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ARTICLE

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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 found that the effects of these structures might vary substantially 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 modeled 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 data set of real-world antagonistic and mutualistic communities.

KEYWORDS
antagonism, ecological networks, metacommunity persistence, modularity, mutualism, nestedness, network structure

INTRODUCTION

How complexity arises and persists in natural communities is a key question in ecology that still lacks a conclusive answer (Allesina & Tang, 2012; May, 1972; McCann, 2000). In particular, the relationship between diversity and stability has fascinated ecologists for a long time. Before the 1970s, ecologists believed that increasing species diversity should enhance community stability (Elton, 1958; MacArthur, 1955; Odum, 1953). Yet this early intuitive idea was challenged by May (1972). Conducting a linear stability analysis on models with randomly structured communities, May (1972) found that diversity tended to destabilize community dynamics. Since then, the so-called diversity–stability debate has become a long-standing theoretical puzzle for ecologists, and numerous researchers have begun exploring the factors contributing to community stability or instability (e.g., Allesina & Tang, 2012; McCann, 2000). For example, Jacquet et al. (2016) performed a stability analysis of 116 quantitative food webs sampled worldwide and found no relationship between community complexity (including species richness, connectance, and interaction strength) and stability. Furthermore, an increasing number of theoretical models have been used to investigate the effects of antagonism, mutualism, nonlinear feedback, and dispersal on stability (Allesina & Tang, 2012; Baron & Galla, 2020; Galla, 2018; Sidhom & Galla, 2020), greatly enriching our understanding of the complexity–stability relationship. In addition, the structure of the interaction networks underlying natural communities can also theoretically affect stability (Allesina & Tang, 2012; Bastolla et al., 2009; Landi et al., 2018; May, 1972; Thébault & Fontaine, 2010). Theoretical studies have identified the level of nestedness and modularity of interaction networks as important determinants of community stability (Allesina & Tang, 2012; Bastolla et al., 2009; Okuyama & Holland, 2008; Santamaría & Rodríguez-Gironés, 2007; Stouffer & Bascompte, 2011; Thébault & Fontaine, 2010). These studies further found structural differences in how network architecture modulated stability in mutualistic versus antagonistic networks. In particular, Thébault and Fontaine (2010) demonstrated that weakly connected, modular network structures promoted the stability of antagonistic communities and high connectance and nestedness could stabilize mutualistic communities.

The aforementioned models focused primarily on a single level of organization (i.e., local scale) by assuming that each species can interact with all potential partners in a network. However, many natural communities consist of relatively isolated subcommunities, linked by species dispersal, within a landscape (Albouy et al., 2019; Baiser et al., 2019; Galiana et al., 2018; Gravel et al., 2011, 2016; Guimarães Jr., 2020; Pillai et al., 2011; Poisot et al., 2014). In this context, there are at least two levels on which an interaction structure can be characterized—first, the interaction networks of individual subcommunities and, second, the structure of the overall meta-network of all possible interactions (Kissling & Schleuning, 2015; Tylianakis & 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. Thus, existing models provide little insight into the effects of the structure of a meta-network on the persistence of the metacommunity (Cagnolo et al., 2009; Fenoglio et al., 2012; Grass et al., 2018; Spiesman & Inouye, 2013; Valverde et al., 2020; Vázquez et al., 2009).

The population dynamics of landscape-scale metacommunities can be straightforwardly modeled using the patch-dynamic framework (Fortuna & Bascompte, 2006; Jabot & Bascompte, 2012; Liao, Bearup, & Blasius, 2017; Liao, Bearup, & Fagan, 2020; Liao, Bearup, Wang, et al., 2017; Pillai et al., 2010, 2011). While this framework is spatially implicit, it can be used to describe the mean-field effects of the spatial partitioning of a metacommunity into subcommunities. In other words, the patch-dynamic framework allows for 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 modeling studies that considered specific aspects of the relationship between interaction network structure and metacommunity persistence (Fortuna & Bascompte, 2006; Grass et al., 2018; Liao, Xi, et al., 2020; McWilliams et al., 2019; Schleuning et al., 2016; Staniczenko et al., 2017). However, a systematic comparative analysis of the architecture–persistence relationship for antagonistic versus mutualistic networks from a metacommunity perspective is still lacking. More importantly, it remains unclear whether the structure of an interaction network plays the same role in regulating the persistence of antagonistic versus mutualistic metacommunities on the landscape scale as it does on a local scale (Thébault & 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, or 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 & May, 1992; Tilman, 1994), the patch occupancy p of a species is given by

$$\frac{\mathrm{d}p}{\mathrm{d}t}=\underbrace{cp(1-p)}_{\text{Colonization}}\ \underbrace{-ep}_{\text{Extinction}}, \tag{1}$$

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, that is, $1-p$. Furthermore, colonization from outside the system is not possible, so species extinction is permanent in this metapopulation model.

Two-species system

First, we consider a mutualistic system with one plant (P) and one animal (A) in the landscape. Following existing patch-dynamic models (Fortuna & Bascompte, 2006), we have

$$\frac{\mathrm{d}P}{\mathrm{d}t}=c^{P}A(1-P)-e^{P}P, \tag{2}$$

$$\frac{\mathrm{d}A}{\mathrm{d}t}=c^{A}A(P-A)-e^{A}A. \tag{3}$$

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 $(P-A)$, that is, 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 & Bascompte, 2002; Pillai et al., 2010, 2011) in the landscape:

$$\frac{\mathrm{d}P}{\mathrm{d}t}=c^{P}P(1-P)-e^{P}P-\mu A, \tag{4}$$

$$\frac{\mathrm{d}A}{\mathrm{d}t}=c^{A}A(P-A)-e^{A}\mathrm{A}, \tag{5}$$

In this case, the plant does not require the presence of the animal for reproduction and colonization, so its colonization term (Equation 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 Equation (5) are the same as in the mutualistic system (Equation 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 $S=n_P+n_A$)

$$\frac{\mathrm{d}A_j}{\mathrm{d}t}=c_j^{A}A_j\left[\Omega_j(t)-A_j\right]-e_j^{A}A_j, \tag{6}$$

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 Equations (3) and (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, that is, $\left[\Omega_j(t)-A_j\right]$. The variable $\Omega_j(t)$ denotes the fraction of patches that 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 (a) the number of plants that the focal animal can interact with, (b) the patch occupancies of these plants (i.e., the probability that a given patch is occupied by a given plant i: P_i), and (c) 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 that can interact with animal j, that is,

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

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

$$\Omega_j(t) = \left[1 - \prod\nolimits_{i=1}^{n_P} \left(1 - \theta_{ji} P_i\right)\right], \tag{7}$$

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

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, that is, the plant colonization and top-down extinction rates do not increase with the number of interacting animals present because 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); and (iv) in antagonistic networks, plant species have an increased rate of extinction when a consumer is present in the same patch (i.e., top-down predation) (Liao, Bearup, & Fagan, 2020; Liao, Xi, et al., 2020; Melián & Bascompte, 2002; Pillai et al., 2010, 2011). Thus, the patch occupancy of a plant (P_i) can be derived by modifying Equations (2) and (4) to obtain

$$\frac{\mathrm{d}P_i}{\mathrm{d}t} = c_i^P \Phi_i(t) P_i (1 - P_i) - e_i^P P_i \tag{8}$$

if the interaction is mutualistic, and

$$\frac{\mathrm{d}P_i}{\mathrm{d}t} = c_i^P P_i (1 - P_i) - \left[e_i^P + \mu_i^P \Phi_i(t)\right] P_i \tag{9}$$

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.

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 that can interact with it. For a mutualistic network, $\Phi_i(t)$ is applied to the colonization rate (Equation 8), while for an antagonistic network it increases the extinction rate (i.e., top-down predation in Equation 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, that is, in a subhabitat 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*

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

in which $\theta_{ij} A_j \frac{P_i}{\Omega_j(t)} \frac{1}{P_i} = \theta_{ij} \frac{A_j}{\Omega_j(t)}$ represents the proportion of the *i*-patches being occupied by 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 animal *j* can establish. Thus the term $\Phi_i(t) P_i$ in Equations (8) and (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 for a 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 nontrivial steady states of systems describing mutualistic and antagonistic metacommunities. The species that survive in these steady states are identified, and in particular the number of such species and, hence, the steady-state species richness are 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 4 network structure metrics: network size (number of species $S = 24$, 64, 96, and 120), connectance (relative number of interactions $C = 0.07$, 0.1, 0.15, and 0.2), nestedness (level of sharing of interaction partners among species $N = \mathrm{NODF}/100$ using the vegan package in R to calculate NODF, i.e., nestedness metric based on overlap and decreasing fill) (Almeida-Neto et al., 2008; Oksanen et al., 2013), and modularity (degree of compartmentalization Q using the igraph R package) (Guimerà & Amaral, 2005; Newman & Girvan, 2004). Network modularity and nestedness are controlled by varying the probabilities that network connections will be made within one of four modules of equal size (*pcomp*) and within a nestedness structure (*pnest*) between 0 and 1 in 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 that 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 using $Z(N) = \frac{N_{\mathrm{obs}} - \overline{N}_{\mathrm{null}}}{\sigma(N_{\mathrm{null}})}$ and $Z(Q) = \frac{Q_{\mathrm{obs}} - \overline{Q}_{\mathrm{null}}}{\sigma(Q_{\mathrm{null}})}$, where N_{obs} and Q_{obs} are nestedness and modularity for an observed network at steady state, $\overline{N}_{\mathrm{null}}$ and $\overline{Q}_{\mathrm{null}}$ are the mean nestedness and modularity of 100 replicates of a particular null model, and $\sigma(N_{\mathrm{null}})$ and $\sigma(Q_{\mathrm{null}})$ are their standard deviations of the 100 null models. While Z-scores are not appropriate for comparing nestedness between different networks (Song et al., 2017), they provide a good means for 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; Payrató-Borràs et al., 2019; Song et al., 2017; Strona et al., 2018; Ulrich et al., 2009).

Initial patch occupancies are equal for all species, and patch dynamics are simulated until the metacommunity reaches a steady state (Appendix S3: Figure S1). For each simulation, the colonization and extinction rates for each species in the metacommunity are drawn randomly from an appropriate uniform distribution. 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 (Figure 1 and Appendix S3: Figures 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 modeling predictions, we compile a large data set 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 conduct statistical analyses for all these empirical data together to check whether our predicted networks (obtained from the 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 ($N = \mathrm{NODF}/100$), and modularity (Q) and their Z-scores. In addition, we compare the nestedness and modularity of the observed networks to the expected nestedness ($\overline{N}_{\mathrm{null}}$) and modularity ($\overline{Q}_{\mathrm{null}}$) of 100 replicates of the null models, again including the equiprobable, probabilistic, and fixed models. As shown in Figures 3 and 4 and Appendix S3: Figures S8–S11, Z-scores derived from different null models can yield different patterns, confirming previous work (Payrató-Borràs et al., 2019; Song et al., 2017; Strona et al., 2018; Strona & Fattorini, 2014). 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: Figures S8–S11), which has been the preferred choice in the majority of work dealing with network structure and stability (Bascompte et al., 2003; Fortuna et al., 2010; Olesen et al., 2007; Rodríguez-Gironés & Santamaría, 2006; Thébault & Fontaine, 2010).

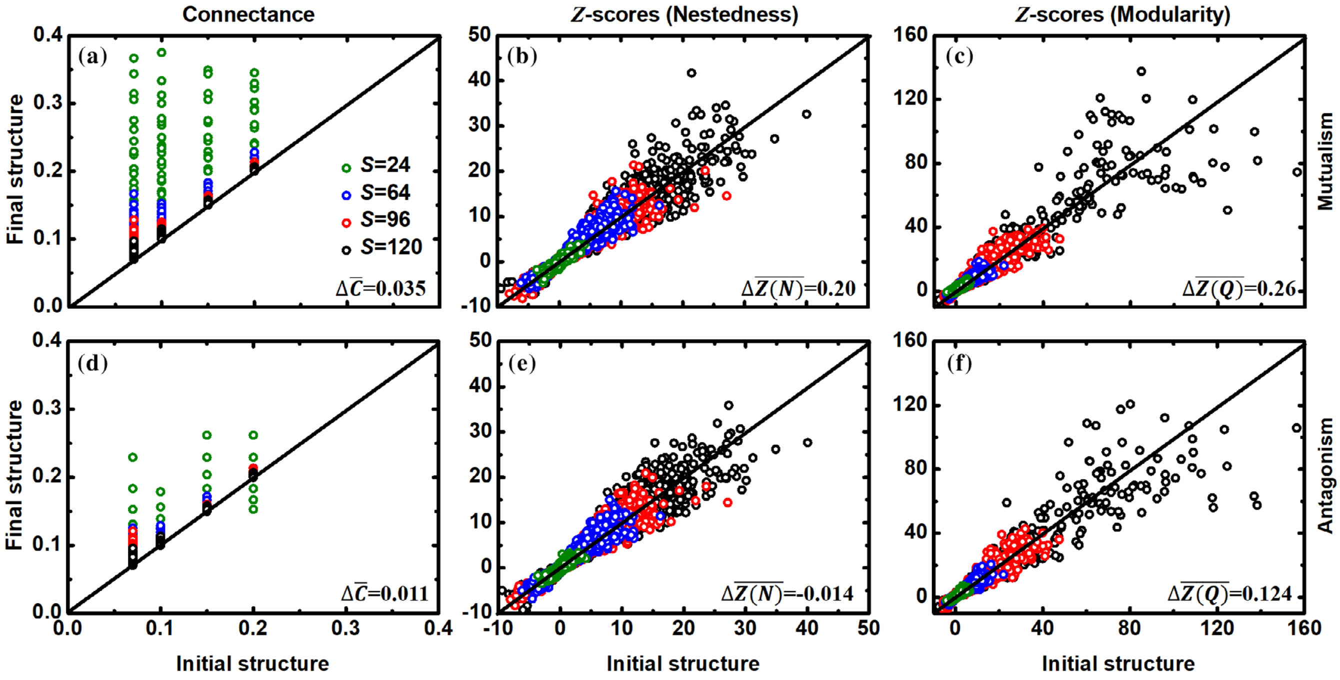

FIGURE 1 Steady-state structure of (a–c) mutualistic and (d–f) antagonistic networks against their initial structure, at different levels of initial community diversity ($S = 24$, 64, 96, 120 in different colors) and connectance ($C = 0.07$, 0.1, 0.15, and 0.2). The mean difference in these characteristics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

TABLE 2 Empirical data sets analyzed in this study

Interaction	Type	No. network	*S*	*C*	*N*	*Q*
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 no. species; *C*, connectance; *N*, nestedness (=NODF/100); *Q*, modularity.

RESULTS

Model analysis

We began by comparing the initial structure of metacommunities with that obtained at steady state (Figure 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: Figures S1 and 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 ($\Delta\overline{Z} = \overline{Z}_{\text{Final}} - \overline{Z}_{\text{Initial}}$) (Figure 1c,f). The nestedness in mutualistic metacommunities also increased ($\Delta\overline{Z(N)} = 0.20$) (Figure 1b) but decreased in antagonistic metacommunities ($\Delta\overline{Z(N)} = -0.014$) (Figure 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 models (SEMs). 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 affect metacommunity persistence. To disentangle the effects of diversity and connectance, we tried different SEMs for path analysis (Figure 2 and Appendix S3: Figures S13 and S14), and the best performing of these models was presented in Figure 2 (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 (Figure 2). Regardless of interaction type, the overall effects (combining direct and indirect effects) of these structural properties on metacommunity persistence were positive (Figure 2), except for the overall effect of nestedness in antagonistic networks (which had a weak negative effect). Comparing these factors, we found that the interaction ($N \times Q$) of nestedness and modularity had a strong positive effect on persistence, with this interaction always promoting final diversity (Figure 2). However, these interactive effects were substantially stronger in mutualistic networks than in antagonistic ones (Figure 2).

The emergent metacommunities were also compared to structures generated from the probabilistic null model (Figure 3). Both mutualistic and antagonistic metacommunities showed a negative linear relationship between network size and connectance (with a log–log scale in Figure 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, that is, networks with low modularity tended to be highly nested, and vice versa (Figure 3b). Both nestedness and modularity in emergent metacommunities were higher than those obtained in the probabilistic null model (see average on Z-scores in Figure 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 (Figure 4). As commonly observed in natural

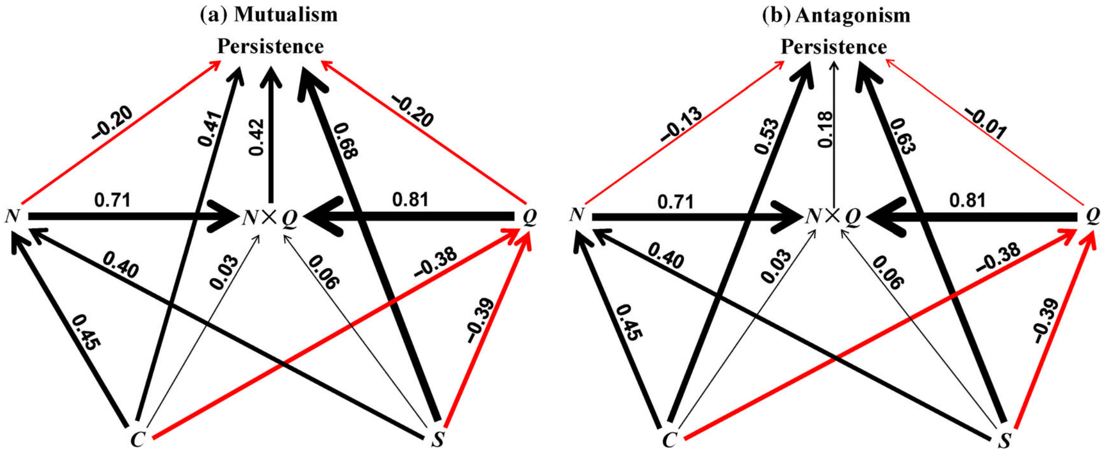

FIGURE 2 Path analysis of initial network architecture on persistence of (a) mutualistic and (b) antagonistic metacommunities (S—diversity, C—connectance, N—nestedness with N = NODF/100, Q—modularity, and $N \times Q$—interaction between nestedness and modularity), obtained from Figure 1. Different structural equation models are used for path analysis, finding that the one presented here is the best-performing one (Appendix S2: Section S1 and Appendix S3: Figures S13 and 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

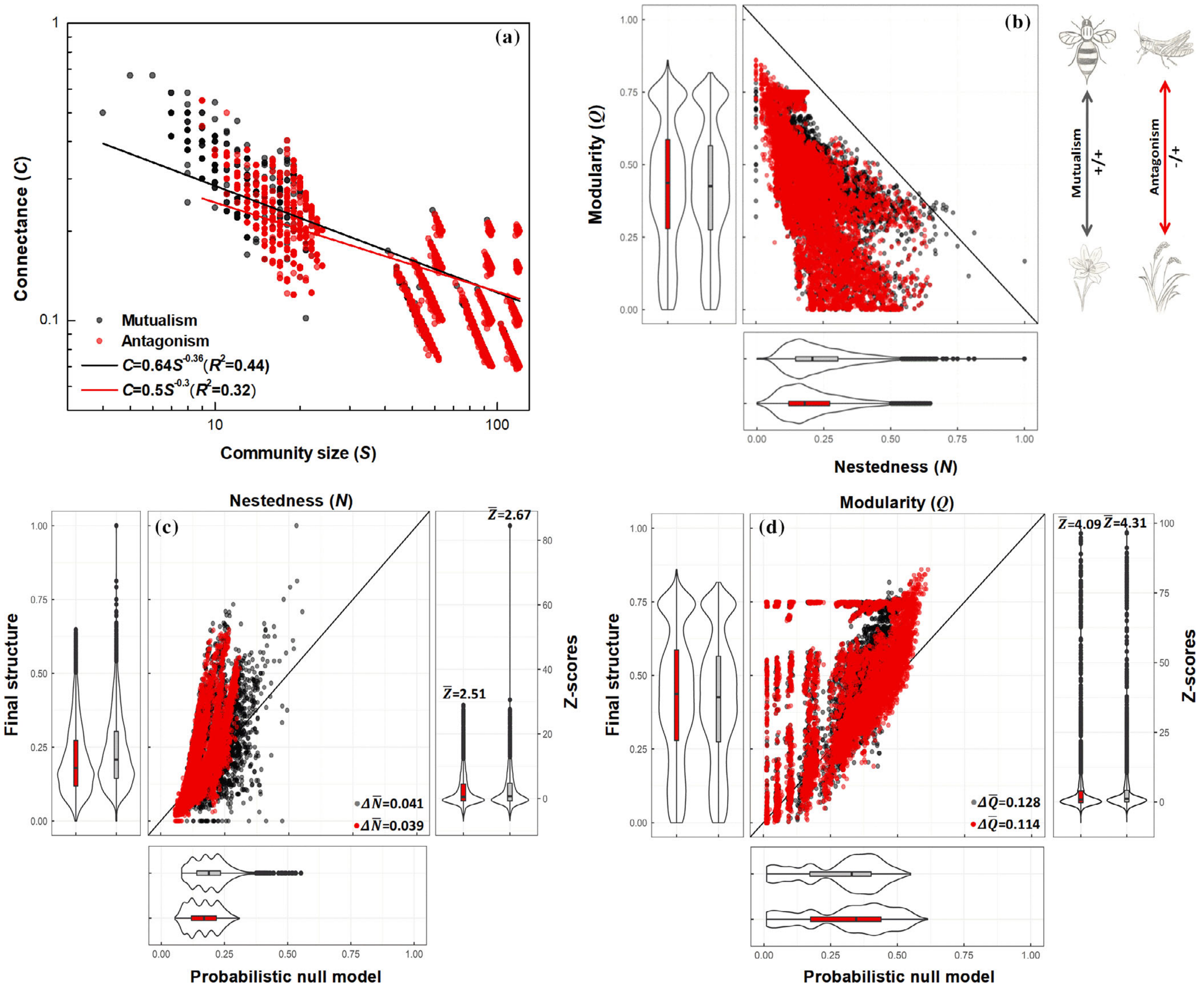

FIGURE 3 Analysis of structural properties of simulated mutualistic and antagonistic bipartite networks at steady state, obtained from Figure 1. Each point corresponds to the steady state of a simulated mutualistic or antagonistic network, with the distribution of each metric being summarized in adjacent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

ecosystems, both types of community displayed a negative linear relationship between community size and connectance (on a log–log scale in Figure 4a), similar to our theoretical results (Figure 3a). However, antagonistic networks tended to be more connected than mutualistic networks if the community size was 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 (Figure 4b), in line with our modeling predictions (Figure 3b). Both types of community were typically more nested and modular than the probabilistic null model (Figure 4c,d), as predicted by our model (Figure 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

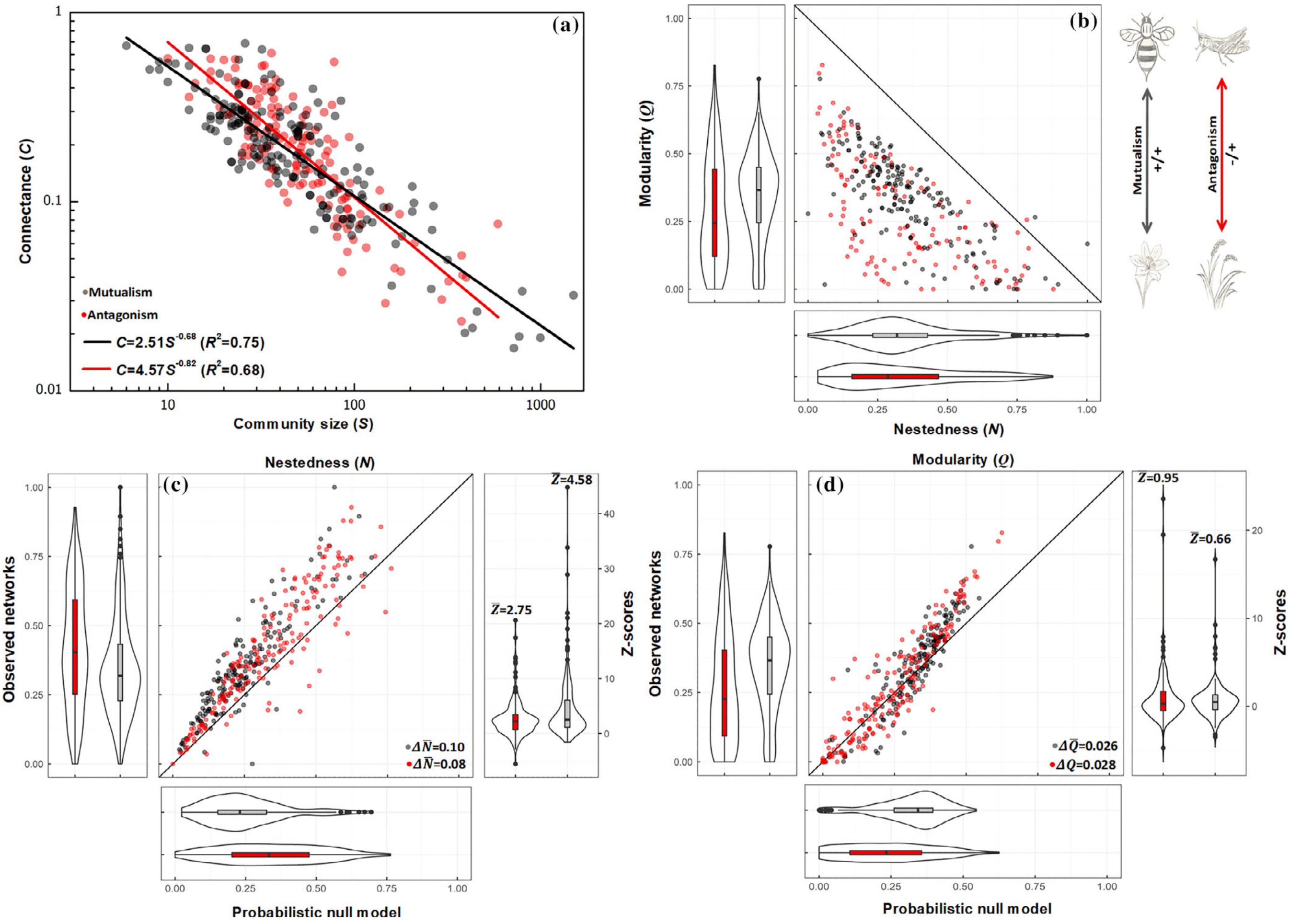

FIGURE 4 Analysis of structural properties of real-world mutualistic and antagonistic bipartite networks. Each point corresponds to an empirically observed network of either mutualistic or antagonistic, with the distribution of each metric being summarized in adjacent violin plots. (a) Relationship between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

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 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 the 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 a 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 the breakage of rare links between highly connected subnetworks (Appendix S3: Figure S12). In a large network with high levels of nestedness, those generalists interact with many other species, thereby forming a dense core that might be very robust to environmental disturbances, such as habitat loss (Fortuna & Bascompte, 2006). In turn, the generalist species can promote the persistence of associated specialists, consistent with Strona et al. (2013) and Strona & 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 & 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 (Figure 2). The interplay between network structure and spatial community assembly strongly affects species that highly depend 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 (Figure 2). This stems from the fact that predated plant species are not dependent on their predators. In fact, 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, plant species linked to many predators are more vulnerable to extinction because of strong top-down control, which reduces network asymmetry (Appendix S1: Section S1). Taken 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. Because 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 (Figure 1). This explains why the overall effect of nestedness switches from promoting (mutualism) to suppressing (antagonism) metacommunity persistence, as predicted by nonspatial models (Thébault & Fontaine, 2010).

The previously described mechanism also drives the changes we observe in network structure at steady state (Figure 3). Because of the vulnerable links between specialists, network connectance, nestedness, and modularity tend to increase, except in antagonistic communities where nestedness declines (Figure 1). These linking patterns have been observed previously (Grass et al., 2018; Spiesman & Inouye, 2013), for example, 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 (Figures 3 and 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 previously (Michalska-Smith & Allesina, 2019).

Our modeling framework relies on several assumptions that require further discussion. First, we assumed that all species could 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 that use more realistic dispersal ranges (e.g., characterized by a dispersal kernel). Second, our model did not consider variation in interaction strength/frequency between each plant–animal pair, nor were intraguild competitive interactions considered (Ghazoul, 2006; van Veen et al., 2006). One could anticipate that a trade-off 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 colonization rate by feeding on seeds or propagules (e.g., Olff & Ritchie, 1998; Ryberg et al., 2012; Ryberg & Chase, 2007). In addition, some field observations find that prey species can even avoid places with perceived high predation risk (e.g., Resetarits & Binckley, 2013). The effects of predators on colonization may have qualitatively different outcomes than their effects on extinction, so future studies could 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 treated 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 nonspatial models (e.g., Thébault & Fontaine, 2010), so it can be used to describe site colonization–extinction dynamics for these empirical communities, despite 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 (Allesina & Tang, 2012; Bastolla et al., 2009; Grass et al., 2018; Thébault & Fontaine, 2010). 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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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Jinbao Liao conceived this study, built the model, wrote the MATLAB codes and performed simulations, and wrote the first draft. Jinbao Liao and Daniel Bearup analyzed the results and rewrote the manuscript. Giovanni Strona discussed the results and contributed substantially to revisions.

DATA AVAILABILITY STATEMENT

Data (Liao et al., 2022) are available on Dryad: https://doi.org/10.5061/dryad.mkkwh7121.

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