

Doctoral Confirmation Report

BUILDING RESILIENCE: HOW DO SPECIES INTERACTIONS SHAPE ECOSYSTEM COLLAPSE?

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Summary

The present report summarises the advances made after the presentation of the PhD proposal in August 2015. Most of the progress has been made towards Objective 3 of the proposed research. The proposed schedule has been kept and there haven't been changes on the research objectives or methodology. I present an updated schedule in which extra funded time is included. The literature review and the description of the research—including the planned methodology and analysis techniques—have already been included in the PhD proposal. For convenience, and because there have not been any modifications, these items will be reproduced here.

Research objectives

Natural ecosystems provide important services—like food and water—we humans depend on to a large extent. Much like the failure of a single key financial institution can trigger unexpected crashes on the stock market, human pressures—such as biological invasions and species extinctions—can cause sudden collapses that severely transform the way ecosystems function. However, despite its importance, we do not completely understand the dynamics that make ecosystems resilient to collapse. Because the functioning of ecosystems is largely determined by the network of interactions between the species that inhabit them, my proposed research aims to quantify the role played by species interactions in determining the resilience of ecosystems. To achieve this, I will focus on networks of mutually beneficial interactions, like those between plants and their pollinators, and use a combination of empirical data, computer simulations and ecological theory. Ultimately I want to understand why, when and how ecosystem collapses occur, and how to recover from them.

Overall objective: The overall objective of my proposed research is to quantify the role played by species interactions in modulating ecosystem resilience. To do so, I will focus on the network of mutualistic interactions between plants and pollinators¹⁻³. These networks, which form the base of pollination systems, play a globally important role in the maintenance of biodiversity and crop production^{2,3}.

I will focus on empirically informed theoretical approaches. Throughout my thesis, I will use computer simulated communities to estimate the population dynamics of the species in the community, and then I will directly quantify stability properties from fluctuations in the species populations^{4,5}. I will develop these ‘synthetic’ communities under a wide range of parameters to answer the specific questions I aim to answer in each chapter of my dissertation.

Objective 1: In the first chapter of my thesis I will concentrate on biotic invasions. Specifically I have a twofold objective: first, I aim to determine which network characteristics shape the its resistance and resilience to invasions, and second to determine how biotic invasions reshape network resistance and resilience by affecting existing interactions in the community.

Objective 2: Remarkably, invaded pollination communities have been shown to have structures that support more species⁶ and can be more robust than those of un-invaded communities⁷. Indeed we know which structures can enhance biodiversity⁴ and delay the onset of catastrophic collapses⁸, but there are still serious mismatches between theoretical predictions and empirical observations. I argue that this can be at least partially explained by the interplay between the degree of redundancy among species in the network and the apparent facilitation and competition between species in a mutualistic network. Therefore, the objective of my second chapter is to evaluate the effects that structural redundancy has on the stability of ecological networks.

Objective 3: The aim of my third chapter is to obtain useful lessons for ecosystem management from a direct analysis the network structure. Ecosystems are complex, non-linear systems that are very difficult to control. On the other hand, recent work in theoretical physics has highlighted that is indeed possible to regulate them using targeted interventions⁹. I propose to build upon these findings to determine the optimal set of management actions—from both a theoretical and a feasibility perspective—that are required to modify an ecosystem state.

Literature Review & Methodology

Objective 1: Ecosystems stability to species invasions

The invasion of naturalized species is changing ecosystems worldwide^{10,11}. Fortunately, during the last four decades, there has been steady progress in understanding the causes and outcomes of biotic invasions^{12,13}. For instance, we now understand that the success of an ecological invasion depends on geographic, bio-climatic, and taxonomic factors, as well as aspects of reproductive biology and general ecology of the introduced organisms^{14–18}. However, we are still unable to successfully predict the outcome of species introductions in a large proportion of cases.

One of the potential explanations for this limited predictive success is that research on both the causes and consequences of invasive species, have focused on the negative interactions between species in the community (for example competition and predator-prey relationships). However, the establishment of an introduced species depends on, or at least is greatly enhanced, by the establishment of mutualistic relationships¹⁵—in which both interacting species have a positive outcome. In fact, there are multiple empirical examples of plants that only become successful invaders when mutualistic partners that pollinate their flowers, or disperse their seeds, are available^{14,19,20}. Understanding the reciprocal relationship between biotic invasions and mutualism is a key step necessary to both improving current predictions of invasion outcomes, as well as evaluating how invasive species are modifying mutualistic systems¹⁵.

Species coexistence theory underpins the invasibility of ecosystems

It has been recently shown that there exists a direct link between the structure of ecological networks and ecosystem stability^{1,4,21–26}. In particular stable species coexistence in mutualistic networks seems to be favoured by highly diverse, connected, and nested structures^{4,22,24,26}. For instance, the nested structure observed in many mutualistic networks—in which specialist species tend to interact with a subset of the species with which a generalist interact—support higher amounts of biodiversity, minimises competition among species in the community and maximises the range of conditions necessary to have a stable community^{4,25}. The unambiguous link between ecosystem stability and the ecosystem response to disturbances is an important argument for investigating the implications of network structure and its vulnerability to drivers of global change.

Perturbations caused by global change are severely modifying the structure of mutualistic networks²⁷. Indeed, current evidence suggests that most of its effects are negative^{23,28}. Although our understanding of the effects of those perturbations is limited, we know that, for instance, climate change, and habitat modification can lead to shifts on species abundances, and mismatches of phenology, behaviour, or geographic ranges of the interacting species^{27–30}. Those changes can in turn disrupt the patterns of interactions that determine the structure of mutualistic networks. Some evidence suggest other factors of global change like biotic invasions can also modify the structure of mutualistic networks, for example through changes in the strength of species interactions, and the degree of network nestedness and connectivity^{31–35}.

I hypothesise that network structure is not only modified by the successive invasion of alien

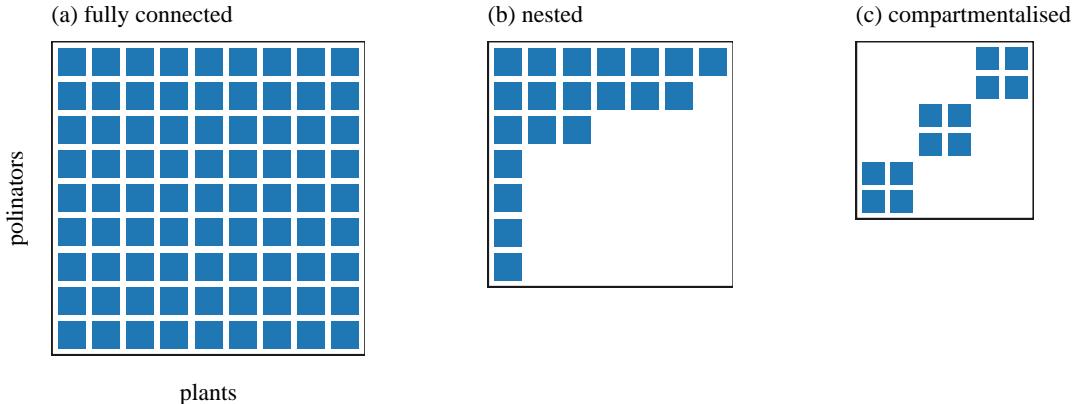


Figure 1: Each panel represents a plantanimal network with different network structures. Plants compete for resources such as nutrients, but also have indirect interactions mediated by their common pollinators. As the number of shared pollinators is higher, positive effects outweigh negative one. Current theory predicts a higher number of coexisting species as indicated by the size of the matrices.

species, but it also plays an important role in determining the invasibility of the community. Two facts provide support to this hypothesis. First, mutualistic interactions are key for the invasion success of introduced species because introduced plants need to have suitable pollinators in the new habitat in order to establish themselves in the community^{15,36}. Second, the structure of mutualistic interactions is known to have direct implications for the number of coexisting species in the community^{1,2,4,37}. Specifically, structures that minimise plant competition seem to facilitate species coexistence and promote biodiversity⁴. Therefore structural attributes—like the degree of specialisation/generalisation, and the contribution to nestedness^a, of available pollinators—should influence the likelihood an introduced species becomes invasive⁶.

Previous studies have found that simpler networks, with fewer species and fewer interactions between species, are easier to invade^{12,18}. However, these studies are strictly limited to trophic networks in which interactions are chiefly antagonistic (prey-predator)^{12,18,39}. Unfortunately, these results cannot be easily extrapolated because mutualistic interactions introduce facilitative and competitive feedbacks that are not present in antagonistic interactions. Here I will fill that gap and study the link between different structural attributes of mutualistic networks—degree of nestedness, contribution to nestedness, and compartmentalisation.

The first step to fill that gap is to construct simulated communities of mutualistic interactions. Initially I will build synthetic communities with a wide range of structural parameters (connectance, nestedness and compartmentalisation; Figure 1). Then I will follow by building communities that copy the structure of a collection of empirically observed mutualistic networks⁶. These two approaches will allow me to evaluate if the network structures that have been found to minimise competition also make the community more vulnerable to invasions.

The second step is to develop models of the population dynamics in mutualistic communities in which the abundances of each species present on the community depends on their growth rate (*births – deaths*). These growth rates can in turn be affected by the feedbacks imposed by the

^aEach species contribution to the nested architecture is defined as the degree to which the organization of their interactions increases overall nestedness³⁸ (Figure 1).

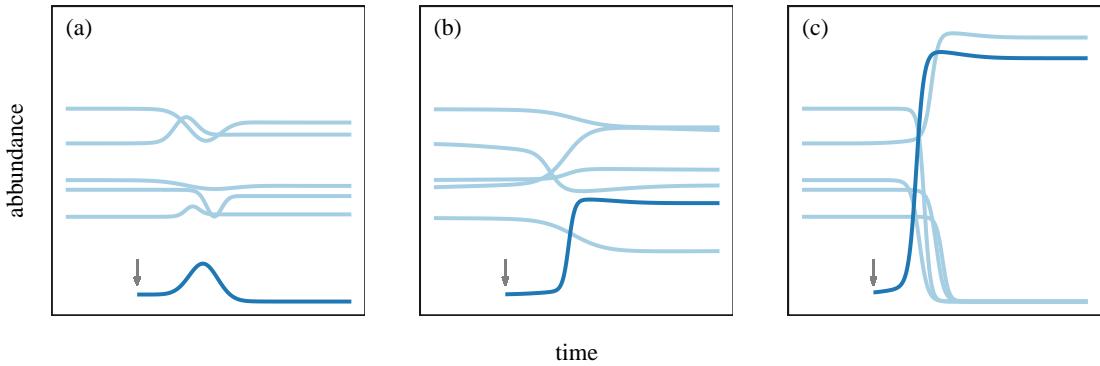


Figure 2: Three possible responses of ecosystems in stable coexistence to the introduction of an alien species (dark blue): (a) the alien species did not succeed to coexist, and caused only minor changes in the abundances of the species already present in the community (light blue); (b) the alien species persisted with the original species; or (c) the alien species became invasive, and four of the original species went extinct.

interactions with other species. In this model, there is competition between species that belong to the same group (plants or pollinators), while facilitation occurs between species that belong to different groups. Specifically I will use a recently introduced logistic model that is mathematically simpler but preserves the dynamic richness of previous models⁵. Like in previous studies using dynamic models^{4,22}, I will assume that the beneficial effect of mutualistic partners saturates at high abundances.

The third step is to analyse the ecosystem response to an alien species. Depending on the network structure, and the traits of the native and alien species, the outcome of an species introduction can vary. One possible outcome option is that alien species is not able to invade the community (Figure 2a). Another possibility is that the alien species becomes an invader, which can, in some instances, have catastrophic consequences for other species in the community (Figure 2b, c). Therefore, I will quantify the invasibility of the community as the likelihood that an invader is successful^{12,40}.

Because a nested structure is thought to maximise the number of species that can stably coexist⁴, I predict that a similar relationship exists between invasibility and nestedness (Figure 3a). Additionally, because a compartmentalised structure might limit the potential for apparent facilitation between the native and invasive species, I argue that there is a negative relationship between invasibility and compartmentalisation (Figure 3b). This hypotheses link concepts of network structure, apparent competition/facilitation and ecosystem stability, and testing them will allow us to put limited and somewhat disparate empirical observations in context.

Despite the general belief that successful invasive species tend to be super-generalists^{7,15,32,34}, a recent meta-analysis has shown that invasive species become very integrated in pollination networks⁶. Specifically, invasive plants seem to interact preferentially with pollinators that are weak contributors to community nestedness, which have been shown to be the less vulnerable to extinction^{6,38}. However, this empirical observation has not yet been explained mechanistically. By testing the hypotheses I propose light be shed on what makes ecosystem vulnerable to invasions. Also, because they deal with fundamental tenets in theoretical ecology, we will also gain a better understanding of the implications of network structure on the persistence of biodiversity, the link

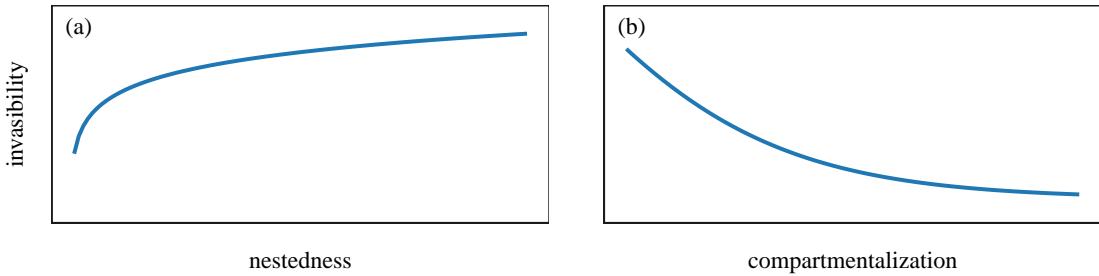


Figure 3: It has been found that (a) an increasingly nested structure enhances the number of species that can stable coexist, while (b) a compartmentalized structure decreases it. I hypothesise that a similar relationship exist between these attributes of network structure and the invasibility of the community.

between stability and biodiversity, and the assembly of ecological communities.

Invasions change the structure of mutualistic networks

After analysing the structures that make an ecological network more or less susceptible to invasions, I will then investigate the consequences for the community when the invasion is successful. On the one hand, I will explore the feedbacks on the structure of mutualistic network after an successful invasion; on the other, I will explore when the invasions lead to a large number of secondary extinctions and ultimately ecosystem collapse (Figure 2c).

Successful invasive species have been shown to have detrimental effects in the native species through changes on pollinator populations and behavior^{34,41–43}. Although they can have facilitative effects by increasing the total visitation rates^{36,42}, they can also have negative effects by decreasing conspecific or increasing heterospecific pollen transfer⁴³. Therefore, changes to the structure of networks are expected.

Although there are few empirical studies that measure the consequences of ecological invasions in network structure, evidence suggest that invasive species have the ability to modify the structure of mutualistic networks. In particular, invaded communities seem to be more nested^{6,33} and less compartmentalised⁷ than their un-invaded counterparts , while also having altered visitation patterns³⁴. Nevertheless, these results are somewhat contradictory⁴⁴, and the limited amount of evidence precludes the generalisation of the patterns observed.

I will use the theoretical results obtained from the population dynamics model to fill the gap on empirical data. Specifically, I will quantify the changes to network structure (nestedness and compartmentalisation) induced by the invasive species, and the contribution to structure of both the invasive species, and the species it interacts with^{6,38}. Therefore, it will be possible to quantify how an initial successful invasion affects the future invasibility of the community. A successful invasion can not only cause changes on network structure, but it can also cause extinction cascades that disrupt mutualisms in the community^{41,45}.

It is also possible to quantify the stability of an ecosystem by measuring the number of species extinctions that follow a successful invasion^{40,46}. Paradoxically, the same structures that I propose

are the most vulnerable to invasions have also been shown to be the most robust to cascading extinctions in ecological networks^{7,23,47}. The research I propose will help disentangle these two seemingly disparate observations.

Objective 2: The effects of structural redundancy on stability

Grouping species by ecological equivalency—such as the way they respond to perturbations, the role they have on ecosystem processes or the structural patterns of their interactions—is a useful device for understanding complexity in ecological systems⁴⁸. One possibility is to group species that have similar roles in ecosystem functioning using traits—morphological, physiological or phenological features that influence individual’s performance^{49–51}. Functional groups (like for example, herbivore grazers in coral reefs, decomposers in a forest, or nitrogen-fixing legumes in agricultural systems) have been widely adopted because of their importance for ecosystem processes and services^{52–54}. However, trait based functional groups are not the only meaningful way to group species. Another possibility is to group species by guilds—based on similarities in the way they exploit environmental resources⁵⁵—or their trophic position⁵⁶.

Ecological interactions are at least partially determined by the traits of the involved species^{57–59}. Moreover, the network of interactions contains substantial information on species niche differentiation (the way species use different resources) and energy pathways in the ecological community⁶⁰. Therefore, grouping species by the structural similarity of their interactions can capture information that is particularly meaningful for the functioning of the community^{24,47}. Structurally, there are also several ways to group species based on their interactions. A global perspective to species grouping separates species by compartments, in which species interact more often with other species in the same compartment than otherwise (Figure 1). Adopting a local perspective, on the other hand, it is possible to group species using “network motifs”^{61–63}, a set of smaller sub-networks which put together can form the original network (Figure 4).

It has been shown that these structural groupings (compartments and motifs) can have important consequences for the stability and persistence of the communities^{24,47,64–66}. In food webs, for example, where most interactions are antagonistic, a high degree of compartmentalisation increases the persistence of the community by buffering the propagation of the effects of species extinctions beyond their compartment⁴⁷. Similarly, a food-web tri-trophic motif^b is more persistent in isolation than an omnivory motif^c. However although less efficient by itself, the omnivory motif increases the persistence of the whole food web by a larger proportion⁶⁶, perhaps because of the redundancy conferred by the omnivorous link. This suggest that regardless of whether the ecological groups are structural or functional redundancy within groups confers an insurance effect to the ecosystem⁶⁷.

Here I propose to explicitly evaluate the effects that structural redundancy has on the stability of ecological networks. Despite the clear positive implications of redundancy in overall stability, from a theoretical point of view it is expected to also have negative effects for individual species because it reduces the niche differentiation with its competitors. Therefore I am interested in

^bA three species food chain with one producer, one consumer and one top predator

^cA three species web with one producer, one consumer and an omnivore that depredate the consumer and the primary producer

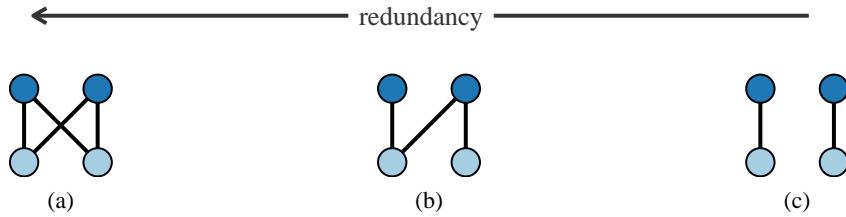


Figure 4: Motifs are sub-networks that represent different patterns of interactions in ecological networks. Motifs can be seen as simple building blocks that show the underlying structure of the community and include different forms redundancy (generalisation/specialisation). The most redundant type of four-species motifs in mutualistic networks is shown on the left and the least redundant on the right.

exploring at the implications that redundancy has on both the conditions for stable coexistence (similar as to the previous section) and on the response of an ecosystem to perturbations. Because there are several ways to quantify the structural redundancy of a species, I aim to identify the type of redundancy that is most relevant to species coexistence and, ultimately, ecosystem collapse.

Several examples outside of ecology highlight the benefits of redundancy on complex systems. In financial markets for example, risk is reduced by investing in a diverse portfolio; even if one or some investments do not generate the expected returns, the risk of possible loss in the total asset value is much smaller than the risk of individual assets. In engineering, the reliability of a system is increased by making components that perform critical functions redundant. Similarly in ecology, redundancy has been proposed to be a key factor contributing to the persistence of the ecosystem^{48,68}, and positive relationship exists between biodiversity and stability^{69–71}.

This “portfolio effect” hypothesis states that aggregated properties of the community (like total biomass or abundances) are less variable than those of independent species when species populations fluctuate asynchronously. There is both theoretical^{71,72} and empirical^{69,73–75} evidence for the insurance outcome of the portfolio effect in ecosystems. Indeed, as mentioned, previous findings in food webs of antagonistic interactions support it.

However, for pollination networks, where interactions are considered to be mutualistic, the effects of structural redundancy have not been thoroughly explored. To date, only one study²⁴ has explicitly looked at the effects of compartmentalisation on the stability of mutualistic networks. Remarkably, contrary to what would be expected in an antagonistic system, some evidence suggest that compartmentalisation decreases both the persistence and resilience of mutualistic networks. This might explain the fact that empirical mutualistic networks are on average less compartmentalised than their antagonistic counterparts²⁴, but it does not explain why a large proportion of observed mutualistic networks are still significantly modular.

Previous theoretical work has largely assumed that the feedbacks of mutualistic interactions increase the growth rates of the focal species, while antagonistic interactions decrease it, which in turns allows the coexistence of a larger number of species (Figure 1)^{4,37}. This assumption, however, ignores that in mutualistic systems, organisms might also compete to optimise the obtained benefits⁷⁶. Indeed, evidence suggests that, in plant-pollinator systems, the increase of mutualistic interactions caused by invasive species does not translate into increased facilitation⁷⁷. Because plant reproduction depends strongly in the quality of the mutualistic service, mutualisms can be

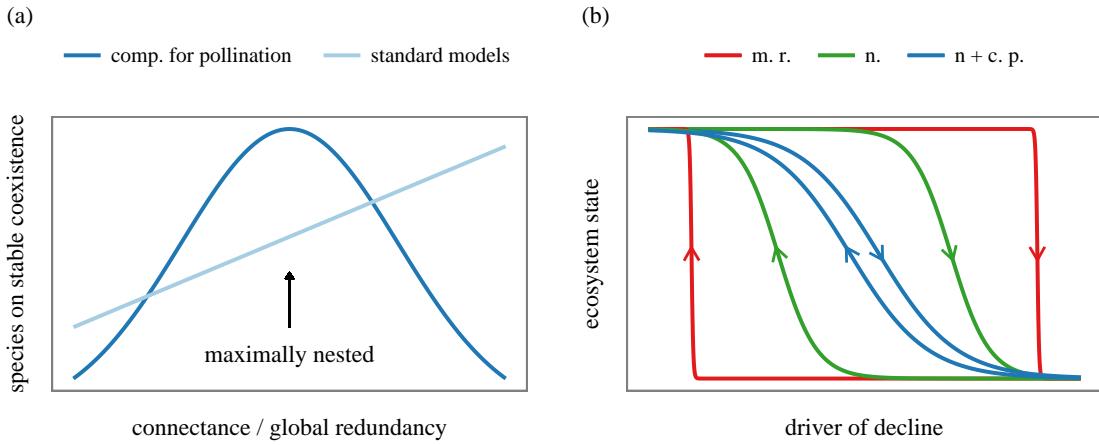


Figure 5: (a) Standard models of mutualism predict a positive relationship between connectance (higher global redundancy) and biodiversity (light blue line), yet this is not observed in empirical communities. I argue that including competition-for-pollination will help explain why this orgy of facilitation is not observed in nature. Also, (b) standard models of pollination have found that the more connected the network (red lines) the more it is resistant to drivers of decline; nested structures (green line) are also able to delay the onset of catastrophic declines more efficiently than random structures with no redundancy, the response to declines when competition for pollination is included (blue line) is however unknown. I predict that because plants that share pollinators are not exclusively facilitating each other, they do not collapse independently. Therefore decline should be more gradual and the hysteresis should be reduced.

strongly altered when co-flowering species compete for the service of shared pollinators^{36,78}. This happens because the visit of some pollinator does not lead to reproduction if pollen is transferred between different species of plants⁷⁹. Even though there are some mechanisms to mitigate the impacts of competition for mutualism and inter-specific pollen transfer^{80–82}, it has been found that invasive species, at high densities, are able to co-opt pollinators from native species⁸³, dominate the networks of pollen transport^{77,84}, and ultimately decrease the seed output of native species⁸⁵.

Standard models of mutualism, which are used in both coexistence and collapse research, have so far only included intra-guild competition (for example competition for resources among plants)^{4,8}. However stability attributes can change drastically if inter-guild interactions are not exclusively facilitative. For instance, if only facilitation is taken into account, a fully connected and maximally redundant structure (Figure 1a, 4a) represents the most favourable conditions for species coexistence⁴, at the same time it successfully delays catastrophic ecosystem collapse⁸. On the other hand, the same structure will be the undesirable if interactions were antagonistic because niche differentiation would be minimal⁶⁶.

Although these standard models have been useful in recognising that, all else being equal, a nested structure is indeed better than a random structure at facilitating biodiversity and delaying the onset of catastrophic collapses^{4,8}, they also predict that a maximally redundant network is better than the nested structure we tend to observe in nature (Figure 5). My hypothesis is that competition for pollinators and its interplay with structural redundancy might be the key for explaining this discrepancy as well as to explain the structural differences between mutualistic and antagonistic networks.

I will use two approaches to evaluate this hypothesis. In the first approach I will make use of motifs as an intuitive local metric of redundancy. In a similar methodology as that used by Stouffer and Bascompte (2010)⁶⁶, I will first evaluate the persistence of individual motifs (Figure 4) with and without competition-for-pollinators when taken in isolation. Then by analysing the frequency at which those motifs are represented in empirical networks, I will quantify their relative contribution to the persistence of the pollination system.

There are several metrics that have been used to assess the structure of functional traits of ecological communities⁵¹. I will use some of those previously developed methods adapt them to quantify the structural redundancy of ecological networks. These include metrics of entropy⁸⁶, specialisation⁸⁷, and originality⁸⁸. In the second approach I will extend the models developed in the previous section to explicitly include competition for pollinators. Then I will construct a large number of synthetic networks of varied structure and numerically determine the relationship between these global metrics of redundancy and the number of coexisting species (Figure 5a). Also, I will explore the consequences that competition-for-pollinators has on delaying the onset of catastrophic collapse (Figure 5b). I predict that the structure of “optimal” networks that include competition-for-pollinators is more consistent with the structure of networks observed in nature. I argue that this empirical structure is the reflection of a balance between the redundancy required to maximise the facilitation effect of shared pollinators and minimise the competitive effects of interspecific pollen transfer.

Summing-up, I expect this research to help clarify the mechanisms that drive the structure of mutualistic networks. While high redundancy might have biodiversity and stability benefits in mutualistic systems, it might also be responsible for the catastrophic collapses that occur once the perturbation has reached critical levels. Ultimately we will be better positioned to understand why high diversity doesn’t necessarily translate in higher redundancy⁸⁹.

Objective 3: Controlling ecosystems for resilience management

Theoretical evidence suggest that ecosystems have stable states on which self-organised processes and structures persist in equilibrium^{40,90}. However, disturbances, when large enough, can cause the ecosystem to move to a critical transition point. When the ecosystem has reached this critical point, it can collapse, or more precisely, it can undergo a regime shift: a large, persistent transformation in ecosystem functioning and structure after which the ecosystem enters an alternate stable state^{90–92} (Figure 6a, 7).

Often, ecosystems enter into these alternate stable states in response to anthropogenic pressures of global change like climate, invasive species, overexploitation or habitat loss (Figure 6b). Unfortunately the frequency of regime shifts is increasing globally, and this trend is likely to continue⁹⁴. Unfortunately, this increase is severely compromising the provision of important ecosystem services we, and other species, strongly depend on⁹⁵. Examples include the diminished production of fish after a food-web or habitat collapse in marine ecosystems^{96–98} or failure of crops after the collapse of pollination services^{8,99}.

Restoration projects that seek to bring back ecosystems to a pre-disturbance state have had limited amount of success¹⁰⁰. Even to restore the community to a more ‘desirable’ state of ecosys-

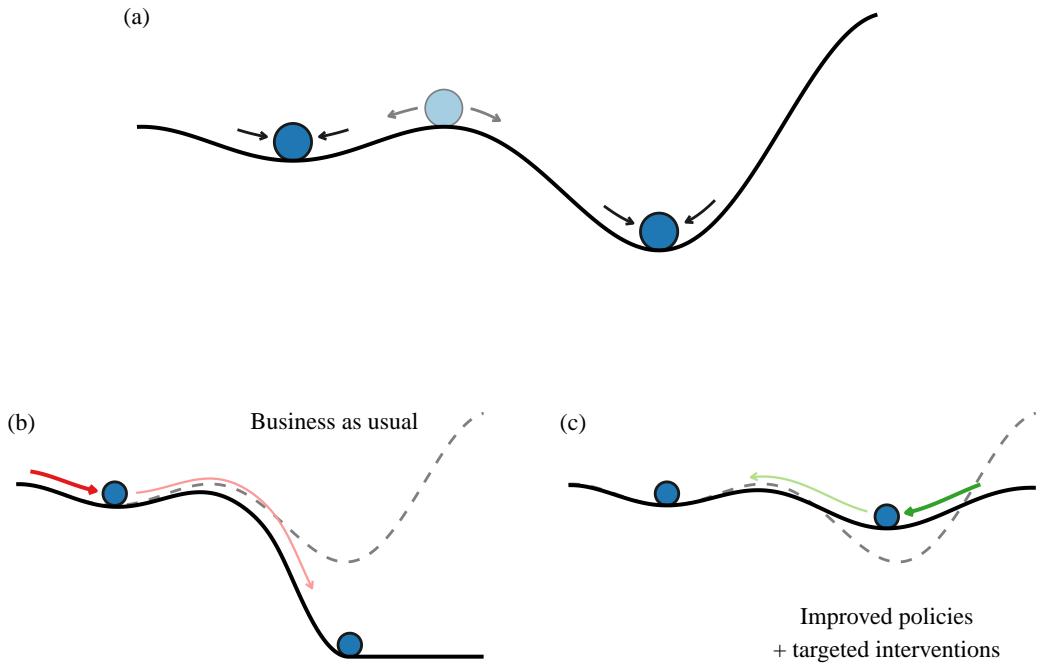


Figure 6: A ball, representing the ecosystem, exists on a surface where any point along the surface represents a possible state⁹³. When the ball is in a valley, or a “domain of attraction”, ecosystems tend to converge into stable states (dark blue circles). (a) After a small disturbance, the ecosystem is likely to return to the original stable state (black arrows) at a rate determined by its resilience (depicted in the figure as the slope of the curve). However, large disturbance (or a combination of smaller ones) can bring the ecosystem into a critical transition point (light blue) from which the ecosystem can undergo a regime shift and enter into an alternate stable state. From a management perspective, under a “business as usual” scenario (b), the resilience of the desired state is diminished and human disturbances (red arrow) can push the ecosystem into an alternate stable state from which recovery is very difficult. By controlling the abundances of a set of key species (c), in theory, it is possible to induce a compensatory perturbation that weakens the resilience of the undesirable alternate stable state, and possibly push the ecosystem into recovery.



(a) Before

(b) After

Figure 7: One example of alternate states in tropical coral reefs, (a) assemblages dominated by corals in the Caribbean in 1979, and (b) the same reef, degraded and smothered by fleshy seaweed two decades later. By definition, regime shifts among alternate states constitute profound and often sudden changes in species composition, with major economic and social consequences. Reproduced from Hughes et al. 2005⁹⁴.

tem function, in which services are somewhat recovered, is a particularly challenging endeavor¹⁰¹. So far we have only small-scale and localised examples of recovery^{102,103}, and in many cases the ecosystem fails to recover even after the disturbances that caused the regime shift are removed⁹⁴. Moreover, some evidence suggest that recovery is at least partially determined by pre-disturbance structure of the community¹⁰⁴, but we do not understand the mechanisms behind. How to recover ecosystems from these undesirable alternate stable state is currently a major question in conservation and theoretical ecology.

The recovery of any ecosystem depends strongly on the interactions between species in the community and the dynamics that arise from these interactions^{100,105}. Therefore, there have been calls to replace the predominant species-level approaches by ecosystem scale approaches to management and conservation^{106,107}. However, perhaps with the exception of the mitigation of human-caused disturbances, ecosystem wide management can be expensive and difficult to attain^{100,108}. Contrastingly, even though the efficacy of conservation measures directed to individual species can be contested, they are more intuitive, tractable, and usually easier to implement.

Unfortunately, we still do not understand how species-level interventions relate to the stability of the ecosystem as a whole. This is important because it will allow us to determine if current interventions are indeed pushing the ecosystem towards recovery or not. Also, scaling up the perspective from individual species to the ecosystem level, will help to elucidate how to weaken the resilience of undesirable stable states, or strengthen the resilience of desirable states¹⁰¹. What is more, it will also help to determine if ecosystem recovery to a pre-disturbance state is even possible and feasible from a management perspective¹⁰⁶. Here, I propose to go one step further, and study the controllability of ecological networks and what network structures best support restoration efforts.

Ecosystems are challenging to “control” because they are large, complex, inhomogeneous, and non-linear systems. However, recent work from theoretical physics has highlighted the possibility of regulating ecological networks by using targeted interventions in just some key species^{9,109}. These species are not necessarily the most or least abundant, or invasive, but rather those that can drive

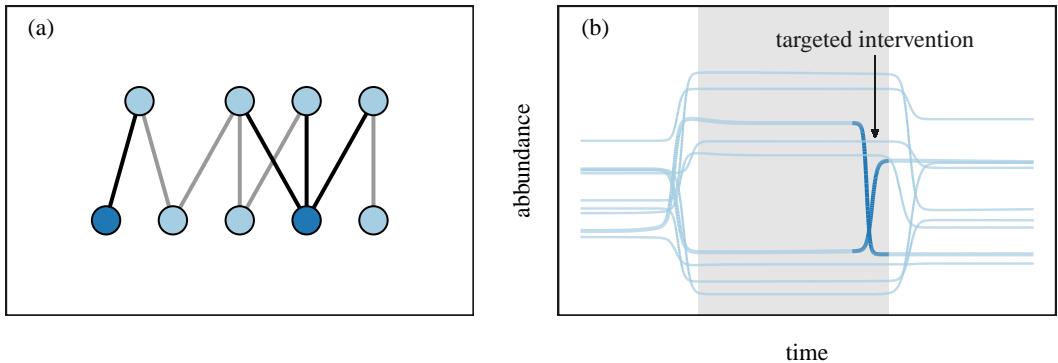


Figure 8: In an ecological network, due to the interactions between species, changes in the abundances of any species are necessarily reflected in the abundances of their direct and indirect partners. (a) It is possible to find a minimal set of species (dark blue), such that the abundances of all other species (light blue) can be modified by interventions on the minimal set. If targeted interventions on those species are feasible (b), it is, in theory, possible to regulate the state of the ecosystem, and therefore reverse a regime shift that has lead an ecosystem into an alternate stable state (shaded area).

the entire ecosystem dynamics¹¹⁰ (Figure 8a). By modifying the abundances of driver species, it is in theory possible to control the state of the ecosystem, and possibly push the ecosystem into a pre-disturbance state or at least a more desirable alternate state of ecosystem function (Figure 6c, 8b).

To achieve that, the first step is to determine the smallest possible set of driver species in which to apply conservation measures that modify their abundance^{109,110}. I will determine these species by using ‘maximally matching’ on the network of interactions—an algorithm that is already commonly used to find minimum sets in diverse areas of graph theory, image processing, and computational chemistry^{111,112}.

By applying this framework to six pairs of invaded and uninvaded pollination networks³³ I will examine the utility of this approach in a real world scenario. Specifically I will explore the characteristics that make species (such as the degree of generalisation or its contribution to nestedness) more or less likely to function as a driver of ecosystem state, and whether these characteristics depend on the presence of an invasive species in the ecosystem.

The second step is to determine which interventions on the driver species are necessary to guide the ecosystem to the desired state. Here, I will use the subset of the population dynamics models developed for the previous research objectives that show multiple alternate stable states. I will then employ a recently developed algorithm that accounts for the non-linear dynamics present in ecological community^{9,113} to find the interventions that are necessary to modify ecosystem state.

However not all interventions are feasible; in reality, they are severely constrained by costs and scale. For example, the an intuitive intervention to restore a coral reef from an algal dominated stable state (Figure 7b) to a coral dominated stable state (Figure 7a) is to simply decrease the abundance of fleshy seaweed and increase the abundance of stony corals. This however is totally impractical; other interventions, for example those focused on species that consume herbivore fishes, are more practical and might lead to similar results¹¹⁴. Therefore, I will focus on the feasible (reasonable from an ecological and management perspective) interventions that allow to

modify the state of an ecosystem even when that state is not directly accessible, or possibly to weaken the resilience of the undesirable state^{101,115,116}.

Nevertheless, I anticipate to find empirical and simulated ecological communities in which none of the feasible interventions can lead to recovery to the original state. In these cases, I will focus on exploring the implications of accepting a ‘novel ecosystem’¹¹⁷. The concept of novel ecosystems highlights the possibility of an intermediate state, different from the original state, but one in which some ecosystem function and services have been restored^{118,119}. As pristine environments become less and less common, restoring some altered ecosystems back seems unrealistic under escalating anthropogenic pressures¹¹⁹. Therefore, I will find the interventions that maximise one ecosystem service, like pollination, while maintaining novel components in the ecosystem like invasive species. Embracing change will “allow conservation and management efforts to be directed more appropriately towards goals that are achievable”¹¹⁸.

Progress

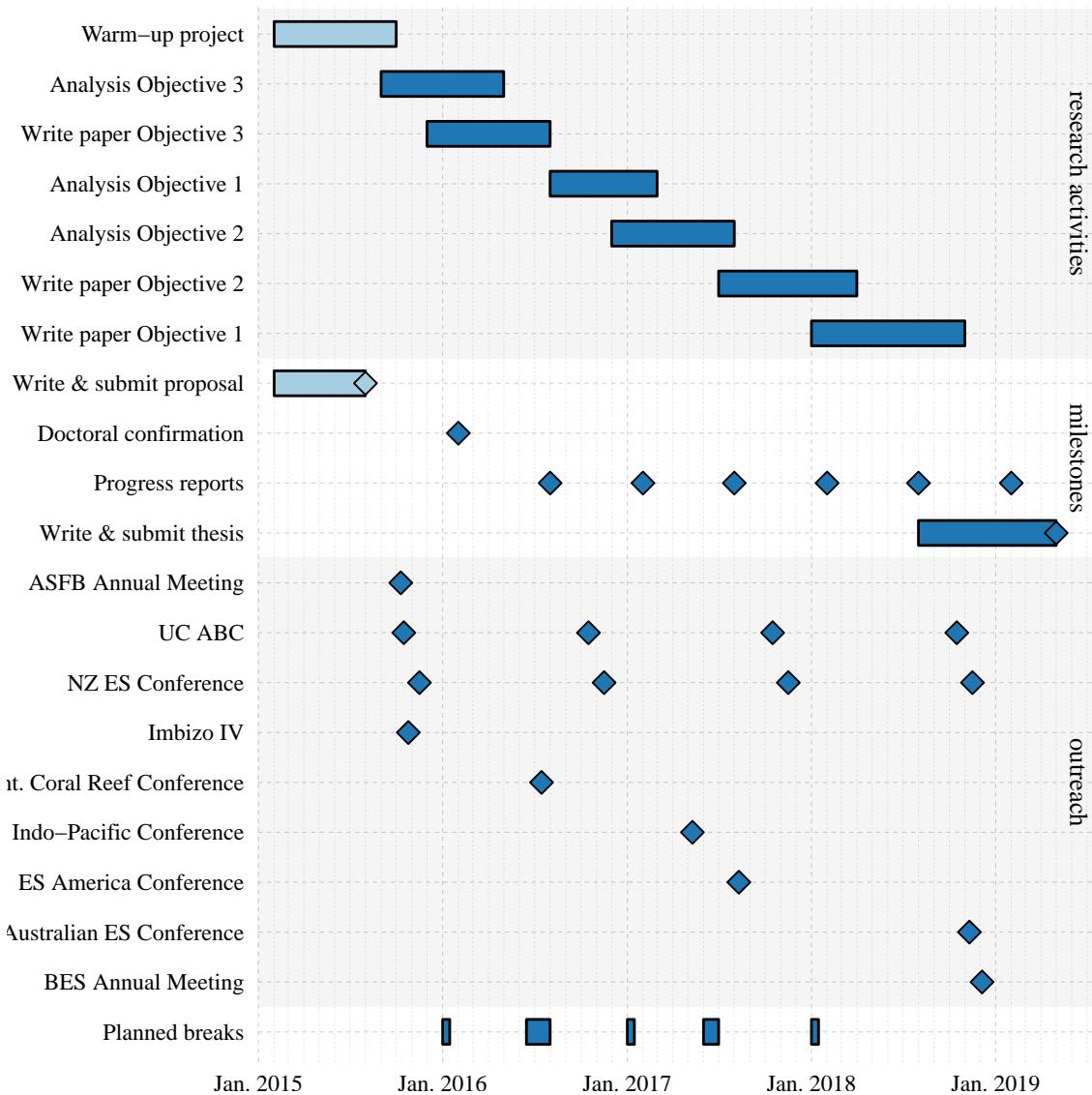
As specified on the PhD proposal schedule, I have started by the third objective of my thesis. Below I describe specific milestones completed or in progress.

- Objective 3: Controlling ecosystems for resilience management
 - Objective 3.1. Determine the set of driver species: To date I have analysed previously published data, and obtained preliminary results. The paper writing is underway, and a preliminary draft has been attached to this report.
 - Objective 3.2. Determine which interventions on the driver species are necessary to guide the ecosystem to the desired state: Ecosystem models are being currently developed by Jenny Shang, an intern under the University of Canterbury Summer Research Scholarship Programme. Results for this component are expected by mid February.
- Warm-up project: Coevolution and modularity in pollination networks
 - The warm-up project was an exploratory piece of research related to the evolution of ecological networks. The work was collaboratively developed with Matt Hutchinson, who initiated the project under the University of Canterbury Summer Research Scholarship Programme in Summer 2014-2015. A manuscript, which is currently under review on *Proceedings of the Royal Society B*, has been attached to this report. Evolution was eventually replaced by resilience as the major topic of my research, and therefore the warm-up project was not included as part of the proposed PhD thesis. However I report it here as well, because it represents a substantial research contribution and a considerable portion of the PhD scheduled time.

Research Plan

So far dates estimated in the proposal research plan have been met. However there are changes in the future milestones as I have been awarded funding to continue the PhD until May 2019. This extra time will be used to deepen the research output in each of the chapters and possibly more freedom to pursue side-projects.

Schedule:



References

- (1) Bascompte, J., Jordano, P., and Olesen, J. M. (2006). Asymmetric Coevolutionary Networks Facilitate Biodiversity Maintenance. *Science* 312, 431–433, DOI: [10.1126/science.1123412](https://doi.org/10.1126/science.1123412).
- (2) Bascompte, J., and Jordano, P. (2007). Plant-Animal Mutualistic Networks: The Architecture of Biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 38, 567–593, DOI: [10.1146/annurev.ecolsys.38.091206.095818](https://doi.org/10.1146/annurev.ecolsys.38.091206.095818).
- (3) Klein, A. M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., and Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B* 274, 303–313, DOI: [10.1098/rspb.2006.3721](https://doi.org/10.1098/rspb.2006.3721).
- (4) Bastolla, U., Fortuna, M. A., Pascual-García, A., Ferrera, A., Luque, B., and Bascompte, J. (2009). The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature* 458, 1018–1020, DOI: [10.1038/nature07950](https://doi.org/10.1038/nature07950).
- (5) Garcia-Algarra, J., Galeano, J., Pastor, J. M., Iriondo, J. M., and Ramasco, J. J. (2013). Rethinking the logistic approach for population dynamics of mutualistic interactions. *Journal of Theoretical Biology* 363, 332–343, DOI: [10.1016/j.jtbi.2014.08.039](https://doi.org/10.1016/j.jtbi.2014.08.039).
- (6) Stouffer, D. B., Cirtwill, A. R., and Bascompte, J. (2014). How exotic plants integrate into pollination networks. *Journal of Ecology* 102, 1442–1450, DOI: [10.1111/1365-2745.12310](https://doi.org/10.1111/1365-2745.12310).
- (7) Albrecht, M., Padrón, B., Bartomeus, I., and Traveset, A. (2014). Consequences of plant invasions on compartmentalization and species' roles in plant-pollinator networks. *Philosophical Transactions of the Royal Society B: Biological Sciences* 381, 20140773, DOI: [10.1098/rspb.2014.0773](https://doi.org/10.1098/rspb.2014.0773).
- (8) Lever, J. J., van Nes, E. H., Scheffer, M., and Bascompte, J. (2014). The sudden collapse of pollinator communities. *Ecology Letters* 17, 350–359, DOI: [10.1111/ele.12236](https://doi.org/10.1111/ele.12236).
- (9) Cornelius, S. P., Kath, W. L., and Motter, A. E. (2013). Realistic control of network dynamics. *Nature Communications* 4, 1942, DOI: [10.1038/ncomms2939](https://doi.org/10.1038/ncomms2939).
- (10) Lövei, G. L. (1997). Global change through invasion. *Nature* 388, 627–628.
- (11) Ehrenfeld, J. G. (2010). Ecosystem Consequences of Biological Invasions. *Annual Review of Ecology, Evolution, and Systematics* 41, 59–80, DOI: [10.1146/annurev-ecolsys-102209-144650](https://doi.org/10.1146/annurev-ecolsys-102209-144650).
- (12) Romanuk, T. N., Zhou, Y., Brose, U., Berlow, E. L., Williams, R. J., and Martinez, N. D. (2009). Predicting invasion success in complex ecological networks. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364, 1743–1754, DOI: [10.1098/rstb.2008.0286](https://doi.org/10.1098/rstb.2008.0286).
- (13) Powell, K. I., Chase, J. M., and Knight, T. M. (2011). A synthesis of plant invasion effects on biodiversity across spatial scales. *American Journal of Botany* 98, 539–548, DOI: [10.3732/ajb.1000402](https://doi.org/10.3732/ajb.1000402).
- (14) Simberloff, D., Simberloff, D., Holle, B. V., and Holle, B. V. (1999). Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions*, 21–32, DOI: [10.1023/a:1010086329619](https://doi.org/10.1023/a:1010086329619).
- (15) Richardson, D. M., Allsopp, N., D'Antonio, C. M., Milton, S. J., and Rejmánek, M. (2000). Plant invasions—the role of mutualisms. *Biological reviews of the Cambridge Philosophical Society* 75, 65–93, DOI: [10.1111/j.1469-185X.1999.tb00041.x](https://doi.org/10.1111/j.1469-185X.1999.tb00041.x).
- (16) Strayer, D. L. (2012). Eight questions about invasions and ecosystem functioning. *Ecology Letters* 15, 1199–1210, DOI: [10.1111/j.1461-0248.2012.01817.x](https://doi.org/10.1111/j.1461-0248.2012.01817.x).
- (17) Thomsen, M. S., Byers, J. E., Schiel, D. R., Bruno, J. F., Olden, J. D., Wernberg, T., and Silliman, B. R. (2014). Impacts of marine invaders on biodiversity depend on trophic position and functional similarity. *Marine Ecology Progress Series* 495, 39–47, DOI: [10.3354/meps10566](https://doi.org/10.3354/meps10566).
- (18) Galiana, N., Lurgi, M., Montoya, J. M., and López, B. C. (2014). Invasions cause biodiversity loss and community simplification in vertebrate food webs. *Oikos* 123, 721–728, DOI: [10.1111/j.1600-0706.2013.00859.x](https://doi.org/10.1111/j.1600-0706.2013.00859.x).
- (19) Simberloff, D. (2006). Invasional meltdown 6 years later: Important phenomenon, unfortunate metaphor, or both? *Ecology Letters* 9, 912–919, DOI: [10.1111/j.1461-0248.2006.00939.x](https://doi.org/10.1111/j.1461-0248.2006.00939.x).

- (20) Prior, K. M., Robinson, J. M., Meadley Dunphy, S. A., and Frederickson, M. E. (2014). Mutualism between co-introduced species facilitates invasion and alters plant community structure. *Proceedings of the Royal Society B* 282, 20142846, DOI: [10.1098/rspb.2014.2846](https://doi.org/10.1098/rspb.2014.2846).
- (21) Rooney, N., McCann, K., Gellner, G., and Moore, J. C. (2006). Structural asymmetry and the stability of diverse food webs. *Nature* 442, 265–269, DOI: [10.1038/nature04887](https://doi.org/10.1038/nature04887).
- (22) Okuyama, T., and Holland, J. N. (2008). Network structural properties mediate the stability of mutualistic communities. *Ecology Letters* 11, 208–216, DOI: [10.1111/j.1461-0248.2007.01137.x](https://doi.org/10.1111/j.1461-0248.2007.01137.x).
- (23) Tylianakis, J. M., Laliberté, E., Nielsen, A., and Bascompte, J. (2010). Conservation of species interaction networks. *Biological Conservation* 143, 2270–2279, DOI: [10.1016/j.biocon.2009.12.004](https://doi.org/10.1016/j.biocon.2009.12.004).
- (24) Thébault, E., and Fontaine, C. (2010). Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* 329, 853–856, DOI: [10.1126/science.1188321](https://doi.org/10.1126/science.1188321).
- (25) Rohr, R. P., Saavedra, S., and Bascompte, J. (2014). On the structural stability of mutualistic systems. *Science* 345, 1253497, DOI: [10.1126/science.1253497](https://doi.org/10.1126/science.1253497).
- (26) Sauve, A. M. C., Fontaine, C., and Thébault, E. (2014). Structure-stability relationships in networks combining mutualistic and antagonistic interactions. *Oikos* 123, 378–384, DOI: [10.1111/j.1600-0706.2013.00743.x](https://doi.org/10.1111/j.1600-0706.2013.00743.x).
- (27) Burkle, L. A., Marlin, J. C., and Knight, T. M. (2013). Plant-pollinator interactions over 120 years: loss of species, co-occurrence, and function. *Science* 339, 1611–5, DOI: [10.1126/science.1232728](https://doi.org/10.1126/science.1232728).
- (28) Tylianakis, J. M., Didham, R. K., Bascompte, J., and Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11, 1351–1363, DOI: [10.1111/j.1461-0248.2008.01250.x](https://doi.org/10.1111/j.1461-0248.2008.01250.x).
- (29) Memmott, J., Craze, P. G., Waser, N. M., and Price, M. V. (2007). Global warming and the disruption of plant-pollinator interactions. *Ecology Letters* 10, 710–717, DOI: [10.1111/j.1461-0248.2007.01061.x](https://doi.org/10.1111/j.1461-0248.2007.01061.x).
- (30) Hegland, S. J., Nielsen, A., Lázaro, A., Bjerknes, A. L., and Totland, O. (2009). How does climate warming affect plant-pollinator interactions? *Ecology Letters* 12, 184–195, DOI: [10.1111/j.1461-0248.2008.01269.x](https://doi.org/10.1111/j.1461-0248.2008.01269.x).
- (31) Olesen, J. M., Eskildsen, L. I., and Venkatasamy, S. (2002). Invasion of pollination networks on oceanic islands: Importance of invader complexes and endemic super generalists. *Diversity and Distributions* 8, 181–192, DOI: [10.1046/j.1472-4642.2002.00148.x](https://doi.org/10.1046/j.1472-4642.2002.00148.x).
- (32) Aizen, M. A., Morales, C. L., and Morales, J. M. (2008). Invasive mutualists erode native pollination webs. *PLoS Biology* 6, 0396–0403, DOI: [10.1371/journal.pbio.0060031](https://doi.org/10.1371/journal.pbio.0060031).
- (33) Bartomeus, I., Vilà, M., and Santamaría, L. (2008). Contrasting effects of invasive plants in plant-pollinator networks. *Oecologia* 155, 761–770, DOI: [10.1007/s00442-007-0946-1](https://doi.org/10.1007/s00442-007-0946-1).
- (34) Vilà, M., Bartomeus, I., Dietzsch, A. C., Petanidou, T., Steffan-Dewenter, I., Stout, J. C., and Tscheulin, T. (2009). Invasive plant integration into native plant-pollinator networks across Europe. *Proceedings of the Royal Society B* 276, 3887–3893, DOI: [10.1098/rspb.2009.1076](https://doi.org/10.1098/rspb.2009.1076).
- (35) Traveset, A., Heleno, R., Chamorro, S., Vargas, P., McMullen, C. K., Nogales, M., Herrera, H. W., Olesen, J. M., and McMullen, K. (2013). Invaders of pollination networks in the Galápagos Islands : emergence of novel communities. *Proceedings of the Royal Society B* 280, 20123040, DOI: [10.1098/rspb.2012.3040](https://doi.org/10.1098/rspb.2012.3040).
- (36) Sargent, R. D., and Ackerly, D. D. (2008). Plant-pollinator interactions and the assembly of plant communities. *Trends in Ecology & Evolution* 23, 123–130, DOI: [10.1016/j.tree.2007.11.003](https://doi.org/10.1016/j.tree.2007.11.003).
- (37) Moeller, D. A. (2004). Facilitative interactions among plants via shared pollinators. *Ecology* 85, 3289–3301, DOI: [10.1890/03-0810](https://doi.org/10.1890/03-0810).
- (38) Saavedra, S., Stouffer, D. B., Uzzi, B., and Bascompte, J. (2011). Strong contributors to network persistence are the most vulnerable to extinction. *Nature* 478, 233–235, DOI: [10.1038/nature10433](https://doi.org/10.1038/nature10433).
- (39) Baiser, B., Russell, G. J., and Lockwood, J. L. (2010). Connectance determines invasion success via trophic interactions in model food webs. *Oikos* 119, 1970–1976, DOI: [10.1111/j.1600-0706.2010.18557.x](https://doi.org/10.1111/j.1600-0706.2010.18557.x).
- (40) Ives, A. R., and Carpenter, S. R. (2007). Stability and diversity of ecosystems. *Science* 317, 58–62, DOI: [10.1126/science.1133258](https://doi.org/10.1126/science.1133258).
- (41) Christian, C. E. (2001). Consequences of a biological invasion reveal the importance of mutualism for plant communities. *Nature* 413, 635–639, DOI: [10.1038/35098093](https://doi.org/10.1038/35098093).

- (42) Bjerknes, A. L., Totland, O., Hegland, S. J., and Nielsen, A. (2007). Do alien plant invasions really affect pollination success in native plant species? *Biological Conservation* 138, 1–12, DOI: [10.1016/j.biocon.2007.04.015](https://doi.org/10.1016/j.biocon.2007.04.015).
- (43) Morales, C. L., and Traveset, A. (2009). A meta-analysis of impacts of alien vs. native plants on pollinator visitation and reproductive success of co-flowering native plants. *Ecology Letters* 12, 716–728, DOI: [10.1111/j.1461-0248.2009.01319.x](https://doi.org/10.1111/j.1461-0248.2009.01319.x).
- (44) Gilberto, G. M., Aguiar, C. M. L., Genini, J., Martins, C. F., Zanella, F. C. V., and Mello, M. A. R. (2012). Invasive Africanized honeybees change the structure of native pollination networks in Brazil. *Biological Invasions* 14, 2369–2378, DOI: [10.1007/s10530-012-0235-8](https://doi.org/10.1007/s10530-012-0235-8).
- (45) Rodriguez-Cabal, M. A., Barrios-Garcia, M. N., Amico, G. C., Aizen, M. A., and Sanders, N. J. (2013). Node-by-node disassembly of a mutualistic interaction web driven by species introductions. *Proceedings of the National Academy of Sciences of the United States of America* 110, 16503–7, DOI: [10.1073/pnas.1300131110](https://doi.org/10.1073/pnas.1300131110).
- (46) Post, W., and Pimm, S. (1983). Community assembly and food web stability. *Mathematical Biosciences* 64, 169–192, DOI: [10.1016/0025-5564\(83\)90002-0](https://doi.org/10.1016/0025-5564(83)90002-0).
- (47) Stouffer, D. B., and Bascompte, J. (Mar. 2011). Compartmentalization increases food-web persistence. *Proceedings of the National Academy of Sciences of the United States of America* 108, 3648–52, DOI: [10.1073/pnas.1014353108](https://doi.org/10.1073/pnas.1014353108).
- (48) Naeem, S. (1998). Species redundancy and ecosystem reliability. *Conservation Biology* 12, 39–45, DOI: [10.1046/j.1523-1739.1998.96379.x](https://doi.org/10.1046/j.1523-1739.1998.96379.x).
- (49) Raunkiaer, C., *Life forms of plants and statistical plant geography*; Clarendon Press: Oxford, 1934, pp 379–424.
- (50) Fonseca, C. R., and Ganade, G. (2001). Species functional redundancy, random extinctions and the stability of ecosystems. *Journal of Ecology* 89, 118–125, DOI: [10.1046/j.1365-2745.2001.00528.x](https://doi.org/10.1046/j.1365-2745.2001.00528.x).
- (51) Mouillot, D., Graham, N. A. J., Villeger, S., Mason, N. W. H., and Bellwood, D. R. (2013). A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution* 28, 167–177, DOI: [10.1016/j.tree.2012.10.004](https://doi.org/10.1016/j.tree.2012.10.004).
- (52) Díaz, S., and Cabido, M. (2001). Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution* 16, 646–655, DOI: [10.1016/S0169-5347\(01\)02283-2](https://doi.org/10.1016/S0169-5347(01)02283-2).
- (53) Tilman, D., Reich, P. B., Knops, J., Wedin, D., Mielke, T., and Lehman, C. (2001). Diversity and productivity in a long-term grassland experiment. *Science* 294, 843–845, DOI: [10.1126/science.1060391](https://doi.org/10.1126/science.1060391).
- (54) Wardle, D. A., and Zackrisson, O. (2005). Effects of species and functional group loss on island ecosystem properties. *Nature* 435, 806–810, DOI: [10.1038/nature03611](https://doi.org/10.1038/nature03611).
- (55) Root, R. B. (Jan. 1967). The Niche Exploitation Pattern of the Blue-Gray Gnatcatcher. *Ecological Monographs* 37, 317, DOI: [10.2307/1942327](https://doi.org/10.2307/1942327).
- (56) Hairston, N. G., Smith, F. E., and Slobodkin, L. B. (1960). Community Structure, Population Control, and Competition. *The American naturalist* 94, 421–425.
- (57) Cohen, J. E., Pimm, S. L., Yodzis, P., and Saldaña, J. (1993). Body Sizes of Animal Predators and Animal Prey in Food Webs. *Journal of Animal Ecology* 62, 67–78, DOI: [10.2307/5483](https://doi.org/10.2307/5483).
- (58) Stang, M., Klinkhamer, P. G., Waser, N. M., Stang, I., and van der Meijden, E. (2009). Size-specific interaction patterns and size matching in a plant-pollinator interaction web. *Annals of botany* 103, 1459–1469, DOI: [10.1093/aob/mcp027](https://doi.org/10.1093/aob/mcp027).
- (59) Edwards, K. F., Klausmeier, C. A., and Litchman, E. (2011). Evidence for a three-way trade-off between nitrogen and phosphorus competitive abilities and cell size in phytoplankton. *Ecology* 92, 2085–2095, DOI: [10.1890/11-0395.1](https://doi.org/10.1890/11-0395.1).
- (60) Gauzens, B., Thébault, E., Lacroix, G., and Legendre, S. (2014). Trophic groups and modules: two levels of group detection in food webs. *Journal of The Royal Society Interface* 12, 20141176, DOI: [10.1098/rsif.2014.1176](https://doi.org/10.1098/rsif.2014.1176).
- (61) Holt, R. D., and Hochberg, M. E. In *Evaluating Indirect Ecological Effects of Biological Control*, Wajnberg, E., Scott, J. K., and Quimby, P. C., Eds.; CABI: 2001; Chapter 2, pp 13–37.

- (62) Milo, R. (2002). Network Motifs: Simple Building Blocks of Complex Networks. *Science* 298, 824–827, DOI: [10.1126/science.298.5594.824](https://doi.org/10.1126/science.298.5594.824).
- (63) Stouffer, D. B., Camacho, J., Jiang, W., and Amaral, L. A. N. (2007). Evidence for the existence of a robust pattern of prey selection in food webs. *Proceedings. Biological sciences / The Royal Society* 274, 1931–1940, DOI: [10.1098/rspb.2007.0571](https://doi.org/10.1098/rspb.2007.0571).
- (64) Neutel, A.-M., Heesterbeek, J. A. P., and De Ruiter, P. C. (2002). Stability in real food webs: weak links in long loops. *Science* 296, 1120–1123, DOI: [10.1126/science.1068326](https://doi.org/10.1126/science.1068326).
- (65) Kondoh, M. (2008). Building trophic modules into a persistent food web. *Proceedings of the National Academy of Sciences of the United States of America* 105, 16631–16635, DOI: [10.1073/pnas.0805870105](https://doi.org/10.1073/pnas.0805870105).
- (66) Stouffer, D. B., and Bascompte, J. (Feb. 2010). Understanding food-web persistence from local to global scales. *Ecology Letters* 13, 154–61, DOI: [10.1111/j.1461-0248.2009.01407.x](https://doi.org/10.1111/j.1461-0248.2009.01407.x).
- (67) Walker, B. H. (Mar. 1992). Biodiversity and Ecological Redundancy. *Conservation Biology* 6, 18–23, DOI: [10.1046/j.1523-1739.1992.610018.x](https://doi.org/10.1046/j.1523-1739.1992.610018.x).
- (68) Naeem, S., and Li, S. (1997). Biodiversity enhances ecosystem reliability. *Nature* 390, 507–509, DOI: [10.1038/37348](https://doi.org/10.1038/37348).
- (69) Tilman, D. (1996). Biodiversity: population versus ecosystem stability. *Ecology* 77, 350–363, DOI: [10.2307/2265614](https://doi.org/10.2307/2265614).
- (70) Doak, D. F., Bigger, D., Harding, E. K., Marvier, M. A., O’Malley, R. E., and Thomson, D. (1998). The statistical inevitability of stability-diversity relationships in community ecology. *The American naturalist* 151, 264–276, DOI: [10.1086/286117](https://doi.org/10.1086/286117).
- (71) Tilman, D., Lehman, C. L., and Bristow, C. E. (1998). Diversity-stability relationships: statistical inevitability or ecological consequence? *The American naturalist* 151, 277–282, DOI: [10.1086/286118](https://doi.org/10.1086/286118).
- (72) Yachi, S., and Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences of the United States of America* 96, 1463–1468, DOI: [10.1073/pnas.96.4.1463](https://doi.org/10.1073/pnas.96.4.1463).
- (73) Tilman, D., Reich, P. B., and Knops, J. M. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* 441, 629–632, DOI: [10.1038/nature04742](https://doi.org/10.1038/nature04742).
- (74) Valone, T. J., and Barber, N. A. (2008). An empirical evaluation of the insurance hypothesis in diversity-stability models. *Ecology* 89, 522–531, DOI: [10.1890/07-0153.1](https://doi.org/10.1890/07-0153.1).
- (75) Hector, A. et al. (2010). General stabilizing effects of plant diversity on grassland productivity through population asynchrony and overyielding. *Ecology* 91, 2213–2220, DOI: [10.1890/09-1162.1](https://doi.org/10.1890/09-1162.1).
- (76) Levin, D. A., and Anderson, W. W. (1970). Competition for Pollinators between Simultaneously Flowering Species. *The American Naturalist* 104, 455–467.
- (77) Lopezaraiza-Mikel, M. E., Hayes, R. B., Whalley, M. R., and Memmott, J. (2007). The impact of an alien plant on a native plant-pollinator network: An experimental approach. *Ecology Letters* 10, 539–550, DOI: [10.1111/j.1461-0248.2007.01055.x](https://doi.org/10.1111/j.1461-0248.2007.01055.x).
- (78) Mitchell, R. J., Flanagan, R. J., Brown, B. J., Waser, N. M., and Karron, J. D. (2009). New frontiers in competition for pollination. *Annals of botany* 103, 1403–1413, DOI: [10.1093/aob/mcp062](https://doi.org/10.1093/aob/mcp062).
- (79) Morales, C. L., and Traveset, A. (2008). Interspecific Pollen Transfer: Magnitude, Prevalence and Consequences for Plant Fitness. *Critical Reviews in Plant Sciences* 27, 221–238, DOI: [10.1080/07352680802205631](https://doi.org/10.1080/07352680802205631).
- (80) Waser, N. M., and Real, L. A. (1979). Effective mutualism between sequentially flowering plant species. *Nature* 281, 670–672, DOI: [10.1038/281670a0](https://doi.org/10.1038/281670a0).
- (81) Ghazoul, J. (2006). Floral diversity and the facilitation of pollination. *Journal of Ecology* 94, 295–304, DOI: [10.1111/j.1365-2745.2006.01098.x](https://doi.org/10.1111/j.1365-2745.2006.01098.x).
- (82) Bartomeus, I., Bosch, J., and Vilà, M. (2008). High invasive pollen transfer, yet low deposition on native stigmas in a Carpobrotus-invaded community. *Annals of Botany* 102, 417–424, DOI: [10.1093/aob/mcn109](https://doi.org/10.1093/aob/mcn109).
- (83) Pyšek, P., Chytrý, J., Milan, V., Danihelka, J., Kühn, I., Pergl, J., Tichý, L., Biesmeijer, J. C., Ellis, W. N., Kunin, W. E., and Settele, J. (2011). Successful invaders co-opt pollinators of native flora and accumulate insect pollinators with increasing residence time. *Ecological Monographs* 81, 277–293, DOI: [10.1890/10-0630.1](https://doi.org/10.1890/10-0630.1).

- (84) Alarcón, R. (2010). Congruence between visitation and pollen-transport networks in a California plant-pollinator community. *Oikos* 119, 35–44, DOI: [10.1111/j.1600-0706.2009.17694.x](https://doi.org/10.1111/j.1600-0706.2009.17694.x).
- (85) Muñoz, A. A., and Cavieres, L. A. (2008). The presence of a showy invasive plant disrupts pollinator service and reproductive output in native alpine species only at high densities. *Journal of Ecology* 96, 459–467, DOI: [10.1111/j.1365-2745.2008.01361.x](https://doi.org/10.1111/j.1365-2745.2008.01361.x).
- (86) Mokany, K., Ash, J., and Roxburgh, S. (2008). Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. *Journal of Ecology* 96, 884–893, DOI: [10.1111/j.1365-2745.2008.01395.x](https://doi.org/10.1111/j.1365-2745.2008.01395.x).
- (87) Villéger, S., Ramos Miranda, J., Flores Hernández, D., and Mouillot, D. (2010). Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecological applications : a publication of the Ecological Society of America* 20, 1512–1522, DOI: [10.1890/09-1310.1](https://doi.org/10.1890/09-1310.1).
- (88) Mouillot, D., Culoli, J. M., Pelletier, D., and Tomasini, J. A. (2008). Do we protect biological originality in protected areas? A new index and an application to the Bonifacio Strait Natural Reserve. *Biological Conservation* 141, 1569–1580, DOI: [10.1016/j.biocon.2008.04.002](https://doi.org/10.1016/j.biocon.2008.04.002).
- (89) Bellwood, D. R., Hoey, A. S., and Howard Choat, J. (2003). Limited functional redundancy in high diversity systems: resilience and ecosystem function of coral reefs. *Ecology Letters* 6, 281–285.
- (90) Gunderson, L. H. (2000). Ecological resilience - in theory and application. *Annual Review of Ecology and Systematics* 31, 425–439, DOI: [10.1146/annurev.ecolsys.31.1.425](https://doi.org/10.1146/annurev.ecolsys.31.1.425).
- (91) Holling, C. S. (1973). Resilience and Stability of Ecological Systems. *Annual Review of Ecology and Systematics* 4, 1–23, DOI: [10.1146/annurev.es.04.110173.000245](https://doi.org/10.1146/annurev.es.04.110173.000245).
- (92) May, R. M. (Oct. 1977). Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature* 269, 471–477, DOI: [10.1038/269471a0](https://doi.org/10.1038/269471a0).
- (93) Holling, C. S., Schindler, D. W., Walker, B. W., and Roughgarden, J. In *Biodiversity loss: economic and ecological issues*, Perrings, C., Maler, K.-G., Folke, C., Holling, C. S., and Jansson, B.-O., Eds.; Cambridge University Press: Cambridge, 1995; Chapter 2, pp 44–89, DOI: [10.1017/CBO9781139174329](https://doi.org/10.1017/CBO9781139174329).
- (94) Hughes, T. P., Bellwood, D. R., Folke, C., Steneck, R. S., and Wilson, J. (2005). New paradigms for supporting the resilience of marine ecosystems. *Trends in Ecology & Evolution* 20, DOI: [10.1016/j.tree.2005.03.022](https://doi.org/10.1016/j.tree.2005.03.022).
- (95) Hughes, T., and Carpenter, S. (2013). Multiscale regime shifts and planetary boundaries. *Trends in Ecology & Evolution* 28, 389–396, DOI: [10.1016/j.tree.2013.05.019](https://doi.org/10.1016/j.tree.2013.05.019).
- (96) Hare, S. R., and Mantua, N. J. (2000). Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography* 47, 103–145, DOI: [10.1016/S0079-6611\(00\)00033-1](https://doi.org/10.1016/S0079-6611(00)00033-1).
- (97) Daskalov, G. M., Grishin, A. N., Rodionov, S., and Mihneva, V. (2007). Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. *Proceedings of the National Academy of Sciences of the United States of America* 104, 10518–10523, DOI: [10.1073/pnas.0701100104](https://doi.org/10.1073/pnas.0701100104).
- (98) MacNeil, M. A., Graham, N. A. J., Cinner, J. E., Wilson, S. K., Williams, I. D., Maina, J., Newman, S., Friedlander, A. M., Jupiter, S., Polunin, N. V. C., and McClanahan, T. R. (2015). Recovery potential of the world's coral reef fishes. *Nature*, DOI: [10.1038/nature14358](https://doi.org/10.1038/nature14358).
- (99) Pauw, A. (2007). Collapse of a pollination web in small conservation areas. *Ecology* 88, 1759–1769, DOI: [10.1890/06-1383.1](https://doi.org/10.1890/06-1383.1).
- (100) Suding, K. N., Gross, K. L., and Houseman, G. R. (2004). Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology and Evolution* 19, 46–53, DOI: [10.1016/j.tree.2003.10.005](https://doi.org/10.1016/j.tree.2003.10.005).
- (101) Graham, N. A. J., Bellwood, D. R., Cinner, J. E., Hughes, T. P., Norström, A. V., and Nyström, M. (Dec. 2013). Managing resilience to reverse phase shifts in coral reefs. *Frontiers in Ecology and the Environment* 11, 541–548, DOI: [10.1890/120305](https://doi.org/10.1890/120305).
- (102) Carpenter, R. C., and Edmunds, P. J. (2006). Local and regional scale recovery of Diadema promotes recruitment of scleractinian corals. *Ecology letters* 9, 271–280, DOI: [10.1111/j.1461-0248.2005.00866.x](https://doi.org/10.1111/j.1461-0248.2005.00866.x).
- (103) Stockwell, B., Jadloc, C. R. L., Abesamis, R. A., Alcala, A. C., and Russ, G. R. (2009). Trophic and benthic responses to no-take marine reserve protection in the Philippines. *Marine Ecology Progress Series* 389, 1–15, DOI: [10.3354/meps08150](https://doi.org/10.3354/meps08150).

- (104) Graham, N. A. J., Jennings, S., Macneil, M. A., Mouillot, D., and Wilson, S. K. (2015). Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature* 518, 94–97, DOI: [10.1038/nature14140](https://doi.org/10.1038/nature14140).
- (105) van de Koppel, J., Rietkerk, M., and Weissling, F. J. (1997). Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems. *Trends in ecology & evolution (Personal edition)* 12, 352–356, DOI: [10.1016/S0169-5347\(97\)01133-6](https://doi.org/10.1016/S0169-5347(97)01133-6).
- (106) Suding, K. N., and Hobbs, R. J. (2009). Threshold models in restoration and conservation: a developing framework. *Trends in Ecology and Evolution* 24, 271–279, DOI: [10.1016/j.tree.2008.11.012](https://doi.org/10.1016/j.tree.2008.11.012).
- (107) Sasaki, T., Furukawa, T., Iwasaki, Y., Seto, M., and Mori, A. S. (2015). Perspectives for ecosystem management based on ecosystem resilience and ecological thresholds against multiple and stochastic disturbances. *Ecological Indicators* 57, 395–408, DOI: [10.1016/j.ecolind.2015.05.019](https://doi.org/10.1016/j.ecolind.2015.05.019).
- (108) Browman, H. I., Stergiou, K. I., Browman, C. H. I., Cury, P. M., Hilborn, R., Jennings, S., Lotze, H. K., Mace, P. M., Murawski, S., Pauly, D., Sissenwine, M., and Zeller, D. (2004). Perspectives on ecosystem-based approaches to the management of marine resources. *Marine Ecology Progress Series* 274, 269–303, DOI: [10.3354/meps274269](https://doi.org/10.3354/meps274269).
- (109) Isbell, F., and Loreau, M. (2013). Human impacts on minimum subsets of species critical for maintaining ecosystem structure. *Basic and Applied Ecology* 14, 623–629, DOI: [10.1016/j.baae.2013.09.001](https://doi.org/10.1016/j.baae.2013.09.001).
- (110) Liu, Y.-Y., Slotine, J.-J., and Barabási, A.-L. (2011). Controllability of complex networks. *Nature* 473, 167–173, DOI: [10.1038/nature10011](https://doi.org/10.1038/nature10011).
- (111) Hopcroft, J. E., and Karp, R. M. (Dec. 1973). An $n^{5/2}$ Algorithm for Maximum Matchings in Bipartite Graphs. *SIAM Journal on Computing* 2, 225–231, DOI: [10.1137/0202019](https://doi.org/10.1137/0202019).
- (112) Neumann, F., and Witt, C. In *Bioinspired Computation in Combinatorial Optimization*, 2010, pp 51–74, DOI: [10.1007/978-3-642-16544-3](https://doi.org/10.1007/978-3-642-16544-3).
- (113) Cornelius, S. P., and Motter, A. E. (June 2013). NECO - A scalable algorithm for NEtwork COntrol. *Protocol Exchange*, 1–6, DOI: [10.1038/protex.2013.063](https://doi.org/10.1038/protex.2013.063).
- (114) Bennett, S., Wernberg, T., Harvey, E. S., Santana-Garcon, J., and Saunders, B. J. (2015). Tropical herbivores provide resilience to a climate-mediated phase shift on temperate reefs. *Ecology Letters* 18, 714–723, DOI: [10.1111/ele.12450](https://doi.org/10.1111/ele.12450).
- (115) Standish, R. J., Hobbs, R. J., Mayfield, M. M., Bestelmeyer, B. T., Suding, K. N., Battaglia, L. L., Eviner, V., Hawkes, C. V., Temperton, V. M., Cramer, V. A., Harris, J. A., Funk, J. L., and Thomas, P. A. (2014). Resilience in ecology: abstraction, distraction, or where the action is? *Biological Conservation* 177, 43–51, DOI: [10.1016/j.biocon.2014.06.008](https://doi.org/10.1016/j.biocon.2014.06.008).
- (116) Selkoe, K. A. et al. (July 2015). Principles for managing marine ecosystems prone to tipping points. *Ecosystem Health and Sustainability* 1, art17, DOI: [10.1890/EHS14-0024.1](https://doi.org/10.1890/EHS14-0024.1).
- (117) Hobbs, R. J. et al. (2006). Novel ecosystems: Theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography* 15, 1–7, DOI: [10.1111/j.1466-822X.2006.00212.x](https://doi.org/10.1111/j.1466-822X.2006.00212.x).
- (118) Graham, N. A. J., Cinner, J. E., Norström, A. V., and Nyström, M. (Apr. 2014). Coral reefs as novel ecosystems: embracing new futures. *Current Opinion in Environmental Sustainability* 7, 9–14, DOI: [10.1016/j.cosust.2013.11.023](https://doi.org/10.1016/j.cosust.2013.11.023).
- (119) Graham, N. A. J., and Hicks, C. C., *Adaptive Management for Novel Ecosystems*; Allen, C. R., and Garmestani, A. S., Eds.; Springer Netherlands: Dordrecht, 2015; Chapter 8, pp 123–146, DOI: [10.1007/978-94-017-9682-8](https://doi.org/10.1007/978-94-017-9682-8).

Attachment 1

STRUCTURAL CONTROLABILITY OF POLLINATION NETWORKS

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1 Introduction

2 Ecological communities are formed by the interconnection of several species.
3 Therefore, changes in the abundances of one species can potentially alter the
4 abundances of the species they interact with. For instance, in a classic example
5 of ecosystem cascades, a reduction on the abundance of sea otters, an important
6 predator or sea urchins, can drive a dramatic reduction on kelp abundances be-
7 cause the sea urchins that consume kelp are released from predation. It has been
8 long established that some species, like the sea otter, have a disproportionate
9 large effect in their environment relative to their abundance.

10 In several ecosystems the relative importance of species have been identified
11 based on empirical observations of long term dynamics. However, in less stud-
12 ied, highly diverse, or where the "keystone" role is shared by several species, it
13 can be challenging to determine which is the set of species that influence the
14 most the ecosystem dynamics. Alternative approaches that recognize a contin-
15 uum of importance and that are less dependent on empirical observations have
16 also been developed. Some of them are based on metrics that evaluate their
17 position in the food web or on mass balance models of functional groups. Nev-
18 ertheless, these approaches are conceptually limited to trophic interactions and

19 in general ignore the structural mechanisms that allow or prevent the spread of
20 perturbations in the ecosystem.

21 From a systems perspective, perturbations like over-exploitation, eutrophication
22 or global warming are equivalent to management actions like culling,
23 no-take areas or captive rearing in the sense that they have the potential to
24 modify the abundances of one or several species in the ecosystem. Therefore
25 identifying these key species is crucial not only to predict how these perturba-
26 tions will spread through the community but also to guide effective conservation
27 efforts.

28 Recent work on the control of complex systems suggest that in principle it
29 is possible to alter any ecological community's composition, by modifying the
30 abundances of just some key species (Isbell and Loreau 2013; Cornelius, Kath,
31 and Motter 2013). Here, we apply these theories to estimate the controllability
32 of different ecological communities and to find driver species: species, that due
33 to the structural characteristics of their interactions are more likely to drive the
34 dynamics of the community.

35 Invasive species have been shown to have a disproportionate effect on the
36 structure of pollination communities. Influencing for example the strength of
37 species interactions, and the degree of network nestedness and connectivity (Jens
38 M. Olesen, Eskildsen, and Venkatasamy 2002; Aizen, C. L. Morales, and J. M.
39 Morales 2008; Bartomeus, Vilà, and Santamaría 2008; Vilà et al. 2009; Traveset
40 et al. 2013). However whether this influence is translated into a driver role
41 has not been tested. Here we use plant pollinator communities to investigate
42 the number of species that should be managed to control population dynamics
43 of the whole community, the characteristics that determine whether a species
44 should be managed or not and how invasive species fit.

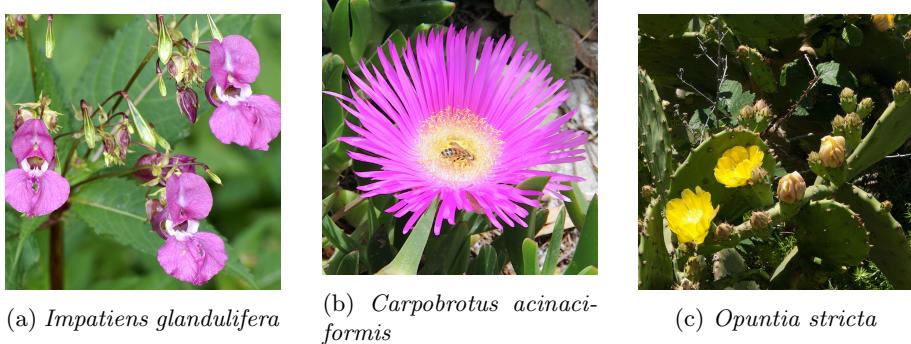


Figure 1: Invasive species present in the studied pollination communities (photographs by Udo Schmidt, Peter Mansfeld, and Tony Rodd).

45 Methods

46 To investigate the dynamic controllability of pollination networks, we used ten
 47 paired plants-pollinator communities. Each pair was composed by a community
 48 invaded by a plant and a community free of the invasive species. Weighted
 49 visitation networks were constructed from previously published visitation data
 50 collected from pollination communities in Bristol, Great Britain (Lopezaraiza-
 51 Mikel et al. 2007) and the National Cap de Creus in Northeastern Spain (Bar-
 52 tomeus, Vilà, and Santamaría 2008). The four British uninvaded communities
 53 the non-invaded plots were obtained by experimentally removing the invasive
 54 species *Impatiens glandulifera* (Figure 1a). Contrastingly, Spanish uninvaded
 55 communities were obtained from plots that were not been colonised by the inva-
 56 sive species *Carpobrotus affine acinaciformis* or *Opuntia stricta* (Figure 1b, c).
 57 In each of the networks we calculated the minimum number of driver species—
 58 species that need to be managed in order to gain full control of the community.

59 We first assigned a direction to each link between plants and pollinators
 60 given by the direction of dependency. For each link between a plant and its
 61 pollinator we quantified the level of dependency of the plant on the pollinator
 62 and vice versa (Bascompte, Jordano, and Jens M Olesen 2006). The link points
 63 to the plant if the its dependency on the pollinator is larger than the pollinator's

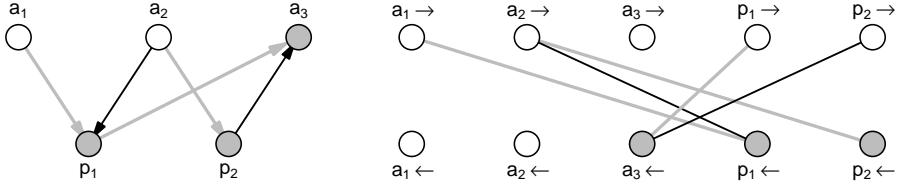


Figure 2: On the left a simple pollination network; the direction of the arrows indicates the direction of the largest dependency between species pairs. On the right the representation of the network used to calculate the maximum matching (in grey). Matched species, i.e. those whose dynamic could be “controlled” by another species are shown in blue. Note that the maximum matching is not necessarily unique.

dependency on the plant. The dependency of plant i on pollinator j is the ratio between the visits coming from pollinator j and all pollinator visits to plant i . The dependency of pollinator j on plant i is the ratio of the visits by pollinator j to plant i and all visits of pollinator j .

In a directed network, a matching is a subset of links in which no two links share a common starting species or a common ending species. A species is matched if it is an ending node of an link in the matching. Otherwise, it is unmatched. It has been shown that the number of driver species can be calculated by counting the number of unmatched nodes in the directed graph representation of the pollination network (Liu, Slotine, and Barabási 2011). We then found a maximum in the an alternative bipartite representation of the pollination network (Csardi and Nepusz 2006) (Figure 2).

We calculated dependencies based on visitation frequency, which has been shown to be an appropriate surrogate of the inter-specific effects (Bascompte, Jordano, and Jens M Olesen 2006; Vázquez, Morris, and Jordano 2005). However, because the degree distribution, and ultimately the number of driver species, can be affected by the sampling method (Blüthgen 2010) we compared the number of driver species in a pollination community in which both visitation frequency and effectiveness were measured (Ballantyne, Baldock, and Willmer 2015).

84 To quantify to what extent the number of driver species is characteristic
85 of the structure of pollination networks we compared them against a set of random
86 null-models. A set of null models were based on network randomisations that
87 maintained the degree of plants, pollinators, and both plants and pollinators. To
88 analyse the effects of the chosen directionality, we devised a null model in which
89 we randomised the visitation patterns and re-calculated the new dependencies.
90 In all cases we computed 999 randomisations.

91 We quantified the relative importance of each species for network dynamics.
92 To do this, we counted the number of times a particular species was a driver
93 species across all possible maximum matchings in the pollination network. The
94 number of maximum matchings were found by generating the line graph of the
95 alternative bipartite network representation ([Figure 2](#)), and then enumerating
96 the maximal cliques in the complement of the line graph (Csardi and Nepusz
97 [2006](#)).

98 Finally, we tackled the question whether some structural properties can pre-
99 dict the relative importance of driver species. Here, we regressed the impor-
100 tance of each species against measures of centrality (degree, betweenness), mea-
101 sures related to network robustness (contribution to nestedness) and measures
102 of strength of association (visitation levels).

103 Preliminary results

104 To date only data from the National Cap de Creus in Northeastern Spain has
105 been analysed. We found that if we were to control the dynamics of the whole
106 community, we would need to control between 55 and 75% of the species in the
107 community. The proportion of driver species did was not significantly different
108 between invaded and uninvaded ecosystems.

109 Empirical pollination networks to randomisations have need significantly
110 more driver species than randomisations that maintain the number of inter-

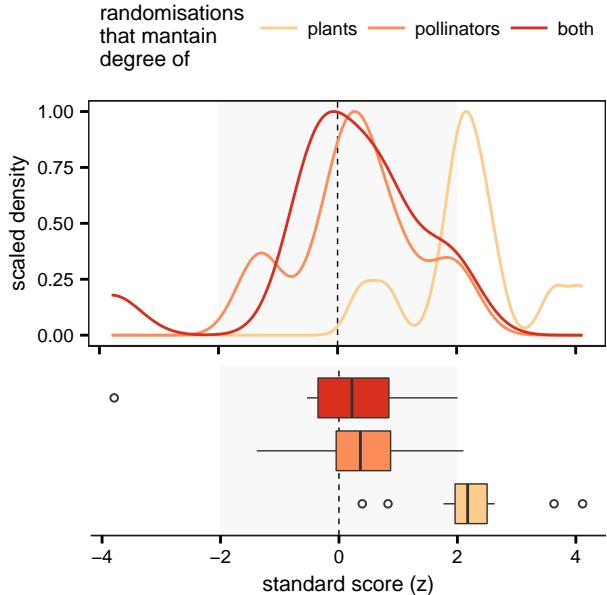


Figure 3: Difference between the number of driver species in the empirical pollination networks versus randomisations of the same networks. The unshaded area ($z < -2, z > 2$) suggest a significant difference at a significance level of $\alpha = 0.05$.

111 acting species per plants. However when the number of interacting species is
 112 maintained in pollinators or in all species, the difference disappear (Figure 3).
 113 This suggest that the number of driver species is determined by the degree dis-
 114 tribution of the species, in particular pollinators. This is consistent to previous
 115 findings that highlight the influence of the degree distribution on the controlabil-
 116 ity of complex networks (Liu, Slotine, and Barabási 2011; Benavides, Diwekar,
 117 and Cabezas 2015).

118 However, when we compared the empirical networks to randomisations that
 119 maintain the network structure but shuffle the directionality of the dependency,
 120 we found that empirical networks need substantially more driver species than the
 121 random counterpart (Figure 4). This highlights the importance of asymmetries
 122 in structuring pollination networks.

123 Not all species have the same importance for network control. Pollinators

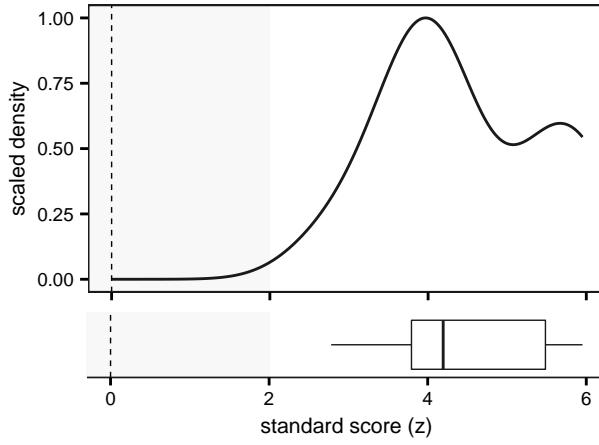


Figure 4: Difference between number of driver species in the empirical networks versus randomisations of the dependencies in the same networks. The unshaded area ($z > 2$) suggest a significant difference at a significance level of $\alpha = 0.05$.

124 in general seem to have a moderate-high role on driving the dynamics of other
 125 species. Plants on the other hand seem to be a skewed distribution, with some
 126 species having a very low and some species having a very high relative impor-
 127 tance (Figure 5).

128 When looking at the relative importance of invasive species we found that,
 129 in all of the six analysed networks, they all have the maximum importance.
 130 They are certainly not unique in this regard, but it is remarkable that invasive

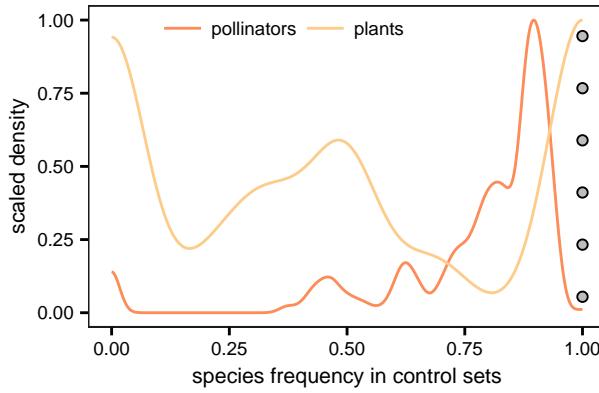


Figure 5: Distribution of the relative frequency a species is present in the set of driver species. Invasive species are depicted as grey points.

131 species integrate this way in the community.

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141 **References**

- 142 Aizen, Marcelo A, Carolina L Morales, and Juan M Morales (2008). “Invasive
143 mutualists erode native pollination webs”. In: *PLoS Biology* 6.2, pp. 0396–
144 0403. DOI: [10.1371/journal.pbio.0060031](https://doi.org/10.1371/journal.pbio.0060031).
- 145 Ballantyne, G, Katherine C R Baldock, and P G Willmer (2015). “Constructing
146 more informative plant-pollinator networks: visitation and pollen deposition
147 networks in a heathland plant community”. In: *Proceedings of the Royal
148 Society B* 282.1814, p. 20151130. DOI: [10.1098/rspb.2015.1130](https://doi.org/10.1098/rspb.2015.1130).
- 149 Bartomeus, Ignasi, Montserrat Vilà, and Luís Santamaría (2008). “Contrasting
150 effects of invasive plants in plant-pollinator networks”. In: *Oecologia* 155.4,
151 pp. 761–770. DOI: [10.1007/s00442-007-0946-1](https://doi.org/10.1007/s00442-007-0946-1).
- 152 Bascompte, Jordi, Pedro Jordano, and Jens M Olesen (2006). “Asymmetric Coevo-
153 lutionary Networks Facilitate Biodiversity Maintenance”. In: *Science* 312.April,
154 pp. 431–433. DOI: [10.1126/science.1123412](https://doi.org/10.1126/science.1123412).

- 155 Benavides, Pahola T, Urmila Diwekar, and Heriberto Cabezas (2015). “Controllability of complex networks for sustainable system dynamics”. In: *Journal of Complex Networks* 3.4, pp. 566–583. DOI: [10.1093/comnet/cnu051](https://doi.org/10.1093/comnet/cnu051).
- 156
- 157
- 158 Blüthgen, Nico (2010). “Why network analysis is often disconnected from community ecology: A critique and an ecologist’s guide”. In: *Basic and Applied Ecology* 11.3, pp. 185–195. DOI: [10.1016/j.baae.2010.01.001](https://doi.org/10.1016/j.baae.2010.01.001).
- 159
- 160
- 161 Cornelius, Sean P, William L Kath, and Adilson E Motter (2013). “Realistic control of network dynamics”. In: *Nature Communications* 4, p. 1942. DOI: [10.1038/ncomms2939](https://doi.org/10.1038/ncomms2939). arXiv: [1307.0015](https://arxiv.org/abs/1307.0015).
- 162
- 163
- 164 Csardi, G and T Nepusz (2006). “The igraph software package for complex network research”. In: *International Journal of Complex Systems* Complex Sy.June, p. 1695. DOI: [10.1109/ICCSN.2010.34](https://doi.org/10.1109/ICCSN.2010.34).
- 165
- 166
- 167 Isbell, Forest and Michel Loreau (2013). “Human impacts on minimum subsets of species critical for maintaining ecosystem structure”. In: *Basic and Applied Ecology* 14.8, pp. 623–629. DOI: [10.1016/j.baae.2013.09.001](https://doi.org/10.1016/j.baae.2013.09.001).
- 168
- 169
- 170 Liu, Yang-Yu, Jean-Jacques Slotine, and Albert-László Barabási (2011). “Controllability of complex networks.” In: *Nature* 473.7346, pp. 167–173. DOI: [10.1038/nature10011](https://doi.org/10.1038/nature10011).
- 171
- 172
- 173 Lopezaraiza-Mikel, Martha E. et al. (2007). “The impact of an alien plant on a native plant-pollinator network: An experimental approach”. In: *Ecology Letters* 10.7, pp. 539–550. DOI: [10.1111/j.1461-0248.2007.01055.x](https://doi.org/10.1111/j.1461-0248.2007.01055.x).
- 174
- 175
- 176 Olesen, Jens M., Louise I. Eskildsen, and Shadila Venkatasamy (2002). “Invasion of pollination networks on oceanic islands: Importance of invader complexes and endemic super generalists”. In: *Diversity and Distributions* 8.3, pp. 181–192. DOI: [10.1046/j.1472-4642.2002.00148.x](https://doi.org/10.1046/j.1472-4642.2002.00148.x).
- 177
- 178
- 179
- 180 Traveset, Anna et al. (2013). “Invaders of pollination networks in the Galápagos Islands : emergence of novel communities”. In: *Proceedings of the Royal Society B* 280.iii, p. 20123040. DOI: [10.1098/rspb.2012.3040](https://doi.org/10.1098/rspb.2012.3040).
- 181
- 182
- 183 Vázquez, Diego P., William F. Morris, and Pedro Jordano (2005). “Interaction frequency as a surrogate for the total effect of animal mutualists on plants”.
- 184

- 185 In: *Ecology Letters* 8.10, pp. 1088–1094. DOI: [10.1111/j.1461-0248.2005.00810.x](https://doi.org/10.1111/j.1461-0248.2005.00810.x).
- 186 Vilà, Montserrat et al. (2009). “Invasive plant integration into native plant-
- 187 pollinator networks across Europe.” In: *Proceedings of the Royal Society B*
- 188 276.1674, pp. 3887–3893. DOI: [10.1098/rspb.2009.1076](https://doi.org/10.1098/rspb.2009.1076).

Attachment 2

THE SCALING UP OF COEVOLUTION IN POLLINATION NETWORKS BEYOND SPECIES PAIRS

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¹ Abstract

² On a macroevolutionary scale, processes such as coevolution can play a large role in determining who
³ interacts with whom in ecological networks. However, it is unclear whether or how these phenomena are
⁴ actually detectable in observed assemblages. Here, we aim to bridge this gap by using cophylogenetic
⁵ analysis to scale up coevolution in 54 empirical pollination networks from the species pair to: *(i)* the
⁶ entire interaction network and *(ii)* the modular structure of those networks. Our results suggest that the
⁷ interaction and phylogenetic structures of pollination networks cannot be considered independent with
⁸ 70% of networks showing significant cophylogeny. These significant patterns of cophylogeny suggest
⁹ that macroscopic coevolution, as opposed to chance or vicariance, is responsible for the structure of
¹⁰ pollination assemblages. At the intermediate scale—modules of tightly interacting groups of species—
¹¹ the patterns expected of macroscopic coevolution are not universally observed. Contrary to previous
¹² hypotheses, this suggests that topological modules as we understand them do not represent a fundamental
¹³ macroscopic unit of coevolution and are more likely determined by multiple eco-evolutionary factors.

¹⁴ • **Keywords:** compartmentalization, diffuse coevolution, ecological networks, guild coevolution,
¹⁵ modularity, mutualism, mutualistic networks, cophylogeny

¹⁶ 1. Introduction

¹⁷ Species do not exist in isolation, but are instead constantly interacting with other species in the commu-
¹⁸ nity. Each of these interactions can impact the fitness of individuals and lead to selection for amplification
¹⁹ or avoidance of future interactions [1, 2]. When two species interact over enough time, reciprocal selec-
²⁰ tion can lead to concurrent evolutionary change in both species [1]. This process is generally referred to
²¹ as coevolution, and it often leads to the evolutionary trajectory of pairs of species, and potentially their
²² descendants, becoming deeply intertwined [1]. The coevolution of species can have multiple outcomes,
²³ although these most simply can be generalised into two categories: microscopic and macroscopic. Akin to
²⁴ marcoecology—the study of large-scale ecological patterns—macroscopic coevolution can be considered
²⁵ the pattern of coupled divergence of interacting clades that implies a large degree of trait complementarity
²⁶ between interaction partners [3, 4, 5]. Conversely, microscopic coevolution—otherwise coadaptation or
²⁷ pairwise coevolution—is the reciprocal trait evolution of interacting species [1, 6].

²⁸ At the microscopic level of species pairs, coevolution has been widely studied [1, 2], from corals and
²⁹ their zooxanthellae to symbiotic organelles in eukaryotes. Comparatively, the degree to which macro-
³⁰ scopic coevolution is responsible for the structure and functioning of entire communities is poorly under-
³¹ stood at the scale of taxonomically rich interacting clades [1, 7]. Among the ecological systems in which
³² one might expect to observe coevolution at a community scale, the mutualistic assemblages of flowering
³³ plants and their pollinators are a logical candidate [8, 9]. This is because the positive feedback of mutu-
³⁴ alisms [9] and myriad examples of extreme pollination-driven coevolution (such as between figs and fig
³⁵ wasps) should make macroscopic coevolutionary signal particularly observable in pollination networks.
³⁶ Furthermore, the notion of diffuse coevolution tenets that, as most species interact with several partners,
³⁷ coevolution should manifest itself above specific pairs of plants and pollinators [1, 6, 10, 11].

³⁸ Assessing the coevolution of communities is a long-standing question in evolutionary biology [1, 3, 7],
³⁹ and the ultimate solution requires consideration of both microscopic and macroscopic coevolutionary

40 processes [1, 12]. Nevertheless, important initial insights can be obtained with the quantification of the
41 macroscopic coevolutionary processes observable in the patterns of species interaction and evolutionary
42 history [3, 13]. Furthermore, extant interactions—that are typically only possible with trait complemen-
43 tarity [1, 5]—can indicate a certain level of codependent trait evolution at the scale of species' pairs or
44 taxonomically higher [3, 13].

45 Cophylogenetic analysis is one common approach that provides insight to the community-wide pat-
46 terns of interaction and evolutionary history between species—the same patterns expected of macroscopic
47 coevolution [3, 14]. At its backbone is the pattern of cospeciation which measures the degree to which
48 two phylogenies match in their speciation and divergence events [13, 15]. However, this pattern alone
49 can arise from several processes including vicariance, chance, and coevolution [1, 12, 13]. Thus, the
50 second aspect of a cophylogenetic pattern that must be present alongside cospeciation is phylogenetic
51 congruence of interactions—that the interactions observed occur between evolutionarily coupled clades
52 [14, 16]. Cophylogeny is therefore more than just phylogenetic signal of interactions for both interacting
53 groups as it simultaneously considers both phylogenies alongside the extant interactions.

54 Though it is a tantalizing possibility, a signal of macroscopic coevolution such as cophylogeny may
55 not extend across an entire pollination network to the same extent that other ecological or evolutionary
56 processes, such as the direct and indirect propagation of disturbance in food webs [17], traverse interaction
57 networks. Nonetheless, it is widely accepted that diffuse coevolutionary processes may still be manifest
58 in pollination networks at the level of subsets of the community [1, 7, 8]. At the same time, it has been
59 observed that closely interacting groups of species, or modules, are a ubiquitous structural feature of
60 ecological communities including pollination networks [8, 18]. Given that coevolution is assumed to act
61 above the level of species pairs [1, 10], it has therefore been hypothesized that modules are an, if not *the*,
62 ecologically relevant product of coevolution [8, 19].

63 Despite theory that provides tentative support for this hypothesis [11], a more directed test of empiri-
64 cal network structure is needed to confirm such results. As with community-wide cophylogeny, multiple

65 constraints must be satisfied for empirically observed modules to show cophylogeny or be considered a
66 product of macroscopic coevolution (Fig. 1). First, they should reflect the cospeciation of the network
67 such that closely related species tend to be found in the same module. This consistency between modules
68 and phylogenies, however, does not take into account the fact that some interactions, and implied trait
69 complementarity, can be considered more consistent with the cophylogenetic narrative than others when
70 they occur between closely coupled clades [5, 13, 14, 16]. Therefore secondly, if modules reflect cophy-
71 logenetic patterns, they should also be comprised of these phylogenetically congruent interactions, with
72 the less congruent interactions falling between modules.

73 Here, we study 54 pollination networks from around the world to quantify the degree to which these
74 networks show a significant cophylogenetic pattern. In particular, we search for evidence of cophylogeny
75 at two specific scales: (i) network cophylogeny—where any observable cospeciation should be embod-
76 ied by the interactions of the entire network—and (ii) modular cophylogeny—where the modules of a
77 network should tend to contain closely related plant species, closely related pollinator species, and the
78 most congruent interactions between them. Addressing patterns of cophylogeny at these two macroscopic
79 scales represents an important step towards a robust, quantitative integration of coevolutionary processes
80 with the modern theory underpinning community ecology.

81 **2. Material and methods**

82 **(a) Empirical data and phylogeny construction**

83 We analyzed a dataset comprised of 54 plant-pollinator mutualistic networks from a wide range of lo-
84 cations around the globe and with diverse species assemblages [20, Table S1]. In each of the networks,
85 the presence or absence of interactions is based on observed visitation of flowering plants by their animal
86 pollinators. In total, these networks include 1,388 species of flowering plants, 2,930 species of flower-
87 visiting animals, and over 15,000 interactions. Studying the cophylogenetic patterns between two sets of
88 interacting species, such as plants and pollinators, requires an understanding of the evolutionary history of

89 both groups. Central to the accuracy and robustness of our method were rigorously resolved phylogenies
90 of flowering plants and their pollinators, and we followed several steps to generate these. First, to ensure
91 all species identifications were up-to-date, we verified all species' names in the original interaction ma-
92 trices. Plant names were checked and corrected with the NCBI database (<http://www.ncbi.nlm.nih.gov/>)
93 whereas we corrected animal names with the gnr_resolve function in the R package taxize, which ac-
94 cessed a range of taxonomic databases [21]. Second, we constructed dated phylogenies for both groups
95 with the verified species' names. To do so, we started with a taxonomic tree given by the classification
96 function in taxize with preferential acceptance of classifications returned by the NCBI database [21]. We
97 compiled estimated divergence times of the flowering plants and insect pollinators from accepted phylo-
98 genies [22, 23]. We then used the bladj function from phylocom [24] to obtain branch length estimates
99 for any clades missing from these two studies. Although some of the divergence times we use should be
100 treated as an approximation [25], the accurate dating of even a subset of phylogenetic tips, which we have
101 achieved with two accepted phylogenies [22, 23] can improve the performance of comparative methods
102 such as ours [26].

103 **(b) Measuring whole-network cophylogeny**

104 To conduct an indirect assessment of macroscopic coevolution in each of our pollination networks, we
105 implemented a recently developed Procrustean method to directly assess cophylogeny in those networks
106 [14]. This approach, referred to as PACo, approaches the cophylogeny problem by optimizing the fit of
107 the phylogeny-interaction graphs of each network [14, 27]. PACo provides a quantification of the global
108 fit of the phylogenetic objects—a measure of cophylogeny and a proxy for macroscopic coevolution—
109 using the sums of squares residual distance between phylogenetic-interaction graphs [14, 27]. The smaller
110 the residual distance, the better the fit of the two graphs (*i.e.* phylogenies) and thus a higher degree of
111 cophylogeny reflected in the extant interactions. Similarly, the phylogenetic congruence of each individ-
112 ual interaction is equal to the residual distance between the two corresponding points on the phylogenetic

113 graphs. PACo offers several analysis options including a choice of whether to superimpose the raw
114 phylogenetic graphs (asymmetric) or to normalize both graphs to the same dimensionality before a super-
115 imposition is done (symmetric) [14]. The order of superimposition can also be specified (*i.e.* plants on
116 pollinators and vice versa), a decision based on the evolutionary assumptions of the system [14]. In this
117 study, we have focused on the results of the symmetric method where the normalized pollinator graph
118 is superimposed on the normalized plant graph. Nonetheless, our results do not differ qualitatively nor
119 quantitatively when selecting alternative configurations (Fig. S1).

120 We determined the significance of cophylogeny at the network level as captured by PACo by compar-
121 ing the sum of squared residuals of the Procrustean superimposition of plant and pollinator phylogenies
122 with the same from an ensemble of 1,000 randomizations of the network of interactions between plants
123 and pollinators. In each randomization, we conserved the number of interactions for each species as
124 well as the total number of interactions [28]. A conservative null model such as this does not rely on
125 an evolutionary assumption about which group is driving the cophylogenetic pattern allowing us to test
126 the hypothesis that both the plant and pollinator phylogenetic histories are constrained by the other via
127 their interactions. However, there are several alternate null models (the results for which do not differ
128 qualitatively from the model we present) and selection depends on the evolutionary assumptions made.
129 For example, in host-parasite systems it is perhaps more appropriate to assume that host speciation drives
130 parasite speciation and implement a less constrained null model [14].

131 **(c) Identifying network modules**

132 To test whether cophylogeny was consistent with modularity, we first needed to identify modules in the
133 interaction networks—compartments in which species are more likely to interact with each other than the
134 rest of the network [18]—given the observed interactions. In order to identify such modules in each of the
135 different networks, we followed the approach proposed by Barber [29] and implemented in MODULAR
136 [30], which partitions nodes with a stochastic optimization procedure. While there are several such

137 methods to assess modularity, the method employed here has been demonstrated to perform as well or
138 better than other contemporary module detection algorithms in bipartite networks [31].

139 To determine whether the observed network structure was significantly modular we implemented the
140 same null model used to assess network-wide cophylogeny and compared observed modularity to an
141 ensemble of 1000 randomisations of each network that maintained the degree distribution. This null
142 model has been widely used to assess the significance of modularity in ecological networks [8, 28], while
143 at the same time it allows for comparison of our results for network cophylogeny and modularity.

144 **(d) Measuring modular cophylogeny**

145 The first step we took to quantify the cophylogeny and infer the degree of macroscopic coevolution in
146 modules was to quantify how modules related to the evolutionary histories of both groups of species.
147 To do so, we fitted a likelihood model for discrete character evolution, using a continuous-time Markov
148 model of trait evolution [32]. Our assessment compared the degree to which the phylogeny predicts
149 covariance among module assignment of species [33], or in other words, the degree to which closely
150 related species tend to share the same module.

151 We determined the significance of the phylogenetic signal of modules by comparing our results to
152 those that would be obtained after randomly assigning module participants. First, we compared the
153 likelihood that the observed species-module assignment was the product of an evolutionary process versus
154 the corresponding likelihood from 1,000 randomized assignments. Therefore, a significant phylogenetic
155 signal of pollination modules implies that the observed modules are more consistent with this evolutionary
156 process than expected at random.

157 While the degree to which networks as a whole show cophylogeny can be established with PACo
158 [14, 27], an assessment of the extent to which cophylogenetic processes characterize topological modules
159 requires subsequent analysis. As noted earlier, the phylogenetic congruence of an interaction is given
160 by the residual of two points in the Procrustean superimposition of the phylogenetic-interaction graphs;

161 therefore, an interaction can be considered more congruent when its contribution to the overall residual
162 of the Procrustean analysis is small [14]. Thus, if modules are the product of cophylogeny, we expected
163 interactions within modules to have a higher degree of congruence (*i.e.* to have smaller residuals on aver-
164 age) than interactions between species in different modules. We tested this assumption using one-factor
165 analysis of variance (ANOVA) of the log-transformed Procrustean partial residuals of each interaction,
166 where the decision to log-transform the data was made to improve the normality but also did not qualita-
167 tively affect our results or conclusions.

168 We determined the significance of the within-module cophylogeny by comparing our results to those
169 that would be obtained after randomly assigning module participants. We compared the Akaike's In-
170 formation Criterion (AIC) of the ANOVA that contrasts the degree of cophylogeny within and between
171 observed modules against an ensemble of 1000 AIC values of the same with the randomized module as-
172 signments. We randomized the species' module assignments using two approaches. In the first approach,
173 we allowed for an arbitrary number of species in each module and an arbitrary number of modules. In the
174 second, more conservative approach we maintained the observed number of modules and the number of
175 species within each of them. Differences between approaches are not substantial and do not qualitatively
176 affect our results or conclusions, therefore we presented the results of the second, more conservative
177 approach. Results for the first approach can be found in the *Supplementary Material* (Fig. S1).

178 **3. Results**

179 Across our dataset, we found that a large proportion of pollination networks (38 out of 54 networks)
180 could be considered cophylogenetic assemblages (Monte Carlo test, $p < 0.05$; Fig. 2A). The observation
181 of high levels of cophylogeny at a network scale, such as this, therefore provided the necessary baseline
182 from which we could assess how cophylogeny was manifest at the modular scale. Implementing the
183 bipartite modularity optimization of Barber [29] and a conservative null model (*Materials and Methods*)
184 we observed that 57% (31 out of 54) of networks in our dataset were significantly modular (Monte Carlo

185 test, $p < 0.05$; Fig. 2B). Furthermore, of the significantly modular networks, 74% also showed significant
186 cophylogeny (Fig. 3).

187 On the surface, these high levels of cophylogeny and modularity would appear to support the hy-
188 pothesis that macroscopic coevolution acts at a modular scale. However, as described earlier, this still
189 amounts to circumstantial evidence and a deeper investigation of the relationships between each interac-
190 tion and the respective phylogenies is required. Specifically, if module participation is the natural result
191 of cophylogeny, we expected that modules based on who tends to interact with whom are consistent with
192 the evolutionary histories of both plants and pollinators—that is, they show cospeciation. Here we in-
193 stead found that the modules of a network are consistent with the plant and pollinator phylogenies in only
194 26% and 54% of networks, respectively (Monte Carlo test, $p < 0.05$; Figs. 2C, 2D, and 4). However,
195 when considering only the 31 significantly modular networks, the proportion of networks that exhibit
196 phylogenetic signal of module assignment increases to 35% and 58%, respectively (Fig. 3).

197 Our second consideration to assess cophylogeny in modules is the degree of phylogenetic congruence
198 of their constituent interactions. In general, we expected that within-module interactions would tend
199 to be more congruent than between-module interactions if modules represented a cophylogenetic unit
200 (Fig. 5). We found that observed modules were significantly better than random at explaining interaction
201 congruence in only 26% of the empirical networks (Monte Carlo test, $p < 0.05$; Figs. 2E, 4). Again,
202 this proportion increases slightly to 29% when considering exclusively networks that were significantly
203 modular (Fig. 3).

204 In total, we have assessed three complementary measures—conservation of the plant phylogeny,
205 conservation of the pollinator phylogeny, and within-module cophylogeny—to quantify whether cophy-
206 logeny is manifest in the modules of pollination networks. Across the 54 networks, varying proportions of
207 networks' modules satisfy these cophylogenetic constraints at a modular scale (Fig. 2 C-E). Though each
208 of these were observed at a greater frequency than would be expected at random ($p < 0.001$ in all cases;
209 [34]) just four networks appear to satisfy constraints for cophylogeny at the modular scale (Fig. 4). As

such, fulfilling one constraint for cophylogeny does not necessarily facilitate fulfilment of others (Chi-squared tests; both phylogenies conserved, $p < 0.001$; plant phylogeny conserved and within-module interaction cophylogeny, $p = 0.201$; pollinator phylogeny conserved and within-module interaction cophylogeny, $p = 0.002$; all three constraints, $p = 0.532$; Figs. 2C-E and 3). When put together, our results indicate that there is limited evidence at best that modules reflect cophylogenetic patterns or represent a definitive unit of macroscopic coevolution (Figs. 3 and S1).

4. Discussion

Coevolution has long been hypothesized to manifest itself in ecological assemblages above the level of species pairs [1, 6, 7, 8, 10]. Here, we address this hypothesis with a formal quantification of cophylogenetic patterns in pollination networks. We have demonstrated that a strong signal is present in pollination networks, with 70% of the networks analyzed exhibiting significant levels of whole-network cophylogeny. Despite current thinking that suggests cophylogeny cannot provide evidence for coevolution [1, 12], our results in taxonomically rich and globally sourced networks provide a potential counter argument. Many previous studies of cophylogeny address these patterns in specific genera and clades rather than across entire trophic groups such as the flowering plants and pollinators that we focus on here [35, 36, 37, 38, 39]. As such, ours is perhaps the first study of cophylogeny in large assemblages of interacting species and the high levels of significantly cophylogenetic networks we observe suggest that this pattern can still arise quite consistently when scaled up.

Furthermore, for patterns of cophylogeny to be this ubiquitous across such distinct systems, Occam's razor would indicate that it arises from a common process. On the one hand, these patterns can arise due to both biogeographical [1, 40] and coevolutionary processes [1, 41]. On the other, multiple previous studies have indicated that phylogenetic congruence in pollination systems is most parsimoniously explained by coevolution [39, 41]. Furthermore, the taxonomically diverse and global nature of our dataset makes it unlikely that vicariance alone can account for the high levels of network cophylogeny we observed here.

234 Likewise, traits are such a strong predictor of interactions in mutualistic networks [42, 43] that strong
235 interaction congruence, like that observed here, is rather unlikely—albeit not impossible—to observe
236 in the complete absence of coupled trait evolution between taxa that maintained trait complementarity
237 across the trees. Our results therefore support the idea that coevolution is indeed an influential process
238 in shaping pollination networks and that many of these communities can be considered macroscopically
239 coevolved assemblages [1]. Our results further suggest that an imprint of coevolution can at times be
240 observed in the topological modules of pollination networks. Having said that, it cannot be considered
241 the pervasive structural force that some have suggested [1, 7, 8, 10, 19].

242 The link between traits and interactions in ecological communities [43, 44] also offers at least two
243 potential explanations as to why we did not universally see macroscopic coevolution in topological mod-
244 ules. First, in the networks we have studied, closely related pollinators tend to co-occur in modules more
245 than twice as often as closely related plants. This result may be a consequence of convergence in polli-
246 nation networks via pollination syndromes, whereby plants are thought to converge on traits selected for
247 by pollinator functional groups [45]. As functional groups of pollinators are often considered to be broad
248 clades that tend to be more closely related than the plants they visit [45], pollination syndromes may ex-
249 plain why we see such a disparity in terms of phylogenetic conservation of modules. Second, it has been
250 suggested that free-living mutualists tend to converge on traits as opposed to species [1]. If traits rather
251 than species converge in pollination networks, future inquiry that incorporates specific trait histories and
252 microscopic coevolutionary dynamics *alongside* phylogenetic and interaction data may perhaps expose a
253 more vivid signal of coevolution [5].

254 Beyond macroscopic coevolution, modularity in ecological networks is also thought to be influenced
255 by several ecological processes including species' abundance [46], body mass [47] and species richness
256 [48]. The collective action of these processes and others may act to effectively layer over the products of
257 coevolution, resulting in the weak signal we tend to observe in network modules. Our results also show
258 variation in the extent to which coevolution within modules is quantifiable—for example, the pollinator

259 phylogeny is conserved by the modular structure in roughly half the networks we assess—suggesting
260 that the contribution of ecological processes to modular structure may differ on both spatial and temporal
261 scales [7]. Therefore, attempts to tease apart the contributions of ecological, evolutionary, and coevolu-
262 tionary processes to the modular structure of ecological networks may be as important as attempts that
263 aim to tease apart the ecological mechanisms alone [49, 50].

264 Conversely, it is also possible that a modular structure will always fail to serve as a definitive unit of
265 macroscopic coevolution in pollination networks when examined at the whole-network scale. For exam-
266 ple, it is entirely plausible, and perhaps even likely, that the role of macroscopic coevolution in contribut-
267 ing to module structure differs between the modules observed in a network. Variation in the strength of
268 macroscopic coevolution observable at a module scale may arise from differences in the period of shared
269 evolutionary history of participant species [19], infiltration of modules by exotic species [51], or merely
270 the aforementioned suite of ecological determinants. Furthermore, the balance of pollinator species to
271 plant species in a module may also indicate the extent to which coevolution has shaped the assemblage,
272 with suggestions that balanced, or symmetrical, modules are more likely the product of coevolution and
273 predisposed to reciprocal selection whereas asymmetrical modules are more likely driven by abundance
274 [52, 53]. Thus, a description of coevolution at a modular scale in ecological networks requires not only
275 a consideration of the multiple determinants of ecological modularity, but also an explicit focus on indi-
276 vidual modules and their constituent species.

277
278 **Data accessibility:** All interaction networks can be found on the Web of Life database (<http://www.web->
279 of-life.es). Summaries of the datasets used in this article can also be found as part of the supplemen-
280 tary material. Both plant and pollinator phylogenies for each interaction network are available through
281 GitHub: <http://github.com/stoufferlab/to-be-added-upon-publication/>

282
283 **Authors' contributions:** M. C. H. and E. F. C. contributed equally to the work; M. C. H. and D. B. S.

284 designed research; M. C. H. and E. F. C. performed research; E. F. C. analyzed data; M. C. H. led the
285 writing; and E. F. C. and D. B. S. contributed substantially to the writing.

286

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288

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298

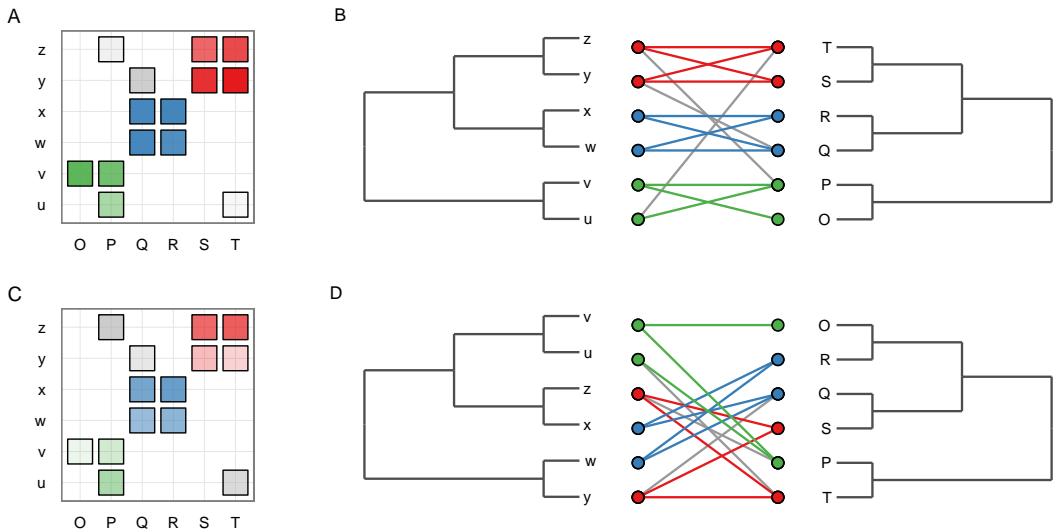


Figure 1: Graphical representation of our key hypotheses for modular cophylogeny in pollination networks. (A) We show a significantly modular network composed of three modules of tightly interacting species as indicated by the different colors (e.g., the green module containing species u, v, O, and P). This matrix format is one way to represent a binary bipartite ecological network; the pollinator species are on the x-axis (O–T), the plants on the y-axis (u–z), and a solid square at their intersection indicates the presence of an interaction between those species. (B) The modules in this network are highly cophylogenetic since they are made up of closely related species in both phylogenies and the evolutionary histories of these interacting species mirror each other strongly. (C and D), Despite the fact that this network is significantly modular, there is no evidence for modular cophylogeny since there is no tendency of its three modules to be composed of closely related species nor for species in extant interactions to exhibit comparable evolutionary histories. In both (A) and (C), the shading of the interactions is indicative of that interactions' cophylogenetic signal where the darker the shade the higher the signal (*Materials and Methods*).

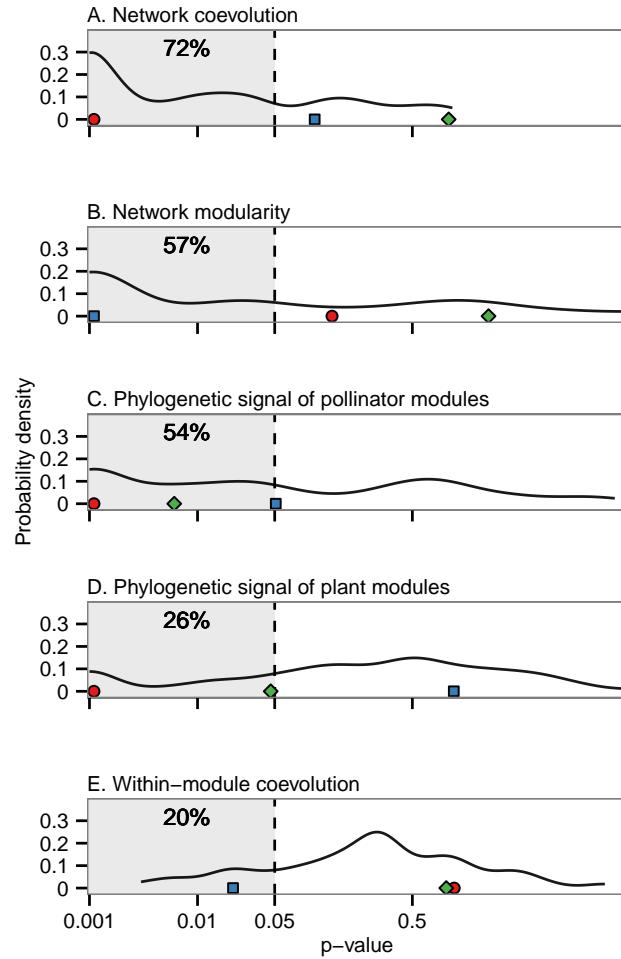


Figure 2: The structure of empirical pollination networks provides varying degrees of support for the different constraints for whole-network and modular cophylogeny. (A)-(E) We show the probability densities of the p-values associated with our hypothesis testing of each criteria: (A) network cophylogeny, (B) network modularity, (C) phylogenetic signal of pollinator modules, (D) phylogenetic signal of plant modules, and (E) within-module cophylogeny. In each panel, we indicate the proportion of networks that are significant for each measure compared to the corresponding null hypothesis (*Materials and Methods*). The red circle, blue square, and green diamond on each plot show the values for three representative networks to indicate the variability within as well as across individual networks.



Figure 3: Graphical summary of the results of our analysis of cophylogeny in empirical pollination networks. Each column is for a different empirical network and the rows show the outcome of different statistical tests. In all rows a dark blue cell indicates a significant result for the network whereas light blue indicates the result was non-significant. Row 1 shows the proportion of significantly modular networks. Row 2 shows the proportion of significantly cophylogenetic networks. Rows 3 & 4 show the proportion of networks with phylogenetic signal of the pollinator and plant modules, respectively. Row 5 shows the support for within-module cophylogeny of the networks.

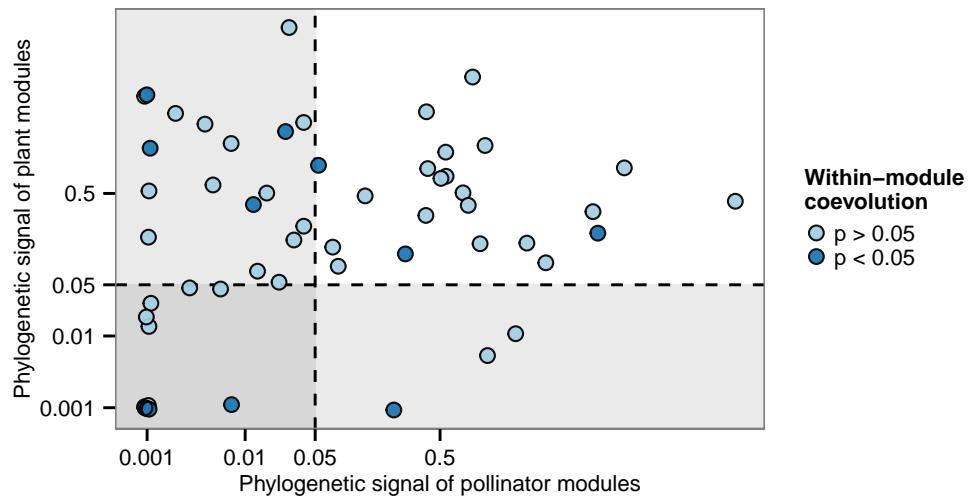


Figure 4: Few empirical pollination networks simultaneously support the hypothesis of substantial modular cophylogeny. For each of the 54 empirical networks, we plot the phylogenetic signal of pollinator modules (on the x-axis) versus the phylogenetic signal of the plant modules (on the y-axis). Networks to the left of the vertical dashed line and below the horizontal dashed line exhibit significant phylogenetic signal for pollinators and plants, respectively. The color of symbol indicates whether the networks' modular structure significantly explained the variation of interaction-level cophylogeny; dark blue indicates those networks whose modules have a significant tendency to contain the most congruent interactions whereas light blue indicates the opposite. Only four of the empirical networks fulfil all three constraints.

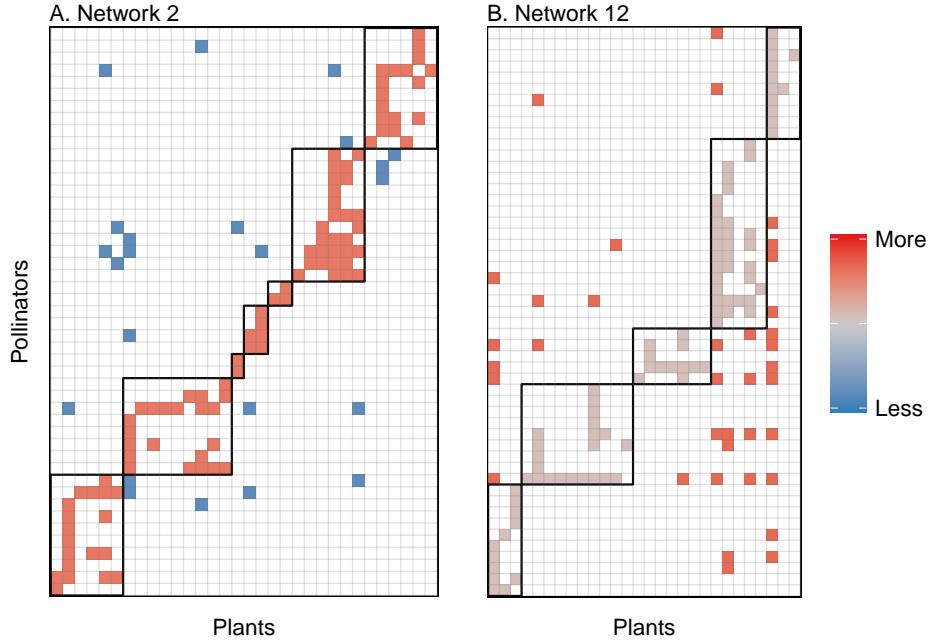


Figure 5: There is substantial variation in the extent to which the modular structure of a network captures macroscopic cophylogeny. We show here how two representative networks fit the constraint that within-module interactions should be more congruent than between-module interactions. The color of the within- and between-module interactions in each network is given by the mean cophylogenetic signal of all interactions in that group. (A) The constraint for within-module cophylogeny is fulfilled by Network 2 since the interactions within modules tend to show significantly more cophylogeny than those falling between modules. (B) In contrast, the constraint for within-module cophylogeny is not fulfilled by Network 12 since within-module interactions tend to show less cophylogeny than the between-module counterparts. In cases like this—which are the norm of our study—the whole network provides stronger support for cophylogeny than do topological modules.

²⁹⁹ **References**

- ³⁰⁰ [1] Thompson, J. N., 2005 *The geographic mosaic of coevolution*. University of Chicago Press,
³⁰¹ Chicago, IL.
- ³⁰² [2] Futuyma, D. J. & Agrawal, A. A., 2009 Macroevolution and the biological diversity of plants and
³⁰³ herbivores. *Proceedings of the National Academy of Sciences* **106**, 18054–18061.
- ³⁰⁴ [3] Futuyma, D. J. & Slatkin, M., 1983 Introduction. In *Coevolution* (eds. D. J. Futuyma & M. Slatkin),
³⁰⁵ pp. 1–13. Sinauer Associates, Sunderland, MA.
- ³⁰⁶ [4] Brooks, D. R. & McLennan, D. A., 1993 Macroevolutionary patterns of morphological diversifica-
³⁰⁷ tion among parasitic flatworms (platyhelminthes: Cercohermida). *Evolution* pp. 495–509.
- ³⁰⁸ [5] Segraves, K. A., 2010 Branching out with coevolutionary trees. *Evolution: Education and Outreach*
³⁰⁹ **3**, 62–70.
- ³¹⁰ [6] Janzen, D. H., 1980 When is it coevolution. *Evolution* **34**, 611–612.
- ³¹¹ [7] Bascompte, J. & Jordano, P., 2014 *Mutualistic Networks*. Princeton University Press, Princeton, NJ.
- ³¹² [8] Olesen, J. M., Bascompte, J., Dupont, Y. L. & Jordano, P., 2007 The modularity of pollination
³¹³ networks. *Proceedings of the National Academy of Sciences* **104**, 19891–19896. (doi:10.1073/pnas.
³¹⁴ 0706375104).
- ³¹⁵ [9] Bascompte, J. & Jordano, P., 2007 Plant-animal mutualistic networks: The architecture of biodiver-
³¹⁶ sity. *Annual Review of Ecology, Evolution, and Systematics* **38**, 567–593. (doi:10.1146/annurev.
³¹⁷ ecolsys.38.091206.095818).
- ³¹⁸ [10] Fox, L. R., 1988 Diffuse coevolution within complex communities. *Ecology* **69**, 906–907.
- ³¹⁹ [11] Nuismer, S. L., Jordano, P. & Bascompte, J., 2013 Coevolution and the architecture of mutualistic
³²⁰ networks. *Evolution* **67**, 338–354.

- 321 [12] Anderson, B., 2015 Coevolution in mutualisms. In *Mutualism* (ed. J. Bronstein), pp. 107–130.
- 322 Oxford University Press.
- 323 [13] Page, R. M., 2003 Introduction. In *Tangled Trees: Phylogeny, Cosppeciation, and Coevolution* (ed.
- 324 R. M. Page), pp. 1–22. University of Chicago Press, Chicago, IL.
- 325 [14] Balbuena, A. J., Miguez-Lozano, R. & Blasco-Costa, I., 2013 Paco: A novel procrustes application
- 326 to cophylogenetic analysis. *PLoS One* **8**, e61048. (doi:10.1371/journal.pone.0061048).
- 327 [15] Clayton, D., Bush, S. & Johnson, K., 2004 Ecology of congruence: Past meets present. *Systematic*
- 328 *Biology* **53**, 165–173. (doi:10.1080/10635150490265102).
- 329 [16] Legendre, P., Desdevises, Y. & Bazin, E., 2002 A statistical test for host–parasite coevolution. *Sys-*
- 330 *tematic Biology* **51**, 217–234.
- 331 [17] Stouffer, D. B. & Bascompte, J., 2011 Compartmentalization increases food-web persistence. *Pro-*
- 332 *ceedings of the National Academy of Sciences* **108**, 3648–3652. (doi:10.1073/pnas.1014353108).
- 333 [18] Guimera, R., Stouffer, D., Sales-Pardo, M., Leicht, E., Newman, M. & Amaral, L., 2010 Origin of
- 334 compartmentalization in food webs. *Ecology* **91**, 2941–2951.
- 335 [19] Bascompte, J. & Olesen, J., 2015 Mutualistic networks. In *Mutualism* (ed. J. Bronstein), pp. 203–
- 336 219. Oxford University Press.
- 337 [20] Rezende, E. L., Lavabre, J. E., Guimaraes, P. R., Jr., Jordano, P. & Bascompte, J., 2007 Non-
- 338 random coextinctions in phylogenetically structured mutualistic networks. *Nature* **448**, 925–U6.
- 339 (doi:10.1038/nature05956).
- 340 [21] Chamberlain, S., Szocs, E., Boettiger, C., Ram, K., Bartomeus, I. & Baumgartner, J., 2014 *taxize:*
- 341 *Taxonomic information from around the web*. R package version 0.3.0.

- 342 [22] Wikström, N., Savolainen, V. & Chase, M. W., 2001 Evolution of the angiosperms: calibrating
343 the family tree. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **268**,
344 2211–2220.
- 345 [23] Misof, B., Liu, S., Meusemann, K., Peters, R. S., Donath, A., Mayer, C., Frandsen, P. B., Ware,
346 J., Flouri, T., Beutel, R. G. *et al.*, 2014 Phylogenomics resolves the timing and pattern of insect
347 evolution. *Science* **346**, 763–767. (doi:10.1126/science.1257570).
- 348 [24] Webb, C. O., Ackerly, D. D. & Kembel, S. W., 2008 Phylocom: software for the analysis of phylo-
349 genetic community structure and trait evolution. *Bioinformatics* **24**, 2098–2100.
- 350 [25] Beaulieu, J. M., Moles, A. T., Leitch, I. J., Bennett, M. D., Dickie, J. B. & Knight, C. A., 2007
351 Correlated evolution of genome size and seed mass. *New Phytologist* **173**, 422–437.
- 352 [26] Webb, C. O., 2000 Exploring the phylogenetic structure of ecological communities: an example for
353 rain forest trees. *The American Naturalist* **156**, 145–155.
- 354 [27] Cagua, E. F., Hutchinson, M. C., Poisot, T. & Balbuena, J.-A., 2015 *paco v0.2.2*. (doi:10.5281/
355 zenodo.31977).
- 356 [28] Fortuna, M. A., Stouffer, D. B., Olesen, J. M., Jordano, P., Mouillot, D., Krasnov, B. R., Poulin, R.
357 & Bascompte, J., 2010 Nestedness versus modularity in ecological networks: two sides of the same
358 coin? *Journal of Animal Ecology* **79**, 811–817. (doi:10.1111/j.1365-2656.2010.01688.x).
- 359 [29] Barber, M. J., 2007 Modularity and community detection in bipartite networks. *Physical Review E*
360 **76**, 066102.
- 361 [30] Marquitti, F. M. D., Guimarães, P. R., Pires, M. M. & Bittencourt, L. F., 2014 Modular: software
362 for the autonomous computation of modularity in large network sets. *Ecography* **37**, 221–224.

- 363 [31] Thébault, E., 2013 Identifying compartments in presence–absence matrices and bipartite networks:
364 insights into modularity measures. *Journal of Biogeography* **40**, 759–768.
- 365 [32] FitzJohn, R. G., Maddison, W. P. & Otto, S. P., 2009 Estimating trait-dependent speciation and
366 extinction rates from incompletely resolved phylogenies. *Systematic Biology* **58**, 595–611.
- 367 [33] Pagel, M., 1999 Inferring the historical patterns of biological evolution. *Nature* **401**, 877–884.
- 368 [34] Moran, M. D., 2003 Arguments for rejecting the sequential bonferroni in ecological studies. *Oikos*
369 **100**, 403–405.
- 370 [35] Hafner, M. S. & Nadler, S. A., 1988 Phylogenetic trees support the coevolution of parasites and
371 their hosts. *Nature* **332**, 258–259. (doi:10.1038/332258a0).
- 372 [36] Cruaud, A., Rønsted, N., Chantarasuwan, B., Chou, L. S., Clement, W. L., Couloux, A., Cousins,
373 B., Genson, G., Harrison, R. D., Hanson, P. E. *et al.*, 2012 An extreme case of plant–insect codiver-
374 sification: figs and fig-pollinating wasps. *Systematic Biology* p. sys068.
- 375 [37] Nishiguchi, M. K., Ruby, E. G. & McFall-Ngai, M. J., 1998 Competitive dominance among strains
376 of luminous bacteria provides an unusual form of evidence for parallel evolution in sepiolid squid-
377 vibrio symbioses. *Applied and environmental microbiology* **64**, 3209–3213.
- 378 [38] Mikheyev, A. S., Mueller, U. G. & Abbot, P., 2010 Comparative dating of attine ant and lepiotaceous
379 cultivar phylogenies reveals coevolutionary synchrony and discord. *The American Naturalist* **175**,
380 E126–E133.
- 381 [39] Smith, C. I., Godsoe, W. K., Tank, S., Yoder, J. B. & Pellmyr, O., 2008 Distinguishing coevolution
382 from covariation in an obligate pollination mutualism: asynchronous divergence in Joshua tree and
383 its pollinators. *Evolution* **62**, 2676–2687.

- 384 [40] Weckstein, J. D., 2004 Biogeography explains cophylogenetic patterns in toucan chewing lice. *Systematic Biology* **53**, 154–164.
- 385
- 386 [41] Godsoe, W., Strand, E., Smith, C. I., Yoder, J. B., Esque, T. C. & Pellmyr, O., 2009 Divergence in an
387 obligate mutualism is not explained by divergent climatic factors. *New Phytologist* **183**, 589–599.
- 388 [42] Eklöf, A., Jacob, U., Kopp, J., Bosch, J., Castro-Urgal, R., Chacoff, N. P., Dalsgaard, B., Sassi,
389 C., Galetti, M., Guimarães, P. R. *et al.*, 2013 The dimensionality of ecological networks. *Ecology*
390 *Letters* **16**, 577–583.
- 391 [43] Dehling, D. M., Töpfer, T., Schaefer, H. M., Jordano, P., Böhning-Gaese, K. & Schleuning, M., 2014
392 Functional relationships beyond species richness patterns: trait matching in plant–bird mutualisms
393 across scales. *Global Ecology and Biogeography* **23**, 1085–1093.
- 394 [44] Guimaraes, P. R., Jr., Jordano, P. & Thompson, J. N., 2011 Evolution and coevolution in mutualistic
395 networks. *Ecology Letters* **14**, 877–885. (doi:10.1111/j.1461-0248.2011.01649.x).
- 396 [45] Fenster, C. B., Armbruster, W. S., Wilson, P., Dudash, M. R. & Thomson, J. D., 2004 Pollination
397 syndromes and floral specialization. *Annual Review of Ecology, Evolution, and Systematics* pp.
398 375–403.
- 399 [46] Krasnov, B. R., Fortuna, M. A., Mouillot, D., Khokhlova, I. S., Shenbrot, G. I. & Poulin, R., 2012
400 Phylogenetic signal in module composition and species connectivity in compartmentalized host-
401 parasite networks. *The American Naturalist* **179**, 501–511. (doi:10.1086/664612).
- 402 [47] Rezende, E. L., Albert, E. M., Fortuna, M. A. & Bascompte, J., 2009 Compartments in a marine
403 food web associated with phylogeny, body mass, and habitat structure. *Ecology Letters* **12**, 779–788.
404 (doi:10.1111/j.1461-0248.2009.01327.x).
- 405 [48] Martín González, A. M., Dalsgaard, B., Nogués-Bravo, D., Graham, C. H., Schleuning, M.,
406 Maruyama, P. K., Abrahamczyk, S., Alarcón, R., Araujo, A. C., Araújo, F. P. *et al.*, 2015 The

- 407 macroecology of phylogenetically structured hummingbird–plant networks. *Global Ecology and*
408 *Biogeography* p. 10.1111/geb.12355.
- 409 [49] Vázquez, D. P., Chacoff, N. P. & Cagnolo, L., 2009 Evaluating multiple determinants of the structure
410 of plant-animal mutualistic networks. *Ecology* **90**, 2039–2046.
- 411 [50] Kaiser-Bunbury, C. N., Vázquez, D. P., Stang, M. & Ghazoul, J., 2014 Determinants of the mi-
412 crostructure of plant-pollinator networks. *Ecology* **95**, 3314–3324.
- 413 [51] Traveset, A., Heleno, R., Chamorro, S., Vargas, P., McMullen, C. K., Castro-Urgal, R., Nogales,
414 M., Herrera, H. W. & Olesen, J. M., 2013 Invaders of pollination networks in the galápagos is-
415 lands: emergence of novel communities. *Proceedings of the Royal Society of London B: Biological
416 Sciences* **280**, 20123040.
- 417 [52] Hagen, M., Kissling, W. D., Rasmussen, C., Carstensen, D., Dupont, Y., Kaiser-Bunbury, C.,
418 O’Gorman, E., Olesen, J., De Aguiar, M., Brown, L. *et al.*, 2012 Biodiversity, species interactions
419 and ecological networks in a fragmented world. *Advances in Ecological Research* **46**, 89–120.
- 420 [53] Rasmussen, C., Dupont, Y. L., Mosbacher, J. B., Trøjelsgaard, K. & Olesen, J. M., 2013 Strong
421 impact of temporal resolution on the structure of an ecological network. *PLoS One* **8**, e81694.