

Consumers' active choice behaviour promotes coevolutionary units in antagonistic networks

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Abstract

Individual behaviour and local context can influence the evolution of ecological interactions and how they structure into networks. In trophic interactions, consumers can increase their fitness by actively choosing resources that they are more likely to explore successfully. Mathematical modelling is often employed in theoretical studies to understand the coevolutionary dynamics between consumers and resources. However, they often disregard the individual consumer behaviour since the complexity of these systems usually requires simplifying assumptions about interaction details. Using an individual-based model, we model a community of several species that interact antagonistically. Each individual has a trait (attack or defence) that is explicitly modelled and the probability of the interaction to occur successfully increases with increased trait-matching. In addition, consumers can actively choose resources that guarantee greater fitness. We show that active consumer choice can generate coevolutionary units over time. It means that the traits of both consumers and resources converge into multiple groups with similar traits and the species interactions stay restricted to these groups over time. We also observed that network structure is more dependent on the parameter that delimits active consumer choice than on the intensity of selective pressure. Thus, our results support the idea that consumer active choice behaviour plays an important role in the ecological and evolutionary processes that structure interacting communities.

KEYWORDS

antagonism, coevolution, interaction network, modularity, resource selection, specialization

1 | INTRODUCTION

Ecological interactions build the architecture of biodiversity in biological communities (Bascompte, 2009). In trophic interactions such as parasitism, parasitoidism, predation or herbivory, individuals of one trophic level (consumers) exploit individuals of the trophic level below, as food resources. Consequently, these interactions result in increased consumer fitness at the expense of resource fitness. A foraging consumer will generally encounter different kinds

of resources, and they can decide which one to choose according to some 'currency' of biological fitness (e.g. rate of net energy intake, handling time, predator avoidance; MacArthur & Pianka, 1966; Pyke & Choe, 2019). This decision-making process known as 'active choice' leads the consumers to use some resources more often than others, given an encounter with each type of resource (Sih & Christensen, 2001), e.g. birds that typically eat molluscs of particular sizes or species (Nagarajan et al., 2015); nest parasites that use the host's nests whose eggs are similar to their own (Avilés et al., 2006;

Soler et al., 2014; Stevens et al., 2013); insects that differ in their oviposition patterns based on plant defence traits (Jaenike, 1978; Jorge et al., 2014; Mayhew, 2001; Scheirs et al., 2000); prey choice by hematophagous insects (Lyimo & Ferguson, 2009) or parasitoid insects that choose their prey through chemical signals (Vet & Dicke, 1992).

Little is known about the evolutionary effects of the active choice on the dynamics and composition of ecological communities (Abrams, 2019). Theoretical studies on active consumer choice have been restricted to population dynamics, not considering its effect on community evolution (Berec & Krivan, 2000; Stephens & Krebs, 1986). However, ecological and evolutionary processes can be combined via natural selection (Schoener, 2011) and occur on contemporary scales (Hendry, 2020). These eco-evolutionary dynamics, such as the relationship between the ecology of populations, communities and the evolution of functional traits, generate information that would not be expected in isolation (Velzen & Brodie, 2019). The outcomes of eco-evolutionary dynamics between antagonistic species are generally related to the strength of selection imposed by the interaction (Abrams, 2000; Andreazzi et al., 2017). The modelling of the active choice is simplified by assuming a random choice behaviour combined with another function that determines the probability of interaction to occur successfully, depending on the trait-matching between consumer and resource (Andreazzi et al., 2017; Nuismer et al., 2013). This assumption implies that the consumer does not evaluate the resource's trait that defines resource quality, which increases the chances that it interacts with a resource that results in small fitness despite the presence of better resources available in its neighbourhood. Such simplification may be understood as equivalent to active choice behaviour since the imposed probability function will favour those interactions with a higher probability of success. A first theoretical step addressing the effect of an active choice on species evolution was made for pairs of antagonistically interacting species, where it was observed that both approaches are not equivalent and active consumer choice has significant consequences on the patterns of trait evolution (Araujo et al., 2020). Nevertheless, the effects of active consumer choice on coevolutionary dynamics of communities remain unknown.

A huge effort has been made to understand the mechanisms that determine the structure of interaction networks in communities (Andreazzi et al., 2017; De Andreazzi et al., 2018; Dupont & Olesen, 2009; Guimarães et al., 2011, 2017; Nuismer et al., 2013). Divergent selection regimes, phylogenetic conservatism (Lewinsohn et al., 2006; Prado & Lewinsohn, 2004), habitat heterogeneity (Thompson, 2005) and morphological traits (Danieli-Silva et al., 2012; Donatti et al., 2011) may lead to nonrandom patterns of interactions and to the tendency of different subsets of species in the network to interact more frequently with each other than with the remaining species (modules), resulting in a modular network (Lewinsohn et al., 2006; Olesen et al., 2007; Pimm, 1980; Thébault, 2013). Modularity plays fundamental roles in ecological community resilience (Thebault & Fontaine,) and persistence since disturbances are not easily spread to other modules (Stouffer &

Bascompte, 2011). Besides that, modules have been suggested to be candidates for coevolutionary units (Dupont & Olesen, 2009), (Olesen et al., 2007). That means that the modules are formed by coevolution and stay stable over time. However, it is not clear to date how such convergence could emerge in antagonistic networks, where the selection pressure upon resource species should tend towards divergence, not convergence.

Here, we integrate individual-based modelling with ecological networks tools to move forward our understanding of the role of the individuals' active choice behaviour in antagonistic network evolution. Our results demonstrate that active consumer choice is a crucial element in giving rise to and promoting the stability of modules, generating coevolutionary units.

2 | METHODS

2.1 | The model

We simulate an ecological system of two trophic levels composed of several species and individuals that interact antagonistically and are explicitly modelled. Consumer attack traits and resource defence traits are subject to selection and mutation. The interactions occur through trait matching, that is, the probability of a successful interaction increases with trait matching between interacting individuals. A closer trait matching between both species is advantageous for the consumer and detrimental for the resource. Consumers actively choose resources within an interacting neighbourhood, which represents the possibility of the consumer to evaluate the resources near them and choose which one will be attacked. In addition to the interaction pressure, we consider a stabilizing external pressure that models all types of pressure outside the interaction. This pressure acts as a selective force on consumer traits and resources towards a favoured trait. Both the pressure of the interaction and the stabilizing pressure result in the fitness of the individuals, i.e. the contribution of these individuals to the next generation.

The model considers M_X resource species with N_X individuals per species and M_Y consumer species with N_Y individuals per species. It assumes the existence of a set of traits that constitute the defence or attack traits of individuals. Such traits may be morphological, physiological, chemical or behavioural and are represented by a real number, Z_{nr}^i , where Z represents the defence (X) or attack (Y) trait, i the individual and n the species. For example, X_2^1 indicates the defence trait of individual 1 belonging to species 2 and Y_3^1 indicates the attack trait of individual 1 belonging to species 3.

2.2 | Dynamics

The dynamics of the model consists of three main steps in the following order: (i) the encounter between individuals; (ii) the fitness outcomes due to the interaction pressure and stabilizing pressure; and (iii) the reproduction (Figure 1).

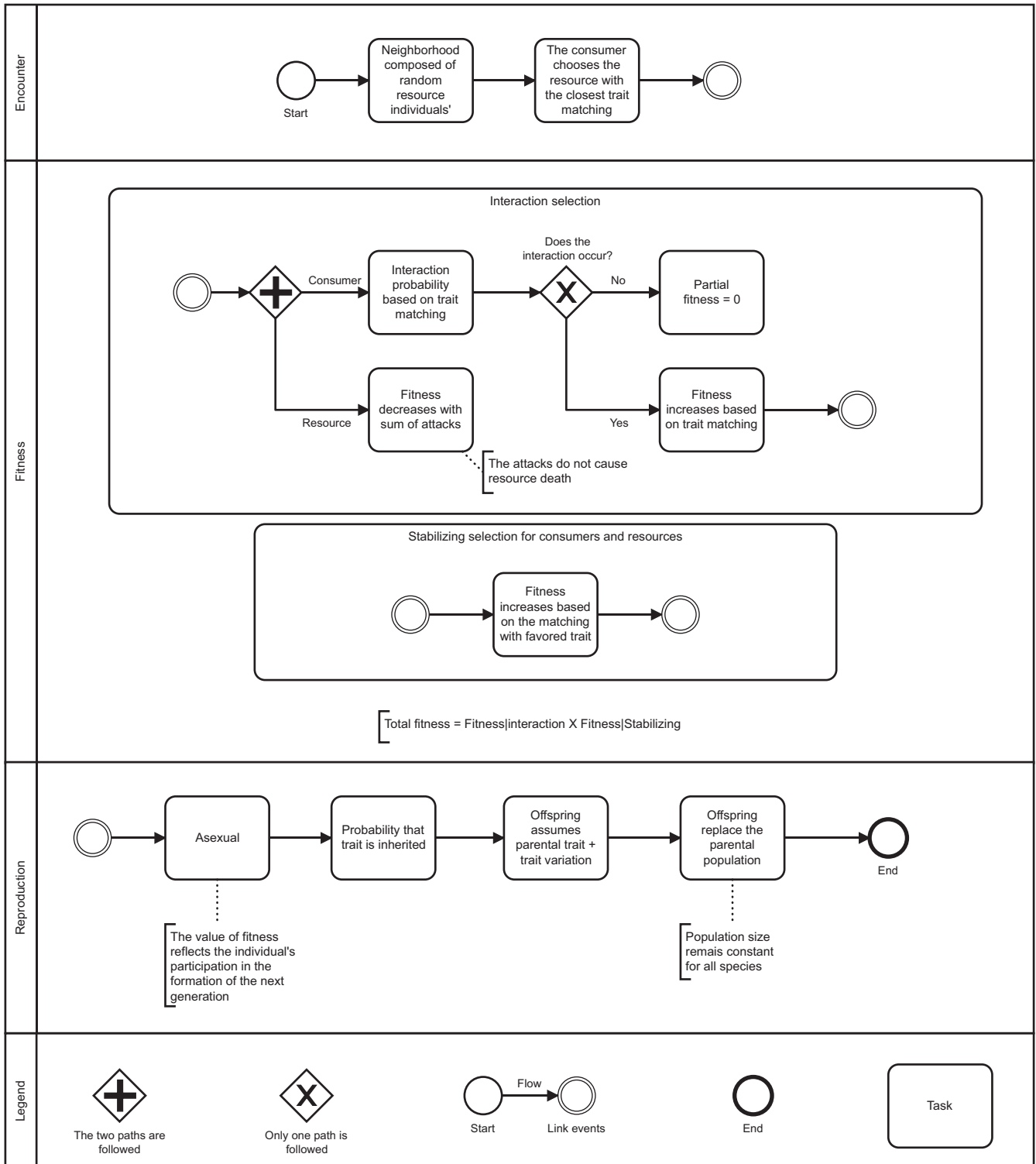


FIGURE 1 Steps of the model. The dynamics start with the encounter between consumers and resources within an interaction neighbourhood. Consumer actively chooses and tries to interact with the resource that maximizes its fitness. Both consumers and resources have their total fitness calculated, composed of the partial fitness due to the interaction and stabilizing pressures. The result of the total fitness is reflected in the individual's contribution to the next generation

2.2.1 | Encounters

The model considers that each consumer individual can detect only a subset of resource individuals that corresponds to the

interaction neighbourhood. For each consumer, the model selects *n* resource individuals regardless of their species, with replacement, to compose the interaction neighbourhood. This means that the same resource individual can be selected more than once,

and the neighbourhood size can vary below n unique individuals. Moreover, the resource individuals can belong to more than one interaction neighbourhood. This resource overlap can be interpreted as the consumer home range overlap or also resource movement among neighbourhoods. We characterized the neighbourhood size ϕ , which corresponds to the maximum fraction of resource that a consumer can access within the community. The size of the interaction neighbourhood is constant across consumer individuals and may represent that the consumers with smaller capacity (smaller neighbourhoods) can detect less resources. It can also represent different environments, in which larger neighbourhoods represent an environment with a higher density of individuals per area.

Here, for simplicity, we assume that every consumer has only one chance to interact, whereas a resource can receive interactions from more than one consumer. The consumers can be herbivores or parasites; that is, consumers who do not kill their resources. If the consumer could interact with all resource in its neighbourhood, the active choice would not play any consequence in the resulting interactions since it would only change the order of the interactions.

We consider that consumers have local omniscience (Berec, 2000). That is, any consumer has exact knowledge of resources only in its neighbourhood. That local omniscience may be due to constraints in the consumer's capacity of detecting its resources, either through visual, olfactory or chemical senses (Berec, 2000) and then allows consumers to choose which resource to interact with. Following the recent approach proposed for pairs of species (Araujo et al., 2020), we incorporate into the model the active choice behaviour of the consumer, in which the consumer will choose, within its interaction neighbourhood, the resource with the smallest trait difference, that yields the highest fitness. Thus, increasing the size of the interaction neighbourhood raises the probability that the consumer will find a resource that yields higher fitness. Note that when the interaction neighbourhood is composed of only one individual, the consumer has no option to choose and the interaction equals a scenario without active choice, where the interactions occur randomly.

2.2.2 | Fitness ($W_{Z_n^i}$)

The total fitness of a resource individual ($W_{X_n^i}$) or a consumer individual ($W_{Y_n^i}$) is given by the product of the performance of its trait due to the interaction and the selective pressure given by the external stabilizing selection:

$$W_{Z_n^i} = W_{Z_n^i}^{\text{int}} \times W_{Z_n^i}^{\text{ext}} \quad (1)$$

where $Z \in X, Y$. The details of both selective pressures are detailed below:

2.3 | Interaction pressure

We model the interaction mechanism based on trait matching, where the probability of the interaction to occur successfully decreases with the difference between consumer and resource traits:

$$P_{Y_n^i \rightarrow X_m^j} = \exp \left[-\alpha (X_m^j - Y_n^i)^2 \right], \quad (2)$$

where α is a parameter that controls the intensity of the selective pressure on the interaction (Figure S1a).

When an interaction occurs successfully, the consumer's fitness due to the interaction also depends on trait-matching. Hence, if the interaction occurs successfully, a consumer's fitness due to the interaction is given by:

$$W_{Y_n^i}^{\text{int}} = P_{Y_n^i \rightarrow X_m^j}, \quad (3)$$

and if the interaction does not occur,

$$W_{Y_n^i}^{\text{int}} = 0. \quad (4)$$

For the resource, both the intensity and number of attacks contribute to a decrease in its fitness. The attacks do not directly imply the death of the resource, but rather a decrease in its fitness:

$$W_{X_m^j}^{\text{int}} = \exp \left[-\beta \left(\sum P_{Y_n^i \rightarrow X_m^j} \right)^2 \right] \quad (5)$$

where β is a parameter that controls the intensity of the interaction pressure on the resource. A higher value of β penalizes resources whose phenotypic compatibility with the consumer is high, as it increases the impact of the attack of a consumer with high phenotypic compatibility with the resource (Figure S1b). The term $\sum P_{Y_n^i \rightarrow X_m^j}$ Eq. (5) represents the sum of all successful attacks weighted by the consumers' interaction fitness. It means that a consumer that possesses greater trait-matching will cause more impact on the resource's fitness than a consumer with smaller trait-matching.

2.4 | Stabilizing pressure

We include a stabilizing selective pressure, which considers all types of pressure outside the interaction and acts as a selective force on traits towards a favoured trait, both in resources and in consumers:

$$W_{Z_n^i}^{\text{ext}} = \exp \left[-\gamma Z_n (Z_n^i - \theta_n)^2 \right] \quad (6)$$

where θ_n is the trait favoured by the external stabilizing selective pressure for a given species n and γ is a parameter that controls the intensity of the pressure to the deviations of θ_n . For simplicity, we assume that γ is constant, but not null, over species and trophic levels.

TABLE 1 Parameters used in the simulations, their values and a short description

Parameter/ variable	Value	Description
M_X, M_Y	50, 50	Number of resource and consumer species.
N_X, N_Y	100, 100	Number of individuals per resource and consumer species
δ	random number that follows a normal distribution probability which standard deviation is σ	Mutation coefficient
σ	0.02	The standard deviation used to calculate phenotypic variation due to reproduction
γ	1	Stabilizing pressure intensity
θ	$\theta \sim \mathcal{N}(0, 1)$ for consumers and resources	Trait favoured by stabilizing pressure
α	0, 0.05, 0.1, 0.2, 0.4, 0.8 ^a , 1.6, 3.2, 6.4	Intensity of interaction pressure on the consumer
β	0, 0.05, 0.1, 0.2 ^a , 0.4, 0.8, 1.6, 3.2, 6.4, 12.8, 25.6, 51.2, 102.4	Intensity of the interaction pressure on the resource
Φ	from 0.02% to 20% an increase by 1% and from 20.2% to 100% an increase by 10%	Size of the interaction neighbourhood (0.02% implies that the attack is without active choice)

^aRepresents values of α and β that were kept constant in simulations where the effects of variation in the interaction neighbourhood size were investigated.

2.4.1 | Reproduction

We assume that all individuals with non-zero fitness can have offspring which will then recompose the population to its original size. Thus, the number of individuals is constant over time, regardless of the number of survivors after the Fitness step. Our analysis considers only those cases in which there was no extinction as, given these dynamics, extinction events occur only in extreme situations. Therefore, the contribution of the individual i to the next generation is proportional to its fitness relative to other individuals of the same species:

$$P_{Z_n^i} = \frac{W_{Z_n^i}}{\sum_{i=1}^{N_2} W_{Z_n^i}} \quad (7)$$

where $P_{Z_n^i}$ is the probability that an individual of the new generation will inherit the trait Z_n^i of the individual i of the n species. $W_{Z_n^i}$ refers to the fitness of the parental individual Eq. (7), and $\sum W_{Z_n^i}$ the sum of the adaptive values of all individuals of the parental species.

For simplicity, the reproduction is asexual and the offspring assumes the same trait value as the parental individual with a mutation coefficient δ , whose value is a random number that follows a normal-probability distribution:

$$P_{(\delta)} = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{\delta^2}{2\sigma^2}} \quad (8)$$

where σ is the standard deviation, which we assume constant between trophic levels. Even though asexual reproduction is widespread as reported for interacting species as bacteria and viruses (Brockhurst et al., 2003; Fortuna et al., 2019; Hochberg & Baalen, 1998; Lopez-Pascua & Buckling, 2008) or bacteria and protists (Chow et al., 2014; Jousset, 2012), bacteria and nematodes (Jensen, 1987; Neher, 2001), daphnias and parasites (Decaestecker et al., 2007; Duffy et al., 2008),

this asexual reproduction simplification can be extrapolated to sexual organisms. In this case, assortative mating to the couples (Doebeli & Dieckmann, 2000) must be assumed; that is, only individuals with similar traits can mate, and the offspring will have about the same trait as their parents.

2.5 | Simulation parameters

The number of species, the number of consumer and resource individuals per species and the intensity of external stabilizing pressure were held constant in all simulations ($M_X = 50$, $M_Y = 50$; $N_X = 100$, $N_Y = 100$, $\gamma = 1$, respectively). The traits favoured by the stabilizing selection on consumer and resource species were obtained from a normal distribution $\theta \sim \mathcal{N}(0, 1)$ (mean equal to 0 and a standard deviation equal to 1). Therefore, the simulated community presented heterogeneity of trait values favoured by the external stabilizing selection.

We ran simulations without active consumer choice under different intensities of interaction pressures (see values of α and β in Table 1) to verify their effect on coevolutionary trait dynamics. We model the absence of choice by assuming the interaction neighbourhood is equal to a single resource individual, which corresponds to $\Phi = 0.02\%$. In simulations with active consumer choice, the intensity of interaction pressure was fixed ($\alpha = 0.8$ and $\beta = 0.2$). These correspond to intermediate interaction pressure values presented in Table 1 approached in the case without active choice. These values refer to a situation where the selection is not so low as to have insignificant consequences, and neither too high, where extinctions become too frequent. Also, different sizes of the interaction neighbourhoods Φ were evaluated. All the values of parameters and variables used in the simulations are described in Table 1. Each simulation consisted of 10 000 generations. To verify the model's sensitivity to random events, five replicates of each simulation were

performed, producing a total of 146 491 communities in models with active choice and 5145 in the model without active choice. The simulations were carried out in the FORTRAN language both in the LCPAD—Central High-Performance Processing Laboratory of the Federal University of Paraná and through the Amazon web service.

2.6 | Data analysis

2.6.1 | Interaction persistence networks

To evaluate the persistence of interactions over time, for each replicate we built an interaction persistence network from the matrix of size $N_x \times N_y$, where each row and column represents a resource and a consumer species, respectively. The value of each cell indicates the number of generations in which at least one interaction between the given pair of species was recorded. To avoid transient effects, we only used the data for the last 4000 generations, sampled at every 200 generations, resulting in 21 networks per simulation. We have also analysed the interaction network for each time, where each cell of the matrix represents the number of interactions between a pair of species (see Supplementary Material, Figures S6 and S7).

The interaction persistence networks were characterized using established network metrics: connectance (C), modularity (M) (Beckett, 2016) and specialization index ($H2'$) (Blüthgen et al., 2006). The measure of all the mentioned metrics was implemented through the bipartite package and performed in an R (R Core Team, 2020) environment. Connectance (C) was calculated as the ratio between the number of non-zero cells and matrix size (Dormann et al., 2020). It represents the proportion of interactions actually realized relative to all potential interactions. Modularity was measured using the DIRTLPAwb+ algorithm using the *computeModules* function (Dormann et al., 2020). This metric ranges from 0 to where the higher value is 1, the more restricted are the interactions into species subsets (modules). We use modularity on the persistence of interaction networks to infer the presence of the coevolutionary units. Specialization $H2'$ was measured using the *H2fun* function (Dormann et al., 2020). This metric also ranges from 0 to 1, and the higher this value, less overlap exists between interacting species. Both modularity and specialization metrics use quantitative matrices. The connectance indicates the percentage of all interaction occurred during the analysed time. Higher values of modularity in the interaction persistence networks indicate that species interactions occur more often (in time) in a subgroup of species than between them. Similarly, the higher the specialization index, it means that a pair of species persists their interaction over time more intensely than expected by the abundance of species.

3 | RESULTS

In most cases, active consumer choice led to coevolutionary trait dynamics with stable groups of tightly interacting species that exert

reciprocal selection on traits. Within each module, the resource traits converge into a narrow range of values, surrounded by consumer traits (Figure 2a and Figure S2). Smaller neighbourhoods induced more extreme trait dynamics (higher trait values), with trait values reaching twofold the amplitudes when compared with larger neighbourhoods (Figure 2a: compare $\phi = 4\%$ with $\phi = 100\%$, or see more cases in Figure S2). In these smaller neighbourhoods, there was a high frequency of interactions (darker colours in Figure 2b and Figure S3) between consumers and resources within each module over generations. That is, all species interact with each other inside the modules in most generations. In larger neighbourhoods, due to a higher opportunity for encounters with preferred resources, the frequency of interactions over generations between all species inside the module decreased (lighter colours). However, the presence of interactions highlights that, among the species in the same module, a consumer species changes its choice of interaction over time. Interaction breakdown occurs because a resource species evolves into a lower trait-matching, leading a different resource species, with greater trait-matching, to be chosen by a given consumer species. Still, the former resource may then become the chosen for another consumer species, restarting the cycle of events. This choice alternation is maintained over the generations, but it is locked inside the module, that is between the same group of interacting species, therefore without breaking the unit of coevolution. Stable coevolutionary units, the modules, were not observed in scenarios without active consumer choice (Figure 2c and Figure S4), and the interactions occur between almost all species regardless of the interaction pressure intensity (Figure 2d). Additionally, we observed that even higher interaction pressure intensities do not promote coevolutionary units, but instead drive species to extinction (Figure S4).

As the size of the interaction neighbourhood increases, the network tends to be more modular, specialized, less connected and consumer success decreases (Figure 3). However, for ϕ between approximately 0.2% and 1%, this trend is inverted for all metrics. This inversion occurs when the first coevolutionary units emerge, but with only two or three modules, which increases the interactions between species, explaining the metric inversions (Figure S2 and S3). For ϕ around 1% and higher, the metrics follow the initial trend again (Figure 3). However, between approximately 1% and 10%, the coevolutionary units oscillate between two and four modules, varying both over time and over replicates. For ϕ around 10% and higher, the coevolutionary units stabilize (Figure S2 and S3 and Figure 2). To avoid this initial variation, we restrict the next results to $\phi > 10$.

The network metrics showed considerable difference according to consumer choice behaviour. Without active choice but varying the interaction pressure (α and β), connectance ranges from 0.94 to 1; modularity from 0.017 to 0.14; and specialization, from 0 to 0.06. With active choice, and $\phi > 10$, connectance ranges from 0.29 to 0.48; modularity from 0.41 to 0.65 and specialization, from 0.19 to 0.32. Thus, networks with active consumer choice were more modular, more specialized and less connected in relation to networks without active choice behaviour (Figure 4). Although all networks have the same size, the number of interactions varied over simulations

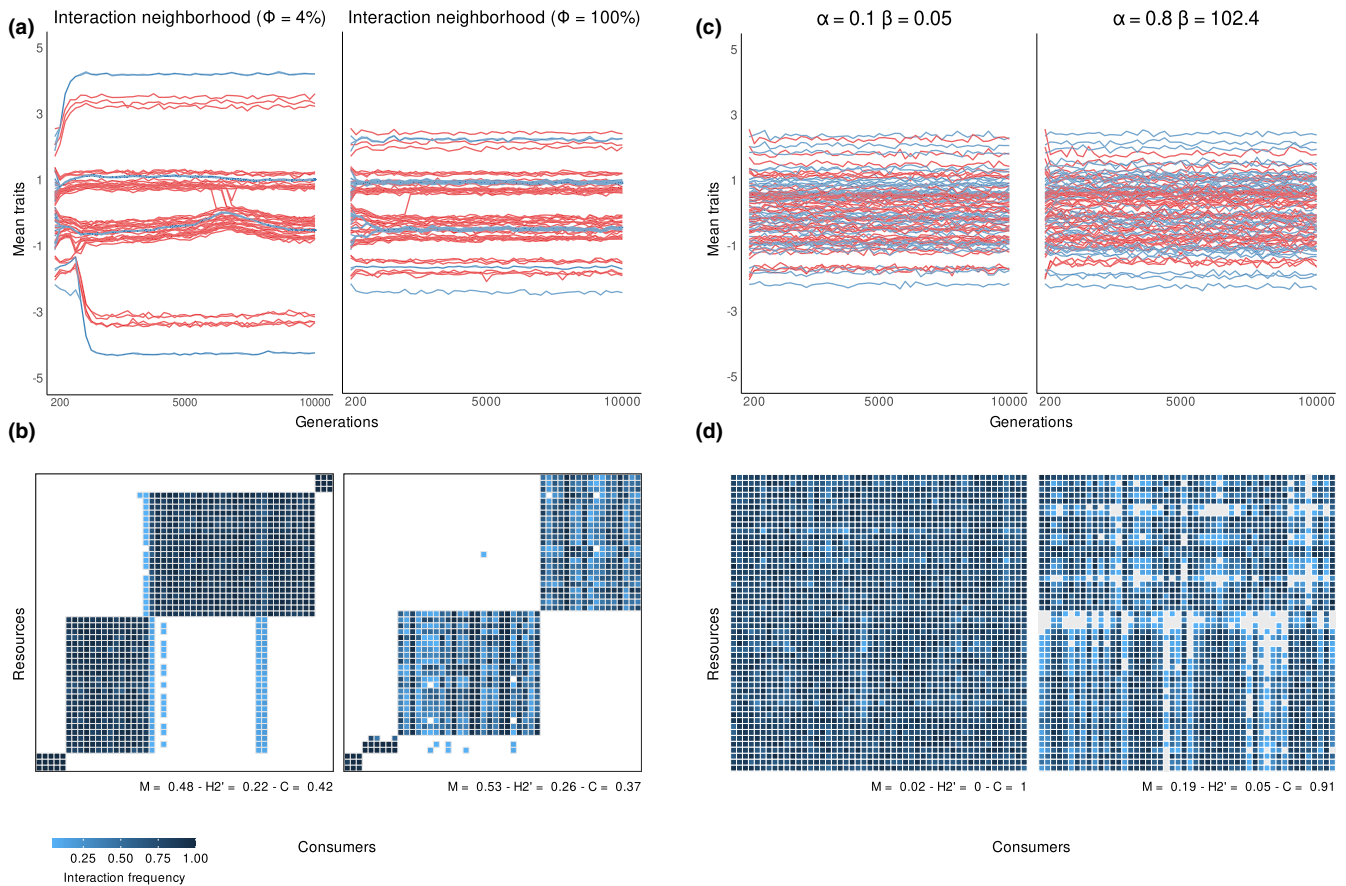


FIGURE 2 Coevolution with and without active consumer choice. (a–b) Example of coevolutionary trait dynamics under active choice in different sizes of interaction neighbourhoods. (c–d) Coevolutionary trait dynamics without active choice behaviour, but under different interaction pressures. (a and c) shows the average trait of each consumer species (red) and each resource species (blue in a given simulation). (b and d) represents the matrices of interaction persistence of the same simulation. Each row and column represent a resource and a consumer species, respectively, and the cell the frequency of generations in which at least one interaction between a pair of species was recorded. The species order in these graphs maximizes the visualization of the modular pattern. The absence of interaction is represented by the colour white. Network metrics: M , Modularity; $H2'$, Specialization; C , Connectance; Note that active choice behaviour limits species interactions to subgroups, evidencing the stability of the evolutionary units

(Consumer success Figure S6). Overall, active choice promotes more interactions since the consumer can choose with whom to interact. It means that if a null model normalized the interaction networks, the discrepancy between with and without active choice scenarios would be even higher.

4 | DISCUSSION

In this study, we investigated the role of individual active choice behaviour on coevolutionary trait dynamics and network structure of species with antagonistic interactions. Our results reveal that active choice can drive significant changes in trait distributions, on the selective regimes and on patterns of interactions that shape the structure and dynamics of antagonistic networks. We demonstrate that the active choice behaviour generates modules that are persistent in evolutionary time, which can be interpreted as coevolutionary units. These results highlight the importance of individual behaviour and the effects of adaptive diet choice on eco-evolutionary dynamics.

The model with active choice behaviour allows each consumer individual to choose to interact with the resource in its neighbourhood that maximizes its fitness. The simulations showed that, under this condition, subgroups of resource species converge their traits around a single value, whereas subgroups of consumer species converge their traits around one of two values—below or above resource traits values—locking the resource trait evolution (Figure 2a). These subgroups of resource and consumer species then form a temporal stable module with almost no interaction between modules. The mechanism behind this stability is probably the same observed for the model with two species (Araujo et al., 2020). That study analytically showed that active choice behaviour locks the resource trait because any variant resource that maximizes consumer fitness will not go unnoticed by the consumer. Here, a small variation in a resource trait makes it a better resource choice for at least part of the surrounding consumers, reducing the resource fitness. On the other hand, without active choice, small variations in the resource trait are more likely to go unnoticed by the consumer, so that the

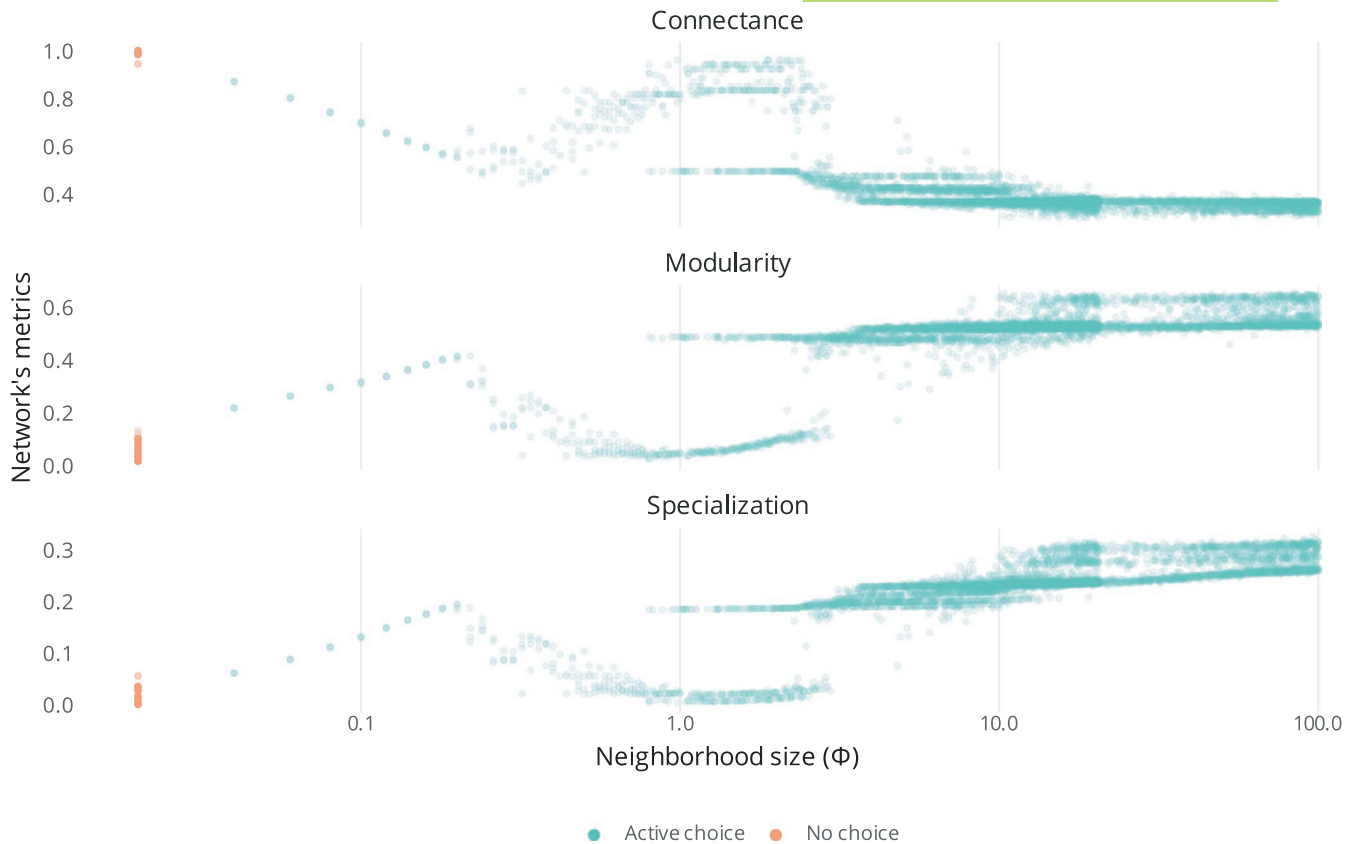


FIGURE 3 Network metrics in different sizes of interaction neighbourhoods. The red dots highlight the cases where the neighbourhood is minimal (just one individual), which is equivalent to the scenario without active choice. As the size of the interaction neighbourhood increases, the network tends to be more modular, specialized, less connected and the consumer success decreases. However, for Φ between approximately 0.22% and 1%, this trend is inverted for all metrics, then it returns to the first trend for $\Phi > 1\%$

temporal stability of the module and the convergence of species traits are never achieved (Figure 2b). Thus, higher pressure intensity on the interaction (α and β) is not enough to increase modularity and trait convergence.

Modules have been suggested to be candidates for coevolutionary units (Andreazzi et al., 2017; Dupont & Olesen, 2009; Olesen et al., 2007), implying that modules are formed by coevolution and stay stable over time. Inside the modules, the species interact with each other, exerting strong reciprocal selection on traits, shaped by a similar regime of selective pressures (Dupont & Olesen, 2009; Thompson, 2005). Andreazzi et al. (2017) proposed a model for antagonistic interactions and observed that coevolutionary units can emerge from antagonistic interaction, but only when the fitness consequence is higher for the consumers than victims. Here, we show that active choice promotes a higher increase in modularity and interaction persistence than in the models without active choice (Figure 3). Since the enlargement of the interaction neighbourhood increases the fitness consequence for the resources, our model supports that evolutionary units can emerge even under high pressure on resources.

Coevolutionary units have been suggested as a product of co-speciation and arms race (Endara et al., 2017; Sweet et al., 2020). Under this hypothesis, the consumers are predicted to have evolutionary patterns of diversification that are congruent with the

patterns of their resources, where closely related resource species would have similar defences and closely related consumers would feed on closely related resources (Endara et al., 2017; Sweet et al., 2020). However, this hypothesis has little support in empirical studies (Braby & Trueman, 2006; Braga et al., 2014; Brooks et al., 2019; Silva-Brandão & Solferini, 2007; Sweet et al., 2020), except for tight specialized interactions (Patra et al., 2018). The incongruence between host and parasite phylogenies, for example, has previously been explained in terms of host switching, extinction, duplication events and failure of the parasite to speciate in response to host speciation (Johnson et al., 2003). Although our model does not approach speciation, it does not support that the interactions are restricted to pairs of species, which would be the first step of co-speciation. We show that the coevolutionary units in antagonistic interactions also produce convergent traits, independently of co-speciation ($\Phi = 100\%$), species interact with almost all other species within the module. Further studies must be done to investigate whether diversification patterns could emerge from our model.

The mechanism behind the coevolutionary units may be the emergence of convergent traits among individuals of the same trophic level, for example the presence of mainly white flowers inside a module in pollination networks (Dupont & Olesen, 2009; Olesen et al., 2007; Thompson, 2005). This arises due to the reciprocal fitness benefit among the two trophic levels, which does not occur

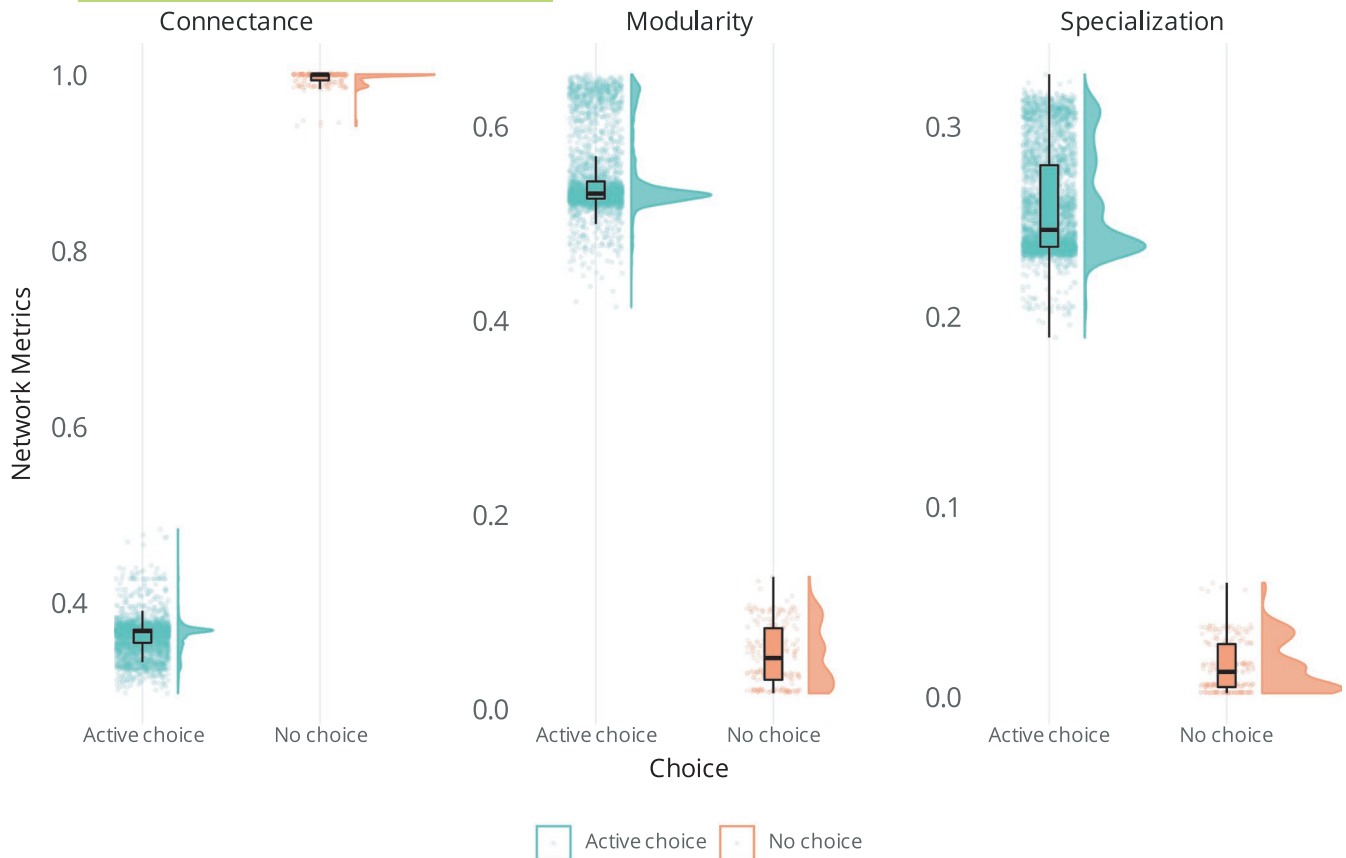


FIGURE 4 Network metrics with and without active choice behaviour. Active choice promotes networks with lower connectance and higher modularity and specialization. The green colour indicates the model with active choice, and the orange colour indicates the model without active choice. The raincloud plot shows the distribution of the data, and the raw data and presents the summary statistics median and interquartile ranges

in antagonistic interactions, and thus, trait convergence is not expected in antagonists. However, it has been observed that when distantly related plant species share a common assemblage of herbivores, they are likely to defend themselves with similar strategies (Agrawal & Fishbein, 2006). Besides, consumers experience a selection pressure to evolve specific traits adapted to consuming the existing resource species (Maliet et al., 2020); that is, they 'track' resource defences and not resource species per se (Endara et al., 2017). For example, closely related herbivores prefer *Inga* host trees with similar defences rather than closely related *Inga* (Coley et al., 2018). Regardless of these examples, there is not yet a mechanistic explanation on why distant-related resources would converge their traits since they could develop different strategies to defend themselves. Our results suggest that resource trait convergence promotes attack dilution: when resources converge their traits, the pool of options for a consumer increases and the chance of a specific individual being attacked decreases. In other words, with different resource species with similar phenotypes, the effects of the attacks of the consumers are diluted among the resources inside the module.

In this study, we were able to evaluate the effects of active choice behaviour in eco-evolutionary dynamics using simplifications (see methods). We suggest that future studies include more modelling ingredients to capture more information about this mechanism. For

example: (i) the spatial homogeneity disregards the differences between landscapes, as well as gene flow limitations (Fernandes et al., 2019; Thompson, 2005); (ii) although the model has an evolutionary time scale, it does not allow speciation, which could reveal how the individual behaviour can promote species diversification; (iii) finally, the equivalence between generations of consumers and resources disregards differences in consumer and resource life spans, when it is common to have several generations of consumers in relation to a single generation of the resource, as in parasite–host relationships (Olesen et al., 2007).

To conclude, we show that consumer active choice of resources that maximize their fitness is a crucial element for the emergence of coevolutionary units, that is, modules formed through the coevolutionary process. Moreover, as far as we know, this work is the first to demonstrate the mechanism of dilution by which traits converge in antagonistic networks.

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CONFLICT OF INTEREST

We declare we have no competing interests.

AUTHORS' CONTRIBUTIONS

SBLA conceived the idea of the project, SBLA, AMSBA and MEB wrote the model and performed the analyzes. AMSBA wrote the R code for the data analyses and AMSBA, MEB, LRJ, IGV and SBLA interpreted the results and contributed to the writing of the manuscript.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/jeb.13956>.

OPEN RESEARCH BADGES





This article has been awarded <Open Materials, Open Data> Badges. All materials and data are publicly accessible via the Open Science Framework at [<http://doi.org/10.5281/zenodo.4606671>].

DATA AVAILABILITY STATEMENT

R-project to reproduce the full paper and FORTRAN input: Allan Maurício Sanches Baptista de Alvarenga, Marcelo Eduardo Borges, Leonardo Ré Jorge, Isabela Galarda Varassin, & Sabrina Borges Lino Araújo. (2021, March 17). Alvarenga et al. 2021 data set and project (Version 1). Zenodo. <http://doi.org/10.5281/zenodo.4606671>.

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