Network Structure and Selection Asymmetry Drive Coevolution in Species-Rich Antagonistic Interactions

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ABSTRACT: Ecological interactions shape and are shaped by the evolution of interacting species. Mathematical models and empirical work have explored the multiple ways coevolution could occur in small sets of species, revealing that the addition of even one species can change the coevolutionary dynamics of a pairwise interaction. As a consequence, one of the current challenges in evolutionary biology is to understand how species-rich assemblages evolve and coevolve as networks of interacting species. We combined an adaptive network framework, a trait evolutionary model, and data on network structure to study how network organization affects and is affected by selection in antagonistic interactions such as parasitism, predation, and herbivory. We explored how selection imposed by interactions shapes the evolution of attack and defense traits, parameterizing our models with structural information from 31 empirical assemblages of antagonistic species. In the simulations, the form of coevolution in antagonistic interactions is affected by the intensity and asymmetry of the selection imposed by the interacting partners. Transient escalation in attack and defensive traits was the most prevalent form of coevolutionary dynamics, especially in networks formed by modules of highly interacting species. Fluctuating evolution of traits was observed when the intensity of selection was higher in exploiters than in victims and was especially favored in nested networks. At the species level, highly connected species experienced higher temporal variation in selection regardless of the network structure, resulting in high trait mismatching with their partners. The mismatched patterns of highly connected species, in turn, may explain the emergence of modularity in antagonistic interactions in which selection is stronger on exploiters than on their victims. Our results highlight the roles of different aspects of network structure on antagonistic coevolution: nestedness shapes coevolutionary dynamics, whereas modularity emerges as one outcome of coevolutionary dynamics.

Keywords: alternation, antagonism, arms race, coevolution, network.

Introduction

Coevolution is phenotypic change driven by reciprocal selection between interacting species (Thompson 1994). Coevolution plays a key role in producing and maintaining species diversity and ecological interactions (Thompson 2005; Yoder and Nuismer 2010). A solid body of theoretical and experimental studies focused on pairwise antagonistic interactions predicts a suite of evolutionary dynamics, such as selective sweeps due to new mutants (Gandon and Michalakis 2002; Ebert 2008), arms races (Brockhurst and Koskella 2013), and negative frequency-dependent selection (Gavrilets 1997). A long-lasting challenge in the study of the evolution of ecological interactions is to understand whether and how the coevolutionary process changes when more than two species are involved (Fox 1988; Iwao and Rausher 1997; Strauss and Irwin 2004). Multiple hypotheses have been proposed that focus on how groups, rather than pairs, of species coevolve (Thompson 2013; Barraclough 2015). In this context, tools derived from network science present a promising approach for investigating coevolution in multispecies interactions and for distinguishing among alternative hypotheses (Loeuille and Loreau 2005; Guimarães et al. 2007; Nuismer et al. 2013).

In species-rich networks, evolutionary and coevolutionary changes are intrinsically interwoven through the cascading effects of selection acting on each species (Guimarães et al. 2011). Variation in the network organization of ecological interactions may alter the structure of selection, which may impact species in the network (Strauss and Irwin 2004; Guimarães et al. 2011; Nuismer et al. 2013). Therefore, the characterization of the structure of ecological networks may allow inferences on coevolutionary dynamics in species-rich assemblages. Among the most widely observed structural patterns in ecological networks are nestedness and modularity (Fortuna et al. 2010). Nestedness is a pattern of

interaction in which specialist species tend to interact with subsets of species that interact with more generalist species (Bascompte et al. 2003). Modularity occurs when groups of species within a network interact more with each other than with other groups (Olesen et al. 2007). Levels of nestedness and modularity vary widely across ecological networks (Fontaine et al. 2011). For instance, antagonistic interactions between plants and gall-making insects form highly modular, nonnested networks, whereas interactions between mammalian predators and their prey form highly nested, nonmodular networks (Pires and Guimarães 2013). The great structural diversity found in antagonistic networks may shape the rate of evolution and coevolution in different ways (Beckett and Williams 2013; Nuwagaba et al. 2015). Theory and empirical work suggest that antagonistic interactions may show rapid and diverse ecological and evolutionary dynamics (Abrams 2000; Woolhouse et al. 2002; Thompson 2013).

Species-rich networks can favor coevolutionary alternation (Thompson 2005), in which reciprocal selection leads to temporal fluctuation in the specialization of exploiters to particular victim species and in the levels of defense of victims against exploiters (Davies and Brooke 1989; Nuismer and Thompson 2006). Coevolutionary alternation is expected to emerge if (1) exploiter preference hierarchies are inherited, (2) victim defenses are costly, (3) selection favors exploiters that preferentially attack the currently more vulnerable victims, and (4) prey defenses evolve faster than exploiter preference hierarchies (Thompson 2005). In contrast, escalating arms races can occur in multispecies interactions if the preference hierarchies of exploiters evolve faster than victim defenses (Davies and Brooke 1989; Nuismer and Thompson 2006). Empirical work supports assumptions and predictions of coevolutionary alternation and escalating arms races. Selection experiments have shown genetic variation in exploiter preference hierarchies at the population level (Strauss and Irwin 2004; Nylin et al. 2005) and rapid evolution of defenses within populations (Trussell and Smith 2000; Rausher 2001; O'Steen et al. 2002; Yoshida et al. 2003; Brockhurst et al. 2004; Koskella et al. 2012). These studies provide evidence that multiple antagonistic species alter the outcomes of pairwise interactions and reorganize patterns of interaction at the community level (Barraclough 2015), reshaping the structure of antagonistic networks. A next challenge in the analysis of coevolutionary dynamics is to understand the specific roles of the feedback between trait evolution and the structure of antagonistic networks in shaping trait evolution in interacting species.

Here we combine an adaptive network framework (Gross and Blasius 2008), a model for single-trait evolution, and information about the structure of 31 empirical antagonistic assemblages to study how antagonistic interactions coevolve by forming networks of multiple species interactions. We address two main questions: (1) Do selection intensity and selection asymmetry affect multispecific coevolution? In coevolutionary models that focus on a few species, selection intensity and asymmetry often lead to qualitatively distinct coevolutionary outcomes. We expect that selection intensity and asymmetry in species-rich networks would influence whether coevolutionary alternation or escalation would emerge. (2) Do network structure and coevolutionary dynamics show reciprocal effects on each other? The networks in our data set encompass a large sample of the diverse natural history of antagonistic interactions, including those between insect and mammalian herbivores and plants, fish and their parasites, and mammalian prey and their predators. Antagonistic networks vary widely in their organization (Pires and Guimarães 2013), and network organization markedly affects dynamical processes in a variety of natural systems (Thébault and Fontaine 2010). Therefore, we expect that network organization would affect the coevolutionary outcomes in antagonisms.

We show that the joint effects of selection imposed by partners and network organization shape species evolutionary and coevolutionary dynamics in predictable ways, favoring escalation, coevolutionary alternation, or both. If selection on exploiters is stronger than on victims, coevolutionary alternation is favored by nested organization, creating asymmetry in specialization between exploiters and victims and generating a hierarchy of preferred victims among exploiters. Coevolution not only is affected by network organization but also reshapes network organization: higher modularity arises in antagonistic networks as an outcome of the coevolutionary process, emerging as a by-product of stronger selective pressures acting on exploiters.

Methods

Model

We modeled the evolution of a single trait in victims and exploiters (fig. 1). We used an adaptive network approach to model evolutionary dynamics, allowing us to track trait changes, quantify the degree of trait matching among species, and measure network structural change. We assumed that natural selection favors exploiters whose attack traits match the defenses of victims in ways that increase the chance of successful attack and that selection favors victims whose defense traits mismatch the exploiters in ways that allow them to escape attack (Nuismer and Thompson 2006; Hanifin et al. 2008). We modeled the evolution of the mean trait value of a population of species i as a real number, z_i^t, representing a defensive trait if species i is a victim or an attack trait if i is an exploiter at time step t. The value of z_i^t was initially sampled from a truncated normal distribution $\mathcal{N}(0, 0.1)$.

At each time step, the trait values of each species were updated in response to selection imposed by the environ-
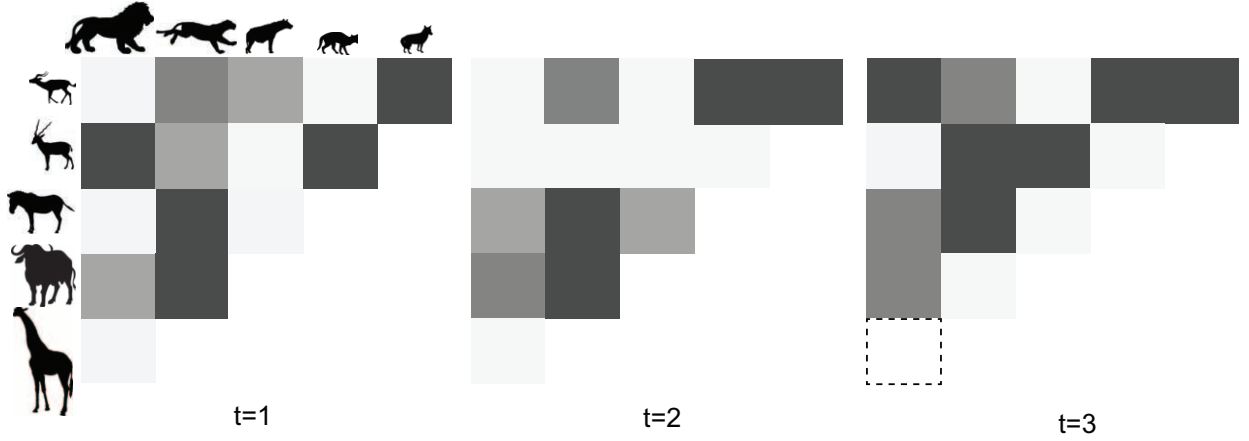
Figure 1: In this hypothetical example of the coevolutionary model, predator-prey interactions are organized as an interaction matrix. The colors of the matrix elements depict the degree of selective pressure of predators on prey. Dark gray cells indicate interactions with the highest trait matching in that time step, which are also the interactions with the highest selection imposed by the interaction partner. Grayscale colors indicate progressively weaker trait matching, from dark to light gray. As the coevolutionary process continues, exploiters can alternate among their selected victims through genetic changes in their preferences, and victims can evolve either greater or reduced defenses, leading to changes in selective pressures and network organization. The white square in $t = 3$ illustrates the evolution of a resistant victim that escaped attack, thus reshaping the network.

ment and antagonistic partners. We assumed that environmental selection favors a fixed trait value, θ_i, and we set $\theta_i = z_i^0$ for simplicity. The partial selection differential caused by environmental selection was defined as

$$S_i^t = \xi_{S_i}(\theta_i - z_i^t), \tag{1}$$

where ξ_{S_i} is the intensity of environmental selection on species i, $0 < \xi_{S_i} < 1$. In our model, the fitness consequences of the interaction for an exploiter i and victim j depend on the degree of trait matching, defined as $z_{ij}^t = |z_i^t - z_j^t|$. Selection by victim j on exploiter i favors matching, and the partial selection differential is described by

$$M_{ij}^t = \xi_{d_i} p_{ij}^t (z_j^t - z_i^t), \tag{2}$$

where ξ_{d_i} is the selection intensity imposed by interacting species. The selection intensities of the environment and antagonistic partners determine the species total selection differential such that $0 < \xi_{d_i} < 1 - \xi_{S_i}$. The selection imposed by victims on exploiters is weighted by the relative degree of matching between species pairs, p_{ij}^t, which depend on phenotypic matching and the exploiter preference, b:

$$p_{ij}^t = \frac{f_{ij}e^{-b(z_j^t - z_i^t)^2}}{\sum_{k=1;\ k \neq i}^{R} f_{ik}e^{-b(z_k^t - z_i^t)^2}}, \tag{3}$$

where f_{ij} is an element of **F** and describes whether the interaction can occur ($f_{ij} = 1$) or not ($f_{ij} = 0$, a so-called forbidden link; Olesen et al. 2011) and R is the network species richness. Ecological interactions are often modulated by multiple traits, and **F** allows us to implicitly introduce the

effect of other traits that prevent an interaction from occurring. Thus, **F** sets a limit on the extent to which the network structure can change. Because the strength of the interactions was determined by trait matching, some co-occurring victims and exploiters may have high trait mismatching with weak effects on fitness. This aspect of the model simulates ecological interactions that occur in nature but that have negligible functional effects on the ecology and evolution of species interactions. Nevertheless, selection on exploiters may favor trait matching, leading to the evolution of a novel strong interaction from functionally negligible interactions. We subsequently explored whether the presence of fixed forbidden links affected our conclusions regarding network structure evolution (see supplementary information, available online). In this later extension of the model, we allowed new interactions to evolve by interaction swaps, exploring the coevolutionary dynamics when niche width is conserved.

For victims, selection favored trait mismatches (large z_{ij}). We assumed that there is a critical mismatch, ε, such that if $|z_i^t - z_j^t| > \varepsilon$, then the exploiter i has a negligible effect on victim j fitness. Therefore, an antagonistic interaction was considered lost if the exploiter no longer exerted selection on the victim. Biologically, this means the exploiter has no fitness effect on the victim, for example, the exploiter is a commensal organism. The partial selection differential caused by selection imposed by exploiter i on victim j was defined as

$$\begin{cases} M_{ji}^t = \xi_{d_j} f_{ji} u_{ji}^t (z_i^t + \varepsilon - z_j^t), & \text{if } z_i^t < z_j^t, \\ M_{ji}^t = \xi_{d_j} f_{ji} u_{ji}^t (z_i^t - \varepsilon - z_j^t), & \text{if } z_i^t > z_j^t, \end{cases} \tag{4}$$

where $u_{ji}^t = 1$, if $|z_i^t - z_j^t| \leq \varepsilon$, and $u_{ji}^t = 0$, if $|z_i^t - z_j^t| > \varepsilon$. Because the trait axis is bidirectional, selection favors increasing trait values for the victim, $z_i^t + \varepsilon$, if $z_j^t > z_i^t$, and decreasing trait values, $z_i^t - \varepsilon$, if $z_j^t < z_i^t$. Combining equations (1)–(4) with the breeder's equation results in a general equation describing trait evolution for both exploiters and victims:

$$z_i^{t+1} = z_i^t + h_i^2 \left(S_i^t + \frac{\sum_{j=1; j \neq i}^R M_{ij}^t}{k_i^t} \right), \qquad (5)$$

where h_i^2 is the heritability of trait z_i, $\sum_{j=1; j \neq i}^R M_{ij}^t / k_i^t$ is the combined effects of the partial selection differentials caused by interacting species, and k_i^t is the number of potential partners of species i. If species i is an exploiter, the number of potential partners at time t is $k_i^t = \sum_{j=1; j \neq i}^R f_{ij}$. If species i is a victim, $k_i^t = \sum_{j=1; j \neq i}^R f_{ij} u_{ij}^t$.

Characterizing Evolutionary Patterns

Coevolutionary escalation is the expected outcome of sustained directional selection on attack and defense traits among interacting species, whereas coevolutionary alternation is expected if there is fluctuating selection on those traits in each species. We characterize the evolutionary dynamics using three evolutionary patterns: the directionality of trait change in a given species, the temporal variation in trait matching of interacting species, and degree of trait disparity across species in the network. We characterized directionality in trait change in a given species i as

$$\delta_i = \frac{|z_i^{t=10,000} - z_i^{t=0}|}{\sum_{t=0}^{t=10,000} |z_i^{t+1} - z_i^t|}, \qquad (6)$$

where $|z_i^{t=10,000} - z_i^{t=0}|$ is the directional trait change after 10,000 time steps and $\sum_{t=0}^{t=10,000} |z_i^{t+1} - z_i^t|$ is the total amount of trait change across all time steps. We used 10,000 time steps because this number of steps allows asymptotic behavior of the model (fig. S1). Coevolutionary escalation predicts values close to one, characterizing directional trait evolution with little fluctuation over time. In contrast, coevolutionary alternation predicts values close to zero, indicating a lack of sustained directional evolution due to fluctuating selection. We investigated the effects of network structure on trait change directionality by calculating the mean directionality for the entire network, $\langle \delta \rangle = \sum_{i=1}^R \delta_i / R$.

We characterized how trait matching varied across time using $c_{ij} = \sum_{t=1}^{t=10,000} f_{ij} |z_{ij}^t - z_{ij}^{t-1}|$. Higher c_{ij} values indicate higher temporal variation in trait matching between interacting species i and j. We estimated trait disparity by describing the breadth of the trait space occupied by all species in the community using the difference between the largest and smallest species trait values z_i in the community, $\max_{i \neq j} |z_{ij}^{t=10,000}|$.

Do Selection Intensity and Selection Asymmetry Affect Multispecific Coevolution?

We explored the effects imposed by selection intensity and selection asymmetry on multispecific antagonistic coevolution by performing simulations using five distinct parameterizations (scenarios) of the model. In the scenario with stronger selection on exploiters than on victims, selection imposed on exploiters i by victims j was stronger than selection imposed on victims by exploiters ($\xi_{d_i} = 0.99$, $\xi_{d_j} = 0.5$). This scenario is rooted in the natural history of several obligatory parasite-host interactions in which the parasite depends fully on the host to survive and reproduce, whereas the host has only slightly to moderately reduced lifespan or reproduction due to the parasite (e.g., Haraguchi and Sasaki 1996). The scenario with stronger selection on victims ($\xi_{d_i} = 0.5$, $\xi_{d_j} = 0.99$) simulates the life-dinner principle (Dawkins and Krebs 1979), which states that the selection pressure on prey defensive traits is stronger than that on predator efficiency. The scenarios with weak symmetric selection ($\xi_{d_i} = \xi_{d_j} = 0.5$) and strong symmetric selection ($\xi_{d_i} = \xi_{d_j} = 0.99$) represent benchmarks that separate the effects of intensity and asymmetry captured in stronger selection on exploiters and stronger selection on victims scenarios. Finally, we considered a null scenario in which interaction selection is symmetric and very weak for both exploiters and victims ($\xi_{d_i} = \xi_{d_j} = 0.01$). Each simulation had 10,000 time steps, and we ran 100 simulations per combination of network and scenario (table 1). Because we were interested in studying the effects of contrasting selection scenarios, and because the sensitivity analysis showed that the remaining parameters (h^2, b, ε) had weaker effects than other parameters on the coevolutionary dynamics (figs. S2–S5 in the supplementary information; figs. S1–S18 are available online), we fixed these parameters at $h^2 = 0.25$, $b = 10$, and $\varepsilon = 0.5$ for all species in the network. We then analyzed how the resulting evolutionary patterns varied across scenarios (see below).

Does Network Structure Affect and Is It Affected by Coevolutionary Dynamics?

We used 31 two-mode antagonistic networks to parameterize the model, exploring the effects of network structure on coevolutionary dynamics. The networks range from small networks of 22 species of mammalian predators and preys to large networks of almost 300 species of leaf-mining herbivores and their host plants (table A1). Some interactions are likely to be associated with particular evolutionary scenarios, for example, the life-dinner principle in predator-

Table 1: List of variables and parameter values used in the coevolutionary model

Notation	Definition	Value
z_i^0	Initial quantitative trait value of species i	Sampled from a normal distribution, mean $= 0$, SD $= 0.1$
Z	Matrix of trait matching between species i and j containing all z_{ij}^t values	Variable
R	Total number of species in network	Parameter from data
F	Empirical matrix of species interactions in which $f_{ij} = 1$, if species i interacts with j, and $f_{ij} = 0$, if i does not interact with j	Estimated from the data
h_i^2	Heritability of trait z_i	.25
k_i^t	Number of species with which i interacts; in the case of victims, if the trait difference is higher than the threshold ($\|z_{ij}^t\| > \varepsilon$), then this interaction will be subtracted from its interaction partners	Initially provided by the data; for victim species, the number can vary during the simulation
S_i	Partial selection differential caused by environmental selection	Variable
M_{ij}	Partial selection differential caused by selection imposed by interaction partners	Variable
θ_i	Trait value of species i (z_i) favored by stabilizing selection	$\theta_i = z_i^0$
ξ_s	Intensity of environmental selection	A value between 0 and 1
ξ_d	Intensity of selection imposed by interaction partners	A value between 0 and 1
p_{ij}	Relative preference of exploiter species i on victim species j	Variable
b	Degree of exploiter preference	10
u_{ji}^t	Indicates whether victim species j will respond to selection pressure exerted by exploiter i at time t	$u_{ji}^t = 1$, if $\|z_{ij}^t\| \leq \varepsilon$; $u_{ji}^t = 0$, if $\|z_{ij}^t\| > \varepsilon$
ε	Maximum $\|z_{ij}^t\|$ value that induces evolutionary response on victim j	.5
C	Matrix of the cumulative change in trait matching between species i and j; contains all c_{ij} values	Variable
δ_i	Directionality of species i trait change	Variable
$\langle\delta\rangle$	Average directionality of species trait change in a network	Variable

prey interactions and simulated by the scenario of stronger selection on victims. However, in this study, we used only the information on network structure to parameterize **F** (table A1), simulating the five evolutionary scenarios described above using each empirical network structure. Later, we discuss the outcomes of the model using as reference the evolutionary ecology of particular types of antagonistic interactions.

We calculated four network descriptors: (i) species richness (R), (ii) connectance, (iii) nestedness, and (iv) modularity (details on each descriptor are provided in the supplementary information). We used the metric NODF (nestedness metric based on overlap and decreasing fill; Almeida-Neto et al. 2008) to estimate nestedness, which was computed using the software application Aninhado (Guimarães and Guimarães 2006). Because asymmetries pervade nested networks (Bascompte et al. 2003; Guimarães et al. 2006), we hypothesized that nestedness may generate a hierarchy of preferred victims among exploiters, thereby favoring coevolutionary alternation. The degree of modularity was estimated using a simulated annealing algorithm to optimize the metric M (Newman and Girvan 2004; Guimerà and Amaral 2005), which was calculated using the software Modular (Marquitti et al. 2014). We expected that modularity would favor coevolutionary escalation because of the limited number of poten-

tial partners within modules and the semi-isolation of each module from other species in the network.

Nestedness and modularity are affected by other network properties. We controlled for these confounding factors using Z-scores to compare levels of nestedness and modularity across different networks, $\text{NODF}_{\text{rel}} = (\text{NODF} - \overline{\text{NODF}_{\text{null}}})/\sigma_{\text{null}}$ and $M_{\text{rel}} = (M - \overline{M_{\text{null}}})/\sigma_{\text{null}}$ (Fortuna et al. 2010), where $\overline{\text{NODF}_{\text{null}}}$ and $\overline{M_{\text{null}}}$ are the metrics' mean values obtained with the null model and σ_{null} represents the standard deviation obtained with the null model for the corresponding metric. We controlled for the effects of heterogeneity in the number of interactions per species, connectance, and species richness on nestedness and modularity using null model 2 of Bascompte et al. (2003), which considers the probability of drawing an interaction as proportional to the number of interactions of both the exploiter and victim species (supplementary information).

We also investigated whether the patterns of interaction affected the evolutionary dynamics of traits using species-level descriptors: (i) normalized degree, which is the number of interactions of the species divided by the number of species in the other trophic level (Martín González et al. 2010); (ii) contribution to nestedness (Almeida-Neto et al. 2008); (iii) standardized within-module degree; and (iv) among-module connectivity (Guimerà and Amaral 2005). These last two

descriptors characterize how interactions of a given species are distributed within and among modules (app. B). We also categorized each species as part of either the network core or the periphery (Díaz-Castelazo et al. 2010) using a categorical core-periphery analysis for bipartite graphs (app. B). Core species are highly connected species that interact with other core species and certain poorly connected species, called peripheral species. Peripheral species, in turn, are not interconnected.

We used a combination of analyses to evaluate how the evolution of traits, the number of interactions between species, and network structure are directly and indirectly interrelated. We first used generalized linear models to explore how directionality in trait evolution, $\langle \delta \rangle$, disparity of traits, and number of lost interactions ($u_{ji}^{t=10,000} = 0$, given that $f_{ji} = 1$) relate to the structure of ecological networks. This analysis allowed us to evaluate the effects of nestedness, modularity, connectance, and richness on trait evolution and changes in specialization.

Because structural descriptors of networks often affect each other, we performed a path analysis (Shipley 2004). We assumed that richness and connectance have direct effects on the directionality of evolutionary change, $\langle \delta \rangle$, and on the degrees of nestedness and modularity, which in turn can also affect $\langle \delta \rangle$. We tested the entire causal structure of the path model simultaneously by estimating model parameters via maximum likelihood (Shipley 2004). We cross-validated our results by exploring the correlated effects of network structure with an alternative approach based on principal components analysis (see supplementary information).

We next used the directionality of evolutionary change for a species, δ_i, and the magnitude of directional change in trait value to characterize the evolutionary dynamics at the species level. We investigated the effects of patterns of interaction of species (species normalized degree, contribution to nestedness, standardized within-module degree, and among-module connectivity) on the species evolutionary dynamics with generalized linear mixed models (GLMMs), using network identity as a random factor. We cross-validated the GLMM results by first performing a principal component analysis (PCA) to synthesize the different aspects of patterns of interaction of species and then correlating the first principal component with the metrics of evolutionary dynamics (supplementary information).

We used the final matrix of trait matching ($\mathbf{Z}^{t=10,000}$) to characterize net evolutionary change and the matrix of cumulative change in trait matching (**C**) to estimate the dynamics of interaction strengths between species. We compared the values of final trait matching and average change in trait matching (c_{ij}) for interactions (*a*) between species that are in the same module or in different modules and (*b*) between core and periphery species using GLMMs that included network identity as a random factor. We do not

report *P* values because, for simulation data, statistical significance is not useful for determining the relative importance or presence/absence of effects of the various predictors (White et al. 2014). Instead, we report the effect sizes and signs of the estimated regression parameters for interpreting the importance of different predictors (White et al. 2014).

Finally, we explored the feedback of coevolution on the structure of interactions by analyzing how coevolutionary dynamics affect descriptors of network organization. We first computed the proportion of interactions that were lost because the victim escaped attack. Then, we investigated how the levels of nestedness and modularity changed due to the loss of interactions by computing the NODF and *M* for all of the replicates of each network. We tested for potential differences between the initial and final structures using paired *t*-tests.

Results

The emergence of coevolutionary alternation or coevolutionary escalation was affected by the interplay between network structure and asymmetries in selection imposed by species interactions on victims and exploiters. Overall, directional trait evolution was the prevalent outcome of the evolutionary dynamics (figs. 2, S14). Fluctuating selection, indicated by fluctuating trait change, occurred more frequently when the selection intensity imposed by exploiters on victims was weaker than that imposed by victims on exploiters (scenario: stronger selection on exploiters; fig. 2). When selection was stronger on exploiters, network structure affected coevolution, with nestedness decreasing the directionality of trait evolution, $\langle \delta \rangle$ (slope [*b*] = -0.05, $F = 17.27$, df $= 29$; fig. 3), and modularity presenting a negligible effect ($b = -0.006$, $F = 0.04$, df $= 29$). Species richness and connectance had a small negative effect on the directionality of trait evolution, indicating that fluctuating selection was more likely to occur in species-rich and highly connected networks (fig. 4). PCA cross-validated these results and suggested that nestedness is the main structural driver allowing the emergence of fluctuating selection (supplementary information).

When selection intensity on victims was stronger and asymmetric (scenario: stronger selection on victims, e.g., life-dinner principle), directional selection was the prevalent dynamic (fig. 3). When selection was stronger on victims, directional evolution emerged independent of network structure, and higher directionality was not associated with nestedness ($b = -0.0015$, $F = 0.551$, df $= 29$) or modularity ($b = -0.0031$, $F = 0.682$, df $= 29$; fig. S6). Similar directional coevolution was observed in both scenarios that assumed symmetric selection intensities (scenarios of weak symmetric selection and strong symmetric se-
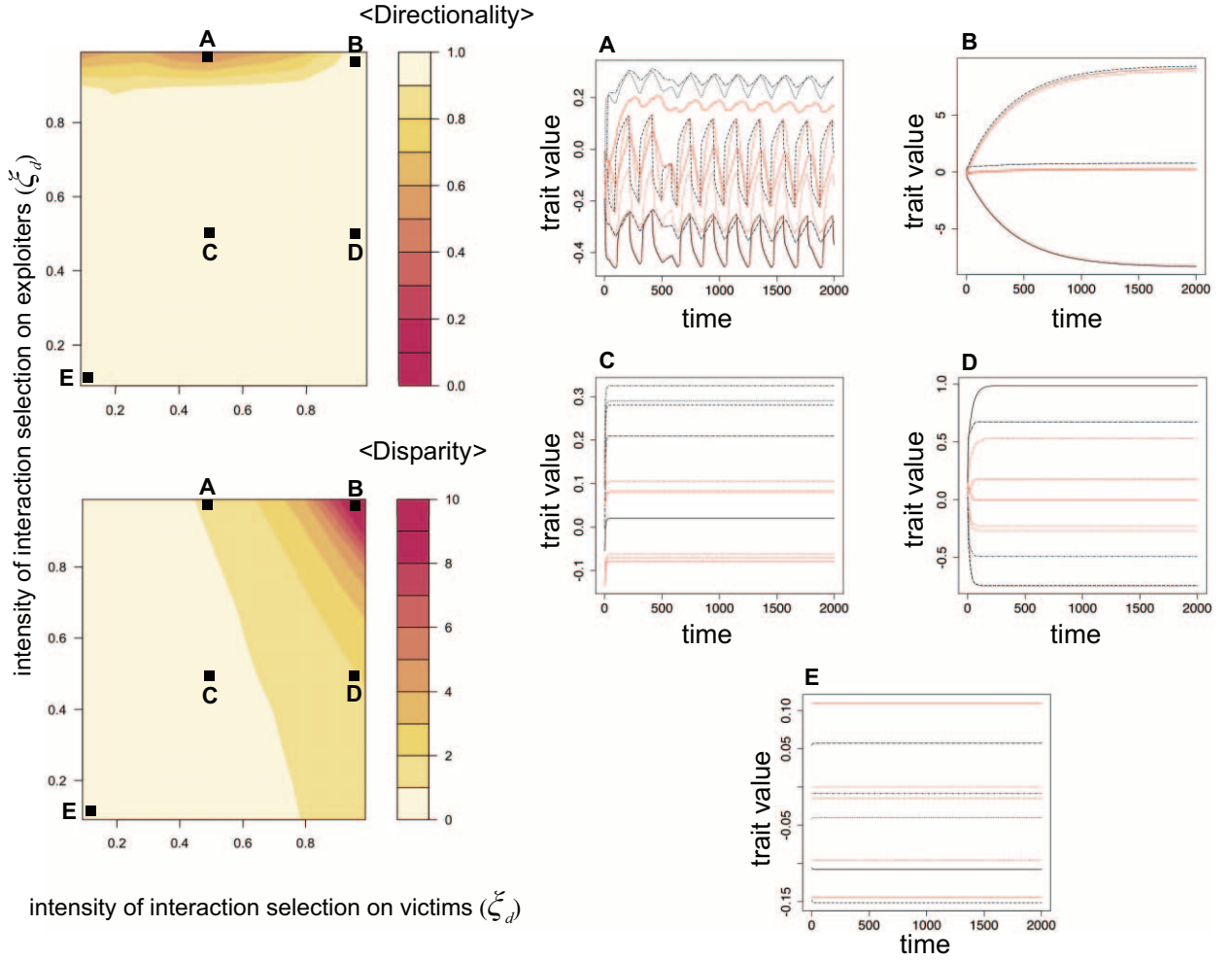
Figure 2: *Left*, average directionality (*top*) and disparity of trait change (*bottom*) among 100 replicates in the 31 antagonistic networks for all combinations of victim and exploiter interaction selection intensity. *Right*, an example of the trait dynamics for one species assuming distinct scenarios: stronger selection on exploiters (*A*), stronger selection on victims (*B*), weak and symmetric selection (*C*), strong and symmetric selection (*D*), and null scenario (*E*) for the 5 × 5 hypothetical network shown in figure 1. Black and red (or gray) lines represent the victim and exploiter trait dynamics, respectively.

lection; fig. 3). Weaker selection (null scenario) reduced the magnitude of directional trait change without qualitatively changing the directionality of coevolutionary dynamics (figs. 2, 3).

The effects of network structure were more pervasive on the other outcomes of coevolutionary dynamics (fig. S7). When the selection imposed by victims and exploiters was nonnegligible (i.e., in all scenarios except the null scenario), nestedness affected trait disparity (fig. S8). The higher the degree of nestedness, the lower was the trait disparity (a negative correlation between nestedness and trait disparity was observed in all scenarios except the null scenario; table S4; fig. S8; tables S1–S5 are available online). In contrast, modularity increased trait disparity only in those scenarios in which selection intensity was weak or negligible (weak

symmetric and null scenarios; table S4; fig. S9). When victims or exploiters faced strong selection, modularity did not affect trait disparity (stronger selection on exploiters, stronger selection on victims, and strong symmetric scenarios; table S4; fig. S9). PCA analysis cross-validated these results (supplementary information).

The coevolutionary dynamics also reorganized network structure where victims had evolved efficient defenses against exploiters ($|z_i^t - z_j^t| > \varepsilon$). The proportion of lost interactions was higher when the selection intensity acting on victims was higher (figs. S10, S11). Higher nestedness resulted in a higher proportion of lost interactions in all scenarios (table S5; fig. S11). Nestedness amplified the loss of interactions by enabling exploiters to specialize on poorly defended victims (higher trait matching), which in turn
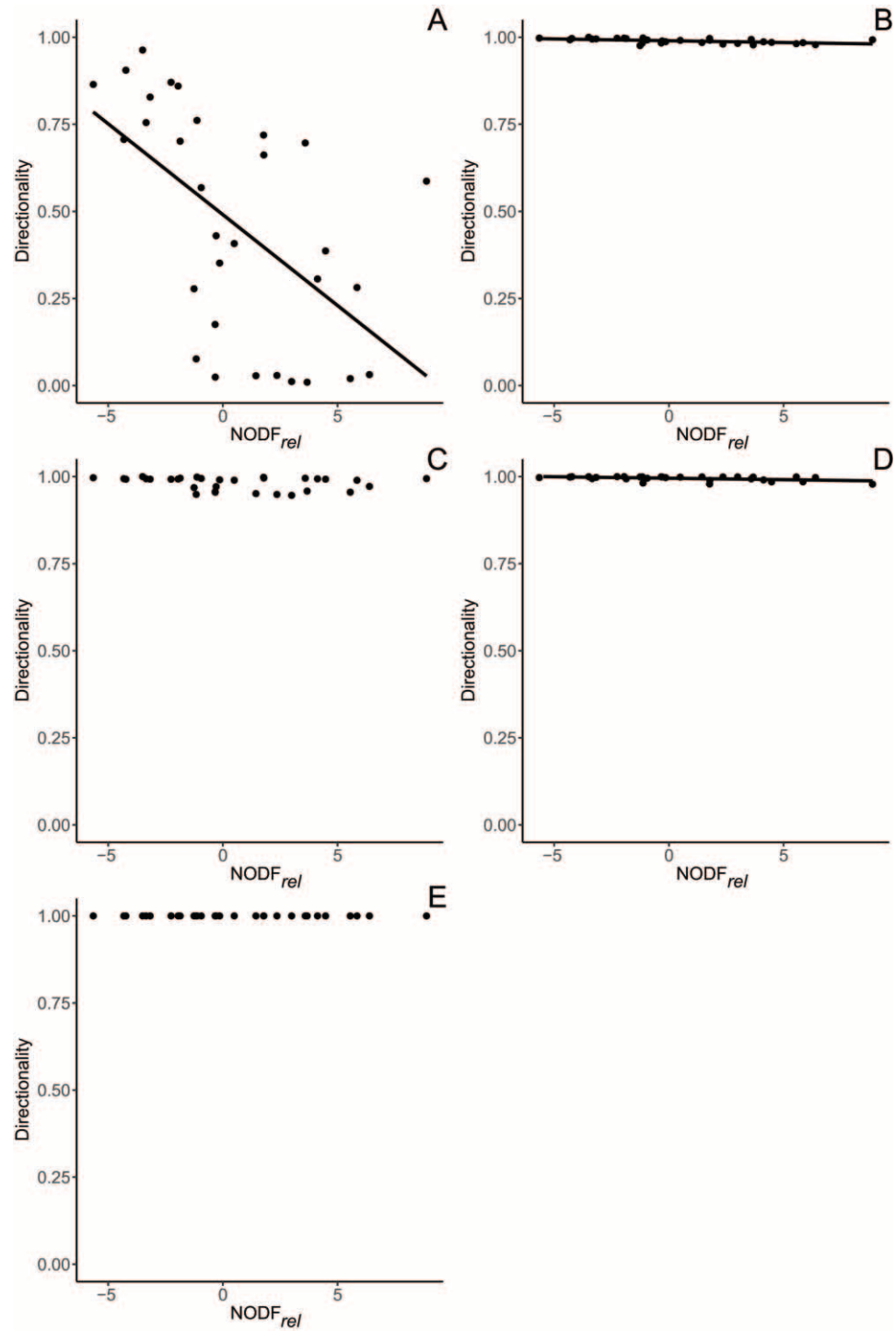
Figure 3: Relationship between network nestedness Z-score ($NODF_{rel}$) and the mean directionality of trait evolution, $\langle\delta\rangle$. Points represent median values for the 100 replicates for simulations parameterized with each network, and lines are the expected values for the significant relationships for each scenario: stronger selection on exploiters (*A*), stronger selection on victims (*B*), weak and symmetric selection (*C*), strong and symmetric selection (*D*), and null scenario (*E*).
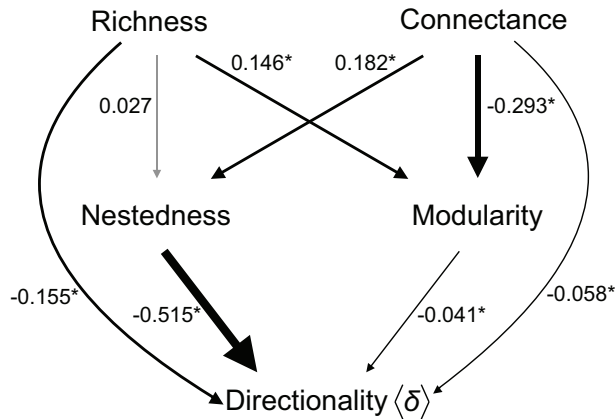
Figure 4: Summary diagram of the effects of different network architectural patterns on the directionality of coevolutionary dynamics of antagonistic networks, $\langle\delta\rangle$. The thickness of the arrows is scaled to the standardized coefficients from the path analysis (goodness of fit = 0.99, root mean square error of approximation = 0.037 [90% confidence interval = 0.012–0.071], standardized root mean square residual = 0.011) and illustrates the relative effect strength. Significant effects are represented by black and are marked with an asterisk, and nonsignificant effects are represented by gray. The effects of connectance and richness are split between direct effects and indirect effects through changes in modularity and nestedness. The strength of the indirect effects was calculated as the product of the coefficients along the path. For example, connectance has a direct effect on strength (-0.058), an indirect effect through modularity on strength (0.012; -0.293×-0.041), and an indirect effect through nestedness on strength (-0.094; 0.182×-0.515), which leads to an overall connectance effect of -0.14.

allowed other victims to escape attack. In contrast, modularity had no effect on the proportion of lost interactions (fig. S11).

We focused on the scenario in which more variable coevolutionary dynamics occurred (stronger selection on exploiters) to explore how the loss of interactions affected network organization. At the end of the simulations, networks had become more modular ($t = 8.06$, df $= 30$; fig. 5A) and less nested ($t = -6.08$, df $= 30$; fig. 5A) than the original network structure. Increased modularity and decreased nestedness did not result from the assumption of fixed forbidden links; rather, they were outcomes of the coevolutionary process. These coevolutionary effects were shown by a model in which forbidden links ($f_{ij} = 0$) were not fixed (as in the standard model) but instead could evolve through time (figs. S15–S17). The temporal decay of nestedness was positively related to initial nestedness ($b = 0.26$, $F = 118.2$, df $= 29$; fig. 5B), whereas the increase in the levels of modularity was negatively related to initial network modularity ($b = -0.118$, $F = 13.69$, df $= 29$; fig. 5C). Thus, highly nested networks tended to become more modular, but the final structure of modular networks remained unchanged.

We next evaluated how network organization shapes trait evolution for species within networks. Trait evolution

for each species depended on the number of other species to which the species was connected within the network. On average, highly connected species had higher fluctuating selection on traits (smaller δ_i). These highly connected species were those that had a high number of interactions (higher normalized degree, $b = -0.21$, $F = 31.91$, df $= 2,371$), connected distinct modules (higher among-module connectivity, $b = -0.2$, $F = 88.71$, df $= 2,363$), and a higher contribution to nestedness ($b = -0.004$, $F = 126.36$, df $= 2,349$) and that were part of the core of the network ($b = -0.04$, $F = 13.87$, df $= 2,354$). The number of interactions within species of the same module was negligible for the directionality of evolutionary dynamics, δ_i (within-module degree, $b = 0.006$, $F = 1.945$, df $= 2,349$).

Network structure modulated the relationships between the patterns of interaction and species coevolution within networks. This modulation was evidenced by the variation among networks in the coefficients of regression between species' structural metrics and the directionality of coevolutionary dynamics, δ_i. As the absolute value of the regression coefficient increased, the average effect of species patterns of interaction on the directionality of evolution became stronger. In nested networks, the directionality of selection, δ_i, was weakly related or unrelated to the number of interactions and the contribution to nestedness of a given species (fig. 6). This result indicated that any species could experience fluctuating selection regardless of its patterns of interaction. In contrast, the directionality of evolutionary dynamics was negatively associated with the species patterns of interaction, and stronger negative relationships were observed in nonnested networks (fig. 6). For example, in modular networks, there was a stronger negative relationship between species among-module connectivity and the directionality of evolution, δ_i (fig. 6C). In contrast, the number of interactions of a species within modules showed no clear relationship with δ_i (fig. 6D).

Directional evolution leading to an escalation of traits was more common among peripheral species ($b = -0.07$, $F = 236.9$, df $= 2,361$) with a low number of interactions (normalized degree, $b = -0.16$, $F = 103.31$, df $= 2,131$), a low contribution to nestedness ($b = -0.002$, $F = 223.83$, df $= 1,686$), and a low number of interactions with species in different modules (among-module connectivity, $b = -0.12$, $F = 153.2$, df $= 2,378$) or within the same module (within-module degree, $b = -0.007$, $F = 12.681$, df $= 2,349$). The results of PCA cross-validated these findings, supporting the conclusion that species that have all of their interactions within one or a few modules are more likely to experience directional selection (supplementary information).

Although network modularity had a negligible effect on coevolutionary dynamics, modular structures emerged as an important outcome of the coevolutionary process. Modules were found to be stable coevolutionary units, and mod-
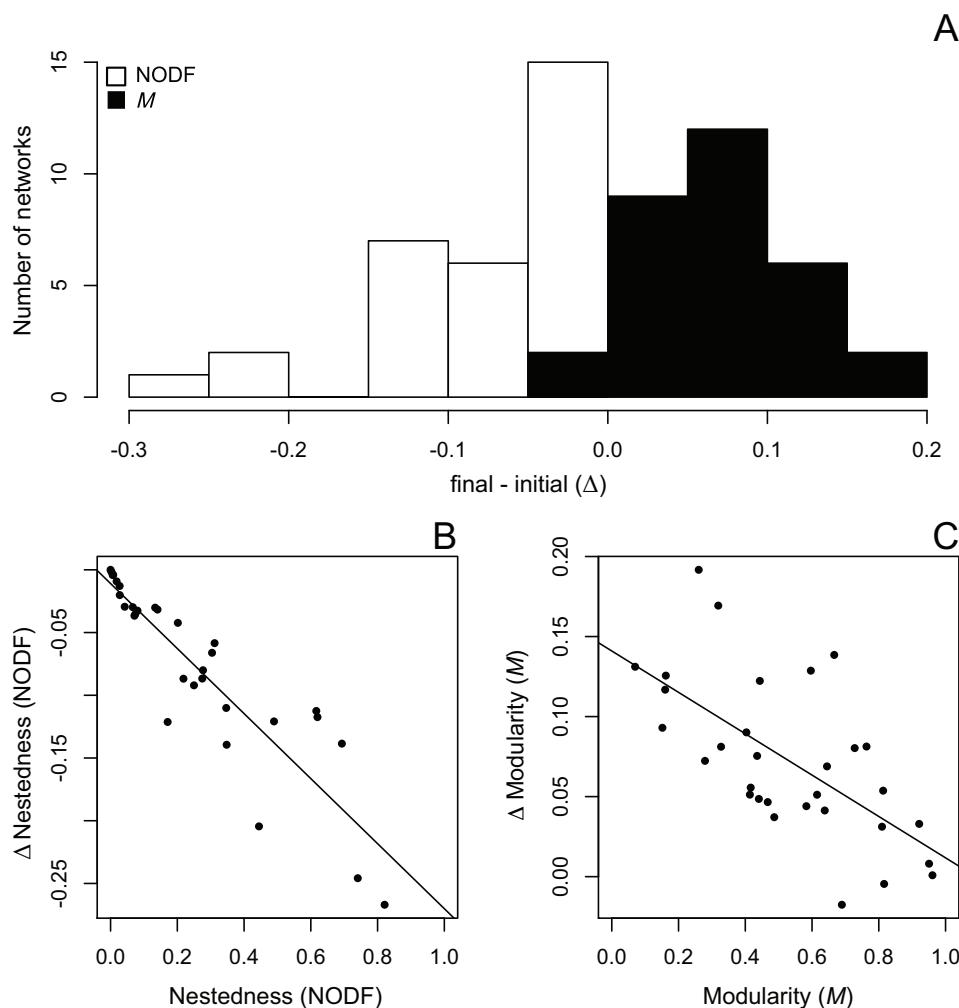
Figure 5: Changes in network nestedness and modularity at the end of the simulations. *A*, Histogram of the difference (Δ) between the initial and final network nestedness (NODF, in white) and modularity (*M*, in black). *B*, Networks with higher NODF values resulted in greater differences between the initial and final values, leading to stronger decay in nestedness. *C*, Networks with low *M* values showed a greater increase in modularity than did networks with initially high *M* values.

ularity had a key role in how trait matching was distributed within networks. Mean trait matching was higher for species interacting within the same module than between species belonging to different modules ($F = 227.6$, df = 3,524; fig. S12*A*). Similarly, when comparing trait matching among core-core, core-peripheral, and peripheral-peripheral species, trait matching was higher between peripheral species, which form modules in networks ($F = 99.9$, df = 3,495; fig. S12*B*). Temporal change in trait matching was more frequent in interactions involving highly connected species. Moreover, the cumulative change in trait matching (c_{ij}) indicates that the strength of selection of interacting species belonging to different modules was more variable over time than that of interacting species within the same module ($F = 132.0$, df = 3,502; fig. S13*A*). Similarly, interactions

between core species frequently changed over time, whereas peripheral-peripheral interactions presented a more constant selection strength ($F = 37.82$, df = 3,504; fig. S13*B*).

Discussion

We identified three central drivers of the trajectories of coevolutionary change within species-rich antagonistic networks. First, we showed that coevolutionary alternation is a possible outcome of coevolutionary dynamics mediated by trait matching if selection is asymmetric between victims and exploiters. Asymmetries in selection also produce asymmetries in evolutionary rates, which can be further amplified by differences in the heritability of coevolving
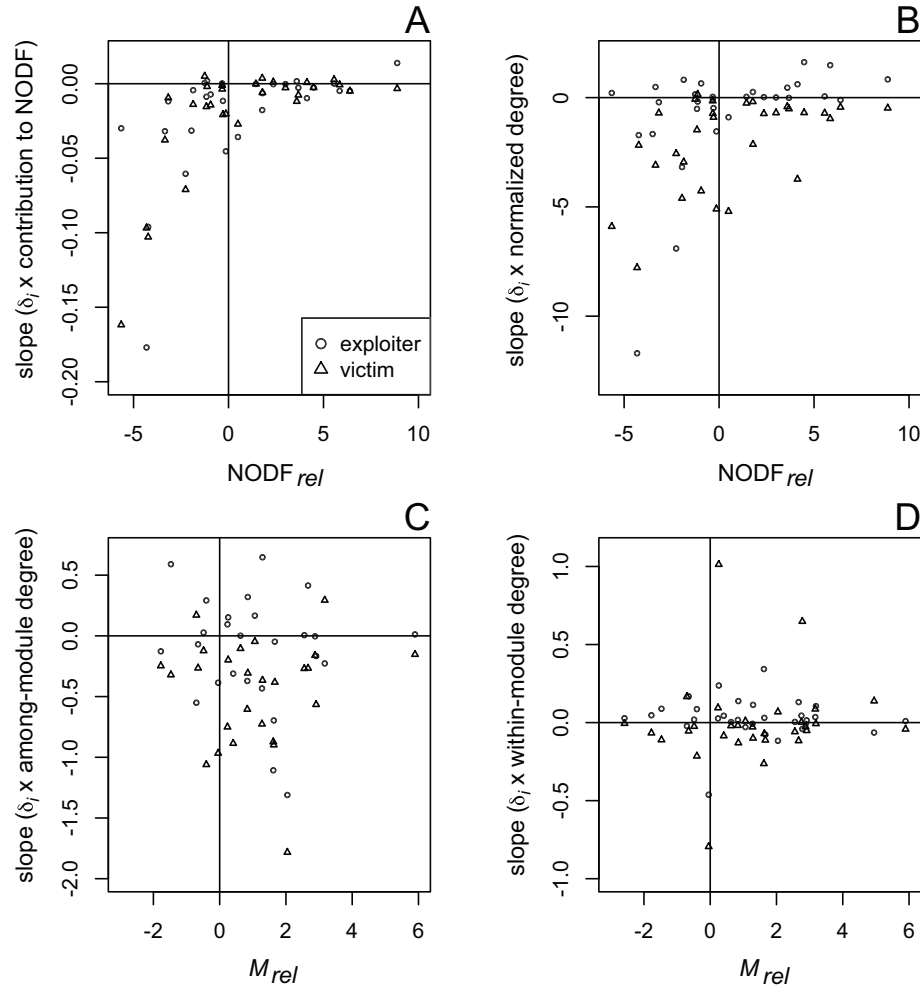
Figure 6: Relationship between the structural roles of victims and exploiters and the directionality of their coevolutionary dynamics, δ_i. *A*, *B*, In networks that are less nested than expected based on a null model that preserves species richness, connectance, and heterogeneity in the number of interactions (negative NODF$_{rel}$ values), there is a negative relationship between δ_i and nestedness contribution and normalized degree, respectively. In contrast, in networks that are more nested than expected based on the null model (positive NODF$_{rel}$ values), the relationship between nestedness contributions and normalized degree and δ_i is lost because trait changes are propagated throughout the entire network. *C*, Among-module degree is negatively related to δ_i and independent of network structure. *D*, Within-module degree is not associated with δ_i.

traits (Nuismer and Thompson 2006). Coevolutionary alternation in systems with few species is supported by both theory (Sasaki 2000; Agrawal and Lively 2002; Nuismer and Thompson 2006) and empirical work (Soler 2014). For instance, fluctuating selection, which is a necessary assumption for coevolutionary alternation, occurs if ecological conditions reduce selection for costly defenses, as is observed in phage-bacteria interactions in nutrient-limited environments (Gómez and Buckling 2011; Hall et al. 2011). In species-rich networks, fluctuating evolution is favored by the nested structure of some antagonisms in combination with asymmetries in selection. Therefore, our results support the no-

tion that coevolution in species-rich antagonistic interactions is neither a simple combination of pairwise interactions nor unstructured selection due to multiple species interactions. Rather, networks favor coevolutionary dynamics that cannot be predicted from pairwise interactions alone (Guimarães et al. 2011). Thus, coevolutionary dynamics in ecological networks may join the set of dynamical processes in complex systems that are affected by network structure, such as the spread of disease in human and animal societies (Keeling and Eames 2005; Craft et al. 2009), the flow of information in technological networks (Watts and Strogatz 1998), the persistence of species in fragmented landscapes

(Urban et al. 2009), and the demographic changes in present and past ecological networks (Thébault and Fontaine 2010; Yeakel et al. 2014).

By favoring coevolutionary alternation, asymmetries in selection and nested network organization lead to deviations from the tendency of coevolution to inherently favor directional evolution in antagonistic networks. Local directional evolution has been found in some pairwise antagonistic interactions involving few species, such as weevils and camellias (Toju 2011), crossbills and lodgepole pine (Benkman et al. 2003), and bacteria and phages (Weitz et al. 2013). Directional trait coevolution is the result of selection that favors increased levels of defense and counter-defense as well as the emergence of local specialization by exploiters to a few partners (Thompson 2005; Nuismer and Thompson 2006). However, costs prevent the levels of defense and counter-defense from escalating indefinitely (Rigby and Jokela 2000; Zuk and Stoehr 2002; Koskella et al. 2012; but see Cogni et al. 2012). Therefore, the degree of trait disparity observed in antagonistic interactions is limited by environmental selection in species-poor systems. As the existence of a network of antagonistic interactions affects coevolutionary dynamics, escalation is also limited by distinct regimes of conflicting selection imposed by multiple partners and the network structure that embeds pairwise interactions.

Second, coevolution due to asymmetries in selection and network organization reshapes the organization of antagonistic networks. This coevolutionary feedback indicates that coevolutionary dynamics in large multispecific networks are an interactive process of ever-changing interactions (Thompson 2013). If the fitness consequences of an interaction are higher for exploiters than for victims, highly nested networks allow exploiters to temporally specialize on victims with whom they currently have better trait matching. Nested structures also enable more victims to escape attack, thus increasing network modularity. Assuming that some degree of nestedness will occur even if interactions among species are ecologically neutral (Krishna et al. 2008), we hypothesize that species-rich antagonistic interactions start as nested networks and that if stronger selection acts on exploiters than on victims at the individual level, specialization and low niche overlap among exploiters will emerge at the population level. This emergence, in turn, will drive network organization from nested to modular. Once modularity is achieved, environmental and biotic selective forces will favor the evolutionary persistence of the modular organization. Available theory suggests that modular networks of antagonistic interaction are ecologically stable and naturally emerge from the ecological dynamics of nonmodular antagonisms (Thébault and Fontaine 2010; Allesina and Tang 2012). Our analyses suggest that modular networks are also a stable consequence of coevolutionary dynamics. Future empirical studies should explore the relative contributions of ecological

and evolutionary processes to the emergence of modularity. Ecological and evolutionary dynamics may have similar (Schoener 2011) or very different timescales (Levin 2000). The more similar the ecological and evolutionary timescales, the more likely it is that eco-evolutionary feedback loops will promote modularity in antagonistic interactions. However, independent of timescale similarity, both processes have the potential to exert synergistic effects on the structure of antagonistic networks.

Our results predict that modularity should be more common in antagonistic networks in which the fitness consequences of an interaction are higher for the exploiter than for the victim. This prediction is corroborated by empirical evidence and could be tested directly in future studies. Interactions between host plants and gall-inducing insects, leaf miners, and endophagous seed predators are often highly modular (Pires and Guimarães 2013). In contrast, nestedness is often observed in interactions that show higher fitness consequences for the victim than for the exploiter, as observed in interactions between mammalian herbivores and their predators and between plants and grasshoppers (Pires and Guimarães 2013). Our theoretical findings may also explain variation in network organization in other consumer-resource relationships, such as mutualisms (Pires et al. 2011). Modularity in mutualistic networks is also associated with stronger selective pressure on the consumers than on the resource, as illustrated by interactions between myrmecophytes and ants (Fonseca and Ganade 1996), plants and floral parasite pollinators (Hembry et al. 2013), and anemones and anemonefish (Ricciardi et al. 2010). In contrast, nestedness is associated with similar or higher fitness consequences for the resource organisms, as observed in interactions among plants and most pollinators and seed dispersers (Bascompte et al. 2003). Future work should investigate whether differences in the fitness consequences of interactions between partners indeed provide a general explanation for the structural variation of antagonisms and mutualisms. The physical integration of antagonistic and mutualistic interactions at the individual level may also affect the fitness consequences that shape the patterns of interaction. We hypothesize that differences in patterns of specialization that result from differences in selection pressures correspond to, at least to some extent, the differences between symbiotic and intimate interactions as compared with interactions among free-living species (Thompson 1994, 2005). For instance, we expect that asymmetries in selection may partially explain why intimate interactions based on the physical integration of consumers with a single host are modular, whereas interactions among free-living species, in which a consumer interacts with multiple individuals, are often nested (Guimarães et al. 2007; Fontaine et al. 2011; Pires and Guimarães 2013). Direct and indirect interactions between species within the same

trophic level, such as competition, may also have consequences for the evolution of networks, and the relative effects of between- and within-trophic level interactions should be further investigated.

Third, directional evolution and trait matching are affected not only by network organization but also by the interaction patterns of the species within the network. Peripheral species in nested networks have higher trait matching in all selection regimes, suggesting that specialized interactions may achieve fixed and high levels of trait matching, even in nested antagonistic networks. In contrast, coevolutionary alternation dynamics were observed in the interactions among species from different modules or between core species, in which we observed variable levels of trait matching (indicated by higher cumulative trait change). Highly connected species—the supergeneralists—are expected to coordinate coevolution in mutualistic networks, promoting convergence and trait complementarity (Guimarães et al. 2011). Our results suggest that in antagonistic networks, supergeneralists experience higher fluctuating selection, which may influence the dynamics of the entire network, depending on the degree of nestedness. Supergeneralists may alternate their interacting partners according to the relative defenses found in the victim community (Thompson 2005). Coevolutionary alternation has been proposed to explain the coevolutionary dynamics among highly diverse, thick-shelled marine invertebrates and their shell-crushing predators (Leighton 2002), the geographically variable interactions between cuckoos and their hosts (Davies and Brooke 1989; Soler et al. 2001), and the chemically and geographically complex interactions between butterflies and ants (Nash et al. 2008). Our work provides a theoretical expectation for the specific set of conditions under which coevolutionary alternation shapes the evolution of preferences and defenses in species-rich interacting assemblages of antagonisms.

In summary, modularity had a negligible effect on coevolutionary dynamics when niche width was conserved. However, our results indicate that modular structures arise in antagonistic networks as outcomes of the coevolutionary process, emerging as the products of conflicting selective pressures acting on antagonistic networks. Nestedness sustains fluctuating trait evolution, and it may occur in interactions in which there is an asymmetry in the selection experienced by interacting exploiters and victims. Therefore, the fitness consequences of interactions and asymmetries therein may determine the patterns of species interactions and shape the structure of ecological networks. The generality of these expectations should be investigated for scenarios in which species niche width itself coevolves and potentially results in niche expansion or contraction. It would also be worthwhile to model coevolution in other types of consumer-resource interaction networks. Approaches derived from evolutionary theory with network-based modeling and empirical data contribute to the emerging field of evolutionary ecology of ecological networks (Kauffman and Johnsen 1991; Loeuille and Loreau 2005; Mckane and Drossel 2006; Santamaría and Rodríguez-Gironés 2007; Gómez et al. 2010; Guimarães et al. 2011; Gómez and Verdú 2012; Nuismer et al. 2013), and they allow predictions to be generated regarding how network structure and the coevolutionary process are related. Experiments and field studies that consider the complex structure of ecological interactions and the geographic mosaic of variation in such interactions are necessary to understand coevolution in natural communities and to test our predictions. To advance our understanding of coevolution in antagonistic systems, it is imperative to consider the interplay between the ecological and evolutionary dynamics of species that interact in species-rich assemblages. At present, we argue that to understand how different selection regimes favor distinct coevolutionary trajectories it is fundamental to consider the network structure of multispecific antagonistic interactions.

APPENDIX A

Data Set Used in the Simulations

Table A1: Data set used to parameterize the matrix **F**, including the type of interaction and network basic characteristics

Data set	Type	N_v	N_e	C	Reference
herb1	Grasshoppers–plants	52	22	.16	Joern 1979
herb2	Mammalian grazers–plants	10	17	.6	Hansen et al. 1985
herb3	Grasshoppers–plants	54	24	.14	Joern 1979
herb4	Leaf-chewing beetles–plants	10	32	.14	Basset and Samuelson 1996
herb5	Gallers–host plants	10	17	.12	Dawah and Hawkins 1995
herb6	Leaf-chewing caterpillars–plants	53	24	.06	Henneman and Memmott 2001
herb7	Leaf-chewing caterpillars–plants	49	26	.06	Henneman and Memmott 2001
herb8	Mining insects–host plants	204	94	.01	Lewis et al. 2002
herb9	Sap-feeding insects–plants	42	35	.05	Loye 1992
herb10	Mining insects–host plants	50	87	.02	Memmott et al. 1994
herb11	Sap-feeding insects–plants	26	25	.07	Muller et al. 1999
herb12	Fruit flies–plants	53	30	.05	Novotny et al. 2005
herb13	Flower feeders–plants	81	34	.06	Prado and Lewinsohn 2004
herb14	Gallers–host plants	10	16	.12	Tscharntke et al. 2001
herb15	Grasshoppers–plants	43	14	.3	Ueckert and Hansen 1971
herb16	Phasmids–plants	38	13	.11	Blüthgen et al. 2006
herb17	Leaf-chewing caterpillars–plants	40	49	.05	Coley et al. 2006
herb18	Gallers–host plants	29	27	.04	Cuevas-Reyes et al. 2007
par1	Fish–parasites	07	29	.38	Arthur 1976
par2	Fish–parasites	10	40	.22	Leong and Holmes 1981
par3	Fish–parasites	14	51	.16	Arai and Mudry 1983
par4	Fish–parasites	17	53	.18	Arai and Mudry 1983
par5	Fish–parasites	33	97	.1	Bangham 1955
par6	Fish–parasites	06	25	.35	Chinniah and Threlfall 1978
pred1[a]	Mammalian predator–prey	16	8	.52	Baskerville et al. 2011
pred2	Mammalian predator–prey	22	5	.8	Owen-Smith and Mills 2008
pred3	Seed predators–plants	98	11	.01	Janzen 1980
pred4	Seed predators–plants	21	30	.17	Nakagawa et al. 2003
pred5	Seed predators–plants	15	37	.17	Nakagawa et al. 2003
pred6	Mammalian predator–prey	18	4	.66	Radloff and du Toit 2004

Note: The data sets are available online at the Interaction Web Database (www.nceas.ucsb.edu/interactionweb/index.html) or available in Pires and Guimarães 2013. N_v = number of victims; N_e = number of exploiters; C = connectance.

[a] Subnetwork depicting predator-prey interactions between mammals weighing >5 kg.

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"The authoress has been fortunate in her sources of information and in her artists. She wields an easy and graceful pen, has the art of vivid description and good generalizing powers. . . . The wood-cuts . . . are by Mr. Carreras." From the review of Buckley's *Winners in Life's Race* (*The American Naturalist*, 1884, 1:47–50).