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Title: A patch-dynamic metacommunity perspective on the persistence of mutualistic and antagonistic bipartite networks

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Abstract

The structure of interactions between species within a community plays a key role in maintaining biodiversity. Previous studies have found that the effects of these structures might substantially differ depending on interaction type, for example, a highly connected and nested architecture stabilizes mutualistic communities, while the stability of antagonistic communities is enhanced in modular and weakly connected structures. Here we show that, when network dynamics are modelled using a patch-dynamic metacommunity framework, the qualitative differences between antagonistic and mutualistic systems disappear, with nestedness and modularity interacting to promote metacommunity persistence. However, the interactive effects are significantly weaker in antagonistic metacommunities. Our model also predicts an increase in connectance, nestedness and modularity over time in both types of interaction, except in antagonistic networks where nestedness declines. At steady state, we find a strong negative correlation between nestedness and modularity in both mutualistic and antagonistic metacommunities. These predictions are consistent with the structural trends found in a large dataset of real-world antagonistic and mutualistic communities.

Keywords: ecological networks, mutualism, antagonism, network structure, metacommunity persistence, nestedness, modularity.

Introduction

How complexity arises and persists in natural communities is a key question in ecology that still lacks a conclusive answer (May 1972, McCann 2000, Allesina and Tang 2012). In particular, the relationship between diversity and stability has fascinated ecologists for a long time. Before 1970s, ecologists believed that increasing species diversity should enhance community stability (Oldum 1953, MacArthur 1955, Elton 1958). Yet, this early intuitive idea was challenged by May (1972). By using a linear stability analysis on models with randomly structured communities, May (1972) found that diversity tends to destabilize community dynamics. Since then, the so-called diversity-stability debate has become a long-standing theoretical puzzle for ecologists, and numerous studies have begun to explore the factors contributing to community stability or instability (e.g., McCann 2000, Allesina and Tang 2012). For example, Jacquet et al. (2016) have performed a stability analysis of 116 quantitative food webs sampled worldwide, finding no relationship between community complexity (including species richness, connectance and interaction strength) and stability. Furthermore, an increasing number of theoretical models have investigated the effects of antagonism, mutualism, nonlinear feedback, and dispersal on stability (Allesina and Tang 2012, Galla 2018, Baron and Galla 2020, Sidhom and Galla 2020), greatly enriching our understanding of the complexity-stability relationship. Besides, the structure of the interaction networks underlying natural communities can also theoretically affect stability (May 1972, Bastolla et al. 2009, Thébault and Fontaine 2010, Allesina and Tang 2012, Landi et al. 2018). Theoretical studies have identified the level of nestedness and modularity of interaction networks as important determinants of community stability (Santamaría and

Rodríguez-Gironés 2007, Okuyama and Holland 2008, Bastolla et al. 2009, Thébault and Fontaine 2010, Stouffer and Bascompte 2011, Allesina and Tang 2012). These studies further found structural differences in how network architecture modulates stability in mutualistic *versus* antagonistic networks. In particular, Thébault and Fontaine (2010) demonstrated that weakly connected, modular network structures promote stability of antagonistic communities, while high connectance and nestedness can stabilize mutualistic communities.

The models mentioned above have focused primarily on a single level of organization (i.e., local scale), by assuming that each species can interact with all potential partners in the network. However, many natural communities consist of relatively isolated subcommunities, linked by species dispersal, within a landscape (Gravel et al. 2011, Pillai et al. 2011, Poisot et al. 2014, Gravel et al. 2016, Galiana et al. 2018, Albouy et al. 2019, Baiser et al. 2019, Guimarães 2020). In this setting, there are at least two levels on which interaction structure can be characterized, firstly the interaction networks of individual subcommunities, and secondly the structure of the overall meta-network of all possible interactions (Kissling and Schleuning 2015, Tylianakis and Morris 2017). The interaction networks of subcommunities are, by definition, subnetworks of the meta-network, but it does not necessarily follow that they have the same structural characteristics. As such, existing models provide little insight into the effects of the structure of the meta-network on the persistence of the metacommunity (Cagnolo et al. 2009, Vázquez et al. 2009, Fenoglio et al. 2012, Spiesman and Inouye 2013, Grass et al. 2018, Valverde et al. 2020).

The population dynamics of landscape-scale metacommunities can be straightforwardly modelled using the patch-dynamic framework (Fortuna and Bascompte 2006, Pillai et al. 2010,

2011, Jabot and Bascompte 2012, Liao et al. 2017a, 2017b, 2020a). While this framework is spatially implicit, it can be used to describe mean-field effects of the spatial partitioning of the metacommunity into subcommunities. In other words, the patch-dynamic framework allows a spatial perspective on ecological networks by viewing networks as the regional assembly of simpler, spatially distributed, subnetworks. This framework has been used as the basis of several modelling studies which have considered specific aspects of the relationship between interaction network structure and metacommunity persistence (Fortuna and Bascompte 2006, Schleuning et al. 2016, Staniczenko et al. 2017, Grass et al. 2018, McWilliams et al. 2019, Liao et al. 2020b). However, a systematic comparative analysis of the architecture-persistence relationship for antagonistic vs. mutualistic networks from a metacommunity perspective is still lacking. More importantly, it remains unclear whether the structure of interaction network plays the same role in regulating the persistence of antagonistic vs. mutualistic metacommunities on the landscape scale as it does on a local scale (Thébault and Fontaine 2010). In this study, we address both of these questions using the models of mutualistic and antagonistic metacommunities, based on the patch-dynamic framework, and compare our predictions to the observed structures of empirical communities.

Methods

Theoretical framework

On the landscape scale, population monitoring is often performed by recording the presence, or absence, of a species on habitat patches. The metapopulation framework, originally developed by

Levins (1969), is ideally suited to describing such data. In this approach, population size is measured in terms of the proportion of patches occupied, *patch occupancy*. Occupancy changes when populations are found in a new patch (*colonization*), or when populations are not observed in a previously occupied patch (*extinction*). As such, in a typical model (Hastings 1980, Nee and May 1992, Tilman 1994), the patch occupancy p of a species is given by

$$\frac{dp}{dt} = \underbrace{cp(1-p)}_{\text{Colonization}} - \underbrace{ep}_{\text{Extinction}}, \quad (1)$$

where c and e denote the rates at which patches transition from unoccupied to occupied and vice versa. Note that colonization is restricted by the availability of unoccupied patches, i.e., $1 - p$. Furthermore, colonization from outside the system is not possible, and thus species extinction is permanent in this metapopulation model.

Two-species system

Firstly, we consider a mutualistic system with one plant (P) and one animal (A) in the landscape.

Following existing patch-dynamic models (Fortuna and Bascompte 2006), we have

$$\frac{dP}{dt} = c^P A(1 - P) - e^P P, \quad (2)$$

$$\frac{dA}{dt} = c^A A(P - A) - e^A A. \quad (3)$$

In the colonization terms, c^P and c^A are the colonization rates of the plant P and the animal A respectively when the plant is pollinated or dispersed by the animal. These colonization terms summarize both reproduction and subsequent patch establishment of offspring via random dispersal across the landscape (e.g., seed long-range dispersal for plants). We assume that the animal cannot survive in a patch without the plant, while the plant can survive in the absence of

the animal but cannot reproduce without it (e.g., plant-pollinator network or plant-seed disperser network). Consequently, the fraction of patches occupied by the animal is a subset of the patches occupied by the plant ($A \subseteq P$). The colonization term for the plant depends on the fraction of patches occupied by both the plant and the animal (e.g., pollination; A), and the fraction of patches unoccupied by the plant ($1 - P$). Similarly, colonization by the animal depends on the fraction of patches occupied by the animal (A) and the fraction of patches available for the animal colonization ($P - A$), i.e., the plant-occupied patches without the animal. In the extinction terms, e^P and e^A are the extinction rates of the plant P and the animal A separately, encapsulating all forms of density-independent mortality experienced by them.

Similarly, we describe the patch dynamics for a trophic system (e.g., herbivory or predation) with one plant (P) and one animal (A) subject to the colonization-extinction-predation processes (Melián and Bascompte 2002, Pillai et al. 2010, 2011) in the landscape

$$\frac{dP}{dt} = c^P P(1 - P) - e^P P - \mu A, \quad (4)$$

$$\frac{dA}{dt} = c^A A(P - A) - e^A A, \quad (5)$$

In this case, the plant does not require the presence of the animal for reproduction and colonization, so its colonization term (Eq. 4) now depends on the fraction of patches it occupies P . However, it is subject to additional extinction pressure due to predation represented by the term $-\mu A$ (μ is the top-down extinction rate). The patch dynamics for the animal in Eq. 5 are the same as in the mutualistic system (Eq. 3).

Multispecies system

We can generalize these two-species models for multispecies metacommunities consisting of two

classes of species, plants and animals, which interact according to a single common relationship type: mutualism or antagonism. In either case, we do not consider competition within classes of species in order to focus on the effects of interactions between these classes, and, as before, assume that animals require suitable plants to be present in a patch in order to colonize it. Thus, each patch in our model can accommodate a local community consisting of multiple interacting species.

Similar to Fortuna and Bascompte (2006), we can write the patch occupancy dynamics of an animal A_j in a metacommunity consisting of n_p plants and n_A animals (i.e., with species richness $S = n_p + n_A$)

$$\frac{dA_j}{dt} = c_j^A A_j [\Omega_j(t) - A_j] - e_j^A A_j, \quad (6)$$

regardless of interaction type (see parameter definitions in Table 1). Apart from defining that each animal species has its own colonization and extinction rate, c_j^A and e_j^A respectively, this formula is very similar to Eqs 3 & 5. The only change is that the habitat available to this animal is not the entire landscape, but rather the patches occupied by a suitable (mutualist or resource) plant species at a given time t , i.e., $[\Omega_j(t) - A_j]$. The variable $\Omega_j(t)$ denotes the fraction of patches which are occupied by at least one of the animal j 's mutualists or resources. This must be continuously determined from the state of the system. Assuming that plants are uniformly distributed across the landscape via random dispersal, the value of $\Omega_j(t)$ can be determined from: (i) the number of plants which the focal animal can interact with; (ii) the patch occupancies of these plants (i.e., the probability that a given patch is occupied by a given plant i , i.e., P_i); and (iii) the overlap among these plants within patches. In particular, we estimate $\Omega_j(t)$ by finding

the probability that a patch is not occupied by any plant species which can interact with animal j , i.e.,

$$\Omega_j(t) = [1 - \prod_{i=1}^{n_p} (1 - \theta_{ji} P_i)], \quad (7)$$

where θ_{ji} is the element of the adjacency matrix of the interaction network, with $\theta_{ji}=1$ if plant i interacts with animal j and 0 otherwise (Fortuna and Bascompte 2006, Liao et al. 2020b).

To derive the patch dynamics of plants, we assume that: (i) those associated animals within the i -patches (occupied by plant i) are uniformly distributed via random dispersal; (ii) in cases where multiple animals interact with a common focal plant, these interactions are not additive, i.e., the plant colonization and top-down extinction rates do not increase with the number of interacting animals present, as they may interact with other plants within patches; (iii) in mutualistic networks, plants are only able to colonize unoccupied patches from patches in which they co-occur with a suitable animal (e.g., plant-pollinator network or plant-seed disperser network); (iv) in antagonistic networks, plant species have an increased rate of extinction when a consumer is present in the same patch (i.e., the top-down predation; Melián and Bascompte 2002, Pillai et al. 2010, 2011, Liao et al. 2020a,b). Thus, the patch occupancy of a plant (P_i) can be derived by modifying Eqs 2 & 4 to obtain

$$\frac{dP_i}{dt} = c_i^P \Phi_i(t) P_i (1 - P_i) - e_i^P P_i, \quad (8)$$

if the interaction is mutualistic, and

$$\frac{dP_i}{dt} = c_i^P P_i (1 - P_i) - [e_i^P + \mu_i^P \Phi_i(t)] P_i, \quad (9)$$

if the interaction is antagonistic (see parameter definitions in Table 1). For simplicity, the

top-down extinction rate for the focal plant i (μ_i^P) does not change when it is consumed by different predators.

In order to account for the effect of animals on plants, a new variable $\Phi_i(t)$ is introduced. This represents the fraction of the i -patches that are also occupied by at least one animal which can interact with it. For a mutualistic network, $\Phi_i(t)$ is applied to the colonization rate (Eq. 8), while for an antagonistic network, it increases the extinction rate (i.e., top-down predation in Eq. 9). Similar to $\Omega_j(t)$, the value of $\Phi_i(t)$ can be estimated from the system state. Animals can only occur in patches where at least one suitable plant is present, i.e., in a sub-habitat of size $\Omega_j(t)$ for animal j . We can then estimate $\Phi_i(t)$ by determining the probability that a given i -patch is not occupied by any animal that can interact with plant i

$$\Phi_i(t) = \left[1 - \prod_{j=1}^{n_A} \left(1 - \theta_{ij} A_j \frac{P_i}{\Omega_j(t) P_i} \right) \right], \quad (10)$$

in which $\theta_{ij} A_j \frac{P_i}{\Omega_j(t) P_i} = \theta_{ij} \frac{A_j}{\Omega_j(t)}$ represents the proportion of the i -patches being occupied by the animal j when both of them can interact ($\theta_{ij} = 1$), with $\frac{P_i}{\Omega_j(t)}$ being the fraction of the i -patches accounting for all the potential patches in which the animal j can establish. Thus, the term $\Phi_i(t)P_i$ in Eqs 8 & 9 represents the probability that a given patch is both occupied by plant i and at least one animal with which it interacts on the landscape scale.

Numerical simulations

Since the resulting models for multispecies metacommunities are difficult to investigate analytically (but see Appendix S1: Section S1 with system analysis of a simplified neutral model), numerical methods are the primary tool with which we analyze these systems. We use

such methods (via ODE45, Matlab 2016a) to derive the non-trivial steady states of systems describing mutualistic and antagonistic metacommunities. The species which survive in these steady states are identified and, in particular, the number of such species and hence the steady state species richness is determined. Using these data, we undertake a systematic analysis of the effects of network structure on the fraction of surviving species at steady state (*metacommunity persistence*) for mutualism and antagonism.

Metacommunity structure is described in the form of bipartite networks of interactions between plants and animals. Following Thébault and Fontaine (2010), we construct an ensemble of 5760 random networks by varying four network structure metrics: network size (the number of species $S=24, 64, 96$ and 120), connectance (the relative number of interactions $C=0.07, 0.1, 0.15$ and 0.2), nestedness (the level of sharing of interaction partners among species $N=NODF/100$; using the ‘*vegan*’ R package to calculate NODF; Almeida-Neto et al. 2008, Oksanen et al. 2013) and modularity (the degree of compartmentalization Q ; using the ‘*igraph*’ R package; Newman and Girvan 2004, Guimerà and Amaral 2005). Network modularity and nestedness are controlled by varying the probabilities that network connections are made within one of four modules of equal size (p_{comp}) and within a nestedness structure (p_{nest}) between 0 and 1 with increments of 0.2. Ten random networks are constructed for each combination of these parameters. These four metrics are also calculated for the steady-state metacommunities which emerge from our simulations, offering complementary information as to how interactions are organized in final stable systems. For standardization, the Z-scores for nestedness (N) and

modularity (Q) are estimated with $Z(N) = \frac{N_{obs} - \bar{N}_{null}}{\sigma(N_{null})}$ and $Z(Q) = \frac{Q_{obs} - \bar{Q}_{null}}{\sigma(Q_{null})}$, where N_{obs} and Q_{obs} are nestedness and modularity for an observed network at steady state, $\bar{N}_{null}$ and $\bar{Q}_{null}$ are the mean nestedness and modularity of 100 replicates of a particular null model, and $\sigma(N_{null})$ and $\sigma(Q_{null})$ are their standard deviation of the 100 null models. While Z-scores are not appropriate for comparing nestedness between different networks (Song et al. 2017), they are a good way of assessing whether there are significant differences in nestedness between observed networks and the null model. Specifically, three types of null model are considered: equiprobable, probabilistic and fixed models, where the equiprobable model assigns the same probability to each potential interaction in the network, the probabilistic model assigns a probability to each potential interaction proportional to the number of observed interactions between species, and the fixed model randomly reshuffles the interactions while preserving the observed number of interacting partners of each species (Bascompte et al. 2003, Ulrich et al. 2009, Song et al. 2017, Strona et al. 2018, Payrat ó-Borr à et al. 2019).

Initial patch occupancies are equal for all species and patch dynamics are simulated until the metacommunity reaches a steady state (Appendix S3: Fig. S1). For each simulation, the colonization and extinction rates for each species in the metacommunity are drawn randomly from an appropriate uniform distribution. In order to explore a broad range of biologically reasonable parameter combinations, several different uniform distributions are used for sensitivity analysis, including setting different ranges of colonization and extinction rates between plants and animals (Fig. 1 and Appendix S3: Figs S2-S7). Generally, results are qualitatively consistent across these simulations, so we present a single representative case

throughout (with parameter values summarized in Table 1).

Analysis of empirical community structure

To compare with our modelling predictions, we compile a large dataset of ecological networks from previously published work, containing 186 mutualistic and 135 antagonistic bipartite networks observed in nature (see details in Table 2; data set and sources seen in Data). The mutualistic communities consist of 148 plant-pollinator, 34 plant-seed disperser, and 4 plant-ant systems, while the antagonistic communities include 17 plant-herbivore, 83 host-parasite, 1 seed-eating bird, 30 fish-parasite, 1 fly-wasp, 1 plant-fly, 1 seed-eating insect and 1 seed-eating rodent systems. In this study, we attempt to make statistical analysis for all these empirical data together to check whether our predicted networks (obtained from initial 5760 networks with diverse architectures) have the same structural trends as these observed networks from diverse natural ecosystems.

We analyze the relationship between the structural properties of these observed networks, including network size (S), connectance (C), nestedness ($N = \text{NODEF}/100$) and modularity (Q) and their Z -scores. In addition, we compare the nestedness and modularity of the observed networks to the expected nestedness ($\bar{N}_{null}$) and modularity ($\bar{Q}_{null}$) of 100 replicates of the null models, again including the equiprobable, probabilistic and fixed models. As shown in Figs 3 & 4 and Appendix S3: Figs S8-S11, Z -scores derived from different null models can yield different patterns, confirming previous work (Strona and Fattorini 2014, Song et al. 2017, Strona et al. 2018, Payrat ó-Borr à et al. 2019). However, both theoretical and empirical networks display, in general, qualitative consistency in their structural trends regardless of the selected null model,

reinforcing our findings. Thus, we focus here on the results stemming from the probabilistic null model (while reporting the results from the alternative null models in Appendix S3: Figs S8-S11), which has been the preferred choice in the majority of work dealing with network structure and stability (Bascompte et al. 2003, Rodríguez-Gironés and Santamaría 2006, Olesen et al. 2007, Fortuna et al. 2010, Thébault and Fontaine 2010).

Results

Model analysis

We began by comparing the initial structure of metacommunities with that obtained at steady state (Fig. 1). Since the links to specialist species are most vulnerable to the metacommunity dynamics, their disruption and the resulting extinctions of these specialists naturally led to changes in the entire community structure (Appendix S3: Figs S1 & S12), particularly in connectance (C), nestedness (N) and modularity (Q). Irrespective of interaction type, metacommunities evolved more connected and modular structures than the initial networks, with the change measured using the difference in mean Z scores ($\Delta\bar{Z} = \bar{Z}_{Final} - \bar{Z}_{Initial}$; Fig. 1C & F). The nestedness in mutualistic metacommunities also increased ($\Delta\overline{Z(N)} = 0.20$; Fig. 1B) but decreased in antagonistic metacommunities ($\Delta\overline{Z(N)} = -0.014$; Fig. 1E).

We then assessed the relative importance of initial community structure in determining *metacommunity persistence* (i.e., fraction of species that are able to survive at steady state relative to initial network size), using structural equation modelling (SEM). Specifically, initial diversity and connectance were hypothesized to be direct potential causes of *metacommunity*

persistence. In addition, they are known to affect the level of network nestedness and modularity (Almeida-Neto et al. 2008), which in turn can influence *metacommunity persistence*. To disentangle the effects of diversity and connectance, we tried different SEMs for path analysis (Fig. 2 and Appendix S3: Figs S13 & S14), and the best performing of these models was presented in Fig. 2 (see Appendix S2: Section S1). Most structural properties, including initial network size (positive), connectance (positive), nestedness (negative) and modularity (negative), showed qualitatively similar direct effects on metacommunity persistence in both mutualistic and antagonistic networks (Fig. 2). Regardless of interaction type, the overall effects (combining direct and indirect effects) of these structural properties on metacommunity persistence were positive (Fig. 2), except for the overall effect of nestedness in antagonistic networks (which has a weak negative effect). Comparing these factors, we found that the interaction ($N \times Q$) of nestedness and modularity has a strong positive effect on persistence, with this interaction always promoting final diversity (Fig. 2). However, these interactive effects were substantially stronger in mutualistic networks than in antagonistic ones (Fig. 2).

The emergent metacommunities were also compared to structures generated from the probabilistic null model (Fig. 3). Both mutualistic and antagonistic metacommunities showed a negative linear relationship between network size and connectance (with a log-log scale in Fig. 3A). Moreover, mutualistic networks tended to be more connected than antagonistic ones, but the magnitude of this difference dwindled and eventually disappeared as network size was increased. For both types of interaction, we also observed a strong negative correlation between nestedness and modularity, i.e., networks with low modularity tended to be highly nested, and vice versa

(Fig. 3B). Both nestedness and modularity in emergent metacommunities were higher than those obtained in the probabilistic null model (see average on Z-scores in Fig. 3C & D).

Analysis of empirical data

To check whether theoretical and empirical networks deviate from the probabilistic null model in the same way, we finally analyzed the structural features of a large set of empirical mutualistic and antagonistic communities (Fig. 4). As commonly observed in natural ecosystems, both types of community displayed a negative linear relationship between community size and connectance (on a log-log scale in Fig. 4A), similar to our theoretical results (Fig. 3A). However, antagonistic networks tended to be more connected than mutualistic networks if the community size is relatively small ($S < 100$), in contrast to the case in highly diverse communities ($S > 100$).

Irrespective of interaction type, the metacommunities showed a negative correlation between nestedness and modularity (Fig. 4B), in line with our modelling predictions (Fig. 3B). Both types of community were typically more nested and modular than the probabilistic null model (Fig. 4C & D), as predicted by our model (Fig. 3C & D). Interestingly, mutualistic networks displayed higher Z-scores in nestedness than antagonistic ones, confirming our model prediction.

Discussion

In our patch-dynamic framework, increasing network size (diversity) and connectance promotes metacommunity persistence, irrespective of whether the underlying ecological interactions are antagonistic or mutualistic. In addition, the interactive effects of nestedness and modularity on metacommunity persistence are also positive in both mutualistic and antagonistic networks. Thus,

these theoretical outcomes generally support the positive complexity-stability relationship found by Gravel et al. (2011) and Pillai et al. (2011), in contrast with the negative relationship that has been typically identified by local stability analysis (May 1972). McCann et al. (2005) and Gravel et al. (2016) demonstrated that a spatially distributed community has increased stability relative to the well-mixed (local) communities studied by May (1972), partially explaining this result. In our model, increasing connectance and diversity essentially increases the number of available resource patches accessible to predators or mutualists, thereby promoting metacommunity persistence.

Our results show little qualitative difference in how interaction network structure affects metacommunity persistence between mutualism and antagonism. This can be explained by considering that, in the patch-dynamic framework, the persistence of animal species depends on finding suitable partner plant species within the landscape. Interactions between specialists are readily disrupted by animal extinctions, regardless of the type of interaction (as observed by Cagnolo et al. 2009). This results in an increase of network connectance, nestedness and modularity, by breaking rare links between highly connected subnetworks (Appendix S3: Fig. S12). In a large network with high levels of nestedness, those generalists interact with many other species, hence forming a dense core which might be very robust to environmental disturbances such as habitat loss (Fortuna and Bascompte 2006). In turn, the generalist species can promote the persistence of associated specialists (consistent with Strona et al. 2013, Strona and Lafferty 2016), further promoting metacommunity persistence. However, specialists that are not involved in this dense core will be very vulnerable to extinction, because of lower effective

patch availability and recolonization opportunities. Similarly, if a large network is divided into small cliques with these generalist cores, and species interact more frequently within cliques than between cliques (i.e., increasing modularity tends to shape more isolated but well-connected subnetworks; Fortuna et al. 2010), each subnetwork will be very robust to perturbation (Stouffer and Bascompte 2011). By contrast, in a less compartmentalized network, species are less tightly linked to such cores and thus more species are at risk of extinction. As a result, the interaction between nestedness and modularity greatly increases metacommunity persistence (Fig. 2). The interplay between network structure and spatial community assembly strongly affects species that highly depends on other species, and thus applies regardless of whether interactions are mutualistic or antagonistic.

Despite having similar qualitative effects on persistence, the interactive effects of modularity and nestedness are much weaker when interactions are antagonistic (Fig. 2). This stems from the fact that predated plant species are not dependent on their predators. In fact, the plant species linked to fewer animal predators can persist more easily because of lower predation pressure, which can strengthen the robustness of links between specialists. In contrast, the plant species linked to many predators are more vulnerable to extinction due to strong top-down control, which reduces network asymmetry (Appendix S1: Section S1). Combined together, these two facts directly result in a decline in nestedness in antagonistic communities. Yet, in mutualistic communities, both the plant and the animal species are strongly dependent on each other. As the links between specialists are disrupted more easily than those involving at least one plant or animal generalist (Appendix S1: Section S1), network nestedness is expected to increase

over time in mutualistic systems. Consequently, metacommunity dynamics increase the level of nestedness for mutualism but decrease nestedness for antagonism (Fig. 1). This explains why the overall effect of nestedness switches from promoting (mutualism) to suppressing (antagonism) metacommunity persistence, as predicted by non-spatial models (Thébault and Fontaine 2010).

The mechanism described above also drives the changes we observe in network structure at steady state (Fig. 3). Because of the vulnerable links between specialists, network connectance, nestedness and modularity tend to increase, except in antagonistic communities where nestedness declines (Fig. 1). These linking patterns have been observed previously (Spiesman and Inouye 2013, Grass et al. 2018), e.g., losses of these links between specialists, resulting from regional habitat loss, can lead to more connected and modular plant-pollinator networks. Both theoretical and empirical analyses show a consistent, strong negative correlation between nestedness and modularity for both mutualistic and antagonistic systems (Figs 3 & 4). The prevalence of these structural patterns confirms that they play an important role in stabilizing communities. More importantly, our results demonstrate how these features could emerge naturally from relatively unstructured communities when they are embedded in a spatial context. These structural similarities in both types of interaction suggest that it should be difficult to differentiate between mutualistic and antagonistic networks based solely on their architecture, as observed before (Michalska-Smith and Allesina 2019).

Our modelling framework relies on several assumptions that require further discussion. First, we assumed that all species can randomly disperse into any patch across the landscape (i.e., global dispersal without restriction). This type of dispersal is too ideal to reflect the broad range

of different dispersal behaviors in nature. This omission could be further explored by comparing our predictions with those models using more realistic dispersal ranges (e.g., characterized by a dispersal kernel). Second, our model did not consider variation in interaction strength/frequency between each pair of a plant and an animal, nor were intraguild competitive interactions considered (Ghazoul 2006, van Veen et al. 2006). One can anticipate that a tradeoff between interaction strength and generalism might have a substantial effect on network persistence, deserving further investigation. Third, it is also common for predators to reduce the prey's colonization rate through feeding on seeds or propagules (e.g., Olff and Ritchie 1998, Ryberg and Chase 2007, Ryberg et al. 2012). In addition, there are some field observations finding that prey species can even avoid places with perceived high predation risk (e.g., Resetarits and Binckley 2013). The effects of predators on colonization may have qualitatively different outcomes than their effects on extinction, thus future study can conceptualize these different effects into models for comparison. Finally, comparing steady-state metacommunities with real-world networks might be inappropriate, because of the different spatial scales (regional vs. local) of the underlying networks. Yet, if we treat each empirical network as an isolated spatial system, these diverse natural systems can be considered as possible instances of our model structure. For example, in these local communities, we assume that each colony site can only accommodate one individual of a species instead of one population, and each species can establish in any site and interact with other species randomly, similar to our patch-dynamic framework. In addition, our spatially implicit framework can characterize mean-field effects as those non-spatial models (e.g., Thébault and Fontaine 2010), thus it can apply to describe the site

colonization-extinction dynamics for these empirical communities, in spite of having different spatial scales.

Our model demonstrates that, at the landscape scale, the architecture-persistence relationships are only partially affected by the type of interaction, which provides a novel perspective complementing and advancing current knowledge (Bastolla et al. 2009, Thébault and Fontaine 2010, Allesina and Tang 2012, Grass et al. 2018). In particular, the structural patterns we predict are in good agreement with those observed in real-world networks, demonstrating the validity of our model. More generally, by integrating both metacommunity and network theories, this study provides a mechanistic explanation for the architecture-persistence relationship from a metacommunity perspective, providing further evidence for the importance of spatial assembly in regulating biodiversity maintenance.

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Literature cited

Albouy, C., et al. 2019. The marine fish food web is globally connected. *Nature Ecology &*

- Evolution 3:1153-1161.
- Allesina, S., and S. Tang. 2012. Stability criteria for complex ecosystems. *Nature* 483:205-208.
- Almeida-Neto, M., P. Guimarães, P. R. Guimarães Jr, R. D. Loyola, and W. Ulrich. 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* 117:227-1239.
- Baiser, B., et al. 2019. Ecogeographical rules and the macroecology of food webs. *Global Ecology & Biogeography* 28:1204-1218.
- Baron, J. W., and T. Galla. 2020. Dispersal-induced instability in complex ecosystems. *Nature Communications* 11:6032.
- Bascompte, J., P. Jordano, C. J. Melián, and J. M. Olesen. 2003. The nested assembly of plant-animal mutualistic networks. *Proceedings of the National Academy of the Sciences USA* 100:9383-9387.
- Bastolla, U., M. A. Fortuna, A. Pascual-García, A. Ferrera, B. Luque, and J. Bascompte. 2009. The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature* 458:1018-1020.
- Cagnolo, L., G. Valladares, A. Salvo, M. Cabido, and M. Zak. 2009. Habitat fragmentation and species loss across three interacting trophic levels: effects of life-history and food-web traits. *Biological Conservation* 23:1167-1175.
- Elton, C. S. 1958. *Ecology of Invasions by Animals and Plants*. Chapman & Hall, London.
- Fenoglio, M. S., D. Srivastava, G. Valladares, L. Cagnolo, and A. Salvo. 2012. Forest fragmentation reduces parasitism via species loss at multiple trophic levels. *Ecology* 93:2407-2420.
- Fortuna, M. A., and J. Bascompte. 2006. Habitat loss and the structure of plant-animal

- mutualistic networks. *Ecology Letters* 9:281-286.
- Fortuna, M. A., et al. 2010. Nestedness versus modularity in ecological networks: two sides of the same coin? *Journal of Animal Ecology* 79:811-817.
- Galiana, N., et al. 2018. The spatial scaling of species interaction networks. *Nature Ecology & Evolution* 2:782-790.
- Galla, T. 2018. Dynamically evolved community size and stability of random Lotka-Volterra ecosystems. *Europhysics Letters* 123:48004.
- Ghazoul, J. 2006. Floral diversity and the facilitation of pollination. *Journal of Ecology* 94:295-304.
- Grass, I., B. Jauker, I. Steffan-Dewenter, T. Tschamtkke, and F. Jauker. 2018. Past and potential future effects of habitat fragmentation on structure and stability of plant-pollinator and host-parasitoid networks. *Nature Ecology & Evolution* 2:1408-1417.
- Gravel, D., E. Canard, F. Guichard, and N. Mouquet. 2011. Persistence increases with diversity and connectance in trophic metacommunities. *PLoS ONE* 6:e19374.
- Gravel, D., F. Massol, and M. A. Leibold. 2016. Stability and complexity in model meta-ecosystems. *Nature Communications* 7:12457.
- Guimarães, P. R. Jr., 2020. The structure of ecological networks across levels of organization. *Annual Reviews of Ecology, Evolution and Systematics* 51:433-460.
- Guimerà R., and L. A. N. Amaral. 2005. Functional cartography of complex metabolic networks. *Nature* 433:895-900.
- Hastings, A. 1980. Disturbance, coexistence, history, and competition for space. *Theoretical Population Biology* 18:363-373.
- Jabot, F., and J. Bascompte. 2012. Bi-trophic interactions shape biodiversity in space.

- Proceedings of the National Academy of the Sciences USA 109:4521-4526.
- Jacquet, C., C. Moritz, L. Morissette, P. Legagneux, F. Massol, P. Archambault, and D. Gravel. 2016. No complexity–stability relationship in empirical ecosystems. *Nature Communications* 7:12573.
- Kissling, W. D., and M. Schleuning. 2015. Multispecies interactions across trophic levels at macroscales: retrospective and future directions. *Ecography* 38:346-357.
- Landi, P., H. O. Minoarivelo, Å. Brännström, C. Hui, and U. Dieckmann. 2018. Complexity and stability of ecological networks: a review of the theory. *Population Ecology* 60:319-345.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15:237-240.
- Liao, J., D. Bearup, and B. Blasius. 2017a. Food web persistence in fragmented landscapes. *Proceedings of the Royal Society B* 284:20170350.
- Liao, J., et al. 2017b. Robustness of metacommunities with omnivory to habitat destruction: disentangling patch fragmentation from patch loss. *Ecology* 98:1631-1639.
- Liao, J., D. Bearup, and W. F. Fagan. 2020a. The role of omnivory in mediating metacommunity robustness to habitat destruction. *Ecology* 101:e03026.
- Liao, J., X. Xi, D. Bearup, and S. Sun. 2020b. Metacommunity robustness of plant–fly–wasp tripartite networks with specialization to habitat loss. *Ecology* 101:e03071.
- Liao, J., D. Bearup, and G. Strona. 2022. Data from: A patch-dynamic metacommunity perspective on the persistence of mutualistic and antagonistic bipartite networks. Dryad, Dataset. <https://doi.org/10.5061/dryad.mkkwh7121>
- MacArthur, R. H. 1955. Fluctuations of animal populations and a measure of community stability. *Ecology* 36:533-536.

- 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.
- Mccann, K. S., J. B. Rasmussen, and J. Umbanhowar. 2005. The dynamics of spatially coupled food webs. *Ecology Letters* 8:513-523.
- McWilliams, C., M. Lurgi, J. M. Montoya, A. Sauve, and D. Montoya. 2019. The stability of multitrophic communities under habitat loss. *Nature Communications* 10:2322.
- Melián, C. J., and J. Bascompte. 2002. Food web structure and habitat loss. *Ecology Letters* 5:37-46.
- Michalska-Smith, M. J., and S. Allesina. 2019. Telling ecological networks apart by their structure: A computational challenge. *PLoS Computational Biology* 15:e1007076.
- Nee, S., and R. M. May. 1992. Dynamics of metapopulations: habitat destruction and competitive coexistence. *Journal of Animal Ecology* 61:37-40.
- Newman, M. E. J., and M. Girvan. 2004. Finding and evaluating community structure in networks. *Physical Review E* 69:026113.
- Odum, E. P. 1953. *Fundamentals of ecology*. Saunders, Philadelphia.
- Oksanen, J. F., et al. 2013. Package ‘vegan’. R package version 2.0-9. Available at: <http://cran.r-project.org/>.
- Okuyama, T., and J. N. Holland. 2008. Network structural properties mediate the stability of mutualistic communities. *Ecology Letters* 11:208-216.
- Olesen, J. M., J. Bascompte, Y. L. Dupont, and P. Jordano. 2007. The modularity of pollination networks. *Proceedings of the National Academy of the Sciences USA* 104:19891-19896.
- Olf, H., and M. E. Ritchie. 1998. Effects of herbivores on grassland plant diversity. *Trends in Ecology & Evolution* 13:261-265.

- Payrat ó-Borr à, C., L. Hern ández, and Y. Moreno. 2019. Breaking the spell of nestedness: the entropic origin of nestedness in mutualistic systems. *Physical Review X* 9:031024.
- Pillai, P., M. Loreau, and A. Gonzalez. 2010. A patch-dynamic framework for food web metacommunities. *Theoretical Ecology* 3:223-237.
- Pillai, P., A. Gonzalez, and M. Loreau. 2011. Metacommunity theory explains the emergence of food web complexity. *Proceedings of the National Academy of the Sciences USA* 108:19293-19298.
- Poisot, T., D. B. Stouffer, and D. Gravel. 2014. Beyond species: why ecological interaction networks vary through space and time. *Oikos* 124:243-251.
- Resetarits, W. J., and C. A. Binckley. 2013. Is the pirate really a ghost? Evidence for generalized chemical camouflage in an aquatic predator, pirate perch *Aphredoderus sayanus*. *American Naturalist* 181:690-699.
- Rodr íguez-Giron és, M. A., and L. Santamar ía. 2006. A new algorithm to calculate the nestedness temperature of presence–absence matrices. *Journal of Biogeography* 33:924-935.
- Ryberg, W. A., and J. M. Chase. 2007. Predator-dependent species-area relationships. *American Naturalist* 170:636-642.
- Ryberg, W. A., K. G. Smith, and J. M. Chase. 2012. Predators alter the scaling of diversity in prey metacommunities. *Oikos* 121:1995-2000.
- Santamar ía, L., and M. A. Rodr íguez-Giron és. 2007. Linkage rules for plant–pollinator networks: trait complementarity or exploitation barriers? *PloS Biology* 5:e31.
- Schleuning, M., et al. 2016. Ecological networks are more sensitive to plant than to animal extinction under climate change. *Nature Communications* 7:13965.
- Sidhom, L., and T. Galla. 2020. Ecological communities from random generalized

- Lotka-Volterra dynamics with nonlinear feedback. *Physical Review E* 101:032101.
- Song, C., R. P. Rohr, and S. Saavedra. 2017. Why are some plant-pollinator networks more nested than others? *Journal of Animal Ecology* 86:1417-1424.
- Spiesman, B. J., and B. D. Inouye. 2013. Habitat loss alters the architecture of plant–pollinator interaction networks. *Ecology* 94:2688-2696.
- Staniczenko, P. P., et al. 2017. Predicting the effect of habitat modification on networks of interacting species. *Nature Communications* 8:792.
- Stouffer, D. B., and J. Bascompte. 2011. Compartmentalization increases food-web persistence. *Proceedings of the National Academy of the Sciences USA* 108:3648-3652.
- Strona, G., P. Galli, and S. Fattorini. 2013. Fish parasites resolve the paradox of missing coextinctions. *Nature Communications* 4:1718.
- Strona, G., and S. Fattorini. 2014. On the methods to assess significance in nestedness analyses. *Theory in Biosciences* 133:179-186.
- Strona, G., and K. Lafferty. 2016. Environmental change makes robust ecological networks fragile. *Nature Communications* 7:12462.
- Strona, G., W. Ulrich, and N. J. Gotelli. 2018. Bi-dimensional null model analysis of presence-absence binary matrices. *Ecology* 99:103-115.
- Thébault, E., and C. Fontaine. 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* 329:853-856.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75:2-16.
- Tylianakis, J. M., and R. J. Morris. 2017. Ecological networks across environmental gradients. *Annual Review of Ecology, Evolution & Systematics* 48:25-48.
- Ulrich, W., M. Almeida-Neto, and N. J. Gotelli. 2009. A consumer's guide to nestedness

analysis. *Oikos* 118:3-17.

van Veen, F. J. F., R. J. Morris, and H. C. J. Godfray. 2006. Apparent competition, quantitative food webs, and the structure of phytophagous insect communities. *Annual Review of Entomology* 51:187-208.

Valverde, S., B. Vidiella, R. Montañez, A. Fraile, S. Sacristán, and F. García-Arenal. 2020. Coexistence of nestedness and modularity in host–pathogen infection networks. *Nature Ecology & Evolution* 4:568-577.

Vázquez, D. P., N. Blüthgen, L. Cagnolo, and N. P. Chacoff. 2009. Uniting pattern and process in plant-animal mutualistic networks: a review. *Annals of Botany* 103:1445-1457.

Tables

Table 1. Definitions and the range of values of variables and parameters in this study

Symbols	Definitions	Range values
P_i	Patch occupancy of the plant species i	[0, 1]
A_j	Patch occupancy of the animal species j	[0, 1]
c_i^P	Colonization rate of the plant species i	[0.4, 0.8]
c_j^A	Colonization rate of the animal species j	[0.4, 0.8]
e_i^P	Extinction rate of the plant species i	[0, 0.3]
e_j^A	Extinction rate of the animal species j	[0, 0.3]
μ_i^P	Top-down extinction rate of the plant species i due to predation in antagonistic metacommunities	[0, 0.2]
θ_{ij}	$\theta_{ij} = 1$ if the plant i can interact with the animal j and 0 otherwise	0 or 1
$\Omega_j(t)$	Fraction of patches being occupied by at least one of the animal j 's mutualists or resources at time t	[0, 1]
$\Phi_i(t)$	Fraction of i -patches (occupied by the plant i) being also occupied by at least one animal that can interact with it	[0, 1]

Table 2. Empirical data sets analyzed in this study

Interaction	Type	Number of network	<i>S</i>	<i>C</i>	<i>N</i>	<i>Q</i>
Mutualism	Plant-pollinator	148	8~1500	0.02~0.64	0~0.85	0~0.62
	Plant-seed disperser	34	6~317	0.05~0.69	0.11~1	0~0.59
	Plant-ant	4	10~89	0.125~0.54	0.04~0.59	0.05~0.78
Antagonism	Plant-herbivore	17	33~590	0.06~0.32	0.09~0.47	0~0.69
	Host-parasite	83	10~95	0.05~0.57	0.08~0.88	0~0.5
	Seed-eating systems	3	25~78	0.18~0.61	0.03~0.75	0~0.65
	Fish-parasite	30	22~399	0.02~0.38	0.039~0.59	0.08~0.83
	Plant-fly	1	38	0.44	0.448	0
	Fly-wasp	1	38	0.40	0.457	0.09

Note: *S* – Total number of species; *C*- Connectance; *N* – Nestedness (=NODEF/100); *Q* – Modularity.

Figures

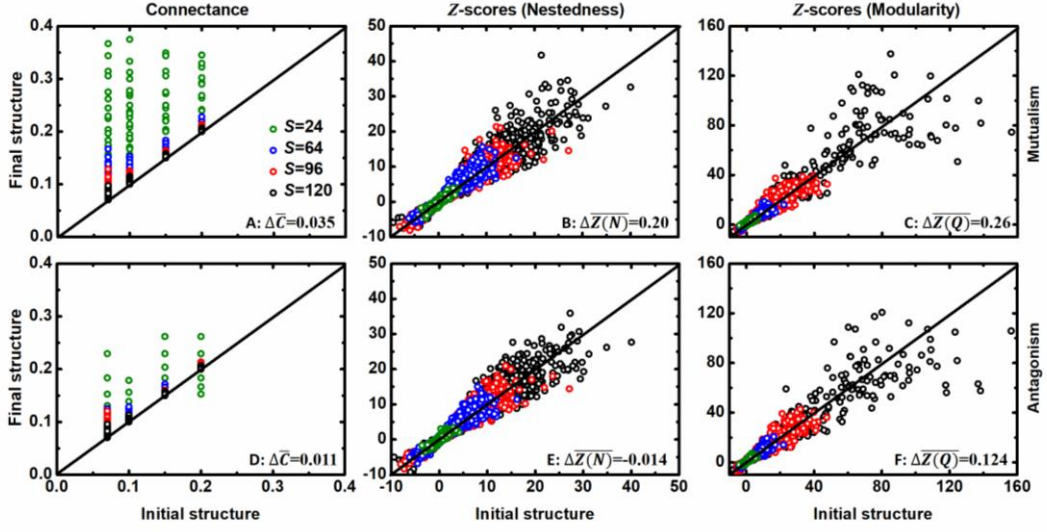


Figure 1. Steady-state structure of mutualistic (A-C) and antagonistic (D-F) networks against their initial structure, at different levels of initial community diversity ($S=24, 64, 96, 120$ in different colors) and connectance ($C=0.07, 0.1, 0.15$ and 0.2). The mean difference in these characteristics ($\Delta\bar{X} = \bar{X}_{Final} - \bar{X}_{Initial}$; including connectance C , Z-scores of nestedness $N=NODF/100$ and modularity Q using the probabilistic null model with average from 100 replicates) indicates the overall change. Parameters: species colonization rates are randomly sampled from the uniform distribution $c_i^P = c_j^A \sim unif[0.4, 0.8]$, species extinction rates $e_i^P = e_j^A \sim unif[0, 0.3]$ and top-down extinction rates $\mu_i^P \sim unif[0, 0.2]$.

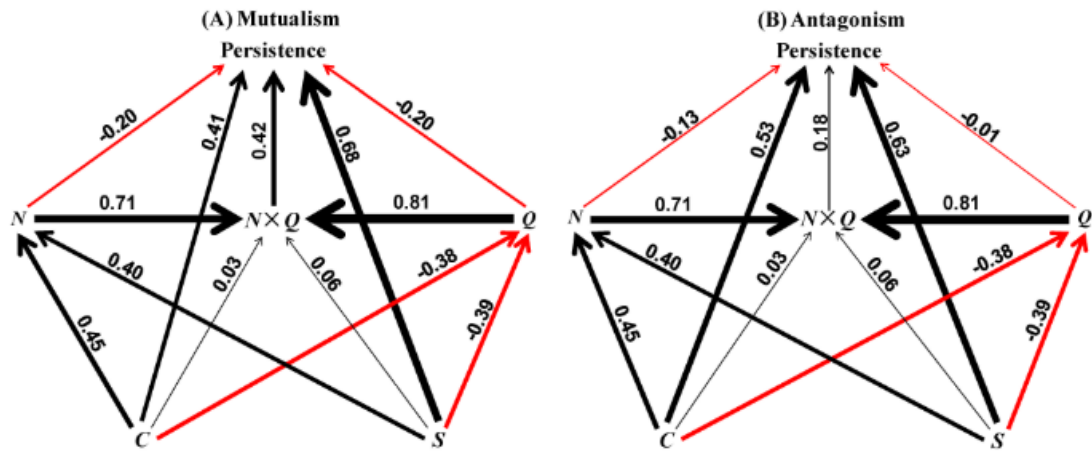


Figure 2. Path analysis of initial network architecture on the persistence of mutualistic (A) and antagonistic (B) metacommunities (S – diversity, C – connectance, N – nestedness with $N = \text{NODEF}/100$, Q – modularity, and $N \times Q$ – the interaction between nestedness and modularity), obtained from Fig. 1. Different SEMs are used for path analysis, finding that the one presented here is the best performing one (Appendix S2: Section S1 and Appendix S3: Figs S13 & S14). The thickness of the arrows is scaled to standardized coefficients from path analysis, indicating the relative effect strength. Negative and positive effects are represented in red and black respectively.

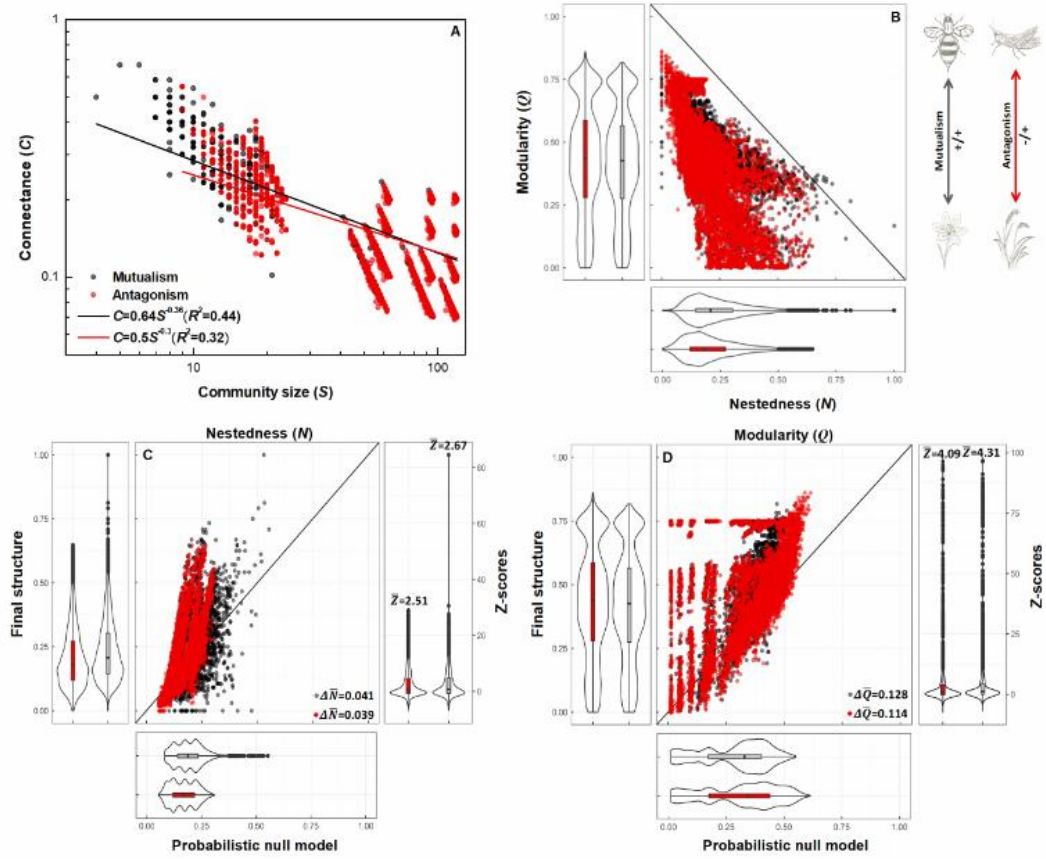


Figure 3. Analysis for the structural properties of simulated mutualistic and antagonistic bipartite networks at steady state, obtained from Fig. 1. Each point corresponds to the steady state of a simulated mutualistic or antagonistic network, with the distribution of each metric being summarized in adjacent violin plots. (A) Relationship between network size (S) and connectance (C). (B) Relationship between nestedness ($N = \text{NODEF}/100$) and modularity (Q). (C & D) Nestedness and modularity of simulated networks against their corresponding probabilistic null models (average from 100 replicates) (right: the distribution of Z-scores for nestedness and modularity with the mean $\bar{Z}$). The mean difference in nestedness ($\Delta \bar{N} = \bar{N}_{\text{Final}} - \bar{N}_{\text{Null}}$) and modularity ($\Delta \bar{Q} = \bar{Q}_{\text{Final}} - \bar{Q}_{\text{Null}}$) between final structures and null models was calculated separately for mutualism and antagonism.

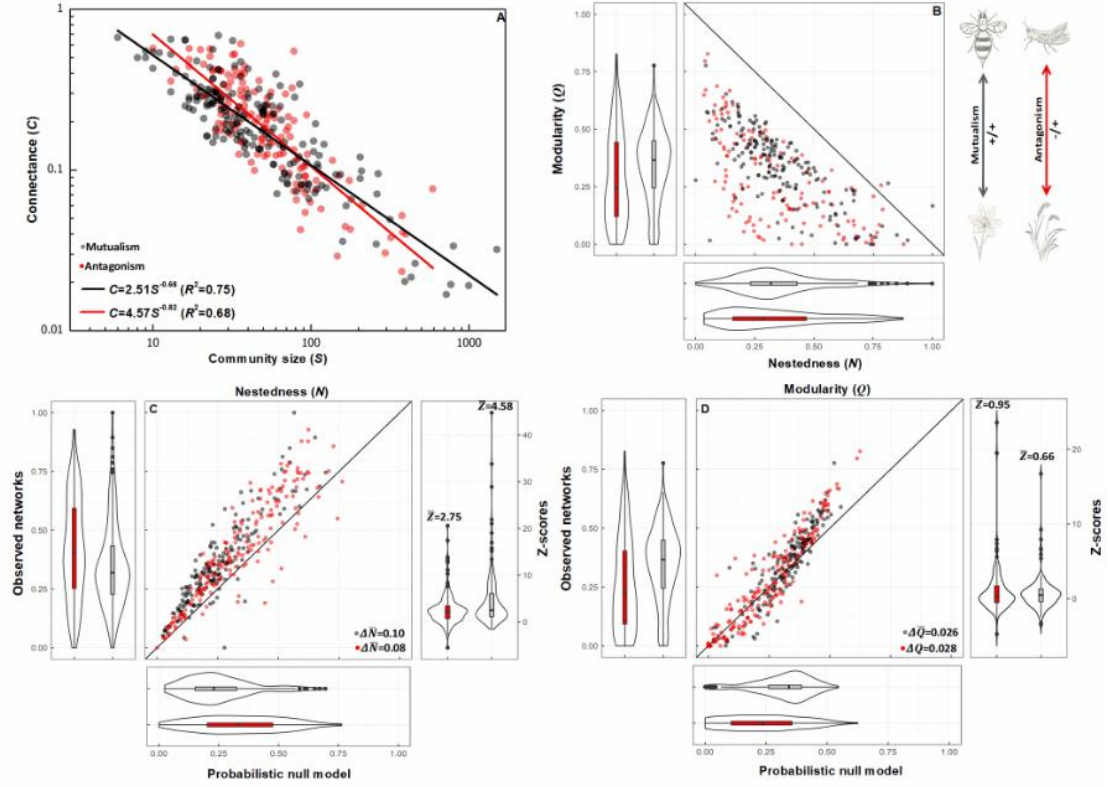


Figure 4. Analysis for the structural properties of real-world mutualistic and antagonistic bipartite networks. Each point corresponds to an empirically observed network of either mutualistic or antagonistic, with the distribution of each metric being summarized in adjacent violin plots. (A) Relationship between network size (S) and connectance (C). (B) Relationship between nestedness ($N = \text{NODF}/100$) and modularity (Q). (C & D) Nestedness and modularity of observed networks against their corresponding probabilistic null models (average from 100 replicates) (right: the distribution of Z-scores for nestedness and modularity with the mean $\bar{Z}$).

Supporting Information. Liao, J., D. Bearup, and G. Strona. 2022. A patch-dynamic metacommunity perspective on the persistence of mutualistic and antagonistic bipartite networks. *Ecology*.

Appendix S1

Section S1. System analysis

For analytical simplicity, we made the neutral assumption that all species, including plants and animals, are equivalent ($c_i^P = c_j^A = c$, $e_i^P = e_j^A = e$, $\mu_i^P = \mu$). Despite being a strong simplification, this assumption has been commonly used in ecology to obtain analytic, general conclusions (Gross and Cardinale 2005, Bascompte et al. 2006). At the steady state, we derived a non-trivial coexistence solution

$$P_i^*(mut) = 1 - \frac{e}{c\Phi_i^*} \text{ \& } P_i^*(ant) = 1 - \frac{e+\mu\Phi_i^*}{c} \quad (0 \leq \Phi_i^* < 1), \quad \text{Equation S1}$$

$$\text{and } A_j^* = \Omega_j^* - \frac{e}{c} \quad \text{Equation S2}$$

for both mutualism and antagonism. The above non-trivial steady state is positive when

$\Phi_i^* > e/c$ & $\Omega_j^* > e/c$ for mutualism, and $\Phi_i^* < (c - e)/\mu$ & $\Omega_j^* > e/c$ for antagonism.

When $0 < \Phi_i^* < \frac{\sqrt{e^2+4e\mu}-e}{2\mu}$, we have $P_i^*(mut) < P_i^*(ant)$, the opposite to the case if

$\frac{\sqrt{e^2+4e\mu}-e}{2\mu} < \Phi_i^* < 1$. Over time, some species would go extinct directly in nested networks

due to the metacommunity dynamics. As such, if the associated plant species remaining at steady state are insufficient to support the animal ($\Omega_j^* < e/c$), then the secondary extinction

for the animal would occur regardless of the type of interaction. In antagonistic

metacommunities, the direct extinctions of animals (e.g. $\Phi_i^* = 0$) do not cause the secondary extinction of the plant species (i.e. $P_i^*(ant) = 1 - \frac{e}{c}$), as the survival of plant species does

not rely on the animals. Yet, in mutualistic metacommunities, the secondary extinctions for

plant species would occur if the associated mutualists at steady state are insufficient to support the plant species, since both plants and animals are highly dependent on each other ($\Phi_i^* < e/c$).

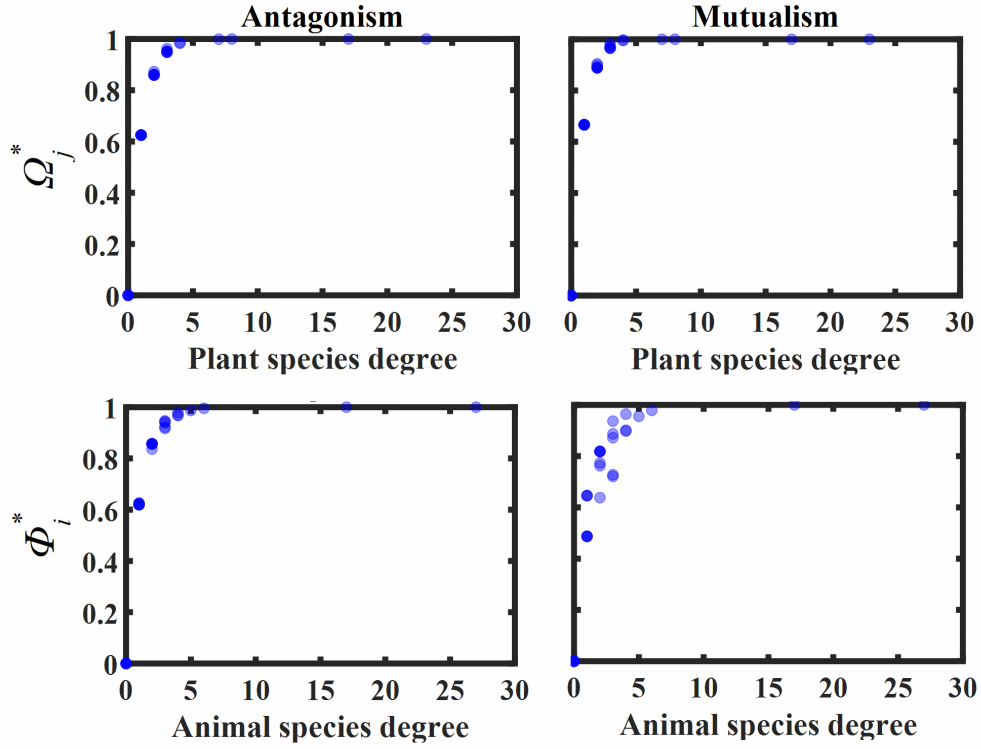


Figure S1. Effect of species degree on both unions Φ_i^* and Ω_j^* at steady state in antagonistic and mutualistic metacommunities. Parameter values: $c=0.6$, $e=0.15$, $\mu=0.1$, $S=32+32=64$, $C=0.1$ and $N=NODF/100=0.73$.

For the plant specialists that interact with few animals, the union Φ_i^* in Appendix S1: Equation S1 generally tends to be smaller at steady state (Appendix S1: Fig. S1), meaning that these specialists are more vulnerable to extinction in mutualistic networks (decreasing their persistence), but less vulnerable to predation in antagonistic networks (increasing their persistence). For the plant generalists that interact with lots of animals, the union Φ_i^* tends to be larger in general at steady state (Appendix S1: Fig. S1), thereby promoting their

survival in mutualistic communities while decreasing their persistence in antagonistic communities. Furthermore, animal specialists linked to specialist plant species are more vulnerable to extinction than animal generalists in both types of interaction (Appendix S1: Fig. S1). Due to the complexity of the highly structured bipartite networks, it was not practical to perform further system analysis algebraically, instead we primarily use numerical methods throughout.

Literature cited

- Gross, K., and B. J. Cardinale. 2005. The functional consequences of random versus ordered species extinctions. *Ecology Letters* 8:409-418.
- Bascompte, J., P. Jordano, and J. M. Olesen. 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* 312:431-433.

Supporting Information. Liao, J., D. Bearup, and G. Strona. 2022. A patch-dynamic metacommunity perspective on the persistence of mutualistic and antagonistic bipartite networks. *Ecology*.

Appendix S2

Section S1. Structural equation modelling (SEM)

Path analysis, a special case structural equation modelling (SEM), is used to analyze the direct and indirect pathways linking metacommunity *persistence* (P – fraction of species that are able to survive at steady state) and initial network architecture (including network size S , connectance C , nestedness $N = \text{NODEF}/100$ and modularity Q) in both mutualistic and antagonistic systems, based on the assumption of linear relationships between variables. Since previous studies have shown that the modularity and nestedness of a community structure influence the proportion of species that can survive within it, i.e. *persistence* (Okuyama and Holland 2008, Thébault and Fontaine 2010). Additionally, it is well-established that network size (diversity) and connectance influence the degree of modularity and nestedness (Fortuna et al. 2010, Thébault and Fontaine 2010, Strona et al. 2017). Furthermore, we observed that candidate model (M5: $P = a_0 + a_1N + a_2Q + a_3NQ$) which includes the interaction of nestedness and modularity (represented by the product NQ) have significantly more explanatory power than those without (Appendix S2: Tables S1-S3). Thus, we also include this composite variable in our path analysis. The SEM analysis was performed using AMOS 210 v5.0.1 (Arbuckle 2003), and the standardized path coefficients displayed in Fig. 2 and Appendix S3: Figs S13-S14 indicate the rate of change in the dependent variable for each standard deviation increase in the independent variable.

Table S1. Summary of candidate models for the relationship between species survival (P), modularity (Q) and nestedness (N).

Linear Models	Mutualism		Antagonism	
	RSE	R^2	RSE	R^2
M1: $P = a_0 + a_1N$	0.1051	0.1663	0.05464	0.1264
M2: $P = a_0 + a_1Q$	0.11	0.08755	0.05588	0.08638
M3: $P = a_0 + a_1N + a_2Q$	0.1051	0.1664	0.05452	0.1304
M4: $P = a_0 + a_1NQ$	0.1128	0.03916	0.05806	0.01359
M5: $P = a_0 + a_1N + a_2Q + a_3NQ$	0.1027	0.2035	0.05391	0.1497

Table S2. Coefficients estimated for model M5: $P = a_0 + a_1N + a_2Q + a_3NQ$.

Mutualistic communities			
Coefficients	Estimate	Standard Error	p
a_0	0.9246	0.0078	$<2 \times 10^{-16}$ (***)
a_1	0.0828	0.0253	0.00108 (**)
a_2	-0.1883	0.0137	$<2 \times 10^{-16}$ (***)
a_3	0.99	0.06	$<2 \times 10^{-16}$ (***)
Antagonistic communities			
Coefficients	Estimate	Standard Error	p
a_0	0.9679	0.004	$<2 \times 10^{-16}$ (***)
a_1	0.0354	0.013	0.0077 (**)
a_2	-0.0885	0.007	$<2 \times 10^{-16}$ (***)
a_3	0.3642	0.0317	$<2 \times 10^{-16}$ (***)

Table S3. Explanatory power of structural equation models for persistence, estimated by adjusted R^2 . Three SEMs are displayed in Fig. 2 and Appendix S3: Figs S13-S14.

SEMs	Mutualism (R^2)	Antagonism (R^2)
Fig. 2	0.668	0.573
Fig. S13	0.631	0.566
Fig. S14	0.655	0.564

Literature cited

- Arbuckle, J. L. 2003. *AMOS 5.0.1*. AMOS Development Corporation, Spring House, Pennsylvania, USA.
- Fortuna, M. A., et al. 2010. Nestedness versus modularity in ecological networks: two sides of the same coin? *Journal of Animal Ecology* 79:811-817.
- Okuyama, T., and J. N. Holland. 2008. Network structural properties mediate the stability of mutualistic communities. *Ecology Letters* 11:208-216.
- Strona, G., W. Ulrich, and N. J. Gotelli. 2017. Bi-dimensional null model analysis of presence-absence binary matrices. *Ecology* 99:103-115.
- Thébault, E., and C. Fontaine. 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* 329:853-856.

Supporting Information. Liao, J., D. Bearup, and G. Strona. 2022. A patch-dynamic metacommunity perspective on the persistence of mutualistic and antagonistic bipartite networks. *Ecology*.

Appendix S3 – Figures S1-S14

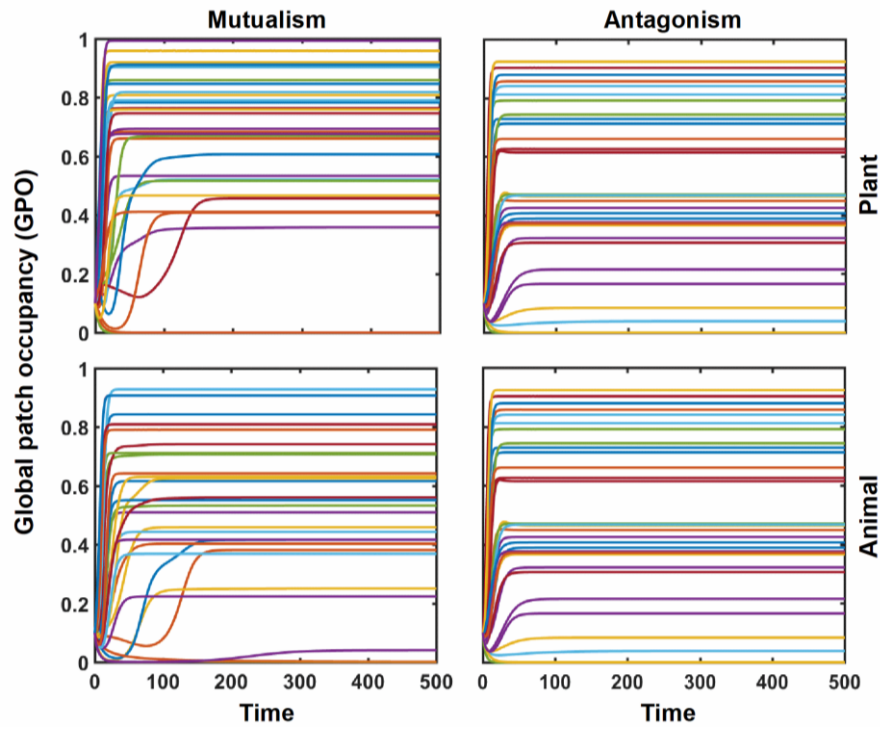


Figure S1. Simulated dynamics of mutualistic (left panels) and antagonistic (right panels) bipartite metacommunities. Parameters: network size $S=64$, initial connectance $C=0.07$, nestedness $N=NODF/100=0.09$, modularity $Q=0.6$ (see *Methods*). Other parameters: see Fig.

1.

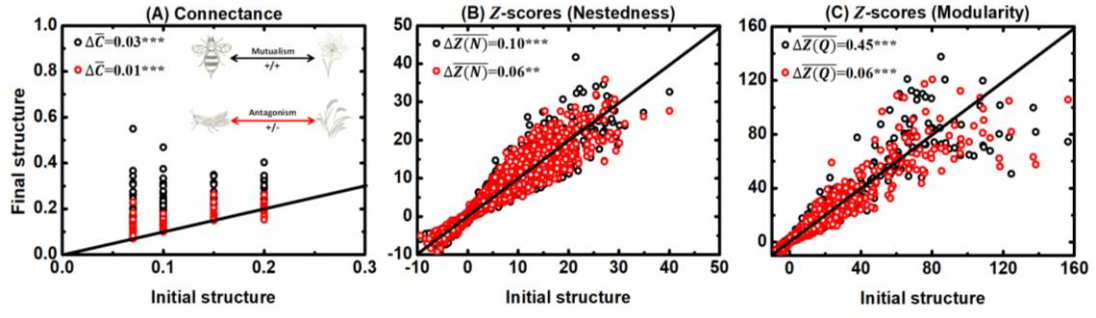


Figure S2. Steady-state structure of mutualistic (black circles) and antagonistic (red circles) bipartite metacommunities, against their initial structure with different levels of network size ($S=24, 64, 96, 120$) and connectance ($C=0.07, 0.1, 0.15$ and 0.2). Three network metrics are included: connectance (C), Z-scores for nestedness ($N=NODF/100$) and modularity (Q) with the probabilistic null model. The mean difference in these characteristics ($\Delta \bar{X}$) indicates the overall change, and statistical significance of these changes was determined using the Wilcoxon signed-rank test ($***-p<0.001$ and $** - 0.001<p<0.01$). Other parameters:

$$c_i^P = c_j^A \sim \text{unif}[0.4, 0.8], \quad e_i^P = e_j^A \sim \text{unif}[0, 0.1] \text{ and } \mu_i^P \sim \text{unif}[0, 0.1].$$

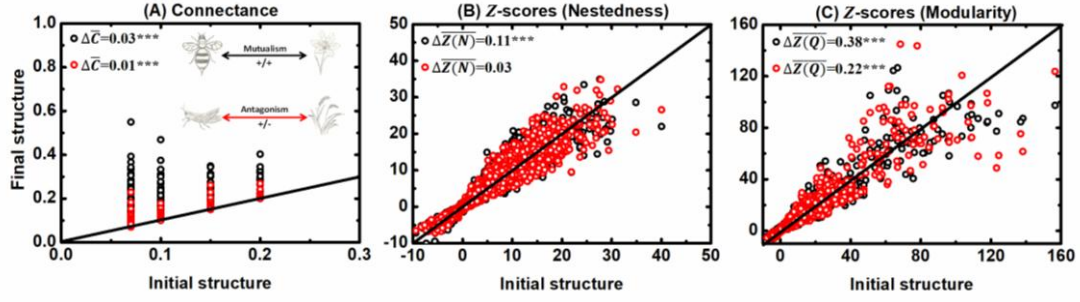


Figure S3. Steady-state structure of mutualistic (black circles) and antagonistic (red circles) bipartite metacommunities, against their initial structure with different levels of network size ($S=24, 64, 96, 120$) and connectance ($C=0.07, 0.1, 0.15$ and 0.2). Three network metrics are included: connectance (C), Z-scores for nestedness ($N=NODF/100$) and modularity (Q) with the probabilistic null model. The mean difference in these characteristics ($\Delta\bar{X}$) indicates the overall change, and statistical significance of these changes was determined using the Wilcoxon signed-rank test (***- $p<0.001$, otherwise non-significance). Other parameters:

$$c_i^P = c_j^A \sim \text{unif}[0.6, 1], \quad e_i^P = e_i^A \sim \text{unif}[0, 0.2] \text{ and } \mu_i^P \sim \text{unif}[0, 0.2].$$

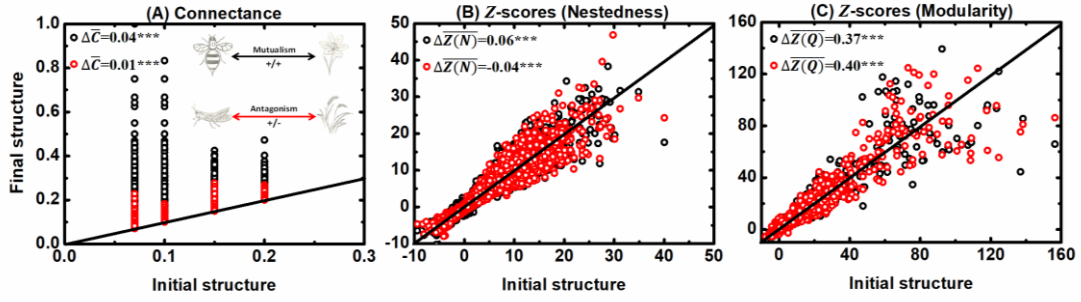


Figure S4. Steady-state structure of mutualistic (black circles) and antagonistic (red circles) bipartite metacommunities, against their initial structure with different levels of network size ($S=24, 64, 96, 120$) and connectance ($C=0.07, 0.1, 0.15$ and 0.2). Three network metrics are included: connectance (C), Z-scores for nestedness ($N=NODF/100$) and modularity (Q) with the probabilistic null model. The mean difference in these characteristics ($\Delta\bar{X}$) indicates the overall change, and statistical significance of these changes was determined using the Wilcoxon signed-rank test (***- $p<0.001$). Other parameters: $c_i^P = c_j^A \sim \text{unif}[0.6, 1]$, $e_i^P = e_j^A \sim \text{unif}[0, 0.5]$ and $\mu_i^P \sim \text{unif}[0, 0.1]$.

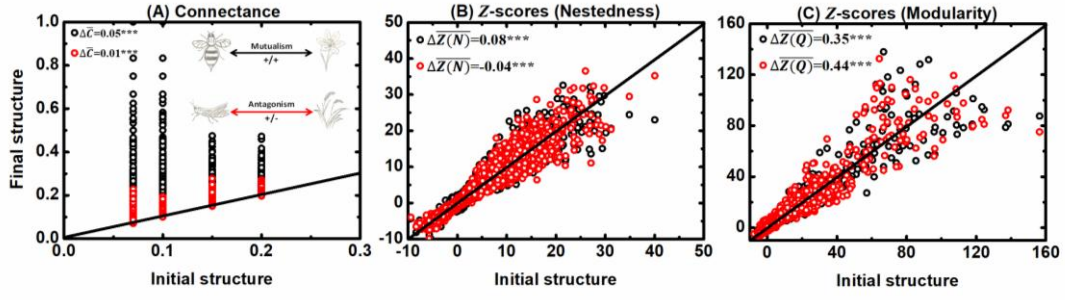


Figure S5. Steady-state structure of mutualistic (black circles) and antagonistic (red circles) bipartite metacommunities, against their initial structure with different levels of network size ($S=24, 64, 96, 120$) and connectance ($C=0.07, 0.1, 0.15$ and 0.2). Three network metrics are included: connectance (C), Z-scores for nestedness ($N=NODF/100$) and modularity (Q) with the probabilistic null model. The mean difference in these characteristics ($\Delta\bar{X}$) indicates the overall change, and statistical significance of these changes was determined using the Wilcoxon signed-rank test (***- $p<0.001$). Other parameters: $c_i^P = c_j^A \sim \text{unif}[0.8, 1]$, $e_i^P = e_j^A \sim \text{unif}[0, 0.6]$ and $\mu_i^P \sim \text{unif}[0, 0.2]$.

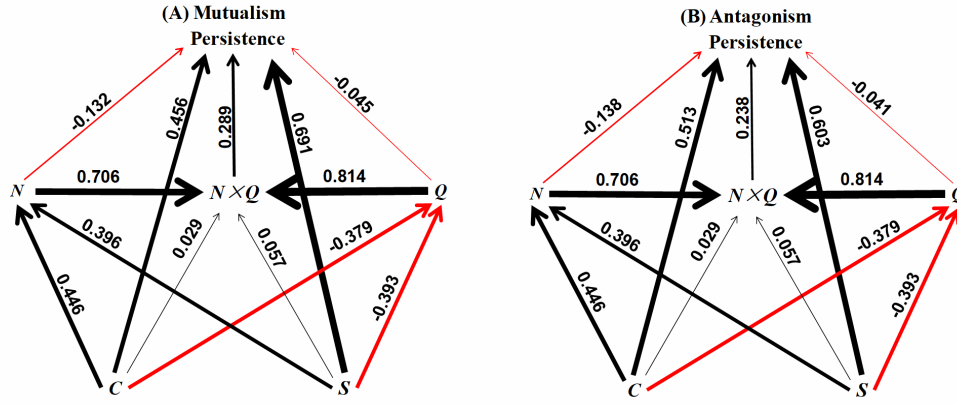


Figure S6. Path analysis of initial network architecture on the persistence of mutualistic (A) and antagonistic (B) metacommunities (S – diversity, C – connectance, N – nestedness with $N = \text{NODEF}/100$, Q – modularity, and $N \times Q$ – the interaction between nestedness and modularity), by separately setting different ranges of colonization and extinction rates between plants and animals. The thickness of the arrows is scaled to standardized coefficients from path analysis, indicating the relative effect strength. Negative and positive effects are represented in red and black respectively. Parameter values: $c_i^P \sim \text{unif}[0.4, 0.8]$, $e_i^P \sim \text{unif}[0, 0.1]$, $\mu_i^P \sim \text{unif}[0, 0.2]$, $c_j^A \sim \text{unif}[0.6, 1]$, and $e_j^A \sim \text{unif}[0, 0.3]$.

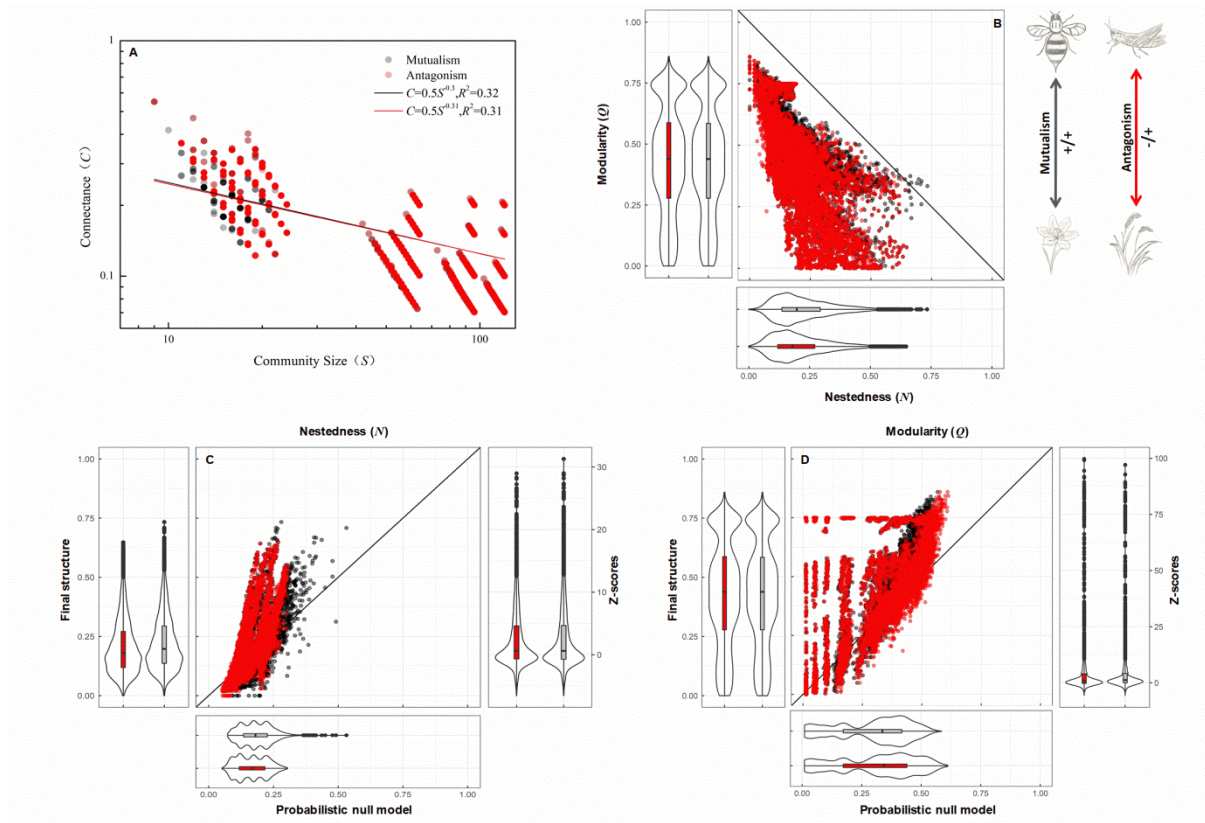


Figure S7. Analysis for the structural properties of simulated mutualistic and antagonistic bipartite networks at steady state, using parameter setting in Appendix S3: Fig. S6 (see above). Each point corresponds to the steady state of a simulated network, with the distribution of each metric being summarized in adjacent violin plots. (A) Relationship between network size (S) and connectance (C). (B) Relationship between nestedness ($N = \text{NODF}/100$) and modularity (Q). (C & D) Nestedness and modularity of simulated networks against their corresponding probabilistic null models (average on 100 replicates) (right: the distribution of Z-scores for nestedness and modularity with the mean $\bar{Z}$). The mean difference in nestedness ($\Delta \bar{N} = \bar{N}_{\text{Final}} - \bar{N}_{\text{Null}}$) and modularity ($\Delta \bar{Q} = \bar{Q}_{\text{Final}} - \bar{Q}_{\text{Null}}$) between final structures and null models was calculated separately for mutualism and antagonism.

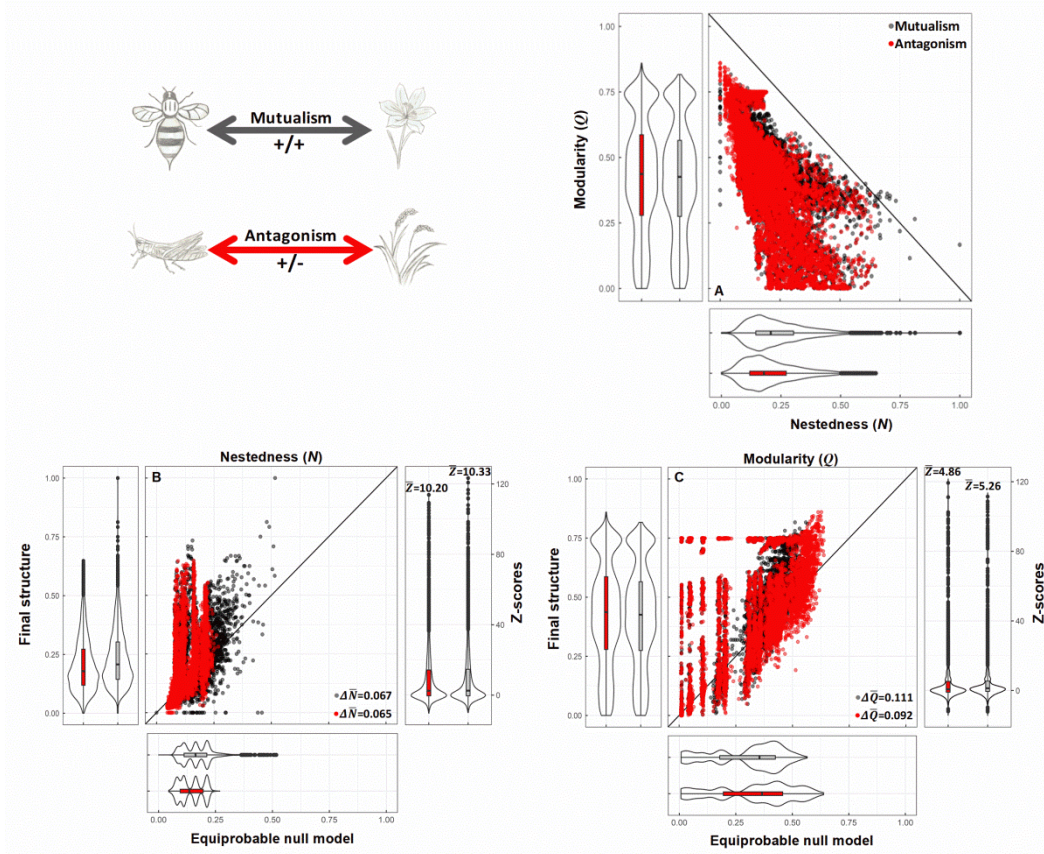


Figure S8. Analysis for the structural properties of steady-state mutualistic and antagonistic bipartite networks (obtained from Fig. 1) relative to the equiprobable null model. Each point corresponds to the steady state of a simulated mutualistic or antagonistic network, with the distribution of each metric being summarized in adjacent violin plots. (A) Relationship between nestedness ($N = \text{NODE}/100$) and modularity (Q). (B & C) Nestedness and modularity of simulated networks against their corresponding equiprobable null models (average from 100 replicates) (right: the distribution of Z-scores for nestedness and modularity with the mean $\bar{Z}$). The mean difference in nestedness ($\Delta \bar{N} = \bar{N}_{Final} - \bar{N}_{Null}$) and modularity ($\Delta \bar{Q} = \bar{Q}_{Final} - \bar{Q}_{Null}$) between final structures and null models was calculated separately for mutualism and antagonism.

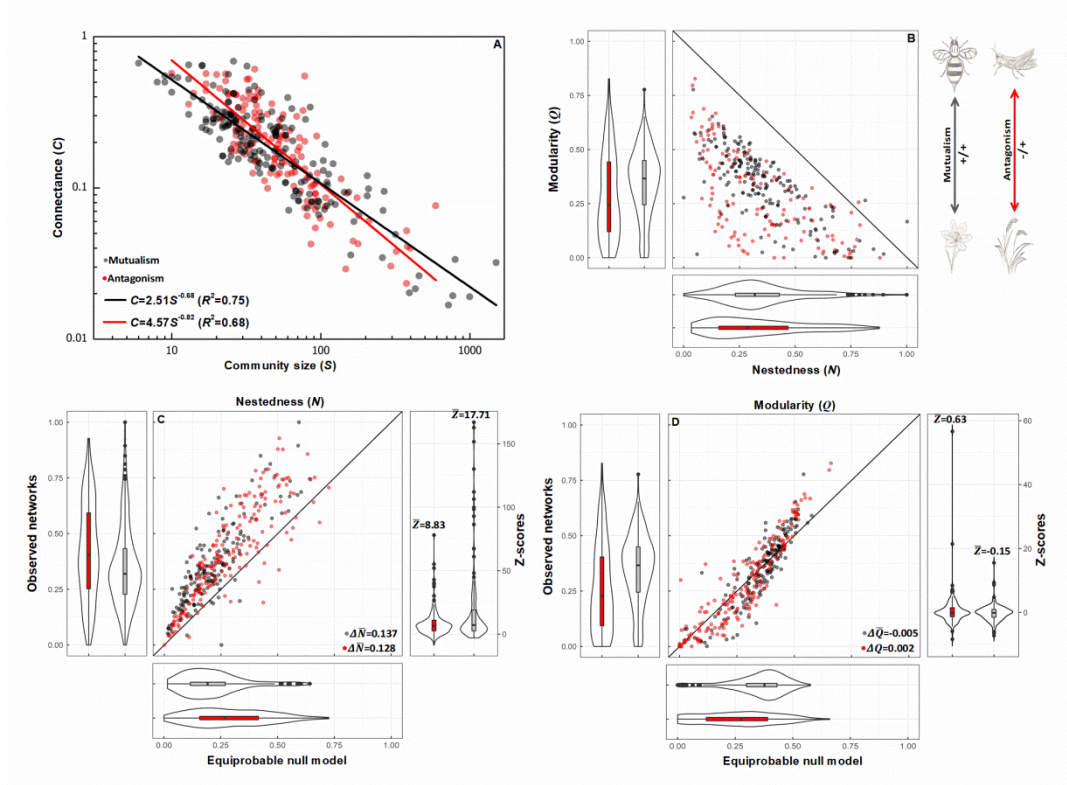


Figure S9. Analysis for the structural properties of real-world mutualistic and antagonistic bipartite networks relative to the equiprobable null model. Each point corresponds to an empirically observed network of either mutualistic or antagonistic, with the distribution of each metric being summarized in adjacent violin plots. (A) Relationship between network size (S) and connectance (C). (B) Relationship between nestedness ($N = \text{NODF}/100$) and modularity (Q). (C & D) Nestedness and modularity of observed networks against their corresponding equiprobable null models (average from 100 replicates) (right: the distribution of Z-scores for nestedness and modularity with the mean $\bar{Z}$).

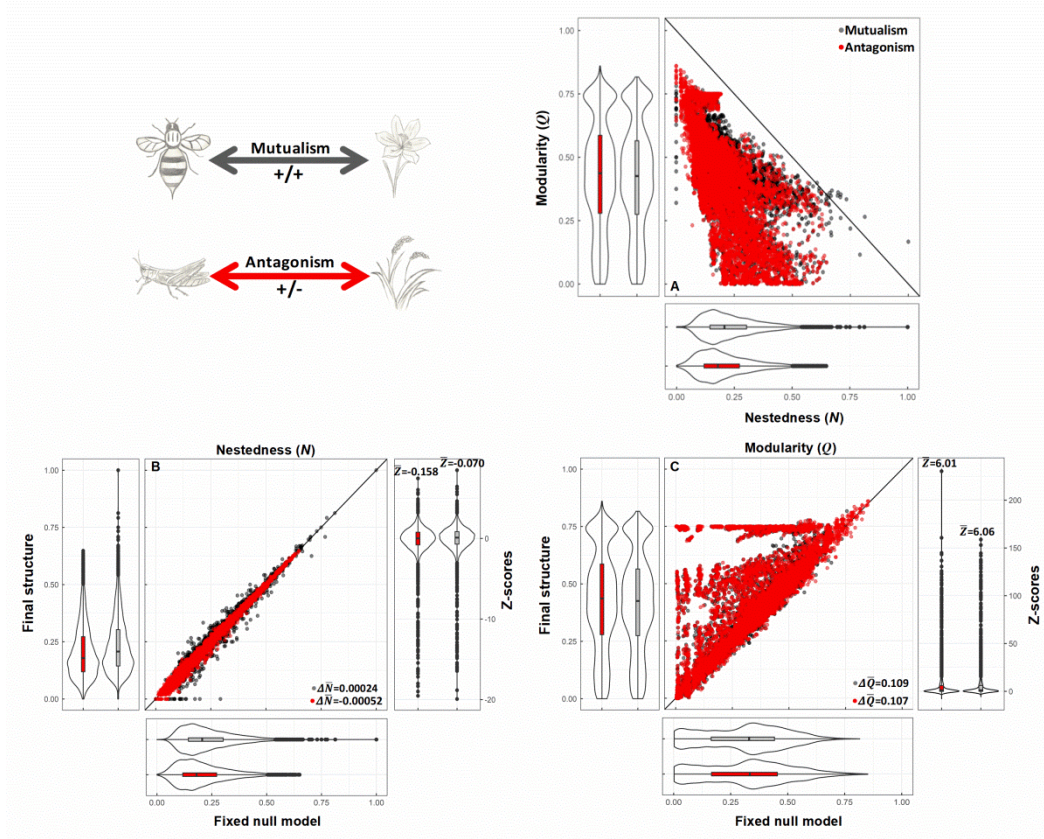


Figure S10. Analysis for the structural properties of steady-state mutualistic and antagonistic bipartite networks (obtained from Fig. 1) relative to the fixed null model. Each point corresponds to the steady state of a simulated mutualistic or antagonistic network, with the distribution of each metric being summarized in adjacent violin plots. (A) Relationship between nestedness ($N = \text{NODE}/100$) and modularity (Q). (B & C) Nestedness and modularity of simulated networks against their corresponding fixed null models (average from 100 replicates) (right: the distribution of Z-scores for nestedness and modularity with the mean $\bar{Z}$). The mean difference in nestedness ($\Delta \bar{N} = \bar{N}_{\text{Final}} - \bar{N}_{\text{Null}}$) and modularity ($\Delta \bar{Q} = \bar{Q}_{\text{Final}} - \bar{Q}_{\text{Null}}$) between final structures and null models was calculated separately for mutualism and antagonism.

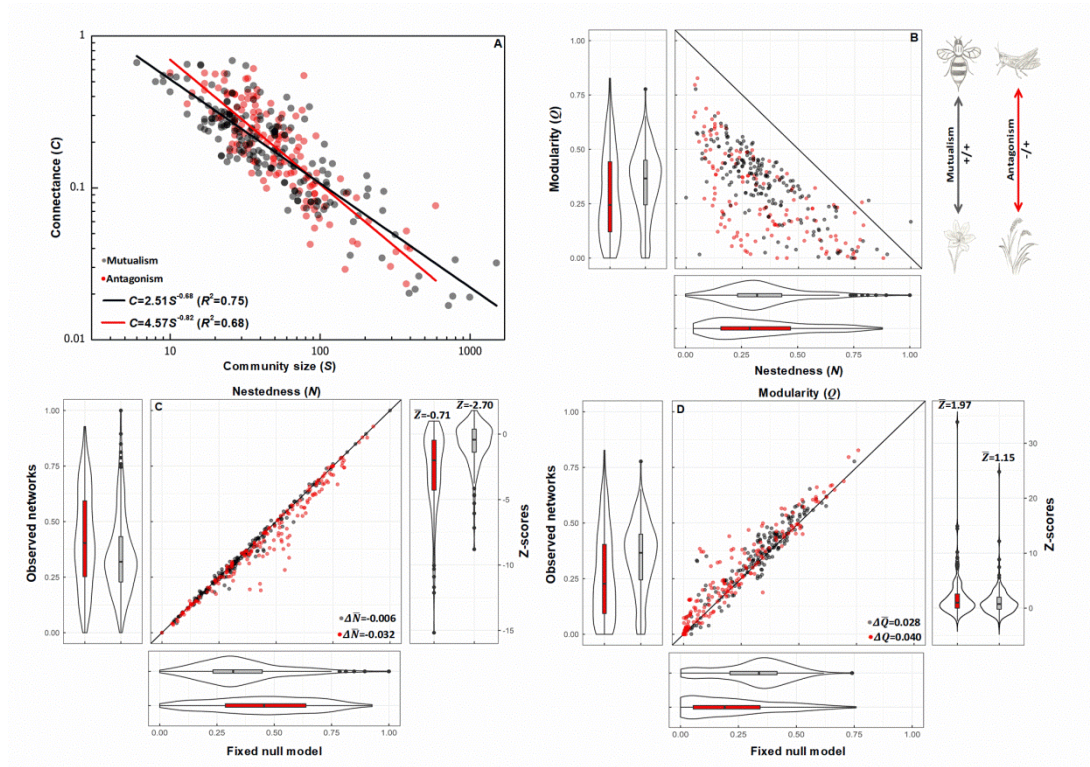


Figure S11. Analysis for the structural properties of real-world mutualistic and antagonistic bipartite networks relative to the fixed null model. Each point corresponds to an empirically observed network of either mutualistic or antagonistic, with the distribution of each metric being summarized in adjacent violin plots. (A) Relationship between network size (S) and connectance (C). (B) Relationship between nestedness ($N = \text{NODF}/100$) and modularity (Q). (C & D) Nestedness and modularity of observed networks against their corresponding fixed null models (average from 100 replicates) (right: the distribution of Z-scores for nestedness and modularity with the mean $\bar{Z}$).

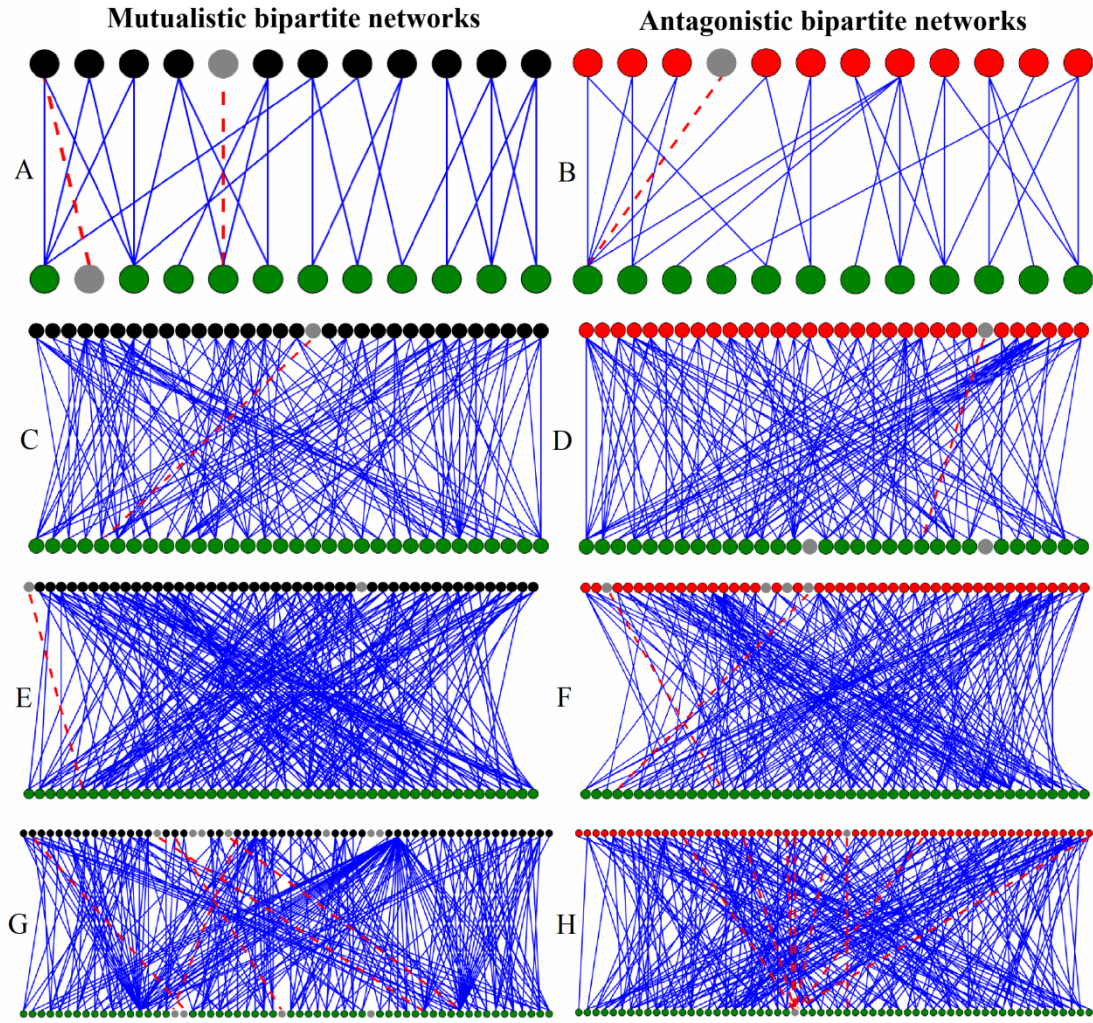


Figure S12. Illustration of species extinction (gray nodes) from mutualistic and antagonistic communities (green nodes – plant species, red nodes – animal species, blue lines – trophic links, and dashed red lines – trophic disruption due to species extinction). As shown, those specialist species with very low linking degree go extinct easily. (A) $S=24$, $C=0.2$; (B) $S=24$, $C=0.2$; (C) $S=64$, $C=0.15$; (D) $S=64$, $C=0.15$; (E) $S=96$, $C=0.1$; (F) $S=96$, $C=0.1$; (G) $S=120$, $C=0.07$; (H) $S=120$, $C=0.07$. Other parameters: see Fig. 1.

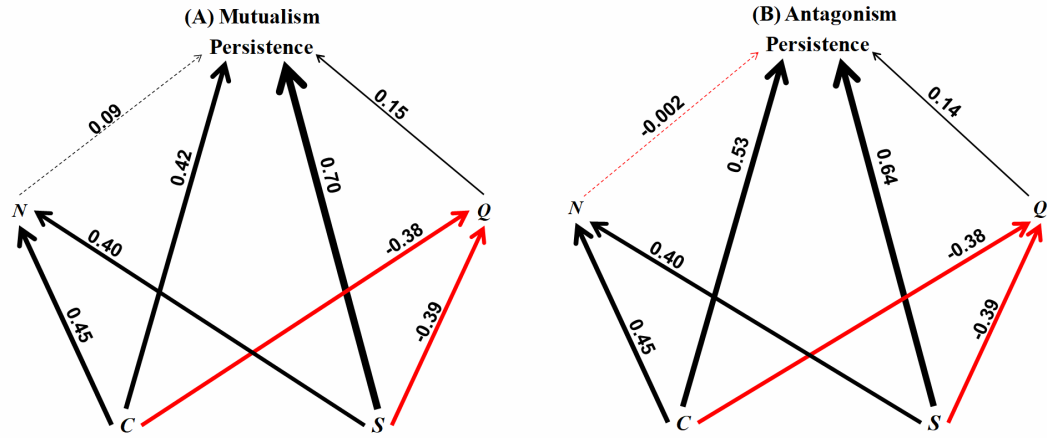


Figure S13. Path analysis of initial metacommunity structure on the persistence of mutualistic (A) and antagonistic (B) networks (obtained from Fig. 1). The thickness of the arrows is scaled to standardized coefficients from path analysis, indicating the relative effect strength (dashed lines – non-significance with $P>0.05$, otherwise $P<0.001$). Negative effects are represented in red and positive effects in black. The effects of connectance (C) and diversity (S) are split between direct effects and indirect effects through changes in nestedness ($N=NODE/100$) and modularity (Q). The strength of the indirect effects is calculated by the product of the coefficients along the path.

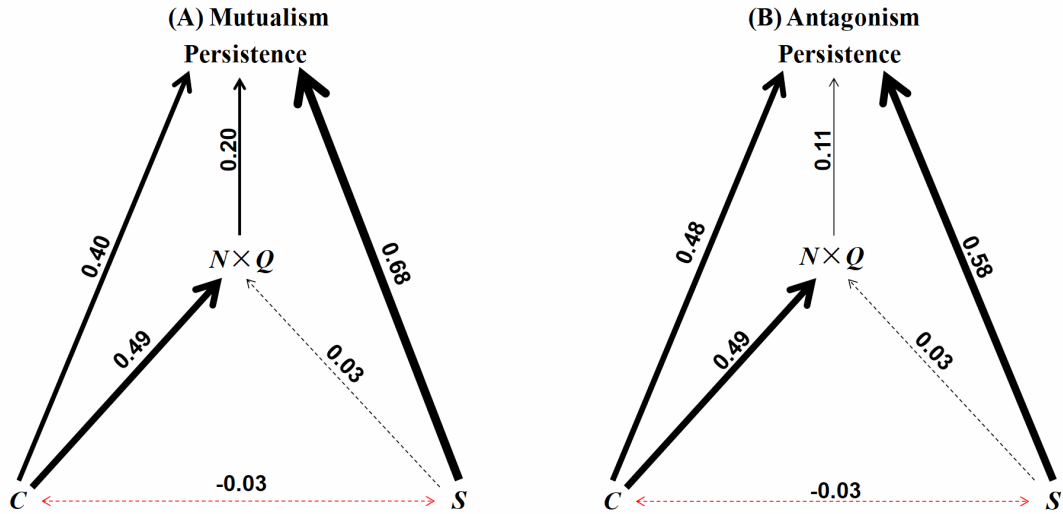


Figure S14. Path analysis of initial metacommunity structure on the persistence of mutualistic (A) and antagonistic (B) networks (obtained from Fig. 1). The thickness of the arrows is scaled to standardized coefficients from path analysis, indicating the relative effect strength (dashed lines – non-significance with $P > 0.05$, otherwise $P < 0.001$). Negative effects are represented in red and positive effects in black. The effects of connectance (C) and diversity (S) are split between direct effects and indirect effects through changes in the interaction of nestedness and modularity, i.e. $N \times Q$. The strength of the indirect effects is calculated by the product of the coefficients along the path.