

Coevolution by different functional mechanisms modulates the structure and dynamics of antagonistic and mutualistic networks

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Abstract

A central problem in the study of species interactions is to understand the underlying ecological and evolutionary mechanisms that shape and are shaped by trait evolution in interacting assemblages. The patterns of interaction among species (i.e. network structure) provide the pathways for evolution and coevolution, which are modulated by how traits affect individual fitness (i.e. functional mechanisms). Functional mechanisms, in turn, also affect the likelihood of an ecological interaction, shaping the structure of interaction networks. Here, we build adaptive network models to explore the potential role of coevolution by two functional mechanisms, trait matching and exploitation barrier, in driving trait evolution and the structure of interaction networks. We use these models to explore how different scenarios of coevolution and functional mechanisms reproduce the empirical network patterns observed in antagonistic and mutualistic interactions and affect trait evolution. Scenarios assuming coevolutionary feedback with a strong effect of functional mechanism better reproduce the empirical structure of networks. Antagonistic and mutualistic networks, however, are better explained by different functional mechanisms and the structure of antagonisms is better reproduced than that of mutualisms. Scenarios assuming coevolution by strong trait matching between interacting partners better explain the structure of antagonistic networks, whereas those assuming strong barrier effects better reproduce the structure of mutualistic networks. The dynamics resulting from the feedback between strong functional mechanisms and coevolution favor the stability of antagonisms and mutualisms. Selection favoring trait matching reduces temporal trait fluctuation and the magnitude of arms races in antagonisms, whereas selection due to exploitation barriers reduces temporal trait fluctuations in mutualisms. Our results indicate that coevolutionary models better reproduce the network structure of antagonisms than those of mutualisms and that different functional mechanisms may favor the persistence of antagonistic and mutualistic interacting assemblages.

Keywords: coevolution, exploitation barrier, functional trait, nestedness, modularity, trait matching

Introduction

Coevolution is the reciprocal trait change resulting from ecological interactions, shaping the adaptive peaks of pairs of interacting species (Guimarães et al. 2017). A fundamental problem in evolutionary ecology is how scaling up coevolutionary dynamics from pairs of species to assemblages forming networks with defined structures that are shaped by and shape ecological and evolutionary processes (Bascompte 2009, Thompson 2013, Barraclough 2015). In this vein, the way that coevolution modulates the structure of networks of interacting species may depend on how species traits determine the likelihood of interactions and impact fitness (hereafter, the functional mechanism; Stang et al. 2006, Dehling et al. 2014, Schleuning et al. 2014). At the same time, the structure of a network represents the pathways through which the effects of selection may create evolutionary cascades that propagate through the network, driving trait evolution of multiple species (Encinas-Viso et al. 2012, Nuismer et al. 2013, Beckett and Williams 2013, Minoarivelo and Hui 2016b, Andreazzi et al. 2017, Guimarães et al. 2017). For example, selection imposed by one parasite species may promote evolutionary changes in a host species, which may lead to changes in another parasite species that share the same host. Thus, exploring how network structure emerges as a result of coevolution by different functional mechanisms and how such structure affects trait evolution is key to elucidate the feedbacks among ecological and evolutionary processes in shaping biodiversity (Thompson 2013).

Here we explore two pervasive network structures that have been widely observed across species assemblages -nestedness and modularity- and that may be affected by coevolutionary processes. Nestedness is a pattern characterized by specialist species interacting with subsets of species interacting with more generalist ones (Bascompte et al.

2003, Vázquez and Aizen 2004). Modularity is a pattern in which there are groups of species having many interactions among themselves and very few interactions with species in other modules (Newman 2006, Olesen et al. 2007). Antagonistic and mutualistic interactions among free-living species (e.g. herbivory by grasshoppers and mammals, frugivory) are often more nested and less modular than intimate interactions among species (e.g. gall-forming and leaf-mining insects and their plants, protective ants and their plants; Fontaine et al. 2011). Thus, no discrete classes of network structure can be strictly associated with different types of interactions (Fontaine et al. 2011, Pires and Guimaraes 2012). However, ecological interactions do vary in such a way that selective pressures lead to different trait evolution, and therefore to different outcomes depending on the functional mechanisms that shape the likelihood of interaction occurrence in nature.

Functional mechanisms describe how physiological, morphological and life-history traits modulate the likelihood of an interaction and affect individual fitness (Williams and Martinez 2000, Stang et al. 2006b, Rezende et al. 2007, Santamaría and Rodríguez-Gironés 2007, Blüthgen et al. 2008, Pires et al. 2011, Eklöf et al. 2013). At the community level, functional mechanisms may lead to specific network patterns across mutualistic and antagonistic interactions (Stang et al. 2006a, Nuismer et al. 2013, Santamaría and Rodríguez-Gironés 2015, Andreazzi et al. 2017). Nestedness can emerge as an outcome of thresholds imposed by how species traits, such as body size (Vázquez et al. 2009, Chamberlain et al. 2010) and prey preferences (Kondoh 2003, Araújo et al. 2010), affect the use of resources by consumers. In contrast, modules may emerge because of constraints imposed by trait matching such as those among attack and defense traits and among plant rewards and the requirements of pollinators and frugivores (Olesen et al. 2007, Donatti et al. 2011, Krasnov et al. 2012, Schleuning et al. 2014).

At evolutionary timescales, the functional mechanism determining network interaction patterns also may drive trait evolution. As a consequence, we should expect that coevolution by different functional mechanisms play a role in shaping nestedness and modularity (Thompson 2005; but see Ponisio and M’Gonigle 2017). For instance, a high matching between cuckoo and host eggs decreases the probability of egg rejection (Krüger 2007, Vikan et al. 2011) and increases the chance of a successful antagonistic interaction. In the same vein, the matching of floral and pollinator traits also increases the fitness effect of the mutualistic interaction (Johnson and Steiner 1997, Stang et al. 2009, Ibanez 2012). Therefore, coevolution selecting for trait matching (i.e. fitness effect of interaction increases with trait similarity) may promote increased levels of reciprocal specialization and segregate communities into semi-independent modules (Nuismer et al. 2013, Nuwagaba et al. 2015, Andreazzi et al. 2017). In contrast, coevolution selecting for exploitation barriers (i.e. fitness effect of interactions depends on whether species traits are larger than the threshold that allows interaction occurrence) may lead to nested structures (Nuismer et al. 2013). For example, weevils successfully infect camellia seeds only if their rostra are longer than the camellia fruit pericarp (Toju 2011). Otherwise, the camellia seeds are protected from predation (Toju 2011). Exploitation barriers have also been documented in mutualisms such as the hawkmoth-plant pollination interaction, which is modulated by hawkmoth mouthparts length and corolla depth (Alexandersson and Johnson 2002, Santamaría and Rodríguez-Gironés 2015). Therefore, trait evolution in mutualisms and antagonisms may be affected by a complex interplay of functional mechanisms, coevolution, and network structure. It has been increasingly recognized that trait coevolution and network structure may ultimately affect the evolutionary dynamics of species interactions (Nuismer et al. 2013, Thompson 2013, Guimarães et al. 2017, Ponisio and M’Gonigle 2017, Andreazzi et al. 2018). These models

have shown that coevolution reduces trait variation in mutualistic networks (Guimarães et al. 2017). In antagonistic networks, trait matching is related to fluctuating selection and increased trait variation (Andreazzi et al. 2018). However, modeling coevolution by different functional mechanisms and evaluating the ability of these mechanisms to reproduce the structures observed in empirical networks is still an open challenge

In this study we explore how coevolution by different functional mechanisms shapes the structure and drives the evolutionary dynamics of antagonistic and mutualistic networks. We use an adaptive network framework (Gross and Blasius 2008) that combines the evolution of species traits and the assembly of interactions, allowing us to study feedbacks between trait evolution and network structure. We study coevolution by two functional mechanisms, trait matching and exploitation barrier, and we evaluate the ability of such models to predict the structure of empirical networks covering a wide spectra of antagonistic and mutualistic ecological interactions. Our aim is to understand (i) how coevolution by different functional mechanisms explains the modular and nested structure of empirical antagonistic and mutualistic networks, and (ii) how these processes may drive species trait evolution.

Methods

Coevolution by functional mechanisms, trait evolution and the structure of networks

The adaptive network framework

We use an adaptive network framework (Raimundo et al. 2018) to study how antagonistic and mutualistic networks are shaped by different functional mechanisms and coevolution. The adaptive network approach combines the evolution of species traits caused

by direct and indirect interactions among species and the feedback between trait evolution and network dynamics (Figure 1).

We define z_i^t as the mean value of a single quantitative trait in species i at time t . We assume that there is evolutionary feedback between species traits and interactions, i.e. that z_i^t shapes interactions between species i and other species of the network and that those interactions affect trait evolution. We initially sample the value of z_i^t from a normal distribution (mean=0, sd=0.1). Species traits determine the probability of pairwise interactions according to a given functional mechanism (described below). Once pairwise interactions have been assigned, traits evolve in response to the selective pressures imposed by the environment and interactions among species. Thus, pairwise interaction probabilities are recalculated at each time step and species interactions are re-assigned following the updated interaction probabilities, which may lead to a new matrix of realized interactions (Figure 1).

Functional mechanisms

We study the effects of coevolution on network structure and trait evolution by considering two different functional mechanisms, trait matching and exploitation barrier. These mechanisms are depicted in the simulations by a matrix with a total of R species (resources in rows and consumers in columns) whose elements are the probabilities of pairwise interaction among species. The trait matching mechanism assumes that the similarity of resource and consumer traits determines the probability of pairwise interaction among them in a given time step (Nuismer and Thompson 2006, Nuismer et al. 2013). Pairwise interaction probabilities are calculated as follows:

$$p_{ij}^t = e^{-\alpha(z_i^t - z_j^t)^2} \quad (1)$$

In this equation α is the strength of the mechanism and measures how the degree of trait matching changes the probability of pairwise interaction.

The exploitation barrier mechanism assumes that the consumer species has to overcome a barrier to successfully interact with a resource species. Thus, the probability of pairwise interaction depends on how large is the difference between trait z_i^t of consumer i and trait z_j^t of resource j , with the interaction successfully occurring only if such difference is higher than a given threshold. Pairwise interaction probabilities are calculated as follows:

$$p_{ij}^t = \frac{1}{1 + e^{-\alpha(z_i^t - z_j^t)}} \quad (2)$$

As in Eq. 2, α measures how the difference in species traits affects the probability of pairwise interaction (Nuismer and Thompson 2006, Nuismer et al. 2013).

Interactions among species in each network are assigned proportionally to interaction probabilities (\mathbf{P}^t , Eq. 1, 2). We initially allocate one interaction for each species with probability proportional to \mathbf{P}^t , therefore ensuring that all species have at least one interaction and then the remaining interactions are assigned according to \mathbf{P}^t .

Trait evolution

We use a time-discrete model that describes trait evolution in the context of selection imposed by environment and species interactions, as in previous coevolutionary network models (Andreazzi et al. 2017, Guimarães et al. 2017). We modify the classical equation for phenotypic evolution (Lande 1976) to calculate the evolutionary change of z_i^t in a given time step (Eq. 3, 4). The selection gradient is composed by environmental and species interaction selection pressures (Andreazzi et al. 2017, Guimarães et al. 2017,). We describe the mean trait

evolution of a given species that interacts with a partner j assuming interactions are affected by trait matching (Eq. 3) and exploitation barrier (Eq. 4) as follows:

$$z_i^{t+1} = z_i^t + \varphi_i(S_i^t + M_{ij}^t) \quad (3)$$

$$z_i^{t+1} = z_i^t + \varphi_i(S_i^t + B_{ij}^t) \quad (4)$$

In Eq. 3 and 4, φ_i is a constant proportional to the slope of the selection gradient and to the additive genetic variance of the trait under selection (Guimarães et al. 2017). Because previous studies have already shown that φ_i has no qualitative effect on coevolutionary dynamics (Guimarães et al. 2017), we assume φ_i is fixed and identical for all species ($\varphi = 0.25$). S_i^t , M_{ij}^t and B_{ij}^t are the partial selection differentials caused by environmental selection, selection imposed by interactions due to trait matching and selection imposed by interactions due to exploitation barriers, respectively.

We assume that environmental selection favors an optimum trait value for each species, θ_i , and that $\theta_i = z_i^{t=0}$ for simplicity. The partial selection differential caused by the environment (S_i^t) is defined as follows:

$$S_i^t = \xi_S(\theta_i - z_i^t) \quad (5)$$

in which ξ_S is the intensity of environmental selection, $0 < \xi_S < 1$, and $\theta_i - z_i^t$ is the difference between environmental optimum and the mean trait value of the population at time step t .

To model coevolution by trait matching, we assume that the consequences of pairwise interactions on fitness depend on the degree of trait matching between interaction partners. Therefore, we are assuming that trait matching affects both the functional viability of the interaction (probability of interaction) and the selective pressures imposed by the ecological

interactions. Selection on consumer i favors trait matching with resource j for both antagonistic and mutualistic interactions. The consumer's partial selection differential (M_{ij}^t) is calculated as:

$$M_{ij}^t = \xi_d a_{ij}^t (z_j^t - z_i^t) \quad (6a)$$

in which ξ_d is the intensity of selection imposed by resource species j , so that $\xi_d + \xi_S = 1$, and a_{ij}^t describes the evolutionary effect of the interaction between species i and j at time t (see below). Similarly, selection also favors trait matching with consumer i in mutualistic interactions for the resource species j :

$$M_{ji}^t = \xi_d a_{ji}^t (z_i^t - z_j^t) \quad (6b)$$

In contrast, in antagonisms selection favor trait mismatching on resource species. To model selection favoring trait mismatches in antagonistic interactions we assume there is a critical mismatch, ε , so that if $|z_i^t - z_j^t| > \varepsilon$ consumer i has a negligible effect on the fitness of resource j (Andreazzi et al. 2017). We assume ε is fixed and identical for all species ($\varepsilon = 0.5$). Because single-trait matching relationships imply bidirectional trait axis, selection acting on the resource j can favor either increasing z_j^t ($z_i^t + \varepsilon$, if $z_j^t > z_i^t$) or decreasing z_j^t ($z_i^t - \varepsilon$, if $z_j^t < z_i^t$), leading to:

$$\begin{cases} M_{ji}^t = \xi_d a_{ji}^t u_{ji}^t (z_i^t + \varepsilon - z_j^t) & \text{if } z_i^t < z_j^t \\ M_{ji}^t = \xi_d a_{ji}^t u_{ji}^t (z_i^t - \varepsilon - z_j^t) & \text{if } z_i^t > z_j^t \end{cases} \quad (6c)$$

in which $u_{ji}^t = 1$ if $|z_i^t - z_j^t| \leq \varepsilon$; $u_{ji}^t = 0$ if $|z_i^t - z_j^t| > \varepsilon$. The evolutionary effect a_{ij}^t is defined as:

$$a_{ij}^t = \frac{l_{ij}^t p_{ij}^t}{\sum_{k=1, k \neq i}^R l_{ik}^t p_{ik}^t} \quad (7)$$

In this equation, $l_{ij}^t = 1$ if species i and j interact at time t and otherwise $l_{ij}^t = 0$. R is the total number of species in the network.

In the model describing coevolution by exploitation barriers, selection on consumers favors a unidirectional larger trait value that overcomes the exploitation barrier determined by the traits of the resource species. We assume that the trait of consumer i , z_i^t , needs to be larger than the trait value of resource j plus a critical value, i.e. $z_j^t + \varepsilon_b$, for the successful occurrence of the pairwise interaction in both mutualistic and antagonistic interactions. The partial selection differential imposed by resources on consumers (B_{ij}^t) is defined as:

$$B_{ij}^t = \xi_d a_{ij}^t (z_j^t + \varepsilon_b - z_i^t) \quad (8a)$$

Selection on resource j favors traits that increase the probability of a successful interaction with consumer i in mutualistic interactions, leading to:

$$B_{ji}^t = \xi_d a_{ji}^t (z_i^t - \varepsilon_b - z_j^t) \quad (8b)$$

In antagonistic interactions, in contrast, selection on resource j favors traits that are sufficiently large to avoid attack so that $z_j^t > z_i^t + \varepsilon_b$ consumer i has a negligible effect on the fitness of resource j ($u_{ji}^t = 0$). The partial selection differential imposed by antagonistic consumer i on resources j is defined as:

$$B_{ji}^t = \xi_d a_{ji}^t u_{ji}^t (z_i^t + \varepsilon_b - z_j^t) \quad (8c)$$

Empirical antagonistic and mutualistic networks

To investigate how coevolution by functional mechanisms shapes the structure and trait dynamics of antagonistic and mutualistic networks we parameterize the models with data from 122 antagonistic (i.e. herbivory, parasitism and predation) and 122 mutualistic (i.e. dispersal, pollination and protective) empirical networks (Supplementary material, Table A1). We use the number of resources (i.e. plants in mutualistic networks; plants, hosts and prey in antagonistic networks), consumers (i.e. pollinators, dispersers and ants in mutualistic networks; herbivores, parasites and predators in antagonistic networks) and realized interactions (i.e. connectance) of these networks to parameterize the dimensions and the total number of interactions of simulated matrices (the \mathbf{L}' matrix of each simulation). The empirical networks range from very small networks of bacteria and phages or protective ants and plants that include less than 10 species to large networks of fishes and their parasites or plants and their pollinators including more than 240 species (Table A1). The structure of each empirical network is characterized by nestedness, estimated using the descriptor NODF (Almeida-Neto et al. 2008), and modularity, estimated using the descriptor Q (Newman 2006, Barber 2007). We estimate the degree of modularity using the fast greedy modularity optimization algorithm for finding community structure (Clauset et al. 2004), which combines fast computing time with adequate performance for characterization of small (< 1000 nodes) networks with similar species richness (Marquitti et al. 2014, Leger et al. 2015).

Numerical simulations

We explore differences between coevolution by trait matching and exploitation barrier models by comparing scenarios of weak ($\alpha = 1$) or strong ($\alpha = 100$) effects of the functional mechanisms on interaction probabilities and moderate or strong interaction selection imposed

by those mechanisms (ζ_d) as described in Table 1. In scenarios with moderate effects of coevolution there is a balance between the selective pressure imposed by interactions and that of the environment ($\zeta_d = \zeta_S = 0.5$). In those scenarios in which coevolution has a strong effect, selection imposed by interacting species is the main force driving species trait evolution ($\zeta_d = 0.99$).

We also explore four null scenarios as theoretical benchmarks to improve our understanding of the effects of coevolution by the two different functional mechanisms on network structure and trait dynamics. In the no effect (random interactions) null scenarios (Table 1) the probability of pairwise species interaction does not depend on traits and is equal for all species ($p_{ij} \sim 1/N_V N_E$), and the intensity of coevolution is either moderate ($\zeta_S = 0.5$) or strong ($\zeta_d = 0.99$). We use no coevolution (fixed traits) null scenarios (Table 1) to understand how networks are assembled by weak ($\alpha = 1$) or strong ($\alpha = 100$) functional mechanisms in the absence of coevolutionary feedback. In the no coevolution null scenarios species traits are fixed at the environmental optimum (θ_i). We run 100 replicates per each combination of network, functional mechanism and selection scenario (Table 1).

We characterize the structure of networks obtained at the end of each simulation by calculating nestedness and modularity as described above for empirical networks. Because interactions can rewire over time and alter network structure, we calculate these structural statistics at different points in time (at $t = 1, 100, 500, 1000$, and every 1000 time steps thereafter) and obtain mean values. We also characterize the outcome of trait evolution at the end of each simulation. Each simulation run ($n=100$) per network replicate implies 10 000 time steps (i.e. generations), which represents the adequate time for the stabilization of the variance of the structural statistics. We compute the magnitude of trait change, $D_i =$

$|z_i^{t=10\,000} - z_i^{t=0}|$, which measures the final outcome of trait evolution, and the total temporal trait fluctuation, $F_i = \sum_{t=0}^{t=10\,000} |z_i^{t+1} - z_i^t|$, which characterizes the trajectory of trait change in time. We obtain the average value of D and F considering all species within each network replicate to evaluate the effects of coevolution by the different functional mechanisms on trait evolutionary dynamics.

Statistical analyses

Performance of models and scenarios in reproducing the structure of empirical networks

We calculate the accuracy of the structural fit between the empirical estimates of network nestedness and modularity and their counterparts in the networks obtained through simulations by computing the normalized model error (NME) between these estimates (Williams and Martinez 2008, Pires et al. 2011). The normalized NME of a given statistic can be defined as the absolute difference between the model's median value and the empirical value divided by the difference between the model's median value and the value at the 2.5% or 97.5% quantiles, depending on whether the empirical value is lower or larger than the model's median (Williams and Martinez 2008, modified by Pires et al. 2011). By using this approach, we do not make particular assumptions about the distribution of values that is generated by the models. The empirical structural statistic is considered significantly different from the distribution of structures obtained through simulations if $NME < -1$ or $NME > 1$, with positive and negative NME values outside this range indicating over and underestimation, respectively. We evaluate the performance of scenarios in reproducing the structural properties of empirical networks by calculating both the significance of the median NME values and the percentage of empirical networks whose structure was significantly reproduced ($|NME| < 1$) by each scenario. We test the significance of differences between

scenarios performances by using Wilcoxon signed rank test which estimates the median of the pairwise difference in NME values from each scenario being compared and its associated 95% confidence intervals. Scenarios' performances are considered different if these confidence intervals do not include the zero value (Hollander and Wolfe 1999).

Model predictions of trait evolution

We analyze the predicted effects of coevolution by different functional mechanism on 1) the magnitude of directional trait change, and 2) the temporal fluctuation of traits by comparing these response variables across the full set of scenarios that are described in Table 1. We test the significance of differences between scenarios by using the same procedure described above.

Results

The empirical antagonistic and mutualistic networks show no difference in mean modularity and nestedness, with both interaction types containing highly nested and modular networks (Figure 2). However, within these interaction types some show higher nestedness, such as mammalian predator-prey and frugivory networks, while others tend to be more modular, such as leafminer-plants and protective networks (Supplementary material Appendix 1 Figure A3).

Scenarios including coevolution with a strong functional mechanism (SM and SS models) have, in general, better performance than other scenarios in predicting the structure of empirical networks, particularly in antagonistic systems (Table 1). These scenarios perform particularly well in predicting the structure of antagonistic networks such as seed predation, chewing herbivory, fish parasitism, bacteriophagy and mammal predation (Supplementary

material Appendix 1 Figure A6-A7). For mutualistic systems the scenario that assume a balance between coevolutionary and environmental selection predict better the structure of those networks (SM model, Table 1). Thus, the effect of coevolution in better reproducing antagonistic and mutualistic networks is evidenced only when there is a strong functional mechanism because scenarios including coevolution with weak functional mechanism (WS and WM models) perform similar to the null scenarios (Table 1, Supplementary material Appendix 1 Figure A4-A5).

Moderate coevolution by trait matching strongly determining interactions has, in general, the best performance for antagonistic networks, reproducing nestedness and modularity of almost 70% of the networks (Table 1, Fig. 3, 4). The modular and nested structure of chewing herbivory, fish parasitism and bacteriophagy networks is reproduced by both mechanisms, with trait matching always performing better (Supplementary material Appendix 1 Fig. A6-A7). Mammal predators and prey interactions are the only antagonistic networks which modularity and nestedness are better predicted by the exploitation barrier mechanism (Supplementary material Appendix 1 Fig. A6-A7). These results are not affected by differences in connectance and size among such interactions as the ability of scenarios to reproduce the structure of empirical networks (i.e. their NME) is not affected by these network structural parameters (Supplementary material Appendix 1 Fig. A10-A13).

Scenarios assuming moderate coevolution by strong exploitation barriers better reproduce mutualistic interactions (Fig. 3, 4), significantly predicting the modular and nested structure of ca. 20% of networks (Table 1). This result is consistent across all types of mutualistic interactions considered (Supplementary material Appendix 1 Figure A8). However, the modularity of mutualistic networks is similarly predicted by scenarios assuming

moderate coevolution by any type of strong functional mechanism (22% of networks; Table 1). In general, trait matching tends to overestimate mutualistic network modularity, while exploitation barrier tends to underestimate it (Supplementary material Appendix 1 Figure A9). Network connectance and size are not related to the ability of scenarios to predict the nested structure of mutualistic networks (i.e do not affect the NME; Supplementary material Appendix 1 Fig. A14, A16). For modularity there is a small effect of network connectance and size on the NME of mutualistic networks ($R^2 = 0.16$ and $R^2 = 0.07$, respectively), with smaller and more connected networks being better predicted by scenarios including coevolution (Supplementary material Appendix 1 Fig. A15, A17).

Trait evolution

In general, strong coevolution boosts trait change in antagonistic interactions while it stabilizes trait change in mutualistic interactions (Figures 5, 6, Supplementary material Appendix 1 A18–A19). Moderate coevolution by strong trait matching, the scenario that better reproduces the structure of antagonistic networks, shows the lowest magnitude of directional trait change and strongly restricts temporal trait fluctuation in such interactions (Fig. 5, 6). In mutualistic networks, the scenario that better reproduces network organization (strong intensity of exploitation barrier with moderate coevolution) reduces temporal trait fluctuations and promotes higher magnitude of directional trait change than other scenarios (Fig. 5, 6). Therefore, the scenarios that better perform in reproducing network structure for both antagonisms and mutualisms are those that often reduce temporal trait fluctuation, increasing the evolutionary stability of ecological networks.

Discussion

Unraveling the importance of trait-based ecological and evolutionary processes in structuring communities is central to understand biodiversity (Thompson 2005, Gravel et al. 2006, Kembel 2009, Venner et al. 2011, Leibold and Chase 2017). In the context of the study of ecological networks there is a growing effort to understand how these processes account for nestedness and modularity in empirical networks (Vázquez et al. 2007, Krishna et al. 2008, Canard et al. 2012, Fort and Mungan 2015, Gilarranz et al. 2015, Nuwagaba et al. 2015, Rohr et al. 2016). In this vein, our study shows that adaptive network models incorporating coevolution and different functional mechanisms underpinning species interactions are useful tools to explore the feedbacks of ecological and evolutionary processes on network structure. In the following, we discuss the three main results about the processes shaping the structure of antagonistic and mutualistic networks that emerge from the implementation of our modeling framework..

First, we show that empirical networks are better reproduced by scenarios considering a balance between coevolutionary and environmental selection strengths together with a strong effect of functional mechanisms, i.e. traits strongly determining interspecific interactions. Previous studies show that neutral assumptions tend to produce networks that are more nested and less modular than empirical networks (Krishna et al. 2008, Canard et al. 2014). On the other hand, trait-based mechanistic models that do not consider trait evolution produce networks with higher modularity and lower nestedness (Santamaría and Rodríguez-Gironés 2007, Nuwagaba et al. 2015). However, those with hybrid linkage rules (trait matching and exploitation barriers) are more efficient in predicting the structure of mutualistic networks (Santamaría and Rodríguez-Gironés 2007). In this regard, we find that our best model better reproduces the structure of antagonistic than mutualistic networks.

Second, we show that although the structures of antagonistic and mutualistic networks are similar, they are differently predicted by moderate coevolution by different functional mechanisms. Moderate coevolution by strong trait matching highly predicts both the nestedness and modularity of antagonisms (70% of networks), particularly of interactions among parasites and fish hosts, seed predators and plants, leaf chewing herbivores and plants, and phages and bacteria. Mammal predator-prey networks are, though, better predicted by coevolution by strong exploitation barrier. In contrast, in mutualistic interactions, coevolution by strong exploitation barrier predicts the nestedness and modularity of 20% of the networks, no matter the type of mutualism considered. Modularity was overestimated by trait matching and underestimated by exploitation barriers in mutualistic networks. Overall, our results partially support those of previous studies suggesting that coevolution and trait matching are important processes generating and maintaining the biodiversity of interactions in nature (Thompson 2005, Barraclough 2015). However, by incorporating a wide spectrum of antagonistic and mutualistic interactions than previous studies (Guimarães et al. 2007, Andreatzi et al. 2017) we show that there is no such a clear link among interaction intimacy, trait matching, reciprocal specialization, and modularity (Hembry et al. 2018). This is because we find that trait matching leads to nested structures in antagonistic networks and modular structures in mutualistic networks emerge with barrier-driven interactions. These results are not or weakly affected by connectance and species richness. Thus, our results suggest that the similar set of structures found in antagonistic and mutualistic empirical interaction networks may be determined by the interplay among functional mechanisms, the fitness effect of interactions, and their natural history.

Previous theoretical models suggest that coevolution by different functional mechanisms can have very different consequences for the structure of simulated species

networks (Nuismer et al. 2013, McPeck 2017). For instance, when antagonistic interactions evolve following a trait matching rule, coevolution tends to increase the mean trait disparity among groups of interacting species and promote modularity (Beckett and Williams 2013, Nuwagaba et al. 2015, Andreazzi et al. 2017). Here we find that, when accounting for the feedbacks between ecological and evolutionary processes, coevolution by strong trait matching reproduces not only the distribution of modularity but also the distribution of nestedness found in most of the antagonistic networks. In mutualistic interactions it was already found that coevolution by trait matching produces anti-nested networks with much higher connectance than the observed in empirical systems (Nuismer et al. 2013). This is one of the reasons why coevolution was predicted to leave a weak signal on the structure of mutualistic networks (Ponisio and M’Gonigle 2017). When an exploitation barrier drives the fitness effect of mutualistic interactions, coevolution is expected to shape networks toward more nested, generalized and highly connected architectures in which specialists are rare (Nuismer et al. 2013). We go one step further by testing how well coevolution by exploitation barriers predicts the empirical structure of mutualistic networks. The low predictive power of our models suggest that the structure of mutualistic networks may be modulated by more complex trait-based processes that have not been included in the current modeling approaches. For instance, incorporating competition among species belonging to the same trophic level could balance the high generalization predicted by current mutualistic coevolutionary models

Third, our results suggest that antagonistic and mutualistic networks experience distinct coevolutionary dynamics, which is affected by the functional mechanism. Coevolution in species-rich antagonistic interactions show diverse outcomes, including escalating traits arms races or fluctuations (McPeck 2017, Andreazzi et al. 2017). We show

that moderate coevolution driven by trait matching reproduces antagonistic networks and leads to more stable interactions with reduced arms races and less intense fluctuating trait dynamics. The occurrence of fluctuating trait dynamics was already found in several pairwise predator-prey coevolutionary models that considered a trait matching mechanism (Abrams 2000, McPeck 2017) and has also been explored as a red queen dynamic (Dieckmann et al. 1995). Fluctuating selection driven by exploitation barrier is likely to occur in antagonistic interactions only when interaction selection is strong, which results in species traits escalating until they reach a level representing a trade-off between interaction and environmental selection. Coevolution by trait matching in mutualistic interactions usually results in a stable state in which species achieve their adaptive peaks characterized by a high complementarity and convergence of species traits (Guimarães et al. 2011). This may explain why we find lower trait change in the strong coevolution models and the low predictability of mutualistic networks. High convergence in species traits tends to homogenize pairwise interaction probabilities across species, which may lead to networks with a more even distribution of degrees and therefore which structure differs from the empirical one (Astegiano et al. 2015). Our results show that moderate coevolution driven by strong exploitation barrier better explains the structure of mutualistic empirical networks. A unidirectional trait axis such as in the exploitation barrier mechanism tends to promote a higher magnitude of trait change, which may increase adaptation, and a lower temporal fluctuation in species traits that stabilizes interactions (Abrams 2000, McPeck 2017) and may explain the better performance of these models in predicting 20% of the mutualistic networks. Incorporating competition among species in the same trophic level may increase the variance in species traits, which could promote a higher diversity of interaction asymmetries and thus increase the predictive power of such coevolutionary models, particularly in mutualistic interactions.

We have evaluated the evolved network structure and temporal dynamics of species traits based on two different functional mechanisms: trait matching and exploitation barrier. The models perform well in predicting the nestedness and modularity of empirical antagonistic networks. Moderate coevolution mediated by strong functional mechanisms seems more likely to generate empirically observed network patterns. To advance our comprehension of the coevolutionary process, future studies should incorporate additional forms of functional mechanisms. Accounting for the joint effect of multiple biotic selective forces, such as in multiplex networks, and feedbacks due to contrasting effects of traits on fitness would also give us important insights about the coevolutionary process in ecological networks. Understanding how the coevolutionary process alters ecosystem dynamics is becoming increasingly important as climate change, fragmentation of environments, and spread of invasive species are changing ecosystems worldwide. In this vein, developing theoretical models that incorporate multiple trait information and empirical patterns is critical to improve our predictions on the importance of different eco-evolutionary processes in shaping the web of life.

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Supplementary material (available online as Appendix oik-06737 at <www.oikosjournal.org/appendix/oik-06737>). Appendix 1

Figure Legends

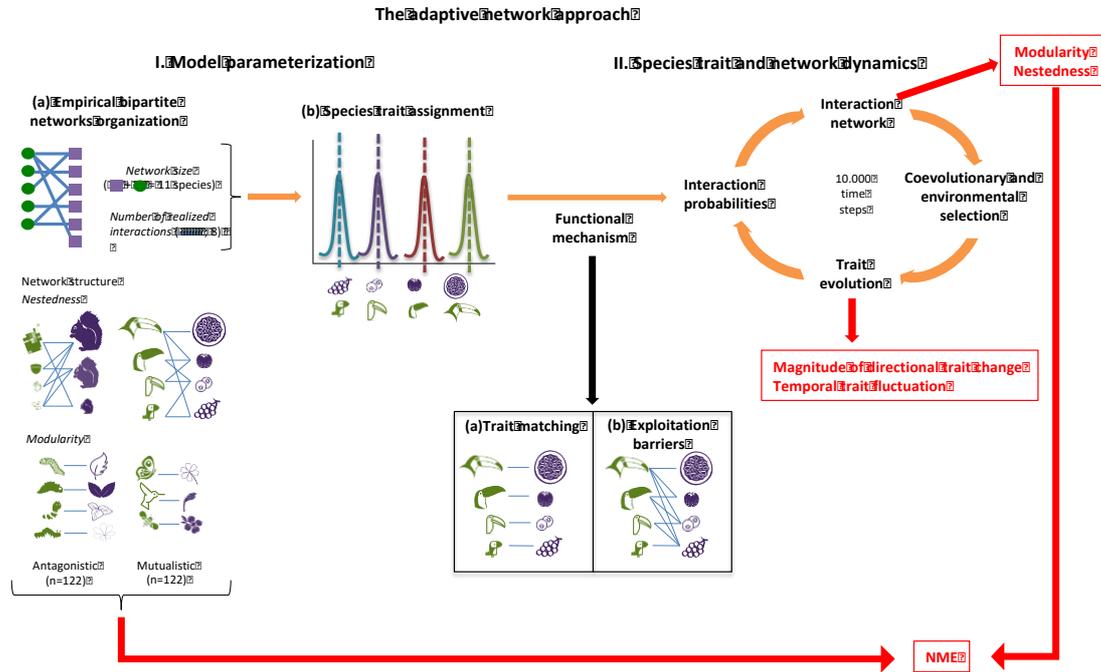


Figure 1: Conceptual representation of the adaptive network approach. (I) Model parameterization: (a) Model network replicates have the same number of species and interactions found in the empirical counterparts; (b) A specific trait value is assigned for each species in the network. (II) Species trait and network dynamics: At each time step, the trait-based probabilities of pairwise interactions are calculated according to the functional mechanisms (trait matching and exploitation barriers). Interactions are assigned according to these probabilities and species traits evolve in response to interaction and environmental selection pressures. Model network structures are compared with empirical ones throughout NME calculation. Model outcomes (Magnitude of directional trait change and Temporal trait fluctuation) are compared among scenarios. See main text for more details.

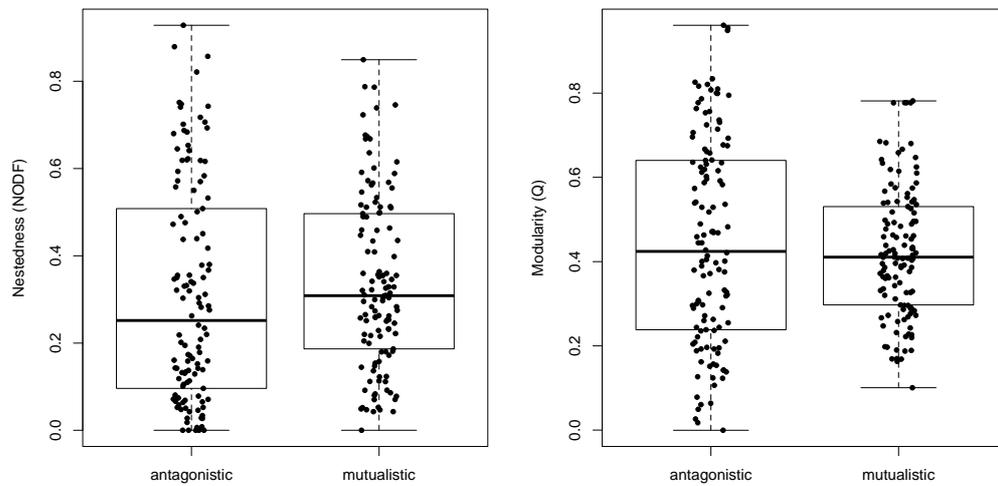


Figure 2: Nestedness (NODF) and modularity (Q) of the 122 antagonistic and 122 mutualistic empirical networks used to parameterize the models. Upper and lower limits of boxes represent 1st and 3rd quartiles, respectively.

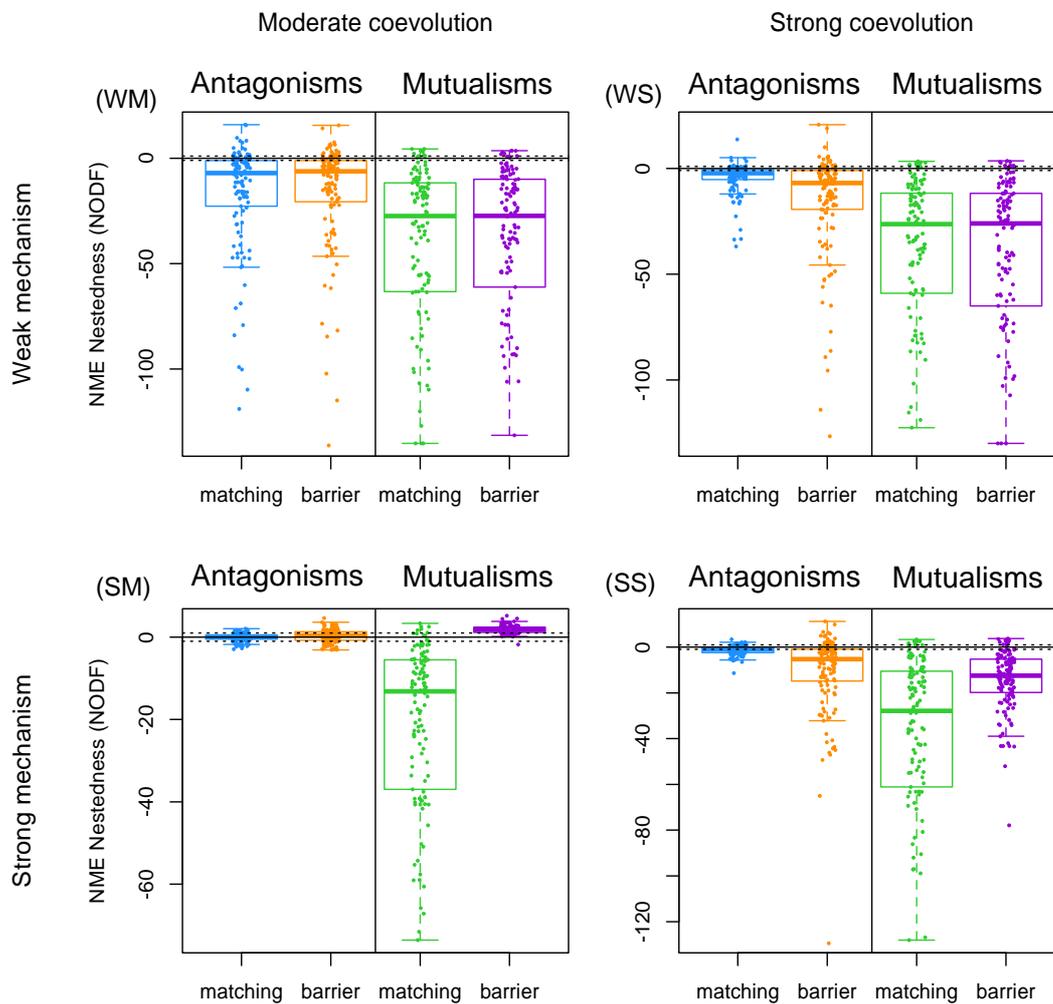


Figure 3: Normalized model error (NME) for nestedness (NODF) measures predicted by trait matching and exploitation barriers functional mechanisms for the antagonistic (blue and orange) and mutualistic (green and purple) networks in the simulated scenarios. (WM): weak mechanism and moderate coevolution ($\alpha = 1$, $\zeta_d = 0.5$); (WS): weak mechanism and strong coevolution ($\alpha = 1$, $\zeta_d = 0.99$); (SM): strong mechanism and moderate coevolution ($\alpha = 100$, $\zeta_d = 0.5$); and (SS): strong mechanism and strong coevolution ($\alpha = 100$, $\zeta_d = 0.99$). Thick lines within boxes represent median NME values for 122 networks. Upper and lower limits of boxes represent 1st and 3rd quartiles, respectively. The black lines highlight the NME values between -1 and 1, which are considered not significantly different from the empirical network structures (See the percentage of networks whose structure is significantly predicted by each scenario in Table 1). Values above and below this interval are overestimating and underestimating the nestedness of empirical networks, respectively.

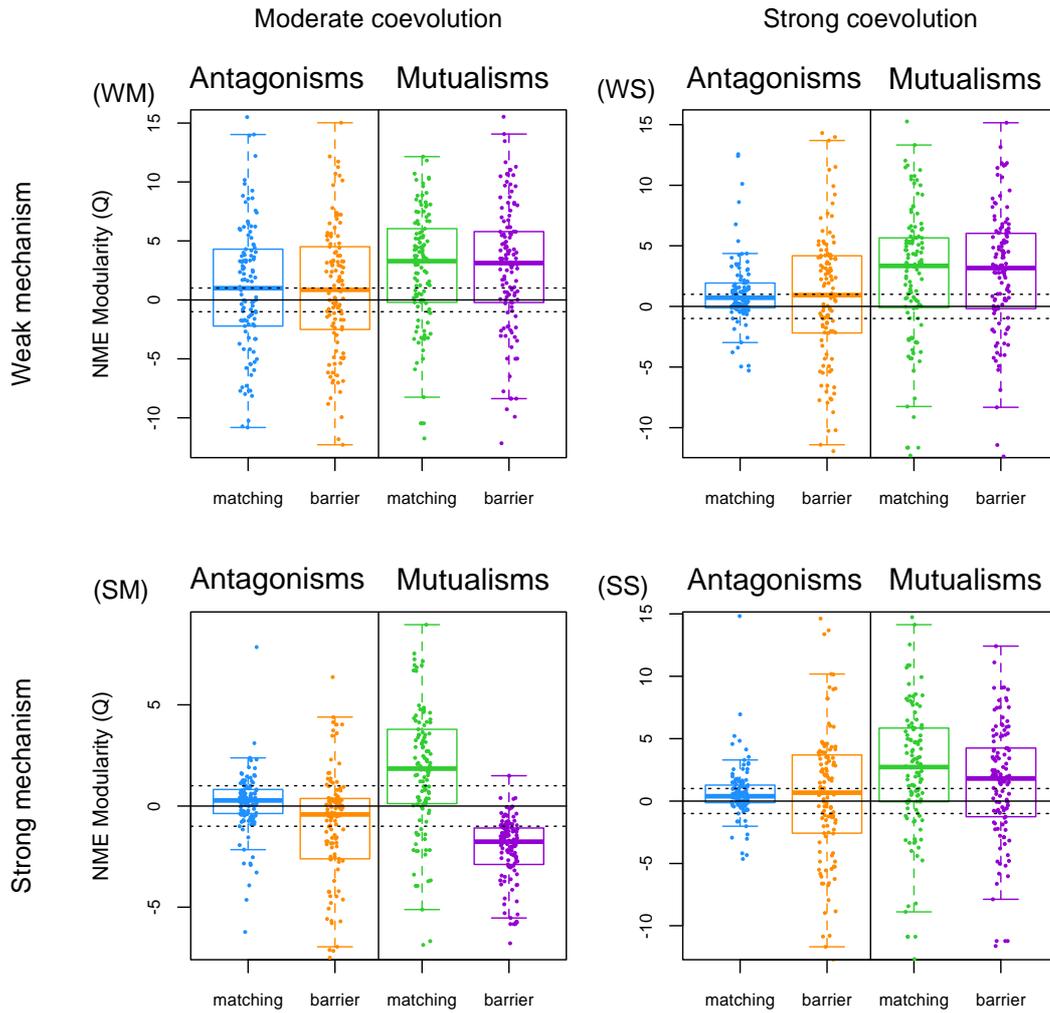


Figure 4: Normalized model error (NME) for modularity (Q) measures predicted by trait matching and exploitation barriers functional mechanisms for the antagonistic (blue and orange) and mutualistic (green and purple) networks in the simulated scenarios: (WM): weak mechanism and moderate coevolution ($\alpha = 1$, $\xi_d = 0.5$); (WS): weak mechanism and strong coevolution ($\alpha = 1$, $\xi_d = 0.99$); (SM): strong mechanism and moderate coevolution ($\alpha = 100$, $\xi_d = 0.5$); and (SS): strong mechanism and strong coevolution ($\alpha = 100$, $\xi_d = 0.99$). Thick lines within boxes represent median NME values for 122 networks. Upper and lower limits of boxes represent 1st and 3rd quartiles, respectively. The black lines highlight the NME values between -1 and 1, which are considered not significantly different from the empirical network structures (See the percentage of networks whose structure is significantly predicted by each scenario in Table 1). Values above and below this interval are overestimating and underestimating the modularity of empirical networks, respectively.

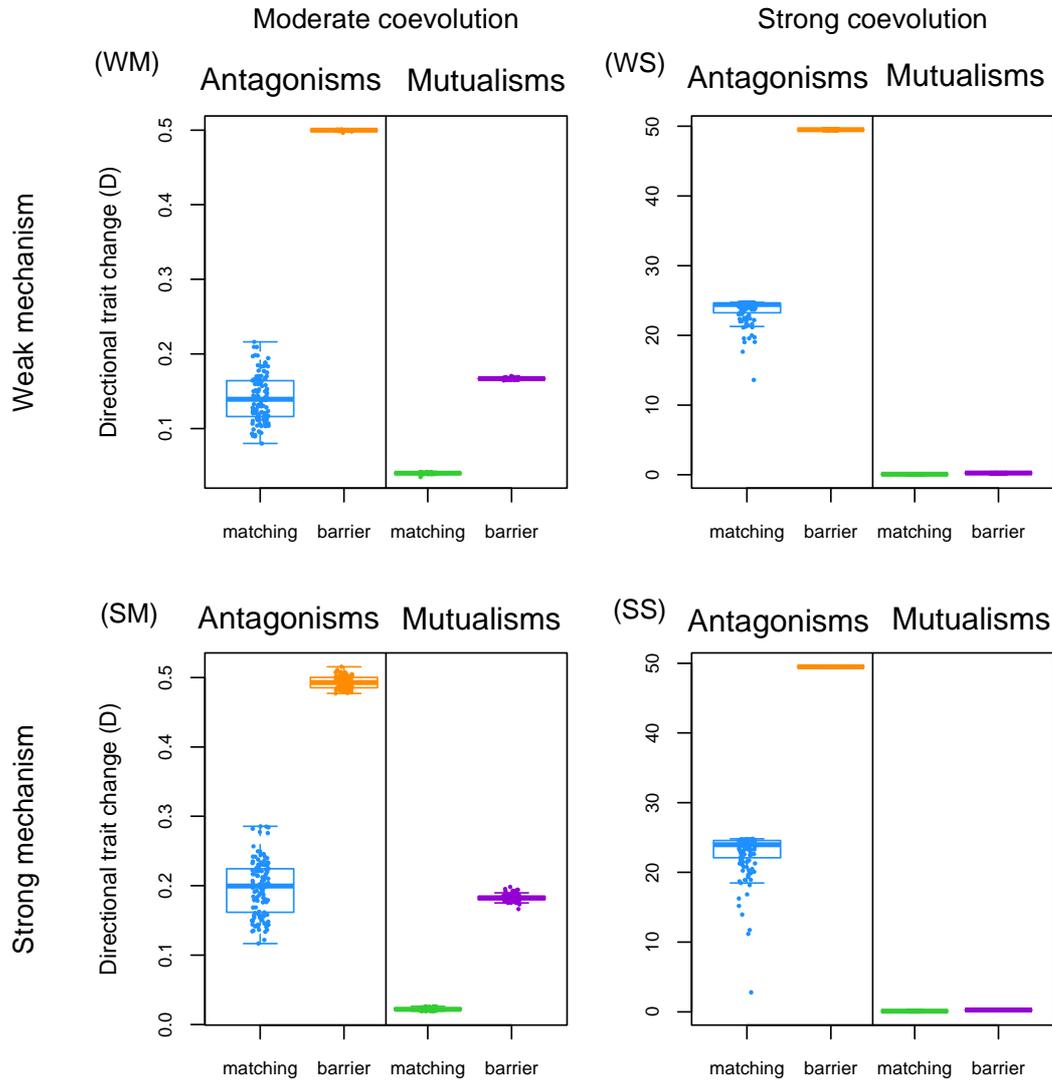


Figure 5: Average magnitude of directional trait change (D) predicted by trait matching and exploitation barriers functional mechanisms for the antagonistic (blue and orange) and mutualistic (green and purple) networks in the simulated scenarios: (WM): weak mechanism and moderate coevolution ($\alpha = 1, \zeta_d = 0.5$); (WS): weak mechanism and strong coevolution ($\alpha = 1, \zeta_d = 0.99$); (SM): strong mechanism and moderate coevolution ($\alpha = 100, \zeta_d = 0.5$); and (SS): strong mechanism and strong coevolution ($\alpha = 100, \zeta_d = 0.99$). Thick lines within boxes represent median values for 122 networks. Upper and lower limits of boxes represent 1st and 3rd quartiles, respectively. The SM trait matching model was the one that better reproduced the structure of antagonistic networks and the SM exploitation barrier model was the one that better reproduced the structure of mutualistic networks (See the percentage of networks whose structure is significantly predicted by each scenario in Table 1).

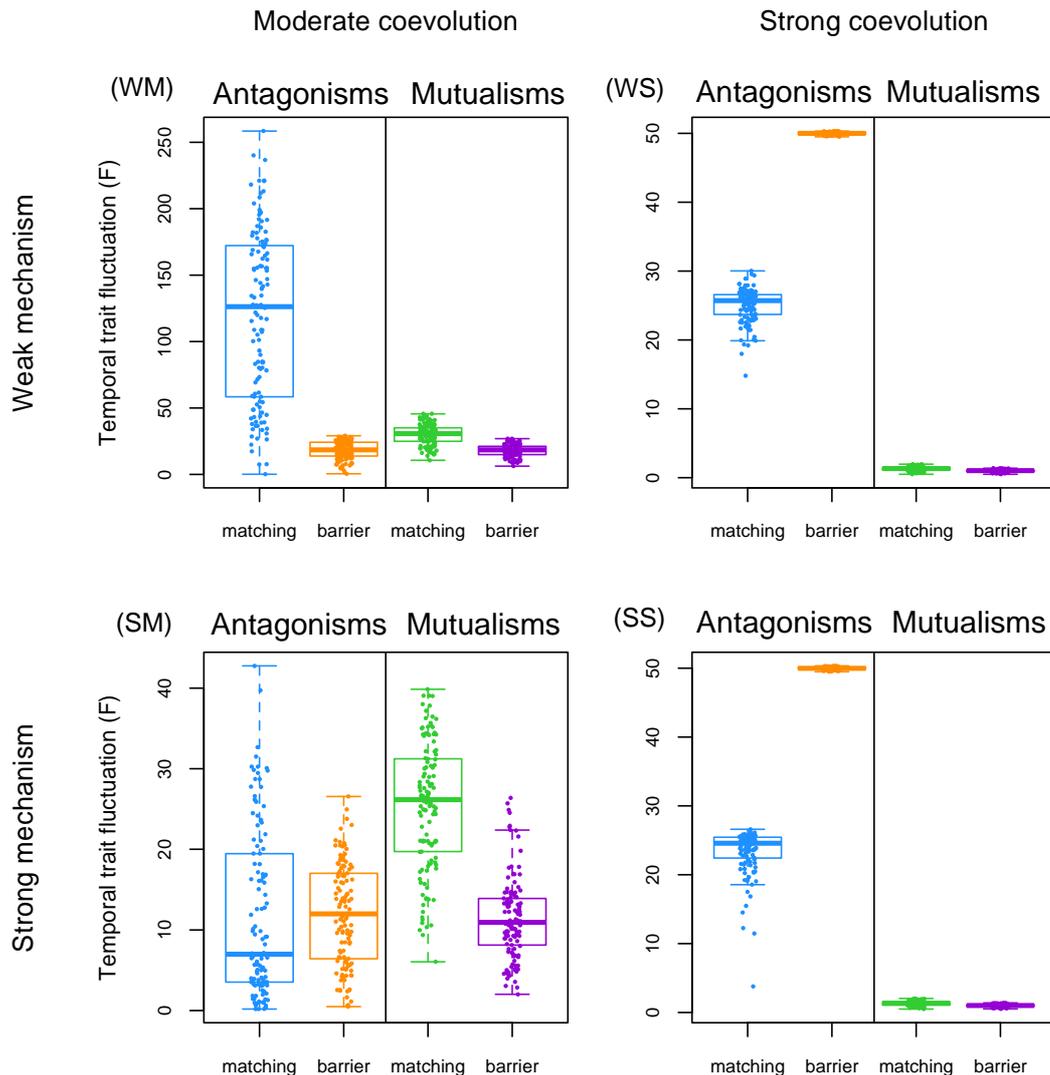


Figure 6: Average temporal trait fluctuation (F) predicted by trait matching and exploitation barriers functional mechanisms for the antagonistic (blue and orange) and mutualistic (green and purple) networks in the simulated scenarios: (WM): weak mechanism and moderate coevolution ($\alpha = 1$, $\zeta_d = 0.5$); (WS): weak mechanism and strong coevolution ($\alpha = 1$, $\zeta_d = 0.99$); (SM): strong mechanism and moderate coevolution ($\alpha = 100$, $\zeta_d = 0.5$); and (SS): strong mechanism and strong coevolution ($\alpha = 100$, $\zeta_d = 0.99$). Thick lines within boxes represent median values for 122 networks. Upper and lower limits of boxes represent 1st and 3rd quartiles, respectively. The SM trait matching model was the one that better reproduced the structure of antagonistic networks and the SM exploitation barrier model was the one that better reproduced the structure of mutualistic networks (See the percentage of networks whose structure is significantly predicted by each scenario in Table 1).

Table Legends

Table 1. Percentage of antagonistic and mutualistic empirical networks whose structure (nestedness and modularity) is significantly reproduced by each model under each scenario. The best functional mechanistic scenario explaining network structure is in bold. Abbreviations: WM = weak mechanism and moderate coevolution; SM = strong mechanism and moderate coevolution; WS = weak mechanism and strong coevolution; SS = strong mechanism and strong coevolution; NM = random interactions and moderate coevolution; NS = random interactions and strong coevolution; WN = weak interactions and fixed traits; SN = strong interactions and fixed trait.

Strength of functional mechanism	Strength of coevolution	Scenarios	Nestedness (NODF)				Modularity (Q)			
			Antagonism (%)		Mutualism (%)		Antagonism (%)		Mutualism (%)	
			matching	barrier	matching	barrier	matching	barrier	matching	barrier
weak ($\alpha = 1$)	moderate ($\xi_d = 0.5$)	WM	10.66	10.66	1.64	2.46	14.75	15.57	12.30	13.11
strong ($\alpha = 100$)	moderate ($\xi_d = 0.5$)	SM	72.13	45.90	4.92	20.49	68.85	40.98	22.13	21.31
weak ($\alpha = 1$)	strong ($\xi_d = 0.99$)	WS	25.41	10.66	1.64	1.64	47.54	17.21	13.93	13.11
strong ($\alpha = 100$)	strong ($\xi_d = 0.99$)	SS	42.62	10.66	3.28	2.46	59.84	13.93	15.57	16.39
random interaction	moderate ($\xi_d = 0.5$)	NM	11.48	11.48	2.46	2.46	15.57	15.57	14.75	14.75
random interaction	strong ($\xi_d = 0.99$)	NS	11.48	11.48	2.46	2.46	15.57	15.57	14.75	14.75
weak ($\alpha = 1$)	fixed traits	WN	12.30	11.48	1.64	2.46	16.39	16.39	14.75	13.93
strong ($\alpha = 100$)	fixed traits	SN	11.48	11.48	2.46	2.46	15.57	15.57	14.75	14.75