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Interaction generalisation and demographic feedbacks drive the resilience of plant-insect networks to extinctions

K. P. Maia*[1,2], F. M. D. Marquitti[3], I. P. Vaughan[4], J. Memmott[1] and R. L. G. Raimundo*[5,6]

[1] School of Biological Sciences, University of Bristol, Bristol, UK

[2] Biosciences Institute, University of Sao Paulo, Sao Paulo, Brazil

[3] Gleb Wataghin Institute of Physics, University of Campinas, Campinas, Brazil

[4] Cardiff School of Biosciences, Cardiff University, Cardiff, UK

[5] Department of Engineering and Environment and Postgraduate Program in Ecology and Environmental Monitoring (PPGEMA), Centre for Applied Sciences and Education, Federal University of Paraíba, Campus IV, Rio Tinto, Brazil

[6] IRIS Research Group, Innovation for Resilience, Inclusion and Sustainability, Federal University of Paraíba, Campus IV, Rio Tinto, Brazil

* Corresponding authors: kate.maia@usp.br, rafael.raimundo@academico.ufpb.br

Abstract

1. Understanding the processes driving ecological resilience, defined as the extent to which systems retain their structure while absorbing perturbations, is a central challenge for theoretical and applied ecologists. Plant-insect assemblages are well-suited for the study of ecological resilience as they are species-rich and encompass a variety of ecological interactions that correspond to essential ecosystem functions.

2. The mechanisms affecting community response to perturbations depend on both the natural history and the structure of ecological interactions. Natural history attributes of interspecific interactions, *e.g.* whether they are mutualistic or antagonistic, may affect ecological resilience by controlling the demographic feedbacks driving ecological dynamics at the community level. Interaction generalisation may also affect resilience, by defining opportunities for interaction rewiring, the extent to which species are able to switch interactions in fluctuating environments. These natural history attributes may also interact with network structure to affect ecological resilience.

3. Using adaptive network models, we investigated the resilience of plant-pollinator and plant-herbivore networks to species loss. We specifically investigated how fundamental natural history differences between these systems, namely the demographic consequences of the interaction and their level of generalisation – mediating rewiring opportunities - affects the resilience of dynamic ecological networks to extinctions. We also create a broad reference for the effect of network structure on resilience using theoretical networks.

4. When network structure was static, pollination networks tended to be less resilient than herbivory networks; this was is related to their high levels of nestedness and the reciprocally positive feedbacks that define mutualisms, which made coextinction cascades more likely and longer in plant-pollinator assemblages. When considering interaction rewiring, the high generalisation and the structure of pollination networks boosted their resilience to extinctions, which approached those of herbivory networks. Finally, results using theoretical networks suggested that the empirical structure of herbivory networks may protect them from collapse.

5. Understanding the ecological and evolutionary processes driving interaction rewiring is key to understanding the resilience of plant-insect assemblages. Accounting for rewiring requires ecologists to combine natural history with network models that incorporate feedbacks between species abundances, traits and interaction patterns. This combination will elucidate how perturbations propagate at community-level, reshaping biodiversity structure and ecosystem functions.

Key-words antagonism, cascade length, coevolutionary networks, forbidden links, interaction rewire, mutualistic network, robustness

Introduction

Ecological resilience can be defined as the ability of a system to maintain its structure, functioning and internal feedbacks when absorbing perturbations (Holling, 1973, 1996). Ecological interactions drive community resilience to perturbations by connecting biodiversity structure with ecosystem functioning. The loss of species and interactions trigger structural changes that can propagate through several trophic levels, reshaping community organisation and eroding ecosystem functions (Janzen, 1974; Jordano, 2016). Assessing community resilience to the loss of species and interactions can help explain how extinctions disassemble the interaction structure of ecological communities and may also reveal strategies for biodiversity restoration (Tylianakis et al., 2018). Plant-insect interactions are excellent model systems to study the mechanisms shaping community resilience to extinctions as they encompass a diversity of natural histories, which reflect their relevance for ecosystem functions (Coley et al., 2006; Del-Claro et al., 1996; Requier et al., 2015; Shepherd & Chapman, 1998).

Networks are powerful tools to investigate how ecological communities are structured and how such structures affect their resilience. Ecological networks representing different interaction types show recurrent structural patterns. For instance, antagonistic networks involving insect herbivores and plants are often modular, *i.e.* include sets of species that interact more frequently among themselves than with other species in the assemblage (Cagnolo et al., 2011; Thébault & Fontaine, 2010). On the other hand, networks depicting free-living mutualisms, such as plant-pollinator interactions, are highly nested (Bascompte et al., 2003; but see Olesen et al., 2007), *i.e.* present a highly connected core of generalist species to which specialist species are connected. Networks' structural patterns partially result from the contrasting natural history attributes of interaction types (Guimarães et al., 2007), which affect their dynamics and resilience in different ways (Burgos et al., 2007; Dunne et al., 2002; Stouffer & Bascompte, 2011; Thébault & Fontaine, 2010; Vieira & Almeida-Neto, 2015).

Ecological networks are dynamic systems and we are only beginning to understand how incorporating dynamics into network studies affects our understanding of biodiversity resilience (Costa et al., 2018; Gilljam et al., 2015; Ramos-Jiliberto et al., 2012; Valdovinos et al., 2016). Adaptive network models (ANMs) are a class of dynamic models that can account for two naturally observable sources of ecological community dynamics: the local dynamics of species' abundances over time, and topological dynamics, referring to alterations in network structure that result from changes in species composition and interaction switches, hereafter referred to as rewiring (Gross & Blasius, 2008). In ANMs there is feedback between these two in-built sources of dynamics, allowing us to investigate how the contrasting dynamical properties of different plant-insect systems affect their resilience.

Mutualisms and antagonisms have contrasting demographic effects that could modulate the long-term persistence of community structure in different ways. These population-level feedbacks that result from interactions are a fundamental natural history attribute potentially affecting the resilience of these systems (Thébault & Fontaine, 2010). In mutualisms, such as pollination, species exploit each other with reciprocal net fitness benefits. The reciprocity of mutualisms may increase the probability and length of extinction cascades because plant population declines would lead to declines in pollinators, leading to further declines in plants (Vieira & Almeida-Neto, 2015). In herbivory, however, as only herbivores benefit from the interaction, plant declines would lead to herbivore declines, but not the inverse, constraining the frequency and length of extinction cascades. Such contrasting population feedbacks are therefore likely key determinants of plant-insect network persistence (Thébault & Fontaine, 2010) and hence resilience (Holling, 1973).

Species abundances continuously affect and are affected by species interactions (Poisot et al., 2015). Interaction rewiring is widespread in free-living mutualisms, such as pollination (Kaiser-Bunbury et al., 2010), given their high levels of generalisation that lead to flexibility in interaction partners (Bascompte & Jordano, 2013). Interaction rewiring between plants and pollinators occurs over time (CaraDonna et al., 2017) and space (Carstensen et al., 2014; Trøjelsgaard et al., 2015), both as a consequence of, or despite, changes in species abundances (Carstensen et al., 2014; MacLeod et al., 2016; Trøjelsgaard et al., 2015). In contrast, whilst rewiring occurs in plant-herbivore interactions (Auerbach & Simberloff, 1988; Murphy & Feeny, 2006), host switches are often phylogenetically constrained involving mostly congeneric plant species (Novotny & Basset, 2005; but see Agosta, 2006). Difference in the pervasiveness of interaction rewiring between pollination and herbivory systems could result from their distinct levels of generalisation – which is embedded on the structure of these networks (Fontaine et al., 2009), as plant defences impose selection on herbivores favouring specialisation (Thompson, 2005).

We combine ANMs and empirical network data to investigate how three properties that differ between pollination and herbivory networks – their network structure (Objective 1), demographic feedbacks (Objective 2), and levels of generalisation (Objective 3) - affect their resilience to species loss. Network robustness is an easy to interpret metric (Memmott et al., 2004), that quantifies how structurally resilient, *i.e.* able to maintain its structure and structuring feedbacks (Holling, 1973; Walker et al., 2004), ecological networks are to the loss of species. We predict that the reciprocally positive demographic feedbacks between plant and insect populations in pollination networks will result in longer and more frequent coextinction cascades in pollination than in herbivory networks, reducing their resilience. We also predict rewiring opportunities to be more limited in herbivory, as a result of their high degree of specialisation, reducing their resilience. Finally, we investigate how the structure of plant-insect networks interacts with population feedbacks and rewiring opportunities to affect network resilience. We complement our analysis with theoretical networks to deepen our understanding on the relationship between network structure and resilience. By accounting for the dynamic nature of ecological systems, and by systematically controlling for the effect of network structure, demographic feedbacks and interaction generalisation, we hope to shed light on how these processes interact to affect the resilience of plant-insect systems to species loss.

Material and methods

We first describe our simulation procedure and model - specifically, how the ANM incorporates local and topological dynamics. We then present our network dataset, composed of empirical and theoretical networks, simulation scenarios and statistical analyses.

Simulation overview

We simulate coextinction cascades following primary extinctions of one randomly removed plant species (Fig. 1). One cascade encompasses all secondary extinctions following a primary extinction, including species from both trophic levels. We removed plants as primary extinctions because plants positively affect insect populations in both pollination and herbivory systems, while the inverse is not true, facilitating the comparison of network collapse between interaction types. Following a primary extinction (Fig. 1; steps I and II), insect species interacting with the extinct plant have the opportunity to rewire their interactions (step III; see *Rewiring algorithm – Topological dynamics*). After changes in network structure due to species loss and rewiring, species abundances are recomputed (numerically solving equation 1, see below) and coextinctions recorded (steps IV and V). Coextinctions can either be abundance-related when abundances approach zero – emulating the process by which rare species are at a higher extinction risk (Pimm et al., 1988) - or interaction-related when species are no longer linked to other species in the network mimicking most models of network robustness. Plants in herbivory networks can remain in the system even if disconnected. We used simulated abundance data (see *Model – Local dynamics*) allowing us to compare two study systems that differ in sampling methods and therefore interaction frequencies, by isolating the elements under investigation: network structure, demographic feedbacks and interaction generalisation. Coextinctions are treated similarly to primary extinctions: the secondary extinction of a plant (step II), gives the insects feeding on that plant the opportunity of rewiring. If insects are lost (step VI), plants do not rewire as rewiring is a direct result of insects' behavioural change. Species abundances are recalculated after changes in network structure and further coextinctions are computed. Coextinction cascades end when (co)extinctions lead to no further coextinctions, and a new cascade starts.

Model – Local dynamics

We use the model developed by Suweis et al. (2013). Interaction networks and matrices (**M**) are interchangeable structures. In **M**, a matrix corresponding to a bipartite network, each animal species, $A = \{A_1, A_2, A_3... A_{SA}\}$, is a row, each plant species, $P = \{P_1, P_2, P_3...P_{SP}\}$ is a column and $m_{ij} = 1$ when insect *i* and plant *j* interact, and $m_{ij} = 0$ otherwise. Species richness in the network is $SM = SA + SP$, where SA and SP are insect and plant richness. At the beginning of each simulation run, we randomly sampled species abundances from a lognormal distribution with mean $\mu = 1$ and standard deviation $\sigma = 1$ (different σ values do not qualitatively affect results, Fig. S1). Coupling species abundances with network structure – *i.e.* distributing species abundances in accordance with their number of interactions – produces similar results (Supplementary Material). A random sample of 100,000 abundance values ranged from 0.039 to 173.68, while abundance-related coextinctions happened if values reached 0.001 or lower values. During simulation, species abundances are an outcome of interactions established with other species. In pollination networks, plants and animals are positively affected by interactions, whereas in herbivory networks only animals benefit, and plants are negatively affected by animals. The population dynamics of species *i* can be described as a function of the per capita effects of ecological interactions on its abundance x_i:

$$\frac{d_{x_i}}{d_t} = x_i\left(a_i + \sum_j^{S_M} \mathbf{T}_{ij} x_j\right) \qquad \text{eqn 1}$$

where a_i describes the intrinsic growth rate of species *i* in the absence of interactions, $\mathbf{T}_{ij}$ represents the effects of species *j* on *i*, and x_j is the abundance of species *j*. We assumed a type I functional response for both interaction types.

Matrix **T** of dimensions *SM* × *SM*, stores information on the per capita effects of each interaction on species abundances ($\mathbf{T}_{ij}$ in equation 1):

$$\mathbf{T} = \begin{bmatrix} \mathbf{\Omega_{AA}} & \mathbf{\Gamma_{AP}} \\ \mathbf{\Gamma_{PA}} & \mathbf{\Omega_{PP}} \end{bmatrix} = \begin{bmatrix} d & \omega_{1,2} & \cdots & \omega_{1,S_A} & \gamma_{1,S_A+1} & \cdots & \cdots & \gamma_{1,S_M} \\ \omega_{2,1} & d & \cdots & \cdots & \gamma_{2,S_A+1} & \cdots & \cdots & \cdots \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ \omega_{S_A,1} & \vdots & \cdots & d & \gamma_{S_A,S_A+1} & \cdots & \cdots & \gamma_{S_A,S_M} \\ \gamma_{S_A+1,1} & \cdots & \cdots & \cdots & d & \omega_{S_A+1,S_A+2} & \cdots & \omega_{S_A+1,S_M} \\ \gamma_{S_A+2,1} & \cdots & \cdots & \cdots & \cdots & d & \cdots & \omega_{S_A+2,S_M} \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ \gamma_{S_M,1} & \cdots & \cdots & \cdots & \omega_{S_M,S_A+1} & \cdots & \cdots & d \end{bmatrix} \text{eqn 2}$$

where $\mathbf{\Gamma_{AP}}$ and $\mathbf{\Gamma_{PA}}$ describe the per capita effects of pollination or herbivory on species abundances, and $\mathbf{\Omega_{AA}}$ and $\mathbf{\Omega_{PP}}$ summarise the per capita effects of competition. Diagonal elements represent intraspecific competition, $d_{ii} = -1$. $\mathbf{\Gamma_{AP}}$ is built from **M:** considering a pair of species *i* $\{i \in A\}$ and *j* $\{j \in P\}$ that interact ($m_{ij} = 1$), if the effect of *j* on the abundance of *i* is positive, $\gamma_{ij} \sim |\mathcal{N}(\mu,\sigma)|$; if it is negative, $\gamma_{ij} \sim -|\mathcal{N}(\mu,\sigma)|$; where $\mathcal{N}(\mu,\sigma)$ is a normal distribution ($\mu = 0$, $\sigma = 0.1$). Within $\mathbf{\Gamma_{PA}}$, the effect of species *i* on the abundance of *j* is defined by a different number: $\gamma_{ji} \sim |\mathcal{N}(\mu,\sigma)|$ if the effect of the interaction is positive and $\gamma_{ji} \sim -|\mathcal{N}(\mu,\sigma)|$ if it is negative. Therefore, pollination is symmetrical regarding its sign, but not its value (Bascompte & Jordano, 2013), whilst herbivory is asymmetric in sign and value. Both $\mathbf{\Omega_{AA}}$ and $\mathbf{\Omega_{PP}}$ were set to zero, assuming there is no interspecific competition (see Appendix S1 for scenarios incorporating competition). Species intrinsic growth rates were defined at the beginning of each simulation as $\vec{a} = \mathbf{T} \cdot \vec{x}$, assuming negative values for all groups but for plants in herbivory networks (Thébault & Fontaine, 2010).

Rewiring algorithm – Topological dynamics

Rewiring opportunities are defined by a matrix of forbidden links, **R**, calculated from **M.** At the beginning of each simulation, we calculated the Jaccard similarity of interactions between all networks' insect pairs. As interactions are partly determined by species attributes such as morphology, physiology and phenology (Cipollini & Peterson, 2018; Cornell & Hawkins, 2003; Olesen et al., 2011; Stang et al., 2006), we assume that species with high interaction similarity are likely to share those attributes and, therefore, to establish similar interactions. Thus, we used the interaction similarity of insect pairs, as the probability each insect in the pair had of mimicking the interactions of the other (Fig. 2a). With increasing similarity, mimicking probability increases, but the number of interactions to be mimicked - not shared by both species - decreases. Given the higher level of specialisation in herbivory compared to pollination networks, we expect a lower interaction overlap in herbivory networks, thus reducing the probability of interaction mimicking (Fig. 2a). Therefore, **R** incorporates the differences in generalisation between pollination and herbivory networks.

Rewiring occurs as a two-step process (Ramos-Jiliberto et al., 2012): step 1 determines which of the insects that lost a resource will rewire and step 2 determines to which plant species each insect will rewire. The rewiring probability of insect species i (Step 1, Fig. 2b) was calculated as $P_i = 1 - n_i$, where n_i is the abundance of i's resources. Insects' resource abundances were normalised to range between 0 and 1. As a result, rewiring probability was inversely proportional to each insect's resource abundance: insects with the highest resource abundance never rewire ($P_i = 1 - 1 = 0$), insects which lost their last resource ($P_i = 1 - 0 = 1$) always rewire, and insects with intermediate resource abundances have an intermediate probability of rewiring. Selected insects rewire to a new plant species (Step 2) in proportion to plants' abundances and respecting **R**.

Network datasets

We compiled pollination networks from the Interaction Web Database and the Web of Life. Herbivory networks were compiled from previous studies (Fontaine et al., 2009; Fontaine & Thébault, 2015; Pires & Guimarães, 2013), and networks of both interaction types were obtained from original papers. We excluded networks: i) in which animal species were not insects, as we focus on plant-insect systems, ii) that were from the same interaction type and author, to use independent networks, and iii) which were collected over more than two years or across large spatial scales (*e.g.* the whole country), so that our networks represent observable ecological communities in which co-occurrence between species is likely and our rewiring assumptions valid. This resulted in 26 pollination and 19 herbivory networks (Table S1). We used binary interaction data as we are comparing systems which are likely to vary in species abundances, detectability and data collection methods (Dáttilo et al., 2016). We characterised four network-level structural attributes of empirical networks: i) species richness; ii) connectance,; iii) nestedness; and iv) modularity (see Appendix S1.1 for details).

We created two additional network collections as references, to which we refer as *null* and *theoretical* datasets. These distinct datasets provide complementary references for the effect of network structure, and for its interaction with population feedbacks and rewiring, on resilience. Null networks serve as a specific reference for our empirical dataset, by keeping the variation in network size, proportion of species in both interacting sets and connectance of our empirical dataset, while lacking its network-level structural patterns, such as nestedness and modularity. We generated 100 null networks for each empirical network using a null model in which interactions are distributed in proportion to species degree, *i.e.* number of interaction partners (null model 2; Bascompte et al., 2003). The resulting null networks therefore, serve as a "control" for the empirical dataset.

Complementarily, theoretical networks act as a broader reference on how network structure affects resilience, providing a benchmark for the effects of network structure on resilience for any type of ecological network regardless of its structural properties. Because in empirical networks structural patterns such as nestedness and modularity may coexist (Fortuna, Lewinsohn, Valverde), and empirical networks may present sampling issues, we created theoretical networks using models which favour a single pattern: nestedness, modularity or none of the two, hereafter called random networks. For each of these patterns we created a set of *even* and *uneven* networks, *i.e.* with equal and differing numbers of "plant" and "insect" nodes, resulting in six sets of theoretical networks' with 100 networks each (see Appendix S1.2 for more information).

Simulations scenarios

To elucidate how population feedbacks, generalisation through rewiring opportunities and network structure affect the resilience of pollination and herbivory networks, we ran twelve simulation scenarios using the empirical and null datasets (Table 1). We ran simulations on empirical networks in half of these scenarios (100 simulation runs per network per simulation scenario), and on null networks in the remaining scenarios.

To investigate how differences in network structure between pollination and herbivory networks affect their resilience (Objective 1), we compare scenarios using empirical networks with scenarios using null networks (S1 to S4, Table 1), in all of which insects did not rewire. To investigate the effect of population feedbacks (Objective 2), we compare the first four scenarios with four new scenarios (S5 to S8, Table 1): equivalent to the first four but in which population feedbacks were switched between the two interaction types, *i.e.* pollination networks were treated as antagonistic, and herbivory networks as mutualistic. To explore the effect of generalisation on rewiring opportunities (Objective 3), the last four scenarios were equivalent to the first four, but insects were allowed to rewire (S9 to S12, Table 1). Additionally, we ran a total of 24 theoretical scenarios: for each of the six sets of theoretical networks we ran four scenarios - two mutualistic and two antagonistic, with and without rewiring.

For all simulation scenarios, we calculated the network robustness, a measure of structural resilience, using the *bipartite* R package (Dormann et al., 2008; R Core Team, 2017). The robustness metric is based on the attack tolerance curve, which describes the percentage of species remaining in the network following sequential primary extinctions. We calculated additional resilience measures for empirical scenarios S1 to S8: (i) the probability of abundance-related secondary extinctions, *i.e.* the number of abundance-related secondary extinctions as a proportion of all secondary extinctions; (ii) the average length of coextinction cascades; (iii) the probability of coextinction cascades, *i.e.* a primary extinction leading to at least one secondary extinction; and (iv) the probability of a long coextinction cascade, *i.e.* a primary extinction leading to at a cascade of length three or more. The loss of plant species is likely to lead to coextinctions of insects (cascades of length two) in networks of both interaction types, while further coextinctions (length three or more) reveal whether cascades continue to propagate across both trophic levels. We expect long cascades to be more common in pollination than in herbivory networks.

Statistical analysis

We investigated the effect of network structure on robustness using simulation results of S1 to S4 (Table 1) and a linear mixed-effects model (LMM), with robustness as the response variable, and structure (empirical vs null), interaction type (pollination vs herbivory) and their interaction as fixed effects. We then tested whether species richness, connectance, nestedness and modularity were associated with network robustness. These linear models had the robustness ratio between empirical and null networks as the response variable, and network metric, interaction type, and their interaction as explanatory variables. The robustness ratio should reveal if a particular network structure is associated with increases (ratio > 1) or decreases (ratio < 1) in robustness.

Using S1 to S8 we investigated the effect of population feedbacks, and its interaction with network structure, on network robustness. With LMMs, we compared the robustness of empirical and null networks of both interaction types (S1-S4) with their robustness when pollination networks were treated as antagonistic, and herbivory as mutualistic (S5-S8). Since we expect the reciprocally positive population feedbacks of mutualisms to cause longer and frequent coextinction cascades, we expect the robustness of pollination networks to increase with reversed feedbacks, and the robustness of herbivory networks to decrease. The two models (one per interaction type) had robustness as response variable, and structure (empirical vs null), population feedbacks (original or reversed), and their interaction as fixed effects. We also looked at the (i) probability of abundance-related secondary extinctions, and the (ii) length and (iii and iv) probability of coextinction cascades. The eight LMMs (four response variables, two interaction types) had structure (empirical or null), population feedbacks (original or reversed), and their interaction as fixed effects. The (i) probability of abundance-related secondary extinctions and (iii) of coextinction cascades was logit transformed.

To understand how differences in generalisation and rewiring opportunities interact with network structure to affect network robustness, we used one LMM. The response variable was the ratio between robustness in scenarios with (S9-S12) and without (S1-S4) rewiring. Ratios larger than one indicate that robustness increased with rewiring. Network structure (empirical or null), interaction type (pollination or herbivory), and their interaction were the fixed effects.

In all analyses, we used the Akaike Information Criteria (AIC) to select between (i) no random structure and (ii) network identity as a random effect (following Zuur et al., 2009), and the *emmeans* R package (Lenth, 2018) to perform *a posteriori* Tukey tests. For theoretical scenarios, we followed a similar statistical approach (see Appendix S1.3 for details).

Results

Pollination networks had 136 species on average (min = 18, max = 451, median = 78), while herbivory networks had 98.5 (min = 17, max = 655, median = 58; Table S1). Species richness (t=0.93, df=36.9, p=0.36) and connectance (t=0.37, df=32.4, p=0.71) were not significantly different in pollination and herbivory networks (Figs S2a-b). Nestedness was more common than modularity in both network types, as 15.8% (3 out of 19) of herbivory and 11.5% (3 out of 26) of pollination networks were significantly modular, while 68.4% (13 out of 19) of herbivory and all pollination networks were significantly nested. Pollination networks were more nested than herbivory networks (t=2.99, df=42.8, p<0.01), while both network types had similar modularity (Figs S2c-d; t=1.31, df=31.1, p=0.2).

The structure of empirical networks had a negative effect on their robustness (Fig. 3; t=4.35, df=43, p<0.001) as null networks had higher robustness than their empirical counterparts. The final model included network identity as a random effect. The negative effect of network structure on robustness, however, was only statistically significant for pollination networks (Fig. 3a; p<0.001). The negative effect of empirical network structure on robustness seems to be mainly associated with nestedness (Fig. S3) since with increasing nestedness (z-scored) networks were less robust ($F_{(3,41)}$=34.63, p<0.001), especially pollination networks (Fig. S3c; t=3.78, p<0.001). Nestedness decreased during network collapse similarly across scenarios (Fig. S4), while network fragmentation in components remained constant (Fig. S5). Simulations with theoretical networks reinforced the findings of empirical networks: nested networks always had lower robustness than random or modular networks (Fig. 4a). The interaction between network structure (random, nested or modular) and population feedbacks (mutualistic and antagonistic) was statistically significant (even: L-ratio=815.8, $p<0.001$; uneven: L-ratio=604.9, $p<0.001$; Fig. 4a). Nestedness had a negative effect on the robustness of even and uneven networks with mutualistic and antagonistic population feedbacks ($p<0.001$ in every comparison). Modularity often had a small positive effect on network robustness, for mutualistic ($p<0.001$ for all comparisons) and antagonistic networks ($p<0.001$ for most comparisons).

Switching population feedbacks of empirical networks, significantly increased the robustness of pollination networks (Fig. 3a; t=3.29, df=75, p=0.001), of both empirical ($p<0.001$) and null networks (p=0.03). Accordingly, treating herbivory networks as mutualistic had a negative effect on network robustness (Fig. 3b; t=4.3, $p<0.001$), similar for empirical and null networks ($p<0.001$). Network identity was selected as a random effect only on the pollination model. Theoretical scenarios support our empirical results, showing that even and uneven networks with antagonistic population feedbacks are more robust than mutualistic networks of any structure ($p<0.001$; Fig 4a).

Extinction cascades in empirical networks highly depended on population feedbacks (Table S2, Fig. S6), since abundance-related extinctions were more common in pollination networks treated as mutualistic (P-M) than in pollination networks treated as antagonistic (P-A; Fig. S6a). Coextinctions cascades were also longer in P-M than in P-A (Fig. S6c), and long cascades were also much more likely in P-M than P-A (Fig. S6g). Similarly, for herbivory networks, cascades were longer when networks were treated as mutualistic (H-M) than when treated as antagonistic (HA; Fig. S6d), and the probability of coextinction cascades of any length was higher in H-M than H-A (Figs S6f, h). Coextinction cascades continued to be longer in mutualistic networks even when competition for resources - to balance potential competitive effects between herbivore insects - is included in pollination systems (Appendix S2).

Allowing insects to rewire, increased the robustness of empirical and null networks of both interaction types (Fig. 5; t=2.95, df=43, p<0.01). The largest observed increase was for empirical pollination networks (27% ± 20, mean ± SD, min=4%, max=74%), followed by null pollination networks (13% ± 5, mean ± SD, min=7%, max=28%), and herbivory networks (empirical: 4% ± 4, mean ± SD, min=-4%, max=11%, null: 2% ± 4, mean ± SD, min=-11%, max=6%). Network structure had a significant effect on pollination networks, since empirical networks benefited more from rewiring than null networks (p<0.001), but it had no effect on herbivory networks (p=0.88). Empirical pollination networks also benefited more from rewiring opportunities than empirical herbivory networks (p<0.001). Only one empirical and two null herbivory networks had lower robustness when herbivores were allowed to rewire.

The effect of adding rewiring to theoretical networks depended on the interaction between network structure and interaction type (even: L-ratio=661.19, p<0.001; uneven: L-ratio=563.33, p<0.001). Interaction rewiring homogenised robustness across network structure and interaction type scenarios (Fig. 4b), strongly benefiting mutualistic networks (Fig. 6), especially with nested structures (p<0.001 for all comparisons). On the other hand, interaction rewiring consistently had a small negative effect on antagonistic networks (Fig. 6). Rewiring slightly decreased the robustness of 89.7% of antagonistic networks: the only 62 antagonistic networks (out of 600) which benefited from rewiring were mostly nested (32 even, 14 uneven), followed by random (7 even, 2 uneven) and modular (4 even, 3 uneven). Tukey results suggest that the effect of network structure on the robustness of antagonistic networks was small: with the exception of nested networks which had higher ratios than modular (p<0.01) and random networks ($p<0.05$) in even scenarios, there was no difference between random and modular even networks ($p=0.99$), or between uneven networks with any structure (all $p>0.05$).

Discussion

We presented a link between the natural history of two plant-insect systems and the processes that shape their network resilience. We combined the ecological resilience concept (Holling, 1973, 1996; Walker et al., 2004) with adaptive network models, to investigate three potential drivers of community resilience to species extinctions. We did this while systematically controlling for the effects of network structure and the type of demographic feedbacks on robustness, a proxy for resilience to extinctions. When species are not allowed to rewire interactions, network structure negatively affects robustness. The higher levels of nestedness observed in our pollination dataset could be a key determinant of their lower resilience, challenging previous results showing that nestedness facilitates biodiversity persistence (Bastolla et al., 2009; Memmott et al., 2004; Rohr et al., 2014; Thébault & Fontaine, 2010). Further, we found that the demographic effects of mutualisms also reduce the resilience of pollination networks, which undergo longer and more frequent extinction cascades. Finally, interaction rewiring enhances network resilience, especially in pollination systems, suggesting that the extent of a system's interaction flexibility is another key determinant of its resilience to extinctions. Our analyses were strengthened by the use of theoretical networks with controlled structures, which indicate the generality of our findings, but also presented new insights.

Our results on theoretical networks support our empirical finding that highly nested networks are less robust than networks with alternative structures. Besides challenging the notion that nestedness promotes biodiversity persistence (Bastolla et al., 2009; Memmott et al., 2004; Rohr et al., 2014; Thébault & Fontaine, 2010; but see Santamaría et al., 2016), our results contribute to the pivotal debate on the relationship between network structure and dynamics (Landi et al., 2018), reinforcing the idea that the positive effect of nestedness on robustness only holds under specific extinction scenarios (Burgos et al., 2007). The diverse set of resilience concepts and their corresponding operational proxies used in ecology could explain the contrasting results presented by studies using network robustness and alternative measures. Nested networks are very sensitive to attacks on generalists (Burgos et al., 2007) and, in robustness analysis, even when randomly targeting species to suffer extinctions, generalists are indirectly affected due to the high level of interaction asymmetry of nested networks (Silva et al., 2007). Therefore, in a scenario of species extinctions and of static topology, nestedness facilitates network collapse, especially of mutualistic networks.

Incorporating interaction rewiring led to a higher increase in the robustness of pollination when compared to herbivory networks, as expected from the high level of generalisation – and hence flexibility - of pollination systems (Fontaine et al., 2009; Waser, 1986). When species switched interactions, the robustness of pollination networks approached those of herbivory networks. Our empirical results support the notion that interaction rewiring generally has positive effects on network persistence (Gilljam et al., 2015; Ramos-Jiliberto et al., 2012; Valdovinos et al., 2013, 2016). The strong positive effect of rewiring on the resilience of pollination networks likely arises from its positive fitness consequences for mutualist species, which without further adaptations can often rapidly readjust to the most abundant partners (Janzen, 1985). The higher increase in robustness in pollination networks stems from their high generalisation level as well from their high nestedness, as the increase was larger in empirical than in null pollination networks. The structure of nested networks – an interaction core held by generalists working as an umbrella for specialists’ interactions - provides the conditions for the continuous adaptive switching of interactions. Importantly, the positive effect of rewiring on robustness also holds for mutualistic theoretical networks especially with nested structures, but not for theoretical antagonistic networks of any structure. This interesting result suggests that the combination of different structural patterns within herbivory networks may act as a buffer to extinctions. This insight could only have arisen from our combined use of empirical and theoretical networks, a combination which should be carefully considered in future network modelling studies.

Switching population feedbacks – i.e., treating pollination as antagonistic and vice-versa – increased the robustness of pollination networks and decreased the robustness of herbivory networks. Theoretical networks support this result, since antagonistic networks were consistently more robust than mutualistic, regardless of network structure. Although this result leads to the conclusion that mutualisms have a negative effect on resilience, in nature, the negative effect of such cascading events may be counterbalanced by other interaction types that influence the demographic dynamics at the community scale (Dáttilo et al., 2016; Sauve et al., 2014). Our results on the frequency and length of extinction cascades reveal that the robustness of systems treated as mutualistic decreases due to the presence of longer extinction cascades, which ricochet between trophic levels. An important question is whether our results are robust to other functional responses. At this point, we can say that assuming a Type I functional response, pollination networks collapse faster due to frequent and longer and extinction cascades than herbivory networks. Most studies looking at network robustness focus on how species in one set (*e.g.* insects) respond to the loss of species on the other set (*e.g.* plants; Traveset et al., 2017; Vieira & Almeida-Neto, 2015). By constraining coextinctions in our modelling frameworks we may be missing these realistic scenarios of horizontal extinction cascades (Sanders et al., 2013).

Adaptive network models can promote theoretical integration by accounting for dynamics at population and community levels, and the structuring feedbacks between species abundances, traits and interactions (Gross & Sayama, 2009; Poisot et al., 2015; Raimundo et al., 2018). We chose a resilience concept - the persistence of community structure and its structuring feedbacks (Holling, 1973; Walker et al., 2004) - that fits the ANM rationale and allows the use of network robustness to describe how ecological resilience is affected by extinctions. To date, ANMs and the effect of interaction rewiring on the dynamics and robustness of networks have been mostly applied to pollination systems (CaraDonna et al., 2017; Ramos-Jiliberto et al., 2012; Valdovinos et al., 2016) or to generalised antagonistic systems such as food webs (Curtsdotter et al., 2011; Gilljam et al., 2015). Importantly, interaction rewiring is pervasive in nature and is not restricted to species that lose interaction partners (CaraDonna et al., 2017; MacLeod et al., 2016). Instead, it happens by a variety of mechanisms, and can be more or less phylogenetically constrained across biological systems (Raimundo et al., 2018). Different mechanisms and timescales of interaction rewiring should be included in future resilience studies.

Ecological theory posits that topology, interaction type, specialisation of target species, and interaction rewiring affect the resilience of ecological networks (Mariani et al., 2019), but simulation studies that systematically control for the effects of each mechanism remain scarce. We sought to untangle the effect of three different interaction attributes on the robustness of ecological networks. Combining natural history information on plant-insect systems with adaptive network models, will help ecologists to apply community ecology theory to conservation and restoration in predictive ways (Raimundo et al., 2018).

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Authors' Contributions

KPM and RLGR conceived the study; KPM, RLGR and FMDM developed and/or checked the code; KPM and IPV analysed the data; KPM, JM and RLGR led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data Availability Statement

Networks, listed at the Supporting Information, are available at the Interaction Web Database (https://www.nceas.ucsb.edu/interactionweb/) and the Web of Life (http://www.web-of-life.es/). EK Del-Val kindly provided network H17 (Table S1).

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Tables and Figures

Table 1. Simulation scenarios of empirical and null networks: network interaction type (pollination or herbivory), structure (empirical or null), population feedbacks (original or reversed), and interaction rewiring (on or off). Objectives for which scenarios were used (Ob1, Ob2 and Ob3) are marked with an X. For theoretical scenarios, refer to Supplementary Information.

Scenario	Type	Structure	Feedback	Rewire	Ob1	Ob2	Ob3
S1	Pollination	Empirical	Original	Off	X	X	X
S2	Herbivory	Empirical	Original	Off	X	X	X
S3	Pollination	Null	Original	Off	X	X	X
S4	Herbivory	Null	Original	Off	X	X	X
S5	Pollination	Empirical	Reversed	Off		X	
S6	Herbivory	Empirical	Reversed	Off		X	
S7	Pollination	Null	Reversed	Off		X	
S8	Herbivory	Null	Reversed	Off		X	
S9	Pollination	Empirical	Original	On			X
S10	Herbivory	Empirical	Original	On			X
S11	Pollination	Null	Original	On			X
S12	Herbivory	Null	Original	On			X

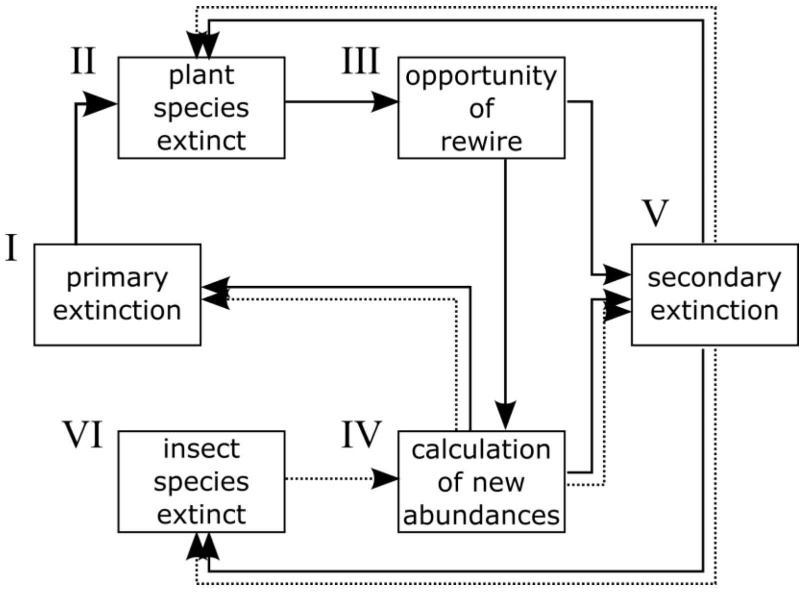

Figure 1. Diagram of extinction cascades. Full arrows indicate consequences of plant species losses and dashed arrows the consequences of animal species losses. Cascades start with the primary extinction of a plant (I and II). Insects interacting with that plant have the chance of rewiring (III). When rewiring is successful, abundances are recalculated (IV), and if new abundances are positive a new cascade begins (I and II). Species that become disconnected or whose abundance reach zero suffer secondary extinctions (V). Secondary plant extinctions lead to a similar sequence of events to primary extinctions. Secondary animal extinctions (VI) lead to the recalculation of abundances.

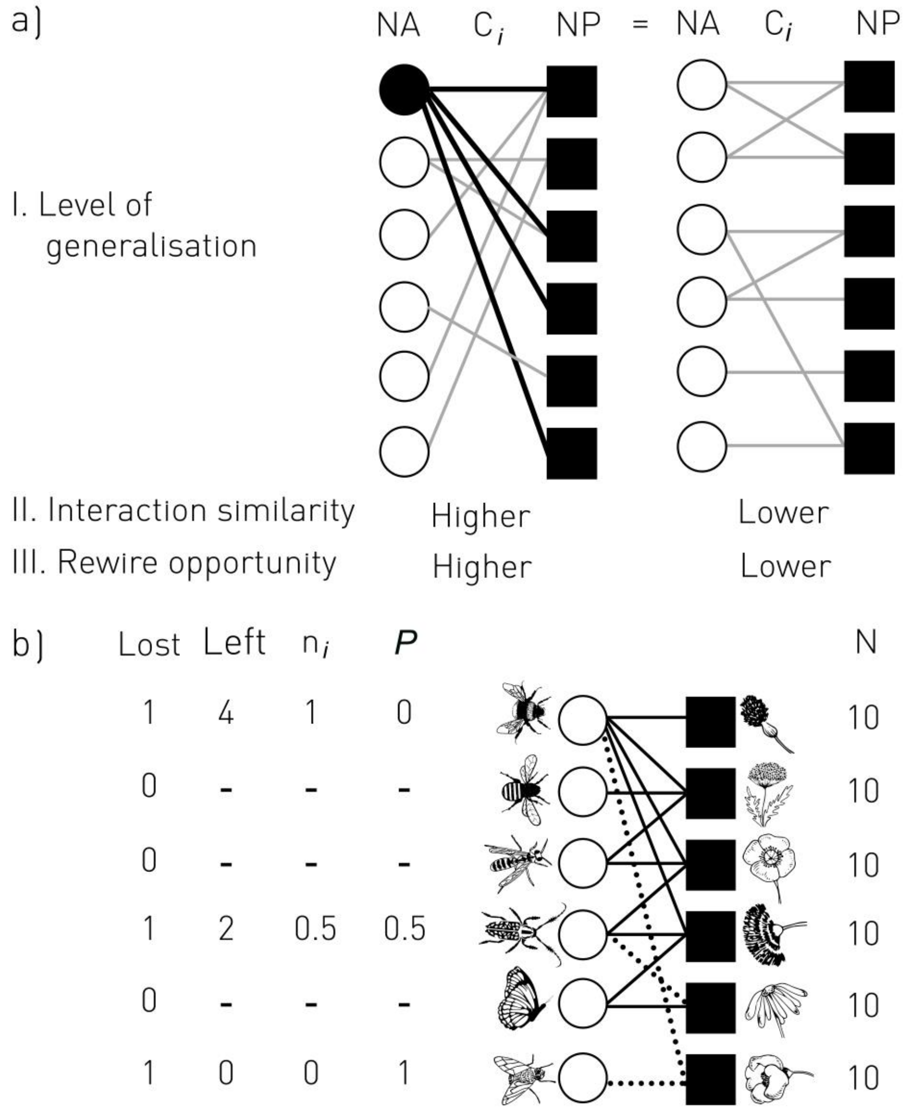

Figure 2. a) Differing levels of generalisation lead to different levels of interaction similarity (niche overlap), resulting in different rewiring opportunities. Both networks have equal connectance (C_i), number of animal (NA) and plant (NP) species, but the presence of a generalist species (black circle), leads to higher interaction similarity and rewiring opportunities. b) The rewiring probability (*P*) of insects that lost interaction partners (dashed lines) is inversely proportional to their resource abundance (n_i: normalised resource abundance of each insect). Number of resources “Lost” and “Left”. In this example, all resources have abundance N = 10.

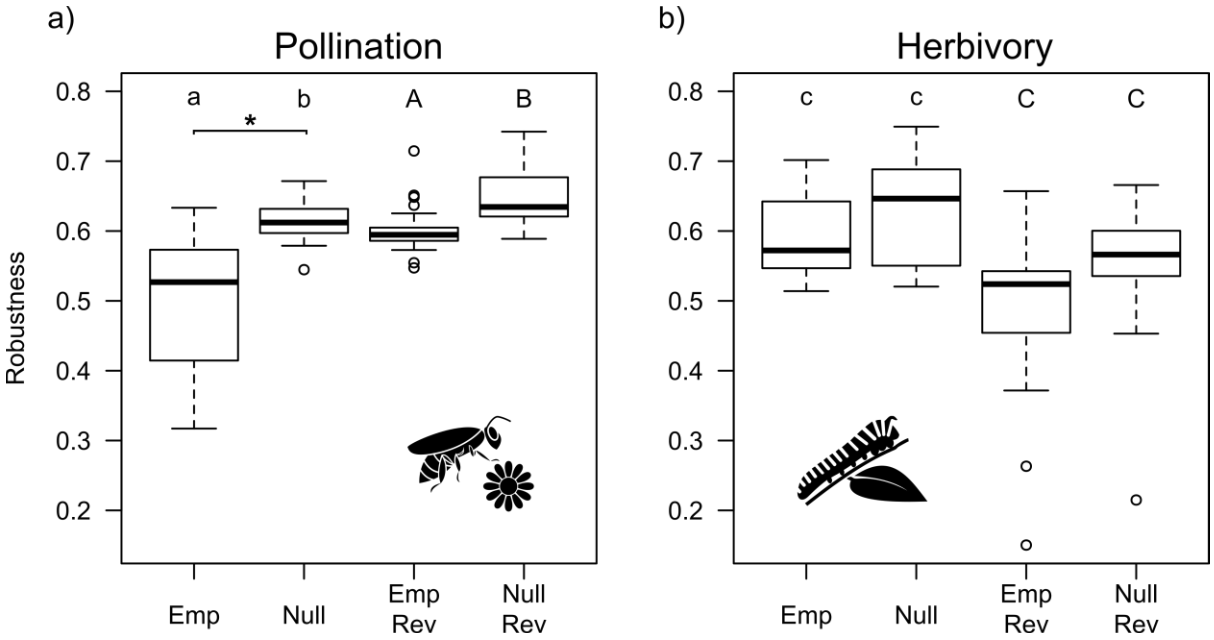

Figure 3. Robustness of a) pollination and b) herbivory networks in the first eight simulation scenarios (Table 1): empirical and null networks, without (Emp and Null) and with (Emp-Rev and Null-Rev) reversed population feedbacks. Objective 1: comparisons between empirical and null networks with non-reversed population feedbacks - Emp vs Null - for pollination and herbivory networks are marked with an asterisk if statistically different (p<0.05). Objective 2: comparisons between non-reversed (Emp and Null) and reversed (Emp-Rev and Null-Rev) population feedbacks scenarios of pollination and herbivory networks are represented by different letters (all c in herbivory as the interaction between network structure and population feedbacks was non-significant). Different letter cases (A vs a) represent p<0.05.

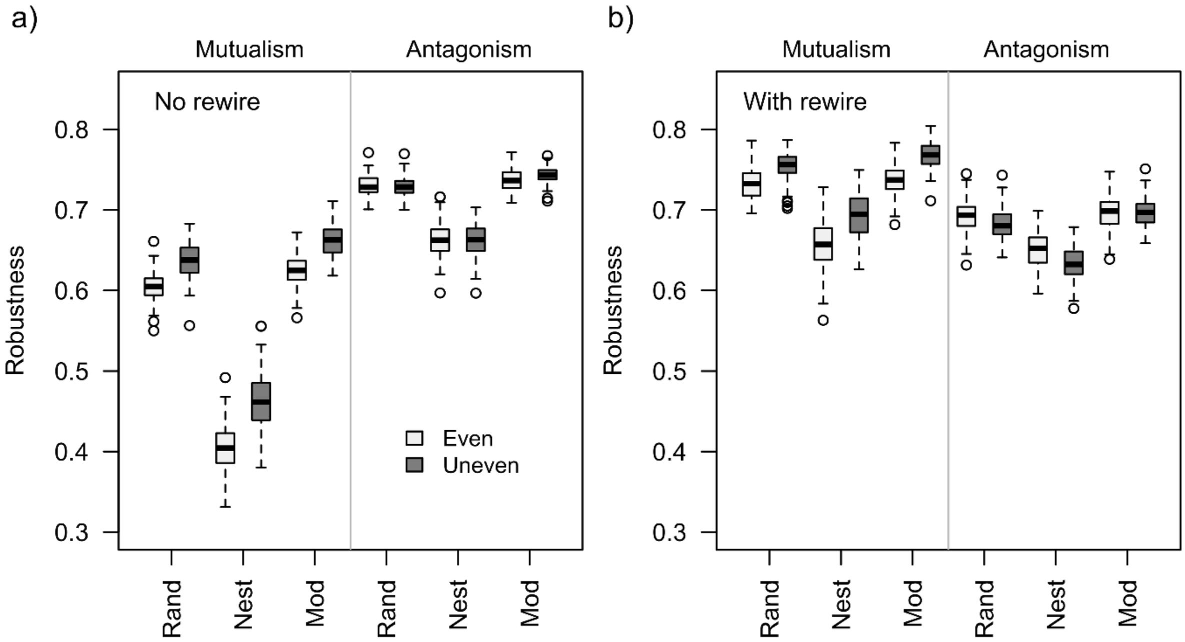

Figure 4. Robustness of theoretical networks in scenarios a) without (12 scenarios) and b) with rewiring (12 scenarios). Light boxes represent scenarios with even networks and dark boxes scenarios with uneven networks. Rand = random structure, Nest = nested and Mod = modular networks.

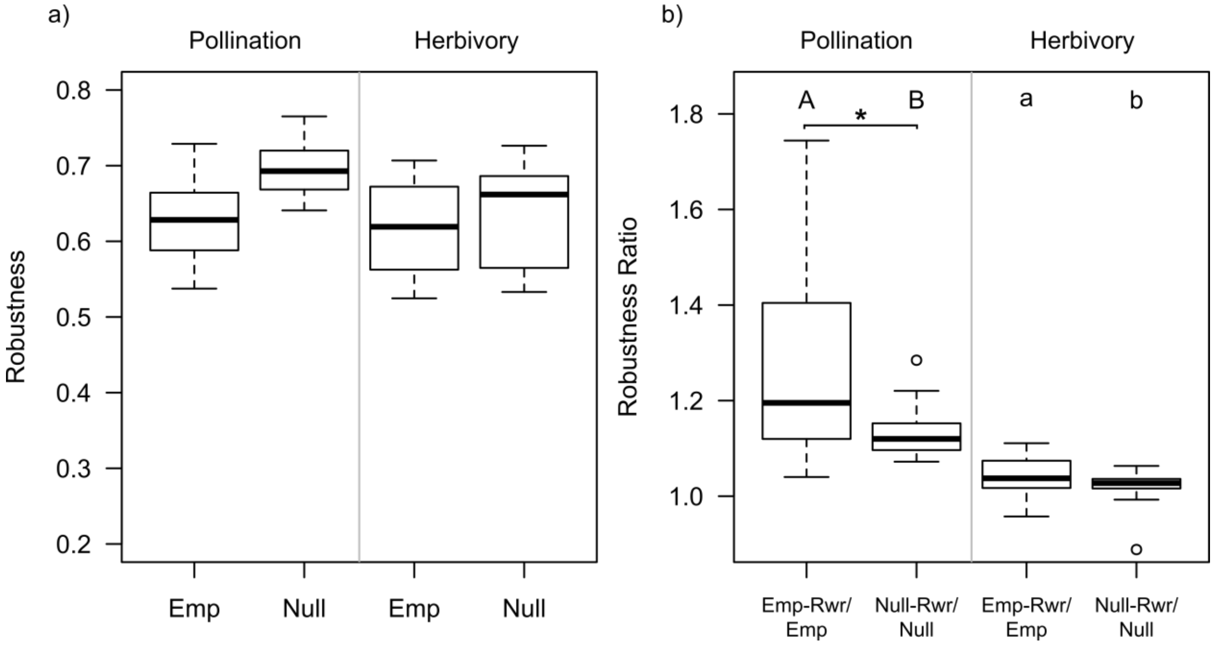

Figure 5. a) Robustness of pollination and herbivory networks in simulation scenarios in which insect species are allowed to rewire (S9 to S12, Table 1) using empirical (Emp) and null (Null) networks. b) Effect of rewiring (Rwr) on network robustness was measured as the ratio between robustness on scenarios with (S9 to S12) and without (S1 to S4) rewiring (Table 1) - *e.g.* in pollination, "Emp-Rwr/Emp" corresponds to the robustness ratio between S9 (scenario with rewire) and S1 (scenario without rewire). Comparisons between empirical and null networks of the same interaction type (*e.g.* Emp-Rwr/Emp vs Null-Rwr/Null for pollination) are marked with an asterisk when $p<0.05$. Comparisons between networks of different interaction types but with similar structure (*e.g.* Emp-Rwr/Emp for pollination vs Emp-Rwr/Emp for herbivory) are represented by different letters. Different letter cases (A vs a) represent $p<0.05$.

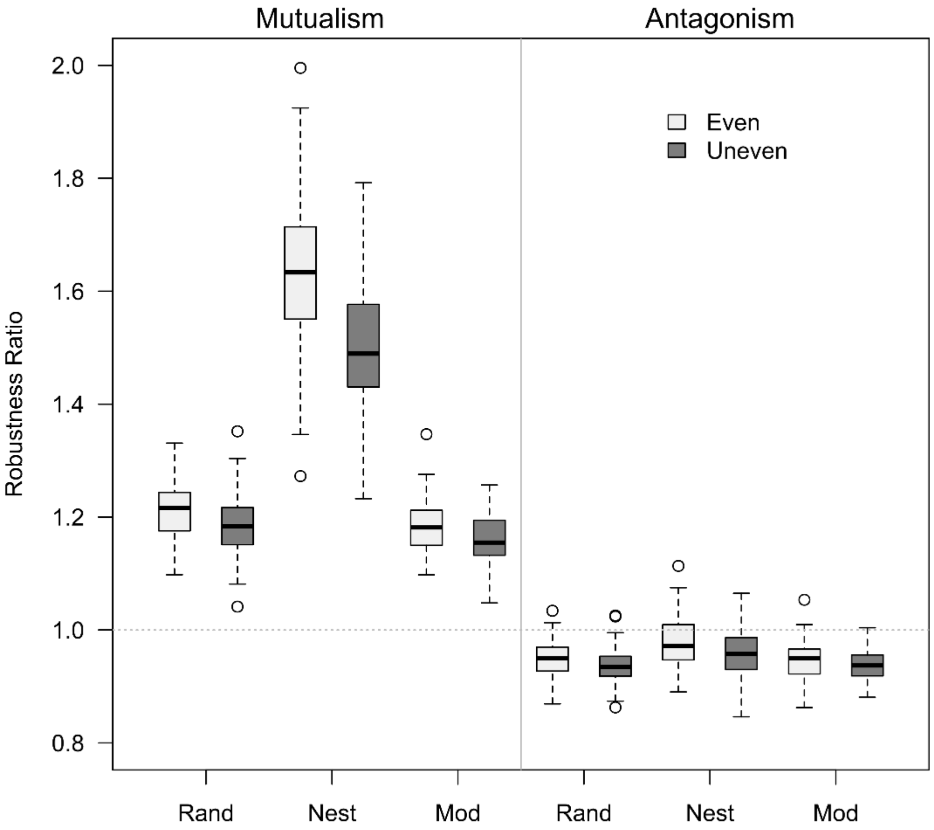

Figure 6. For theoretical networks, the effect of rewiring on network robustness was also measured as the ratio between robustness on the 12 scenarios with and 12 scenarios without rewiring. Light boxes represent scenarios with even and dark boxes scenarios with uneven networks. The horizontal dashed line marks the transition between positive and negative effects of interaction rewiring (ratio = 1). Rand = random structure, Nest = nested and Mod = modular networks.