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Phylogenetic tree shape and the structure of mutualistic networks

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Summary

1. Species community composition is known to alter the network of interactions between two trophic levels, potentially affecting its functioning (e.g. plant pollination success) and the stability of communities. Phylogenies vary in shape with regard to the rate of evolutionary change across a tree (influencing tree balance) and variation in the timing of branching events (affecting the distribution of node ages in trees), both of which may influence the structure of species interaction networks. Because related species are likely to share many of the traits that regulate interactions, the shape of phylogenetic trees may provide some insights into the distribution of traits within communities, and hence the likelihood of interaction among species. However, little attention has been paid to the potential effects of changes in phylogenetic diversity (PD) on interaction networks.
2. Phylogenetic diversity is influenced by species diversity within a community, but also how distantly-related the constituent species are from one another. Here, we evaluate the relationship between two important measures of phylogenetic diversity (tree shape and age of nodes) and the structure of plant-pollinator interaction networks using empirical and simulated data. Whereas the former allows us to evaluate patterns in real communities, the latter allows us to evaluate more systematically the relationship between tree shape and network structure under three different models of trait evolution.
3. In empirical networks, less balanced plant phylogenies were associated with lower connectance in interaction networks indicating that communities with the descendants of recent radiations are more diverged and specialized in their partnerships. In simulations, tree balance and the distribution of nodes through time were included in the best models for modularity, and the second best models for connectance and nestedness. In models assuming random evolutionary

change through time (i.e., Brownian motion), less balanced trees and trees with nodes near the tips exhibited greater modularity, whereas in models with an early burst of radiation followed by relative stasis (i.e. early-burst models) more balanced trees and trees with nodes near roots had greater modularity.

4. *Synthesis*: Overall, these results suggest that the shape of phylogenies can influence the structure of plant-pollinator interaction networks. However, the mismatch between simulations and empirical data indicate that no simple model of trait evolution mimics that observed in real communities.

Key-words: connectance, diversity, modularity, nestedness, network structure, phylogeny imbalance, plant-pollinator interactions, plant population and community dynamics

Introduction

Species in ecological communities form networks of interactions. Interactions can be shaped by multiple factors including species abundances, phenology, spatial distribution and phenotypes (Hooper, Chapin & Ewel 2005; Stang, Klinkhamer & Van Der Meijden 2006; Stang *et al.* 2009; Memmott *et al.* 2007; Vázquez, Chacoff & Cagnolo 2009). These factors are in part determined by the evolutionary history, and trait adaptation, of the interacting species. Morphological traits can be a particularly important predictor of the structure of mutualistic networks, and some of these traits show a strong phylogenetic signal (Rezende *et al.* 2009; Rohr *et al.* 2010). Phylogenetic history may influence species interactions, underlying any analysis of network structure (Maherali & Klironomos 2007; Cadotte *et al.* 2009).

However, little is known about how phylogenetic relationships of species within a community (which are

reflected by the variation in the distribution of branching events upon a phylogenetic tree) shape the structure of interaction networks (Davies & Buckley 2012).

Two aspects are crucial in the evolution of a given community: variation in evolutionary rates among clades within a phylogeny, which determine tree balance and the timing of speciation events, which determine the distribution of node ages (Mooers & Heard 1997). These two simple phylogeny attributes reflect the evolutionary history of an ecological community (Mooers & Heard 1997). Balanced phylogenies exhibit high evenness in the distribution of diversification events among clades, and of phylogenetic distance among species. Trees with ancient speciation events have branching events largely clustered deeper in the tree, hence older average node age. In such trees, species have had more time to diverge, and hence should have lower trait similarity among species than trees with more recent speciation events (Davies *et al.* 2011).

Trait similarity within trophic levels can have an important influence on network metrics. With higher trait similarity, there is a higher probability of species sharing interaction partners (Gibson *et al.* 2011; Junker *et al.* 2013). Communities with imbalanced phylogenies and with older node ages should have low trait similarity among coexisting species (Davies *et al.* 2012), leading to low similarity in the identities of interaction partners of different species. However, there is evidence for the opposite – balanced phylogenies with young nodes on average have low trait similarity and thus low similarity in the identity of interaction partners (Davies *et al.* 2012). Such effects due to similarities of interaction partners should be reflected in the structure of interaction networks. Given that there is contrasting evidence for the relationship between traits and phylogenies, we predict two alternative scenarios. If trait similarity increases with increasing node age and tree imbalance, greater average node age and more imbalanced trees could result in higher connectance (the proportion of realized connections of those possible), higher nestedness (the tendency for specialist species to interact with a subset of

generalist species that interact among each other and with specialists), and less modularity (a network pattern in which groups of species are more connected to each other than with other groups, forming modules). Alternatively, if trait similarity decreases with decreasing node age and tree imbalance (more balanced trees), greater average node age and more imbalanced trees could result in lower connectance, lower nestedness, and greater modularity.

Tree shape is affected by the evolutionary process under which species have diverged. Thus, it is useful to consider various evolutionary models that make contrasting assumptions about how evolution occurs. Here, we consider three such models: Brownian motion (BM), which assumes trait evolution is a random walk and cumulative trait change proportional to time (Cavalli-Sforza & Edwards 1967); Early-burst (EB) which assumes evolution occurs at an accelerating-decelerating rate, with an early-burst of diversification early in time, followed by relative stasis (Harmon *et al.* 2010); and Ornstein-Uhlenbeck [OU], which assumes that traits evolve towards one to many optima imposed by, for example, convergent selection (Hansen 1997; Butler & King 2004). These three evolutionary models will have varying effects on the phylogenetic signal of a trait; thus, if species traits determine species interactions, the above evolutionary models should lead to contrasting patterns in network structure. Specifically, we predict that the EB model will cause the greatest phylogenetic signal, BM less so, and the OU model the least signal (Harmon *et al.* 2010). Given this prediction, the EB model should lead to networks with lower connectance, lower nestedness, and greater modularity, whereas the OU model will lead to networks with greater connectance, greater nestedness, and lower modularity, with the BM model leading to intermediate patterns.

Here we evaluate the relationship between phylogenetic tree shape and mutualistic network structure. We ask the two following questions: i) Does phylogenetic tree shape (tree balance and node age) affect the structure of empirical mutualistic networks?; and ii) Does the effect of phylogenetic tree

shape on the structure of simulated mutualistic networks depend on the evolutionary model under which traits have evolved?

Materials and Methods

1. Empirical networks

1.1 Published networks

We included a total of 65 empirical networks in our analysis. All networks were binary, with cells with ones indicating occurrence of an interspecific interaction and zeros indicating no interaction. Fifty-five interaction matrices were retrieved from the database of mutualistic interaction networks compiled in Rezende *et al.* (2007). Rezende *et al.* (2007) considered 59 networks consisting of many different study organisms and methods of construction. As our study asks what effect phylogenetic tree shape has on network structures, a biased choice towards any particular taxonomic group may bias our results. Thus, we excluded datasets limited to a particular taxonomic group (see Appendix A), and excluded studies where we could not discover their collection method confidently, after which we were left with 50 networks.

1.2 Unpublished networks

An additional 15 mutualistic plant-pollinator networks were included in our analysis from studies in 4 regions of western Canada. Thus, we used a total of 65 networks. The details of these networks, including methods, are in a paper in preparation (Chamberlain *et al.*, *in review*; see Appendix F). As the sampling method (transects and timed observations) used to construct the networks could bias the data, we included sampling method as a predictor variable in our analyses (see below).

2. Empirical phylogenetic trees

2.1 Plants

Plant phylogenies were built using Phylomatic (see <http://phylodiversity.net/phylomatic>; Webb & Donoghue 2004). Phylomatic is an online interface to retrieve a phylogeny based on a user-defined set of plant species taxonomic names. Branch lengths were estimated for the master plant phylogeny using the branch length adjustment algorithm (BLADJ) in the software Phylocom (Webb, Ackerly & Kembel 2008), which fixes a set of nodes in the tree to specified ages and evenly distributes the ages of the remaining nodes. We used node age estimates from Wikström *et al.* (2001) as incorporated in the “ages” file in the Phylocom installation. The tree file we used to run the `bladj` command in Phylocom is provided in multiple formats in Appendix B. See the master plant phylogeny in Appendix B, on Figshare.org (http://figshare.com/articles/Animal_and_Plant_Phylogenies/1015787), and in Dryad (see Data accessibility section). We pruned the master phylogeny for each network.

2.2 Pollinators

For pollinator phylogenies for the unpublished Canadian networks we built a master phylogeny of all animal pollinators across all networks in the study in Mesquite v.2.75 (Maddison & Maddison 2011), based on a variety of published phylogenies. We then pruned the master phylogeny for each network. Pollinator phylogenies from Rezende *et al.* (2007) were built using a variety of sources (see Rezende *et al.* 2007 for details). No information on branch lengths was available for pollinator phylogenies, so we assumed all branch lengths equaled one time unit. See the master plant phylogeny in Appendix B, on Figshare.org (http://figshare.com/articles/Animal_and_Plant_Phylogenies/1015787), and in Dryad (see Data accessibility section).

3. Network structures

We calculated three measures of network structure for each of the mutualistic networks: connectance, nestedness, and modularity. Connectance is the proportion of possible interspecific interactions that are realized. Nestedness quantifies the degree to which specialists tend to interact with a subset of the species with which generalists interact. Nestedness was calculated using *NODF*, a robust algorithm, insensitive to network shape and size. Nestedness values range between 0 and 100; greater values indicate greater nestedness. Modularity (M) measures the extent to which a network is organized into clearly delimited modules. We used a modularity-detecting algorithm, which maximized modularity using simulated annealing (SA) implemented in the command line function *netcarto_cl* in the C program Rgraph (Guimera & Amaral 2005a; b).

4. Tree shape metrics

There is a large suite of metrics used to quantify phylogenetic diversity of trees (Cadotte *et al.* 2010). We chose to go with metrics that are traditionally used to quantify tree shape (*sensu* Mooers & Heard 1997), that quantify complementary aspects of tree shape, and quickly convey information about a phylogeny. One of the most widely used metrics to quantify tree balance is Colless' index (I_c), as it often has the highest statistical power (Mooers & Heard 1997). A smaller value of I_c suggests that speciation is balanced across the clades, while a higher value of I_c suggests speciation differs among clades (trees are more unbalanced; Fig. 1). Values of I_c can range between $-\infty$ and $+\infty$. For the distribution of nodes in time, the gamma index (γ) is widely used and considered the most reliable. γ describes the distribution of internode distances from the root to the tips. γ values equal to zero indicate that speciation events occur more or less midway through the evolution of the tree; values greater than zero indicate that nodes are closer to tips than expected (indicating recent speciation events), while values smaller than zero indicate that nodes are closer to the root than expected (indicating ancient speciation events;

under a pure birth process, in which births are constant and there are no deaths). As we did not have branch length data for animal phylogenies, we only calculated I_c of shape for animal data, while we calculated both I_c and γ for empirical plant data and simulation data (below).

5. Simulated trees and networks

Although empirical data are crucial in examining real-world relationships between tree shape and interaction network structure, the explanatory variables (our two tree shape metrics) cannot be manipulated. That is, the relationship based on empirical networks can only be assumed to be correlational, leaving open the possibility that other variables correlated with tree shape are responsible for the relationship with network structure. Thus, we performed a simulation analysis, asking if tree shape could be a mechanism contributing to interaction network structure.

First, we simulated phylogenetic trees. As network asymmetry (i.e., the ratio between number of plant to animal species) is a common property of mutualistic networks, we simulated trees with realistic network asymmetry values. From our empirical set of 65 mutualistic networks (described above), the average ratio of animals to plants was 2.47. We used 21 community size levels ($n = 30, 40, 50, 60, 70, 80, 90, 100, 110, 120, 130, 140, 150, 175, 200, 240, 280, 350, 425, 500, \text{ and } 600$), where animals are 2.47 times more diverse than plants in each community size level. Within each community size level we simulated phylogenetic trees for plants and animals separately. We simulated pure-birth (aka Yule process) phylogenies of n species for each of plants and animals, with all lineages having an equal probability of diversifying and the death rate = 0, using function *pbtree* in the package *phytools*. Note that simulation runs did not differ for plant and animal phylogenies, so there is no reason to expect that the trees that were created are any different, on average.

Second, within each set of trees at each level of community size, we calculated balance (I_c) and node age (γ). For each measure, we defined a threshold to distinguish between balanced and

unbalanced trees, determined by simulating 1000 trees and examining the distribution of the resulting I_c and γ values. A cutoff was set at 15-17% of trees in each the left and right tails of the distribution of each metric (see Appendix B). If the tree shape metric fell below the lower threshold or above the upper threshold for each metric, we kept the phylogeny, but if not, we discarded the phylogeny and created a new one (we were in essence manipulating phylogeny shape, so we discarded those that did not fit the cutoff values). New phylogenies were created until 200 trees were created below the lower threshold and 200 above the upper threshold for each metric. This process resulted in two sets of trees: 1) a set of "balanced" and "unbalanced" trees based on I_c , and 2) a set of trees with very recent nodes and very old nodes based on γ (see Fig. 1).

Colless' metric values for empirical phylogenetic trees in this study were mostly above zero, or mostly unbalanced phylogenies. Thus, most of the empirical phylogenies align closely with the unbalanced set of trees for each simulation. For Gamma, most values for empirical are less than zero, or mostly phylogenies with nodes near the root. Thus, most of the empirical phylogenies align closely with the set of trees for each simulation that have nodes close to the root.

We chose to simulate a set of balanced and unbalanced trees and a set of trees with shallow and deep nodes instead of trees with a gradient of Colless and Gamma values because we the first task that needed to be done was determine if network structure changed at all with changes in phylogenetic tree shape. It should be noted that this simulation process does not lead by default to trees that are biased in one direction on the I_c or γ axis (see <https://gist.github.com/sckott/9698127>). Our tree selection process is what created a set of trees that were biased towards more or less balanced, and with nodes deeper or more shallower.

Third, we simulated a trait on each tree, under each of three models of evolution: a) "Brownian motion" (BM), b) "Ornstein-Uhlenbeck" (OU), and c) "Early-burst" (EB). In the BM model, traits evolved

randomly on the phylogeny. In the EB model, traits followed an accelerating-decelerating model of trait evolution (ACDC model, with parameter $g=1.05$, where g is the rate at which character change declines). In the OU model, traits evolved toward an optimum, rather than with constant rates without an optimum (BM) or bursts of evolution (EB).

Fourth, we simulated interaction networks among plants and animals with a model for species interactions based on matching of their trait values. We used a combined complementarity/barrier model following Santamaría and Rodríguez-Gironés (2007). Under this model, an interaction occurs only between the plant and animal if their trait values are similar enough, and the animal trait value is larger than the plant trait value. The resulting matrices are binary, with 0 for lack of an interaction, and 1 for an interaction. Next, we calculated network structural metrics on each matrix: connectance, nestedness, and modularity (see *Network structures* above). Last, we calculated means and 95% confidence intervals across replicates for each model of trait evolution, each network structural metric, each level of number of species, and each level of tree balance (balanced and unbalanced). Simulations were done under R v.2.15.3 (R Development Core R 2012), using packages *phytools*, *geiger*, *ape*, *apTreeshape*, *bipartite*, and *picante* (Paradis, Claude & Strimmer 2004; Harmon *et al.* 2008, 2009; Kembel *et al.* 2010; Dormann 2011; Revell 2012). An R package called *treeshape* is available (<https://github.com/sckott/treeshape>) to reproduce the simulations done in this paper.

6. Data analyses

6.1 Empirical data

We analysed to what extent tree shape (I_c and γ) was related to network structural properties (connectance, nestedness, and modularity) by conducting general linear mixed effects models using *lme* function from the package *nlme* in R v.2.15.3 (R Development Core R 2012). Three separate models were run for each network structural property: connectance, modularity, and nestedness. For each property

we tested the effect of network size, I_c and γ , considering also all possible interactions among these variables. Moreover, collection method (transects vs. timed observations) was included as a fixed factor to account for any bias due to collection method. To account for the nested structure of the data study was included as a random factor. For animals γ could not be measured as their phylogenies did not have branch lengths. All response variables, and network size, were linearized by \log_{10} transforming them to improve normality and homoscedasticity. However, we present the results in figures using raw data to allow easier interpretation. A significant main effect of I_c or γ , or their interactions with network size, suggests a significant effect of phylogenetic tree shape on network structure.

6.1 Simulated data

We analysed if tree shape influenced network structural properties using general linear models. We considered network size, network shape and type of evolutionary model (BM, EB, or OU) as fixed variables, also considering any interaction between them. Shape is a factor of tree balance (unbalanced vs. balanced) or average node age (recent or old). We ran separate models for each network structural property (connectance, nestedness, modularity) and for each tree shape metric (balance, node age), resulting in six sets of models. We linearized (using \log_{10} transformation to improve normality and homoscedasticity) the response network structures and network size to meet assumptions. We then compared models with all possible combinations of the terms described above and selected the most parsimonious model (best model) based on the Bayesian Information Criterion (BIC). The inclusion of a main effect of shape (balanced vs. unbalanced, or recent vs. old node age), two-way interaction with community size, or three-way interaction with community size and evolutionary model in the best model suggests an effect of tree shape on network structural properties. Analyses were done using the function *lm* in R v.2.15.3 (R Development Core R 2012). As before, we present the results in figures using untransformed data for ease of interpretation.

As we manipulated only one tree shape metric in each simulation run (either node age or tree balance), the other measure of tree shape is free to vary. We checked for this issue with a separate simulation run following the same simulation protocol as above. We simulated 300 trees each for each run. In the run manipulating balance, we measured node age, and in the simulation manipulating node age we measured balance. Results show that there is no significant pattern to one tree shape metric when the other is manipulated (Appendix E). That is, there is no reason to expect that, for example, in a simulation manipulating tree shape, node age may be heavily influencing the result.

Results

Empirical data

For the plant phylogenies, connectance was not related to node age (γ), but was, as expected, significantly negatively related to tree balance (I_c). That is, connectance decreased with increasing I_c (Fig. 2). In addition, there was a significantly negative relationship between connectance and network size; that is, small networks had higher connectance than larger networks. The negative effect of I_c depended on network size (i.e. there was a significant interaction between I_c and size). There was a significant positive effect of I_c on modularity. That is, modularity increased with larger I_c values, or more unbalanced trees. There was no significant effect of γ on any of the three network structures. Web asymmetry was important for nestedness only – there was a positive relationship between web asymmetry and nestedness such that networks with more plant species were more nested. Collection method significantly affected connectance and nestedness, but did not affect modularity (Table 1).

For the animal phylogenies, we could not examine γ because we did not have branch length data, so we present results based only on the relationship between network structure and I_c . There was no effect of I_c on connectance, nestedness, or modularity (Table 1). There was a significant negative relationship between connectance and network size, with larger networks less connected. In addition,

connectance was negatively related to web asymmetry such that networks that had more plant species (and fewer pollinator species) were less connected. There was a significant negative relationship between modularity and network size, such that larger networks were less modular.

Simulated data

In the simulations, we were able to manipulate phylogenetic tree shape, both in tree balance (I_c) and node age (γ) (Fig. 3; Appendix C).

For modularity analyses, tree balance (I_c) was included in the best model (Appendix C). For nestedness and connectance analyses, although I_c was not included in the best model, it was included in the second best model for each metric (nestedness $\Delta\text{BIC} = 4.7$, connectance $\Delta\text{BIC} = 3.8$; see Appendix C).

Node age had an effect on modularity, being included in the best model. For nestedness and connectance analyses, node age was only included in the second best model ($\Delta\text{BIC} = 4.8$ in both cases; see Appendix C). The effect sizes of both I_c and γ were not large (Fig. 3; Appendix Table C2). However, it is common sense that over evolutionary time very small effect sizes can have large consequences.

The type of evolutionary model also explained a substantial part of the variance of the data, being always included in the best model of all network metrics. This suggests that the evolutionary process behind phylogenetic patterns can also influence the structure of species interactions. We predicted that, if trait similarity increases with increasing tree imbalance, more balanced trees would be less modular, and this is what we found with Brownian motion (Fig. 3); however, we found the opposite for early-burst (greater modularity in unbalanced trees), and no effect of tree balance on modularity under the Ornstein-Uhlenbeck model. For distribution of nodes, we predicted lower modularity in trees with younger nodes, and this is what we found with early-burst, but not with Brownian motion, for which we found greater modularity in trees with younger nodes (Fig. 3). There was no effect of I_c on modularity under the Ornstein-Uhlenbeck model.

Although network size was in many of the top models for all network structures (Appendix C), for both measures of tree shape (I_c and γ), the effect of tree shape on network structure did not greatly vary with network size alone (Fig. 3), in contrast to empirical data. Moreover, the effect of network size depended on the evolutionary model used (i.e. the interaction between evolutionary model and network size was selected in the best model). For example, for both measures of tree shape, modularity increased with increasing network size to an asymptote at relatively small network size (~ 150 species) in the Brownian motion model, but decreased for the other two evolutionary models (Fig. 3). Note that the effect of tree balance and node age on network metrics are somewhat correlated (see Fig. 3).

Discussion

In analyses using empirical data, we found that after taking into account the effect of network size and data collection method, network properties were affected by phylogenetic history of plants and pollinators. The results of the effect of plant phylogeny demonstrated that network properties were more correlated with tree balance than the distribution of nodes in time. Importantly, we manipulated tree shape in simulations, showing that at least under some evolutionary models, there is a causal link between tree shape and network structure. In addition, the effect of phylogenetic history on network structure (modularity) depended on the trait evolution model. Although previous studies have shown a relationship between network structure and some measure of phylogenetic signal (Rezende *et al.* 2007, 2009; Verdú & Valiente-Banuet 2011), the finding that tree shape matters to network architecture begs explanation. We discuss the biological relevance of these main findings below.

Empirical data - Tree balance

Tree balance represents the extent to which clades within a tree differ in diversification rates, and associated richness as well as the assembly processes that might reflect habitat filtering or competition

(Webb 2000). Plant species within communities with more balanced phylogenies may have higher trait similarity, leading to more interactions due to trait overlaps; our simulations show that trait similarity across phylogenies is greater in imbalanced phylogenies under the Brownian motion model, but greater in balanced phylogenies under the Early Burst (EB) model (Appendix D). When phylogenies are very imbalanced (evolutionary rates vary among clades), the community plant phylogeny is likely to have few basal angiosperm species and many members of derived clades (e.g., many species of Asteraceae), which may interact with a greater subset of the animal community. Basal angiosperms are pollinated largely by flies and beetles more than derived families of flowering plants are (Thien *et al.* 2009) and flies and beetles are potentially more generalized than bees in their floral visiting patterns (Willmer 2011; but see Vamosi *et al.* In press). These general tendencies could bring about the overall patterns between increasing imbalance and decreasing connectance. Whether specialization has been increasing over evolutionary time scales through coevolutionary processes is a question we are only now beginning to answer (Guimarães Jr, Jordano & Thompson 2011). Of course additional factors not accounted for such as abundance could play a role (Verdú & Valiente-Banuet 2011).

Empirical data – Differences between plant and pollinator results

Selection pressures from major clades of pollinators have produced convergence of floral characters towards pollination syndromes (Fenster *et al.* 2004), consistent with the Ornstein-Uhlenbeck model, and likely a weakened phylogenetic signal for floral traits when a broad sampling of angiosperms is examined. For example, even basal clades of angiosperms (e.g., Ranunculaceae) include all pollinator syndromes within them, as do more derived clades. This process could produce community plant phylogenies with nodes concentrated at the tips having members with floral forms that attract all functional groups of pollinators, producing weak patterns with modularity. However, we detected no

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significant effect of the distribution of nodes on network structures. Connectance was greater with more balanced plant phylogenies, but the effect was not significant for animals. If we assume this means there is in fact no relationship for animals (and not a result of lack of statistical power), then this suggests a role for balance in plant phylogenies with respect to conservation. That is, we know high connectance can make a network robust to perturbations (Dunne, Williams & Martinez 2002), so plant communities with increasingly imbalanced phylogenies can be highly susceptible to loss of network robustness. Note that we did not have branch length information for pollinators, while we did for plants. We don't know for sure how this affects results and our conclusions drawn on them.

Simulations

Simulations allowed us to do two things beyond what could be done with empirical data: manipulate tree shape to determine if there is a causal link between tree shape and network structures, and determine whether the choice of an evolutionary model changes the relationship between tree shape and network structure. First, we did find that both manipulated I_c and γ can alter modularity, though the direction of the effect depends on the evolutionary model. For modularity, tree shape had a significant effect on network structures only for BM (random diversification at constant rate through time) and EB models (early burst of diversification followed by relative stasis). It is trait similarity within clades that leads to closely related species within a phylogeny (e.g., plants) interacting with similar species in another phylogeny (e.g., pollinators), which explains the lack of effect under the OU model, which leads to greater trait similarity among clades relative to BM and EB models.

Interestingly, BM and EB models lead to opposite patterns of modularity for both I_c and γ . That is, BM models lead to greater modularity in unbalanced trees, while EB models lead to greater modularity in balanced trees. Likewise, BM models lead to greater modularity when nodes are nearer to tips, while EB

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models lead to greater modularity when nodes are closer to the root. The differences between BM and EB trait evolution models could be related with the fact that while for BM trait variation between species is greater when nodes are near the tips of the phylogenetic tree; for EB we found greater trait variation when nodes are near the root (Appendix D). Such differences could play a role in determining modularity. When trait evolution followed an OU model, trait variation did not greatly differ due to node age (Appendix D), and modularity was not significantly affected by node age (Fig. 3). The trait variation in the EB model is likely due to earlier branching on average in a phylogeny leading to greater trait variation; whereas when nodes are nearer tips on average, trait variation is less. It is important to note that we did not model the possibility that network properties could alter the tempo of evolution. Previous studies have found that super-generalists can apply selection pressures that increase the rate of trait convergence (Guimaraes *et al.* 2011) and thus may be the root cause of associations observed between network properties, trait variation, and tree shape.

Nonetheless, Harmon *et al.* (2010) found that EB models were rarely supported in real phylogenies, whereas OU models were supported more often, suggesting that effects of tree shape on network structure should in most cases match either BM or OU evolution processes. Future studies are needed to explore why different evolutionary processes lead to opposing effects on modularity.

Comparison between empirical results and simulations

While in empirical networks we found a correlation between the shape of the phylogenetic trees and two of three network structure properties, with simulations we found only a significant effect of phylogeny on modularity. A major difference between real networks and simulated ones is that our simulated networks were based solely on interaction rules and trait values, whereas real networks are generated from more complicated rules. In real communities pollinators visit only a fraction of available

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plants because of optimal foraging, floral constancy, and time constraints/sampling effort (Chittka, Thomson & Waser 1999; Spaethe, Tautz & Chittka 2001). Additionally, we did not explore species abundances, which often partly explain network structure (Vázquez *et al.* 2009; Verdú & Valiente-Banuet 2011).

In our simulations, modularity varied with tree balance and distribution of nodes, while in the empirical networks modularity was affected only by tree balance. The direction of the effect of tree balance on modularity was the same for simulation and empirical data only if simulations followed the BM model. This result suggests that trait evolution within the empirical networks used in this study is more likely to have followed a BM model. Indeed, Harmon *et al.* (2010) found that EB models were rarely supported in real phylogenies. Further studies involving careful trait evaluations in empirical networks would help clarify these results.

Olesen *et al.* (2007) found that modularity tended to increase with network size in real networks. Intriguingly, our empirical networks do not tend to show this effect, perhaps because the effects of tree shape override the effects of network size. The strong effects of tree shape (and the resulting trait distributions) on network structure in our empirical dataset indicate that community composition of one trophic level can heavily influence whether members of the other trophic level are incorporated into the community (Sargent & Ackerly 2008). Intriguingly, this sets the stage for populations of any given species to be in different ecological contexts in terms of mutualists and competitors, which may provide an additional source of divergent selection pressures that could in turn affect the rates of evolution (Thompson 2005). When adaptations in interacting clades co-evolve (e.g., “pollination syndromes”), we may also observe increased trait matching between trophic levels. For example, it is often observed that bee abundance and diversity declines with elevation (Arnold,

Savolainen & Chittka 2009; Hoiss *et al.* 2012), leaving flies as more predominant pollinators. The prevalence of flies presents a potential constraint on the establishment of species with zygomorphic flowers into high elevation sites (Vamosi *et al.* In press). The ultimate constraint on these dynamics is the rate of evolution of tolerance of high elevation environments in bees and the loss of zygomorphic flowers in plants, and unraveling the genetics of these transitions presents the next frontier that will link the patterns we observe between trait evolution, community assembly, and network structure.

Conclusion

As related species are more likely to share traits through common ancestry, the extent to which history affects the structure of plant-pollinator mutualistic networks is dependent on the model of trait evolution as well as the tempo and distribution of lineage splitting along the course of a lineage's evolutionary history. Our findings suggest that variation in phylogeny balance, or variation in the number of lineages among sister taxa, and the distribution of nodes in time in phylogenies, are associated with variation in network metrics. In addition, our simulations revealed that there is a potential causal link between both tree shape measures and network metrics under some evolutionary models, assuming that interactions between species do not affect the evolution of the trait involved in those interactions. Future studies should explore the mechanisms behind the relationship between tree shape and network structures.

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Data accessibility

All phylogenies are in Figshare (http://figshare.com/articles/Animal_and_Plant_Phylogenies/1015787) as well as Dryad. Networks and phylogenies are in Dryad, and will be embargoed for a period of one year (and will also be deposited in Figshare upon the end of the embargo period). Data deposited in the Dryad repository: <http://datadryad.org/resource/doi:10.5061/dryad.gm7p3>.

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Table 1. Effect of phylogeny (tree balance, l_c and node age, γ), network size (S), web asymmetry (WA), and collection method (CM) on the structure of empirical networks. Three metrics of network structure were considered: connectance, nestedness, modularity. Models for plants followed the equation: network metric $\sim S * l_c * \gamma + \text{web asymmetry} + \text{CM} + \text{study}$. Models for animals followed the equation: network structure $\sim S * l_c + \text{WA} + \text{CM} + \text{study}$. In all models, CM was a fixed factor (transect or timed observation method), and study was a random factor. Values given are regression (linear) slope estimates. Significance ($P < 0.05$) is indicated by bold type. l_c : larger values indicate more imbalanced trees; γ : values increase as nodes get closer to tips.

Plants	Connectance		Nestedness		Modularity	
	Est.	P	Est.	P	Est.	P
			-			
Network size (S)	-0.09	<0.001	0.32	0.169	0.04	0.409
			-			
Balance (l_c)	-0.04	0.032	0.64	0.019	0.14	0.014
Distribution of nodes (γ)	0.02	0.083	0.35	0.069	0.07	0.078
					-	
Web asymmetry	-0.01	0.149	0.22	0.022	0.02	0.179
					-	
Coll. Method	0.02	0.043	0.20	0.034	0.03	0.051
					-	
$S \times l_c$	0.02	0.037	0.30	0.028	0.07	0.019
			-			
$S \times \gamma$	-0.01	0.096	0.18	0.084	0.03	0.102
			-			
$l_c \times \gamma$	-0.01	0.239	0.19	0.047	0.04	0.039
					-	
$S \times l_c \times \gamma$	0.00	0.216	0.10	0.037	0.02	0.036
Animals						
					-	
Network size (S)	-0.05	<0.001	0.05	0.638	0.04	0.037
					-	
Balance (l_c)	-0.01	0.422	0.12	0.334	0.01	0.537
Web asymmetry	-0.02	0.002	0.01	0.917	0.01	0.507
					-	
Coll. Method	0.02	0.084	0.17	0.079	0.03	0.111
			-			
$S \times l_c$	0.00	0.416	0.05	0.395	0.01	0.619

Figure Captions

Fig 1. Two measures of tree shape. Tree balance is quantified using Colless' tree balance metric (I_c), while the distribution of node ages is quantified using gamma (γ). Smaller values of I_c represent more balanced trees, while larger values represent more imbalanced trees. Smaller values of γ represent trees with nodes on average closer to the root, while larger values represent more trees with nodes on average closer to the tips.

Fig 2. Empirical results examining the effect of phylogenetic tree shape (balance and distribution of nodes; see Methods for details) on network structural properties (connectance, modularity, and nestedness), using plant phylogenies. Letters in each panel indicate which factors were significant (see Table 1): S = network size; I_c = tree balance; γ = distribution of nodes. The size of the dots is proportional to network size.

Fig 3. Simulation results examining the effect of phylogenetic tree balance (A-C; based on I_c ; see Methods) and distribution of nodes (D-F; based on γ , see Methods) on network modularity, under three models of evolution (Brownian Motion (A,D), Early-Burst (B,E), and Ornstein-Uhlenbeck (C,F)). Additional network structures connectance and nestedness were examined, but are not shown here. Symbols: plots on the left (grey symbols: balanced trees; black symbols: unbalanced trees); plots on the right (grey symbols: nodes near root on average; black symbols: nodes near tips on average).

Fig. 1.

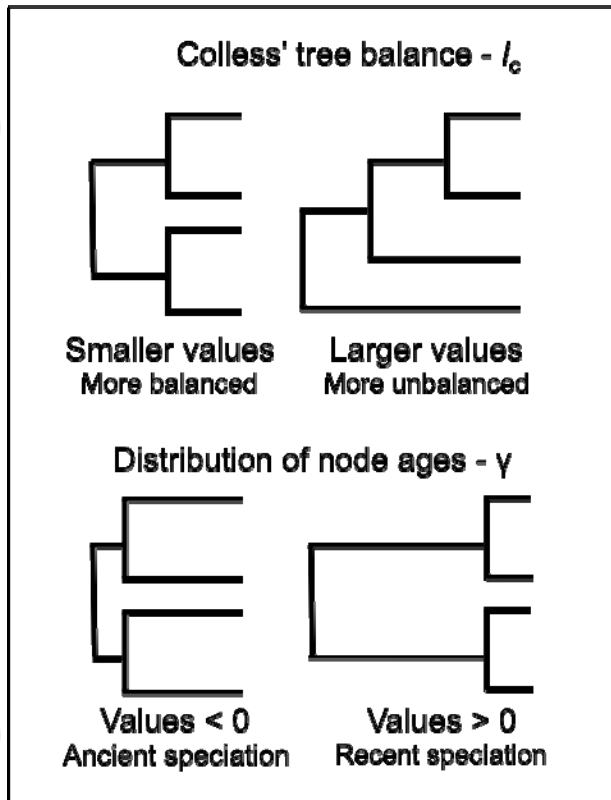


Fig. 2.

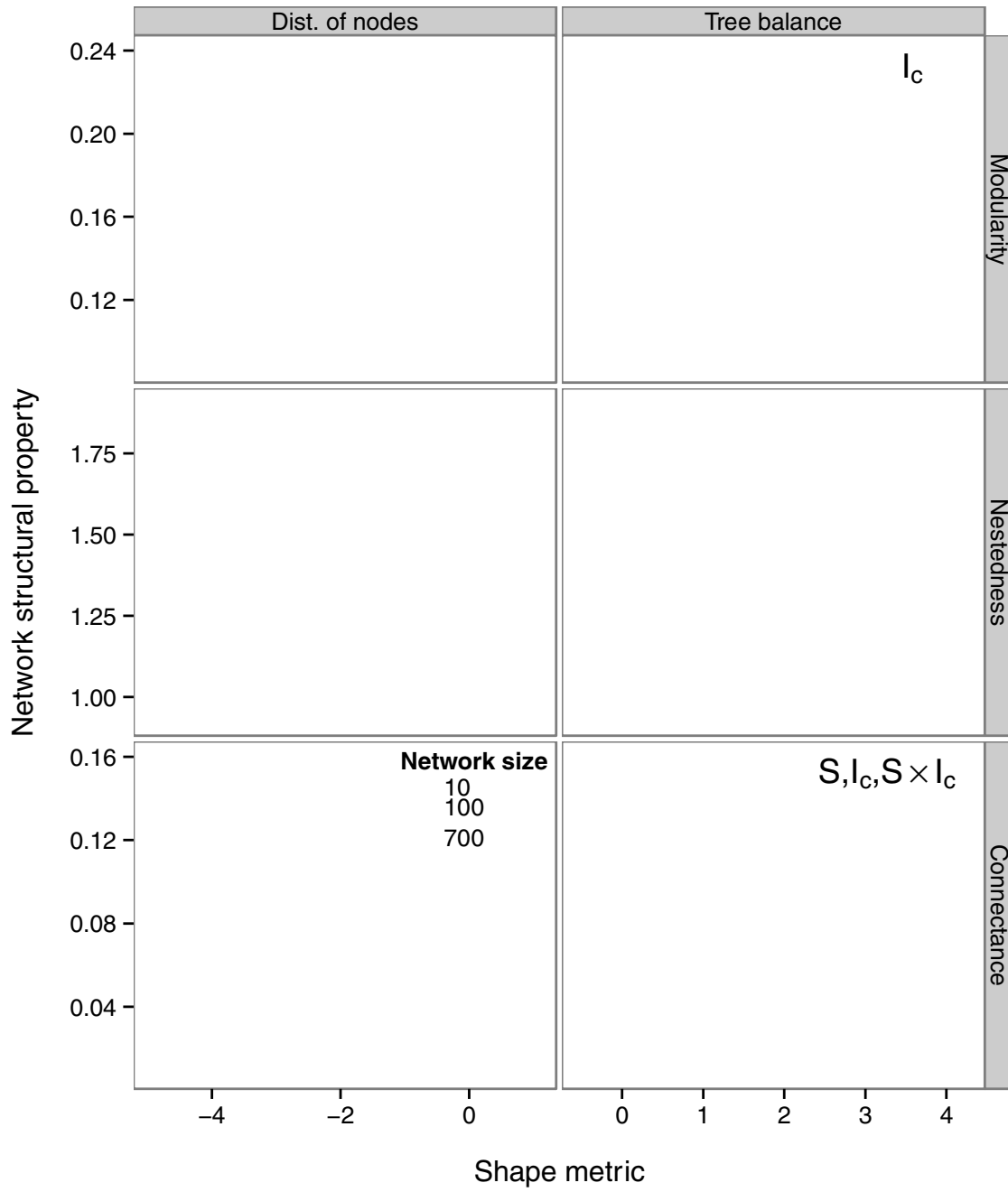


Fig. 3.

