Drezner & Drezner, 2016), all of
354 these slopes remain significant (*Notes S6*). There was no significant relationship between
355 overlap and phylogenetic distance in a further 34 plant families (see *Notes S6* for further
356 details). Finally, the overlap between pairs of *Apiaceae* and *Poaceae* increased signifi-
357 cantly with increasing phylogenetic distance.

358 Of the nine plant families that were well-represented in herbivory networks, overlap

359 decreased significantly with increasing phylogenetic distance in four (Table 2; Fig. 3). Four
360 families did not show significant relationships between phylogenetic distance and overlap,
361 and in one family, *Fabaceae*, overlap of interaction partners increased significantly with
362 increasing phylogenetic distance. If we again apply the correlated Bonferroni correction,
363 all five significant slopes remain significant (*Supportin information 6*).

364 Discussion

365 We found general support for the hypothesis that more closely-related pairs of plants
366 have a higher degree of niche overlap. Taking all networks together, the probability of
367 two plants sharing the same animal interaction partners decreased with increasing phy-
368 logenetic distance. Considering networks separately, $\approx 56\%$ of pollination and $\approx 64\%$ of
369 herbivory networks showed the expected trend of decreasing overlap with increasing dis-
370 tance. This variation between networks echoes earlier studies (e.g., Fontaine & Thébaud,
371 2015; Hutchinson *et al.*, 2017), which also found broad evidence for phylogenetic conser-
372 vation of interaction partners despite variation between particular networks. The lack of
373 a significant relationship between phylogenetic distance and niche overlap in many net-
374 works could be partly due to the large number of extreme specialist insects, especially
375 in the pollination networks. These species interact with only one plant and therefore
376 weaken any signal of niche overlap. The herbivory networks did not contain as many
377 obligate specialists, but we note that herbivores, like pollinators, often interact with only
378 a few closely-related plants (Novotny & Basset, 2005; Brändle & Brandl, 2006; Astegiano
379 *et al.*, 2017). These oligotrophs may affect overall phylogenetic signal in the same way as
380 the strict specialists: in both cases plants that are not very closely related are unlikely
381 to share interaction partners. Note that some of the apparent specialists in our dataset
382 may actually be rare species involved in more interactions which have not yet been ob-
383 served (Blüthgen *et al.*, 2006; Poisot *et al.*, 2015). Without information on the sampling
384 completeness of the networks in our dataset, it is difficult to estimate the size of this effect.

385 It is possible, however, that we might observe stronger relationships between phylogenetic
386 distance and niche overlap with more complete data on rare species.

387 In our dataset, the slope of the relationship between phylogenetic distance and niche
388 overlap was not related to the composition of the plant community in each network. Com-
389 bined with the overall trend for conservation of interaction partners above, this suggests
390 that trends among closely-related plants (e.g., congeners or members of the same subfam-
391 ilies) are more important than phylogenetic signal from deeper within the phylogenetic
392 tree. This echoes earlier results relating plant phylogeny to predation by particular insect
393 species (Novotny *et al.*, 2002, 2004; Ødegaard *et al.*, 2005) and in whole herbivory net-
394 works (Volf *et al.*, 2017). As we did not find any relationship between the families present
395 in a network and the relationship between phylogenetic distance and niche overlap in
396 either pollination or herbivory networks, the greater importance of shallow phylogeny (as
397 reported for leaf miners and galls in Volf *et al.* (2017)) may be a general feature of
398 plant-insect interaction networks. This contrasts with Chamberlain *et al.* (2014), who
399 found that the *shape* of the phylogenetic tree had a larger effect on network structure
400 than the timing of speciation. As Chamberlain *et al.* (2014) were interested in overall
401 structural properties of networks rather than niche overlap, this discrepancy may indi-
402 cate that different aspects of plant-insect interaction networks are influenced by different
403 aspects of plant phylogenies.

404 The variability of the strength of phylogenetic signal across networks and the lack of
405 influence of community composition on the strength of this signal could be partly due
406 to different trends within families. More than half of the plant families in each network
407 type behaved as we hypothesised, with more closely-related plants having greater niche
408 overlap than distantly related plants. This relationship between overlap and phyloge-
409 netic distance is consistent with the idea that traits affecting interactions are heritable
410 and change gradually such that closely related plants resemble their common ancestor—
411 and each other —more than they do distantly related plants (Schemske & Bradshaw,

1999; Gilbert *et al.*, 2015; Ponisio *et al.*, 2017). The degree of heritability of key traits may, however, differ between families. In some families, such as *Asteraceae* in pollination networks, the positive slope of this relationship was very shallow while in others, such as *Melastomataceae* in herbivory networks, the positive slope was extremely steep. This could indicate different rates of phenotypic drift or evolution in different families (or their interaction partners). In other families, there was no significant relationship between phylogenetic distance and niche overlap. In these cases, key traits affecting plant-insect interactions may be highly labile or plastic (environmentally determined). These possibilities are supported by several studies showing a stronger relationship between niche overlap and trait similarity than niche overlap and phylogenetic similarity (Junker *et al.*, 2015; Ibanez *et al.*, 2016; Endara *et al.*, 2017).

While the majority of plant families in our dataset showed the expected trend, two (*Polygonaceae* in pollination networks and *Fabaceae* in herbivory networks) showed the opposite pattern. In these families, closely-related plants had *lower* overlap than more distantly-related pairs of plants. There are several possible explanations for this pattern. First, part of the family may have recently undergone a period of rapid diversification with closely-related species developing novel phenotypes and attracting different interaction partners (Linder, 2008; Breitkopf *et al.*, 2015). Likewise, the animals may have undergone an adaptive radiation to specialise on their most profitable partner (Janz *et al.*, 2006). Alternatively, plants in these families could have undergone convergent evolution or ancestral traits could be strongly preserved. Either case would allow distantly-related *Polygonaceae* and *Fabaceae* to interact with the same insects. Finally, this pattern could be the result of ecological or environmental filtering (Ackerly, 2003; Mayfield *et al.*, 2009). Closely-related species with strong niche overlap might compete too severely to coexist. This is especially likely for plants sharing pollinators, where the loss of pollen to related species might severely limit reproductive success (Levin & Anderson, 1970; Bell *et al.*, 2005; Mitchell *et al.*, 2009). Indeed, animal pollination and seed dispersal have

439 been shown to act as filters for several plant clades (Mayfield *et al.*, 2009). Selection to
440 avoid competition and restrict numbers of interaction partners may lead to more intimate
441 or specialised interactions (Ponisio *et al.*, 2017). This is particularly the case in highly
442 intimate interactions, where both partners may specialise (Hembry *et al.*, 2018). Past
443 selection to avoid competition is consistent with the relatively high proportion of extreme
444 specialists we observed in the pollination networks. As described above, these specialists
445 likely weaken the relationship between phylogenetic distance and niche overlap.

446 The remaining families did not show significant relationships in either direction. That
447 is, the niche overlap between two plants did not vary linearly over phylogenetic distance.
448 Once again, there are several possible explanations for this result. These plants might be
449 highly specialised on different interaction partners and therefore have low overlap at all
450 levels of relatedness. In other plant families with more moderate levels of specialisation, it
451 is possible that pollination and/or herbivory do not exert large selection pressures on the
452 plants. If traits affecting pollination or herbivory are not heritable in these groups [Kursar
453 *et al.*, 2009] or their phenotypes are constrained by other factors (e.g., environmental con-
454 ditions, trade-offs with other traits, ontogenic change [Kariñho-Betancourt *et al.*, 2015]),
455 then we should not expect a relationship between phylogenetic distance and overlap of
456 interaction partners. Alternatively, pollination and/or herbivory might exert large pres-
457 sures that maintain the clade within a single pollination or defensive syndrome. These
458 syndromes are commonly believed to predict the pollinators or herbivores with which a
459 plant will interact (Waser *et al.*, 1996; Fenster *et al.*, 2004; Ollerton *et al.*, 2009; Johnson
460 *et al.*, 2014). As some recent studies have suggested that pollination syndromes do not
461 accurately predict plants' visitors in all plant families (Ollerton *et al.*, 2009), it may be of
462 interest for future researchers to test whether syndromes are better predictors in families
463 with weak relationships between overlap and phylogenetic distance.

464 For those few families which were well-represented in *both* pollination and herbivory
465 networks, we can also contrast the trends in the two network types. Notably, all families

466 except *Asteraceae* showed different trends in different network types. This could be be-
467 cause of conflicting selection from pollinators and herbivores, with one type of selection
468 placing greater constraints on plant traits than the other. Multiple types of interactions
469 (e.g., pollination, herbivory, nectar robbing) and even environmental factors can influ-
470 ence traits such as flower colour, nectar abundance, and flowering phenology (Strauss &
471 Whittall, 2006). These influences can act in the same or different directions (Strauss
472 & Whittall, 2006). Plant phenotypes in turn affect which species participate in both
473 pollination and herbivory (Strauss, 1997; Strauss *et al.*, 2002; Adler & Bronstein, 2004;
474 Adler *et al.*, 2006; Theis, 2006). The interplay between these different selective pres-
475 sures may mean that plants cannot evolve to respond optimally to both pollinators and
476 herbivores. Put another way, stronger selective pressure from herbivores might cause
477 phenotypic changes that disrupt phylogenetic signal in pollinators, or vice versa. This
478 could result from asymmetric degree distributions: within a single system, most plants
479 tend to interact with many pollinators *or* many herbivores but not both (Melián *et al.*,
480 2009; Pocock *et al.*, 2012; Astegiano *et al.*, 2017). These asymmetric interactions may also
481 affect higher-order network structures such as modularity or nestedness (Astegiano *et al.*,
482 2017). The nature of the effects of multiple interaction types on both phylogenetic signal
483 in interactions and overall network structure is, however, still an open question deserving
484 of much more research.

485 Altogether, our study has revealed general trends for conservation of interaction part-
486 ners between closely-related species, with some networks and plant families showing dif-
487 ferent trends. This overall similarity between closely-related species has a potential appli-
488 cation in ecological restoration. Close relatives could be used interchangeably to restore
489 missing interactions and fill ecosystem functions. This may be advantageous when a tar-
490 get plant is more difficult to establish than its relatives, or if the restoration site is not
491 large enough to support viable populations of many species. We should urge caution,
492 however, since plants which support the same pollinators may also support similar sets

493 of herbivores. To avoid unwanted indirect effects, all interactions involving the target
494 species should be considered. Although here we considered only the presence or absence
495 of interactions, (i.e., qualitative networks) recent work also suggests that the phylogenetic
496 composition of a plant community can also affect the strength of interactions, and that the
497 spatial arrangement of plants within a community may be particularly important (Yguel
498 *et al.*, 2011; Castagneyrol *et al.*, 2014). These further nuances in the relationship between
499 phylogenetic distance and niche overlap could also strongly affect the ability of closely-
500 related species to fill the same functions in restoration efforts. This is clearly a topic with
501 many unresolved questions, deserving of further study.

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510 **Author Contribution**

511 ARC, DBS, GVDR, and NJB designed the research. ARC, MO, IN, IMW, and JAT col-
512 lected published data. ARC and GVDR performed the analyses. All authors contributed
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Notes legends

Notes 1: Sources for networks. Original sources for all networks used in this study.

Notes 2: R implementation of tuple-form regression. Further details and R code for our statistical model.

Notes 3: Repeating our analyses with proportion of shared partners. Results when niche overlap is defined as the proportion of shared interaction partners rather than by a tuple of shared and unshared partners.

Notes 4: A test of connectance. Methods and results for a test as to whether the connectance of a network affects the relationship between phylogenetic distance and niche overlap.

Notes 5: Distributions of p -values for permuted networks. Figures showing the distributions of p -values in permuted networks referenced in Figs. 1-2.

Notes 6: Details of within-family regressions. Supplemental results for within-family regressions, including a comparison of p -values and critical values for the sequential correlated Bonferroni test.

Tables

Table 1: Change (Δ) in log odds (per million years of phylogenetic distance) of a pair of plants in the same family sharing a pollinator.

Family	Δ log odds	<i>P</i> -value	Family	Δ log odds	<i>P</i> -value
<i>Adoxaceae</i>	-65.8	0.163	<i>Malvaceae</i>	-5.56	0.363
<i>Amaryllidaceae</i>	-17.9	0.015	<i>Melastomataceae*</i>	5.19	0.577
<i>Apiaceae</i>	10.9	0.006	<i>Montiaceae</i>	-1.12	0.87
<i>Apocynaceae</i>	-6.96	0.037	<i>Myrtaceae</i>	8.55	0.071
<i>Asparagaceae</i>	-6.23	0.189	<i>Oleaceae</i>	0.995	0.855
<i>Asteraceae*</i>	-1.47	<0.001	<i>Onagraceae</i>	-556	>0.999
<i>Berberidaceae</i>	-1.48×10^3	>0.999	<i>Orchidaceae</i>	-14.5	0.145
<i>Boraginaceae</i>	-5.15	<0.001	<i>Orobanchaceae</i>	24.2	0.326
<i>Brassicaceae</i>	-11.2	0.072	<i>Papaveraceae</i>	-11.2	0.511
<i>Calceolariaceae</i>	156	0.998	<i>Phyllanthaceae</i>	9.99	0.433
<i>Campanulaceae</i>	334	0.999	<i>Plantaginaceae</i>	-8.48	0.001
<i>Caprifoliaceae</i>	0.31	0.959	<i>Poaceae*</i>	69.2	0.003
<i>Caryophyllaceae</i>	2.09	0.644	<i>Polygonaceae</i>	-14.8	<0.001
<i>Cistaceae</i>	-11.4	<0.001	<i>Primulaceae</i>	14.9	0.343
<i>Convolvulaceae</i>	-1.84	0.837	<i>Ranunculaceae</i>	-38	<0.001
<i>Ericaceae</i>	4.61	0.116	<i>Rosaceae</i>	0.759	0.735
<i>Fabaceae*</i>	-12.9	<0.001	<i>Rubiaceae*</i>	-13	0.026
<i>Geraniaceae</i>	-3.31	0.624	<i>Salicaceae</i>	-1.9	0.545
<i>Hydrangeaceae</i>	0.057	0.982	<i>Sapindaceae</i>	821	0.999
<i>Iridaceae</i>	-27.9	0.078	<i>Saxifragaceae</i>	-0.092	0.992
<i>Lamiaceae</i>	-5.01	<0.001	<i>Solanaceae</i>	-21.9	0.189
<i>Lauraceae</i>	-79.9	<0.001	<i>Tropaeolaceae</i>	192	0.997
<i>Loasaceae</i>	-865	>0.999	<i>Verbenaceae</i>	-9.03	0.627
<i>Malpighiaceae</i>	2.8	0.168	<i>Violaceae</i>	-0.487	0.974

We were able to fit these models to 48 plant families (see *Materials and Methods* for details). Families marked with an asterisk were also sufficiently diverse to model in herbivory networks. Statistically significant values are indicated in bold.

Table 2: Change (Δ) in log odds (per million years of phylogenetic distance) of a pair of plants in the same family sharing a herbivore.

Family	Δ log odds	<i>P</i> -value
<i>Asteraceae</i>	-1.73	0.550
<i>Euphorbiaceae</i>	-19.2	<0.001
<i>Fabaceae</i>	18.7	0.046
<i>Melastomataceae</i>	-13.2	0.022
<i>Moraceae</i>	-2.13	0.092
<i>Nothofagaceae</i>	-595	>0.999
<i>Pinaceae</i>	-25.8	0.733
<i>Poaceae</i>	-4.50	0.020
<i>Rubiaceae</i>	-8.16	0.006

Nine plant families were sufficiently diverse in our dataset to permit this analysis (see *Materials and Methods* for details). For each pattern of overlap, we show the change in log odds per million years and the associated *P*-value. Statistically significant values are indicated in bold.

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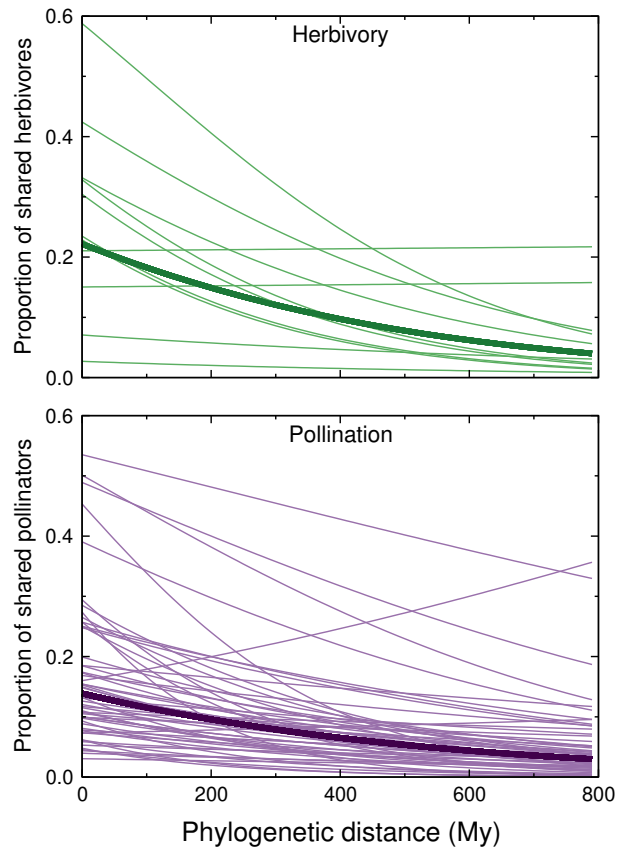


Figure 1: Results of a mixed-effects logistic regression of pairwise niche overlap against phylogenetic distance for plants in 11 herbivory networks (top; green) and 59 pollination networks (bottom; purple). In both network types, the probability of a pair of plants sharing an interaction partner decreased with increasing phylogenetic distance (thick, dark lines). There was substantial variation among networks (thin, pale lines) of both types. The slope of the regression for each network was significantly more extreme than that obtained from 999 permutations of that network (slopes obtained from the permuted networks ranged between -1.34×10^{-12} and 9.19×10^{-13}).

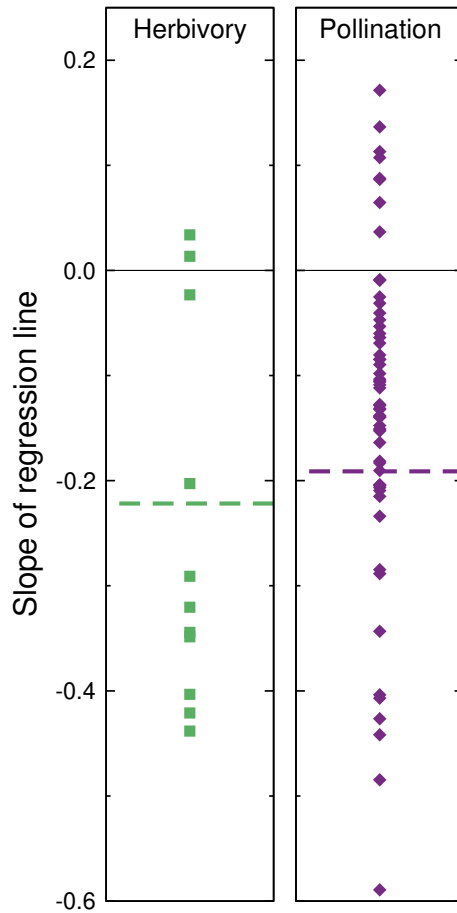


Figure 2: The slopes of the mixed-effect logistic regression of pairwise niche overlap against phylogenetic distance (representing the change in log odds of a pair of plants sharing an interaction partner) was significantly different from 0 for each network. Here we show the observed slopes for herbivory (green squares) and pollination (purple diamonds) networks. Thick, dashed lines represent the mean slopes across all networks of each type. The maximum and minimum slopes obtained from 999 permutations of each network are depicted by thin, black lines. For both network types, the slopes obtained from permuted networks were always very close to 0 (range -1.34×10^{-12} to 9.19×10^{-13}).

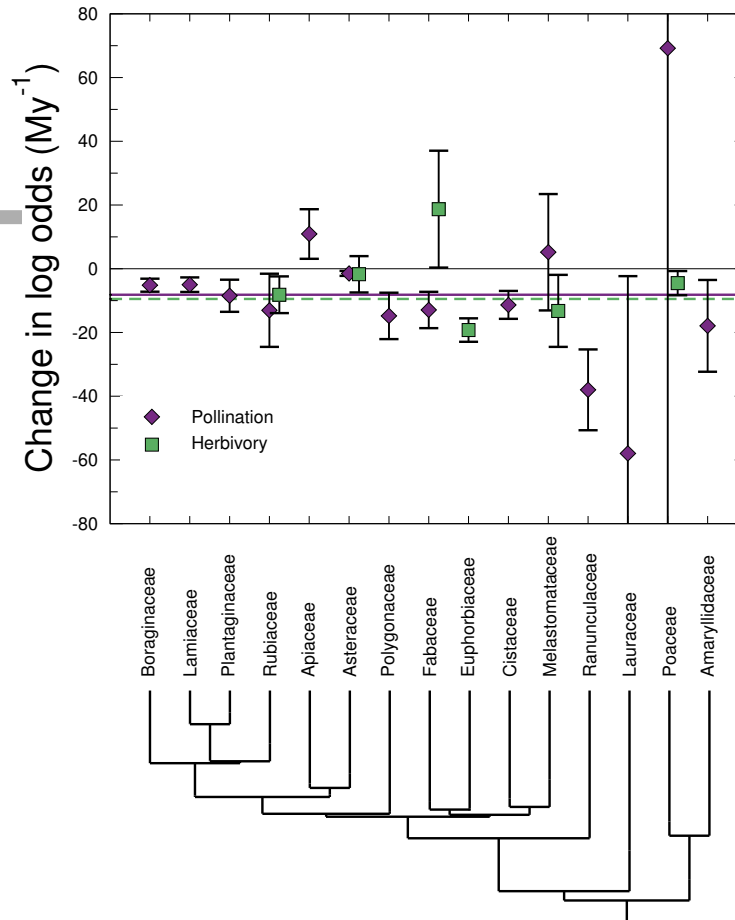
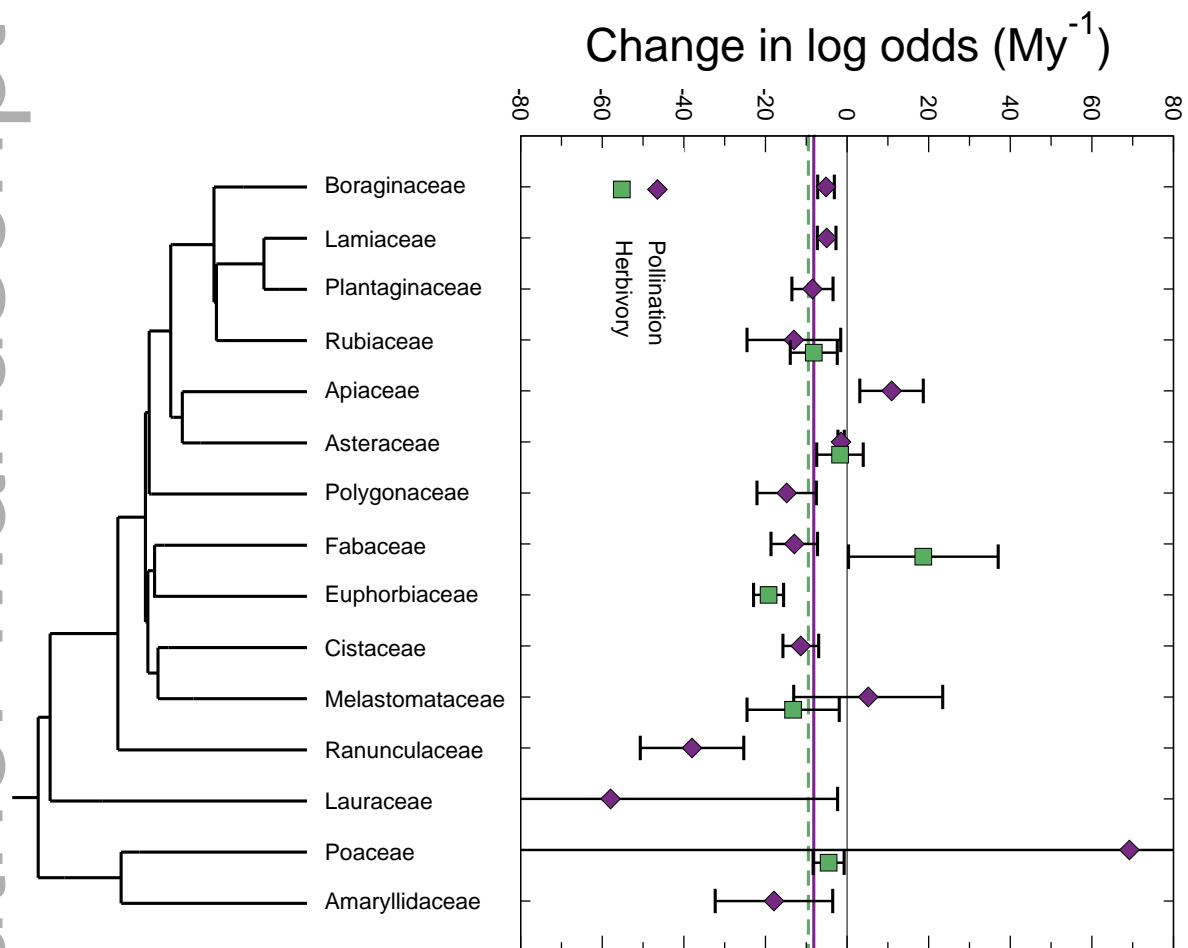
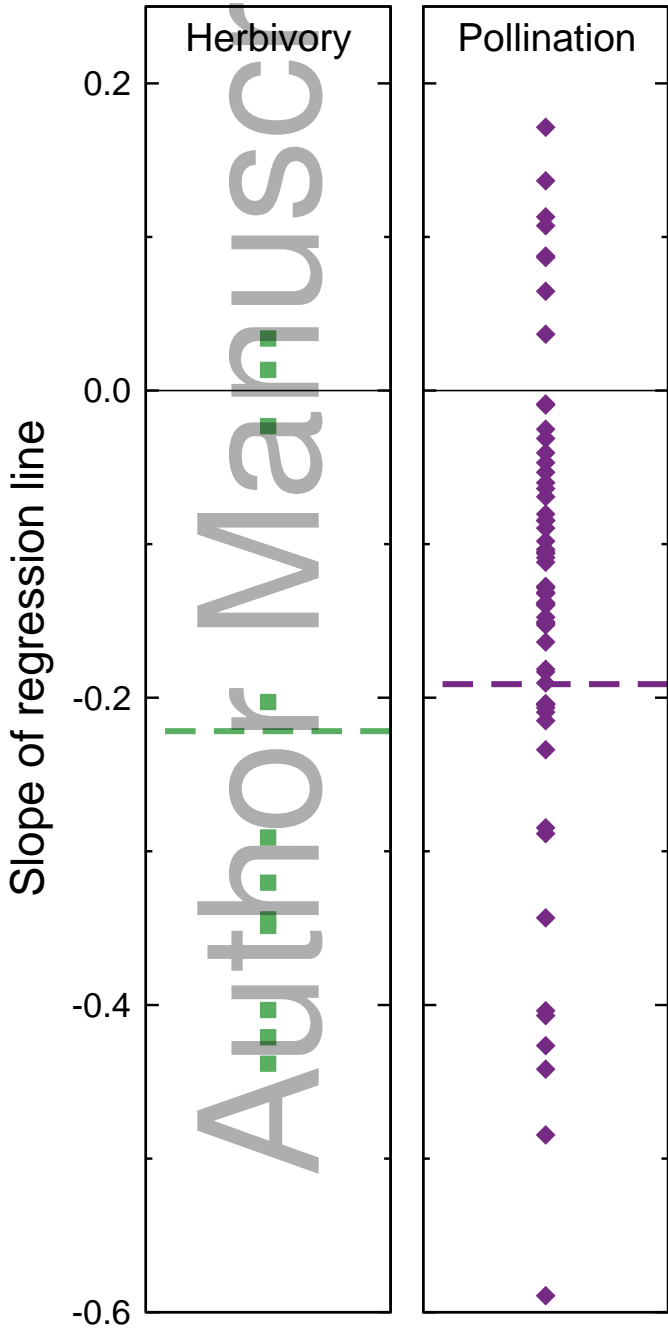
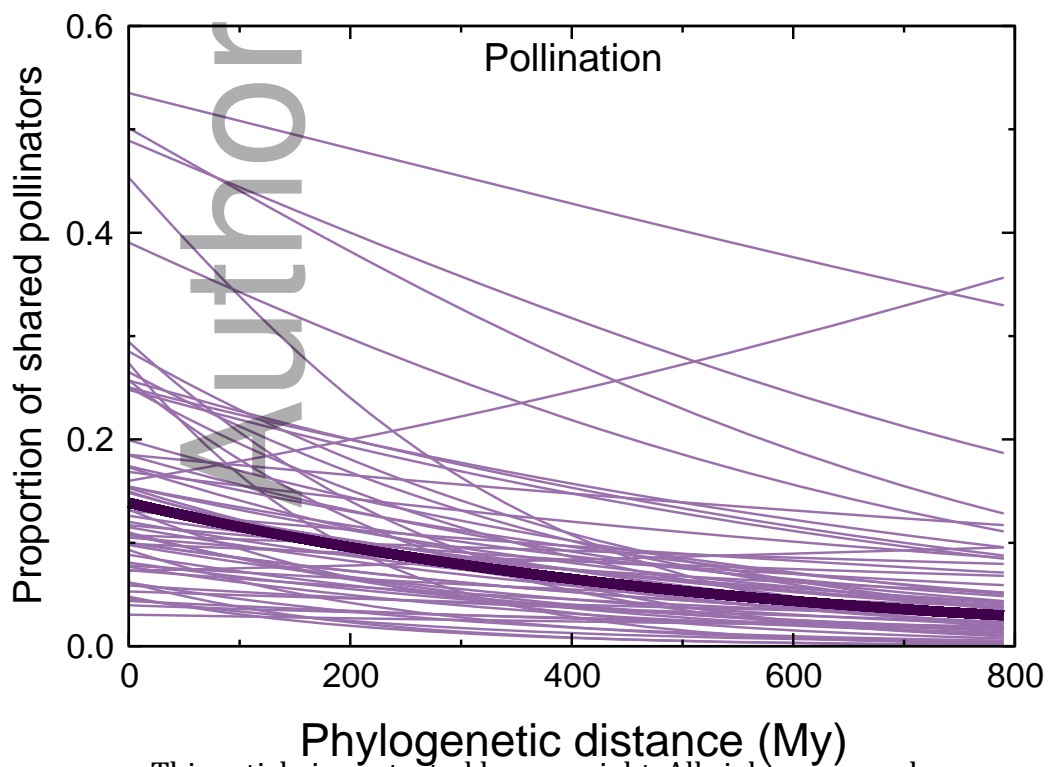
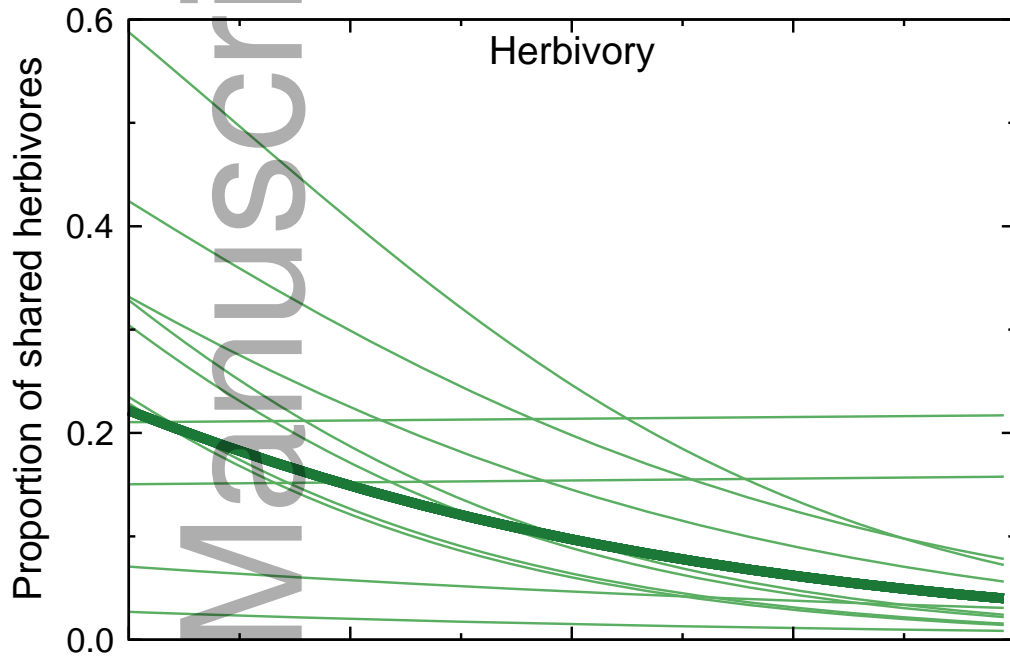


Figure 3: Change in the log odds of a pair of plants sharing a pollinator or herbivore (i.e., the slopes of the mixed-effect logistic regressions) as phylogenetic distance between the plants increases. These values are analogous to the slopes of the regression lines from Eq. 2-3 and represent the change in the probability of observing shared interaction partners per million years of divergence time. For clarity, we show only the 15 plant families for which the slope of the regression of the proportion of shared interaction partners against phylogenetic distance was significant in at least one network type. Note that the change in log odds for *Asteraceae* in herbivory networks and *Melastomataceae* in pollination networks are not significantly different from zero; we present these values only for comparison across network types. All other plant families were well-represented in only one network type. Families in pollination networks are indicated by dark purple diamonds while families in herbivory networks are indicated by pale green circles. We also show the slope of the relationship between the log-odds of observing each overlap pattern and phylogenetic distance across all plant families in herbivory (pale, green horizontal line) and pollination (dark, purple horizontal line) networks. The phylogenetic tree below the plots indicates the relatedness between these plant families. Error bars represent 95% confidence intervals.









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