Cophylogenetic signal is detectable in pollination interactions across ecological scales

Matthew C. Hutchinson,[1,2] Edgar Fernando Cagua,[1] and Daniel B. Stouffer[1,3]

[1]*Center for Integrative Ecology, School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch, New Zealand*
[2]*Department of Ecology and Evolutionary Biology, Princeton University, 106A Guyot Hall, Princeton, New Jersey 08540 USA*

Abstract. That evolutionary history can influence the way that species interact is a basic tenet of evolutionary ecology. However, when the role of evolution in determining ecological interactions is investigated, focus typically centers on just one side of the interaction. A cophylogenetic signal, the congruence of evolutionary history across both sides of an ecological interaction, extends these previous explorations and provides a more complete picture of how evolutionary patterns influence the way species interact. To date, cophylogenetic signal has most typically been studied in interactions that occur between fine taxonomic clades that show high intimacy. In this study, we took an alternative approach and made an exhaustive assessment of cophylogeny in pollination interactions. To do so, we assessed the strength of cophylogenetic signal at four distinct scales of pollination interaction: (1) across plant–pollinator associations globally, (2) in local pollination communities, (3) within the modular structure of those communities, and (4) in individual modules. We did so using a globally distributed dataset comprised of 54 pollination networks, over 4000 species, and over 12,000 interactions. Within these data, we detected cophylogenetic signal at all four scales. Cophylogenetic signal was found at the level of plant–pollinator interactions on a global scale and in the majority of pollination communities. At the scale defined by the modular structure within those communities, however, we observed a much weaker cophylogenetic signal. Cophylogenetic signal was detectable in a significant proportion of individual modules and most typically when within-module phylogenetic diversity was low. In sum, the detection of cophylogenetic signal in pollination interactions across scales provides a new dimension to the story of how past evolution shapes extant pollinator–angiosperm interactions.

Key words: compartmentalization; co-speciation; modularity; mutualism; mutualistic networks; phylogenetic structure; pollination syndromes.

Introduction

Populations do not exist in isolation but are instead constantly interacting with each other. Each of these interactions can impact the fitness of individuals and hence lead to selection for amplification or avoidance of future interactions (Thompson 2005, Gervasi and Schiestl 2017). Furthermore, when interactions directly influence the reproductive isolation of one or both species, selection can be powerful enough to cause speciation or extinction events that can potentially intertwine the evolutionary trajectories of pairs of taxa and their descendants (Thompson 2005). Where selection, regardless of its origin, is strong enough to drive coupled speciation in two interacting clades, the resultant macroscopic pattern is synonymously referred to as cophylogeny, cospeciation, or parallel cladogenesis (Page 2003, Thompson 2005).

A cophylogenetic signal implies two observations: that the phylogenies of interacting clades are congruent in structure and that extant interactions occur between evolutionarily coupled taxa (Page 2003, Desdevises 2007, Balbuena et al. 2013). A cophylogenetic signal suggests that contemporary ecological associations among species are the product of coupled evolutionary history such that ancestral forms of each species experienced and responded to shared selection pressures (Page 2003, Aizen et al. 2016). In contrast, the current paradigm of phylogenetic signal of species interactions suggests only that more closely related species interact in more similar ways (Rezende et al. 2007, Gómez et al. 2010, Rafferty and Ives 2013). Therefore, cophylogenetic signal in ecological networks would suggest that coupled evolutionary history as well as relatedness can determine species interactions, thereby providing additional insights into the role past evolution plays in determining contemporary ecological associations.

To date, the vast majority of studies of cophylogeny have centered on host–parasite relationships (Hafner and Nadler 1988, Vienne et al. 2013), where the focus is often at the relatively fine scale of families and genera (Weckstein 2004, Desdevises 2007, Hughes et al. 2007, but see

Page 2003, Chomicki et al. 2015). If cophylogenetic signal can also be considered a relevant predictor of ecological interactions, it should be detectable in other types of ecological associations. In particular, there is an increasing focus on the mutualistic assemblages of flowering plants and their pollinators as another system in which one might expect to detect a cophylogenetic pattern. Several recent studies have demonstrated the presence of cophylogeny at the scales of fig-wasp (Marussich and Machado 2007, Jousselin et al. 2008, Cruaud et al. 2012)

and yucca-moth (Althoff et al. 2012) pollination interactions (and see Aizen et al. 2016). Findings such as these, coupled with the facts that the association of angiosperms and pollinators dates back to the Cretaceous period (Crane et al. 1995, Grimaldi 1999) and that there is reasonable evidence to expect that at least some angiosperms and pollinators co-diverged (Grimaldi 1999), suggest a cophylogenetic signal may be widely identifiable between these groups (Fig. 1a). On the other hand, perfect congruence of speciation patterns cannot be expected across
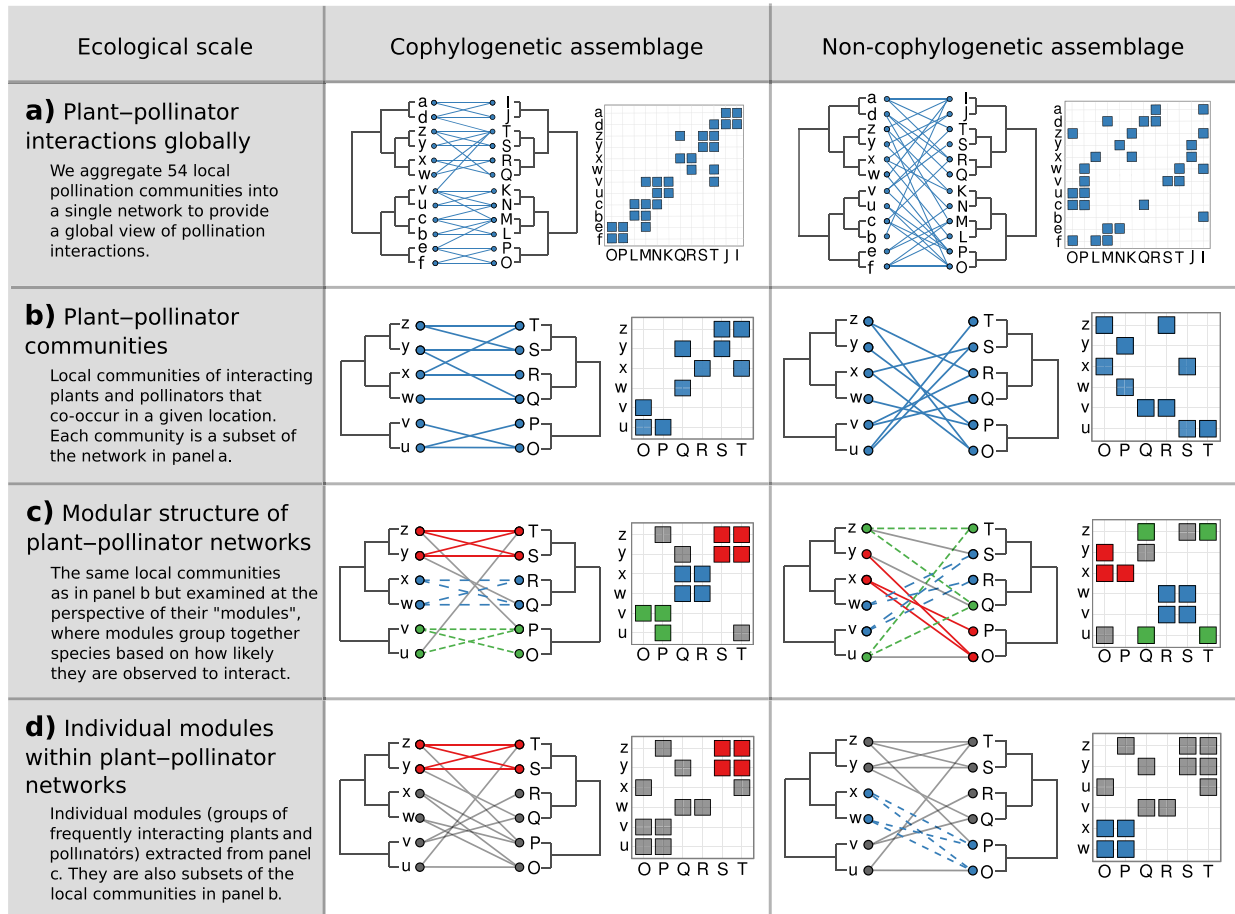

Fig. 1. Conceptual overview of our study in terms of the ecological scales at which we tested for cophylogenetic signal and what cophylogenetic and non-cophylogenetic assemblages look like at each scale. From top to bottom, the scales of investigation are (a) plant and pollinator interactions globally, (b) local pollination communities, (c) the modular structure of those pollination communities, and (d) individual modules within the communities. For each of these levels of organization, we provide a short description of the ecological scale of the analysis (column 1) and show representative examples of pollination-interaction structures that are cophylogenetic and non-cophylogenetic (in columns 2 and 3, respectively). Across all scales, the key to cophylogenetic signal is that the observed interactions tend to occur between species that show coupled evolutionary history (i.e., their speciation patterns match). Though the general idea is similar across them, our hypothesis tests at each scale address a slightly different question regarding the presence of cophylogenetic signal in pollination interactions. First, when we zoom out to plant–pollinator interactions globally, we are asking if observed pollination interactions, in general, tend to occur between taxa whose evolutionary history is congruent despite the fact that most of these species present in this interaction network do not co-occur and that this matching may occur at deep phylogenetic scales. Second, at the level of pollination communities, we are asking if those interactions that are realized in local communities tend to occur between plants and pollinators with the most congruent evolutionary histories. Third, we examine how the modular structure of those communities captures cophylogenetic signal. Our hypothesis here derives from the suggestion that the module is the fundamental unit of coevolution (Olesen et al. 2007) and asks whether interactions within modules tend to occur between those species with congruent evolutionary history and vice versa for interactions that fall between modules. Finally, many factors are thought to contribute to module formation and cophylogenetic signal may therefore not be observable across all modules in a community. As a result, we assess cophylogenetic signal in individual modules where the interactions of a module should occur between species with congruent evolutionary history more than would be expected by chance.

such rich and diverse groups after more than 100 mya of association. Nevertheless, even a weak cophylogenetic signal between angiosperms and their pollinators (i.e., at taxonomic scales above the species level) would provide important evidence that coupled evolution between taxa is an important correlate of their tendency to interact.

The most relevant scale at which cophylogenetic signal could characterize ecological interactions is that of the community. It is already well established that elements of community composition, such as evenness, functional trait diversity and interaction structure have an element of phylogenetic determinism (Webb et al. 2002, Emerson and Gillespie 2008, Vamosi et al. 2009, Harmon-Threatt and Ackerly 2013, Eklöf and Stouffer 2015). Hence, even when recognizing the various caveats of a phylogenetic approach to community ecology (Mayfield and Levine 2010, Losos 2011), there are clear implications should cophylogenetic signal be detectable in ecological communities. For instance, many studies have focused on how the evolutionary history of a single group (e.g., forest trees, pollinators) influences community structure (Cavender-Bares et al. 2006, Kembel and Hubbell 2006, Vamosi et al. 2009, Danieli-Silva et al. 2012); in contrast, detectable cophylogenetic signal would suggest that observed interactions tend to occur between taxa that show coupled evolutionary history and therefore that the structure of pollination networks is, at least partially, the by-product of this evolutionary coupling of taxa (Fig. 1b). Although recent findings for a set of related networks indicate that cophylogenetic signal may be detectable in pollination networks (Aizen et al. 2016), it is currently unclear whether or not this is generally the case.

At the same time, ecological communities can also be stochastic assemblages of species and interactions (Hubbell 2001, Cottenie 2005) and the value of examining smaller groups of closely interacting species has been shown time and again (Paine 1966, Estes and Palmisano 1974, Olesen et al. 2007, Rezende et al. 2009). Therefore, it is entirely possible that a cophylogenetic signal also permeates to finer scales within a community. Indeed, ecological networks are known to have identifiable structural features including being characterized by modules of closely interacting subsets of the community (Barber 2007, Thébault and Fontaine 2010). Modules, a pervasive feature in pollination networks (Olesen et al. 2007), are thought to play crucial roles in ecological community resilience (Thébault and Fontaine 2010) and may represent a fundamental unit of coevolution (Olesen et al. 2007, Bascompte and Jordano 2014). As such, these tight sets of interacting species may provide a more ecologically relevant scale at which cophylogenetic signal could act. On the one hand, a network's modular structure may show the clearest cophylogenetic signal (Fig. 1c). On the other hand, many different processes have been causally attributed to ecological module formation (Olesen et al. 2007, Rezende et al. 2009, Krasnov et al. 2012, Rohr and Bascompte 2014, Schleuning et al. 2014), implying that some individual modules

within networks may be better characterized by cophylogenetic signal than others (Fig. 1d).

For a network's modular structure to show a cophylogenetic pattern, two constraints must be satisfied (Fig. 1c). First, the modular structure should embody the phylogenetic congruence of the network such that modules represent groupings of closely related species on each side of the network. However, this mapping of each side of the modules to phylogenies does not take into account the degree to which those interactions within modules occur between evolutionarily coupled plants and pollinators. Thus second, a network's modules should also be comprised of the interactions that contribute most to the cophylogenetic signal of the network while interactions that contribute less should tend to fall between modules. At the even finer scale of individual modules, a module could be considered to show cophylogenetic signal when just its interactions show greater cophylogenetic signal than expected by chance (Fig. 1d).

Here, we explore cophylogenetic signal between plants and their pollinators in 54 pollination networks from around the world that together provide a taxonomically and geographically diverse data set (*available online*)[4]. In particular, we leverage these data to quantify the evidence of cophylogenetic signal at the four distinct scales mentioned previously (Fig. 1): (1) cophylogenetic signal between angiosperms and pollinators globally, (2) community cophylogenetic signal, where evolutionary congruence between species should be embodied by the interactions of the entire network, (3) cophylogenetic signal of a network's modular structure, where the modular structure of a network should tend to contain more closely related plant species, more closely related pollinator species, and the most evolutionarily congruent interactions between them, and (4) individual module cophylogenetic signal, where interactions within a module should be more cophylogenetic than expected by chance. Detectable cophylogenetic signal across these four scales suggests that, at least in plant–pollinator associations, the evolutionary determinants of extant interactions are a product of both interacting species rather than arising from only the phylogenetic relatedness on one side of the interaction.

METHODS

Empirical data and phylogeny construction

We analyzed a data set comprised of 54 binary, plant–pollinator mutualistic networks from a wide range of locations around the globe and with diverse species assemblages (Appendix S1: Sections S4 and S5). In each of the networks, the presence or absence of interactions is based on observed visitation of flowering plants by their animal pollinators. In total, these networks include

[4] http://www.web-of-life.es/

1,318 species of flowering plants, 2,930 species of pollinators, and over 12,000 unique interactions.

Studying cophylogenetic signal between two sets of interacting species, such as the flowering plants and pollinators that we examine here, requires an understanding of the evolutionary history of both groups. We followed several steps to generate sufficiently well-resolved phylogenies of flowering plants and their pollinators. First, to ensure all species identifications were up to date, we verified all species' names in the original interaction matrices. Plant names were checked and corrected with the NCBI database whereas we corrected animal names with the gnr_resolve function in the R package taxize, which accessed a range of taxonomic databases (Chamberlain et al. 2014; database available online http://www.ncbi.nlm.nih.gov/). We combined these species lists with published mega-phylogenies of plants (Zanne et al. 2014) and insects (Misof et al. 2014) to generate dated phylogenetic trees of our data. The two published trees provide a backbone for the construction of our phylogenies in that divergence patterns and dates of major lineages can be used as the basis of the phylogenies specific to our data. For the plants, major nodes are fully resolved down to the family level (with some dating below the family level). For the insect pollinators, the backbone tree provides resolution to the order level. It is most important for cophylogenetic analysis that these major nodes are dated accurately as it is thought that matching at these deeper phylogenetic scales drives observable cophylogenetic signal (Aizen et al. 2016). Below the family and order level, respectively, we largely rely on taxonomic information to infer evolutionary relationships between taxa. Full details of phylogeny construction are available in Appendix S1: Section S1.

Measuring cophylogenetic signal

To conduct a direct assessment of cophylogenetic signal between angiosperms and pollinators across these four scales, we implemented a recently developed Procrustean method: Procrustean Approach to Cophylogeny (PACo; Balbuena et al. 2013). This approach addresses the cophylogeny problem by optimizing the fit of the phylogeny-interaction graphs of each network (Balbuena et al. 2013). The cophylogenetic signal of each individual interaction is given by the squared residual distance (r^2) between the two corresponding points in the phylogenetic graphs. PACo thus returns a quantification of the global fit of the phylogenetic objects based on observed interactions as the sum of squared residual distances ($R = \sum r^2$) between phylogenetic-interaction graphs (Balbuena et al. 2013). As in regression, the smaller the residual distance, the better the fit of the two phylogenies to each other and the more support for a hypothesis of cophylogenetic signal as reflected by the extant interactions.

PACo, as implemented in R, offers several configuration options (Hutchinson et al. 2017). In this study, we have focused on the results of the symmetric method where the normalized plant graph is superimposed on the normalized pollinator graph. This means that we assessed cophylogenetic signal in terms of the plant phylogeny tracking the pollinator phylogeny since insect lineages preceded angiosperms (Misof et al. 2014) and pollinators have been shown to drive the evolution of plants (Gervasi and Schiestl 2017). It also implies that R is standardized with respect to the two phylogenies rather than in units relative to the pollinator phylogeny (as it would with an asymmetric superimposition). Importantly, our results do not differ qualitatively when selecting alternative configuration of PACo arguments (Appendix S1: Section S6).

Currently, there are a range of tools available for undertaking cophylogenetic analysis, and these methods can mainly be sorted into event-based and global-fit methods. Event-based methods reconcile one phylogenetic tree with the other by directly assessing evolutionary events (i.e., cospeciation, duplication, host switches) that are explicit in the tree topology (Conow et al. 2010, Drinkwater and Charleston 2016). Conversely, global-fit methods, such as ParaFit and PACo, aim to assess cophylogeny based on the congruence of observed interactions relative to the phylogenies rather than with the specifics of the phylogenetic topologies (Legendre et al. 2002, Balbuena et al. 2013). An important consequence of this difference in approaches is the manner in which significance of the observed cophylogenetic statistic tends to be inferred. The randomization approach implemented in PACo (and other global-fit methods) maintains the topology of the phylogeny of each group while shuffling the associations (i.e., interactions) between species to generate random instances of the observed data (Balbuena et al. 2013, Hutchinson et al. 2017). Conversely, event-based methods such as Jane (Conow et al. 2010) and CoRe-PA Merkle et al. 2010) instead permute the topology of the phylogenies due to their explicit focus on specific events. Both approaches have limitations (Balbuena et al. 2013, Drinkwater and Charleston 2016) and we take a global-fit approach here because it is the most amenable to the data we have and network-centric questions we explore.

Consequently, the approach that we adopt to study cophylogeny necessitates the shuffling of the association matrix to estimate the null distribution (Balbuena et al. 2013, Hutchinson et al. 2017). Rather than allow the results to be driven by variation in species' specificity or generalism, we also constrain this randomization so that each species' number of interactions is maintained when the associations are shuffled (Fortuna et al. 2010). For all instances of shuffling the association matrix, we use 1,000 permutations of the data to generate the null (and hence to infer significance of the observed pattern); we determined that this number of permutations was sufficient, here and in the related tests that follow below, by assessing convergence of the resulting P-values used for inference (Appendix S1: Section S11).

Global-scale cophylogenetic signal

We first used PACo to make a global assessment of cophylogenetic signal between flowering plants and pollinators using the global-scale phylogenies and the aggregate interaction network of our dataset, where all observed interactions between angiosperms and pollinators are represented. We assessed the significance of observed cophylogenetic signal at a global scale with a Monte Carlo approach whereby the observed (R) was compared to the same value (R*) from an ensemble of 1,000 randomizations of the aggregated interaction network. In each of these randomizations, we conserved the number of interactions for each species as well as the total number of interactions in the network (Fortuna et al. 2010). A conservative null model such as this preserves any influence on cophylogenetic signal of the total number of species interactions or the degree distribution meaning that deviation from the null model can be interpreted as due to properties of the particular species that interact rather than network topology. We considered the cophylogenetic signal of the observed network to be significant if R was smaller than the null distribution of R*, at $\alpha = 0.05$. Since our hypothesis of significant cophylogenetic signal at the global scale implies that R should be significantly smaller than the null expectation, we performed one-tailed tests for this global analysis.

To further examine any large-scale geographic patterns, we also constructed continent-specific phylogenies and networks. With the same statistical approach as for the global data, we examined cophylogenetic signal between plants and pollinators at the continental scale. The extent to which the interactions between plants and pollinators at a regional scale showed cophylogenetic signal was assessed for the six continents from which the empirical networks originate (Africa, Asia, Europe, North America, Oceania, South America). We followed the same approach as for the global scale. We assessed whether empirical R at the regional scale was smaller than its null expectation (i.e., the same null model as above), at $\alpha = 0.05$.

Community cophylogenetic signal

We next explored cophylogenetic signal at the scale of pollination communities from two angles. First, we assessed the cophylogenetic signal of the species assemblages themselves while maintaining the observed interaction structure, i.e., do the species present in each network represent a more cophylogenetic assemblage than if we were to draw the same number of species randomly from our full phylogenies? Second, we assessed the cophylogenetic signal of the interaction network itself, i.e., do the interactions observed in each network occur between more evolutionarily coupled species than we would expect by chance? To address these questions, we first quantified the cophylogenetic signal of each of the 54 empirical networks.

Cophylogenetic signal based on interaction network

The first assessment of cophylogenetic signal at the community scale was the degree to which realized interactions between plants and pollinators showed a greater cophylogenetic signal than expected by chance. If coupled evolution is an important determinant of species interactions, then we would expect that the interactions observed in a network show a stronger cophylogenetic signal than expected by chance. To make this assessment in our data set, we constructed a null model whereby observed interactions between pollinators and plants within a network were shuffled to create a randomization of the empirical network. The shuffling procedure, identical to that used for the global-scale analysis of cophylogenetic signal, fixes the total number of interactions as well as the degree of plants and pollinators. We used a Monte Carlo approach to compare the cophylogenetic signal of observed communities to the same (R*) from an ensemble of 1,000 randomizations of the network. We considered the cophylogenetic signal of the observed interaction network to be significant if its R was smaller than the null distribution, at $\alpha = 0.05$.

Cophylogenetic signal based on species assemblage

As mentioned earlier, a cophylogenetic signal may be detectable between two species purely because of coupled evolution of their ancestors (rather than the two species themselves). Therefore, it was also important to assess whether cophylogenetic signal seen at the community scale was different from that produced by the chance co-occurrence of species and evolutionary coupling between their ancestral states. To do so, we constructed a null model whereby pollinators and plants were randomly sampled from the full phylogenies (in equivalent numbers to those observed in the assemblage) and assigned to the interaction network. We used a Monte Carlo approach to assess whether or not the cophylogenetic signal seen in observed communities was different to those created by chance with the comparison of an empirical network's R to the same (R*) from an ensemble of 1,000 randomizations of that network following the outlined approach. We considered the cophylogenetic signal of an empirical species assemblage to be significant if its R was smaller than the null distribution, at $\alpha = 0.05$.

Modules in pollination networks

To test whether the modular structure of each network and individual modules themselves show a cophylogenetic signal, we first needed to identify modules in each of the interaction networks. To do so, we followed the approach proposed by Barber (2007) and implemented in MODULAR (Marquitti et al. 2014), where nodes in binary bipartite networks are partitioned across modules via a stochastic-optimization procedure, simulated annealing,

to maximize the modularity measure, Q_B (Marquitti et al. 2014). While there are several such methods to assess modularity, the method employed here has been shown to perform as well or better than other contemporary module detection algorithms in binary bipartite networks (Thébault 2013). Although by and large we use binary interaction networks in our analysis, quantitative networks can provide additional information with which to identify modules (Dormann and Strauss 2014). To assess the influence of a quantitative interaction network approach, we also studied the quantitative versions available for 15 of the networks in our data set. For each of these, we followed the same approach to cophylogenetic signal at the modular scale as for binary networks. We undertook all of the analyses that we outline in the following methodological sections for both our full dataset of binary networks and this subset of quantitative networks.

Cophylogenetic signal of a network's modular structure

While the degree to which communities as a whole show cophylogenetic signal could be established purely with PACo (Balbuena et al. 2013), an assessment of the extent to which cophylogenetic signal is manifest in the modular structure of those networks required subsequent analysis. To do so, we tested two aspects of a network's modular structure: the degree to which closely related species co-occur in modules (for both plants and pollinators) and the degree to which interactions within modules tend to show a stronger cophylogenetic signal than interactions between modules. Finally, we used chi-squared tests to assess the degree to which a significant test statistic for modular structure cophylogenetic signal, plant module phylogenetic signal, or pollinator module phylogenetic signal was related to a significant test statistic in the other two measures.

Phylogenetic congruence of module assignments

The first step we took was to quantify how plant and pollinator modules reflect the evolutionary history of each group. To do so, we inferred the phylogenetic signal present in species' module assignments using a likelihood-ratio test (LRT; Cadotte and Davies 2016). In the case of phylogenetic signal of a discrete trait, such as module assignment, significant phylogenetic signal is based on the comparison of two candidate models of trait evolution using Pagel's lambda (Pagel 1999). In the first model, λ is optimized based on the observed tree and observed traits. In the second model, the tree is first transformed based on $\lambda = 0$ (i.e., the tree is transformed into a star phylogeny, or, a single, large polytomy) and λ is again optimized. The degree of phylogenetic signal in the trait, module assignment, can then be inferred with a likelihood-ratio test (LRT) that compares how well each model, or version of the tree, explains the trait data. The LRT, therefore, assesses the degree to which the observed tree topology provides a better explanation of module assignment than an uninformative phylogeny. We considered the module assignment of the plant or pollinator species in a network to show significant phylogenetic signal if the fit of the model with the observed tree was significantly better than the fit of the model with the star phylogeny, at $\alpha = 0.05$. Both models and tree transformations were implemented with the ape::fitDiscrete function in R with the lambda transformation and equal-rates model (Paradis et al. 2004, R Core Team 2013) and followed the approach suggested by (1999) and reiterated by Cadotte and Davies (2016).

Cophylogenetic signal within and between modules

The previous analysis describes the degree to which closely related plants and/or pollinators co-occur in modules. However, it does not consider the degree to which the interactions within those modules occur between evolutionarily coupled taxa. Therefore, alongside our assessment of module phylogenetic signal, we also assessed the degree to which the modular structure of a pollination network is characterized by cophylogenetic interactions. If the modular structure of a network is characterized by a cophylogenetic signal, we expected interactions within modules to have a higher degree of congruence (i.e., have smaller residuals r on average) than interactions between species in different modules. To assess whether there was in fact a relationship between r and modular structure in each network, we calculated the average residual distance of interactions within modules $\bar{r}_w$, the average residual distance of interactions that occur between modules $\bar{r}_b$ and defined a test statistic $d_m = \bar{r}_w - \bar{r}_b$. We then compared the value of this test statistic to the same (d_m^*) for 1,000 instances of the empirical network with randomized module assignments. Since our hypothesis of significant cophylogenetic signal in the modular structure of a network implies that the empirical d_m should be significantly smaller than the null expectation, we performed a one-tailed test here.

To generate null expectations for both of these analyses, we randomized the species' module assignments using two approaches. In the first, more conservative, approach we created random modules for each network by maintaining the observed number of modules and the number of species within each of them ("same-sizes" null model). This approach preserves the modular structure of the network and just shuffles species between modules. In the second approach, we created random modules for each network by allowing for a random number of species in each module and a random number of modules ("all-sizes" null model). An approach such as this reconfigures the network's modular structure by potentially changing the number and size of its modules. Differences between approaches are not substantial and do not qualitatively affect our results or conclusions, therefore we present the results of the first, more conservative approach here. Results for the second approach can be found in Appendix S1: Section S6.

Cophylogenetic signal of individual modules

Finally, we wanted to understand whether and how individual modules within the same network varied in their cophylogenetic signal. To do so, we assessed the degree to which each empirical module tends to show a greater cophylogenetic signal than expected by chance. For each empirical module, we first generated a distribution of the relationships between the cophylogenetic signal of its interactions and the cophylogenetic signal of interactions in each of 1,000 random modules with an equivalent number of randomly sampled interactions. Random modules were drawn from randomizations of the networks that preserved connectance and degree distribution (the same null model described earlier for our assessment of cophylogenetic signal the global and community scales). In each case, we assessed whether the empirical module shows a stronger cophylogenetic signal than an equivalent random module by comparing the r of all the interactions within the empirical module (r_i) to the same for a random module (r_i^*) with a Wilcoxon-signed rank test. If our hypothesis of stronger cophylogenetic signal in the empirical module can be supported, then r_i should tend to be smaller than r_i^*. From this distribution of 1,000 comparisons of the empirical module with a random module, we were able to characterize a module as significantly cophylogenetic if its interactions tended to be smaller than their random counterparts, at $\alpha = 0.05$. Since our hypothesis of significant cophylogenetic signal within a module implies that empirical modules should always show a greater cophylogenetic signal than chance, we performed a one-tailed test here.

Determinants of cophylogenetic signal in individual modules

To better understand variation in cophylogenetic signal between modules, we quantified several module characteristics. For each module, we calculated module size (total number of species, plant richness, pollinator richness), module degree (the number of interactions within the module and the total number of interactions of participant species), and the phylogenetic diversity of the module for both plants and pollinators (Faith's PD divided by the total species richness of the module to correct for module size; Faith 1992). After checking for correlation or near co-linearity between explanatory variables (Pearson's $r < 0.7$), we used a logistic regression to assess the relationship, at $\alpha = 0.05$, of overall species richness of the module, the proportion of participant species' interactions that occur within the module, and phylogenetic diversity (Faith 1992) of both flowering plants and pollinators with module cophylogenetic signal.

Distribution of participation in cophylogenetic modules across the phylogeny

Last, we examined how the species that made up these modules were distributed across the plant and pollinator phylogenies to assess whether participation in a cophylogenetic module is phylogenetically clustered for either the plants or pollinators. To do so, we treated the participation of species in a significantly cophylogenetic module as a binary trait, 0 if never found in such a module and 1 if found in at least one such module. Based on this trait, we constructed a distance matrix m_d of cophylogenetic module assignment across all plant species, and the same across all pollinator species. Note that, in these symmetric distance matrices, species pairs are assigned a 0 if they both participated in any cophylogenetic module or if they both did not, and a 1 otherwise. We then used a Mantel test to gauge whether or not cophylogenetic module participation as given by the distance matrix m_d was predicted by the phylogenetic relatedness of plants and pollinators, respectively, as captured by the phylogenetic variance covariance matrix m_v. We then compared the Z statistic of the observed matrices to the same (Z^*) from an ensemble of 1,000 matrix randomizations, which preserved the non-independence of the underlying distances with ape::mantel.test (Paradis et al. 2004). A significant Z statistic (at $\alpha = 0.05$) here indicates that participation in cophylogenetic modules is clustered on the phylogeny more than expected by chance. As participation in cophylogenetic modules may either clustered or over-dispersed on the phylogeny, we undertook a two-tailed test here.

The effect of exotic species on cophylogenetic signal

The final analyses we undertook were an exploration of the effect that exotic species had on the cophylogenetic signal that we detect. To do so, we identified those networks in our analysis that contained exotic species. Specifically, we found references to particular exotic species in the original publications of these networks and used that subset of our data to answer this question. In all, nine networks out of the full set of 54 explicitly identified exotic species. For these networks, we removed the exotic species identified by the original authors and re-analyzed the data at all scales. We assessed cophylogenetic signal at the community scale, at the scale of the modular structure of the community, and within individual modules. As these results do not show meaningful differences from the case where exotic species are included, we present the corresponding results in Appendix S1: Section S10.

RESULTS

We first present cophylogenetic analysis of pollination interactions at the global scale where local interaction networks were aggregated into a single conglomerate network. While our data set is extensive, it does not fully encompass all flowering plant and pollinator species. In terms of representativeness, our global-scale plant phylogeny contains 38 out of 68 recognized orders, 133 out of 489 recognized families, and 761 genera. The global-

scale pollinator tree contains 24 orders, 263 families, and 1595 genera. More detail regarding taxonomic diversity can be found in Appendix S1: Section S5. Despite leaving some taxa unrepresented, there is nonetheless a significant cophylogenetic signal between plants and pollinators at the global scale (Monte Carlo test, $P < 0.001$). Moreover, we split this global dataset into continent specific trees and networks to examine regional patterns in cophylogenetic signal. In each region, we see that interactions between pollinators and plants show the same pattern of significant cophylogenetic signal that is seen at the global scale (Monte Carlo tests; all $P < 0.001$).

At the community level, our results show that most pollination communities exhibit a significant cophylogenetic signal. The observed interaction patterns of a majority of empirical pollination networks show significant cophylogenetic signal compared to an ensemble of random network structures (38 out of 54 networks; Monte Carlo test, $P < 0.05$; Fig. 2). Similarly, a large proportion of empirical networks show significantly stronger cophylogenetic signal than assemblages of plants and pollinators randomly sampled from the full phylogenies (24 out of 54 pollination networks, Monte Carlo test, $P < 0.05$; Fig. 2).

The frequent observation of significant cophylogenetic signal at a network scale, such as this, suggests that cophylogenetic signal should also be manifest in the modules of these networks and perhaps more so, given that modules are groups of closely interacting species. If module participation is a direct result of cophylogenetic association, we first expected that modules based on who interacts with whom are consistent with the evolutionary histories of both flowering plants and pollinators. Here, we instead see that the modular structure of a network is consistent with the pollinator and plant phylogenies in only 43% and 17% of networks, respectively (Monte Carlo test, $P < 0.05$; Fig. 2). Our second consideration to assess the cophylogenetic signal of a network's modular structure was the degree to which within-module interactions are more congruent with a cophylogenetic hypothesis than those interactions between modules. Here, we

find that the modular structure of a network shows a significant cophylogenetic signal in only 9% of the empirical networks (Monte Carlo test, $P < 0.05$; Fig. 2).

Across our data set, networks tend to vary in the degree to which their modular structure shows cophylogenetic signal (Fig. 2). Phylogenetic signal of modules for both pollinators and flowering plants is observed at a greater frequency than would be expected at random (χ^2 test, $P < 0.001$ in both cases); however, just two networks appear to satisfy all three constraints for cophylogenetic signal at the scale of a network's modular structure (Fig. 2). As such, a significant result for one aspect of cophylogenetic signal at this scale does not make it more likely for other aspects to also support a hypothesis of cophylogenetic signal (χ^2 tests of both phylogenies conserved, $P < 0.001$; plant phylogeny conserved and cophylogenetic grouping of interactions, $P = 0.662$; pollinator phylogeny conserved and cophylogenetic grouping of interactions, $P = 0.417$; all three constraints, $P = 0.662$; Fig. 2). When put together, our results provide rather limited evidence that the entire modular structure of a pollination network is the product of a cophylogenetic association.

A lack of signal at the scale of a network's modular structure does not imply that individual modules within those networks are also poorly characterized by a cophylogenetic signal. Indeed, most networks show significant cophylogenetic congruence in at least one module (Fig. 3). Similarly, significantly more modules (88 out of 349; χ^2 test, $P < 0.05$) show a detectable cophylogenetic signal, when aggregating across networks, than would be expected at random (Fig. 3). Our exploration of the characteristics of cophylogenetic modules with a logistic regression shows that module size and the proportion of participant species' interactions that are within the module are not related to module cophylogenetic signal ($z = 0.136$, $P = 0.892$ and $z = -0.920$, $P = 0.358$, respectively). However, the phylogenetic diversities of both flowering plants and pollinators do significantly influence module cophylogenetic signal with increased diversity making cophylogenetic signal less likely ($z = 2.225$, $P = 0.026$ and $z = 4.426$, $P < 0.001$, respectively). Furthermore, we see that the probability of
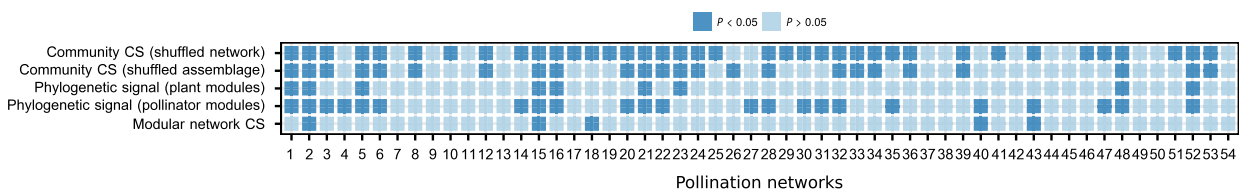

Fig. 2. The degree to which each of the 54 networks in our data set show cophylogenetic signal (CS) at the scale of local communities and their modular structure. On the *y*-axis, we show these measures of cophylogenetic signal starting with community level cophylogenetic signal of the observed species interaction network and community level cophylogenetic signal of the observed species assemblage. The measures that follow, the phylogenetic signal of both plants and pollinators in the observed modular structure of a network, and the degree to which a network's modular structure is cophylogenetic, pertain to the assessment of cophylogenetic signal in a community's modular structure. In each case, a light blue square indicates that a network is no different than a null expectation with respect to the measure of interest while a dark blue square indicates that the empirical network shows a significantly higher level of the measure than expected by chance (always at $\alpha = 0.05$).
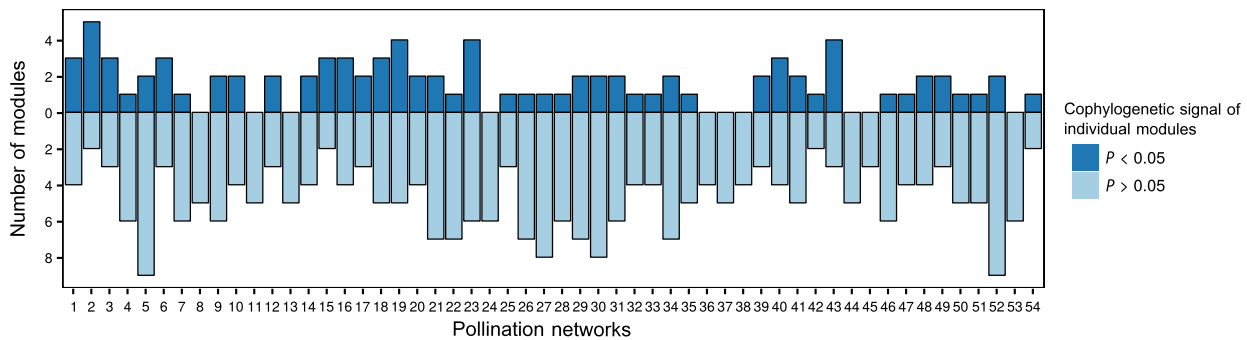
F<small>IG</small>. 3. There is substantial variation in the extent to which individual modules within networks show cophylogenetic signal. For each of the 54 networks (x-axis), we show the number of modules with significant cophylogenetic signal (dark blue) and the number that are non-significant (light blue). The majority of modules in almost all networks do not show a cophylogenetic signal (261 of 349). However, in 44 of 54 networks at least one module shows a stronger cophylogenetic signal than expected by chance.

species appearing in cophylogenetic modules is not equivalent for plants and pollinators. For the pollinators, there is a significant correlation between cophylogenetic module participation and phylogeny (Mantel test; $P < 0.001$) indicating that cophylogenetic module participation is clustered on the phylogeny. Indeed, although the 1151 pollinator species that participate in cophylogenetic modules come from eight orders, 946 of those species are either hymenopterans or dipterans. For the flowering plants, the opposite is true: participation in cophylogenetic modules is not influenced by phylogeny and hence is well distributed across the phylogeny (Mantel test; $P = 0.650$).

We also explored the degree to which modules show cophylogenetic signal when those modules are identified from quantitative rather than bipartite interaction networks. In all cases, we see qualitatively the same results between binary and quantitative networks. In terms of a network's modular structure, the partitioning of species into modules is at least slightly different between the two approaches (Appendix S1: Section S7). However, for cophylogenetic signal at the scale of a network's modular structure, the results are nearly identical. Cophylogenetic signal at the scale of a network's modular structure was assessed with three separate analyses for each network (*Methods*). In the 45 analyses across these 15 networks, there are only five qualitative changes in the result of an analysis between binary and quantitative versions of a network (i.e., from significant to non-significant or vice versa; Appendix S1: Section S7). At the scale of individual modules, we see similar results. The proportion of a network's modules that show significant cophylogenetic signal is often different between binary and quantitative networks but there does not appear to be much consistency to this difference (e.g., four networks show more cophylogenetic modules in the binary version than the quantitative, seven show the opposite pattern, and four are identical; Appendix S1: Section S7).

Last, we saw that exotic species do not appear to have a marked effect on the cophylogenetic signal that we see in pollination communities or in their modular structure (Appendix S1: Section S10). The only exception is that

the presence of exotic species does appear to dampen cophylogenetic signal at the scale of individual modules (Appendix S1: Section S10). However, these analyses should likely be treated as exploratory since exotic species were only found in a small subset of the networks that we studied here.

DISCUSSION

The primary goal of this study was to examine the potential role of cophylogeny as an evolutionary determinant of ecological interactions. Specifically, we have set out to quantify the degree to which a cophylogenetic signal is manifest between flowering plants and their pollinators across a broad dataset and at a range of ecological scales. We found that cophylogenetic signal in pollination interactions appears quite commonplace, from the global level of interactions between flowering plants and pollinators to the scale of ecological communities and their internal structure. In particular, we find that local communities tend to exhibit a greater degree of cophylogenetic signal than both randomly assembled communities of plants and pollinators with the same network structure and observed pollination communities with a shuffled network structure. As such, it appears that the role that evolutionary history plays in determining pollination interactions is not just on one side of the interaction or the other, but can instead be the product of both taxa and the coupled evolutionary history they share.

In its most basic sense, a cophylogenetic pattern is a macro-evolutionary signature of coupled evolutionary divergence between interacting taxa. In some cases, for instance between Toucans and chewing lice (Weckstein 2004) or amphibians and *Polystoma* (Bentz et al. 2006), the congruence in phylogenies of interacting clades has been attributed to shared biogeographical pressure such as vicariance (Weckstein 2004) or habitat acquisition (Bentz et al. 2006). Given the purported role of biogeographical forces in producing phylogenetic signal (Cavender-Bares et al. 2009), the significant cophylogenetic signal that we see at the global scale may be

explained by the co-occurence of taxa that have diversified in the same regions and interact due to proximity. On the other hand, if clumping of lineages by biogeographical filtering is a strong determinant of the signal that we see, we might expect to see a greater proportion of local communities showing significant signal when compared to random assemablages of species. Our results instead suggest that the proportion of local communities showing significant cophylogenetic signal is greater when the null expectation is a randomization of the observed community's interactions rather than when it is a random assemblage of species.

It has also been hypothesized that cophylogenetic signal is most parsimoniously explained by a coevolutionary process (Thompson 2005, Smith et al. 2008, Godsoe et al. 2009, Aizen et al. 2016), even when reciprocal selection need not always result in cospeciation (Thompson 2005). Indeed, Page (2003) suggests that "it is difficult to imagine that cospeciation can occur without at least some degree of coevolution." Clearly, the process or processes that underpin cophylogenetic signal remain an open question. As such, we focus here on the various implications of cophylogenetic signal across a gradient of ecological scales rather than speculate about the underlying mechanism.

Pollination is a comparatively less intimate and a more variable interaction type (Bascompte and Jordano 2014) than other systems in which cophylogeny has been studied (Hafner and Nadler 1988, Weckstein 2004, Desdevises 2007, Hughes et al. 2007). Accordingly, the strength of cophylogenetic signal observed here is not as extreme as levels seen in other systems (Hafner and Nadler 1988). Nonetheless, empirical associations of plants and pollinators still tend to show a significant cophylogenetic signal. Indeed, even when exotic species, who presumably have little coupled evolutionary history with native species, are present, a cophylogenetic signal can still be observed either due to potential evolutionary matching of deep phylogenetic branches between exotic and native taxa (Aizen et al. 2016), or due to the qualitative nature of our assessment of cophylogenetic signal (i.e., significant vs. non-significant). Interestingly however, the dampening of cophylogenetic signal by nonnative species was more obvious at the scale of individual modules of plants and pollinators.

Across ecological scales, we observe cophylogenetic signal between plants and pollinators. At all scales of pollination association, this implies that, while interactions may be predicted by co-occurrence (Gotelli and McCabe 2002) or functional traits (Dehling et al. 2014), it is also important to consider the evolutionary coupling of two taxa as a determinant of their likelihood to interact. Perhaps most importantly, when a community does show cophylogenetic signal, it also implies that there is phylogenetic congruence on both sides of its pollination interactions rather than only one. Our results therefore extend previous conclusions that closely related species in ecological networks tend to interact in

similar ways (Rezende et al. 2007, Gómez et al. 2010, Fontaine and Thébault 2015) and that phylogenetic relatedness influences community assembly (Emerson and Gillespie 2008) by suggesting that the role of past evolution in determining species interactions is not limited to one side of the interaction but can instead traverse the interaction.

The scale at which we see a less clear-cut cophylogenetic signal is at the level of modules. Undoubtedly, modules have fundamental roles in ecological networks as they describe groups of tightly bound interaction partners (Olesen et al. 2007). However, a network's modular structure appears to poorly reflect a cophylogenetic signal. Perhaps this is unsurprising. We know that modules in ecological networks can be the product of a suite of processes ranging from ecological to evolutionary and back again (Olesen et al. 2007, Rezende et al. 2009, Krasnov et al. 2012, Rohr and Bascompte 2014, Schleuning et al. 2014). Therefore, the weak cophylogenetic signal that we observe in the modular structure of pollination networks may be due to the fact that the modules of a community can be the result of a melting pot of ecological and evolutionary processes (Olesen et al. 2007, Krasnov et al. 2012, Traveset et al. 2013, Schleuning et al. 2014). Having said that, recent work that highlights the differences in the determinants and characterization of modules within a network (Olesen et al. 2007, Rezende et al. 2009) suggests the need to focus less on modular structure and more on individual modules themselves. In particular, if individual modules can be thought of as distinct entities then examining cophylogenetic signal across the modules of an entire community may unnecessarily blur the patterns of cophylogenetic signal present in the modules themselves and the community as a whole.

Accordingly, we find substantial variation in cophylogenetic signal across individual modules. While a significant proportion of observed modules are cophylogenetic, they may be closer to the exception than the rule. These cophylogenetic modules, that typically show low phylogenetic diversity on both sides of the interaction, appear to be tightly interacting and closely related groups of flowering plants and pollinators that exhibit both historical *and* contemporary associations. The constituent species in these modules appear to be more phylogenetically constrained for the case of pollinators than for plants as most pollinators that participate in cophylogenetic modules belong to the orders Diptera and Hymenoptera.

Given that the pollinators in pollination syndromes are thought to be more phylogenetically delimited than plants (Fenster et al. 2004), that Hymenoptera and Diptera account for four out of 11 pollination syndromes recognized by Ollerton and Watts (2000), and that these syndromes are thought to be represented by modules (Olesen et al. 2007), we conclude that future work should aim to understand whether or not the cophylogenetic modules we observe are in fact the manifestation of distinct pollination syndromes. Such work

could also incorporate the traits of these species alongside their evolutionary history and ecological associations. A clear pattern of cophylogenetic signal and trait-matching within modules may provide the clearest evidence to date in support of Olesen et al.'s (2007) hypothesis that modules represent a fundamental unit of coevolution in pollination networks.

Our results contribute a new consideration to the prediction of ecological interactions. In the face of accelerating global change, the ability to understand why species interact in the way they do has become particularly imperative to ecologists (Tylianakis et al. 2008). The breakdown of ecological networks that occurs when species become locally extinct or upon the addition of species through introduction poses a similar challenge to ecologists: how will the community respond? In an attempt to address these questions, much work has focused on predicting species interactions and network rewiring (Lopezaraiza-Mikel et al. 2007, Memmott et al. 2007, Tylianakis et al. 2008, Kaiser-Bunbury et al. 2010, Aizen et al. 2016). The cophylogenetic signal that we have seen in pollination interactions suggests that the coupled evolutionary history of taxa may play an important role in determining whether or not they can and will interact as the community around them changes. Given that pollination interactions represent a key ecosystem service, it is particularly important to improve our understanding of why and how particular species interact in the way that they do. We expect that our observation of cophylogenetic signal between plants and pollinators provides another valuable step in this process.

Literature Cited

Aizen, M. A., G. Gleiser, M. Sabatino, L. J. Gilarranz, J. Bascompte, and M. Verdú. 2016. The phylogenetic structure of plant–pollinator networks increases with habitat size and isolation. Ecology Letters 19:29–36.

Althoff, D. M., K. A. Segraves, C. I. Smith, J. Leebens-Mack, and O. Pellmyr. 2012. Geographic isolation trumps coevolution as a driver of yucca and yucca moth diversification. Molecular Phylogenetics and Evolution 62:898–906.

Balbuena, A. J., R. Miguez-Lozano, and I. Blasco-Costa. 2013. PACo: a novel procrustes application to cophylogenetic analysis. PLoS ONE 8:e61048.

Barber, M. J. 2007. Modularity and community detection in bipartite networks. Physical Review E 76:066102.

Bascompte, J., and P. Jordano. 2014. Mutualistic networks. Princeton University Press, Princeton, New Jersey, USA.

Bentz, S., N. D. Sinnappah-Kang, L.-H. S. Lim, B. Lebedev, C. Combes, and O. Verneau. 2006. Historical biogeography of amphibian parasites, genus Polystoma (Monogenea: Polystomatidae). Journal of Biogeography 33:742–749.

Cadotte, M. W., and T. J. Davies. 2016. Phylogenies in ecology: a guide to concepts and methods. Princeton University Press, Princeton, New Jersey, USA.

Cavender-Bares, J., A. Keen, and B. Miles. 2006. Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. Ecology 87:S109–S122.

Cavender-Bares, J., K. H. Kozak, P. V. Fine, and S. W. Kembel. 2009. The merging of community ecology and phylogenetic biology. Ecology Letters 12:693–715.

Chamberlain, S., E. Szocs, C. Boettiger, K. Ram, I. Bartomeus, and J. Baumgartner. 2014. taxize: Taxonomic information from around the web. https://github.com/ropensci/taxize.

Chomicki, G., P. S. Ward, and S. S. Renner. 2015. Macroevolutionary assembly of ant/plant symbioses: Pseudomyrmex ants and their ant-housing plants in the Neotropics. Proceedings of the Royal Society B 282:2015–2200.

Conow, C., D. Fielder, Y. Ovadia, and R. Libeskind-Hadas. 2010. Jane: a new tool for the cophylogeny reconstruction problem. Algorithms for Molecular Biology 5:16.

Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. Ecology Letters 8:1175–1182.

Crane, P. R., E. M. Friis, and K. R. Pedersen. 1995. The origin and early diversification of angiosperms. Nature 374:27–33.

Cruaud, A., et al. 2012. An extreme case of plant–insect codiversification: figs and fig-pollinating wasps. Systematic Biology 61:1029–1047.

Danieli-Silva, A., J. M. T. de Souza, A. J. Donatti, R. P. Campos, J. Vicente-Silva, L. Freitas, and I. G. Varassin. 2012. Do pollination syndromes cause modularity and predict interactions in a pollination network in tropical high-altitude grasslands? Oikos 121:35–43.

Dehling, D. M., T. Töpfer, H. M. Schaefer, P. Jordano, K. Böhning-Gaese, and M. Schleuning. 2014. Functional relationships beyond species richness patterns: trait matching in plant–bird mutualisms across scales. Global Ecology and Biogeography 23:1085–1093.

Desdevises, Y. 2007. Cophylogeny: insights from fish-parasite systems. Parasitologia 49:125.

Dormann, C. F., and R. Strauss. 2014. A method for detecting modules in quantitative bipartite networks. Methods in Ecology and Evolution 5:90–98.

Drinkwater, B., and M. A. Charleston. 2016. Towards sub-quadratic time and space complexity solutions for the dated tree reconciliation problem. Algorithms for Molecular Biology 11:15.

Eklöf, A., and D. B. Stouffer. 2015. The phylogenetic component of food web structure and intervality. Theoretical Ecology 9:107–115.

Emerson, B. C., and R. G. Gillespie. 2008. Phylogenetic analysis of community assembly and structure over space and time. Trends in Ecology and Evolution 23:619–630.

Estes, J. A., and J. F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. Science 185:1058–1060.

Faith, D. P. 1992. Conservation evaluation and phylogenetic diversity. Biological Conservation 61:1–10.

Fenster, C. B., W. S. Armbruster, P. Wilson, M. R. Dudash, and J. D. Thomson. 2004. Pollination syndromes and floral specialization. Annual Review of Ecology, Evolution, and Systematics 35:375–403.

Fontaine, C., and E. Thébault. 2015. Comparing the conservatism of ecological interactions in plant–pollinator and plant–herbivore networks. Population Ecology 57:29–36.

Fortuna, M. A., D. B. Stouffer, J. M. Olesen, P. Jordano, D. Mouillot, B. R. Krasnov, R. Poulin, and J. Bascompte. 2010. Nestedness versus modularity in ecological networks: Two sides of the same coin? Journal of Animal Ecology 79:811–817.

Gervasi, D. D., and F. P. Schiestl. 2017. Real-time divergent evolution in plants driven by pollinators. Nature Communications 8:14691.

Godsoe, W., E. Strand, C. I. Smith, J. B. Yoder, T. C. Esque, and O. Pellmyr. 2009. Divergence in an obligate mutualism is not explained by divergent climatic factors. New Phytologist 183:589–599.

Gómez, J. M., M. Verdú, and F. Perfectti. 2010. Ecological interactions are evolutionarily conserved across the entire tree of life. Nature 465:918–921.

Gotelli, N. J., and D. J. McCabe. 2002. Species co-occurrence: a meta-analysis of JM Diamond's assembly rules. Ecology 83:2091–2096.

Grimaldi, D. 1999. The co-radiations of pollinating insects and angiosperms in the Cretaceous. Annals of the Missouri Botanical Garden 86:373–406.

Hafner, M. S., and S. A. Nadler. 1988. Phylogenetic trees support the coevolution of parasites and their hosts. Nature 332:258–259.

Harmon-Threatt, A. N., and D. D. Ackerly. 2013. Filtering across spatial scales: phylogeny, biogeography and community structure in bumble bees. PLoS ONE 8:e60446.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography (MPB-32). Princeton University Press, Princeton, New Jersey, USA.

Hughes, J., M. Kennedy, K. P. Johnson, R. L. Palma, and R. D. Page. 2007. Multiple cophylogenetic analyses reveal frequent cospeciation between pelecaniform birds and Pectinopygus lice. Systematic Biology 56:232–251.

Hutchinson, M. C., E. F. Cagua, J. A. Balbuena, D. B. Stouffer, and T. Poisot. 2017. paco: implementing procrustean approach to cophylogeny in R. Methods in Ecology and Evolution 8:932–940.

Jousselin, E., S. Van Noort, V. Berry, J.-Y. Rasplus, N. Rønsted, J. C. Erasmus, and J. M. Greeff. 2008. One fig to bind them all: host conservatism in a fig wasp community unraveled by cospeciation analyses among pollinating and nonpollinating fig wasps. Evolution 62:1777–1797.

Kaiser-Bunbury, C. N., S. Muff, J. Memmott, C. B. Müller, and A. Caflisch. 2010. The robustness of pollination networks to the loss of species and interactions: a quantitative approach incorporating pollinator behaviour. Ecology Letters 13:442–452.

Kembel, S. W., and S. P. Hubbell. 2006. The phylogenetic structure of a neotropical forest tree community. Ecology 87: S86–S99.

Krasnov, B. R., M. A. Fortuna, D. Mouillot, I. S. Khokhlova, G. I. Shenbrot, and R. Poulin. 2012. Phylogenetic signal in module composition and species connectivity in compartmentalized host-parasite networks. American Naturalist 179: 501–511.

Legendre, P., Y. Desdevises, and E. Bazin. 2002. A statistical test for host–parasite coevolution. Systematic Biology 51:217–234.

Lopezaraiza-Mikel, M. E., R. B. Hayes, M. R. Whalley, and J. Memmott. 2007. The impact of an alien plant on a native plant–pollinator network: an experimental approach. Ecology Letters 10:539–550.

Losos, J. B.. 2011. Seeing the forest for the trees: the limitations of phylogenies in comparative biology. American Naturalist 177:709–727.

Marquitti, F. M. D., P. R. Guimarães, M. M. Pires, and L. F. Bittencourt. 2014. MODULAR: software for the autonomous computation of modularity in large network sets. Ecography 37:221–224.

Marussich, W. A., and C. A. Machado. 2007. Host-specificity and coevolution among pollinating and nonpollinating new world fig wasps. Molecular Ecology 16:1925–1946.

Mayfield, M. M., and J. M. Levine. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. Ecology Letters 13:1085–1093.

Memmott, J., P. G. Craze, N. M. Waser, and M. V. Price. 2007. Global warming and the disruption of plant–pollinator interactions. Ecology Letters 10:710–717.

Merkle, D., M. Middendorf, and N. Wieseke. 2010. A parameter-adaptive dynamic programming approach for inferring cophylogenies. BMC Bioinformatics 11:S60.

Misof, B., et al. 2014. Phylogenomics resolves the timing and pattern of insect evolution. Science 346:763–767.

Olesen, J. M., J. Bascompte, Y. L. Dupont, and P. Jordano. 2007. The modularity of pollination networks. Proceedings of the National Academy of Sciences USA 104:19891–19896.

Ollerton, J., and S. Watts. 2000. Phenotype space and floral typology: towards an objective assessment of pollination syndromes. Det Norske Videnskaps-Akademi. I. Matematisk-Naturvidenskapelige Klasse. Skrifter, Ny Serie 39:149–159.

Page, R. M. 2003. Introduction. Pages 1–22 in R. M. Page, editor. Tangled trees: phylogeny, cospeciation, and coevolution. University of Chicago Press, Chicago, Illinois, USA.

Pagel, M. 1999. Inferring the historical patterns of biological evolution. Nature 401:877–884.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist 100:65–75.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20:289–290.

R Core Team. 2013. R: A language and environment for statistical computing. R Project for Statistical Computing, Vienna, Austria. www.r-project.org

Rafferty, N. E., and A. R. Ives. 2013. Phylogenetic trait-based analyses of ecological networks. Ecology 94:2321–2333.

Rezende, E. L., J. E. Lavabre, P. R. Guimaraes Jr., P. Jordano, and J. Bascompte. 2007. Non-random coextinctions in phylogenetically structured mutualistic networks. Nature 448: 925–928.

Rezende, E. L., E. M. Albert, M. A. Fortuna, and J. Bascompte. 2009. Compartments in a marine food web associated with phylogeny, body mass, and habitat structure. Ecology Letters 12:779–788.

Rohr, R. P., and J. Bascompte. 2014. Components of phylogenetic signal in antagonistic and mutualistic networks. American Naturalist 184:556–564.

Schleuning, M., et al. 2014. Ecological, historical and evolutionary determinants of modularity in weighted seed-dispersal networks. Ecology Letters 17:454–463.

Smith, C. I., W. K. Godsoe, S. Tank, J. B. Yoder, and O. Pellmyr. 2008. Distinguishing coevolution from covariance in an obligate pollination mutualism: asynchronous divergence in Joshua tree and its pollinators. Evolution 62:2676–2687.

Thébault, E. 2013. Identifying compartments in presence–absence matrices and bipartite networks: insights into modularity measures. Journal of Biogeography 40:759.

Thébault, E., and C. Fontaine. 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. Science 329:853–856.

Thompson, J. N. 2005. The geographic mosaic of coevolution. University of Chicago Press, Chicago, Illinois, USA.

Traveset, A., R. Heleno, S. Chamorro, P. Vargas, C. K. McMullen, R. Castro-Urgal, M. Nogales, H. W. Herrera, and J. M. Olesen. 2013. Invaders of pollination networks in the Galaʹpagos Islands: emergence of novel communities. Proceedings of the Royal Society B 280:20123040.

Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. Ecology Letters 11:1351–1363.

Vamosi, S., S. Heard, J. Vamosi, and C. Webb. 2009. Emerging patterns in the comparative analysis of phylogenetic community structure. Molecular Ecology 18:572–592.

Vienne, D., G. Refrégier, M. López-Villavicencio, A. Tellier, M. Hood, and T. Giraud. 2013. Cospeciation vs host-shift speciation: methods for testing, evidence from natural associations and relation to coevolution. New Phytologist 198: 347–385.

Webb, C. O., D. D. Ackerly, M. A. McPeek, and M. J. Donoghue. 2002. Phylogenies and community ecology. Annual Review of Ecology and Systematics 33:475–505.

Weckstein, J. D. 2004. Biogeography explains cophylogenetic patterns in toucan chewing lice. Systematic Biology 53: 154–164.

Zanne, A. E., et al. 2014. Three keys to the radiation of angiosperms into freezing environments. Nature 506:89–92.

Supporting Information

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Data Accessibility

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.8n3q3