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**Cheating interactions favor modularity in mutualistic networks**

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**Abstract**

A fundamental fact about mutualisms is that these mutually beneficial interactions often harbor cheaters that benefit from the use of resources and services without providing any positive feedback to other species. The role of cheaters in the evolutionary dynamics of mutualisms has long been recognized, yet their broader impacts at the community level, beyond species they directly interact with, is still poorly understood. Because mutualisms form networks often involving dozens of species, indirect effects generated by cheaters may cascade through the whole community, reshaping trait evolution. Here, we study how harboring cheating interactions can influence coevolution in mutualistic networks. For that, we combined a coevolutionary model, empirical data on animal-plant mutualistic networks, and numerical simulations. We show that high trait disparity emerges as a consequence of the negative effect of cheaters on victim fitness, which in turn fueling selection favoring victim traits that are increasingly different from cheaters traits. Intermediate levels of cheating interactions in a network can lead to the formation of groups of species phenotypically similar to each other and distinct from species in other groups, generating clustered trait patterns. The resulting clustered trait pattern, in turn, changes the pattern of interaction in simulated networks, fostering the formation of modules of interacting species and reducing nestedness. Our results indicate that directional selection imposed by cheaters on their victims counteracts selection for trait convergence imposed by mutualists, leading to the emergence of modules of phenotypically similar interacting species. Based on these results, we suggest that cheaters might be a fundamental missing element for our understanding of how multispecies selection shapes the trait distribution and structure of mutualistic networks.

**Keywords:** Coevolution, Ecological network, Modularity, Mutualism, Network structure

**Introduction**

Selection imposed by ecological interactions is one of the main forces impacting phenotypic patterns observed across levels of biological organization (Thompson 2005). Selection imposed by ecological interactions partially shapes trait matching among interacting individuals (Zhang *et al.* 2012), trait distributions within interacting populations (Bronstein *et al.* 2003), trait variation across populations of the same species (Thompson 2005), and trait patterns at the community level (Strauss & Irwin 2004). At the community level, ecological interactions can be a driving force of selection leading to trait convergence (Wilson *et al.* 2012) and trait disparity (Siepielski & Benkman 2010). In this sense, theoretical and empirical results indicate that distinct ecological interactions (e.g., mutualistic, antagonistic) may favor different trait outcomes due to coevolution, *i.e.*, the reciprocal evolutionary change between interacting species (Thompson 1994, Yoder & Nuismer 2010, Wechsler & Bascompte 2021).

Mutualistic interactions, for example, can favor trait matching, which is the trait similarity between interacting species, *e.g.,* the size of the proboscis of a pollinator matching the depth of the flower it pollinates. Although mutualisms may also generate other trait patterns, such as intensification of traits (Anderson & Johnson 2008), trait matching is an observed pattern in a variety of mutualistic systems, such as pollination by flies and bees (Santamaria & Rodríguez-Gironés 2007, Zhang *et al.* 2012), seed dispersal by birds and bats (Mello *et al.* 2011, Galetti *et al.* 2013), and Müllerian rings in velvet ants (Wilson *et al.* 2012). Hence, trait matching is an expected outcome of reciprocal selection that could favor higher interaction efficiency in mutualisms (Thompson 1994, Zhang *et al.* 2012). In contrast, antagonistic interactions, such as among parasites and their hosts, favor trait matching from the parasite perspective, while favoring trait mismatching from the host perspective (but see Anderson 2005, Anderson and Johnson 2008). In fact, antagonisms may lead to coevolutionary dynamics such as alternation and escalation (Nuismer *et al.* 1999), which can result in the maintenance or the increase in trait variation across and within species (Andreazzi *et al.* 2017).

Antagonisms and mutualisms are not isolated in nature but coexist in many ways. Studies have explored the effects of combining mutualisms and antagonisms on population dynamics (e.g., Melián *et al.* 2009), community stability (e.g., Wilson *et al.* 2003), and network structure (e.g., Genini *et al.* 2010). These studies highlight the importance of considering multiple outcomes that interactions may have in a community and the extremes of a gradient between mutualism and antagonism (Fontaine *et al.* 2011, Rodríguez-Rodríguez *et al.* 2017). In some situations, individuals of the same species can be antagonistic or mutualistic partners of the same interacting species, e.g., seed-caching rodents can be either seed predators, or seed dispersers of the same plant species (Loayza *et al.* 2014). In other situations, individuals may act as antagonists of some species and as mutualists of others (Gómez *et al.* 2014, Montesinos-Navarro *et al.* 2017, Gómez *et al.* 2018). Finally, there are species in which individuals are specialized cheaters, exploiting mutualistic interactions without providing any benefit in return like some fig wasps (Bronstein 2001). Thus, selection may favor the evolution of life histories that exploit the resources and services provided by mutualistic partners without providing any benefits, converting mutualistic into cheating interactions (Bronstein 2001, Vieira *et al.* 2003).

We are beginning to understand how cheating interactions may affect evolutionary dynamics in mutualisms, as species playing a cheater or mutualist role may result in different coevolutionary outcomes with distinct local adaptations. For example, the interaction between the plant *Lithophragma parviflorum* (Saxifragaceae) and the floral-parasitic moth *Greya politella* changes from parasitism to mutualism if the legitimate pollinators of *L. parviflorum* are absent in the community, with coevolutionary consequences to the species (Thompson & Cunningham 2002). By exploring the role of cheaters in three-species systems we progressed in our understanding on how cheaters fuel novel evolutionary dynamics (Anderson 2005). A next step in the understanding of the importance of cheaters in mutualisms is to explore what are the evolutionary roles that cheaters play in species-rich communities. In species-rich communities, networks generate pathways connecting species that do not interact directly with each other, allowing evolutionary cascades to affect how species traits evolve (Guimarães *et al.* 2017). Yet, the impact of the cheating interactions at the community level, beyond their impact on the species they directly interact with is still poorly understood. Here, we use a single trait coevolutionary model, empirical ecological networks of species interactions, and numerical simulations to investigate how cheating interactions may affect coevolution in mutualistic networks. Specifically, we explore two main questions: *i)* How does the frequency of cheating interactions affect coevolutionary dynamics? Due to the arms race dynamics favored by directional antagonistic selection, we expect a higher trait mismatch in scenarios with elevated frequencies of cheating interactions. *ii)* What is the effect of cheating interactions on the structure of mutualistic networks? By assuming that cheating interactions may favor arms race dynamics, we expect higher trait disparity fueled by the presence of cheaters. This increase in trait disparity, in turn, may disrupt both mutualistic and antagonistic interactions, leading to the loss of interactions due to phenotypic mismatch. Thus, we expect that higher frequencies of cheating interactions will generate higher arms race dynamics and consequently, higher frequency of interaction loss, generating networks with higher modularity (Figure 1b).

**Methods**

*Evolutionary model*

Our discrete-time, evolutionary model describes how the average trait of a species *i*, *Zi*, evolves due to reciprocal selection imposed by ecological interactions and other environmental factors (e.g., abiotic conditions). In our model, the selection differential, *S*, and the additive genetic variance of the trait governs trait change across generations (Lande 1976). Here, the model states that the species abundances are in equilibrium, having no ecological feedback in trait evolution. Having said that, we show that variation in the abundances across species in a network does not qualitatively change the results we reported here (see Supporting Information). We assumed *S* has three components potentially affecting the evolution of the trait Zi: the selection imposed by (i) mutualisms, (ii) cheating interactions, and (iii) an environmental factor. As a first approximation, we assume that, for a given interaction, species are either mutualistic partners or cheaters, but the same species *i* may behave as a cheater for species *j* but as a mutualistic partner to species *k*.

The mutualism component, is defined as the sum of selective effects caused by all mutualistic partners of species *i*. We assume that selection imposed by mutualism favors trait matching among mutualistic partners. We also assume that perfect trait matching between species *i* and *j* occurs if |*Zj-Zi*| = 0 (Guimarães *et al.* 2011). A given species may have multiple mutualistic partners and each partner may contribute differently to selection, where the contribution of partner *j* to selection on species *i* is described by *mij.* The total contribution of mutualistic interactions to selection on *Zi* at time *t* is defined as:

, (1)

where N is the total number of species in the community, is an element of the adjacency matrix **A**, is contribution of partner *j* to selection on species *i* at time *t*, and is the mean trait of species *i* at time *t*.

In the cheating component , selection favors trait matching for the cheater species *j* (as in equation 1) but favors trait mismatch for the victim species *i,* defined asthe species exploited by the cheater. The contribution of a cheater *j* for the selection on species *i*, , affects trait evolution. Selection for trait mismatching of cheater *j* on victim *i* is given by*:*

, (2)

where represents a trait barrier (e.g., Santamaria & Rodríguez-Gironés 2007), preventing the antagonistic effects of the interaction to impose selective pressures on the victim. To do so, we assume that if the trait difference between *i* and *j* is higher than or equal to , |*Zj(t)-Zi(t)*| , then *δij*=0, and the cheater species imposes no selection on the victim. However, if |*Zj(t)-Zi(t)*|< , then δij=1 and selection on victim *i* will favor the increase or decrease of trait values depending on *Zj(t)-Zi(t)*. If *Zj(t)-Zi(t)* is positive, the sign of will be negative. Contrarily, if *Zj(t)-Zi(t)* is negative, the sign of will be positive (Andreazzi *et al.* 2017). The equations describing the relations between species trait differences and are in the Supporting Information, S4 and S5. Importantly, if , species *j* is a mutualistic partner of species *i*, whereas if , species *j* is a cheater and species *i* is its victim. Finally, we assumed that the environmental component is the combined effects of all other selective pressures, which favor an optimum environmental trait value for each species, *θi*:

. (3)

Combining the three selection components described above (equations 1, 2, and 3), the evolutionary change of Zi from time *t* to *t+1* is given by:

, (4)

in which *φi* () is a compound parameter formed by additive genetic variance and the slope of the adaptive landscape (Guimarães *et al.* 2017). The parameter *()* dictates the importance of ecological interactions versus environmental factors as selective pressures. Both and assume a single value in our simulations (Table 1, but sensitivity analysis show that these parameters do not qualitatively affect the overall patterns reported here).

Trait evolution, in our model, is defined as:

. (5)

The evolutionary effects *mij(t)*and *vij(t)* that affect the magnitude of trait change due to the mutualistic and cheating interactions, respectively, are defined as the relative effect of species *j* on *i*, such that *mij(t)*= and *vij(t)*= . The term = 1 if = 1 (i.e., species *j* is a mutualistic partner of species *i*) and 0 otherwise, whereas the term = 1 if = -1 (i.e., species *j* is a cheater and species *i* is its victim) and 0 otherwise. The term *qij(t)* is defined as:

, (6)

where the parameter controls the sensitivity of the evolutionary effect due to trait matching between species *i* and *j* and |*aik|*=1 if there is a mutualistic or a cheating interaction between *i* and *k* and |*aik* |= 0, otherwise. The values and the description of the model parameters are depicted in Table 1. The numerator of equation 6 is the evolutionary effect between species *i* and *j* considering the trait difference between them, whereas the denominator is the sum of evolutionary effects of all species that interact with species *i*. Thus, is the normalized evolutionary effect between *i* and *j* due to the trait difference between these species. The sensitivity analysis of the model parameters can be found in the Supporting Information.

*Mutualistic networks*

We use 24 empirical mutualistic networks available at the databases Web of Life (<http://www.web-of-life.es/>) and Interaction Web Database (<http://ecologia.ib.usp.br/iwdb/index.html>). These 24 networks include eight plant-pollinator networks, eight plant-frugivore networks, and eight ant-myrmecophyte networks. Each network is represented by an adjacency matrix (**A**) in which each species is represented by a single row and a single column of the matrix; each element of this matrix represents the presence () or absence () of the corresponding animal-plant interaction. Ant-myrmecophyte networks are commonly less connected, more modular, and less nested in comparison to seed dispersal and pollination networks, while seed dispersal networks are usually more nested and have a higher connectance than pollination and ant-myrmecophyte networks (Supporting Information). We used these 24 networks to parametrize the network structure in our simulations. Specifically, if there is a interaction between two species in the network, then in our simulations the , , or , and zero is otherwise. Thus, knowing which species are empirically interacting, we can simulate the coevolutionary process between these species. We emphasize that we did not have information if the recorded interactions are cheating interactions and therefore, we only used the empirical information to parameterize the structure of the mutualistic networks (see next section).

*Simulations*

Our simulations describe how the mean trait *Zi* evolves in time (Figure 1a). Each simulation ends after 1000 timesteps, which is enough time to generate asymptotic trait values. In most simulations, however, the equilibrium was reached before 1000 timesteps. The simulation stops when the condition of equilibrium, |Zi(t+1) - Zi(t)|<10-4, is achieved for every species *i* in the network. We run 72.000 simulations, 3.000 per empirical network, where each simulation tracks how species traits change in time due to coevolution and the selective pressures from the environment (Figure 1a). All the simulations were performed in R v. 3.5.3 (R Core Team 2018). In what follows, we explain how we used this modeling approach to explore our two questions. All the simulation results are available at Zenodo under open access license.

*i) How does the frequency of cheating interactions affect coevolutionary dynamics?*

We ran simulations with different frequencies of cheating interactions for each mutualistic network to evaluate the impact of cheaters on the coevolutionary process. In each simulation, we defined a probability *p* for an interaction within a “mutualistic network” changing from mutualistic to cheating interaction. We explored values of *p* ranging from 0.01 to 1 to test how different frequencies of cheating interactions affect trait evolution and, in turn, network structure. We assumed that cheating interactions are randomly distributed across all interactions in the mutualism network and that the frequency of cheating interactions in the network is fixed in each simulation. This process of defining the outcome of interactions based on *p* generates a network with both positive and negative effects (i.e., = 1 or = -1), merging the effect of mutualism and cheaters in a single network (Melián *et al.* 2009). Because we are defining a cheating interaction as interactions with a negative effect on one partner and positive effect on the other one (i.e., an antagonism), we prohibit the occurrence of double-negative effects between two species. For this purpose, we only applied the transformation from positive to negative effect based on *p* in the lower triangle of the adjacency matrix, therefore maintaining cheating interactions as a combination of positive and negative effects. We also assumed that the outcome of the interaction does not change over time. Although such an approach does not allow us to explore the effects of conditional outcomes of many interactions, it is a starting point to unravel how cheating interactions change the outcome of coevolution in mutualisms. We performed a set of sensitivity analyses where we relaxed this assumption by allowing interactions to shift from positive and negative outcomes during simulations (Supporting Information, Interaction Shifts). These analyses suggest that temporal variability on the interaction outcome does not influence our main results.

We characterized the outcome of coevolutionary dynamics by describing patterns in trait distributions across species. We first measured the average trait distance between pairs of species as a proxy for trait disparity in the network. We computed the mean pairwise distance (*D*) as the sum of the Euclidean distances of species traits of all possible pairwise combinations between all species divided by the total number of pairwise combinations (Ciampaglio *et al.* 2001):

. (7)

Because antagonisms are expected to generate trait mismatching in networks (Andreazzi *et al.* 2017), whereas mutualisms are expected to generate trait matching (Guimarães *et al.* 2017), we perform an analysis to detect the number of trait clusters (i.e., groups of species with similar traits) and we measure how species traits are becoming different due to cheating or similar due to mutualisms. In this way, we can measure trait disparity (*D*) and the number of trait clusters in a single network. To compute the number of trait clusters among interacting species, we used Ward's hierarchical clustering analysis (Ward 1963) along with the GAP validation index (following Tibshirani *et al.* 2001). Both algorithms organize trait values and create clusters which minimize the intra-cluster variation, generating clusters of species with high trait matching. Finally, we explored if the distribution of cheating interactions across species in the network affects the coevolutionary outcome. We performed a sensitivity analysis in which we compared the results of our baseline simulations, in which cheating interactions are randomly distributed across species with simulations in which highly connected, central species harbor most of the cheating interactions (Supporting Information). The results of these analyses led to similar results, suggesting no strong effect of the distribution of cheating interactions across species in shaping the network-level patterns of trait distributions (Supporting Information).

*ii) What is the effect of cheating interactions on the structure of mutualistic networks?*

In our baseline coevolutionary model, the trait barrier indicates whether the evolutionary effects of a cheater species on a victim becomes negligible. To explore the effect of cheating interactions on the network structure, we changed our baseline coevolutionary model to add an additional trait barrier, *bij*, defining the maximum absolute trait mismatch between two species traits so they can interact:

. (8)

Note that from equation 2 represents a trait barrier that dictates if there is a selection on a victim by a cheater species. In contrast, *bij* describes that a potential mutualism or cheating interaction cannot occur because of a large trait dissimilarity between partners. By incorporating *bij* in our model we explored how network structure changes through time as an outcome of the coevolutionary process. With this approach, at each time *t* in our simulations, we verified if there were interacting species with differences in trait values higher than *bij*. Following equation 8, we disconnected those interactions generating an interaction loss. Because we focus on how the network changes due to interaction loss, once the interaction is lost, it remains lost and cannot reconnect during the simulations. Thus, at the end of a simulation, we may have an interaction network with a different structure generated through the removal of links. We then compared the initial and final network structure in each simulation. We performed a sensitivity analysis allowing the reconnection of interactions that led to qualitatively similar results (Supporting Information).

We characterized the structure of the networks calculating two common measures of network structure: nestedness and modularity (Almeida-Neto *et al.* 2008, Blondel *et al.* 2008). For each simulation, we computed the number of interactions loss, here called *F*. These interactions are lost due to the simulated coevolutionary dynamics. We computed measures based on nestedness and modularity describing structural change between the final and initial network for each simulation. We used two measures of network structure change: **Δ**NODF and **Δ**Q. For each network, these measures were calculated as the difference between the network nestedness (NODF, Almeida-Neto *et al.* 2008) and modularity (Q, Blondel *et al.* 2008) at the end and at the beginning of the simulations:

(9)

Coevolutionary dynamics, in our model, therefore, may reduce the total number of interactions, favoring specialization. We then explored if the removal of interactions by coevolutionary dynamics deviates from random removal of interactions from the initial network. To do so, for each simulation, we created a third network generated by randomly removing *F* interactions from the initial network. This network, therefore, has the same number of interactions as the coevolved network but the set of interactions removed was randomly defined. We then compared how network structure changes with random loss of interactions and loss of interactions due to trait dissimilarity from the coevolutionary dynamics.

**Results**

*i) How does the frequency of cheating interactions affect coevolutionary dynamics?*

We find that the higher the proportion of cheating interactions, the higher the trait disparity observed across animal and plant species in the networks (Figure 2a-c). This effect of cheating interactions is similar for the three types of networks studied here (Table 2). Thus, cheating interactions increase trait disparity across species (Figure 2), and this effect did not change among networks of different types of mutualism.

We observed that the frequency of cheating interactions affects the number of species trait clusters. At low levels of cheating interactions (*p* = 0.01, with *p* being the frequency of cheating interactions in the networks), we found a low number of clusters (2.430.62, Figure 2d-f). At intermediate levels of cheating interactions, the number of trait clusters increased (*p* = 0.5, 3.030.79). Finally, if most of the networks formed by cheating interactions then, on average, we saw the formation of lower numbers of species trait clusters, similar to when there was low frequency of cheating interactions (2.690.74, *p* = 0.9, Figure 2d-f). Thus, increasing the frequency of cheating interactions fuels trait disparity in mutualistic networks by promoting the emergence of trait clusters. However, the number of trait clusters decreases with higher frequencies of cheating interactions.

*ii) What is the effect of cheating interactions on the structure of mutualistic networks?*

We found that when assuming *p* = 0 (no cheating interactions), coevolutionary dynamics led to almost no change in the structure of the network [**Δ**Q ≅ 0; **Δ**NODF ≅ 0]. In contrast, as we increase the frequency of cheating interactions, mutualistic networks become more modular and less nested (Figure 3; Table 3). This increasing modularity and reduced nestedness observed was not reproduced by randomly removing interactions (colored versus black points in Figure 3). Moreover, the increase in modularity and reduction in nestedness was not equally distributed across mutualisms. In mutualisms where the empirical network was initially very modular and not nested (e.g., ant-myrmecophyte networks) changes in network structure were weaker than in mutualisms that initially showed higher nestedness (e.g., pollination and seed dispersal). Hence, in mutualistic networks containing a high frequency of cheating interactions, coevolution can enhance modularity and decrease nestedness (Table 3). Having said that, for networks composed by almost only cheaters, the levels of modularity show a small decayment (Figure 3). Sensitivity analysis taking into account the species abundance does not change qualitatively our results from the higher trait disparity and higher modularity with decreased nestedness from simulated networks (Supporting Information).

**Discussion**

In this study, we explored the coevolutionary outcomes of cheating interactions in mutualistic networks. Our results show how trait evolution and network structure can change due to cheating lifestyles that emerge in mutualistic systems. Previous studies have already explored the effect of mutualistic and cheating interactions on population dynamics (Law *et al.* 2001, Bronstein *et al.* 2003, Wilson *et al.* 2003, Lee 2015) and phenotypic evolution (Ferriere *et al.* 2002). In this context, our work contributes to further our understanding of the coevolutionary dynamics of multispecies assemblages in three different ways.

First, we showed that cheating interactions promote higher community-level trait disparity in mutualistic networks. By imposing selection favoring trait mismatching, the presence of cheating interactions leads to an increase in species trait disparity in mutualistic assemblages. The arms race dynamics promoted by cheaters partially offsets selection favoring convergence and trait matching in mutualisms (Guimarães *et al.* 2011, Zhang *et al.* 2012). Therefore, cheating interactions may provide one of the mechanisms preventing the emergence of perfect trait matching in empirical mutualistic communities (Law *et al.* 2001). Yet, trait disparity cannot increase indefinitely due to factors related to the environmental pressures and distinct selection regimes (Andreazzi *et al.* 2017). For instance, limited genetic variation or limited anatomical and physiological mechanisms restricts fruit sugar content and flower size (Jordano 1995), which could limit the potential for trait change in time and consequently restrict trait matching. In addition, annual variation in soil nutrients limit the pulp composition of fleshy fruits and, consequently, represents a restriction for the development of sugar-rich fruits that are highly attractive to frugivores (Herrera 1998), limiting trait matching in plant-frugivore systems. Finally, the way species are organized in mutualistic networks change the resulting trait matching or trait disparity of species. However, we explored the effects of cheater species centrality on trait coevolution and did not find a clear effect on either trait matching or disparity of species (Supporting Information).

Second, cheating interactions promote, under intermediate frequencies, an increase in the number of trait clusters in mutualistic networks. Under intermediate frequencies of cheating interactions, the joint effect of mutualistic selection favoring trait matching and cheating interactions favoring trait mismatching creates clusters of species traits. There is evidence that the proportion of positive and negative effects between species is similar in empirical communities (Dodds 1997). Applying these empirical proportions to our results, i.e., communities having the same proportion of mutualistic and cheating interactions, our results predict high trait disparity due to the formation of trait clusters. This prediction can be tested by measuring the level of trait disparity and the frequency of cheating interactions across different interacting assemblages.

However, it is noteworthy that the presence of cheaters may be underestimated in empirical networks (Genini *et al.* 2010), partially because there is great behavioral plasticity among interacting individuals (Bronstein 2001). Thus, intraspecific variation generating behavioral plasticity may play an important role in individual fitness and lead to occasional cheating.

Third, the presence of cheating interactions in mutualistic networks may lead to the reorganization of network patterns due to the increased trait dissimilarity. We found that cheating leads to increased modularity and reduced nestedness in mutualistic networks. The emergence of modularity was also observed as an outcome of coevolutionary dynamics in antagonistic networks depending on the selection intensity between victim and exploiter species (Andreazzi *et al.* 2017). Our results propose an alternative path to the emergence of modularity in mutualistic networks, which depends on how much cheating interactions the mutualistic network supports. The structure of interaction networks can be explained by several factors, such as species abundance distribution (Dátillo *et al.* 2014), differences in species richness between species sets (Guimarães *et al.* 2007), match and mismatch between traits of plants and animals (Stang *et al.* 2007), phylogenetic and phenology-based constraints (Jordano 1995, Jordano *et al.* 2003), and more recently, ecological niche adaptation (Cai *et al.* 2020). Here we show that cheating interactions could also change the structure of mutualistic networks through the coevolutionary process. Cai and collaborators (2020) showed that, in mutualistic networks showing simultaneously modularity and nestedness, both structures can change the robustness of the network when facing either invasion or extinction. Future studies could test the influence of cheating interactions in network robustness due to the re-organization of modularity and nestedness.

Our results suggest that the incorporation of the selection imposed by cheating interactions that naturally emerge from mutualisms is pivotal to a deep understanding of the coevolutionary dynamics in species-rich mutualisms. Cheating interactions change the outcomes of mutualistic coevolution, leading to increased interspecific trait variation and clustering. We provided insights on the effect of multiple interaction types in a network and how it may shape trait diversity by the contrasting selective forces favoring convergence and disparity across interacting species (Sauve *et al.* 2016). The structure of simulated networks significantly changed when we increased the frequency of cheating interactions, and this result opens new questions on which is the balance of positive and negative effects that maintains the structure of empirical networks. There is theoretical evidence showing that nestedness could, in part, increase network robustness to species extinction and invasions (Lever *et al.* 2014) but also modularity can moderately increase network stability (Stouffer & Bascompte 2011, Grilli *et al.* 2016). Also, theoretical and empirical evidence shows that the identity and type of interaction changes over time, consequently changing the robustness of the network (Montesinos-Navarro *et al.* 2017, Ponisio *et al.* 2017, Baruah 2022). If so, different interaction types or the initial loss of nestedness with higher frequencies of cheaters that we highlight could impact the robustness of communities, impacting ecosystem functioning and services. Here, we contribute to understanding which factors and how the network structure could change. Our theoretical predictions may also help us to understand how networks might evolve under a rapidly changing world, creating modularity and nestedness depending on, for instance, historical factors (Dalsgaard *et al.* 2013). Interactions are changing due to several anthropogenic impacts with unknown consequences for ecosystem functioning and species evolution.

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**Table 1.** Variables and parameters of the model and their baseline values.

|  |  |  |
| --- | --- | --- |
| **Parameter** | **Description** | **Baseline values** |
| *Zi(t)* | Initial mean trait value of specie *i* | (0 ≤ Zi(t) ≤ 10) |
|  | Parameter composed of the additive genetic variance and phenotypic variance of *Z* | 0.2 [0, 1] |
|  | Trait barrier to happen the cheating interaction between species *i* and *j* | 5 |
|  | Strength of abiotic selection for trait change of species *i* | 0.1 [0, 1] |
| *θi* | Zi optimum value for the environmental selection | (0 ≤θi ≤ 10) |
|  | Sensibility of evolutionary effect due to the trait matching between interacting species | 0.2 |
| *p* | Probability of a positive effect become negative in a mutualistic network | 0.01 ≤ *p* ≤ 1 |
| *b* | Trait barrier for any interaction happen between species in the network | 7 |

**Table 2.** Average ± SD values of D and statistical fit of a linear model between D and frequency of cheating interactions in the networks for three types of mutualisms.

|  |  |  |  |
| --- | --- | --- | --- |
| **Mutualisms** | **Average D ± SD** | **Slope** | **R2** |
| **Ant-Myrmecophyte (n = 8)** | 12.94 ± 6.68 | 19.12 | 0.68 |
| **Pollination (n = 8)** | 10.86 ± 6.37 | 18.89 | 0.73 |
| **Seed dispersal (n = 8)** | 9.82 ± 6.66 | 19.39 | 0.70 |

**Table 3.** Average ± SD **Δ**Q and **Δ**NODF for random interaction removal and trait barrier interaction removal for three types of mutualisms

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | **ΔQ ± SD** | | **ΔNODF ± SD** | |
| **Mutualisms** | **Random** | **Simulations** | **Random** | **Simulations** |
| **Ant-Myrmecophyte (n = 8)** | 0.007 ± 0.035 | 0.037 ± 0.056 | -1.65 ± 2.52 | -2.96 ± 3.39 |
| **Pollination (n = 8)** | 0.058 ± 0.072 | 0.14 ± 0.12 | -14.9 ± 13.5 | -19.4 ± 15.4 |
| **Seed dispersal (n = 8)** | 0.095 ± 0.081 | 0.18 ± 0.14 | -23.06 ± 17.02 | -26.3 ± 19.0 |