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ABSTRACT: The web of interactions in a community drives the coevolution of species. Yet it is unclear how the outcome of species interactions influences the coevolutionary dynamics of communities. This is a pressing matter, as changes to the outcome of interactions may become more common with human-induced global change. Here, we combine network and evolutionary theory to explore coevolutionary outcomes in communities harboring mutualistic and antagonistic interactions. We show that as the ratio of mutualistic to antagonistic interactions decreases, selection imposed by direct partners outweighs that imposed by indirect partners. This weakening of indirect effects results in communities composed of species with dissimilar traits and fast rates of adaptation. These changes are more pronounced when specialist consumers are the first species to engage in antagonistic interactions. Hence, a shift in the outcome of species interactions may reverberate across communities and alter the direction and speed of coevolution.

Keywords: ecological networks, species interactions, trait matching.

Introduction

Interactions fuel coevolution. Classic examples of pairwise associations that drive reciprocal evolutionary change include figs and fig wasps (Weiblen 2002) or yuccas and yucca moths (Pellmyr et al. 1996). Yet species are not restricted to pairwise interactions. Instead, they constitute communities of interacting species. In such communities, species can potentially coevolve in response to all other species. For example, a species may exert selective pressures on as many species as it interacts with. But a species can also affect all other species in the community through indirect

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pathways. Together, direct and indirect interactions shape the outcome of coevolution in communities.

Several studies have examined how direct interactions alter coevolutionary dynamics (see references in terHorst et al. 2018). For example, Gómez (2003) showed that the selective pressure imposed by pollinators on floral traits of *Erysimummedio hispanicum* breaks down when ungulate herbivores are present. Yet the question of how indirect interactions alter evolutionary dynamics has been less explored. Work on small communities suggests that indirect effects can drive the evolutionary dynamics between predators and competitors (terHorst 2010), plants and their herbivores (Bonte et al. 2010), and native and exotic plants (Lau 2012). But experiments including large communities are challenging because of the difficulties of tracing the evolutionary trajectories of many species in response to many partners (Miller and Travis 1996; Walsh 2013).

Work merging network and evolutionary theory has provided insights into the coevolutionary dynamics of large communities (Andreazzi et al. 2017, 2020; Guimarães et al. 2017). Andreazzi et al. (2020) showed that the structure of interaction networks can shape the coevolutionary outcome of antagonistic interactions. Furthermore, Guimarães et al. (2017) showed that, depending on the structure of the interaction network, indirect interactions may outweigh direct interactions in shaping the coevolution of mutualistic communities. Moreover, the strength of indirect effects may modulate the rate at which traits evolve in a community and the degree of trait similarity arising from coevolution (Guimarães et al. 2017). Yet these insights on how indirect effects shape coevolution apply to communities that harbor only mutualistic interactions.

The outcome of species interactions determines how coevolution operates (Vermeij 1994; Jordano 1995; Dalsgaard et al. 2008; Luijckx et al. 2013). So communities composed

entirely of mutualistic interactions or antagonistic interactions should exhibit different coevolutionary dynamics. However, these differences remain unexplored. Moreover, it is unlikely that communities contain species that engage in only one type of interaction (Genrich et al. 2017; Montesinos-Navarro et al. 2017).

The outcome of biotic interactions falls along a continuum, from mutualistic to antagonistic. Yet the ultimate result of an interaction depends on its costs and benefits (Bronstein 1994). When these cost-benefit relations change, so does the outcome of an interaction (Hoeksema and Bruna 2015). Interactions can have variable outcomes in pollination (Spira et al. 1992), grazing (Delibes et al. 2017), synzoochory (Gómez et al. 2019), parasitism (Molina-Morales et al. 2014), competition (Butterfield and Callaway 2013), or predation (Mukherjee and Heithaus 2013). Thus, the outcome of most interactions is context dependent (Chamberlain et al. 2014; Maron et al. 2014).

If interactions are context dependent, then communities must harbor associations with different outcomes. For example, while frugivores are the backbone of mutualistic seed-disperser interactions, they can become seed predators (Perea et al. 2013). In fact, nonmutualistic interactions can account for almost half of the interactions of plant-frugivore networks thought to be mutualistic (Simmons et al. 2018). Moreover, under human-induced global change, the outcomes of interactions could change (Kiers et al. 2010 and references therein). For example, ants have been found to switch to an antagonistic relationship with *Acacia* trees in the absence of large herbivores (Palmer et al. 2008), while invasive pollinators can damage flowers impacting plant reproduction (Aizen et al. 2014; Morales et al. 2017). Thus, antagonistic interactions may become more prevalent in otherwise mutualistic communities. The ratio of mutualists to antagonists in a community influences its ecological dynamics (Melián et al. 2009; Lurgi et al. 2016). Yet the evolutionary implications are unclear.

Since coevolution operates through direct and indirect effects, a single antagonistic interaction could change the coevolutionary dynamics of a mutualistic community, and vice versa. Moreover, some species may disproportionately shape the coevolutionary dynamics of communities. For instance, indirect effects play a more prominent role in specialists (species with few interactions) than in generalists (species with many interactions; Guimarães et al. 2017). Hence, the identity of a species could modulate its impact on the rest of the species in the community.

Here, we simulate the coevolutionary consequences of communities (i.e., interacting guilds of species) harboring different interaction types. We investigate how the ratio of mutualists to antagonists alters coevolutionary dynamics. First, we ask how indirect effects change under different ratios of mutualists to antagonists, and we relate these

changes to trait distributions and network structure. Second, we ask how species identity modulates changes to dynamics. We explore this question by simulating two scenarios. In the first, the most specialist species are more likely to be the antagonists. In the second, the most generalist species are more likely to be the antagonists.

Methods

Our workflow consisted of five stages. First, we modified a set of empirical mutualistic networks to include different ratios of mutualistic to antagonistic interactions (see fig. 1). We did this by making either the most specialist or most generalist species in the community antagonistic. Second, we simulated species coevolution in each network. Third, for each network and each species in each network, we measured the role of indirect effects in driving coevolution, the degree of trait matching arising from coevolution, and the rate of coevolution. Fourth, we related the extent to which indirect effects drive coevolution and the degree of trait matching arising from coevolution with the structural properties of the network where coevolution is unfolding. Fifth, we analyzed how these relationships change as networks become progressively antagonistic. We compared the size of these differences in scenarios where the most specialist or most generalist species became antagonistic.

Dataset and Conversion of Interaction Types

We used a set of mutualistic networks (seed dispersal networks, $n = 34$) found in the Web of Life repository (http://www.web-of-life.es/; Fortuna et al. 2014). In these networks, the species are linked by mutualistic interactions. To obtain networks with a mix of antagonistic and mutualistic interactions, we converted a proportion of links from mutualistic to antagonistic (e.g., to obtain a network with 20% antagonistic interactions, we chose 20% of the links of the network and reassigned them as antagonistic interactions). These transformations did not alter network structure; they merely changed the type of link connecting species. We assume that mutualistic and antagonistic interactions differ in how they affect trait evolution. Mutualistic interactions favor trait convergence, while antagonistic interactions select for trait convergence of consumers and trait divergence of resources (see "Model Description" for a detailed account). Because we do not allow these transformations to alter network structure, we can isolate the effect of different ratios of interaction types on coevolutionary dynamics.

We transformed each mutualistic network to obtain an equivalent network with 20%, 40%, 60%, 80%, and 100% of antagonistic interactions. This allowed us to explore how
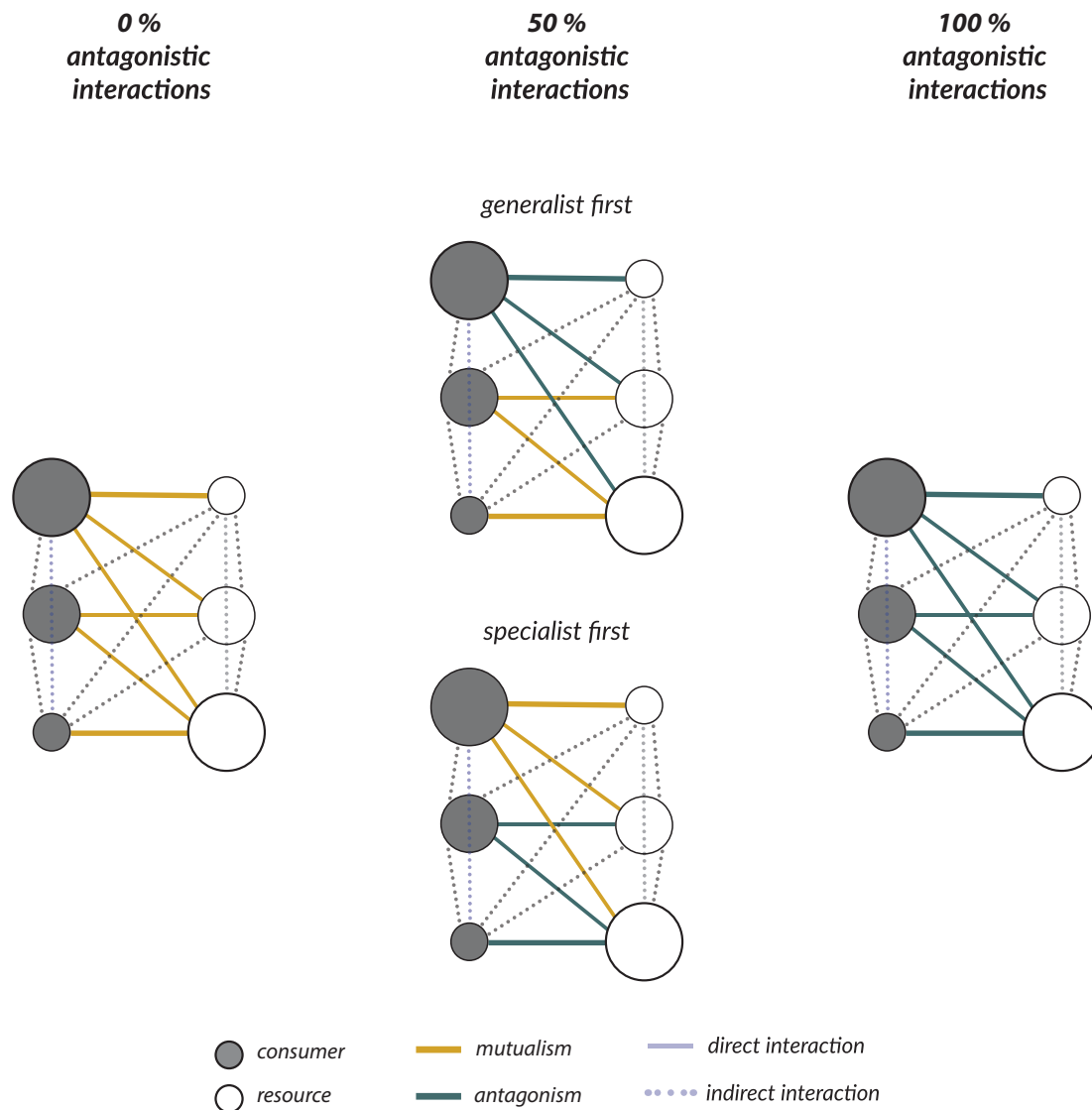
Figure 1: This figure illustrates how we transform a mutualistic network (*left*) to an antagonistic one (*right*). At each fraction of antagonistic interactions (here we show 50% as an example), we convert the corresponding number of links from mutualistic to antagonistic following two strategies. The generalist first strategy (*top*) converts the links of the consumer species with the largest number of interactions first. The specialist first strategy (*bottom*) converts the links of the consumer species with the smallest number of interactions first. At any fraction of antagonistic interactions, both strategies result in networks with an equal number of antagonistic interactions but differ in their distribution. Note that in addition to direct interactions (solid lines), species embedded in networks can also interact indirectly (dotted lines).

coevolutionary dynamics differ among communities with higher and lower proportions of mutualisms and antagonisms. Furthermore, given that specialist and generalist species shape the evolution of communities in different ways (Guimarães et al. 2017), we transform networks following two strategies. In the "generalist first" strategy, we converted the interactions of the consumer species with the most interactions in the network first (fig. 1, *top*). In the "specialist first" strategy, we prioritized the consumer

species with the fewest interactions in the network (fig. 1, *bottom*). Both strategies assume that any switch from mutualism to antagonism is driven by consumers—we refer to seed dispersers as "consumers" and seed producers as "resources." For completeness, we also converted interactions at random. However, as we found that the other two strategies represent the two extreme scenarios and as the results from this "random" strategy followed the same trends, they are not shown here for brevity.

To rule out the possibility that the trends we observed were driven by the structure of the mutualistic networks selected as opposed to the conversion of interactions to antagonistic, we also transformed a set of antagonistic networks ($n = 55$, 51 host-parasite and 4 plant-herbivore networks) from the Web of Life repository. In this case, we converted the originally antagonistic interactions into mutualistic ones and performed the same workflow outlined above. The results of these simulations are qualitatively similar to those where we converted mutualistic networks, thus suggesting that the observed trends are indeed an outcome of interaction types changing. For brevity, we present these results in the supplemental PDF (figs. S1–S12, available online).

Coevolutionary Framework

Model Description. Many models have been proposed to study the evolutionary context of communities, with approaches including genetic population models (Nuismer et al. 2013), individual-based models (Nuismer et al. 2013), models based on assembly rules (Santamaría and Rodríguez-Gironés 2007), and coevolutionary network models (Guimarães et al. 2011; Nuismer et al. 2013). Here, we use a coevolutionary model for networks based on selection gradients (Andreazzi et al. 2017, 2020; Guimarães et al. 2017) for two reasons. First, they allow us to model trait changes resulting from interactions at the scale of communities by expressing coevolution as a coupling of adaptive landscapes due to species interactions, such that adaptive changes by one species deform the landscapes of its partners (Kauffman and Johnsen 1991). Second, they enable us to directly quantify the extent to which indirect interactions reshape adaptive landscapes in ecological networks. Thus, this approach allows us to study how species' traits change as a result of direct and indirect interactions with the rest of the species in their communities. We next describe how the models work and later how we quantify indirect effects.

We used models proposed by Guimarães et al. (2017) and Andreazzi et al. (2017, 2020) to simulate mutualistic and antagonistic coevolution, respectively. These discrete-time models use a selection gradient approach to link the evolution of a single quantitative trait with the fitness consequences of interactions and all other selective pressures that are not related to interactions (hereafter referred to as the "environment"). In other words, we assume that the trait that is evolving affects the fitness benefits derived from both interactions with the individuals and interactions with the environment.

We define the mean trait (Z) evolution of species i over a time step t as

$$Z_i^{t+1} = Z_i^t + \varphi_i(S_i^t + E_i^t), \qquad (1)$$

where φ_i is a compound parameter that affects the slope of the selection gradient and is proportional to the additive genetic variance, while S_i^t and E_i^t are the partial selection differentials attributed to selection imposed by interactions and environment, respectively.

We assume that the change in species' traits due to interactions, S_i^t, depends on the degree of trait matching between interacting species:

$$S_i^t = \sum_{j, j \neq i}^{N} q_{ij}^t I_{ij}^t, \qquad (2)$$

where N is the number of species in the network and I_{ij}^t is the trait value selected by the interaction of species i with species j (this depends on the type of interaction between species and is detailed below). The term q_{ij}^t describes the evolutionary effect of species j on species i, and it serves to weigh the relative importance of the selection imposed by species j to the selection gradient compared with all other sources of selection. We define q_{ij}^t as

$$q_{ij}^t = m_i \frac{a_{ij} e^{-\alpha(Z_j^t - Z_i^t)^2}}{\sum_{k, i \neq k}^{N} a_{ik} e^{-\alpha(Z_k^t - Z_i^t)^2}}, \qquad (3)$$

where m_i is the level of coevolutionary selection and is a measure of the relative importance of interactions in shaping trait evolution. At the extreme values of m_i, trait evolution is completely driven either by the environment ($m_i = 0$) or by the interactions ($m_i = 1$). The term a_{ij} is an element of the symmetric binary adjacency matrix, A, of the network (where $a_{ij} = 1$ if species i and species j interact and $a_{ij} = 0$ otherwise). The term α is a constant that determines the sensitivity of the evolutionary effect to differences in species' traits.

We assume that mutualistic and antagonistic interactions differ in how they affect trait evolution. That is, the phenotype selected by the interaction of species j with species i (I_{ij}^t in eq. [2]) depends on the type of interaction.

For mutualistic interactions, following past theoretical work (Guimarães et al. 2011; Nuismer et al. 2013), we assume that selection imposed by partners favors trait complementarity. Phenotypic matching has been observed between mutualistic partners in nature, such as in the matching between the depth of floral corolla and the length of hummingbird bills (Dalsgaard et al. 2008) or the size of seeds and body mass of frugivores (Jordano 1995). In such scenarios, phenotypic matching of traits may be necessary for the successful interaction of mutualistic partners (Jordano et al. 2003; Agosta and Janzen 2005). We assume that higher trait matching between partners leads to more frequent interactions, which in turn leads to stronger reciprocal selection between species. We define the effect of species j on species i at time t as

$$I_{ij}^t = Z_j^t - Z_i^t. \tag{4}$$

For antagonistic interactions, following past theoretical work (Andreazzi et al. 2017, 2020), we assume that selection imposed by interactions favors trait similarity for consumers and mismatch for resource species. This assumption represents systems where the chance of a successful attack of a consumer on its resources increases when its traits match the defences of its victims, while the chances of a resource escaping its consumer increases if its traits mismatch those of its consumer (Nuismer and Thompson 2006; Hanifin et al. 2008). Examples of these dynamics can be observed in the interaction between hard-shelled invertebrates and their shell-destroying predators (Vermeij 1994) or between crustaceans and their parasitic bacteria (Luijckx et al. 2013). We assume that the reciprocal selection between consumers and resources will be stronger when successful attacks are more common (i.e., when trait matching is high).

From the consumer perspective, the effect of resource j on consumer i at time t is defined by equation (4). From the resource perspective, trait mismatch results in its traits either increasing (if $Z_i^t > Z_j^t$) or decreasing (if $Z_i^t < Z_j^t$). As Andreazzi et al. (2017, 2020), we define a critical mismatch value ε. If $|Z_i^t - Z_j^t| > \varepsilon$, then the consumer species has a negligible effect on the resource's fitness ($I_{ij}^t = 0$). This condition represents a scenario where a consumer no longer has an effect on the fitness of its victim, as in commensalism. Otherwise (if $|Z_i^t - Z_j^t| \leq \varepsilon$), the effect of consumer j on resource i at time t is expressed as

$$I_{ij}^t = Z_j^t + \varepsilon - Z_i^t \quad \text{if } Z_i^t > Z_j^t \tag{5}$$

or

$$I_{ij}^t = Z_j^t - \varepsilon - Z_i^t \quad \text{if } Z_i^t < Z_j^t. \tag{6}$$

Finally, we define the trait change imposed by the environment, E_i^t, as

$$E_i^t = \left(1 - \sum_{j,j \neq i}^N q_{ij}^t\right)(\theta_i - Z_i^t), \tag{7}$$

where θ_i is the environmental optimum of species i (i.e., the phenotype favored by the environmental selection).

Simulation Setup. At the start of each simulation, we sampled the environmental optimum value (θ_i) and the initial trait value of each species in the network (Z_i^0) from a uniform distribution ($\mathcal{U}_{[0,10]}$) and φ_i from a normal distribution ($\mathcal{N}(\mu = 0.7, \sigma = 0.01)$). Note that the coevolution model yields qualitatively similar results when traits are drawn from different distributions (Pedraza and Bas-

compte 2021). Using equation (1), we simulated coevolution in all networks at each particular fraction of antagonistic interactions. We stopped the simulations once they reached equilibrium, defined as $|Z_i^t - Z_i^{t+1}| \leq \tau$, with $\tau = 1 \times 10^{-5}$. At the end of each simulation, we recorded the equilibrium trait values of each species, which allowed us to quantify the contribution of indirect effects to trait evolution and the degree of trait matching arising from coevolution (see following sections). For each network, we ran 100 replicate simulations for a total of 40,800 simulations (34 networks × 6 mutualism-to-antagonism ratios × 2 strategies), where each simulation differed in the sampled θ_i, Z_i^0, and φ_i.

We performed sensitivity analyses by varying (i) the strength of coevolution (m), (ii) the sensitivity of the evolutionary effects to trait differences (α), and (iii) the sensitivity of resources to their consumers (ε). While we observed quantitative differences depending on the parameter values, the qualitative trends were the same. For brevity, here we present the results of simulating coevolution with intermediate parameter values ($m = 0.7$, $\alpha = 0.2$, and $\varepsilon = 10$), while the equivalent results for extreme parameter values are shown in the supplemental PDF (figs. S10–S12).

Measurement of Indirect Effects. The coevolutionary framework we use has an analytical approximation that enables one to quantify the extent to which direct and indirect species interactions shape the adaptive landscapes of species in a network (for the analytical derivation, see the supplementary information in Guimarães et al. 2017). In other words, the model allows for the measurement of the evolutionary consequences of both direct and indirect pathways linking species in a network.

To measure the contribution of indirect effects to trait evolution, we first obtained the Q matrix, which is an $N \times N$ matrix containing the direct coevolutionary effects of interactions (eq. [3]; fig. 2). Thus, q_{ij} represents the evolutionary effect of the direct interaction between species i and species j and is weighed by how similar the traits of species i and species j are relative to the rest of the partners of species i. We assume that interactions between species with more similar traits have a stronger role in shaping species coevolution than interactions between species with more dissimilar traits. For each simulation, we obtained the Q matrix at equilibrium.

Next, we used Q to obtain the T matrix—the coevolutionary matrix. The T matrix contains both direct and indirect coevolutionary effects of interactions (fig. 2) and is defined as

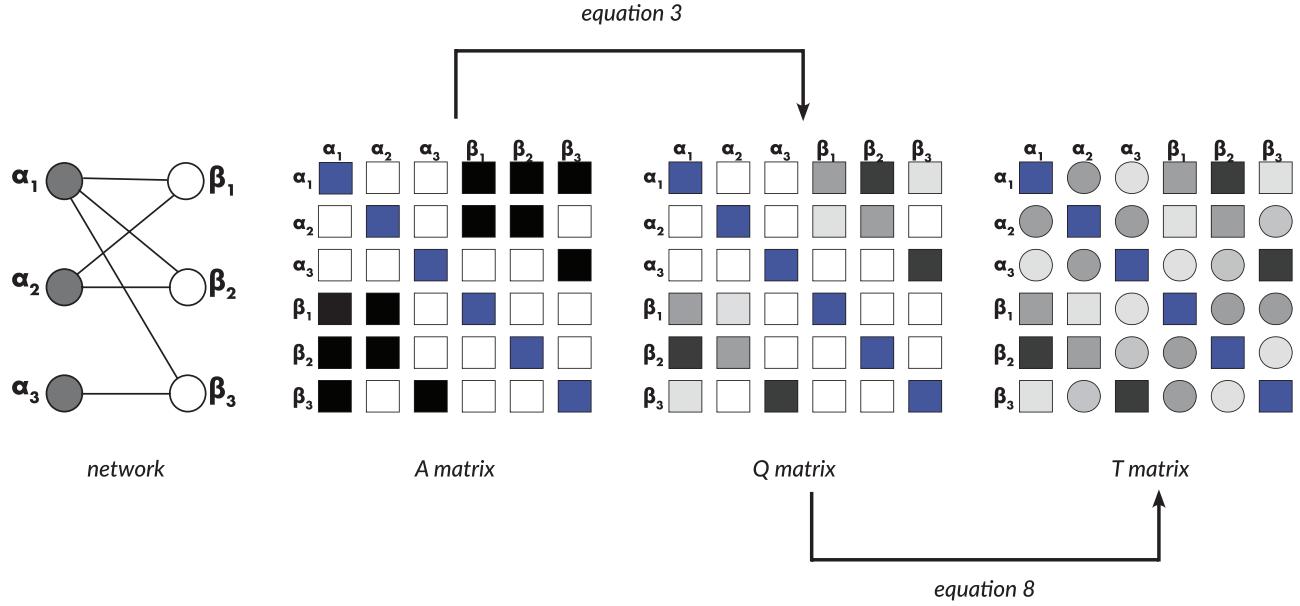$$T = (I - Q)^{-1}\Psi, \tag{8}$$

equation 3

equation 8

Figure 2: This figure illustrates how we measure the indirect evolutionary effects in a network. Shaded cells denote interactions, and the diagonal is highlighted in blue. To measure indirect effects, we first simulate coevolution in a network. Next, we use equation (3) to link the coevolved traits and the adjacency matrix of the network (*A* matrix) to obtain the *Q* matrix. The *Q* matrix contains the coevolutionary effects of direct interactions. These are weighted by the trait difference between species. Dark gray shades indicate strong coevolutionary effects, while light gray shades indicate weak coevolutionary effects. Finally, we use equation (8) and *Q* to obtain the *T* matrix. The *T* matrix contains both direct and indirect coevolutionary effects of interactions. Squares represent direct coevolutionary effects, while circles denote indirect coevolutionary effects. The coevolutionary strength of an interaction is symbolized by shades of gray as in *Q*.

where I is the identity matrix and Ψ is an $N \times N$ diagonal matrix with $\Psi_{ii} = 1 - m_i$ for species i (note that as in the coevolution model, m represents the level of coevolutionary selection). Thus, the elements of T represent the evolutionary effects of interactions between species, be they direct or indirect links.

Using the adjacency matrix (a_{ij}), we identified elements of T corresponding to direct and indirect effects. This allows us to study the indirect effects occurring between species without a direct interaction (i.e., where $a_{ij} = 0$). We measured the contribution of indirect effects to (i) the coevolution of all species in the network and (ii) each species in the network.

At the scale of networks, we define the relative contribution of indirect effects to trait evolution in a network as

$$\kappa = \frac{\sum_i^N \sum_{j,i\neq j}^N (1 - a_{ij})t_{ij}}{\sum_i^N \sum_{j,i\neq j}^N t_{ij}}. \qquad (9)$$

In other words, we compute the ratio (κ) between the aggregate evolutionary effects of all indirect interactions in a network and the aggregate evolutionary effects of all direct and indirect interactions in a network. This ratio (κ) is our measure of the contribution of indirect effects to coevolution at the network scale.

At the scale of species, we define the contribution of species i to the proliferation of indirect effects in the network as

$$\kappa_i = \frac{\sum_{j,i\neq j}^N (1 - a_{ij})t_{ij}}{\sum_{j,i\neq j}^N t_{ij}}. \qquad (10)$$

In other words, for each species, we compute the ratio (κ_i) between all the indirect evolutionary effects and all the evolutionary effects—both direct and indirect—it exerts on the species in the network. This ratio is our measure of each species' contribution to the proliferation of indirect effects in the network. For each network and species, we calculated the average contribution of indirect effects to trait evolution across replicates.

Measurement of Trait Matching. We calculated the degree of trait matching between all pairs of species in the network when simulations reached equilibrium. We defined trait matching between a pair of species i and j as

$$M_{ij} = e^{-\alpha\left(z_i^t - z_j^t\right)^2}. \qquad (11)$$

We used equation (11) to calculate the degree of trait matching arising at the network level and at the species level. At the network level, we calculated the trait matching between all pairs of species in the network and computed

the average (M). At the species level, we calculated the trait matching between a focal species and the rest of the species in the network (M_i).

The degree of trait matching arising from the model is the outcome of how species interactions shape trait evolution (see "Model Description"). The term M summarizes the outcome of all evolutionary effects of all interactions on all species. At a smaller scale, M_i summarizes the outcome of all evolutionary effects of all interactions on species i. Moreover, because trait matching weighs the evolutionary effect of each interaction (see "Measurement of Indirect Effects"), we can relate the degree of trait matching with the importance of direct and indirect interactions.

Data Analysis

In our data analysis we relate (i) the extent to which indirect effects drive coevolution and (ii) the degree of trait matching arising from coevolution with the structural properties of the network. We performed these analyses at the scale of networks and species. We next detail the properties measured at each scale and how we analyzed the data.

Network Structure. At the network scale, we measured four structural properties. These were network size (i.e., the number of species in the network), connectance (i.e., the proportion of realized interactions from the pool of all possible interactions between the species of a network), modularity, and nestedness. To identify modules and quantify the modularity of a network, we used the Q metric (Newman and Girvan 2004; Marquitti et al. 2014). The Q metric measures the difference between the observed fraction of interactions between species in the same module and the expected fraction of interactions connecting species in the same module if interactions were established at random. We used the igraph package (Csardi and Nepusz 2006) in R (R Core Team 2020) to implement a multilevel optimization algorithm (Blondel et al. 2008) to find the network partition where Q is maximized and recorded the Q value of the network partition. Nestedness is a measure of the extent to which more specialist species interact only with subsets of those species interacting with more generalist species (Bascompte et al. 2003). We quantified network nestedness using a metric proposed by Fortuna et al. (2019), which is equivalent to the NODF metric (nestedness metric based on overlap and decreasing fill; Almeida-Neto et al. 2008). This allowed us to measure nestedness as the average overlap between interactions of consumers (resources), without penalizing the contribution to nestedness of consumers (resources) able to interact with the same number of resources (consumers). We controlled for the effect of network size on nestedness and modularity by standardizing them using a null model approach (Bascompte et al. 2003). For each network, we computed its observed (x) nestedness (or modularity). Then we randomized each network using a null model where the probability of each cell being occupied is the average of the probabilities of occupancy of its row and column (Bascompte et al. 2003). We generated 100 randomizations of each network and computed the average (μ) and standard deviation (σ) of nestedness (or modularity) across all randomizations. We then computed the standardized Z nestedness (or modularity) value of each network:

$$Z = \frac{x - \mu}{\sigma}. \tag{12}$$

At the species scale, we measured the number of interactions each species had in each network (i.e., the degree of each species). We analyzed the relationship between species' degree and (i) species' contribution to the proliferation of indirect effects and (ii) species' trait matching to the rest of the species in the network.

Statistical Analyses. We used simple linear regressions to determine whether the relationship between each network descriptor (i.e., size, connectance, modularity, and nestedness) and indirect effects or trait matching changed with the fraction of antagonistic interactions in the network. We fitted a single linear model for each fraction of antagonistic interactions with indirect effects (or trait matching) as the response variable and the corresponding network descriptor as the explanatory variable. For each model, we extracted the estimated slope coefficients and their respective confidence intervals (95%). We performed all simulations, analyses, and visualizations in R (ver. 4.0.2; R Core Team 2020).

Results

We begin by analyzing how coevolutionary dynamics change in communities with different ratios of mutualists to antagonists. We found that higher fractions of antagonistic interactions increased the rate of adaptive change (i.e., the average amount of trait change per time step; fig. 3*C*), increased the variance in trait values (fig. 3*D*), and consequently decreased trait matching in the network (fig. 3*B*). These changes are expected from our model, given that antagonistic interactions can give way to runaway trait dynamics between consumer and resources, thus speeding up coevolution and favoring trait mismatch. Surprisingly, the reduction in trait matching in communities appears to be nonlinear, with the largest changes in trait matching occurring when the first 20% of interactions were converted to antagonism. We found that higher fractions of antagonistic interactions also reduced the contribution of indirect effects to trait evolution (fig. 3*A*). Moreover, the
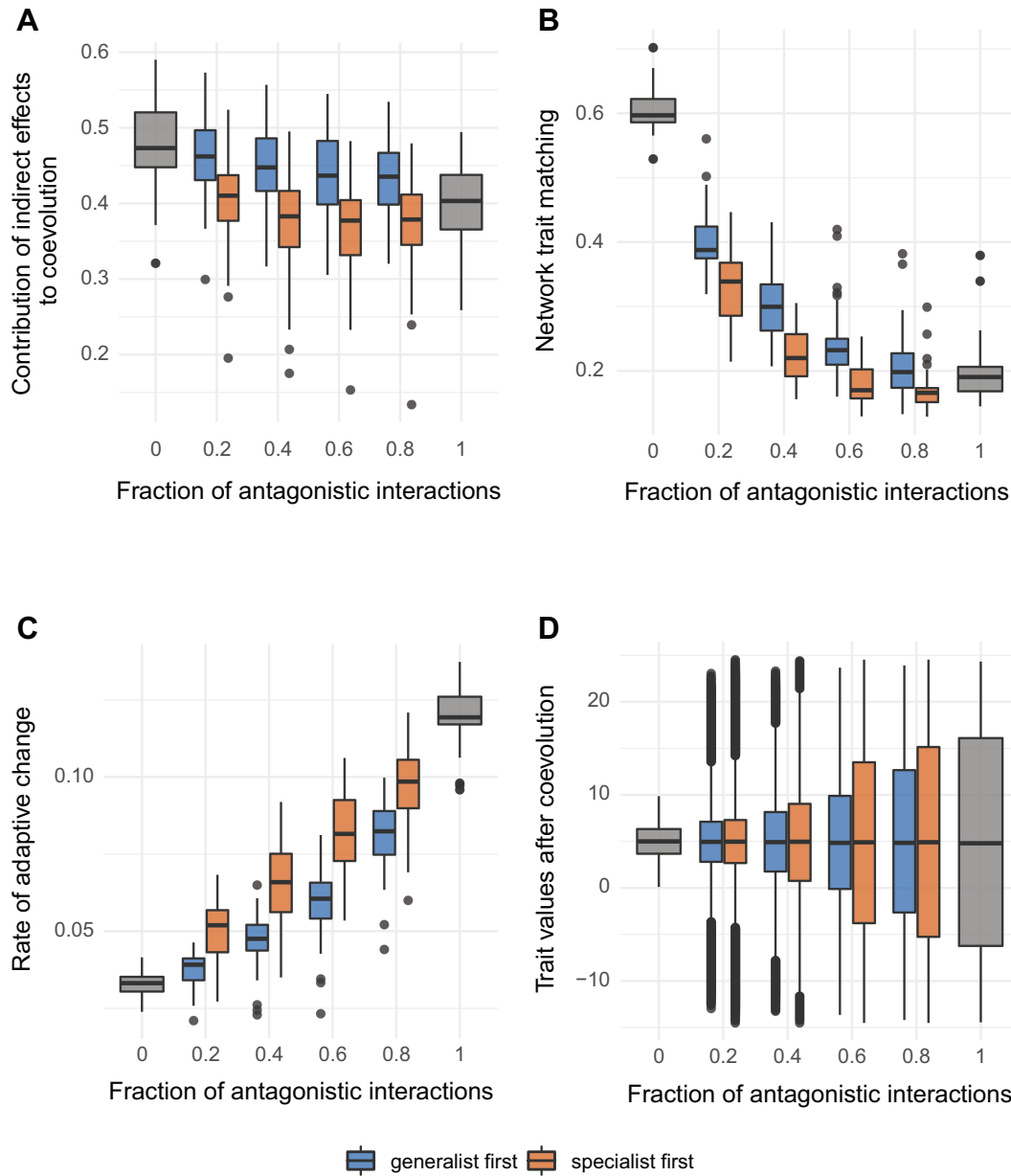
Figure 3: Evolutionary implications of converting mutualistic interactions to antagonistic ones. At a given fraction of antagonistic interactions, boxplots summarize the network-level contribution of indirect effects to coevolution (κ; A), the network-level trait matching (M; B), the rate of adaptive change (the average amount of trait change per time step; C), and the trait values measured after simulating coevolution in a set of empirical networks ($n = 34$; D). Each point corresponds to the result of simulations with $m = 0.7$, $\alpha = 0.2$, and $\varepsilon = 10$, averaged across 100 replicas that differed in θ_i, Z_i^0, and φ_i. Gray boxplots represent either fully mutualistic (*leftmost*) or fully antagonistic (*rightmost*) networks. Networks with both interaction types are depicted in blue and orange, according to the strategy used to convert mutualistic interactions to antagonistic interactions.

changes to coevolutionary dynamics were more drastic when specialist consumers were the first to be converted to antagonism (fig. 3).

First, we investigated why indirect effects were less influential in antagonism than in mutualism (fig. 3A). The contribution of indirect effects to coevolution depends on two factors: the structure of the networks and the trait distributions of communities (fig. 2). In our simulations we used the same set of networks across all fractions of antagonistic interactions. Thus, the changes to indirect effects cannot be due to changes in network structure. This leaves two potential explanations for the weakening of indirect effects.

As communities harbor more antagonistic interactions, there is either (1) a change in the relationship between network structure and indirect effects or (2) a change in the trait distribution of the communities.

Our first proposition is that indirect effects are weakened because of a change in how network structure shapes indirect effects. However, we found no evidence for this

(figs. 4, S5). The effect of each network descriptor on indirect effects was the same ($P > .01$) regardless of the fraction of antagonistic interactions in the network (fig. 4). Network size and nestedness increased the contributions of indirect effects, connectance decreased them, and modularity did not meaningfully affect indirect effects (fig. 4). For all networks analyzed, the effect of each network
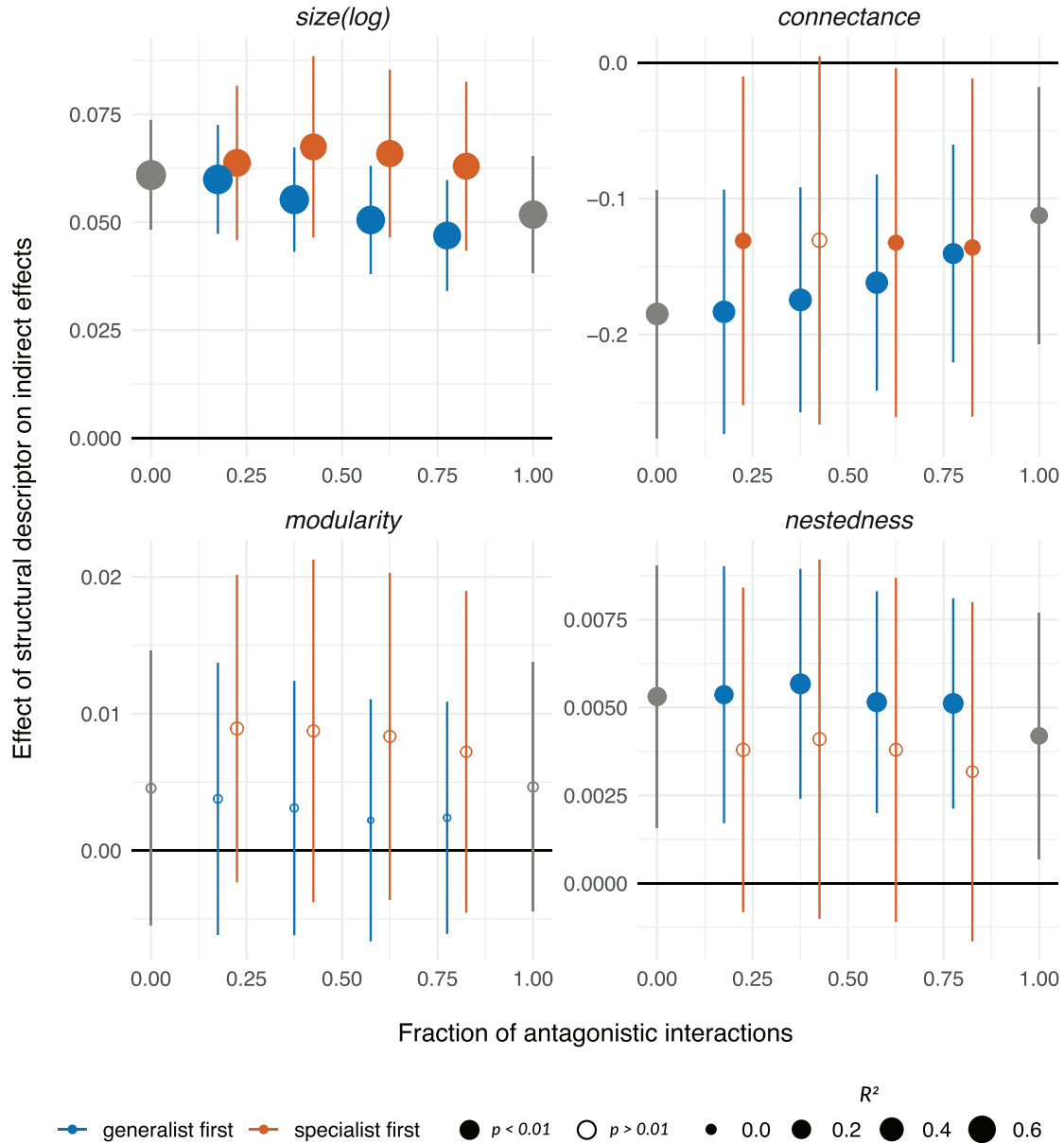

Figure 4: Effect of network structure across fractions of antagonistic interactions estimated from the slope of linear models. At a given fraction of antagonistic interactions, points represent the slope of the linear relationship between a particular structural descriptor and the network-level contribution of indirect effects (κ). Lines show the confidence intervals (95%) of the estimate. The size of the points indicates the model R^2, while filled and open circles correspond to significant ($P < .01$) and nonsignificant effects, respectively. Gray points and lines represent either fully mutualistic networks or fully antagonistic networks. Networks with both interaction types are depicted in blue and orange, according to the strategy used to convert mutualistic interactions to antagonistic interactions.

descriptor on indirect effects did not depend on the ratio of mutualistic interactions to antagonistic interactions (fig. 4), so we disregard our first proposition.

Our second proposition is that indirect effects are weakened because of a change in the trait distribution of communities. We observed that increasing the fraction of antagonistic interactions leads to a decrease in trait matching and weaker indirect effects (fig. 3*B*, 3*A*). On further inspection, we found a positive association between the trait matching arising in a network and the importance of indirect effects in driving coevolution (fig. 5 shows the correlation for one network, while fig. S2 shows the correlation across all networks). This relationship is nonlinear, with the largest increase in indirect effects occurring at low values of trait matching. These results support our second proposition; as communities become increasingly antagonistic, species' traits become more dissimilar, which leads to a weaker role of indirect effects in shaping coevolution.

We then investigated why indirect effects are less influential when the most specialist species are the antagonists (fig. 3*A*). Having shown that trait matching is associated with indirect effects, we conjectured that when specialist consumers became antagonistic first, this resulted in a community with more dissimilar traits compared with when generalist consumers became antagonistic first. We found this to be true; both consumers and resource species had greater variation in traits when specialist consumers became antagonistic compared with when generalist consumers did so (fig. S3, differences between strategies for a given guild).

Diving deeper, we explored how traits evolved inside a community when either specialist species or generalist species were antagonists. Figure 6 shows the trait matching of a single network with 20% antagonistic interactions under both scenarios (fig. S8 shows trends for all networks). As expected, we found that trait matching across the community was lowest when specialist consumers were the antagonists (fig. 6). This is due to how the antagonistic interactions were distributed inside the community. In the generalist first scenario, two consumer species became antagonistic. This resulted in all resource species receiving a single antagonistic interaction while maintaining the rest of their interactions as mutualistic. This allowed trait matching to remain high between mutualistic partners, especially in the case of generalist resources. Yet in the specialist first scenario, 10 consumer species became
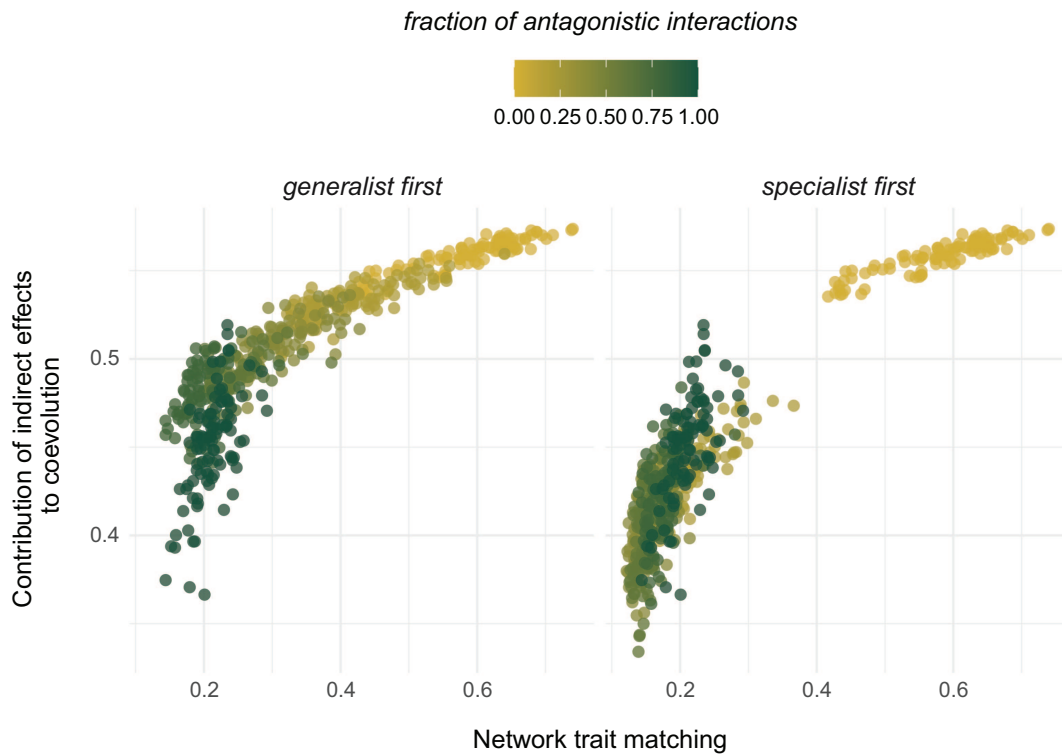

Figure 5: Relationship between the network-level trait matching (*M*) and contribution of indirect effects to coevolution (*κ*). The results shown are the outcome of simulating coevolution in a single network. Points represent different replicates, while the color of points indicates the fraction of antagonistic interactions in the network. Two strategies used to convert the network from mutualism to antagonism are shown.
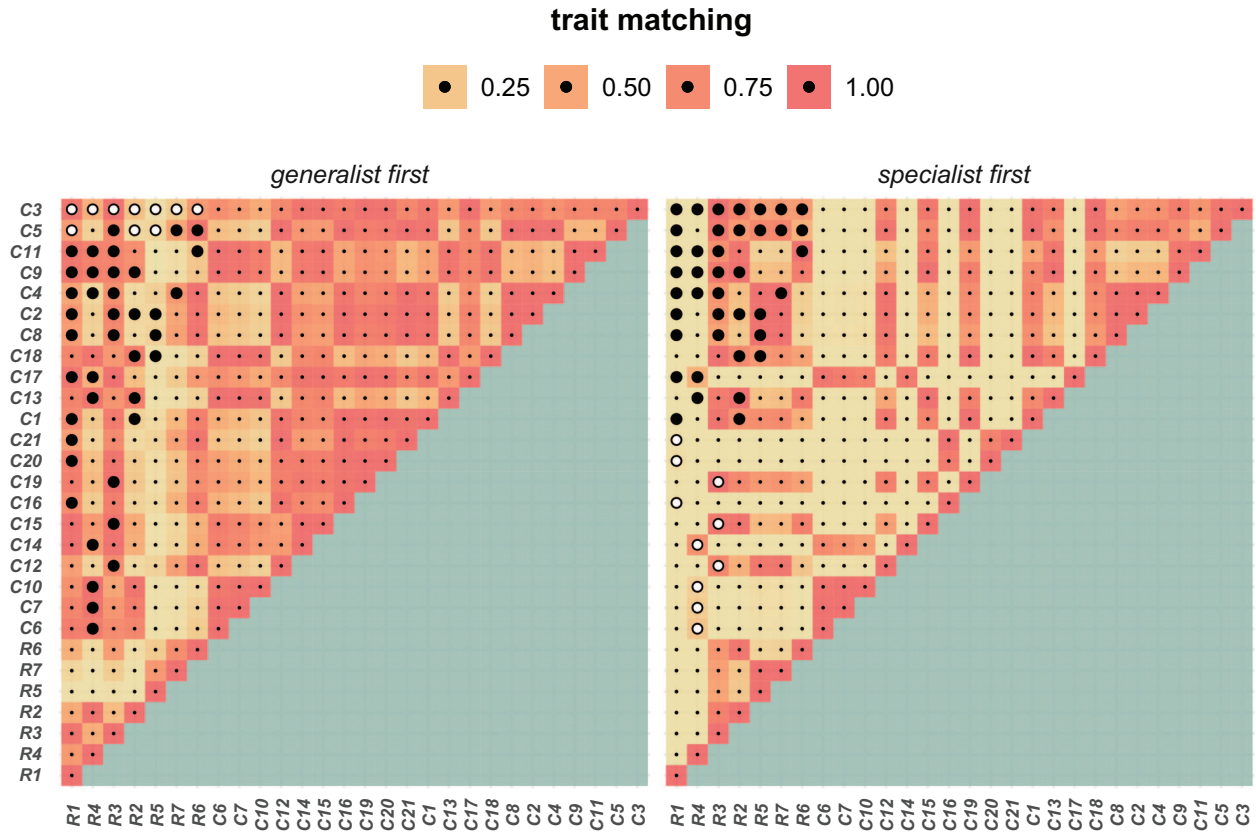
Figure 6: Trait matching between all pairs of species in a network (M_{ij}). The results shown are the outcome of simulating coevolution in a single network with 20% antagonistic interactions. Consumer and resource species are labeled C and R, respectively. The colors indicate the degree of trait matching (M_{ij}). Large black circles denote direct mutualistic interactions, white circles represent direct antagonistic interactions, and small black circles indicate indirect interactions. As the matrix is symmetric, only the upper triangle is shown. Two strategies used to convert the network from mutualism to antagonism are shown.

antagonistic. This resulted in the three most generalist resource species receiving all the antagonistic interactions. Because of the selective pressures of the antagonists, these generalist resource species became very dissimilar to all partners, including their mutualistic ones. In summary, the extent to which antagonistic interactions change coevolutionary dynamics depends on the identity of the antagonists.

Discussion

We highlight two main insights from our work on the coevolutionary consequences of communities harboring different interaction types. First, the contribution of indirect effects to trait evolution is greater in mutualism than in antagonism (fig. 3A). Second, the influence of indirect effects on coevolution is lowest when the specialist consumers are antagonists (fig. 3A).

Experimental studies, focusing primarily on small communities, have shown that indirect interactions result in

evolutionary changes of focal species, as shown in protozoans (terHorst 2010), plants (Lau 2012), and fishes (Walsh and Reznick 2010). At the scale of communities, indirect interactions may drive the coevolution of mutualistic communities (Guimarães et al. 2017). Incorporating antagonistic interactions, we show that mutualistic communities are shaped to a greater extent by indirect effects than antagonistic ones (fig. 3A). Thus, the importance of indirect effects depends on how species interactions affect trait evolution. Mutualistic coevolution leads to high trait similarity (fig. 3B), which is associated with a strong role of noninteracting partners (fig. 5). In turn, antagonistic coevolution leads to lower trait similarity (fig. 3B), which is associated with a weaker role of noninteracting partners (fig. 5).

Communities can harbor both mutualistic interactions and antagonistic interactions at the same time. The evolutionary effects of these contrasting interactions are expected to propagate across the community. For example, the indirect interactions between pollinators and seed

predators (Cariveau et al. 2004) or pollinators and nectar robbers (Irwin 2006) have been shown to alter the evolution of the plant species they visit. We show that the evolutionary implications of such indirect interactions are not restricted to a shared partner; rather, they affect the entire community. Strikingly, we find that the largest reduction in trait similarity in a community occurs when only 20% of the interactions in the network are antagonistic (fig. 3*B*). This suggests that only a few antagonistic interactions can substantially reshape the evolutionary trajectories of groups of mutualistic partners.

The identity of a species determines how it influences the evolution of its partners. In mutualistic communities, indirect effects have been shown to play a more prominent role in specialists than in generalists (Guimarães et al. 2017). This is due, in part, to the fact that species with few direct partners have many indirect partners. We show that regardless of interaction type, indirect effects are always highest for specialists (fig. S9). In addition, we find specialist species disproportionately shape the coevolution of communities. When embedded in a mutualistic community, specialist antagonists alter evolutionary dynamics more than generalist antagonists (figs. 3, 6, S8). Our results highlight the fact that the evolutionary dynamics of communities depend not only on the interaction type between species but also on the role that species play in the network.

It is important to keep in mind that the trait changes we observe are, to an extent, a result of how we assume interactions shape trait evolution. However, mutualism does not always lead to trait matching (e.g., exploitation barriers, as in the case of hawkmoths and the flowers they forage; Alexandersson and Johnson 2002), and neither does antagonism (Thompson 2005; Nuismer and Thompson 2006). It is thus crucial to test our predictions for systems where traits evolve in other ways. In this regard, using a model similar to the one described here, Andreazzi et al. (2020) showed that antagonistic and mutualistic communities experience stronger directional trait change under exploitation barriers than under trait matching. This could suggest that the trends described here may be more pronounced in communities where traits evolve under exploitation barriers. Yet future work must test this prediction. Moreover, our model considers the evolution of only a single quantitative trait. A further extension of this approach could explore the coevolutionary dynamics of communities when interactions drive the evolution of multiple traits (Assis et al. 2020). Last, we did not allow networks to be rewired as a result of interactions switching from mutualism to antagonism. Yet there is ample evidence of differences in network structure between interaction types (Pimm et al. 1991; Bascompte et al. 2003; Thébault and Fontaine 2010). Allowing the rewiring of networks as interaction types change (Kiers et al. 2010; Fontaine et al.

2011) could impact the role of indirect effects and the trait patterns resulting from coevolution. Nonetheless, despite its simplifications, our approach allowed us to begin exploring how a shift in the outcome of species interactions can alter the evolution of entire communities. Future empirical work should test our predictions, ideally in biological systems where mutualism and antagonism are common and where evolutionary dynamics are practically tractable. Microbial communities meet both criteria. First, interactions in such systems range from mutualistic to antagonistic, and their relative frequency oftentimes change across time (Coyte and Rakoff-Nahoum 2019; Drew et al. 2021). For example, interactions between *Escherichia coli* and bacteriophages can be induced experimentally to shift from parasitic to mutualistic and back (Bull et al. 1991; Shapiro and Turner 2018). Second, the coevolutionary dynamics of such systems can be measured with a mix of experimental analyses and genomic approaches (Hall et al. 2020). Experimental work could aim to determine the extent to which the coevolutionary dynamics of microbial communities shift as the relative frequency of mutualistic and antagonistic interactions changes.

We know that interactions shift between mutualism and antagonism (Thompson 1988; Bronstein 1994; Chamberlain et al. 2014). Yet we still do not fully understand when, where, and why these shifts happen (Frederickson 2017). While theoretical (Song et al. 2020; Hale and Valdovinos 2021; Gómez et al. 2023) and experimental (Maestre et al. 2005) work has explored these questions, we are unequipped to predict the likelihood of interactions shifting in a community. To explore the coevolutionary implications of such shifts, we decided to explore a wide range of scenarios—different fractions of interactions shifting and different species shifting. However, these scenarios are very general and need further refinements. For example, we would benefit from knowing the extent to which communities can harbor mutualistic and antagonistic interactions and how this depends on the type of community. Moreover, we should explore other factors that affect a species' likelihood of changing their interactions, such as the nature of the associations (facultative/obligate or symbiotic/free living). Last, we require a more nuanced understanding of the extent to which changes to the outcome of species interactions at the ecological scale affect evolutionary processes. Further empirical and theoretical work addressing these points will fine-tune our insights into the possible coevolutionary outcomes of communities harboring different interaction types.

Conclusion

While indirect effects drive coevolution in mutualisms (Guimarães et al. 2017), we show that they have a weaker

role in antagonisms. In other words, as communities harbor more antagonists, selection imposed by direct partners outweighs that of indirect partners. This hinders the emergence of community-wide trait convergence and accelerates the pace of coevolution. We show that the coevolutionary dynamics of mutualistic communities are modified most drastically when only a few interactions become antagonistic. Furthermore, the effects of these conversions could be amplified if the specialist consumers are the antagonists. Our results are particularly timely, as anthropogenic drivers, such as climate change, habitat transformation, and invasive species, have already been shown to cause transitions from mutualistic to antagonistic interactions (Sachs and Simms 2006; Kiers et al. 2010; Weese et al. 2015; Chomicki and Renner 2017; Sawaya et al. 2018). Thus, conditions that alter the outcome of species interactions may modify the direction and speed of coevolution of entire communities.

Acknowledgments

Statement of Authorship

F.P., H.L., K.A.G., and J.B. designed the research. F.P. and H.L. performed the research. F.P. and K.A.G. analyzed the data. F.P. wrote the first draft of the manuscript, and all authors contributed substantially to the final version.

Data and Code Availability

Data and code for this work are available on Zenodo (https://zenodo.org/record/8131615; Pedraza et al. 2023).

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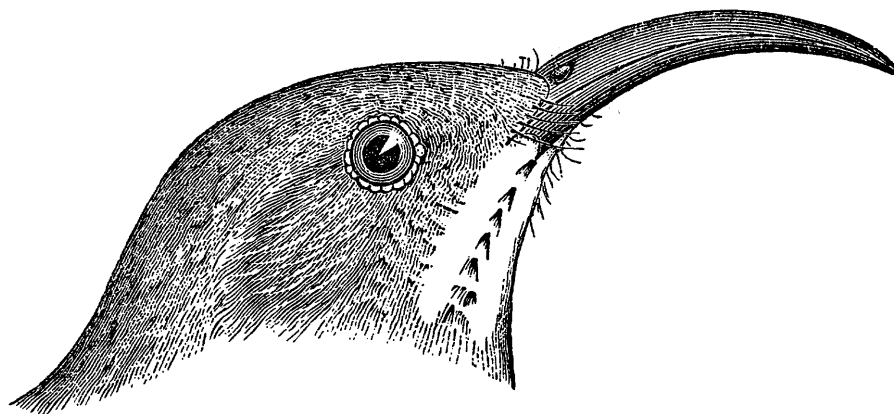
"Next comes the Red-vented, or Crissal Thrush (*H. crissalis*); also inhabiting the Colorado and Gila valleys. It is fully as large as *redivivus* or var. *Lecontei*, with the tail even longer, and the bill, if not larger, at least slenderer and more arcuate, as shown." From "Some United States Birds, New to Science, and Other Things Ornithological" by Elliott Coues (*The American Naturalist*, 1873, 7:321–331).