

At a global scale, conservation of pollinators and herbivores between related plants varies widely across communities and between plant families.

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## Summary

- Related plants are often hypothesised to interact with similar sets of pollinators and herbivores, but empirical support for this idea is mixed. We argue that this may be because plant families vary in their tendency to share interaction partners.
- We introduce a novel way to quantify overlap of interaction partners for each pair of plants in 59 pollination and 11 herbivory networks based on the numbers of shared and unshared interaction partners. We test for relationships between phylogenetic distance and partner overlap within each network, and whether these relationships varied with the composition of the plant community. Finally, we test for different relationships within well-represented plant families.
- Across all networks, more closely-related plants tended to have greater overlap, especially in herbivory networks. The strength of this relationship within a network was unrelated to the composition of the network's plant component, but 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 the dominant plant families within a community may be the key to understanding the distribution of interactions.

## Keywords

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

# Introduction

Interactions with animals affect plants' life cycles in several critical ways (Mayr, 2001; Sauve *et al.*, 2016). On one hand, pollination and other mutualistic interactions contribute to the reproductive success of many angiosperms (Ollerton *et al.*, 2011). On the other, herbivores consume plant tissues (McCall & Irwin, 2006) which costs plants energy and likely lowers their fitness (Strauss *et al.*, 2002). In both cases, these interactions do not occur randomly but are strongly influenced by plants' phenotypes (Fontaine & Thébault, 2015). For example, plants that produce abundant or high-quality nectar may receive more visits from pollinators (Robertson *et al.*, 1999) whereas plants that produce noxious secondary metabolites may have fewer herbivores (Johnson *et al.*, 2014). A plant's traits are also likely to determine *which* specific pollinators and herbivores interact with that plant. Plants with different defences (e.g., thorns vs. chemical defences) may deter different groups of herbivores (Ehrlich & Raven, 1964; Johnson *et al.*, 2014), and the concept of pollination syndromes has often been used to group plants into phenotypic classes believed to attract certain groups of pollinators (Waser *et al.*, 1996; Fenster *et al.*, 2004; Ollerton *et al.*, 2009).

If attractive and/or defensive traits are heritable, then we can reasonably expect that related plants will have similar patterns of interactions with animals, especially if there is some selection in either group to avoid competition or the number of potential partners is limited (Schemske & Bradshaw, 1999; Ponisio *et al.*, 2017). That is, there may be *phylogenetic signal* in plants' interactions such that closely-related plants may tend to have similar interaction partners. Recent studies that have investigated this question at the level of whole communities, however, have yielded mixed results (Rezende *et al.*, 2007b; Gómez *et al.*, 2010; Rohr & Bascompte, 2014; Fontaine & Thébault, 2015; Lind *et al.*, 2015; Ibanez *et al.*, 2016; Bergamini *et al.*, 2017; Sydenham *et al.*, 2018; Volf *et al.*, 2017; Hutchinson *et al.*, 2017). In particular, significant phylogenetic signal in plants' sets of interaction partners tends to be rare in empirical networks (Rezende *et al.*, 2007b;

Lind *et al.*, 2015; Ibanez *et al.*, 2016; but see Elias *et al.*, 2013; Fontaine & Thébault, 2015; Hutchinson *et al.*, 2017). Moreover, statistically significant degrees of phylogenetic signal or coevolution may only result in small differences in network structure, adding to the difficulty of understanding patterns in species' interaction partners (Ponisio *et al.*, 2017). Further, the plant and animal components of networks can show different degrees of phylogenetic conservation of interaction partners. In mutualistic networks, animals often show a stronger phylogenetic signal in their partners than do plants (Rezende *et al.*, 2007b; Chamberlain *et al.*, 2014; Rohr *et al.*, 2014; Vamosi *et al.*, 2014; Lind *et al.*, 2015; Fontaine & Thébault, 2015) (but see Rafferty & Ives (2013) for a counterexample). In antagonistic networks, however, actively-foraging consumers tend to show less phylogenetic signal than their prey (Ives & Godfray, 2006; Cagnolo *et al.*, 2011; Naisbit *et al.*, 2011; Fontaine & Thébault, 2015). Thus, it is not straightforward to assume that interactions will always be similar among related species.

Several mechanisms that might weaken the conservation of interactions have been identified in the literature. Pollination and herbivory may be affected by a wide variety of traits, and not all of these are likely to be phylogenetically conserved (Rezende *et al.*, 2007a; Kursar *et al.*, 2009; Ibanez *et al.*, 2016). If, for example, floral displays are strongly affected by environmental conditions (Canto *et al.*, 2004), then pollinators may not be predicted by plants' phylogenies. Even if the traits affecting pollination and herbivory are heritable, plants may experience conflicting selection pressures that weaken the overall association between plant phylogeny and interaction partners (Armbruster, 1997; Lankau, 2007; Siepielski *et al.*, 2010; Wise & Rausher, 2013; Kariñho-Betancourt *et al.*, 2015). For instance, floral traits that are attractive to pollinators can also increase herbivory (Strauss *et al.*, 2002; Adler & Bronstein, 2004; Theis, 2006). Conversely, herbivory can reduce pollination by inducing chemical defences (Adler *et al.*, 2006) or altering floral display or nectar availability (Strauss, 1997). There may also be trade-offs between chemical and physical defences, or defences at different life stages, that weaken the overall

heritability of plants' sets of herbivores (Kariñho-Betancourt *et al.*, 2015; Endara *et al.*, 2017). Observed patterns of similarity in plants' interaction partners therefore represent a mixture of environmental effects and various selection pressures as well as plants' shared phylogenetic history.

A further complication is the possibility that the relationship between plants' relatedness and the similarity of their interaction partners is not constant across plant clades. Closely-related plants in one clade might be under strong selection to favour dissimilar sets of pollinators to avoid exchanging pollen with other species (Levin & Anderson, 1970; Bell *et al.*, 2005; Mitchell *et al.*, 2009). Similarly, plants may experience disruptive selection on defences against herbivores if congeners tend to grow in the same places such that herbivore able to consume one species could easily spread to close relatives (Kursar *et al.*, 2009). Unrelated plants might also converge upon similar phenotypes, attracting a particularly efficient or abundant pollinator (Ollerton, 1996; Wilson *et al.*, 2007; Ollerton *et al.*, 2009; Ibanez *et al.*, 2016). Likewise, unrelated plants may converge upon similar defences, leading them to share those herbivores which can overcome these defences (Pichersky & Gang, 2000). In either case, dissimilarity of interactions among related species or similarity of interactions among unrelated species could result in weaker phylogenetic signal across an entire plant community. Moreover, all of the aforementioned hypotheses are non-exclusive; different processes likely affect different clades, and these processes might be associated with different pressures imposed by pollination and herbivory (Fontaine & Thébault, 2015).

Here we investigate how overlap in interaction partners between pairs of plants (henceforth "niche overlap") varies over phylogenetic distance and how this differs between plant families. Whereas previous studies have focused on the presence or absence of phylogenetic signal across entire networks, we take a pairwise perspective in order to obtain a more detailed picture of how plant phylogeny relates to network structure. Specifically, we test 1) whether niche overlap decreases over increasing phylogenetic distance in a large

dataset of pollination and herbivory networks, 2) whether the plant family composition of a community affects the relationship between niche overlap and phylogenetic distance in that community, and 3) whether the relationship between niche overlap and phylogenetic distance differs systematically across plant families. This fine-grained approach gives more detailed information than previous studies.

## Materials and Methods

### Network data

We tested for phylogenetic signal in niche overlap within a set of 59 pollination and 11 herbivory networks. These networks span a range of biomes (desert to scrub forest to grassland) and countries (Sweden to Australia). The herbivory networks included a variety of types of herbivores but were dominated by insects consuming leaves. To ensure that we were analysing interactions influenced by similar sets of traits across networks, we restricted our herbivory networks to insects consuming leaves and excluded sap-sucking, leaf-mining, and galling insects as well as seed predators and xylophagous insects; all of these interactions involve different plant tissues and means of feeding than leaf consumption and so may be influenced by different plant and insect traits. Specifically, we removed any non-leaf consuming insects and any plants which had no interaction partners after removing other types of herbivores. The adjusted networks range in size between 19 and 997 total species (mean=162, median=97) with between 8 and 132 plant species (mean=39.1, median=29.5). See *Table S1, Supporting information 1* for details on the original sources of all networks.

### Phylogenetic data

In order to fit the plant species in all networks to a common phylogeny, we first compared all species and genus names with the National Center for Biotechnology Information and

Taxonomic Name Resolution Service databases to ensure correctness. This was done using the function ‘get\_tsn’ in the R (R Core Team, 2016) package *taxize* (Chamberlain & Szocs, 2013; Chamberlain *et al.*, 2019). Species which could not be assigned to an accepted taxonomic name (e.g., ‘Unknown Forb’) were discarded, as were those with non-unique common names and no binomial name given (e.g., ‘Ragwort’) or binomial names that could not be definitively linked to higher taxa (e.g., ‘*Salpiglossus sp.*’). We were left with 2341 unique species in 1027 genera and 195 families. On average, 11.43% of plants were removed from each network (median 4.60%, range 0-55.10%).

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

## Calculating niche overlap within communities

We calculated niche overlap for each pair of species within a community using a Jaccard index to describe the number of shared interaction partners, augmented with the number of interaction partners which were not shared. The Jaccard index  $J_{ij}$  describes the

proportion of shared interaction partners for species  $i$  and  $j$  and is defined as:

$$J_{ij} = \frac{M_{ij}}{P_i + P_j - M_{ij}}, \quad (1)$$

where  $M_{ij}$  is the set of *mutual* (shared) interaction partners of species  $i$  and  $j$  and  $P_i$  and  $P_j$  are the sizes of the sets of interaction *partners* for species  $i$  and  $j$  respectively. We wished to give more weight to species sharing a large number of interaction partners as well as those sharing a large proportion (i.e., to emphasise pairs of generalists sharing most of their interaction partners over specialists sharing a single interaction partner). Note that species sharing a large *number* of interaction partners may not share a large *proportion* of interaction partners if the number of interaction partners that are not shared is also large. To capture all of this information for each species pair, we therefore recorded the number of shared interaction partners ( $M_{ij}$ ) and the number of interaction partners that were not shared ( $U_{ij} = P_i + P_j - 2M_{ij}$ ). Instead of a single index  $J_{ij}$ , we thus kept track of the full information needed to compute niche overlap between species  $i$  and  $j$  as a tuple:  $(M_{ij}, U_{ij})$ .

## Statistical analysis

We modelled the relationship between niche overlap and phylogenetic distance using a logistic regression. We used both the numbers of shared ( $M_{ij}$ ) and non-shared ( $U_{ij}$ ) partners as dependent variables and centred, scaled phylogenetic distance as the independent variable. This approach is conceptually similar to modelling successes and failures in a binomial-distributed process. Accordingly, we assumed a binomially-distributed error structure and used a logit link function to model the probability  $\omega_{ij}$  of plants  $i$  and  $j$  sharing an interaction partner. Regressions of niche overlap and phylogenetic distance within each network were fit using the R (R Core Team, 2016) base function “glm” and



took the form

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

where  $\delta_{ij}$  is the phylogenetic distance between plants  $i$  and  $j$ . The fixed effect of distance in this regression,  $\beta_{\text{distance}}$ , can be understood as the change in log odds of sharing an interaction partner per million-year change in phylogenetic distance.

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

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

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

To demonstrate the power of defining  $\omega_{ij}$  as a tuple of  $M_{ij}$  and  $U_{ij}$ , we repeated the above analyses instead defining  $\omega_{ij}$  as the proportion of interaction partners that are shared (i.e.,  $M_{ij}/[M_{ij}+U_{ij}]$ ). We observed similar trends but, notably, the tuple definition of  $\omega_{ij}$  had greater power to detect weak relationships (*Supporting information 2*). We therefore show only the results when defining  $\omega_{ij}$  as a tuple in the main text.

Note that pairs of plants are not always independent: the same plant will appear in

many pairs. This violates the assumption of independence used when calculating the significance of logistic regressions within the R (R Core Team, 2016) base package or the package *lme4* (Bates *et al.*, 2015). To calculate significance of the regression coefficients we observed, it was therefore necessary to compare the observed relationships to those in a suite of appropriately permuted networks. To create these networks, we shuffled interactions among species while preserving row and column totals. That is, each species retained the same number of interaction partners as in the observed network but the exact set of partners (and therefore niche overlaps with all other species) varied across permuted networks. We preserved the observed phylogenetic relationships between species in all cases. For each observed network, we created 999 such permuted networks and calculated the relationship between niche overlap and phylogenetic distance. This gave us a null distribution for each observed network with which to determine the significance of the observed relationship.

This permutation approach also allows us to estimate type I and type II error for our analysis. To do this, we created 500 permutations of each permuted network and, again keeping the observed phylogenetic distances between plant species, repeated our analyses. We can then determine the number of permuted networks which appear to have significant overlap-phylogenetic distance relationships relative to the permutations of these permuted networks (type I error). Type II error can be determined from the distribution of p-values obtained when comparing the permuted networks to permutations of the permuted networks. Although calculating the exact type II error requires a specific alternative hypothesis, the uniform distribution of p-values we obtained after permuting the permuted networks means that the type II error would increase linearly as the alternative hypothesis was set farther from zero.

To test whether the relationship between phylogenetic distance and niche overlap depended on network size, we fit a general linear model for the slope of this relationship inferred from the glm models against the number of plant pairs for which distances could

be calculated (hereafter “network size”), network type (again using herbivory networks as a baseline), and their interaction:

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

where  $\eta_N$  is the number of plant pairs in network  $N$  for which distances could be calculated,  $I_N$  is an indicator equal to 1 if network  $N$  is a pollination network and 0 otherwise.

As the interaction between network type and network size was strong and opposite to the direction of the main effect of network size, we fit an additional general linear model using only data from pollination networks and including only the effect of network size (herbivory networks were the baseline in the full glm). Both models were fit using the R (R Core Team, 2016) base function “glm”.

## Linking network-level trends and community composition

Next, we examined the connection between our network-level observations and the plant families present in each community. Specifically, we tested the hypothesis that varying relationships between phylogenetic distance and pairwise niche overlap are due to the different distributions of families across networks. We defined the relationship between phylogenetic distance and niche overlap as the change in log odds of two plants in a given network sharing an interaction partner per million years of divergence (i.e., the slope  $\beta_{distance}$  from the regression of niche overlap against phylogenetic distance within a single network). We then related differences in this relationship to differences in the composition of the plant community in each network using a non-parametric permutational multi-variate analysis of variance (PERMANOVA; Anderson, 2001). As we did not wish to inflate the perceived similarity between pairs of networks which did not include many of the same families, we used Bray-Curtis dissimilarity to define differences in plant community composition. Bray-Curtis dissimilarity considers only those plant families which

appear in at least one of a pair of networks (Anderson, 2001; Cirtwill & Stouffer, 2015), ensuring that the shared absence of rare plant families will not make two networks appear more similar than they actually are.

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

## Calculating niche overlap within families

Finally, we wished to compare the breakdown of overlap of interactions in different plant families. To do this, we used the same definitions of overlap and phylogenetic distance as in the within-network analysis but restricted our regressions to pairs of plants from the same family and the same network. Unlike in our previous analysis, we analysed data from pollination and herbivory networks separately as most well-represented plant families appeared in only one network type. For those families which appeared in both network types, we ran separate analyses on each subset of data.

For each plant family, within each network type, we then fit one of two similar sets of models. If family  $f$  was found in several networks of the same type (e.g., several pollination networks), we fit a mixed-effects logistic regression relating niche overlap to a

fixed effect of phylogenetic distance and a random effect for each network using the R (R Core Team, 2016) function “glmer” from package *lme4* (Bates *et al.*, 2015). If family  $f$  was found in only one network (and therefore only one network type), we omitted the network-level random effect and fit a logistic regression using the R (R Core Team, 2016) base function “glm”. These equations took the same form as equation 2.

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

## 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. 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 partly due to the greater proportion of specialist pollinators than specialist herbivores. 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). As extreme specialists by definition are never shared by more than one plant, a large proportion of specialists would decrease interaction partner overlap.

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 distance in only a single pollination network.

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

Comparing the results in the observed networks to those obtained after permuting phylogenetic distances across pairs of plants, the observed slope of the relationship between phylogenetic distance and interaction partner overlap was always more extreme (i.e., always lesser or always greater) than that obtained in the permuted networks (Fig. 2). Observed networks with a negative relationship between phylogenetic distance and overlap

always had a more negative slope than that obtained from the permuted networks, while the 10 networks with positive relationships between phylogenetic distance and overlap always had more positive relationships than the permuted networks. This suggests that even in the networks with non-significant relationships, the association between niche overlap and phylogenetic distance was not random. When the slopes of the permuted networks were compared to those obtained from permutations of the permuted networks, there was no relationship, which speaks to the robustness of our methodology (*Supporting information 3*).

## Linking network-level trends and community composition

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

## Within-family conservation of niche overlap

Taking all families together, the probability of species in the same family sharing interaction partners was not significantly related to phylogenetic distance ( $\beta_{distance}=-6.48$ ,  $p=0.087$ ). Pollination networks did not show a significantly different trend from the herbivory networks ( $\beta_{distance:pollination}=1.73$ ,  $p=0.681$ ). More closely-related pollinators did, however, tend to share fewer interaction partners ( $\beta_{pollination}=-0.776$ ,  $p=0.007$ ), similar to our within-network results above.

Considering each family separately, the relationship between within-family niche overlap and phylogenetic distance varied widely in both pollination and herbivory networks.

For the 48 families that were well represented in pollination networks, overlap decreased significantly with increasing phylogenetic distance in 12 (Table 2). There was no significant relationship between overlap and phylogenetic distance in a further 34 plant families (see *Supporting information 4* for further details). Finally, the overlap between pairs of *Apiaceae* and *Poaceae* increased significantly with increasing phylogenetic distance.

Of the nine plant families that were sufficiently well represented in herbivory networks, overlap decreased significantly with increasing phylogenetic distance in four (Table 1; Fig. 3). Four families did not show significant relationships between phylogenetic distance and overlap, and in one family, *Fabaceae*, overlap of interaction partners increased significantly with increasing phylogenetic distance.

## Discussion

We found broad support for the hypothesis that more closely-related pairs of plants have a higher degree of niche overlap. Using a novel method which considers all pairs of plants together, the probability of two plants sharing the same animal interaction partners generally decreased with increasing phylogenetic distance. Considering networks separately,  $\approx 56\%$  of the pollination and  $\approx 64\%$  of the herbivory networks exhibited the expected trend of decreasing overlap with increasing distance. This variation between networks echoes earlier studies (e.g., Fontaine & Thébaud, 2015; Hutchinson *et al.*, 2017), which also found broad evidence for phylogenetic conservation of interaction partners despite variation between particular networks. The lack of a significant relationship between phylogenetic distance and interaction partner overlap in many networks could be partly due to the large number of extreme specialists, especially among the pollination networks. These species interact with only one plant and therefore weaken any signal of interaction partner overlap. The herbivory networks did not contain as many obligate specialists, but we note that many herbivorous insects are oligotrophs which consume only a few closely-related hosts (Novotny & Basset, 2005; Yguel *et al.*, 2011). These oligotrophs may



affect overall phylogenetic signal in the same way as the specialist partners: in both cases plants in different families are unlikely to share interaction partners.

We found that the composition of plant families in a network was not related to the slope of the relationship between phylogenetic distance and interaction partner overlap. This suggests that conservation of interaction partners among closely related plants (e.g., congeners or members of the same subfamilies) is more important than phylogenetic signal from deeper within the phylogenetic tree. This echoes earlier results relating plant phylogeny to predation by particular insect species (Novotny *et al.*, 2002, 2004; Ødegaard *et al.*, 2005) and in whole herbivory networks (Volf *et al.*, 2017). As we did not find any relationship between the families present in a network and the relationship between phylogenetic distance and interaction partner overlap in either pollination or herbivory networks, the greater importance of shallow phylogeny (as reported for leaf miners and gallers in Volf *et al.* (2017)) may be a general feature of plant-insect interaction networks. This contrasts with the findings of Chamberlain *et al.* (2014), who found that the *shape* of the phylogenetic tree rather than whether speciation was more or less recent had a larger effect on network structure. As Chamberlain *et al.* (2014) were interested in overall structural properties of networks rather than interaction partner overlap, this discrepancy may indicate that different aspects of plant-insect interaction networks are influenced by different aspects of plant phylogenies.

The variability of the strength of phylogenetic signal across networks and the lack of influence of community composition on the strength of the relationship between phylogenetic distance and interaction partner overlap could be partly due to the different trends within families. More than half of the plant families in each network type behaved as we hypothesised, with more closely-related plants having greater niche overlap than distantly related plants. This relationship between overlap and phylogenetic distance is consistent with the idea that traits affecting interactions are heritable and change gradually such that closely related plants resemble their common ancestor— 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. In other families, there was no significant relationship between phylogenetic distance and interaction partner overlap. In these cases, key traits affecting plant-insect interactions may not be strongly conserved. Studies showing a stronger relationship between trait similarity and shared interaction partners than phylogenetic similarity and shared interaction partners suggest that traits may indeed be evolutionarily labile (Junker *et al.*, 2015; Ibanez *et al.*, 2016; Endara *et al.*, 2017).

Moreover, *Polygonaceae* in pollination networks and *Fabaceae* in herbivory networks showed the opposite pattern to what we expected. In these families, closely-related plants had *lower* overlap than more distantly-related pairs of plants. There are several possible reasons a plant family might display this pattern. First, part of the family may have recently undergone a period of rapid diversification with closely-related species developing novel phenotypes that attract different animal interaction partners (Linder, 2008; Breitkopf *et al.*, 2015). It is also possible that the animals have undergone an adaptive radiation to specialise on their most profitable partner (Janz *et al.*, 2006). Second, this pattern could be the result of ecological or environmental filtering (Ackerly, 2003; Mayfield *et al.*, 2009). Closely-related species which have high degrees of overlap in their interaction partners 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 been shown to act as filters for several plant clades (Mayfield *et al.*, 2009), while selection to avoid competition and restriction on num-

bers of interaction partners may lead to more intimate or specialised interactions (Ponisio *et al.*, 2017). This is consistent with the relatively high proportion of extreme specialists we observed in the pollination networks, which likely contributes to the weak relationships between phylogenetic distance and interaction partner overlap in many networks. Finally, although we do not have information about plants' traits in these networks, it is possible that convergence or a high degree of ancestral trait conservation has occurred allowing distantly-related *Polygonaceae* and *Fabaceae* to interact with the same insects.

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

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

showed the expected decrease in interaction partner overlap with increasing phylogenetic distance, the other families showed different trends in different network types. This may indicate that one type of interaction places greater constraints upon these families than the other, similar to the expectation that greater constraints upon consumers than upon their resources explains the asymmetry in conservation of interaction partners (Fontaine & Thébault, 2015). Plants may not be able to respond to selection on both types of interaction simultaneously because traits affecting pollination can also affect herbivory, and vice versa (Strauss, 1997; Strauss *et al.*, 2002; Adler & Bronstein, 2004; Adler *et al.*, 2006; Theis, 2006). Associations with pollinators and herbivores may also be constrained by the larger structure of the community. In one recent study, plants which are visited by many pollinators are also consumed by many herbivores (Sauve *et al.*, 2016). This may be because pairing antagonistic and mutualistic interactions balances the indirect effects of these interactions, leading to a more stable community (Sauve *et al.*, 2014). As more networks describing pollination and herbivory in the same community become available, it will be interesting to test this hypothesis more thoroughly.

Altogether, our study has revealed a wide variety of relationships between overlap of interaction partners and phylogenetic distance between plants in the same family. Regardless of the precise mechanisms behind these relationships, it is clear that the differences between families can affect the relationship between overlap and phylogenetic distance at the network level. Although here we considered only the presence or absence of interactions, recent work also suggests that the phylogenetic composition of a plant community can affect the strength of interactions, and that the spatial arrangement of plants within a community may be particularly important (Yguel *et al.*, 2011; Castagneyrol *et al.*, 2014). If so, then the study of how phylogenetic relationships between plants affect their interactions with animals has only just begun.

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## Author Contribution

ARC, DBS, GVDR, and NJB designed the research. ARC, MO, IN, IMW, and JAT collected published data. ARC and GVDR performed the analyses. All authors contributed to the manuscript.

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# Tables

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

Family	Change in log odds	<i>P</i> -value
<i>Asteraceae</i>	-1.73	0.550
<i>Euphorbiaceae</i>	-19.2	<b>&lt;0.001</b>
<i>Fabaceae</i>	18.7	<b>0.046</b>
<i>Melastomataceae</i>	-13.2	<b>0.022</b>
<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	<b>0.020</b>
<i>Rubiaceae</i>	-8.16	<b>0.006</b>

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.

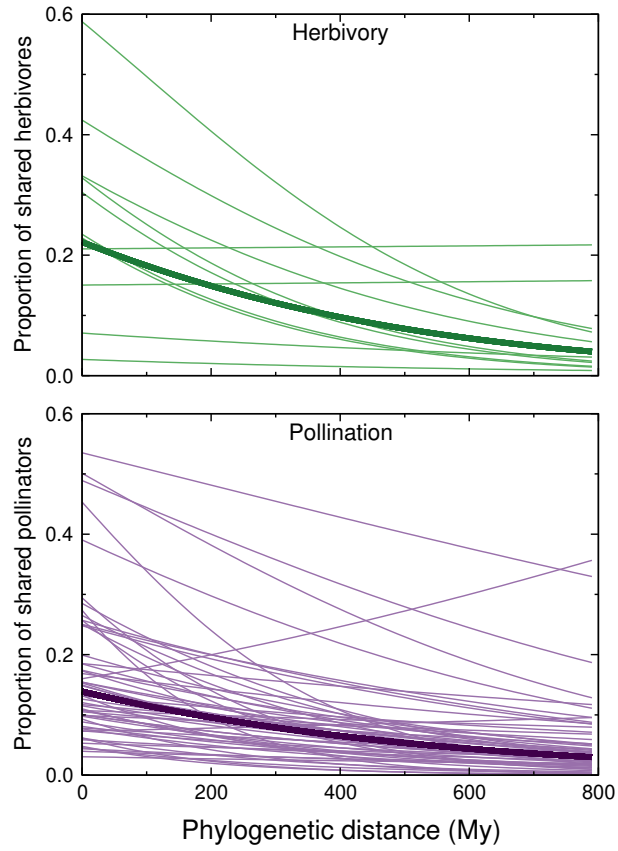
**Table 2:** Change in log odds (per million years of phylogenetic distance) of a pair of plants in the same family sharing a pollinator.

Family	Change in log odds	<i>P</i> -value	Family	Change in 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	<b>0.015</b>	<i>Melastomataceae</i> *	5.19	0.577
<i>Apiaceae</i>	10.9	<b>0.006</b>	<i>Montiaceae</i>	-1.12	0.87
<i>Apocynaceae</i>	-6.96	<b>0.037</b>	<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	<b>&lt;0.001</b>	<i>Onagraceae</i>	-556	>0.999
<i>Berberidaceae</i>	-1.48×10 <sup>3</sup>	>0.999	<i>Orchidaceae</i>	-14.5	0.145
<i>Boraginaceae</i>	-5.15	<b>&lt;0.001</b>	<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	<b>0.001</b>
<i>Caprifoliaceae</i>	0.31	0.959	<i>Poaceae</i> *	69.2	<b>0.003</b>
<i>Caryophyllaceae</i>	2.09	0.644	<i>Polygonaceae</i>	-14.8	<b>&lt;0.001</b>
<i>Cistaceae</i>	-11.4	<b>&lt;0.001</b>	<i>Primulaceae</i>	14.9	0.343
<i>Convolvulaceae</i>	-1.84	0.837	<i>Ranunculaceae</i>	-38	<b>&lt;0.001</b>
<i>Ericaceae</i>	4.61	0.116	<i>Rosaceae</i>	0.759	0.735
<i>Fabaceae</i> *	-12.9	<b>&lt;0.001</b>	<i>Rubiaceae</i> *	-13	<b>0.026</b>
<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	<b>&lt;0.001</b>	<i>Solanaceae</i>	-21.9	0.189
<i>Lauraceae</i>	-79.9	<b>&lt;0.001</b>	<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

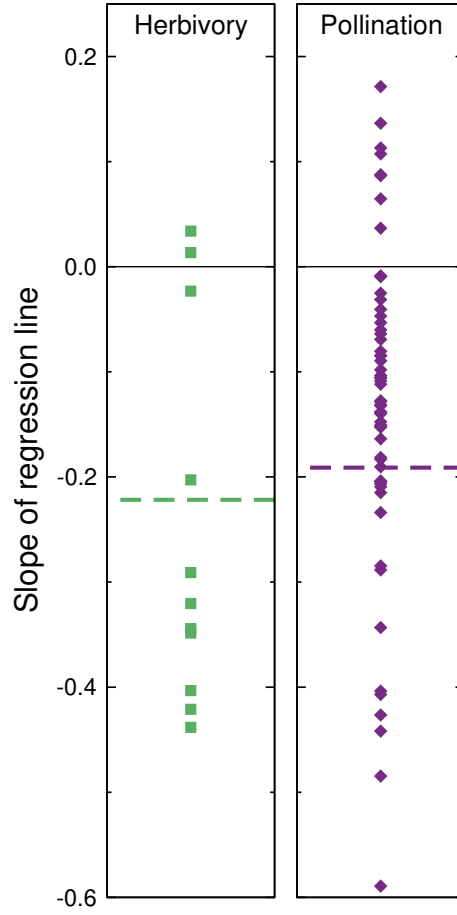
We were able to fit these models to 48 plant families (see *Materials and Methods* for details). Families marked with an asterisk were also sufficiently diverse to model in herbivory networks. Statistically significant values are indicated in bold.



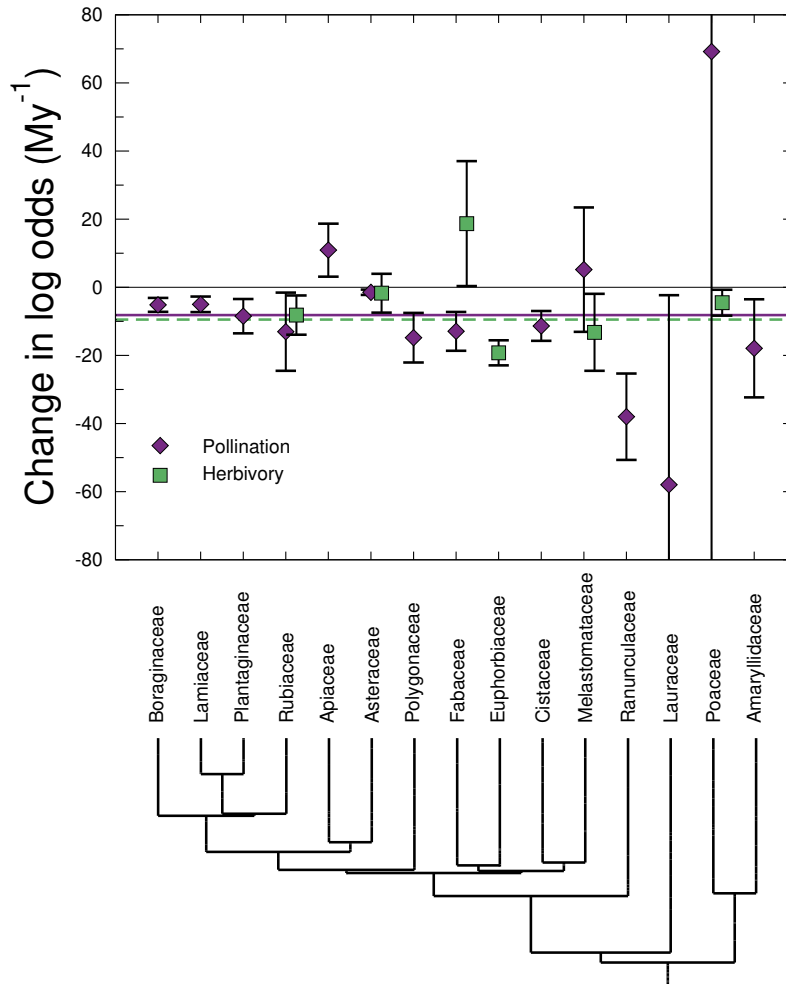
## Figures



**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 increased 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  $-1.34 \times 10^{-12}$  and  $9.19 \times 10^{-13}$ ).



**Figure 2:** The slopes of the mixed-effect logistic regression of pairwise niche overlap against phylogenetic distance 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.



**Figure 3:** Change in the log odds of a pair of plants sharing a pollinator or herbivore 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* and *Poaceae* 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.