

THE STRUCTURE OF POLLINATION NETWORKS

causes & consequences



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Con amor, en memoria de Betty Helena Bermudez.

1964 – 2009

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SUMMARY

PUBLICATIONS

The following peer-reviewed publications have been published by the candidate during the PhD term.

- Cagua, Edgar Fernando, J. E. M. Cochran, C. A. Rohner, C. E. M. Prebble, T. H. Sinclair-Taylor, S. J. Pierce and M. L. Berumen (2015). 'Acoustic Telemetry Reveals Cryptic Residency of Whale Sharks'. In: *Biology Letters* 11.4, pp. 20150092–20150092. DOI: [10.1098/rsbl.2015.0092](https://doi.org/10.1098/rsbl.2015.0092).
- Cagua, Edgar Fernando, Kate L. Wootton and Daniel B. Stouffer (2019). 'Keystoneness, Centrality, and the Structural Controllability of Ecological Networks'. In: *Journal of Ecology*, pp. 1365–2745. DOI: [10.1111/1365-2745.13147](https://doi.org/10.1111/1365-2745.13147).
- Cirtwill, Alyssa R., Giulio Valentino Dalla Riva, Marilia P. Gaiarsa, Malyon D. Bimler, Edgar Fernando Cagua, Camille Coux and D. Matthias Dehling (2018). 'A Review of Species Role Concepts in Food Webs'. In: *Food Webs* 16, e00093. DOI: [10.1016/j.fooweb.2018.e00093](https://doi.org/10.1016/j.fooweb.2018.e00093).
- Cochran, Jesse E. M., Camrin D. Braun, Edgar Fernando Cagua, Michael F. Campbell, Royale S. Hardenstine, Alexander Kattan, Mark A. Priest, Tane H. Sinclair-Taylor, Gregory B. Skomal, Sahar Sultan, Lu Sun, Simon R. Thorrold and Michael L. Berumen (2019). 'Multi-Method Assessment of Whale Shark (*Rhincodon Typus*) Residency, Distribution, and Dispersal Behavior at an Aggregation Site in the Red Sea'. In: *PLOS ONE* 14.9. Ed. by Johann Mourier, e0222285. DOI: [10.1371/journal.pone.0222285](https://doi.org/10.1371/journal.pone.0222285).
- Couturier, Lie, P Newman, Fra Jaine, Mb Bennett, Wn Venables, Edgar Fernando Cagua, Ka Townsend, Sj Weeks and Aj Richardson (2018). 'Variation in Occupancy and Habitat Use of *Mobula Alfredi* at a Major Aggregation Site'. In: *Marine Ecology Progress Series* 599, pp. 125–145. DOI: [10.3354/meps12610](https://doi.org/10.3354/meps12610).

- Hutchinson, Matthew C., Edgar Fernando Cagua, Juan A. Balbuena, Daniel B. Stouffer and Timothée Poisot (2017). 'Paco: Implementing Procrustean Approach to Cophylogeny in R'. In: *Methods in Ecology and Evolution* 8.8. Ed. by Richard Fitzjohn, pp. 932–940. DOI: [10.1111/2041-210X.12736](https://doi.org/10.1111/2041-210X.12736).
- Hutchinson, Matthew C., Edgar Fernando Cagua and Daniel B. Stouffer (2017). 'Cophylogenetic Signal Is Detectable in Pollination Interactions across Ecological Scales'. In: *Ecology* 98.10, pp. 2640–2652. DOI: [10.1002/ecy.1955](https://doi.org/10.1002/ecy.1955).
- López-Angarita, Juliana, Alexander Tilley, Juan M. Díaz, Julie P. Hawkins, Edgar Fernando Cagua and Callum M. Roberts (2018). 'Winners and Losers in Area-Based Management of a Small-Scale Fishery in the Colombian Pacific'. In: *Frontiers in Marine Science* 5. DOI: [10.3389/fmars.2018.00023](https://doi.org/10.3389/fmars.2018.00023).
- Rohner, Christoph A., Amelia J. Armstrong, Simon J. Pierce, Clare E. M. Prebble, Edgar Fernando Cagua, Jesse E. M. Cochran, Michael L. Berumen and Anthony J. Richardson (2015). 'Whale Sharks Target Dense Prey Patches of Sergestid Shrimp off Tanzania'. In: *Journal of Plankton Research* 37.2, pp. 352–362. DOI: [10.1093/plankt/fbv010](https://doi.org/10.1093/plankt/fbv010).

Not everything is a straight line.

— Tukey (1977)

COAUTHORSHIP DECLARATION

Chapter 1 (Cagua, Wootton and Stouffer 2019) and **Appendix A** (Hutchinson, Cagua and Stouffer 2017) have been extracted from co-authored work.

Cagua, Edgar Fernando, Kate L. Wootton and Daniel B. Stouffer (2019). 'Keystoneness, Centrality, and the Structural Controllability of Ecological Networks'. In: *Journal of Ecology*, pp. 1365–2745.13147. DOI: [10.1111/1365-2745.13147](https://doi.org/10.1111/1365-2745.13147).

Hutchinson, Matthew C., Edgar Fernando Cagua and Daniel B. Stouffer (2017). 'Cophylogenetic Signal Is Detectable in Pollination Interactions across Ecological Scales'. In: *Ecology* 98.10, pp. 2640–2652. DOI: [10.1002/ecy.1955](https://doi.org/10.1002/ecy.1955).

For **Chapter 1**, the candidate's contribution is 95%. The candidate performed all analysis and wrote the manuscript and contributed to the development of the theoretical framework.

For **Appendix A**, the candidate's contribution is 45%. The candidate contributed to the analysis and writing the manuscript.

On behalf of all co-authors, the undersigned certifies that:

- The above statement correctly reflects the nature and extent of the PhD candidate's contribution to this co-authored work.
- In cases where the candidate was the lead author of the co-authored work he or she wrote the text.

Christchurch, New Zealand, December 2019

Daniel B. Stouffer

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To all of those with which we smiled together over the last five years, you all make New Zealand feel home.

*We don't see things as they are
we see them as we are.*

— anonymous

THE STRUCTURE OF POLLINATION NETWORKS

1

STRUCTURAL CONTROLLABILITY

*However, not everything that can be counted counts,
and not everything that counts can be counted.*

— Cameron (1963)

SUMMARY

An important dimension of a species' role is its ability to alter the state and maintain the diversity of its community. Centrality metrics have often been used to identify these species, which are sometimes referred as "keystone" species. However, the relationship between centrality and keystone-ness is largely phenomenological and based mostly on our intuition regarding what constitutes an important species. Here we introduce structural controllability, an approach that allows us to quantify the extent to which network topology can be harnessed to achieve a desired state. It also allows us to quantify a species' control capacity—its relative importance—and identify the set of species that are critical in this context because they have the largest possible control capacity. We found that species with high control capacity, and in particular critical species, contribute the most to the stable coexistence of their community. This result was true, even when controlling for the species' degree, abundance/interaction strength, and the relative dependence of their partners. Structural controllability is strongly related to the stability of a network and measures the difficulty of managing an ecological community. It also identifies species that are critical to sustain biodiversity and to change or maintain the state of their community and are therefore likely to be very relevant for management and conservation.

1.1 INTRODUCTION

A major goal in ecology is to understand the roles played by different species in the biotic environment. Within community ecology, a complex-systems approach has led to the development of a variety of analytical and simulation tools with which to compare and contrast the roles of species embedded in a network of interactions (Guimerà and Amaral 2005; Bascompte and Stouffer 2009; Stouffer, Sales-Pardo et al. 2012; Coux et al. 2016). A particularly relevant dimension of any species' role is its ability to alter the abundance of other species and the state of the community—since changes of this nature can have knock-on effects on ecosystem function, diversity, processes, and services (R. M. Thompson et al. 2012; Tylianakis, Didham et al. 2008; Tylianakis, Laliberté et al. 2010). This ability is sometimes referred to as a species' "keystoneness" (Mills and Doak 1993).

A significant proportion of the network tools used to estimate species' roles in this context rely on the calculation of a species' centrality—a relative ranking of its positional importance that originally stems from social-network research (Friedkin 1991; Martín González, Dalsgaard and Olesen 2010). Generally speaking, central species tend to be better connected and consequently are more likely to participate in the network's "food chains". Because species that participate in more chains are more likely to affect the abundances of other species, centrality metrics have often been used to identify keystone species in the community (Jordán, Benedek and Podani 2007). Centrality metrics have been shown to be useful tools to rank species in regard to their potential to alter the abundances of other species, in particular when estimating the probability of secondary extinctions that may follow the loss of a species (Dunne, Williams and Martinez 2002; Kaiser-Bunbury, Muff et al. 2010).

Despite being conceptually intuitive, the relationship between centrality and a species' presumed impact on the state of the community is largely phenomenological. On the one hand, substantive changes in ecosystem functioning can also occur without complete removal of a species (Mouillot et al. 2013). On the other, we are often interested in a *specific* state of the community

that might be desirable to attain (or preserve) because of its biodiversity, resilience, functioning, or the ecosystem services it provides. In these cases, it might be less useful to understand which species may cause *any* change in the community. Instead, we are better served by understanding how the structure of the network can be harnessed to achieve the desired state and which species may play the largest role in this targeted process. When the state of a community is underpinned by more than a single species (often the case in real communities) and we move beyond single-species removals, we might expect the accuracy of centrality to diminish. As a result, community ecology could arguably benefit from an alternative, perhaps more mechanistically-grounded, approach to understand how species affect each other's abundance.

Species' abundances—and consequently the state of the community as a whole—are influenced both by the structure of their interactions and the dynamics of these interactions, including the mechanisms of self-regulation (Lever et al. 2014). However, community and population dynamics can be modelled in innumerable ways, and empirical support for one versus another is often still ambiguous (Holland, DeAngelis and Bronstein 2002). The alternative approach should, therefore, ideally acknowledge ecosystem dynamics, but without being overly dependent on the particular choices of how they are characterised. Among the various possibilities *structural controllability*, a branch of **network control** theory, appears to be a strong candidate (Isbell and Loreau 2013). Control theory is a widely-studied branch of engineering used to determine and supervise the behaviour of dynamical systems (Motter 2015). It is inherently designed to deal with system feedbacks and its application has recently been expanded to complex networks (Lin 1974; Liu and Barabási 2016). Consistent with long-standing ecological questions, advances in structural controllability have established a clear link between the structure of the network and the way nodes affect each other. Unlike centrality indices, however, this link is not based on a priori assumptions between network metrics and keystone-ness but is instead based on well-established advances in both dynamical and complex-systems theory (Motter 2015).

At its fundamental level, structural controllability first determines whether a system is controllable or not; that is, it asks if a system could ever be driven to a desired state within a finite amount of time. Although the controllability of a network is a whole-system property, it has recently been shown that asking for the controllability of a complex-system is equivalent to finding a particular set of relevant nodes: the set with which is possible to control the state of the whole network (Liu and Barabási 2016). Importantly, this set of nodes is not always unique for a given network. This implies that an examination of the distinct sets provides a means to connect nodes with their *general* ability to modify the system to which they belong.

Here, we apply methods from structural controllability to a particular ecological problem and show how it can be used to generate insight into the role of species in an ecological network. Specifically, we outline the approach using a set of ten pairs of uninvaded and invaded plant-pollinator communities. We use invaded communities because there is strong empirical evidence showing that invasive species play an important role shaping the abundances of other species, something which is particularly true in these ten networks (Lopezaraiza-Mikel et al. 2007; Bartomeus, Vilà and Santamaría 2008). This choice thus offers us an opportunity to explicitly contrast our theoretical observations with empirical evidence. Moreover, empirical observations indicate that steering the state of some communities—for example during ecosystem restoration or invasive species removal—can be a very difficult task (Woodford et al. 2016). Therefore, we first ask whether there are differences between the controllability of invaded and uninvaded networks. We then expand existing methods from control theory to effectively link the **controllability** (see Glossary) of a network with the role of its constituent species. We ask—from a control-theoretic perspective—whether there are key differences between species in the role they play at driving the state of the community and explore the ecological factors related to these differences. This allows us to identify species that might be critical for network control and show that they have a larger than expected impact on the stable coexistence of the community. Finally, we compare the proposed approach to current methods based on species' centrality and show how

these methods are indeed valuable but ultimately paint a limited picture in regard to the “keystoneness” of a species.

1.2 METHODS

We used ten paired pollination communities to apply the control-theoretic approach. Each community pair was composed of a community invaded by a plant and a community free of the invasive species. Four pairs correspond to natural or semi-natural vegetation communities in the city of Bristol, UK (Lopezaraiza-Mikel et al. 2007). These communities comprised 19–87 species (mean 55), and non-invaded plots were obtained by experimentally removing all the flowers of the invasive species *Impatiens grandulifera*. The other six pairs were obtained from lower diversity Mediterranean shrublands in Cap de Creus National Park, Spain (Bartomeus, Vilà and Santamaría 2008). These communities comprised 30–57 species (mean 38); in contrast to the above, uninvaded communities were obtained from plots that had not yet been colonised by either of the invasive species *Carpobrotus affine acinaciformis* or *Opuntia stricta*. The structure of all these communities was defined by the pollinator visitation frequency, which has been shown to be an appropriate surrogate for inter-specific effects in pollination networks (Diego P Vázquez, Morris and Jordano 2005; Bascompte, Jordano and Olesen 2006).

The first step in applying methods of control theory is to construct a directed network that is able to provide an indication of the extent to which species affect each other’s abundance. In some ecological networks, establishing the directionality can be relatively straightforward, for example when links represent biomass transfer or energy flow (Isbell and Loreau 2013). In pollination networks, however, this directionality is less obvious as both species can, in theory, benefit from the interaction. We overcome that obstacle by noting that the extent to which species i affects species j relative to the extent to which j affects i can be

summarised by their interaction asymmetry (Bascompte, Jordano and Olesen 2006). This asymmetry is given by

$$a(i, j) = a(j, i) = \frac{|d_{ij} - d_{ji}|}{\max(d_{ij}, d_{ji})},$$

where the dependence of plant i on pollinator j , d_{ij} , is the proportion of the visits from pollinator j compared to all pollinator visits to plant i . Previous research has shown that mutualistic interactions are often highly asymmetric in natural communities; in other words, if a plant species is largely dependent on a pollinator species, that pollinator tends to depend rather weakly on the plant (and vice versa). We therefore create a directed link from species i to species j when $d_{ij} - d_{ji} \geq 0$ to establish the most likely direction of control between a species pair (Figure 1.1). Sometimes (2.4% of the observed interactions in our datasets) there is no observed asymmetry between species pairs ($d_{ij} = d_{ji}$), and we cannot infer a dominant direction of control. When this occurs, we deem both species to be equally likely to affect each other and leave a reciprocal interaction between them (a link from i to j and another from j to i). By basing the direction of the links on the asymmetry of their dependence, we are able to generate a network that is consistent with the dynamics of the community while satisfying the requirements of structural controllability. This allows us to calculate the controllability of the networks and investigate whether there are differences between invaded and uninvaded communities.

1.2.1 Controllability

A system is said to be controllable if it is possible to steer it from an initial to an arbitrary final state within finite time (Kalman 1963). A simple version of such a system can be described by $\frac{dx}{dt} = Ax + Bu(t)$, where the change of its state over time ($\frac{dx}{dt}$) depends on its current state x (for example the species' abundances), an external time-varying input $u(t)$ (the control signal), and two matrices A and B , which encode information about the network structure and how species respond to external inputs, respectively. In classic control theory, determining whether

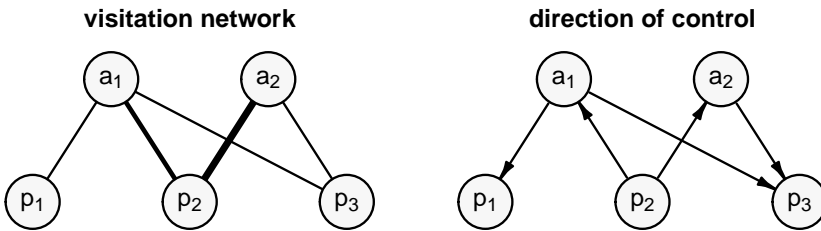


Figure 1.1: The direction of control. To establish the direction of control, we start with a weighted visitation network (on the left). In this network, the width of the links corresponds to the frequency of visitation between animals a_i and plants p_i , with wider links indicating more visits. Plant p_1 is visited exclusively by a_1 but p_1 represents only a small fraction of the floral resources exploited by a_1 . Therefore, the population of p_1 is more likely to be affected by a_1 than vice versa. We represent this with a directed link from a_1 to p_1 in the control network (on the right). The direction of control between all other species pairs can be similarly determined by inspecting the difference between their relative dependences.

this system is controllable can be achieved by checking that its controllability matrix

$$R = [B \quad AB \quad A^2B \quad \dots \quad A^{n-1}B]$$

has full rank. In complex systems, however, employing this rank condition, or numerical approximations of it is infeasible because it is hard to fully parameterise A and B (either because the weight of the links changes over time or because they are difficult to measure). Here, we use an approach based on the structural controllability theorem (Lin 1974), which assumes that we are confident about which elements of A and B have either non-zero or zero values (there is an interaction or not), but that we are less sure about the precise magnitude of the non-zero values. Using this structural approach, we can find out the controllability of a system for every non-zero realisation of the parameters.

We are often able to estimate A in ecological networks, as this matrix represents the interactions between species. Part of the control problem thus resides in estimating a supportable estimation of B , which represents the links between external inputs and species. Naively, any ecological community (and any system for that matter) could be controlled if we control the state of every species independently, but such an approach is typically impractical. Here, we are interested in finding a **minimum driver-node set** (effectively finding B) with which to make the system controllable. The brute-force search for this minimum driver-node set is computationally prohibitive for most networks as it involves the evaluation of 2^N different controllability matrices where N is the number of species in the community. We therefore instead employ a recently-developed approach that shows that the control problem of finding the minimum driver-node set can be mapped into a graph-theoretic problem: maximum matching (Liu, Slotine and Barabási 2011; Liu and Barabási 2016).

Maximum matching is a widely studied topic in graph theory and is commonly used in multiple applications, ranging from dating apps and wireless communications to organ transplant allocation and peer-to-peer file sharing. A matching in an un-weighted directed graph is defined as a set of links that do not

share common start or end nodes; the largest possible matching is called a maximum matching. For example, in a network composed of jobs and job applicants, a matching is any pairing between applicants and positions that satisfies one basic constraint: an applicant can be assigned to at most one position and vice versa. Consequently, a maximum matching is an optimal pairing, one that maximises the number of applicants with jobs and the number of positions filled. Admittedly, the link between matchings and structural controllability may appear far from straightforward.

This link becomes apparent after examining the graphical interpretation of structural controllability: from a topological perspective, a network is structurally controllable if there are no inaccessible nodes—that is, nodes without incoming links—or dilations—*expansions* of the network (Figure 1.2). The key is to note that these two fundamental conditions of structural controllability imply that there is a one-to-one relationship between *superior* and *subordinate* nodes just like the one-to-one relationship between jobs and applicants (Figure 1.2, left). We thus use the maximum-matching algorithm to find an optimal pairing of **superior nodes** (those that can control another node) and subordinate nodes (those that can be controlled by another node) in a manner consistent with the controllability conditions. Given the result, we can further decompose the matching into a set of paths that reveal how a control signal can flow across the links in a network to reach every node within it. As recently shown (Liu, Slotine and Barabási 2011), the minimum driver-node set—those to which an external control input should be applied to make the system controllable—corresponds exactly to the *unmatched* nodes in the network (Figure 1.3).

1.2.2 Differences between invaded and uninvaded networks

Our first objective is to investigate whether the controllability of a community is associated with invasion status or not. Finding out exactly how difficult it is to control a network depends strongly on the particularities of the desired control trajectory (i.e. the path

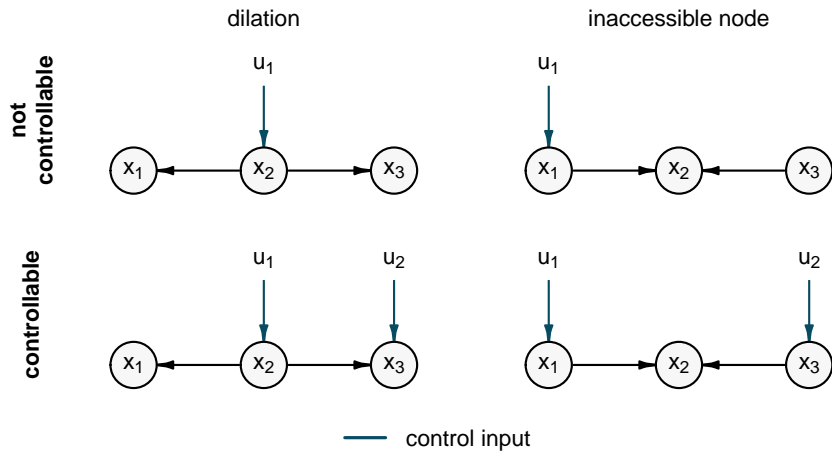


Figure 1.2: Controllability conditions. Once we have established the directions of control, we can determine whether the network is controllable or not. Any system defined by a directed network (with state nodes x_i ; species' populations in an ecological context) and external control inputs (nodes u_i , orange links) is structurally controllable if it satisfies two conditions: it has no dilations (expansions in the network) and no inaccessible nodes. The system on the top left is not controllable because there is a dilation since node x_2 is being used to control two nodes simultaneously; in other words, there are fewer superiors (x_2) than subordinates (x_1 and x_3). The network on the top right is not controllable because node x_3 is inaccessible for the only input node u_1 in the system. Both systems can be made controllable by adding an extra input node (u_2 in both bottom networks).

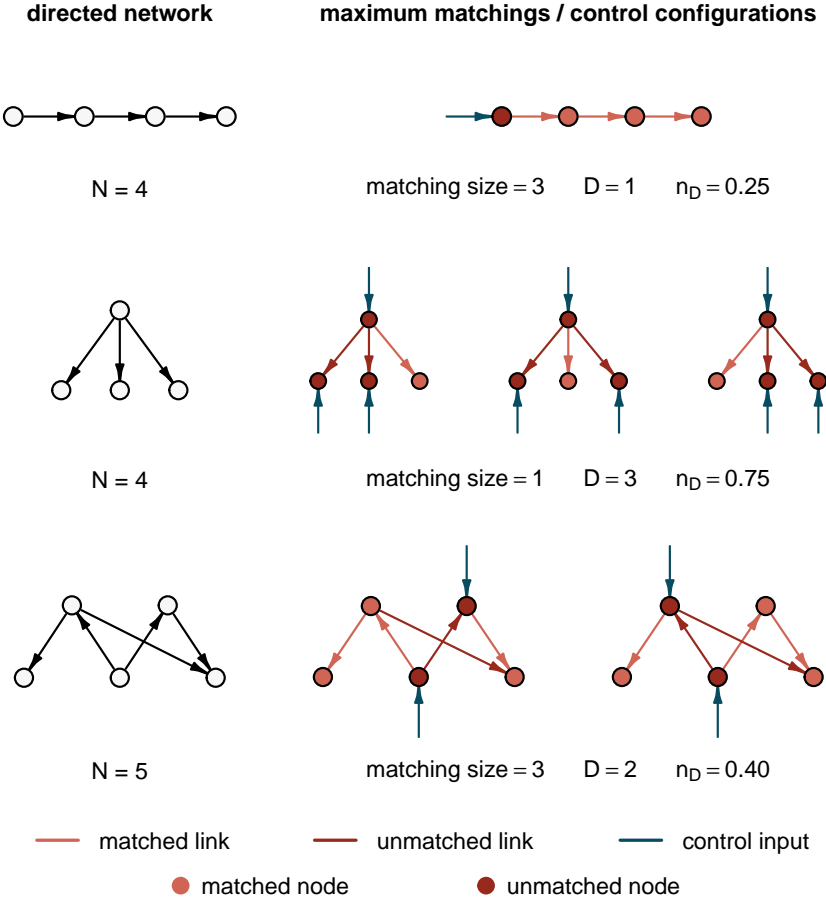


Figure 1.3: Maximum matchings and control configurations. In directed networks, a maximum matching is the largest possible set of links that do not share start or end nodes (dark purple). Maximum matchings are not necessarily unique; instead, each of them is related to a possible minimum driver-node set in the network (the nodes to which an external control input, in orange, should be applied in order to ensure controllability). The size of the minimum driver-node set D corresponds exactly to the number of unmatched nodes (the number of nodes in the network N minus the matching size). To account for network size, we use the size of the minimum driver-node set relative to the total number of nodes $n_D = D/N$ as a measure of the extent to which the network structure can be harnessed to control the system.

to the desired final state) as well as the dynamical relationship between nodes. However, we are interested in understanding the controllability of a network in a more general sense, such that it can be applied even when the precise control scenario is known only incompletely. To this end, we chose an indicator that follows directly from our approach: the size of the minimum driver-node set. This simple metric provides a general indication of how difficult controlling a network might be, as systems that require a large number of external inputs to be fully controlled are intuitively more difficult or costly to manage. For instance, achieving full control in a “network” in which species do not interact at all is relatively more difficult as we would require an intervention for every single species. Conversely, the structure of a linear trophic chain can be harnessed to achieve full control using just one intervention targeted at the top species; a suitable control signal could then cascade through the trophic levels and reach other species in the community. Specifically, drawing from the structural-controllability literature, we use the size of the minimum driver-node set relative to the total number of species $n_D = \frac{D}{N}$ as a measure of the *controllability* of a network—the extent to which the network structure can be harnessed to control the community. The lower n_D the more controllable the community. In an ecological context, external inputs can be thought of as management interventions that modify the abundance of a particular species.

After finding the minimum driver-node set in each of our networks, we wanted to test whether invasion status or other predictors are correlated to controllability. We do this using a set of generalised linear models with Gaussian errors and a logit link function. The response variable was the relative size of the minimum driver-node set n_D of the twenty empirical networks (ten invaded and ten uninvaded), and we included invasion status as a predictor. As predictors, we also include the network connectance, the network nestedness (NODF), the number of species (since one might naively expect to see a negative relationship between richness and controllability; Menge 1995), the network asymmetry (an indication of the balance between plant and pollinator diversity), and the interaction strength asymmetry (the asymmetry on the dependences between trophic levels; Blüthgen

et al. 2007). We compared models using the Akaike Information Criterion for small sample sizes (AICc).

In addition, we also explored whether real networks differ in their architecture from random ones in a concerted way that could impact these results. Specifically, we used two null models each with 99 randomisations per network. In the first, we followed Diego P. Vázquez et al. (2007) and maintained the connectance of the network but randomised the visits across species such that the relative probabilities of interactions were maintained. We then re-estimated the direction of control and the corresponding size of the minimum driver-node set, n_D . For the second null model, we used the empirical directed network described above and randomly shuffled the direction of control between a species pair prior to re-estimating the size of the minimum driver-node set.

1.2.3 Species' roles

Our second objective is related to how species differ in their ability to drive the population dynamics of the community. We in turn examine whether these differences are also reflected in the role species play at supporting the stable coexistence of other species in the community. Ecologically, these differences are relevant because resources and data are limited, and therefore full control is infeasible. While calculating the size of the minimum drive-node set can measure the controllability of an ecological community, it does not provide information about the roles that particular species play.

To answer this question, we harness the fact there may be multiple maximum matchings for a given network, and each of these maximum matchings indicates a unique combination of species with which it is possible to control the network. Moreover, some species belong to these combinations more often than do others. We call this property a species' **control capacity**, ϕ . The higher a species' control capacity, the greater the likelihood that it would need to be directly managed to change (or maintain) the ecological state of their community. Therefore, a species'

control capacity provides an estimation of its relative importance at driving the state of the community (Jia and Barabási 2013).

To calculate a species' control capacity ϕ , we must first enumerate all possible maximum matchings. Unfortunately, enumerating all maximum matchings is extremely expensive from a computational perspective, a network with a couple dozen species has several hundred million unique maximum matchings. To solve this problem, we employ a recently-developed algorithm that reveals the control correlations between the nodes in the graph while requiring considerably less computational resources (Zhang, Lv and Pu 2016). Using this algorithm, we are able to identify species that are possible control inputs—those that belong to the minimum driver-node set in at least one of the possible **control configurations**. Here, we extend this algorithm such that it is possible to calculate a highly accurate approximation of the control capacity ϕ of every species in the network. In the networks that contained reciprocal links (because there was no asymmetry in the dependences of a species pair), we averaged a species' control capacity ϕ across every possible “non-reciprocal” version of the network.

We then examined how species-level properties were related to control capacity using a set of candidate generalised linear models with binomial error structure. These models included five predictor variables that mirror the network-level predictors. First, the species' contribution to nestedness, which has been proposed as a key feature that promotes stability and robustness in mutualistic networks (Saavedra, Stouffer et al. 2011). Second, the species' strength (the sum of a species' visits), which quantifies the strength of a species' associations and is indirectly related to its abundance (Poisot et al. 2012). Third, the direction of asymmetry which quantifies the net balance in dependencies; that is, it indicates if a species affects other species more than what they affect it or not (Diego P. Vázquez et al. 2007). Fourth, the species' degree in order to account for the intrinsic centrality of a species. Finally, we included a categorical variable for the species' trophic level (plant or pollinator) and an interaction term between trophic level and the previous four variables. To facilitate comparison between predictors, degree and visitation

strength were log-transformed and all four continuous variables were scaled to have a mean of zero and a standard deviation of one. In these models, species from all networks were analysed together. We initially included random effects to account for possible variation across communities. Specifically, we tested structures that allowed for a random intercept for the network, site, and the study it comes from. However, we found that in all cases the among-group variance was effectively zero, and therefore we did not include any random effect in further analyses. We then generated all possible candidate models across the space of models with all, some, and none of the predictor variables. To identify the models that were best supported by the data, we first determined the most parsimonious random structure using the AICc. The relative importance of variables was then assessed by looking at their effect sizes in the top-ranked models and the cumulative weight of the models in which they are present.

In addition, we wanted to understand how a species' control capacity ϕ described above relates to metrics of keystoneity based on centrality. Specifically, in each network, we calculated the species' degree, betweenness, closeness centrality (Martín González, Dalsgaard and Olesen 2010), page rank (McDonald-Madden et al. 2016), and eigen centrality (Jordano, Bascompte and Olesen 2006). We then calculated the spearman correlation coefficient between control capacity and each of these centrality metrics.

Our analysis revealed that some species have a control capacity $\phi = 1$. These species are critical to controlling their community because they are part of the minimum driver-node set in *every* control scenario. In other words, it is theoretically impossible to drive the state of the community to a desired state without directly managing the abundance of these species. We thus anticipate that these species have a disproportionately large impact on the community dynamics. To test this hypothesis, we identified these **critical species** in each of the networks and investigated whether they have a larger than average impact on the stable coexistence of species in the community. Within mutualistic networks, one useful measure of stable coexistence is called structural stability (Rohr, Saavedra and Bascompte 2014). Mathematically,

the structural stability of a network represents the size of the parameter space (i.e., growth rates, carrying capacities, etc.) under which all species can sustain positive abundances (Saavedra, Rohr et al. 2016). The contribution of any given species i to stable coexistence can be estimated by calculating the structural stability of the community when the focal species i is removed. To allow comparison across communities, the structural stability values were scaled within each network to have a mean of zero and a standard deviation of one. Given these species-specific estimates of structural stability, we then used a t-test to compare the contribution to stable coexistence of critical and non-critical species.

1.2.4 Testing assumptions

Just like the centrality metrics, the information obtained by applying structural controllability depends on the ability of the network to accurately represent the ecological community. We thus tested the sensitivity of our approach to two fundamental assumptions. First, we tested that visitation is an appropriate proxy to infer interspecific effects by comparing the results obtained using visitation to two alternative metrics in a separate dataset that lacked invasive species (Ballantyne, Baldock and Willmer 2015). Specifically, we also calculated the controllability (the size of the minimum driver node-set) and the control capacity of networks constructed using pollinator efficiency (which measures the pollen deposition of an interaction) and pollinator importance (which accounts for both pollen deposition and visitation and hence is regarded as a more accurate estimation of the pollination service received by plants; Ne'eman et al. 2010).

Second, because interspecific dependencies themselves depend on the network topology and consequently on the accurate sampling of interactions, we tested the robustness of structural controllability to the uncertainty involved with the sampling of interactions. Here, we compared the results obtained when using the full network and when randomly removing interactions from

the weakest links in the network. This effectively removed the rare interactions from the networks.

1.3 RESULTS

1.3.1 Controllability

The size of the minimum driver-node set relative to the number of species in each network n_D ranged between $n_D = 0.58$ and $n_D = 0.88$ (median 0.74).

1.3.2 Differences between invaded and uninvaded networks

We found that the relative size of the minimum driver-node set of invaded communities was not significantly different from that of communities that have not been invaded (Figure 1.4a). In contrast, there was a large negative relationship between n_D and the network asymmetry (Figure 1.4b). Furthermore, there were also negative, albeit weaker, relationships between n_D and connectance, nestedness and species richness. The relative size of the minimum driver-node set n_D of empirical networks did not differ from that of a null model that roughly preserved the degree distribution and fully preserved the network connectance ($p = 0.66$; Figure 1.4c). However, empirical networks had a larger n_D than null models that preserved the interactions but shuffled the direction of control of the empirical network ($p = 2.4 \times 10^{-7}$).

1.3.3 Species' roles

Species varied widely in their control capacity (Figure 1.5). Pollinators had, in average, larger control capacities than plants. That said, almost no pollinator was critical for network control, (where a species is critical for control if it has control capacity $\phi_i = 1$). Plants had a multimodal distribution of control capacity with

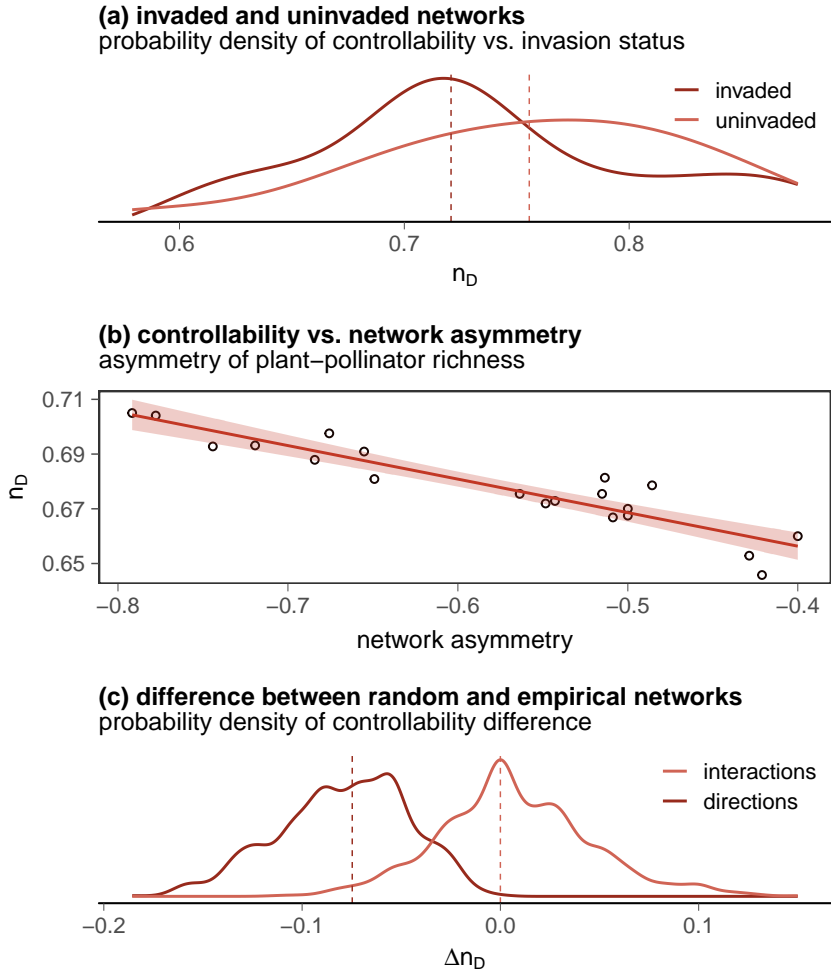


Figure 1.4: Drivers of network controllability. (a) Probability density of the relative size of the minimum driver-node set n_D in the invaded (light) and uninvaded (dark) empirical networks. (b) Relationship between the asymmetry plant/pollinator richness and n_D . (c) Probability density of the difference between the relative size of the minimum driver-node set of random networks and that of empirical networks. We randomised either the species visitation patterns (light line) or randomised the direction of control between a species pair (dark line). The vertical dashed lines in (a) and (c) indicate the median values of the distributions.

Table 1.1: Selection table of the binomial generalised linear models of species’ control capacity, ϕ . Only models with a weight larger or equal to 0.01 are shown.

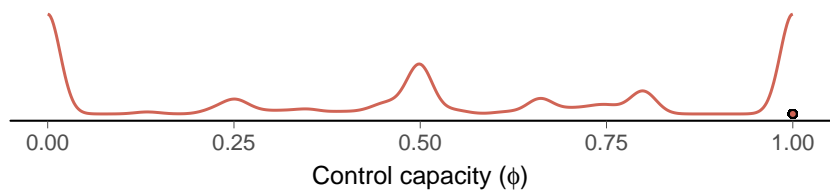
Model terms										$\Delta AICc$	W.
int.	k	l	a	n	s	$k:l$	$l:a$	$l:n$	$l:s$		
-1.20		+	0.80	0.15	0.29		+	+		0.00	0.48
-1.19		+	0.76	0.13	0.35		+	+	+	1.52	0.22
-1.26	-1.24	+	1.44	0.39	1.07	+	+		+	4.09	0.06
-1.37	-0.66	+	1.03		1.06	+	+		+	4.39	0.05
-1.27	-1.15	+	1.37	0.33	1.07	+	+	+	+	4.92	0.04
-1.37	-0.10	+	0.90		0.43	+	+			6.36	0.02
-1.25	-0.28	+	1.24	0.40		+	+			6.47	0.02
-1.24	-0.62	+	1.29	0.38	0.40	+	+			6.50	0.02
-1.39	0.30	+	0.83			+	+			6.72	0.02
-1.28	-0.17	+	1.16	0.32		+	+	+		7.03	0.01
-1.26	-0.53	+	1.23	0.32	0.39	+	+	+		7.42	0.01
-1.02		+	0.69	0.30	0.31		+			7.48	0.01

Note. Terms: intercept (int), degree (k), trophic level (l), asymmetry (a), contribution to nestedness (n), visitation strength (s). Model weight indicated with (W.)

maxima at both extremes of the distribution (Figure 1.5a). Intriguingly, every invasive species was critical for network control in each of their communities. The species-level models identified a positive relationship between control capacity ϕ and a species’ contribution to nestedness, visitation strength, and the asymmetry of its dependences (Table 1.1; Figure 1.6). Comparatively, species’ degree was only weakly associated with control capacity. In fact, many species with a low degree, especially pollinators, exhibited a large control capacity in their communities.

Species’ control capacity ϕ was only weakly correlated with commonly used centrality metrics. The Spearman correlation between these ranged between -0.14 (with betweenness centrality) and 0.42 (with eigen centrality). The correlation coefficient with degree was 0.13, however most species with high degree also tended to attain a high control capacity.

(a) control capacity of plants
probability density



(b) control capacity of pollinators
probability density

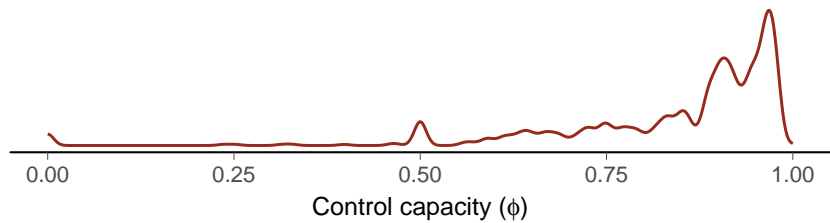


Figure 1.5: Probability density of the control capacity ϕ of (a) plants and (b) pollinators across all networks. The control capacity of all invasive species is $\phi = 1$ and is depicted with solid circles.

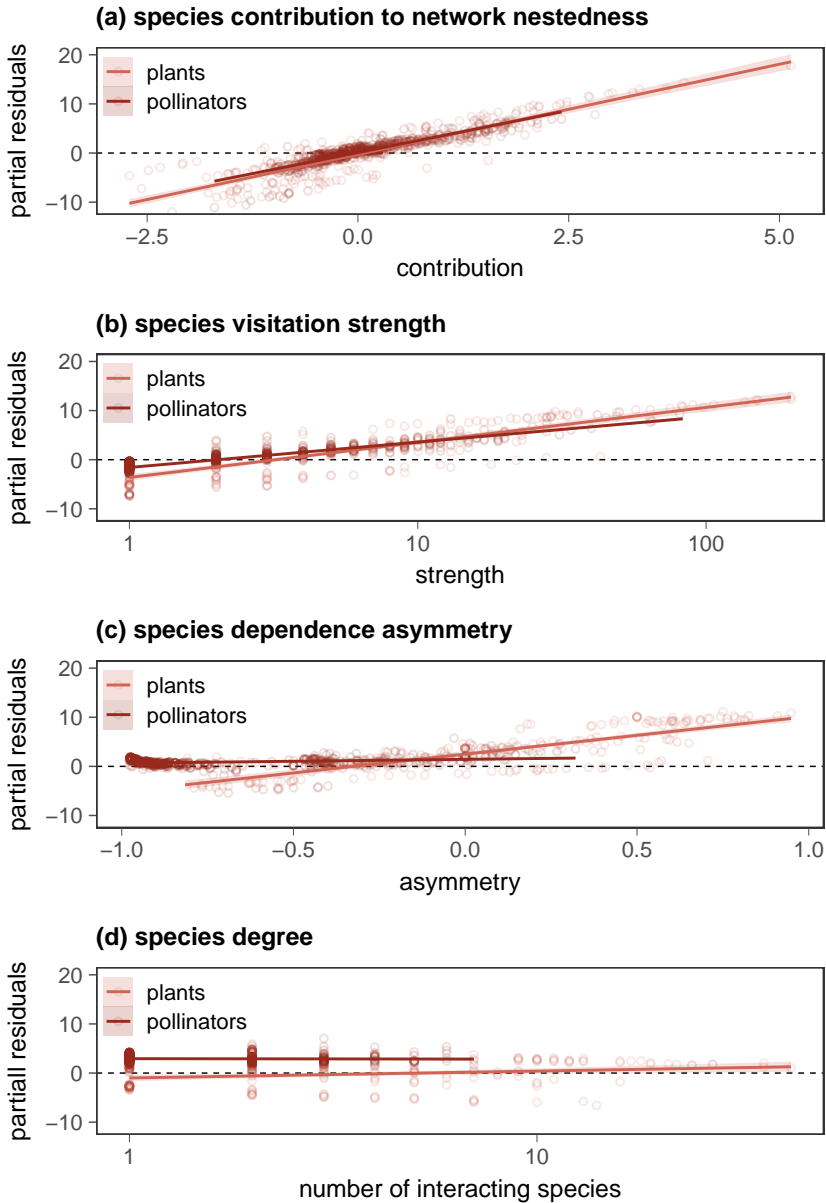


Figure 1.6: Partial-residual plots for the independent variables: (a) contribution to nestedness, (b) visitation strength, (c) asymmetry of dependences, and (d) degree. Partial-residual plots show the relationship between control capacity and each of the independent variables while accounting for all other remaining variables. Plotted values correspond to the predictions of the models weighted average.

structural stability of species removal

probability density

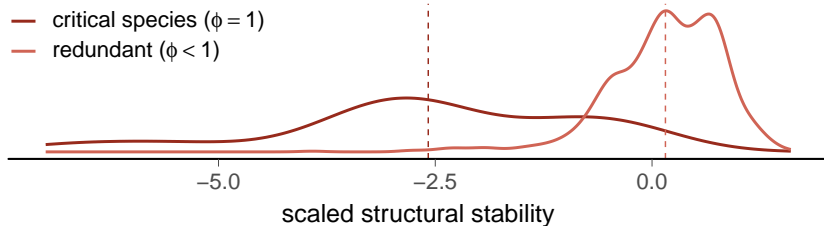


Figure 1.7: Probability density of the structural stability of the communities after a single focal species is removed. Mathematically, the structural stability of a network represents the size of the parameter space (i.e., growth rates, carrying capacities, etc.) under which all species can sustain positive abundances. The structural stability of communities in which critical species have been removed (darker line) is considerably smaller than that of communities in which non-critical species have been removed. This indicates that critical species contribute more to the stable coexistence of their communities. To allow comparison across communities, the structural stability values were scaled within each network to have a mean of zero and a standard deviation of one. Here, we assume values of the mutualistic trade-off and mean interspecific competition of $\delta = 0$ and $\rho = 0.01$ respectively. However, the choice of these parameters does not affect the results.

Finally, we found that critical species have a particularly large impact on species coexistence when compared to non-critical species. Indeed, the structural stability of the networks where critical species were removed was considerably lower than those where non-critical species were removed ($p = 2 \times 10^{-5}$; Figure 1.7).

1.3.4 Testing assumptions

We found that using visitation as a proxy for the strength of species' interactions leads to similar results than those obtained using pollinator importance (regarded as an accurate measure of the pollination service to plants; Ne'eman et al. 2010). Im-

portantly, we also found that structural stability is robust to incomplete sampling of interactions. Indeed, we found strong agreement between results obtained using the complete empirical networks and those obtained by randomly removing the weakest interactions. Despite removing rare interactions and species, the relative size of the minimum driver-node set, the superior species, and the relative rankings of control capacity were generally maintained. Of particular note, we found that critical species in the full network were also critical in the vast majority of rarefied networks.

1.4 DISCUSSION

Our main goal was to understand the role that species play in both modifying the abundance of the species they interact with and the state of the community as a whole. To achieve that goal we applied *structural controllability*, a field at the intersection between control and complex theory that allowed us to obtain two key pieces of information: the *controllability* of a network and a species' *control capacity* (Table ??). We found that the controllability of a network does not depend on its invasion status and that the species that are critical to altering the state of the community are also the ones that most sustain the stable coexistence of species in their communities.

Our results indicate that fully controlling ecological networks might currently be out of reach for all but the smallest communities (Motter 2015). Indeed, the median size of the relative minimum driver-node set in our dataset was $n_D = 0.74$, a high value when compared to other complex systems in which controllability has been investigated (the lower n_D the more controllable the community). For instance, only gene regulation networks appear to achieve similar levels of controllability while most social, power transmission, Internet, neuronal, and even metabolic networks seem to be “easier” to control ($0.1 < n_D < 0.35$) (Liu, Slotine and Barabási 2011). Structural controllability provides solid theoretical rationale for the many difficulties encountered in

the management and restoration of natural communities (Woodford et al. 2016). Nevertheless, structural controllability might be helpful at identifying communities in which changes in the ecological state are more likely to occur.

The differences between the controllability across networks are likely to arise from differences in their structure rather than their invasion status. Specifically, when controlling for network structure, we found no difference between the controllability of invaded and uninvaded networks. Instead controllability is almost completely constrained by the patterns of species richness at each trophic guild and their degree distributions (Melián and Bascompte 2002; Blüthgen et al. 2007). These two factors are particularly relevant because they govern the asymmetric nature of mutual dependences, which themselves provide the foundation of structure and stability in mutualistic networks (Bascompte, Jordano and Olesen 2006; Memmott, Waser and Price 2004; Astegiano et al. 2015).

Accordingly, our results suggest that structural controllability is closely related to the persistence of an ecological community based on two lines of evidence. First, we found a comparatively small but thought-provoking negative relationship between the controllability of a network and its nestedness. Previous studies indicate that nestedness promotes species coexistence and confers robustness to extinction (Bastolla et al. 2009; Memmott, Waser and Price 2004) even at the expense of the dynamic stability of the mutualistic community (Saavedra, Rohr et al. 2016). These observations are in agreement with our results, as we would expect the dynamic stability (the ability to return to equilibrium after a perturbation in species abundances) of a community to be correlated to the difficulty to control it. Second, species' control capacity was strongly correlated to their contribution to nestedness and critical species had the largest impact to the stable coexistence of species in their communities. Therefore, species that play a key role at determining the state of the community might also be more key to "maintain the organization and diversity of their ecological communities", one of the hallmarks of keystone species (Mills and Doak 1993).

When controlling for a species' visitation strength (the sum of a species' visits), which is indirectly a proxy of its abundance, and the net balance of its dependencies, we found that control capacity could not be easily predicted by species' degree or other metrics of centrality. For instance, some species with a low degree achieved the maximum control capacity and were critical for control in their communities. At first glance, our findings challenge numerous studies that highlight the role that central species play in the dynamics of their communities and their utility at predicting species extinctions (Jordan 2009). However, further inspection shows that our results do not contradict these findings; most species with a large degree also have a large control capacity and all of them were classified as superior nodes which corroborates the utility of classic centrality metrics. Putting these observations together, our results therefore take previous findings one step further and suggest that centrality might paint an incomplete picture of the relevance of species.

Other conceptual differences between structural controllability and centrality metrics provide three key insights into the conservation of ecological networks. First, structural controllability emphasizes that the effect a species has on other species is not independent of the effects that the other species have in the community. The rankings provided by centrality metrics and other heuristics fail to account for the collective influence of several species at once. Second, it demonstrates that to ensure the persistence of a community it is often necessary to consider the abundances of more than a single species, even when full control is infeasible or undesired (for example 90% of our communities contained more than one critical species). Third, structural controllability explicitly acknowledges the existence of multiple management strategies and some will be better than others depending on the context. Approaches to prioritise species for conservation and reintroduction based on traits or centrality are still useful and are likely to overlap with species' control capacity (Pires, Marquitti and Guimarães 2017; Devoto et al. 2012). Stepping back, our results also provide support to the idea that management decisions should not be based on a single technique but indicate that focusing on ecosystem processes and interactions may be more effective than traditional ranking-based

approaches (Harvey et al. 2017). As much potential as any metric or metrics to summarise species' importance might appear to have, it's clear that we also need more empirical studies in different types of networks in order to build intuition and ground truth their usefulness.

Our choice of studying invaded/uninvaded networks was based on a desire to contrast the extensive empirical evidence of the role of invasive plants with our theoretical results. We found that invasive plants were always critical for network control and as such our results were in line with our expectations. Invasive plants have been previously found to exacerbate the asymmetries in their communities (Aizen, C. L. Morales and J. M. Morales 2008; Bartomeus, Vilà and Santamaría 2008; Henriksson et al. 2016) and to attain high centrality in their communities (Vila et al. 2009; Palacio, Valderrama-Ardila and Kattan 2016). We found, however, that it is not that invasive plants have some different mechanism for influencing the community compared to their native counterparts (Emer et al. 2016; Stouffer, Cirtwill and Bascompte 2014). Both native species and invasive plants tended to attain a high control capacity if they were important to network persistence, were abundant, and depended little on other species. Furthermore, our observation that changes in the abundance of invasive plants (and presumably all critical species) are crucial to modify the state of the community agrees with recent evidence showing that ecosystem restoration focused on the eradication of invasive plants can have transformative desirable effects in plant-pollinator communities (Kaiser-Bunbury, Mougil et al. 2017). However, our results also suggest that removals must be exercised with caution. Not only it is hard to predict the direction in which the system will change, but we also show that critical species can underpin the coexistence of species and therefore some communities may be acutely vulnerable to their eradication (Traveset et al. 2013; Albrecht et al. 2014).

Structural controllability assumes that the networks can be approximated using linear functional responses (Liu and Barabási 2016). The ramifications of this assumption imply that, while structural controllability is useful to identify species that are relevant for network control, it cannot be used to design the *exact*

interventions that should be applied to these species in order to achieve a desired state. In an ideal scenario, we would completely incorporate the species' dynamics into the controllability analysis (Cornelius, Kath and Motter 2013); the reality is that such information is rarely available in most ecological scenarios. In contrast, structural controllability only requires a quantitative approximation of the network's interactions to gain valuable insight from the community. Furthermore, while the relationship between centrality and keystoneity is based on an intuitive understanding of what a keystone species is, the assumptions of structural controllability are explicit and the estimation of a species' importance arises from a mechanistic understanding of the population dynamics between species. By accounting for network dynamics (even if in a simple way), structural stability incorporates more ecological realism, especially in the extreme scenario in which the structure of interactions within the community only marginally affects the community's state.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article (<https://doi.org/10.1111/1365-2745.13147>).

DATA ACCESSIBILITY

All data used in this manuscript have already been published by Lopezaraiza-Mikel et al. (2007), Bartomeus, Vilà and Santamaría (2008), and Ballantyne, Baldock and Willmer (2015). The reader should refer to the original sources to access the data.

A

APPENDIX: COPHYLOGENY

Después reflexioné que todas las cosas le suceden a uno precisamente, precisamente ahora. Siglos de siglos y sólo en el presente ocurren los hechos; innumerables hombres en el aire, en la tierra y el mar, y todo lo que realmente pasa me pasa a mí...

— Borges (1941)

SUMMARY

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: (i) across plant-pollinator associations globally, (ii) in local pollination communities, (iii) within the modular structure of those communities, and (iv) 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.

A.1 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 (Gervasi and Schiestl 2017; J. N. Thompson 2005). 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 (J. N. 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 (J. N. Thompson 2005; Page 2003).

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, Míguez-Lozano and Blasco-Costa 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, Gleiser 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, Lavabre et al. 2007; Gómez, Verdú and Perfectti 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; de Vienne et al. 2013), where the focus is often at the relatively fine scale of families and genera (Weckstein 2004; Desdèvises 2007; Hughes et al. 2007; but see Page 2003; Chomicki, Ward and Renner 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; Jousset et al. 2008; Cruaud et al. 2012) and yucca-moth (Althoff et al. 2012) pollination interactions (and see Aizen, Gleiser 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, Friis and Pedersen 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 (Figure A.1). On the other hand, perfect congruence of speciation patterns cannot be expected across such rich and diverse groups after more than 100mya 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 composi-

ecological scale: plant–pollinator interactions globally
conceptual overview

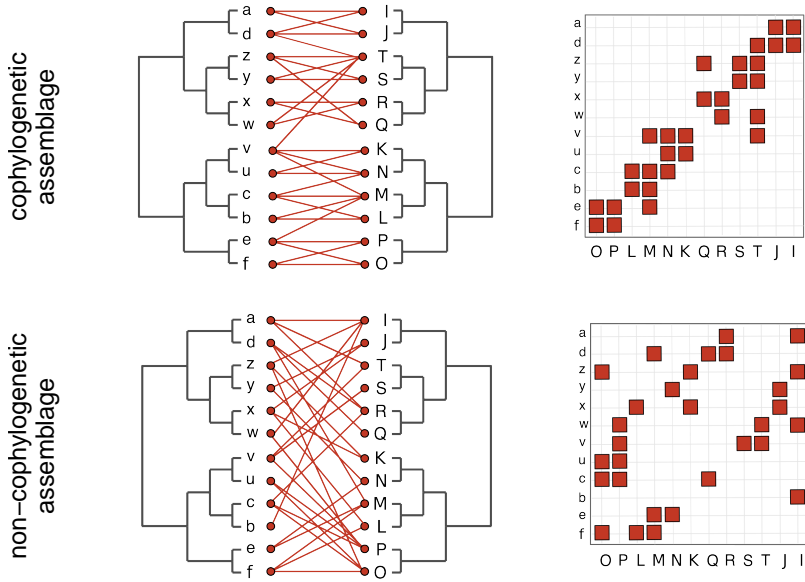


Figure A.1: The first scale of investigation is plant and pollinator interactions globally. We aggregate 54 local pollination communities into a single network to provide a global view of pollination interactions. Here and in the following conceptual figures, we provide a representative example of pollination-interaction structures that are cophylogenetic and non-cophylogenetic. Across all four scales (shown here and in Figure A.2, A.3, and A.4) 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.

tion, such as evenness, functional trait diversity and interaction structure have an element of phylogenetic determinism (Webb et al. 2002; Eklöf and Stouffer 2016; Harmon-Threatt and Ackerly 2013; Emerson and Gillespie 2008; Vamosi et al. 2009). 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, Keen and Miles 2006; Kembel and Hubbell 2006; 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 (Figure A.2). Although recent findings for a set of related networks indicate that cophylogenetic signal may be detectable in pollination networks (Aizen, Gleiser 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, Albert 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; Thebault and Fontaine 2010). Modules—a pervasive feature in pollination networks (Olesen et al. 2007)—are thought to play crucial roles in ecological community resilience (Thebault 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 (Figure A.3). On the other hand, many

ecological scale: plant–pollinator communities
conceptual overview

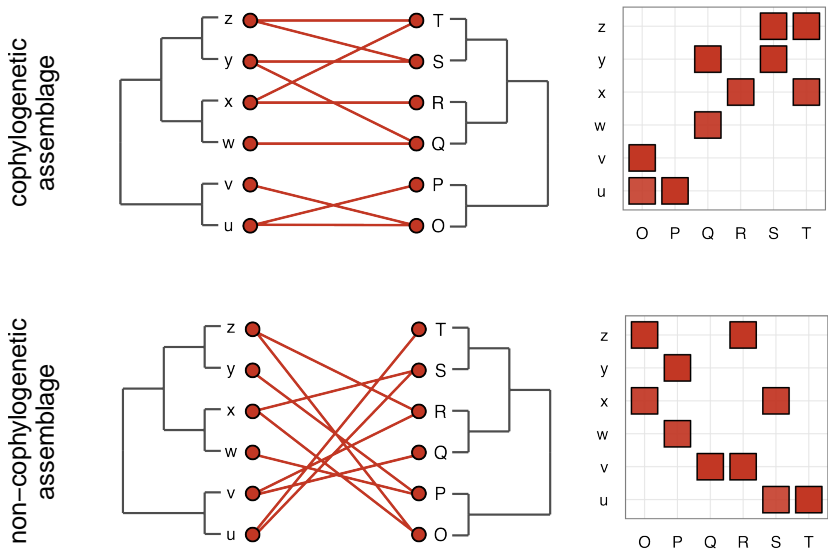


Figure A.2: The second scale of investigation are local communities of interacting plants and pollinators that co-occur in a given location. Each community is a subset of the network in [A.1](#). At this level, we are asking if those interactions that are realized in local communities tend to occur between plants and pollinators with the most congruent evolutionary histories.

different processes have been causally attributed to ecological module formation (Olesen et al. 2007; Rezende, Albert et al. 2009; Krasnov et al. 2012; Rohr, Saavedra and Bascompte 2014; Schleuning et al. 2014), implying that some individual modules within networks may be better characterized by cophylogenetic signal than others (Figure A.4).

For a network's modular structure to show a cophylogenetic pattern, two constraints must be satisfied (Figure A.3). 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 (Figure A.4).

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 dataset. In particular, we leverage these data to quantify the evidence of cophylogenetic signal at the four distinct scales mentioned previously (Figure A.1, A.2, A.3, and A.4): (i) cophylogenetic signal between angiosperms and pollinators globally, (ii) community cophylogenetic signal—where evolutionary congruence between species should be embodied by the interactions of the entire network, (iii) 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 (iv) 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

ecological scale: modular structure of plant–pollinator networks
conceptual overview

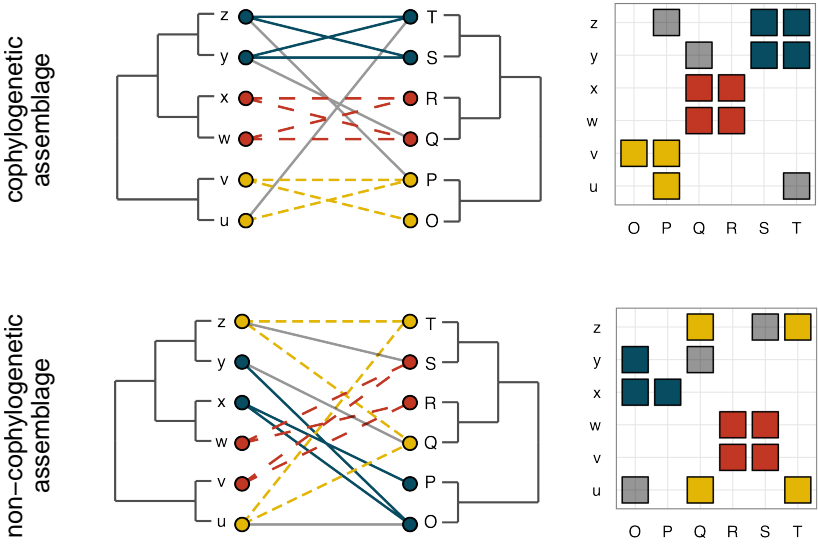


Figure A.3: The third scale of investigation is with the same local communities as in Figure A.2 but examined at the perspective of their modules, where modules group together species based on how likely they are observed to interact. At this scale, we examine how the modular structure of those communities captures cophylogenetic signal. Our hypothesis here derives from the suggestion that the module is the fundamental unit of coevolution 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.

ecological scale: individual modules within plant–pollinator network
conceptual overview

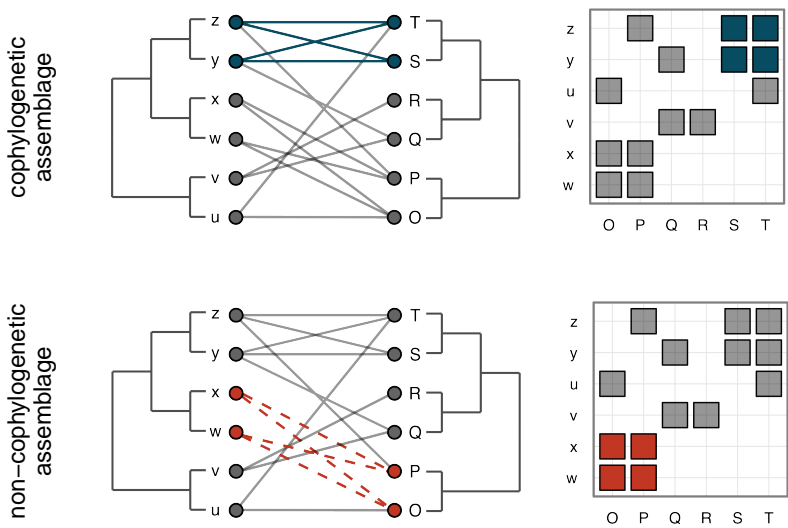


Figure A.4: The fourth and final scale of investigation is at individual modules (groups of frequently interacting plants and pollinators) extracted from Figure A.3. They are also subsets of the local communities in Figure A.2. Many factors are thought to contribute to module formation and cophylogenetic 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.

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.

A.2 METHODS

A.2.1 Empirical data and phylogeny construction

We analyzed a dataset comprised of 54 binary, plant-pollinator mutualistic networks from a wide range of locations around the globe and with diverse species assemblages. In each of the networks, the presence or absence of interactions is based on observed visitation of flowering plants by their animal pollinators. In total, these networks include 1,318 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 (<http://www.ncbi.nlm.nih.gov/>) whereas we corrected animal names with the `resolve` function in the R package `taxize`, which accessed a range of taxonomic databases (Chamberlain et al. 2014). 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, Gleiser et al. 2016). Below the family- and order-level, respectively, we largely rely on taxonomic information to infer evolutionary relationships between taxa.

A.2.2 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, Míguez-Lozano and Blasco-Costa 2013). This approach addresses the cophylogeny problem by optimizing the fit of the phylogeny-interaction graphs of each network (Balbuena, Míguez-Lozano and Blasco-Costa 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 ($\mathcal{R} = \sum r^2$) between phylogenetic-interaction graphs (Balbuena, Míguez-Lozano and Blasco-Costa 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 \mathcal{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.

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 (Balbuena, Míguez-Lozano and Blasco-Costa 2013; Legendre, Desdevises and Bazin 2002). 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, Míguez-Lozano and Blasco-Costa 2013; Hutchinson et al. 2017). Conversely, event-based methods such as Jane (Conow et al. 2010) and CoRe-PA (Merkle, Middendorf and Wieseke 2010) instead permute the topology of the phylogenies due to their explicit focus on specific events. Both approaches have limitations (Balbuena, Míguez-Lozano and Blasco-Costa 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, Míguez-Lozano and Blasco-Costa 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 1000 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.

A.2.3 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 (\mathcal{R}) was compared to the same value (\mathcal{R}^*) from an ensemble of 1000 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 \mathcal{R} was smaller than the null distribution of \mathcal{R}^* , at $\alpha = 0.05$. Since our hypothesis of significant cophylogenetic signal at the global scale implies that \mathcal{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 \mathcal{R} at the regional scale was smaller than its null expectation (i.e., the same null model as above), at $\alpha = 0.05$.

A.2.4 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.

A.2.4.1 *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 dataset, 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 (\mathcal{R}^*) from an ensemble of 1000 randomizations of the network. We considered the cophylogenetic signal of the observed interaction network to be significant if its \mathcal{R} was smaller than the null distribution, at $\alpha = 0.05$.

A.2.4.2 *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 to 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 \mathcal{R} to the same (\mathcal{R}^*) from an ensemble of 1000 randomizations of that network following the outlined approach. We considered the cophylogenetic signal of an empirical species assemblage to be significant if its \mathcal{R} was smaller than the null distribution, at $\alpha = 0.05$.

A.2.5 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 dataset. 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.

A.2.6 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, Míguez-Lozano and Blasco-Costa 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: i) the degree to which closely related species co-occur in modules (for both plants and pollinators) and ii) 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.

A.2.6.1 *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 (LTR; Cadotte and Davies 2018). 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, Claude and Strimmer 2004) and followed the approach suggested by Pagel (1999) and reiterated by Cadotte and Davies (2018).

A.2.6.2 *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 1000 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.

A.2.7 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 sig-

nal 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 1000 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 1000 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.

A.2.7.1 *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 (i)

overall species richness of the module, (ii) the proportion of participant species' interactions that occur within the module, and (iii) phylogenetic diversity (Faith 1992) of both flowering plants and pollinators with module cophylogenetic signal.

A.2.7.2 *Distribution of participation in cophylogenetic modules across the phylogeny*

Lastly, 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 1000 matrix randomizations which preserved the non-independence of the underlying distances with `ape::mantel.test` (Paradis, Claude and Strimmer 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.

A.2.8 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. These results do not show meaningful differences from the case where exotic species are included.

A.3 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 dataset 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. 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, $p < 0.05$; Figure A.5). 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, $p < 0.05$; Figure A.5).

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, $p < 0.05$; Figure A.5). 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, $p < 0.05$; Figure A.5).

Across our dataset, networks tend to vary in the degree to which their modular structure shows cophylogenetic signal (Figure A.5). 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 (Figure A.5). 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

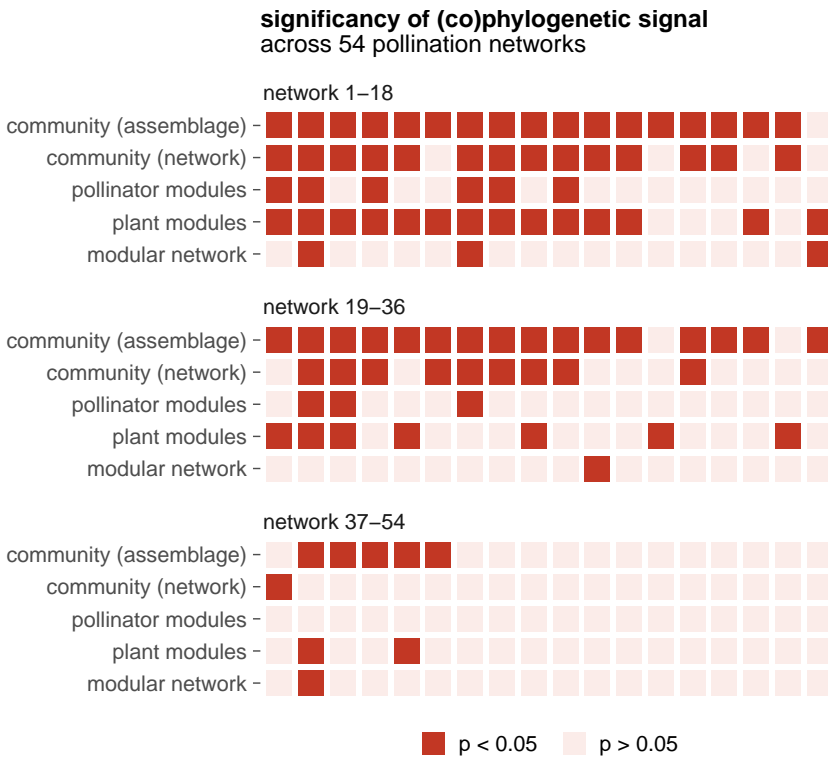


Figure A.5: The degree to which each of the 54 networks in our data set show cophylogenetic signal (CS) at the scale of local communities and their modular structure. On the y-axis, we show these measures of cophylogenetic signal starting with community level cophylogenetic signal of the observed species 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 red square indicates that a network is no different than a null expectation with respect to the measure of interest while a darker red square indicates that the empirical network shows a significantly higher level of the measure than expected by chance. Networks were ordered by overall

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, $p = 0.662$; Figure A.5). 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 (Figure A.6). 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 (Figure A.6). 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 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 8 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

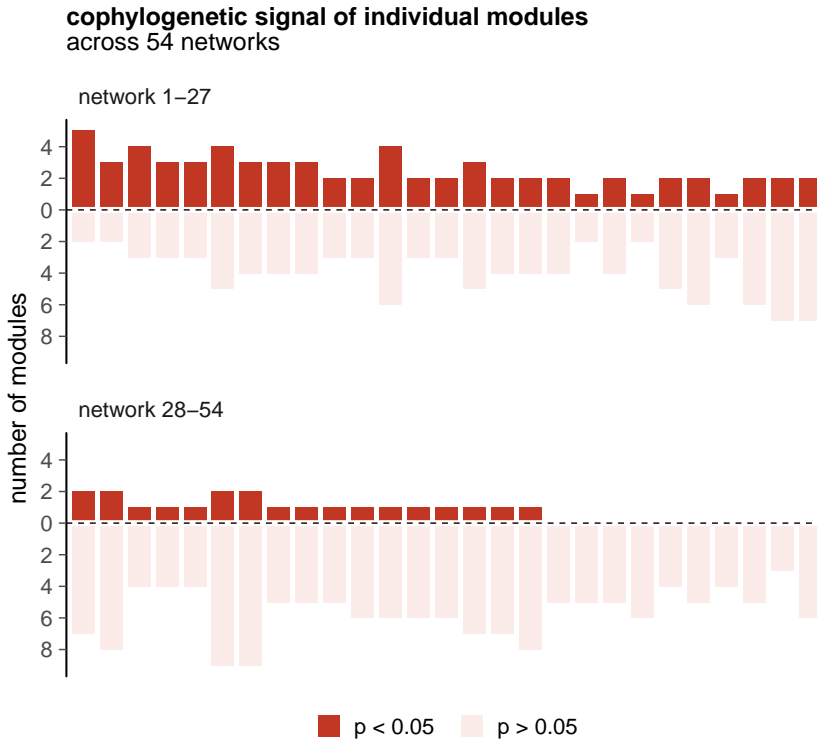


Figure A.6: There is substantial variation in the extent to which individual modules within networks show cophylogenetic signal. For each of the 54 networks (x-axis), we show the number of modules with significant cophylogenetic signal (darker red) and the number that are non-significant (lighter red). 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.

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. 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). 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).

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. The only exception is that the presence of exotic species does appear to dampen cophylogenetic signal at the scale of individual modules. 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.

A.4 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, Kozak et al. 2009), the significant cophylogenetic signal that we see at the global scale may be explained by the co-occurrence 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 assemblages 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 (J. N. Thompson 2005; Smith et al. 2008; Godsoe et al. 2009; Aizen, Gleiser et al. 2016), even when reciprocal selection need not always result in cospeciation (J. N. Thompson 2005). Indeed, Page (2003) suggests that “it is difficult to imagine that cospe-

ciation 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, Gleiser 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 non-native 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, Lavabre et al. 2007; Gómez, Verdú and Perfectti 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, Albert et al. 2009; Krasnov et al. 2012; Rohr, Saavedra 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, Albert 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 4 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. (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, Didham 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, Craze et al. 2007; Tylianakis, Didham et al. 2008; Kaiser-Bunbury, Muff et al. 2010; Aizen, Gleiser 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.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.1955/supinfo>

DATA ACCESSIBILITY

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

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Hypothesen sind Netze, nur der wird fangen, der auswirft

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GLOSSARY

network control a network is said to be controllable if it is possible to steer it from an initial to an arbitrary final state within finite time. 3

controllability the intrinsic difficulty of controlling an ecological community. It is measured by the relative size of the minimum driver-node set, n_D . It also indicates the extent to which network structure can be harnessed for network control. 4

minimum driver-node set one of the sets of species whose abundances need to be directly managed in order to achieve full control of the community. The minimum driver-node sets can be obtained by finding all maximum matchings in a network. 8

maximum matching a matching is a set of links that do not share any common start or end nodes; the largest possible matching is called a maximum matching. 8

superior node a species is a superior node if it can internally affect the abundance of other species in the network. Superior nodes make up the chains that propagate the control signals through the network. 9

control capacity the relative frequency (ϕ) which with a species is part of the optimal control configurations of a network. 13

control configuration one of the species combinations with which is possible to achieve network control. Optimal control configurations are given by the minimum driver-node sets. 14

critical species a species with a maximal control capacity ($\phi = 1$). 15

COLOPHON

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