

Structure–stability relationships in networks combining mutualistic and antagonistic interactions

Alix M. C. Sauve, Colin Fontaine and Elisa Thébault

A. M. C. Sauve (sauve@biologie.ens.fr) and C. Fontaine, Dépt Écologie et Gestion de la Biodiversité, Laboratoire Conservation des Espèces, Restauration et Suivi des Populations, UMR 7204 CNRS-MNHN, Muséum National d'Histoire Naturelle, 61 rue Buffon, FR-75005 Paris, France. – AMCS and E. Thébault, Biogéochimie et Écologie des Milieux Continentaux, UMR 7618 (CNRS, UPMC, ENS, IRD, AgroParisTech), École Normale Supérieure, 46 rue d'Ulm, FR-75005 Paris, France.

The relationship between the structure of ecological networks and community stability has been studied for decades. Recent developments highlighted that this relationship depended on whether interactions were antagonistic or mutualistic. Different structures promoting stability in different types of ecological networks, i.e. mutualistic or antagonistic, have been pointed out. However, these findings come from studies considering mutualistic and antagonistic interactions separately whereas we know that species are part of both types of networks simultaneously. Understanding the relationship between network structure and community stability, when mutualistic and antagonistic interactions are merged in a single network, thus appears as the next challenge to improve our understanding of the dynamics of natural communities. Using a theoretical approach, we test whether the structural characteristics known to promote stability in networks made of a single interaction type still hold for network merging mutualistic and antagonistic interactions. We show that the effects of diversity and connectance remain unchanged. But the effects of nestedness and modularity are strongly weakened in networks combining mutualistic and antagonistic interactions. By challenging the stabilizing mechanisms proposed for networks with a single interaction type, our study calls for new measures of structure for networks that integrate the diversity of interaction.

Stability is a key issue in ecology, directly related to the study of ecosystem response to disturbances and to the understanding of species coexistence in diverse communities. The link between community complexity and stability has been a long held debate (McCann 2000, Ives and Carpenter 2007). Classical theory initiated by May forty years ago demonstrated that high complexity triggers instability (May 1972), a prediction that is in contradiction with the inherent complexity of natural communities. Because May's theory was based on random interactions among species, ecologists have tried to identify non-random patterns that could promote stability in complex communities. In the past decades, the detailed analysis of empirical datasets has highlighted such non-random patterns in the structure of ecological networks (Bascompte et al. 2003, Krause et al. 2003). Recent studies bring two important insights to the complexity–stability debate. First, the link between complexity and stability depends on the type of interaction considered (Thébault and Fontaine 2010, Allesina and Tang 2012), with the effects of complexity of antagonistic and mutualistic networks on stability being opposite. Second, beyond traditional measures of network complexity (i.e. diversity and connectance), finer measures of network structure, such as nestedness and modularity, can strongly affect stability. On one hand, nestedness, that characterizes the tendency for specialist species

to interact with a subset of the species that interact with more generalist ones (Bascompte et al. 2003), tends to beget stability in mutualistic networks (Memmott et al. 2004, Okuyama and Holland 2008). On the other hand, modularity, that characterizes the organization of networks into subgroups of species that interact more with each other than with other species (Newman and Girvan 2004), promotes food web stability (Stouffer and Bascompte 2011).

Contrary to May's seminal work, most recent studies on the relationship between network structure and stability consider one single type of interaction at a time, studying separately mutualistic and antagonistic networks. Since all species can be involved in both mutualistic and antagonistic networks, considering them separately is artificial and leads to ignore an important aspect of the organisation in real communities (Fontaine et al. 2011, Kéfi et al. 2012). Very few studies have considered community dynamics with both mutualistic and antagonistic interactions (but see, Ringel et al. 1996, Jang 2002, Allesina and Pascual 2008, Melián et al. 2009, Mougi and Kondoh 2012). These studies showed that antagonistic interactions can indirectly affect the dynamics of mutualistic interactions (Ringel et al. 1996, Jang 2002). They also revealed that the proportion of mutualistic to antagonistic interactions matters for community stability (Allesina and Pascual 2008, Melián et al.

2009, Mougi and Kondoh 2012) and can further modify complexity–stability relationships (Mougi and Kondoh 2012). However, this research has focused on topological properties that either do not differentiate interaction types, such as the overall network connectance (May 1972), either do not take into account the heterogeneity in degree distributions, such as the relative proportion of interaction types in the network (Allesina and Pascual 2008, Mougi and Kondoh 2012). They have omitted the importance of the respective structures of mutualistic and antagonistic sub-networks on the stability of networks merging both types of interactions. In particular, we ignore whether the links between network structure and stability found in isolated mutualistic or antagonistic networks (Okuyama and Holland 2008, Thébault and Fontaine 2010, Stouffer and Bascompte 2011) still hold when they are considered together.

Herein, we investigate the effect of network structures on community stability focusing on the respective role of mutualistic and antagonistic interactions. Specifically, we test whether combining mutualistic and antagonistic interactions within the same super-network changes the relationship between network structure and community stability known for networks with a single interaction type. We answer this question thanks to a dynamical model of interaction networks that mimics interactions among three guilds: a mutualistic guild M , an antagonistic guild H , and a guild P which species have both mutualistic and antagonistic interactions (Fig. 1). Although this type of network is still a simplified version of natural ecological networks, the structure corresponds to that of the few existing empirical datasets describing networks of different interaction types (i.e. plants interacting with pollinators and phytophagous animals, such as in Melián et al. 2009, Fontaine et al. 2011 and Pockock et al. 2012). We tested the effects of four aspects of structure in the antagonistic and mutualistic sub-networks – connectance, diversity, modularity and nestedness – on two measures of stability – persistence and resilience.

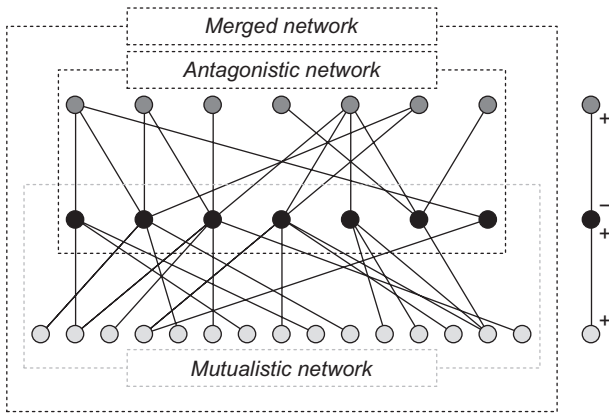


Figure 1. A merged network including an antagonistic sub-network and a mutualistic sub-network, here the example of the interconnection of a pollination network with a herbivory network. Black nodes are species with both mutualistic and antagonistic interactions (for instance plant species), light grey nodes are mutualistic species M (for instance pollinator species), and dark grey nodes are antagonistic species H (for instance herbivore species).

Material and methods

Model

Our aim is to test whether structure–stability relationships found in networks with one single type of interaction still hold in the context of networks with both mutualistic and antagonistic interactions. To do so, we build tripartite networks resulting from merging two bipartite networks, a mutualistic and an antagonistic networks, that share the same interconnecting species (Fig. 1). We analyse their stability with a dynamical model that followed the same assumptions than previous models used to assess structure–stability relationships in isolated mutualistic and antagonistic networks (Okuyama and Holland 2008, Bastolla et al. 2009, Thébault and Fontaine 2010). Our approach thus allows direct comparison of the results with previous ones obtained for isolated mutualistic or antagonistic networks. As modifying such assumptions can change the structure–stability relationship (Thébault and Loreau 2005), we verified the robustness of our results with another model respecting the constant interaction effort hypothesis (as in Mougi and Kondoh 2012, Supplementary material Appendix 1 Fig. A1, A2).

Mutualistic and antagonistic networks are constructed separately, each one with a given structure that is not random but varies in diversity, connectance, nestedness and modularity, following the method of Thébault and Fontaine (2010, see Supplementary material). Simulation of species dynamics is based on a consumer–resource model with a saturating functional response for all interactions, as was done in previous models for mutualistic and antagonistic networks (Holland et al. 2002, Bastolla et al. 2009, Thébault and Fontaine 2010). Species dynamics in a given merged network can be described by the following set of equations:

$$\begin{aligned}
 (1) \quad \frac{dM_i}{dt} &= r_{M_i} M_i - I_{M_i} M_i^2 + \sum_{j=1}^{S_p} \frac{c_{ji}^{(mut)} M_i P_j}{(\alpha_{ji}^{(mut)})^{-1} + \sum_{P_k \in \text{mut}(M_i)} P_k} \\
 (2) \quad \frac{dH_i}{dt} &= r_{H_i} H_i - I_{H_i} H_i^2 + \sum_{j=1}^{S_p} \frac{c_{ji}^{(ant)} H_i P_j}{(\alpha_{ji}^{(ant)})^{-1} + \sum_{P_k \in \text{preys}(H_i)} P_k} \\
 (3) \quad \frac{dP_i}{dt} &= r_{P_i} P_i - I_{P_i} P_i^2 - \sum_{j=1}^{S_H} \frac{c_{ij}^{(ant)} H_j P_i}{(\alpha_{ij}^{(ant)})^{-1} + \sum_{P_k \in \text{preys}(H_j)} P_k} \\
 &\quad + \sum_{j=1}^{S_M} \frac{c_{ij}^{(mut)} M_j P_i}{(\alpha_{ij}^{(mut)})^{-1} + \sum_{M_k \in \text{mut}(P_i)} M_k}
 \end{aligned}$$

H_p , M_p and P_i are the densities of antagonistic species i ($i \in [1; S_H]$, with S_H the diversity of antagonists), mutualistic species i ($i \in [1; S_M]$, with S_M the diversity of mutualists), and interconnecting species i ($i \in [1; S_p]$, with S_p the diversity of interconnecting species). The first term of the equations is the intrinsic growth rate. We assume that we have

obligate mutualism and antagonism for the respective guilds of mutualists and antagonists ($r_{H_i} < 0$ and $r_{M_i} < 0$). Interconnecting species are supposed to be facultative mutualists ($r_{P_i} > 0$). The second term is self-limitation, which is density dependent. The last terms are the interaction terms that saturate with mutualistic partners densities for the mutualistic interactions, or with interconnecting species densities for the antagonistic interactions. Within these interaction terms, $\alpha_{ij}^{(mut,ant)}$ is the half-saturation constant of the functional response, and $c_{ij}^{(mut,ant)}$ is the maximum rate of mutualism or antagonism. It is set to zero if the species i and j do not interact. Parameter values are given in Supplementary material Appendix 2 Table A1, and were chosen to allow comparison with previous studies (Okuyama and Holland 2008, Thébault and Fontaine 2010). The initial conditions of species densities are sampled according to a uniform distribution, between 10^{-12} (the extinction threshold) and 1, a range that is the same as for the final densities at equilibrium. The model was simulated numerically in C++ using functions of *GSL* (GNU Scientific Library). Numerical solutions were obtained with a Runge–Kutta method of order 4 with an adaptive step size. The dynamics of each merged network were simulated until a stable equilibrium was reached (coefficient of variation of each species density $< 10^{-6}$).

Simulations

To understand how the different structural patterns of mutualistic and antagonistic networks (each defined by their diversity, connectance, modularity and nestedness) affect the stability of complex merged networks, we performed two types of simulations, each with the same number of interconnecting species ($S_p = 24$). Our results remain qualitatively the same for different values of S_p .

1) *Antagonistic sub-network centred simulations* allow answering the following questions: what is the relationship between antagonistic structure and the whole community stability depending on mutualistic sub-network complexity? How does the initial structure of the mutualistic sub-network affect the persistence of the antagonistic sub-network? To do so, antagonistic networks, with varying diversity, connectance, nestedness and modularity, are associated with mutualistic networks of contrasted connectance and diversity. We define four cases for the structure of the mutualistic networks, combining different cases of diversity and connectance $\{S_M, C_{mut}\} = \{[40, 0.10], [40, 0.25], [16, 0.10], [16, 0.25]\}$.

2) *Mutualistic sub-network centred simulations* are similar to the previous one, and allow answering the following questions: what is the relationship between mutualistic structure and the whole community stability depending on antagonistic sub-network complexity? How does the initial structure of the antagonistic sub-network affect the persistence of the mutualistic sub-network? To do so, mutualistic networks, with various structures are associated with antagonistic networks of contrasted connectance and diversity $\{S_H, C_{ant}\} = \{[40, 0.10], [40, 0.25], [16, 0.10], [16, 0.25]\}$.

We performed these two types of simulations for three cases: 1) when the average maximum rates of interaction

are equal between mutualistic and antagonistic sub-networks ($\bar{c}^{(mut)} = \bar{c}^{(ant)}$), 2) when average mutualism rate is superior to the antagonism rate ($\bar{c}^{(mut)} > \bar{c}^{(ant)}$), and 3) when the average mutualism rate is inferior to the antagonism rate ($\bar{c}^{(mut)} < \bar{c}^{(ant)}$). The average value \bar{c} of maximum rate of interaction c_{ij} is here used as a proxy of interaction strength. Overall, for the two types of simulations (antagonistic or mutualistic sub-network centred), we cross the four cases of combined diversity and connectance with the three cases of relative interaction strengths, giving us a total of 24 distinct sets of simulations (Supplementary material Appendix 2 Table A2). This simulation design allows us as well to test the sensitivity of the results to the relative interaction strengths in both sub-networks and to different combinations of initial structures of each sub-network (Supplementary material Appendix 3 Fig. A3, A4; Supplementary material Appendix 4 Fig. A5).

Analysis of the network structure

We characterize the structure of each sub-network using the following indices. Species diversity S for the mutualistic and antagonistic sub-networks are defined as follows: $S_{mut} = S_p + S_M$ and $S_{ant} = S_p + S_H$. Connectance C is the proportion of realized links among the possible ones, and is calculated as follows for mutualistic and antagonistic sub-networks: $C_{mut} = L_{mut}/(S_p \times S_M)$ and $C_{ant} = L_{ant}/(S_p \times S_H)$, with L the number of links of each sub-network. Each sub-network is also characterized by its nestedness N and its modularity Q . A network is nested when species connected with specialists belong to a proper subset of the species connected with generalists (Almeida-Neto et al. 2008, Joppa et al. 2009, Tylianakis et al. 2010). NODF metric (nestedness metric based on overlap and decreasing fill) of Almeida-Neto et al. (2008) is used to estimate the nestedness in the networks we model. The modularity Q of a network measures the strength of community structure, in other words how much a network is divided into sub-groups (Newman and Girvan 2004). Modularity Q is calculated using the formula developed for bipartite networks (Thébault 2013, Barber 2008).

Stability of the network

We consider network persistence which is the proportion of species persisting at the end of the simulation of community dynamics. At equilibrium, we also measure network resilience, the capacity of the system to return to equilibrium after a short and small disturbance, expressed as the absolute value of the greatest real part of eigenvalues λ of the jacobian matrix J ($|\max(\text{Re}(\lambda(J)))|$, Gunderson 2000). These two measures of stability give two very different insights of community stability (Grimm and Wissel 1997) and are traditionally used to evaluate the links between structure and stability of ecological networks.

Stability–structure relationship: dealing with multicollinearity of variables

Connectance, diversity, modularity and nestedness measures are known to be tightly correlated (Fortuna et al. 2010, James et al. 2012). We use path analyses to understand the relationships between the structure variables and network

stability, and to go beyond the problematic multicollinearity of variables (Wright 1934). In a path analysis, a model that relates variables in a path diagram is tested. For instance, in our path diagram, $(S_{mut} \rightarrow N_{mut})$ corresponds to the direct effect of mutualistic diversity on mutualistic nestedness. This effect is associated with a path coefficient c that quantifies the relationship between the two variables. This analysis allows confirming relationships among variables, and considering effects of a given variable as mediated through other variables of the model (Grace and Pugsek 1998). The methods to calculate the effect mediated through other variables is explained in figure legends. We use here the same path diagram as Thébault and Fontaine (2010): we consider that connectance, diversity, nestedness and modularity of both mutualistic and antagonistic networks can affect stability, and that the effects of connectance and diversity can be mediated through the influence of nestedness and modularity on stability. We make the assumption that we can compare different path analysis outcomes when they are obtained with the same model, and when the regression coefficients are standardized.

As during the dynamics some species go extinct, the structure changes in both sub-networks which leads to differences between initial (i.e. before the simulation of species dynamics) and final (i.e. at equilibrium) sub-network structures. Therefore, for the analyses on persistence we consider the initial structures, as they define the starting point of the dynamics. For the analyses on resilience we have to consider the final sub-network structures, as resilience is a local measure of stability, at the final state of the network. We take into account the effect of the structure of both mutualistic and antagonistic sub-networks in one single path analysis (Fig. 3, 4).

These path analyses are performed using the sem package of R (software environment for statistical computing and graphics).

Results

Effects of mutualistic and antagonistic sub-network complexity on species persistence

Our networks always reach a stationary equilibrium after running the population dynamics. During the transient dynamics, some species go extinct leading to persistence values that depend on the initial sub-network structures (Fig. 2). For more simplicity, connectance and diversity of each sub-network are gathered in the term $S \times C$ in Fig. 2, related to May's definition of complexity (May 1972). The initial antagonistic diversity S_{ant} and connectance C_{ant} decrease the persistence of the merged network (Fig. 2a), whereas the initial mutualistic diversity S_{mut} and connectance C_{mut} increase its persistence (Fig. 2b). The antagonistic and the mutualistic parts of merged networks affect each other's persistence as the antagonistic diversity and connectance decrease the persistence of both mutualists and antagonists (Fig. 2a) and the diversity and connectance of mutualistic sub-networks increases the persistence of both mutualists and antagonists (Fig. 2b). This result holds for different relative interaction strengths in mutualistic and antagonistic sub-networks.

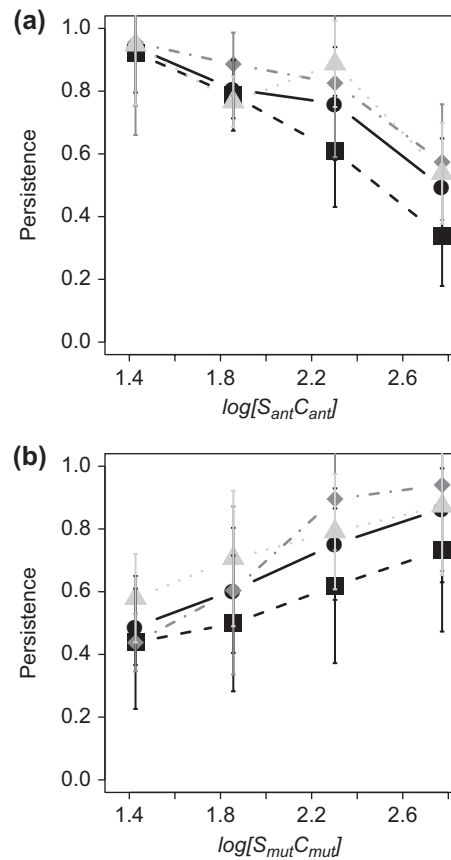


Figure 2. (a) effects of antagonistic complexity on persistence (mean \pm SD) for the mutualistic sub-network centred simulations; (b) effects of mutualistic complexity on persistence (mean \pm SD) for the antagonistic sub-network centred simulations. Complexity of a given sub-network is expressed here as the product of its connectance and diversity. The antagonistic complexity is $S_{ant} \times C_{ant}$ where $S_{ant} = S_p + S_H$ is the antagonistic diversity and C_{ant} the antagonistic connectance. The mutualistic complexity is $S_{mut} \times C_{mut}$ where $S_{mut} = S_p + S_M$ is the mutualistic diversity and C_{mut} the mutualistic connectance. Solid and black lines correspond to total persistence, dark grey and dashed lines to interconnecting species persistence, grey and dot-dashed lines to mutualist persistence, light grey and dotted lines to antagonist persistence.

Overall persistence increases as the relative strength of mutualistic interactions increases over antagonistic interaction strength (Supplementary material Appendix 3 Fig. A3).

Contributions of connectance, diversity, nestedness and modularity of both mutualistic and antagonistic sub-networks on overall community stability

Antagonistic initial connectance and diversity always decrease the persistence of the whole system (Fig. 3). Opposite effects are found for mutualistic connectance and diversity (Fig. 3).

Modularity and nestedness effects on persistence are always weak (or null) (Fig. 3). These effects are negative for mutualistic modularity and antagonistic nestedness, and null for mutualistic nestedness and antagonistic modularity (Fig. 3). These results hold for varying relative interaction strengths in mutualistic and antagonistic sub-networks

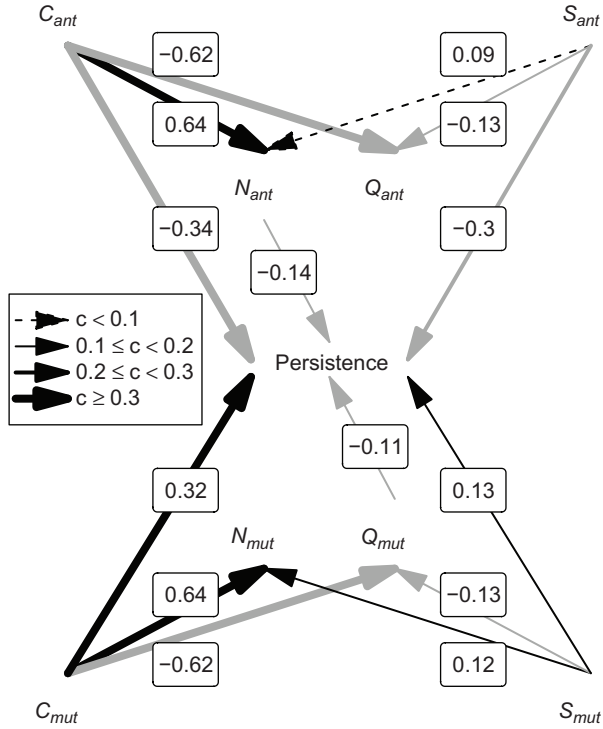


Figure 3. Path diagram of the effects on persistence of the initial structure of the mutualistic sub-network and the antagonistic sub-network, when average interaction strengths are the same in both sub-networks. The legend box indicates the relation between the strength of path-coefficients c and arrow thickness. The negative effects are coloured in grey, and the positive ones in black. The path diagram allows considering the direct effects of antagonistic and mutualistic connectance C and diversity S ($C \rightarrow Stability$, $S \rightarrow Stability$), and their effects mediated by nestedness N and modularity Q (respectively for connectance and diversity ($C \rightarrow N$) \times ($N \rightarrow Stability$) + ($C \rightarrow Q$) \times ($Q \rightarrow Stability$) and ($S \rightarrow N$) \times ($N \rightarrow Stability$) + ($S \rightarrow Q$) \times ($Q \rightarrow Stability$)). Hence, the net effect of connectance or diversity is given by the sum of direct effects and effects mediated by nestedness and diversity on stability (for instance, the net effect of mutualistic connectance is $(C_{mut} \rightarrow Stability) + (C_{mut} \rightarrow N_{mut}) \times (N_{mut} \rightarrow Stability) + (C_{mut} \rightarrow Q_{mut}) \times (Q_{mut} \rightarrow Stability)$). [NB: X_{mut} = mutualistic X ; X_{ant} = antagonistic X . e.g.: C_{mut} = mutualistic connectance].

(Supplementary material Appendix 3 Fig. A4) and are not affected qualitatively by the relative complexity of each sub-network: the effects of connectance and diversity are always stronger than the effects of nestedness and modularity for both sub-networks (Supplementary material Appendix 4 Fig. A5).

The final structures of both mutualistic and antagonistic sub-networks also influence the resilience of the merged network. Greater antagonistic connectance and diversity lower the resilience (Fig. 4). In contrast, the more connected and diverse the mutualistic sub-network is, the more resilient the merged network is (Fig. 4). As for persistence, the effects of mutualistic and antagonistic structures on resilience are mostly due to connectance and diversity effects rather than effects of nestedness and modularity that are weak or null (Fig. 4). Finally, it is interesting to note that for both persistence and resilience the effects of sub-network structure on stability are of similar magnitude, although opposite, for antagonistic and mutualistic sub-networks.

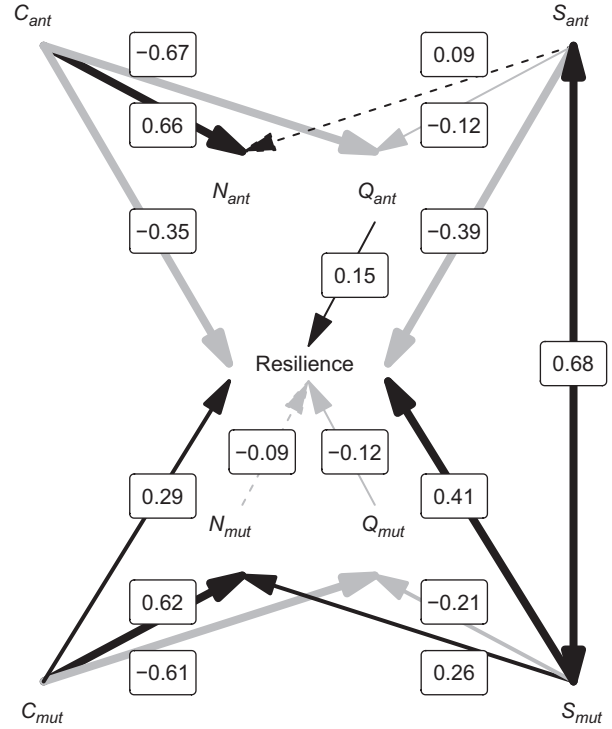


Figure 4. Path diagram of the effects on resilience of the final structure of the mutualistic sub-network and the antagonistic sub-network, when average interaction strengths are the same in both sub-networks. Legend as in Fig. 3.

In merged networks, the observed changes in structures of sub-networks during the dynamics at first appear to be the same as in isolated communities (Thébault and Fontaine 2010, Supplementary material Appendix 5, Fig. A6A–B, Fig. A7A–B). The mutualistic sub-network tends to be more nested and less modular whereas the antagonistic sub-network tends to be less nested and more compartmented. However, when taking into account changes in connectance and diversity that are known to influence changes in nestedness and modularity, only the decrease in antagonistic nestedness is confirmed while the other trends are modified or disappear (Supplementary material Appendix 5 Fig. A6C–D, Fig. A7C–D).

Discussion

In this study, we test if the structure–stability relationships known for mutualistic and antagonistic bipartite networks in isolation are robust when they are merged into a single super-network. On one hand, our results challenge the relevance of nestedness and modularity of mutualistic and antagonistic sub-networks when they are part of a single super-network. This suggests that stabilizing mechanisms proposed for networks with a single interaction type are not necessarily true when considering networks that include both mutualistic and antagonistic interactions. On the other hand, our result also unveils the robustness of the relationships between complexity (in terms of connectance and diversity) and stability known for networks with a single interaction type.

The complexity of the mutualistic part of the super-network fosters its stability, in contrast with the complexity of the antagonistic part. In what follows, we discuss mechanisms explaining our results in the light of recent literature. We conclude with suggestions on ways to deepen our understanding of the structure–stability relationship for networks merging mutualistic and antagonistic interactions.

The relevance of nestedness for community stability has been strongly questioned during the past years. While some studies emphasized that nestedness was related with mutualistic or antagonistic network stability (Bastolla et al. 2009, Thébault and Fontaine 2010, Allesina and Tang 2012), others found weak links between nestedness and stability (James et al. 2012). To a lesser extent, the same debate exists for modularity (Stouffer and Bascompte 2011, Alcantara and Rey 2012). One reason for this debate is the correlation between network nestedness and connectance: effects of connectance on stability can be mistaken with effects of nestedness (James et al. 2012). Following Thébault and Fontaine approach (2010), here we performed path analysis to distinguish the effects of connectance and diversity from the effects of nestedness and modularity on stability. Our results reveal that although the effects of antagonistic nestedness and mutualistic modularity are qualitatively coherent with what was found in isolated networks (Thébault and Fontaine 2010, and Supplementary material Appendix 6 Fig. A8, A9), the strength of their effects, relative to the strength of the connectance and diversity effects, is much weaker. Additionally, the observed changes in nestedness and modularity of both sub-networks, due to species extinctions over the dynamics, are coherent with the patterns exhibited by natural communities (Bascompte et al. 2003, Krause et al. 2003, Supplementary material Appendix 5 Fig. A6A–B, Fig. A7A–B). But they are mostly due to changes in connectance and diversity contrary to what was found when focusing on a single interaction type (Thébault and Fontaine 2010, Supplementary material Appendix 5 Fig. A6C–D, Fig. A7C–D). Our results are thus in agreement with recent studies that question the importance of nestedness for network stability (Allesina and Tang 2012, James et al. 2012). However the mechanisms that could explain this loss of effect are likely to differ from previous studies. Here the weak effects of modularity and nestedness appear to be the consequence of merging antagonistic and mutualistic sub-networks together, since the model of Thébault and Fontaine (2010) and our model are similar except for this merging. Understanding precisely the loss of modularity and nestedness effects remains nevertheless challenging. The decrease in modularity effect in one sub-network could be understood as merging a modular sub-network to another sub-network increases the connection among the compartments via shared partners in this other sub-network (Fontaine et al. 2011). This in turn, could facilitate the propagation of disturbances among the compartments of the sub-network, leading to a loss of effects of modularity on stability. The positive effects of nestedness on stability in mutualistic networks are related to strong positive indirect interactions among species due to interaction overlap in a nested network (Bastolla et al. 2009). As species also share antagonistic partners in the other sub-network, the negative indirect interactions resulting from this sharing might outweigh the positive ones occurring in

the nested sub-network. Explaining the loss of nestedness is however complicated, as the understanding of such indirect effects is intricate (Wootton 1994), and further developments are needed to test our hypothesis.

We further show that the stability of a super-network combining both mutualistic and antagonistic interactions is enhanced by the connectance and diversity of its mutualistic part whereas it is decreased by the connectance and diversity of its antagonistic part. These findings are coherent with what was found for antagonistic networks and mutualistic networks when studied in isolation (Allesina and Pascual 2008, Okuyama and Holland 2008, Gross et al. 2009, Thébault and Fontaine 2010). Thus, complexity–stability relationships, in terms of the net effects of connectance and diversity on stability, are the same whether considering interaction type diversity or not. One has to keep in mind that assumptions made about the interaction strengths might affect the nature of structure–stability relationship (Thébault and Loreau 2005, Allesina and Tang 2012). However, the preservation of complexity–stability relationships is robust to different stability measures, to changes in the relative strength of both interaction types, and to different assumptions made about the interaction strengths (Supplementary material Appendix 1 Fig. A1, A2). Mutualistic and antagonistic sub-networks also influence each other's dynamics, in agreement with the results suggested by previous studies integrating diverse interaction types in the same framework (Ringel et al. 1996, Jang 2002). With the interconnecting guild as the backbone of merged networks (Fig. 1), diversity and connectance effects in one sub-network are transmitted to the other part through this interface. For instance, plants can be pointed out as an interconnecting guild between pollination and phytopygy networks, with a potential key role for stability (Pocock et al. 2012). Furthermore, the puzzling issue of the coexistence of numerous species in food webs (McCann 2000) could be partly explained by this positive effect of mutualistic complexity on the persistence of antagonist species and on the resilience of the overall community as our results suggest. Our findings thus fuel the idea that studying super-networks merging different types of interaction is a way to better understand the dynamics of the single interaction type networks it is made of.

Overall, our study highlights the need to develop new metrics able to capture the structural characteristics of networks merging mutualistic and antagonistic interactions that are relevant for community stability. As we demonstrated, although some simple metrics such as connectance can still be relevant for super-networks, finer structural patterns such as nestedness and modularity are not. It is important to notice that it is not the overall connectance of the super-network that affect its stability (as done in May 1972), but the connectance of each mutualistic and antagonistic sub-network (Fig. 2, Supplementary material Appendix 7 Fig. A10). It is thus crucial to take into account interaction types when characterising the architecture of super-networks combining different interaction types. We suggest that a fruitful avenue might be to develop new metrics focusing on the species involved both in mutualistic and antagonistic interactions. Three recent studies deal with super-networks and propose new indices that take into account the diversity of interaction. Melian et al. (2009) suggested the distribution

of the mutualistic to antagonistic ratio of plant generalism degrees. Fontaine et al. (2011) put forward two supplementary measures: the correlation of mutualistic and antagonistic generalism degrees of the linking species, and the overlap in compartments composition between the two sub-networks for linking species. Still at the level of the interconnecting guild, key species for community maintenance could also be targeted and characterized in terms of traits and position in the network of interactions (Pocock et al. 2012). Such indices might bring new insight for the understanding of how disturbances propagate in such super-networks that could not be captured by current indices such as nestedness and modularity. Hence, if we reveal that research can only partly rely on results of studies considering one single type of network, studying networks that integrate interaction diversity might thus challenge the way we envision the structure–stability debate.

Acknowledgements – We thank Benoît Gauzens, Sonia Kéfi, Stéphane Legendre, Nicolas Loeuille and Peter de Ruiter for their comments and their suggestions which greatly improved this work, the analyses and finally this paper. AMCS was supported with a fellowship by the Chaire “Modélisation Mathématique et Biodiversité” of Veolia Environnement – École Polytechnique – Museum National d’Histoire Naturelle – Fondation X.

References

- Alcantara, J. M. and Rey, P. J. 2012. Linking topological structure and dynamics in ecological networks. – *Am. Nat.* 120: 186–199.
- Allesina, S. and Pascual, M. 2008. Network structure, predator–prey modules, and stability in large food webs. – *Theor. Ecol.* 1: 55–64.
- Allesina, S. and Tang, S. 2012. Stability criteria for complex ecosystems. – *Nature* 483: 205–208.
- Almeida-Neto, M. et al. 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. – *Oikos* 117: 1227–1239.
- Barber, M. J. 2008. Modularity and community detection in bipartite networks. – *Phys. Rev. E*: 1–11.
- Bascompte, J. et al. 2003. The nested assembly of plant–animal mutualistic networks. – *Proc. Natl Acad. Sci. USA* 100: 9383–9387.
- Bastolla, U. et al. 2009. The architecture of mutualistic networks minimizes competition and increases biodiversity. – *Nature* 458: 1018–1020.
- Fontaine, C. et al. 2011. The ecological and evolutionary implications of merging different types of networks. – *Ecol. Lett.* 14: 1170–1181.
- Fortuna, M. A. et al. 2010. Nestedness versus modularity in ecological networks: two sides of the same coin? – *J. Anim. Ecol.* 79: 811–817.
- Grace, J. B. and Pugesek, B. H. 1998. On the use of path analysis and related procedures for the investigation of ecological problems. – *Am. Nat.* 152: 151–159.
- Grimm, V. and Wissel, C. 1997. Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. – *Environ. Res.* 109: 323–334.
- Gross, T. et al. 2009. Generalized models reveal stabilizing factors in food webs. – *Science* 325: 747–750.
- Gunderson, L. H. 2000. Ecological resilience – in theory and application. – *Annu. Rev. Ecol. Evol. Syst.* 31: 425–439.
- Holland, J. N. et al. 2002. Population dynamics and mutualism: functional responses of benefits and costs. – *Am. Nat.* 159: 231–244.
- Ives, A. R. and Carpenter, S. R. 2007. Stability and diversity of ecosystems. – *Science* 317: 58–62.
- James, A. et al. 2012. Disentangling nestedness from models of ecological complexity. – *Nature* 487: 227–230.
- Jang, S. R. J. 2002. Dynamics of herbivore–plant–pollinator models. – *J. Math. Biol.* 44: 129–149.
- Joppa, L. N. et al. 2009. Reciprocal specialization in ecological networks. – *Ecol. Lett.* 12: 961–969.
- Kéfi, S. et al. 2012. More than a meal... integrating non-feeding interactions into food webs. – *Ecol. Lett.* 15: 291–300.
- Krause, A. E. et al. 2003. Compartments revealed in food-web structure. – *Nature* 426: 282–285.
- May, R. M. 1972. Will a large complex system be stable? – *Nature* 238: 413–414.
- McCann, K. S. 2000. The diversity–stability debate. – *Nature* 405: 228–233.
- Melián, C. J. et al. 2009. Diversity in a complex ecological network with two interaction types. – *Oikos* 118: 122–130.
- Memmott, J. et al. 2004. Tolerance of pollination networks to species extinctions. – *Proc. R. Soc. B* 271: 2605–2611.
- Mougi, a. and Kondoh, M. 2012. Diversity of interaction types and ecological community stability. – *Science* 337: 349–351.
- Newman, M. E. J. and Girvan, M. 2004. Finding and evaluating community structure in networks. – *Phys. Rev. E* 69: 1–16.
- Okuyama, T. and Holland, J. N. 2008. Network structural properties mediate the stability of mutualistic communities. – *Ecol. Lett.* 11: 208–216.
- Pocock, M. J. O. et al. 2012. The robustness and restoration of a network of ecological networks. – *Science* 335: 973–977.
- Ringel, M. S. et al. 1996. The stability and persistence of mutualisms embedded in community interactions. – *Theor. Popul. Biol.* 50: 281–297.
- Stouffer, D. B. and Bascompte, J. 2011. Compartmentalization increases food-web persistence. – *Proc. Natl Acad. Sci. USA* 108: 3648–3652.
- Thébault, E. 2013. Identifying compartments in presence–absence matrices and bipartite networks: insights into modularity measures. – *J. Biogeogr.* 40: 759–768.
- Thébault, E. and Loreau, M. 2005. Trophic interactions and the relationship between diversity and ecosystem stability. – *Am. Nat.* 166: E95–E114.
- Thébault, E. and Fontaine, C. 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. – *Science* 329: 853–856.
- Tylianakis, J. M. et al. 2010. Conservation of species interaction networks. – *Biol. Conserv.* 143: 2270–2279.
- Wootton, J. T. 1994. The nature and consequences of indirect effects in ecological communities. – *Annu. Rev. Ecol. Syst.* 25: 443–466.
- Wright, S. 1934. The method of path coefficients. – *Ann. Math. Stat.* 5: 161–215.

Supplementary material (Appendix oik-00743 at <www.oikosoffice.lu.se/appendix>). Appendix A1–A7.