

Research

No such thing as a free lunch: interaction costs and the structure and stability of mutualistic networks

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Different modelling approaches have been used to relate the structure of mutualistic interactions with the stability of communities. However, inconsistencies arise when we compare modelling outcomes with the patterns of interactions observed in empirical studies. To shed light on these inconsistencies, we explored the network structure–stability relationship by incorporating the cost of mutualistic interactions, a long ignored feature of mutualisms, into population dynamics models. We assessed the changes in the relationship between network structure (species richness, connectance, modularity) and community stability (species persistence, resilience), and between network structure and community structural attributes (average abundance), using models with increasing levels of cost for mutualistic communities. We found that adding the potential cost of mutualistic interactions affected the strength of the network structure–stability relationship. Our results revive the question of whether the structure of mutualistic networks determines community stability.

Keywords: abundance, network structure, persistence, plant–pollinator interactions, population dynamics, resilience

Introduction

The study of community stability has captivated ecologists for a long time (MacArthur 1955, May 1973). This long history of research on stability has led to the development of multiple definitions of stability (MacArthur 1955, May 1973, Brose et al. 2006, Gravel et al. 2011) and many lines of research dedicated to understand what drives community stability. A prominent conclusion of this body of research is that species interaction patterns are associated with stability in a variety of ways (McCann et al. 1998, Kondoh 2003, Rooney et al. 2006, Okuyama and Holland 2008, Thébault and Fontaine 2010, Gravel et al. 2011, Stouffer and Bascompte 2011, Sauve et al. 2014, Grilli et al. 2016). In particular, many of the studies assessing the relationship between the structure of ecological networks and community stability have been focused on two measures of stability: persistence (the proportion of species that persist)

and resilience (the capacity of the system to return to equilibrium after disturbance).

The response of persistence and resilience to different interaction network structures has been largely studied for different interaction types. Although some measures of network structure (e.g. nestedness) have the same effect on the stability of different interaction types, e.g. antagonistic and mutualistic interactions, most measures of network structure seem to have opposite effects according to the interaction type considered. For instance, nestedness has negative effects on the persistence and positive effects on the resilience of both antagonistic and mutualistic networks (Okuyama and Holland 2008, Thébault and Fontaine 2010). Conversely, species richness has negative effects on the persistence and resilience of antagonistic networks, but positive effects on that of mutualistic networks (Okuyama and Holland 2008, Thébault and Fontaine 2010). Similarly, the modularity of interaction networks (i.e. the extent to which subsets of species interact most frequently among themselves) has been reported to have positive (Stouffer and Bascompte 2011) or neutral (Thébault and Fontaine 2010) effects on both persistence and resilience of antagonistic networks, whereas it seems to decrease that of mutualistic networks (Thébault and Fontaine 2010). If the effects of network structure on community stability differ across interaction types, we would expect to see striking differences in the structure of empirical networks. For instance, mutualistic networks should have greater species diversity than antagonistic networks, and yet there is no evidence that supports this. Furthermore, we would not necessarily expect empirical mutualistic networks to be modular, or at least that mutualistic networks were less modular than antagonistic networks; yet many mutualistic networks, especially those with higher number of species (Olesen et al. 2007), exhibit significant modularity (Olesen et al. 2007, Dupont and Olesen 2009, Chacoff et al. 2012, Watts et al. 2016). In addition, there seems to be no difference in relative modularity between antagonistic (herbivory) and mutualistic (pollination) networks (Thébault and Fontaine 2010), and even higher levels of modularity have been found in intimate mutualisms compared to intimate antagonisms (Fontaine et al. 2011).

Many explanations are possible for this lack of consistency between the structure–stability relationship in mutualistic networks based on modelling outcomes and what we observe in nature. Some of these explanations propose that network structure is the result of historical assembly processes that do not necessarily reflect selection for stability (Maynard et al. 2018). Others advocate that current models could be too simple to accurately reflect nature patterns, as models must be relatively complex to make predictions about real ecological systems (Evans et al. 2013). Here we focus on the latter and, specifically, in adding a key piece of complexity to mutualistic interaction models: incorporating the interaction cost into mutualistic dynamics. Mutualistic interactions are usually modelled as strictly mutually beneficial for the interacting partners. Mutualisms, however, involve both benefits and costs for the interacting species (Bronstein

2001, Morris et al. 2010, Aizen et al. 2014). Multiple costs can be associated with mutualistic interactions (Young and Young 1992, Gross and Mackay 1998, Traveset et al. 1998, Montesinos-Navarro et al. 2017), from competition for resources (Benadi et al. 2012, Valdovinos et al. 2013, 2016) to negative effects associated with the provision of resources (Sáez et al. 2014, Magrach et al. 2017). Hence, the inclusion of the cost of mutualistic interactions could directly affect the network structure–stability relationship, as the benefit of having more and more partners will not necessarily increase linearly, and could even decrease with increasing the number of interactions (Morris et al. 2010, Valdovinos et al. 2016).

The cost of mutualistic interactions can be easily incorporated using a consumer–resource approach (Holland et al. 2005, Chamberlain and Holland 2008, Holland and DeAngelis 2010), whereby the consumer species (e.g. pollinator) exploits a resource (e.g. pollen or nectar) supplied by the other partner species (e.g. plant) and in return provides a resource or a service (e.g. pollination). This approach has been used in studies assessing how changes in pollinators' behaviour (i.e. competition among consumers) affect species persistence (Valdovinos et al. 2013, 2016) and structural aspects of communities, such as population densities. However, it remains unknown whether costs inflicted by consumers to resources, e.g. those observed in plant–pollinator interactions where too many visits of pollinators diminish plant reproductive success (Sáez et al. 2014, Rollin and Garibaldi 2019), would impact the network structure–stability relationship. Even though the final outcome might be still beneficial for both partners, the incorporation of the cost into models of mutualistic dynamics could have a strong influence on the dynamics of the populations that interact within a community (Holland and DeAngelis 2010), ultimately affecting community stability and structural attributes.

In this study, we evaluate how the incorporation of the costs of mutualistic interactions affects the relationships between network structure and community stability and structural attributes. In particular, we tested whether the effect that species richness, connectance and modularity have on community stability and population densities change when including a cost function in a mutualistic dynamics model. To this end, we compared how alternative network structures differing in their species richness, connectance and modularity affect community persistence, resilience and average abundance (population density) of the mutualistic community, as well as persistence and average abundance of each mutualistic partner, by simulating the dynamics of mutualistic populations while taking into account the cost of these interactions.

Methods

Interaction networks

We used the algorithm of Thébault and Fontaine (2010) to generate interaction networks with different structure, varying species richness (number of species), connectance

(proportion of realized interactions) and modularity (degree of compartmentalization as in Stouffer et al. 2012, Douclicr and Stouffer 2015) across the extent of empirically observed ranges (Olesen et al. 2007). For each combination of species richness (20, 40, 80), connectance (0.1, 0.15, 0.2) and modularity (0.2, 0.3, 0.4, 0.5, 0.6) we generated 100 networks (i.e. 4500 interaction networks in total distributed around those parameter combinations). Even though nestedness has been related to community stability in mutualistic networks (Okuyama and Holland 2008, Thébault and Fontaine 2010), we did not include it in our study as built-in dynamical stability has been found for this metric in similar models to the one we used (Staniczenko et al. 2013) (see the Supplementary material Appendix 1 for more details).

Dynamic model

We used a population dynamics model that has been previously used to study the relationship between network structure and stability of mutualistic communities (Okuyama and Holland 2008, Thébault and Fontaine 2010), allowing us to compare our results with previous ones. This previous model includes a term that describes the mutualistic benefit that each species obtain from each interaction (described as a type II functional response) and simulates changes in species abundance of obligate mutualistic communities (i.e. where interacting species cannot survive without their interacting partners). To this model, we incorporated a term that accounts for the potential effects that the cost of mutualistic interactions can have on population dynamics, i.e. the negative effects on a species population change due to supplying resources to other species (Holland and DeAngelis 2010). Even though this model could be applicable to different mutualistic communities (e.g. plant–frugivore, plant–mycorrhizal), hereafter we refer to plant–pollinator communities as our study system for simplicity. In plant–pollinator systems, the plant provides resources to the pollinator, typically pollen or nectar and the pollinator provides the plant with pollen they carry from other plants. In this process, costs to the plant associated with the provision of a resource include damage to floral structures, removal of pollen that was already deposited in the stigmas, reward production, etc., while for pollinators pollen deposition (resource provision to the plant) does not seem to affect their population growth (Holland and DeAngelis 2010). Although there might be costs associated with pollinators due to the service of pollen dispersal, for simplicity we considered only costs associated with resource supply.

Because empirical information on the cost of mutualistic interactions is scarce, modelling each potential cause of cost separately becomes problematic. We therefore based our modelling approach on net benefit curves for which empirical evidence exists. In particular, we used a type II functional response to model interaction cost that combined with the type II functional response of the mutualistic benefit produce net-benefit curves that matched those empirically observed in plant–pollinator communities (Morris et al. 2010, Rollin

and Garibaldi 2019). When interaction cost is assumed to be absent, then the saturating benefit curve equals the net-benefit curve; when the cost is different from zero, the combination of the benefit and cost type II functional response curves may generate a unimodal curve (Supplementary material Appendix 1 Fig. A1), i.e. a net-benefit peak is followed by a decrease when increasing the frequency of interactions (Morris et al. 2010). Studies showing that higher number of visits can lead to flower damage causing a decrease in fruit production (Aizen et al. 2014, Sáez et al. 2014) also offer an example of such unimodal curve. While this shape qualitatively matches empirical observations, it is ultimately phenomenological. Our approach therefore constitutes a first step towards incorporating the cost of interactions into dynamics models, an essential yet absent feature from ecological and evolutionary mutualistic models in general.

The dynamic model we used is applicable to bipartite mutualistic communities, consisting of two groups of species, P and A , representing plants and pollinators (animals), respectively. The numbers of species within each group are represented by N_P and N_A respectively. P_i and A_j likewise represent the densities of plant species i and pollinator species j . The model was fully specified by the following set of ordinary differential equations:

$$\frac{dP_i}{dt} = P_i r_i - d_i P_i^2 + \sum_{j=1}^{N_A} \frac{c_{ij} A_j P_i}{\alpha_{ij}^{-1} + \sum A_k} - \sum_{j=1}^{N_A} \frac{q_{ij} A_j P_i}{\beta_{ij}^{-1} + \sum P_k} \quad (1)$$

$$\frac{dA_j}{dt} = A_j r_j - d_j A_j^2 + \sum_{i=1}^{N_P} \frac{c_{ji} P_i A_j}{\alpha_{ji}^{-1} + \sum P_k} \quad (2)$$

where r_i and r_j represent intrinsic growth rates of species i and j ; d_i and d_j are their density-dependent self-limitation; c_{ij} and c_{ji} are the maximum rate of mutualistic benefit (i.e. saturation level of the benefit); and α_{ij} and α_{ji} are the half saturation constants of mutualistic benefit. The last term on the right hand side of the plant equation (Eq. 1) represents the cost of the interactions with pollinators, where q_{ij} is the maximum rate of cost (i.e. saturation level of the cost, equals the saturation level of the benefit c_{ij} , except when assuming no cost where $q_{ij}=0$) and β_{ij} is the half saturation constant of the cost. Pollinator density changes are defined by Eq. 2 and do not include cost. Costs and benefits of the interaction between P_i and A_j saturate with the sum of the abundances (i.e. densities) of all the interaction partners (k) of P_i and A_j respectively, i.e. A_k and P_k . Hence, the cost on a given plant depends on the plants with which pollinators are shared, i.e. the sum in the denominator of the cost excludes plant species that do not interact with pollinator A_j .

Parameter values and initial species densities were randomly generated from uniform distributions within defined ranges based on previous studies (Okuyama and Holland 2008, Thébault and Fontaine 2010) (Supplementary material

Appendix 1 Table A1). To test for different levels of cost, we modified the half saturation constant of the cost (β_{ij}). In interaction terms, β_{ij} translates the number of pollinators from species j that need to interact with plant species i in order to attain a particular cost. In other words, low β_{ij} causes the saturation of the cost to occur slowly and, hence, more individuals of a pollinator species j will need to interact with plant species i to inflict a particular cost, which is equivalent to having a low cost. Conversely, high β_{ij} implies that fewer individuals of pollinator species j need to interact with plant species i to inflict a particular cost, which is equivalent to having a high cost. Values of β_{ij} were also selected from a uniform distribution where its maximum range was a proportion of α_{ij} , which allowed us to keep the cost lower than the benefit, such that the net benefit was positive, and to have different increasing levels of cost: minimum cost ($\beta_{ij} = [0.1, 0.25] \times \alpha_{ij}$), medium cost ($\beta_{ij} = [0.1, 0.5] \times \alpha_{ij}$) and maximum cost ($\beta_{ij} = [0.1, 0.75] \times \alpha_{ij}$). When cost was selected from a distribution with wider ranges, indicating even higher levels of cost ($\beta_{ij} = [0.1, 1] \times \alpha_{ij}$), this caused all species to go extinct. No cost was defined as $q_{ij} = 0$, such that the entire cost term of Eq. 1 equalled zero when no cost was assumed. Model simulations were carried out using the ode function (rkMethod=rk45dp7) of the deSolve package (Soetaert et al. 2010) in the R environment (<www.r-project.org>). Numerical solutions were obtained with a Runge–Kutta method of order 4. A time step of 0.01 was used to ensure solution stability. Simulations were run over 100 000 time steps.

Model analysis

For each of the 4500 networks with different interaction network structure, we ran the model four times, once with no cost and once with each level of half saturation constant of the cost (β_{ij}), while keeping all other parameters and initial abundances constant. At the end of each simulation (once stable equilibrium was reached), we recorded species persistence (the proportion of species that persisted with density $> 10^{-13}$), community resilience (dominant eigenvalue of the Jacobian matrix of the system at the final time step) and average species abundance (total abundance, i.e. density, divided by the number of species that persisted). We also recorded the species persistence and average species abundance within each interacting group, i.e. persistence of plants, persistence of pollinators, average plant species abundance (total plant abundance divided by the number of plant species that persisted) and average pollinator species abundance (total pollinator abundance divided by the number of pollinator species that persisted). We used the jacobian function from the numDeriv (Gilbert and Varadhan 2019) R package to numerically estimate the Jacobian matrices.

To assess the effects of incorporating the cost of mutualistic interactions on the network structure–community stability relationship, we fit structural equation models (SEMs) (Shipley 2000), using the piecewiseSEM (Lefcheck 2016) and lme4 (Bates et al. 2015) R packages. We built seven SEMs, one for each measure of community stability,

and each of the SEMs was formed by two linear models. The first linear model in all SEMs included modularity as the response variable and connectance and species richness as predictors, to take into account both the influence that connectance and species richness has on modularity as well as the indirect effects of these variables on the stability metric. The second linear model of each of the SEMs included one stability measure as the response variable (persistence, resilience, average abundance, persistence of plants, persistence of pollinators, average abundance of plants and average abundance of pollinators) and connectance, species richness, modularity, the interactions between these three factors and the cost of interactions (i.e. the average cost of all interactions on each network) as the predictor variables. The interaction terms in particular tell us how the inclusion of the cost in the models changes the effects that network structure has on community stability. The network structure metrics used as predictor variables were calculated based on the initial network structure, except for the resilience model, in which the network structure predictor variables were calculated at equilibrium, as resilience is a local stability measure and might thus be affected by network structure at equilibrium. We used a Gaussian distribution for all models.

In addition, to better understand the emergent changes in the relationship between network structure and resilience, we tested whether the mean and standard deviation of the Jacobian elements changed with increasing cost of interactions using linear regressions. Finally, to assess whether the cost of mutualistic interactions affects the dimensionality of ecological stability (Donohue et al. 2013), we tested for correlations between stability measures within each level of cost, i.e. no cost, low, medium and high cost. Changes in the correlation coefficients would indicate that the cost of interactions affect the dimensionality of ecological stability.

Results

We found that including the cost of mutualistic interactions into population dynamics models significantly affected the quantifiable relationship between network structure and community stability. In particular, when considering all species together, both connectance and species richness had significantly positive effects on persistence (persistence of all species, Fig. 1a, 2) and abundance (average abundance of all species, Fig. 1c, 2), and these effects were significantly reduced when increasing interaction costs. The significantly negative effect of modularity on abundance (Fig. 1c, 2) also became less negative when considering interaction costs. On the other hand, resilience was significantly negatively affected by connectance and modularity, and positively by species richness (Fig. 1b, 2), and all these effects of network structure were accentuated when taking into account the cost of species interactions.

In addition, higher interaction costs increased the mean and decreased the standard deviation of the Jacobian matrix elements ($t = 78.860$, $p < 0.001$; $t = -92.000$, $p < 0.001$, respectively), which may help explain the particularly strong

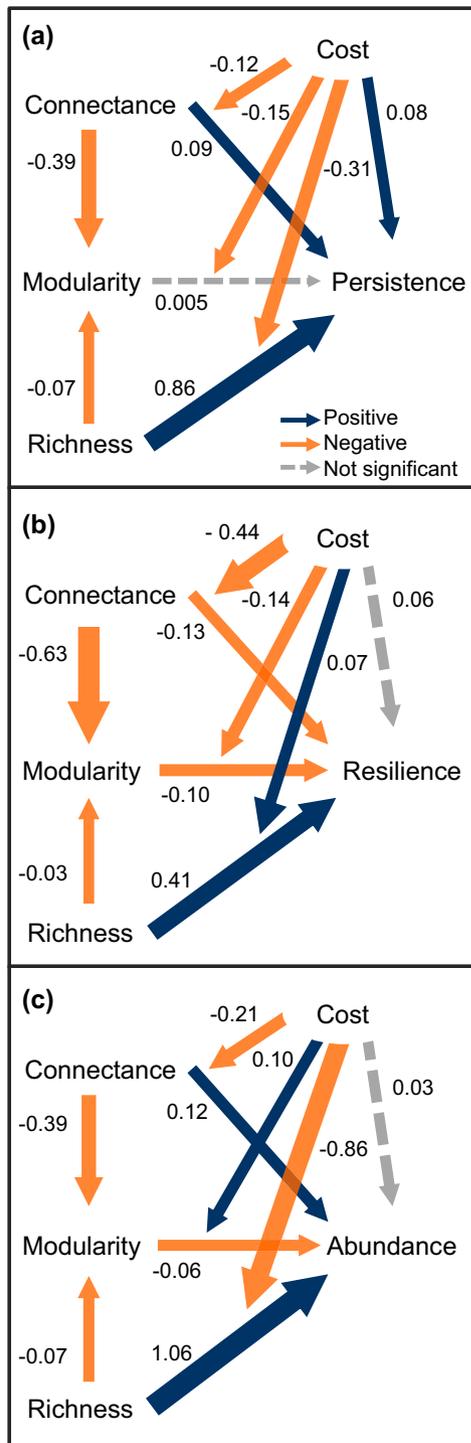


Figure 1. Structural equation models examining the effects of mutualistic interactions cost on the network structure–community stability and network structure–structural attributes relationships. We evaluated two measures of community stability, (a) species persistence and (b) resilience, and one measure of community structure, (c) abundance. Arrows pointing to other arrows represent interaction terms, i.e. changes in slope. Solid arrows represent unidirectional statistically significant relationships ($p < 0.05$), while dashed arrows represent non-significant relationships. Arrow width is proportional to the standardised path coefficient, which is shown next to each arrow.

relationship between resilience and our network metrics. Furthermore, the cost of interactions did not strongly affect the correlations between stability metrics (persistence, resilience and abundance), suggesting minimal changes occurred in the dimensionality of ecological stability of these mutualistic networks (Supplementary material Appendix 1 Fig. A2).

When assessing the effects of network structure on the persistence and abundance of plants and pollinators separately, we found the same general trends as for the entire assemblage (Fig. 3, Supplementary material Appendix 1 Fig. A3, A4). Specifically, the positive effects of species richness and connectance on the persistence and abundance of plant and pollinator species significantly decreased when considering the cost of interactions. Furthermore, the significantly negative effect that modularity had on the abundance of plants (Fig. 3b) and pollinators (Fig. 3d) was diminished, i.e. became less negative, when increasing the cost of interactions (Supplementary material Appendix 1 Fig. A3, A4).

Discussion

We found that including the cost of mutualistic interactions into population dynamics models has a strong impact on the relationship between network structure and community stability, and network structure and community structural attributes, both when considering all species together as well as each interacting group (plants and pollinators) separately. In particular, after including interaction costs, species richness, connectance and modularity did not seem to have such strong effects on species persistence and abundance as previously thought (Okuyama and Holland 2008, Thébaud and Fontaine 2010). Incorporating costs into mutualisms makes the dynamics of mutualisms look more like the dynamics of antagonisms, thus diluting the differences in network structure–stability relationships between antagonistic versus mutualistic communities. Furthermore, by analysing the effects of network structure on persistence and abundance of each interacting group separately, it became clear that even though we only included the interaction cost on one interacting partner (plant), the effects of costs easily spill over to the entire community.

Higher species richness and higher connectance had a less positive effect on species persistence and abundance when taking into account the cost of interactions, as more links between species might not necessarily imply greater net benefits. For example, a plant might receive greater net benefits from one specific interaction and be better off by maximising just that interaction, rather than interacting with many pollinator species. It has been suggested that apparent facilitation in mutualistic communities could be one of the reasons favouring highly connected communities (Thébaud and Fontaine 2010). However, although sharing interaction partners in a network could be particularly beneficial for certain species, it could also involve additional costs for other species (Vilà et al. 2009), such as competition for pollinators among plants (Levin and Anderson 1970, Brown et al. 2002,

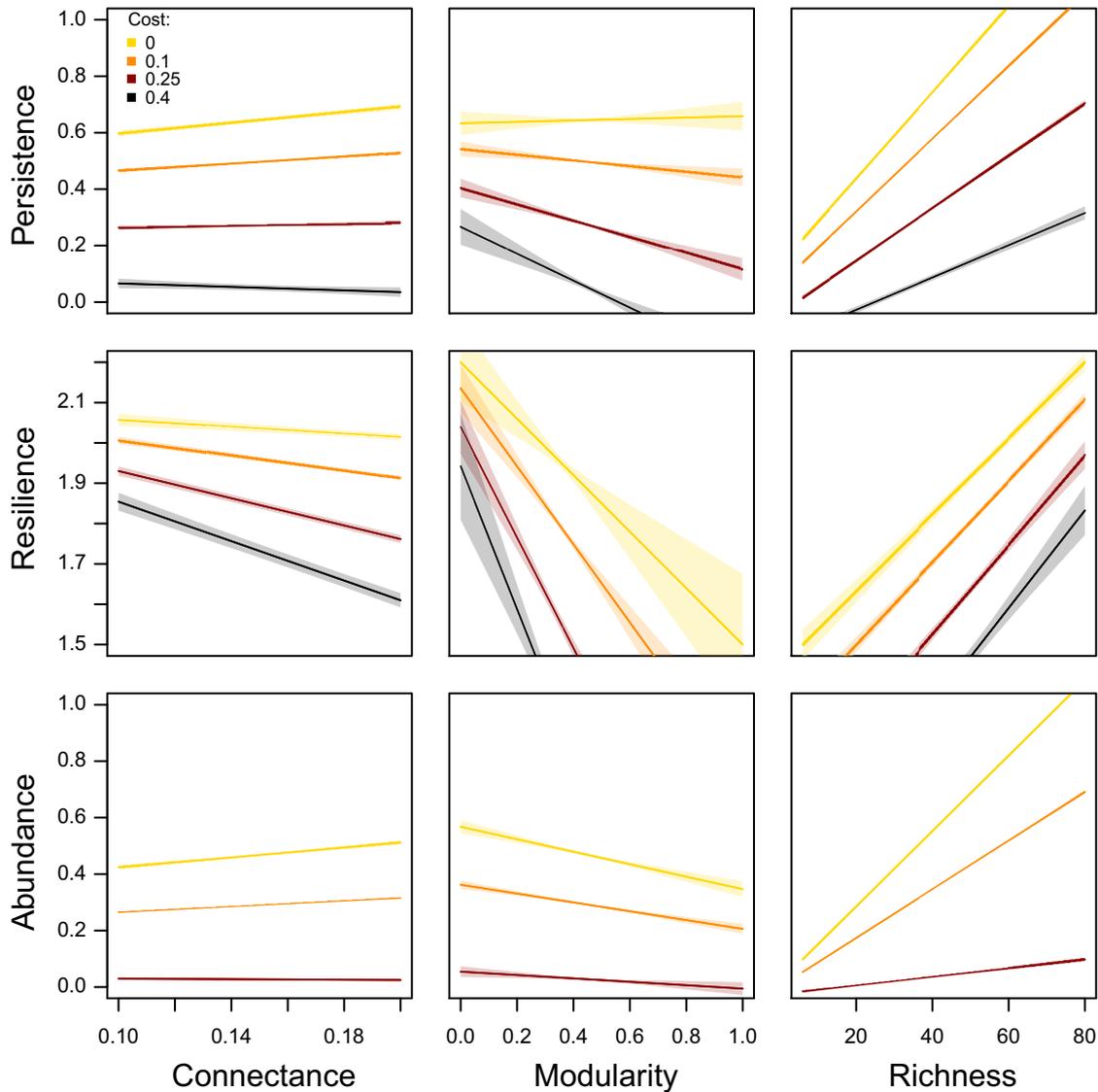


Figure 2. Relationships between predicted persistence, resilience or abundance and network structure (connectance, modularity, species richness) under increasing levels of cost (0, 0.1, 0.25, 0.4). Cost values indicate the average value of all interaction costs within a network. Predicted values were estimated based on the second linear model of each of the SEMs, using the predict R function, where only values of one network attribute were allowed to change while values from the other network attributes were kept constant at their mean across all simulated networks. Predicted abundance values for the highest level of cost (0.4) are not shown as they were mostly below 0.

Mitchell et al. 2009), pathogen transmission between plant (or pollinator) species via pollinators (or plants) (Durrer and Schmid-Hempel 1994, Card et al. 2007), and hetero-specific pollen deposition (Arceo-Gómez and Ashman 2011, Briggs et al. 2016). Similarly, reducing competition among pollinators via adaptive foraging eliminates the link between connectance and pollinators' persistence (Valdovinos et al. 2016). In addition, having more interacting partners means that there are more 'channels' by which a species is susceptible to negative effects, e.g. via sudden changes in the abundance of a partner.

Incorporating the cost of interactions also reduced the negative effect that modularity has on species abundance

when considering all species together, as well as when looking at plants and pollinators separately. The modularity pattern in empirical mutualistic communities has been widely observed (Olesen et al. 2007, Dupont and Olesen 2009, Watts et al. 2016), and the fact that this pattern has persisted in nature over time suggests that its effect on community stability ought not to be exceedingly detrimental, as it should have otherwise driven these communities to extinction. Therefore, even if modularity decreases the persistence of species (Thébaud and Fontaine 2010 and our study), it probably compensates by having low or no effects on the abundance of species in a community. Moreover, modularity has been shown to decrease the rate of spread of negative effects in

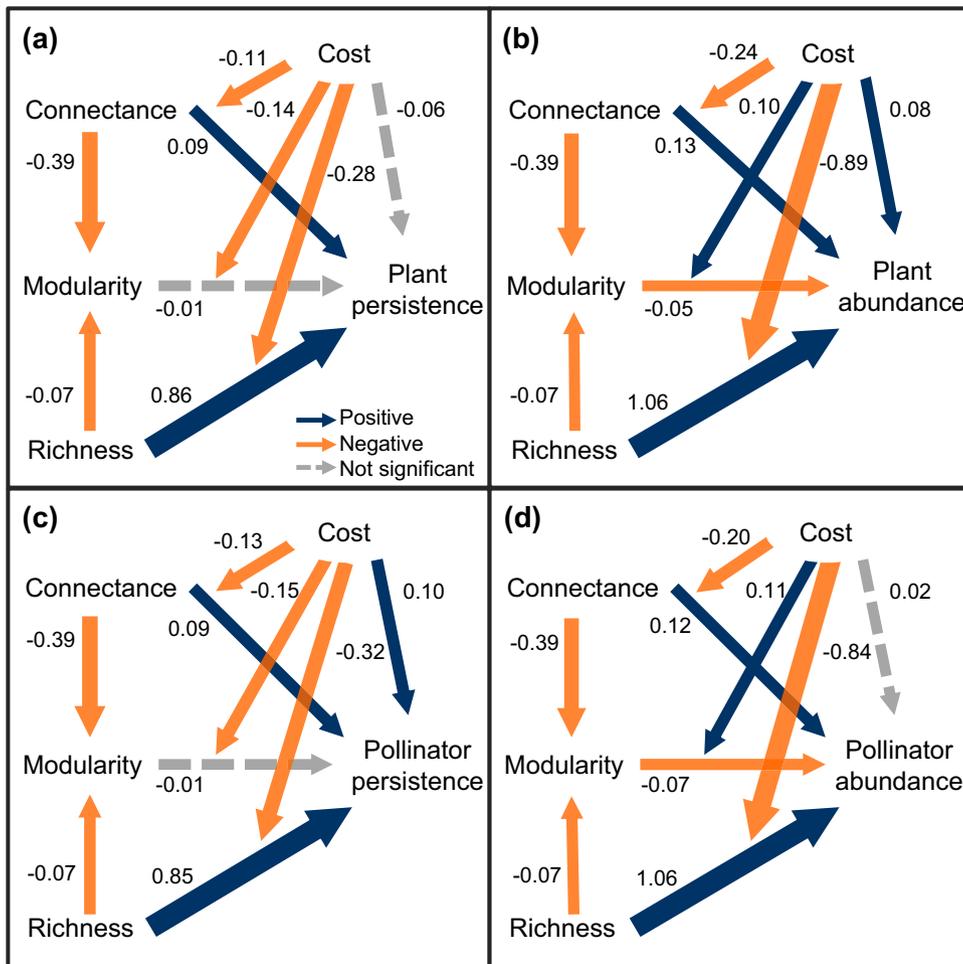


Figure 3. Structural equation models examining the effects of mutualistic interactions cost on the network structure–community stability and network structure–structural attributes relationships of plants (a–b) and pollinators (c–d). Legend as in Fig. 1.

antagonistic (Stouffer and Bascompte 2011) and, recently, on mutualistic communities (Gaiarsa and Guimarães 2019) which could favour stability.

Our study also shows that the incorporation of interaction costs increases the positive effect of species richness, and the negative effects that modularity and connectance have on resilience. Incorporating the cost of interactions implies that interaction networks move from a complete set of positive indirect effects, such as apparent facilitation, to a mixed set of both positive and negative indirect effects. The presence and intensity of indirect effects can affect local community stability (Grilli et al. 2016), suggesting that a higher proportion of negative indirect effects potentially reduces the ability of communities to return to equilibrium after disturbance. It is also possible that the positive effect of cost on the mean Jacobian values mediates the decrease in resilience.

Our results indicate that different measures of stability, such as persistence and resilience, may have different responses to interaction network structure. In addition, local stability measures, such as resilience, can be calculated in different ways, which can lead to different conclusions about the network structure effect on local stability (Thébault and Fontaine 2010,

Feng and Takemoto 2014). Hence, the effect of network structure on community stability might not be as generalisable as we thought, but rather specific to the stability measured used. Despite the differences in the changes observed for the network structure–stability relationship according to the stability metric used, the strong correlations between our different measures of stability did not change when taking into account the cost of interactions. The absence of changes in these correlations suggests that the cost of interactions does not affect the dimensionality of ecological stability. Furthermore, the strong correlations observed among stability measures indicate the dimensionality of ecological stability is low, and hence that similar processes may be affecting the multiple components of stability (Donohue et al. 2013).

Empirical research on food webs has suggested that network attributes might not be associated with food-web stability, and that this absence of a complexity–stability relationship is due to the intrinsic energetic organization of these food webs (Neutel and Thorne 2014, Jacquet et al. 2016). Although these findings apply only to antagonistic networks, and are based on only one measurement of community stability, it remains to be explored whether empirical mutualistic

networks present the same patterns. In addition, some studies suggest that any network structure can have different effects on stability, and that the differences strictly depend on the parameters choice (Grilli et al. 2016). Furthermore, it has been recently proposed that network patterns could be a relic of assembly processes, such that network attributes would result from the mechanisms that determine how species are incorporated into the community rather than by selective forces (Maynard et al. 2018). Even though the interaction coefficients used in this previous study were negative (representing competition), they bring up important questions that need to be addressed in studies incorporating the positive (benefit) and negative (cost) aspects of mutualistic interactions.

Overall, we found that taking into account the cost-benefit nature of mutualistic interactions, which represents more accurately the functional response for the net benefits of mutualisms (Holland and DeAngelis 2010, Morris et al. 2010), reduced the strength of the relationship between network structure (species richness, connectance and modularity) and species persistence, and network structure and population densities. These results demonstrate the need to take into consideration the cost of mutualisms as an essential feature of these interactions. In this respect, even though our model is phenomenological and restricted to obligatory mutualisms, it represents a starting point for the incorporation of costs associated with the provision of a resource into population dynamics models, a component largely absent from ecological and evolutionary interaction network models (Valdovinos 2019). Our study also calls for greater emphasis of empirical research on the quantification of costs associated with mutualistic interactions, necessary for the development of mechanistic models with which to assess, for instance, the effects of costs in facultative mutualisms. Finally, by including the cost of interactions in mutualistic models, either at the consumer level via resource competition (Valdovinos et al. 2016) or, as we do here, at the resource level via costs associated with the provision of a resource, we revive the question of whether the structure of mutualistic networks determines community stability or whether we need to rethink what information the network needs to contain so that it can reveal something about system function.

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Author contributions – GP, DPV, EB designed the study; GP performed modelling work, analysed output data and wrote the first

draft of the manuscript; DBS contributed to modelling; all authors contributed substantially to revisions.

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Supplementary material (available online as Appendix oik-06503 at <www.oikosjournal.org/appendix/oik-06503>). Appendix 1.