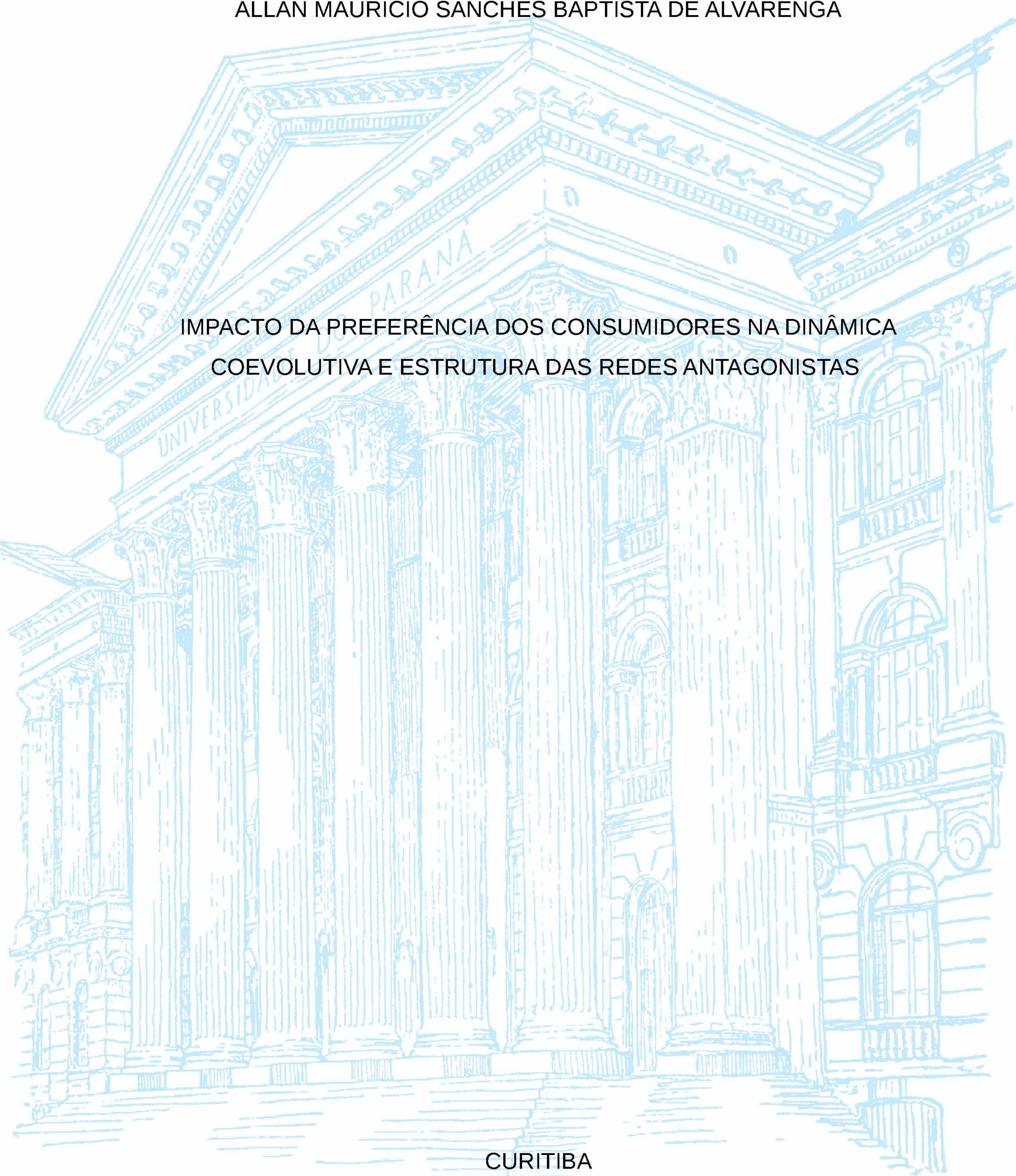
UNIVERSIDADE FEDERAL DO PARANÁ

ALLAN MAURÍCIO SANCHES BAPTISTA DE ALVARENGA



IMPACTO DA PREFERÊNCIA DOS CONSUMIDORES NA DINÂMICA COEVOLUTIVA E ESTRUTURA DAS REDES ANTAGONISTAS

CURITIBA
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O IMPACTO DA PREFERÊNCIA DOS CONSUMIDORES NA DINÂMICA COEVOLUTIVA E ESTRUTURA DAS REDES ANTAGONISTAS

Tese apresentada ao Curso de Pós-Graduação em Ecologia e Conservação, Setor de Ciências Biológicas, da Universidade Federal do Paraná, como requisito parcial à obtenção do título de Doutor em Ecologia e Conservação.

Orientadora: Profª. Dra. Sabrina Borges Lino Araújo

Coorientadora: Profª. Dra. Isabela Galarda Varassin

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Os membros da Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação em ECOLOGIA E CONSERVAÇÃO da Universidade Federal do Paraná foram convocados para realizar a arguição da tese de Doutorado de **ALLAN MAURICIO SANCHES BAPTISTA DE ALVARENGA** intitulada: **O impacto da preferência dos consumidores na dinâmica coevolutiva e estrutura das redes antagonistas**, sob orientação da Profa. Dra. SABRINA BORGES LINO ARAÚJO, que após após terem inquirido o aluno e realizado a avaliação do trabalho, são de parecer pela sua APROVAÇÃO no rito de defesa.
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CURITIBA, 26 de Setembro de 2019.

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Para minha família, amigos, professores e meu amor.

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Politische Grammatik[2]

> “Verfolgung Verfolger verfolgen die Verfolgten. Aus Verfolgten werden Verfolger. Weil Verfolger Verfolgte verfolgen machten Verfolger Verfolgte zu Verfolgten. Weil Verfolgte zu Verfolgern werden (weil Verfolger mit Verfolgen angefangen haben) werden aus Verfolgten verfolgende Verfolgte und aus Verfolgern verfolgte Verfolger. Aber weil verfolgende Verfolgte verfolgte Verfolger verfolgen: werden schließlich die verfolgten Verfolger wiederum zu Verfolgern. Zu verfolgenden verfolgten Verfolgern. Werden schließlich aus verfolgenden Verfolgten wiederum Verfolgte. Verfolgte verfolgende Verfolgte. Machen Verfolger Verfolgte. Machen Verfolger verfolgende Verfolgte. Machen verfolgende Verfolgte verfolgte Verfolger. Machen verfolgende Verfolgte verfolgende verfolgte Verfolger. Machen verfolgende verfolgte Verfolger: verfolgte verfolgende Verfolgte. Usw.”

Gramática política[3]

> “Perseguidores perseguem os perseguidos. De perseguidos surgem perseguidores. Porque perseguidores perseguem perseguidos fizeram os perseguidores dos perseguidos perseguidos. Porque perseguidos tornam-se perseguidores (porque os perseguidores começaram a perseguir) surgem de perseguidos perseguidos que perseguem e de perseguidores perseguidores perseguidos. Mas porque perseguidos que perseguem perseguem perseguidores perseguidos; perseguidores perseguidos tornam-se afinal de novo perseguidores. Perseguidores perseguidos perseguintes. Afinal de perseguidos que perseguem tornam-se de novo perseguidos. Perseguidos perseguintes perseguidos. Perseguidores fazem perseguidos. Perseguidores fazem perseguidos que perseguem. Perseguidos perseguindo fazem perseguidores perseguidos. Perseguidos perseguindo fazem perseguidores perseguidos perseguintes. Fazem perseguidores perseguidos perseguintes: perseguidos perseguidos perseguindo. Etc.”

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[2] Helmut Heissenbüttel, Politische Grammatik. In: Lesebuch. Deutsche Literatur zwischen 1945 und 1969. Hg. Klaus Wagenbach. Berlin 1980 (zuerst 1959).

[3] Traduzido por Haroldo de Campos.

RESUMO

O comportamento dos indivíduos, a organização espaço-temporal e o contexto local são processos que podem influenciar na estrutura e evolução das interações ecológicas. Em interações tróficas, os consumidores podem aumentar sua aptidão ao escolher ativamente os recursos que maximizam suas chances em utilizá-los com sucesso. Por isso, ao encontrá-los, decidem qual utilizar de acordo com seu valor e maneabilidade. A modelagem matemática é frequentemente empregada em estudos teóricos com o intuito de entender as dinâmicas coevolutivas entre essas espécies. Entretanto, esse comportamento individual dos consumidores na modelagem de comunidades é frequentemente ignorado, devido à complexidade desses sistemas exigir simplificações na construção dos mesmos. Nós avaliamos como o comportamento de escolha ativa do consumidor por recursos afeta as dinâmicas coevolutivas e a estrutura das interações em comunidades. Através de um modelo baseado em indivíduos nós simulamos uma comunidade composta por "consumidores" e "recursos". A dinâmica do modelo consiste em cinco etapas principais na seguinte ordem: o encontro entre os indivíduos, a pressão sobre a interação, a pressão estabilizadora, o cálculo da aptidão total, a reprodução e a recomposição da população. Os consumidores encontram os recursos em vizinhanças de interações. Estas são compostas aleatoriamente por um número de indivíduos recursos de qualquer espécie e pode variar desde um único indivíduo recurso, que implica em um cenário sem escolha ativa, até o total de recursos. A aptidão dos consumidores e recursos depende do grau de ajuste entre seus fenótipos e resulta na participação destes na formação da geração seguinte. Aqui, nós mostramos que a escolha ativa do consumidor pode gerar unidades ecológicas e coevolutivas estáveis ao longo do tempo. Ou seja, a convergência dos fenótipos de espécies de consumidores e recursos que exercem pressões seletivas recíprocas. As espécies se ligam preferencialmente a determinados núcleos nas redes, separados pelas diferenças em seus nichos fundamentais, dependendo do tamanho e composição das vizinhanças de interações. As métricas das redes não seguiram uma tendência única e não são diretamente correlacionadas com a intensidade da pressão coevolutiva imposta pelo comportamento dos consumidores. Nossos resultados demonstraram que a modelagem explícita da escolha ativa do consumidor gera dinâmicas coevolutivas e estruturas das interações congruentes, além de gerar amplitudes maiores das métricas de redes, que melhor descrevem as redes reais, diferentemente dos modelos que ignoram este ingrediente. Desse modo, consideramos relevante a inclusão do comportamento de escolha ativa dos consumidores nos modelos, visto que o mesmo desempenha papel fundamental nos processos ecológicos e evolutivos que estruturam as comunidades.

Palavras-chave: Antagonismo; Coevolução; Dinâmicas coevolutivas; Diversificação fenotípica; Escolha ativa; Redes ecológicas.

ABSTRACT

Individual behavior, temporal organization, and local context are processes that can influence the structure and evolution of ecological interactions. In trophic interactions, consumers can increase their fitness by actively choosing resources that enhance their chances of exploring them successfully. Upon searching for potential resources, they are able to decide which one to choose according to their fitness benefit and maneuverability. Mathematical modeling is often employed in theoretical studies to understand the coevolutionary dynamics between these species. However, they often disregard the individual consumer behavior 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. The trait of each individual is modeled explicitly and is subjected to the interaction pressure. In addition, consumers can actively choose the 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, exerting reciprocal selective pressure between them. We also observed that network structure has a greater dependence on the parameter that delimits active consumer choice than on the intensity of selective pressure. As a consequence, this parameter can closely match empirical networks. Thus, we consider that the inclusion of consumers' active choice behavior in the models plays an important role in the ecological and evolutionary processes that structure these communities.

Keywords: Antagonism; Active choice; Coevolution; Coevolutionary dynamics; Ecological networks; Phenotypic diversification.

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Conteúdo

PREFÁCIO

Quando a gente entra na pós graduação, muitas vezes não temos ideia de como é ser um pesquisador. Misturamos aquela ideia de cientista “maluco” que vive nos porões e grita “eureka!”, com os nerds que vemos na tv, a maioria dotados de alta racionalidade e baixas habilidades emocionais. Lá no começo, quando escrevemos um projeto e fazemos o cronograma, inocentemente acreditamos que seguiremos tudo à risca “Daqui 2 anos, no segundo semestre estarei finalizando a etapa de campo”. Pode até acontecer, mas geralmente não é o que acontece. O que ninguém nos conta é que quando vemos uma tese pronta ou um artigo publicado o caminho não-linear percorrido até esse final é omitido. Dessa forma, quando começamos nosso próprio projeto e os experimentos, os trabalhos de campo ou as perguntas que planejamos responder começam a dar errado, nos sentimos frustrados e ninguém conversa sobre isso. O biólogo Uri Alon[1] chama essa fase de “a nuvem”, quando nós nos sentimos desmotivados, desacreditados e empacados.

Como sair dessa nuvem? Como se tornar mais resistente às frustrações? A resposta é simples! Precisamos falar sobre isso. É normal que aconteçam imprevistos, eventos que não somos capazes de controlar. Caminhos diferentes do que planejamos sempre estão abertos e nem sempre são opções ruins a serem seguidas. Pode acontecer desde a mudança de uma pergunta, um método, um objeto de estudo ou até mesmo o projeto todo, mais e uma vez. Aconteceu comigo, vou contar de forma resumida:

Meu projeto inicial de tese foi na área de biomecânica de plantas, com outros orientadorxes. Eu decidi que embarcaria neste tema pois era o tema do pós doutorado da minha orientadora e ela gostaria de criar uma linha de pesquisa na universidade com o tema. Então juntei o útil ao agradável. Havia uma família de plantas Araceae, que eu gostava muito (e ainda gosto). Eu teria que coletar diversas espécies ao longo de todo Estado do Paraná e então avaliar as propriedades biomecânicas dessas plantas, tanto nos pecíolos, quanto nos caules. A ideia era verificar se as propriedades biomecânicas variam entre as plantas com diferentes formas de crescimento.

A primeira dificuldade para pôr em prática o projeto foi o tamanho do esforço do trabalho de campo, percebemos que apesar de inúmeras espécies que poderíamos avaliar, as condições para isso não eram favoráveis. A segunda dificuldade foi fazer as medidas propriamente ditas (three point bending), visto que não tínhamos o equipamento disponível. Decidimos construir nosso próprio equipamento, que não era nada automatizado e sempre nos trazia muitas dúvidas sobre a validade das medições realizadas. Mesmo assim eu queria seguir em frente, diminuimos o esforço de campo e realizamos as medições nas espécies que estavam mais próximas. Meu projeto foi aprovado, apresentei pôsteres sobre o andamento do trabalho. Além disso, consegui uma bolsa sanduíche para passar um tempo

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[1] ALON, U. How To Choose a Good Scientific Problem. Molecular Cell, v. 35, n. 6, p. 726–728, 2009. Disponível em: https://linkinghub.elsevier.com/retrieve/pii/S1097276509006418.

na França com meu coorientador.

Após alguns acontecimentos, decidi trocar de projeto e orientação, nisso eu ja estava com o tempo do curso avançado, $3^{\underline{o}}$ ano do doutorado. Entrei numa área completamente nova, com muitos cálculos, muita linguagem de programação e uma orientadora que era física! Tivemos o apoio da minha nova co orientadora, a Isabela. Novamente eu apresentei o novo projeto, modelamos interações mutualísticas e tentamos avaliar os efeitos de perturbações na estrutura das redes formadas. Realizei as simulações, mas nos deparamos com um erro que dificultava nosso trabalho devido a forma que o modelo era construído, mais uma vez alteramos o projeto. Passamos a trabalhar em um modelo que já estava escrito, mas que precisava de alterações para podermos responder a pergunta: “Qual o efeito do comportamento de escolha ativa do consumidor sobre as dinâmicas coevolutivas e estrutura das redes de interações antagonistas?” Agora nós tínhamos pouco tempo, mas eu consegui ganhar certa independência na hora de rodar e analisar meus modelos. Eu sempre ficava com uma pulga atrás da orelha, pois nossa primeira conclusão era que não havia padrões nas métricas das redes no que dizia respeito à escolha do consumidor. Foi aí que eu saí da “nuvem”, decidi utilizar um cluster poderoso, da Amazon e acabar com qualquer “e se. . . ” que a gente tivesse. Foram mais de 2TB de dados, mais de 500 mil redes analisadas. Foi quando vimos que nosso trabalho possuia resultados muito interessantes, mas ainda havia a dificuldade de filtrar todo esse conteúdo e contar a história de uma forma melhor.

Me orgulho muito do trabalho que realizamos nesse curto período de tempo, claro que gostaria de ter passado os quatro anos do doutorado aprendendo e desenvolvendo a tese, vendo os desdobramentos que encontraríamos pela frente. Agora, depois de corrigi-la, de tentar seguir ao máximo os comentários feitos por todos membros da banca, espero que este documento tenha atingido um maior nível de qualidade. A tese possui um único capítulo: *"Consumers' active choice behaviour promotes eco-evolutionary units"*. Espero que esse documento apesar de todas limitações, dê um passo adiante no caminho do conhecimento sobre o comportamento animal, coevolução e interações antagonistas em comunidades.

APRESENTAÇÃO

Os processos ecológicos e evolutivos podem ser combinados via seleção natural[1] e ocorrerem na mesma escala temporal[2]. Essas dinâmicas eco-evolutivas, como por exemplo, a relação entre a ecologia de populações, comunidades e a evolução de características orgânicas, geram informações que não seriam esperadas de forma isolada[3].

É reconhecido que as interações ecológicas formam a arquitetura da biodiversidade em comunidades[4] e que a coevolução pode modificá-las[5,6]. Dessa forma, interações como parasitismo, mutualismo parasitoidismo, ou herbivoria, são exemplos comuns de dinâmicas eco-evolutivas porque os fenótipos de ambos os níveis tróficos estão frequentemente sob forte pressão seletiva recíproca e portanto, podem evoluir muito rapidamente[3,7]. Um exemplo clássico desse tipo de dinâmica é a evolução rápida do tamanho do bico e corpo dos tentilhões das ilhas de Galápagos em relação à distribuição do tamanho das sementes e das condições ecológicas[8]. Os resultados dessas dinâmicas entre espécies geralmente estão relacionados à força da seleção imposta pela interação sobre cada indivíduo[6,9].

Um consumidor geralmente encontra diferentes tipos de recursos e pode decidir qual escolher de acordo com alguma 'moeda' de aptidão biológica (por exemplo, taxa de consumo líquido de energia, tempo de manuseio, prevenção de predadores), gerando interações não aleatórias[10,11]. A probabilidade de utilizar esse recurso com sucesso depende do seu ajuste às características fenotípicas do recurso. Dessa forma, alguns recursos são utilizados com maior frequência do que são ofertados no ambiente, sendo então considerados como preferidos. Tal preferência depende do comportamento de busca ativa por recurso de cada indivíduo, e pode refletir no padrão de escolha da espécie[12]. Diversos exemplos da escolha ativa do consumidor são encontrados empiricamente como por exemplo: aves predadoras de moluscos, que preferem se alimentar de espécies e tamanhos específicos de moluscos[13]; parasitas de ninho preferem utilizar os ninhos dos hospedeiros cujos ovos ou seus filhotes sejam similares aos seus próprios[14–16]; e os padrões de oviposição de insetos baseados nas defesas das plantas[17–20].

Em comunidades o contexto local, como a presença de determinadas espécies, pode alterar os regimes de pressões seletivas e consequentemente a evolução dos fenótipos e os padrões das interações entre as espécies[21]. De fato, interações entre diversos parceiros podem acarretar pressões seletivas conflitantes em direção e/ou magnitude[22,23]. Ainda, a presença de um parceiro pode reduzir a pressão seletiva imposta pelo outro[24]. Por exemplo, a pressão seletiva imposta por aves, como o cruza-bico (*Loxia curvirostra*), favorece pinheiros (*Pinus contorta ssp. latifolia*) com pinhas grandes e com escalas distais grossas. Por outro lado, a seleção por esquilos vermelhos (*Tamiasciurus hudsonicus*) favorece pinhas curtas, largas e com poucas sementes. Já a seleção imposta pelas mariposas (*Eucosma recissoriana*) favorecem pinhas estreitas e leves[25–28]. Quando esses predadores coocorrem, a maximização da aptidão representa os tradeoffs entre as pressões seletivas conflitantes que os mesmos impõem sobre as árvores, favorecendo pinhas com características intermediárias (optimalidade[29]). Em relações planta-herbívoro, as plantas podem apresentar níveis intermediários de defesa (metabólitos especializados, tricomas, ceras, etc.) em relação aos múltiplos herbívoros[30–34]. Além disso, os efeitos indiretos da seleção imposta pelos esquilos sobre os pinheiros influenciam a evolução das características do bico das aves[28], como resultado de efeitos em cascata que se propagam pela rede e que podem direcionar a evolução dos fenótipos de múltiplas espécies[5,6,35,36]. Nesse contexto, identificar os processos responsáveis pelas formação dos padrões dos regimes de pressões seletivas e consequentemente da evolução dos fenótipos e das interações nas comunidades torna-se altamente relevante.

Foi feito um grande esforço para entender os mecanismos que determinam a estrutura das redes de interação nas comunidades[5,6,35,37–39]. Para descrever as topologias das redes, geralmente utiliza-se as métricas de especialização, aninhamento e modularidade. A especialização representa o quanto as espécies interagem preferencialmente com um conjunto restrito de espécies, numa frequência maior do que esperado pelas suas abundâncias[40]. Já o aninhamento ocorre quando espécies especialistas interagem com subgrupos de espécies que interagem com espécies generalistas e sugere que as espécies generalistas possam exercer pressões seletivas sobre toda a comunidade[41]. A modularidade mede o quanto as espécies são organizadas em grupos que são internamente mais conectados quando comparados com as demais espécies da rede[42,43]. É hipotetizado que esses módulos possam ser formados devido à regimes de pressão seletiva divergentes, conservação filogenética[44], heterogeneidade de habitat[45] e atributos morfológicos[46,47].

Os módulos nas redes podem ser considerados unidades coevolutivas básicas, ou seja, são hipotetizados a emergirem por coevolução[37,48]. Para isso ser verdade, a dinâmica evolutiva de uma comunidade precisa levar à formação de módulos, e esses módulos devem ser persistentes no tempo[37,45]. Embora não seja ingrediente necessário para a formação das unidades coevolutivas, a formação de módulos através da complementaridade e convergência dos fenótipos de espécies não relacionadas já é reconhecida na literatura em estudos de interações mutualísticas[5,45]. Por exemplo, uma das candidaturas dos módulos à unidades coevolutivas é devido ao fato de fenótipos sob seleção convergente serem frequentemente similares geograficamente[45] e os autores observaram que os módulos apresentaram estabilidade da composição de espécies ao longo de pequenas áreas geográficas[37]. O registro de padrões cofilogenéticos bem definidos e a compatibilidade dos fenótipos dentro dos módulos em redes mutualísticas[49] é considerada a evidência mais clara que suporta essa hipótese. No entanto, não está claro até o momento como essa convergência poderia emergir em redes antagonistas, onde a pressão de seleção de espécies de recursos deveria tender então à divergência, não à convergência. Afinal, a seleção da interação depende dos fenótipos do consumidor e do recurso e, uma vez que a interação é antagônica, não favorece a convergência entre os fenótipos dos recursos e consumidores[50].

Modelos matemáticos combinados às análises de redes são ferramentas que trazem entendimento sobre os efeitos dos processos ecológicos e evolutivos na estrutura das comunidades. Atualmente, a abordagem utilizada nesses modelos desconsidera o comportamento individual dos consumidores devido à complexidade da implementação e ao fato da modelagem ser fundada em simplificações de observações empíricas. Por outro lado, um estudo recente propôs uma modelagem deste comportamento para pares de espécies[50]. A modelagem explícita da escolha ativa do consumidor mostrou que o comportamento individual possui importantes consequências ecológicas e evolutivas. Os efeitos podem ser por exemplo, a quebra da simetria da dinâmica coevolutiva (divisão assimétrica das linhagens em direção a cada polo do espaço fenotípico) e evolução dos fenótipos para amplitudes maiores em relação às dinâmicas sem esse comportamento[50]. Entretanto, os estudos teóricos sobre a escolha ativa do consumidor restringiram-se à dinâmica da população, sem considerar seu efeito na evolução da comunidade[51,52]. Portanto, pouco se sabe sobre os efeitos evolutivos da escolha de dieta adaptativa, especialmente seus efeitos mais amplos sobre a dinâmica e composição das comunidades ecológicas[53].

Nesse contexto, o objetivo desta tese foi verificar quais os efeitos do comportamento de escolha ativa do consumidor sobre as dinâmicas eco-evolutivas em redes de interações antagonistas. Utilizamos um modelo baseado em indivíduos com modelagem explícita do comportamento de escolha ativa dos consumidores para avançar nossa compreensão do papel do comportamento dos indivíduos na estrutura da comunidade. Modelamos uma comunidade de várias espécies que interagem antagonisticamente. A característica de cada indivíduo é modelada explicitamente, herdável e sujeita à interação e pressões estabilizadoras, o que permite adaptações das espécies. Além disso, cada consumidor pode escolher ativamente, dentre os recursos que estão em sua vizinhança de interação e interagir com aquele que maximiza sua aptidão. Investigamos o papel da pressão sobre interação e da vizinhança da interação na evolução dos fenótipos e redes de interação. Identificar como esse comportamento atua sobre os processos ecológicos e evolutivos permitirá o desenvolvimento de novas hipóteses, bem como poderá ampliar o conhecimento já obtido através dos modelos atuais.

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Consumers' active choice behavior promotes coevolutionary units

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1. Introduction

Ecological interactions build the architecture of biodiversity in biological communities[1]. 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. As a consequence, these interactions result in increased consumer fitness at the expense of a reduction in resource fitness. A foraging consumer will generally encounter different kinds of resources and they are able to decide which one to choose according to some 'currency' of biological fitness (e.g. rate of net energy intake, handling time, predator avoidance)[2,3]. This decision-making process known as 'active predator choice', leads the consumers to use some resources more often than others, given an encounter with each type of resource[4], e.g., birds that typically eat mollusks of particular sizes or species[5]; nest parasites that use the host's nests whose eggs are similar to their own[6–8]; insects that differ in their oviposition patterns based on plant defense traits[9–12]; prey choice by hematophagous insects[13] or parasitoid insects that choose their prey through chemical signals[14]. When a consumer uses a resource disproportionately to their relative abundance in comparison to alternative resources then this resource is considered preferred by the consumer[4].

Little is known about the evolutionary effects of adaptive diet choice, especially their broader effects on the dynamics and composition ecological communities[15]. Theoretical studies on active consumer choice have been restricted to population dynamics, not considering its effect on community evolution[16,17]. However, ecological and evolutionary processes can be combined via natural selection[18] and interact strongly on short timescales[19]. These eco-evolutionary dynamics, such as the relationship between the ecology of populations, communities and the evolution of organic characteristics, generate information that would not be expected in isolation[20]. The outcomes of eco-evolutionary dynamics between antagonistic species are generally related to the strength of selection imposed by the interaction[21,22]. The modeling of the active choice is simplified by assuming a random choice behavior combined with another function that determines the probability of interaction to occur successfully, depending on the adjustment of traits between consumer and resource[22]. This assumption implies that the consumer does not evaluate the resource's trait, which increases the chances that it interacts with a resource that results in small fitness despite the presence of better resources available in its neighborhood. Such simplification may be understood as equivalent to active choice behavior since the imposed probability function will favor those interactions with a higher probability of success. However, this simplification does not limit the trait range that a consumer will try to interact and choice behaviour is not under selection. A first theoretical step addressing the effect of active choice on species evolution was made for pairs of antagonistic interacting species[23], where it was observed that active consumer choice has evolutionary consequences. One of them, for example, is a unexpectable pattern where the resource trait is locked in only one of two evolutionary stable trait solutions[23]. Nevertheless, a theoretical framework investigating the effects of active consumer choice on coevolutionary dynamics in communities remains unknown.

A huge effort has been made to understand the mechanisms that determine the structure of interaction networks in communities[22,24–28]. Divergent selection regimes, phylogenetic conservation[29,30], habitat heterogeneity[31] and morphological attributes[32,33] may lead to nonrandom patterns of interactions and in the tendency of different subsets of species in the network to interact more frequently with each other than with the remaining species in the network[29,34]. The modules play fundamental roles in ecological community resilience[35] and persistence since disturbances are not easily spread to other modules[36].

Modules have been suggested candidates for coevolutionary units[24,34]. For this to be the case, these species would tightly interact with each other over time, exerting strong reciprocal selection on traits, shaped by this similar regime of selective pressures[24,31]. That means that the modules are formed by coevolution and stay stable over time. The clear pattern of co-phylogenetic signal and trait matching within modules in mutualistic networks was considered the clearest evidence to date to support this hypothesis[37]. However, it is not clear to date how such a convergence could emerge in antagonistic networks, where the resource species selection pressure should tend towards divergence, not convergence.

Here, we integrate individual-based modeling with ecological networks tools to move forward our understanding on the role of the individuals' active choice behavior in antagonistic network evolution. Our results demonstrate that the active consumer choice is a crucial element that promotes the stability of the modules generating coevolutionary units. Also, the active choice generates high variation on network structure in a non linear tendency of values in response to intensity of pressure imposed by neighborhood size.

2. Methods

2.1 The model

We simulate an ecological system considering a network consisting of two trophic levels that interact antagonistically, composed of several species and individuals that are explicitly modeled. Consumer attack traits and resource defense traits are subject to selection and mutation. The interactions occur through trait matching, that is,the probability of a successful interaction increases with the adjustment between the traits of the interacting individuals. A closer adjustment between both species traits is advantageous for the consumer and detrimental for the resource. In other words, resources are favored by smaller trait matching and consumers are penalized for it. The effect of the interaction on each individual's fitness is set by their phenotypic match and the strength of the interaction pressure. Consumers actively choose resources within an interaction neighborhood, 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 favored trait. Both the pressure of the interaction and the stabilizing pressure result in the fitness of the individuals, i.e. the probability of these individuals having offspring.

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 characters that constitute the defense or attack traits of individuals. Such characters may be morphological, physiological, chemical or behavioral and are represented by a real number, Z_n^i, where Z represents the defense (X) or attack (Y) trait, i the individual and n the species. For example, X_2^1 indicates the defense trait X of individual 1 belonging to species 2 and Y_3^1 indicates the attack trait Y of individual 1 belonging to species 3.

2.1.1 Dynamics

The dynamics of the model consists of five main steps in the following order: the encounter between individuals; the interaction pressure; the stabilizing pressure; the calculation of total fitness and the reproduction (Fig.1). The encounter takes place within the interaction neighborhood and the consumer can either choose the resource actively in order to increase trait matching or select it by chance. Through the selective pressures, the fitness of the individuals is used to calculate the probability that it will produce an offspring to the next generation.

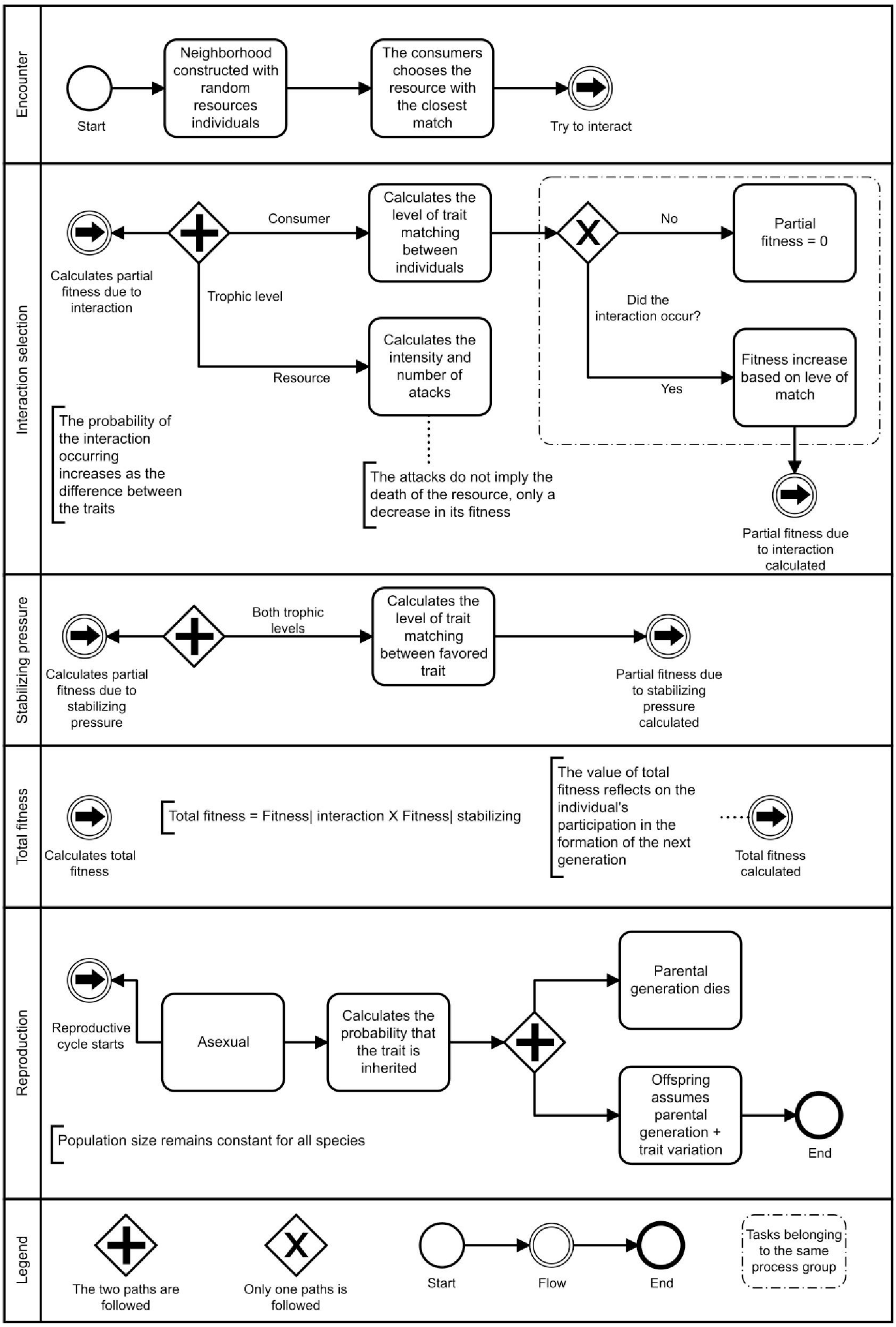

Fig.1| Stages of the dynamics of the coevolutionary model in antagonistic interactions. The dynamics starts with the encounter between consumers and resources in a given neighborhood size of consumer interactions. After the consumer actively chooses and tries to interact with the resource that results in greater matching with the resource trait, both the consumer and the resource have their total fitness calculated, composed of the partial fitness due to the interaction pressure and the stabilizing pressure. The result of the total fitness is reflected in the individual's participation to the next generation, where the parental generation dies and the offspring with the trait value of its parent plus a variation due to mutation recompose the population.

Interaction Neighbourhood and active consumer choice

The model considers that each consumer individual can detect only a subset of resource individuals, that corresponds to the interaction neighborhood. The neighborhoods are randomly composed of a number of resource individuals of any species from the resource community. We characterized it by the parameter Φ, which corresponds to the fraction of resources that a consumer can access within the community. Its size may range from a single resource individual to the total number of resources. The size of the interaction neighborhoods is constant among consumer individuals and throughout a simulation. Larger neighborhoods represent that the consumer is able to detect more resources while smaller neighborhoods may represent consumers with smaller capacity to detect resources. It can also represent different environments, in which larger neighborhoods represent an environment with a higher density of individuals per area.

Due to the consumer's handling time, satiety or energy spent in obtaining the food, the consumer cannot interact with all consumers in its neighborhood. In each generation, every consumer has only one chance to interact, while a resource can receive interactions from more than one consumer.

We consider that consumers have a local omniscience[17]. That is, any consumer has exact knowledge of resources only in its neighborhood. That local omniscience may be due to constraints in the consumer's capacity of detecting its resources, either through visual, olfactory or chemical senses[17] and then allows consumers to choose which resource to interact. Following the recent approach proposed for pairs of species[23], we incorporate into the model the active choice behavior of the consumer, in which the consumer will choose, within its interaction neighborhood, the resource with the smallest trait difference, that yields the highest fitness. Thus, increasing the size of the interaction neighborhood raises the probability that the consumer will find a resource that yields higher fitness. Note that when the interaction neighborhood is composed of only one individual the consumer has no option to choose and the interaction equals a scenario without active choice.

Fitness

The total fitness of a resource individual $\left(W_{X_n^i}\right)$ or a consumer individual $\left(W_{Y_n^i}\right)$ 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:

$$W_{Z_n^i} = W_{Z_n^i}^{int} \times W_{Z_n^i}^{ext}, \tag{2.1}$$

Here, $W_{Z_n^i}^{int}$ is the fitness contribution of the interaction pressure on individual i of species n, and $W_{Z_n^i}^{ext}$ is the fitness contribution of the external stabilizing pressure to the same individual. The details of both selective pressures are detailed below:

Interaction pressure

We model the interaction mechanism based on trait matching, where the probability that the interaction occurs successfully increases as the difference of the consumer trait on resource decreases, according to:

$$P_{Y_n^i \to X_m^j} = \exp\left[-\alpha \left(X_m^j - Y_n^i\right)^2\right]. \tag{2.2}$$

where α s a parameter that controls the intensity of the selective pressure on the interaction. Higher values favor consumers whose trait matching with the resource is high, decreasing the probability of an interaction occurring successfully with low trait matching (Fig.2a).

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

$$W_{Y_n^i}^{int} = P_{Y_n^i \to X_m^j}, \tag{2.3}$$

and if the interaction does not occur,

$$W_{Y_n^i \to X_m^j}^{int} = 0. \tag{2.4}$$

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:

$$W_{X_m^j}^{int} = \exp\left[-\beta \left(\Sigma P_{Y_n^i \to X_m^j}\right)^2\right]. \tag{2.5}$$

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 (Fig.2b). The term $\Sigma P_{Y_n^i \to X_m^j}$ (Eq. 2.5), 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 consumer's fitness than a consumer with smaller trait matching.

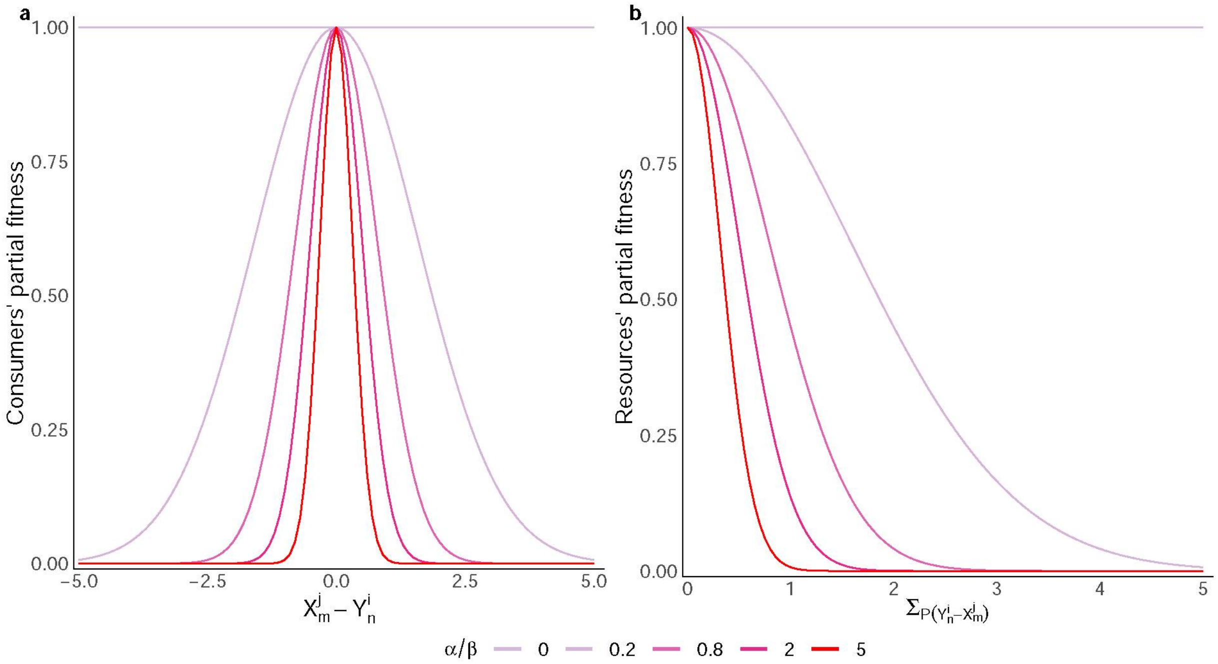

Fig.2| Fitness functions due to interaction. (a) Part of the consumer's partial fitness as a function of phenotypic differences between interacting individuals. (b) resource interaction pressure as a function of the intensity of the attacks (sum of all successful attacks weighted by the consumers' interaction fitness (Eq. 2.5). The lines represent distinct values of the intensity of the selective pressure on the consumer (α) and on the resource (β) used in the simulations.

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 favored trait, both in resources and consumers:

$$W^{ext}_{Z^i_{n \to \theta_n}} = \exp\left[-\gamma_{Zn}\left(Z^i_n - \theta_n\right)^2\right], \tag{2.6}$$

where θ_n it is the trait favored by the external stabilizing selective pressure for a given species n and γ it is a parameter that controls the intensity of the pressure to the deviations of θ_n. The level of match between the individual's trait and the optimal trait makes an additional contribution to their fitness.

Reproduction

We assume that all individuals with non-null 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 surviving a given generation. Our analyzes consider only those cases in which there was no extinction as, given these dynamics, extinction events occur only in extreme situations. Therefore, the participation of the individual i to the next generation is proportional to its fitness relative to other individuals of the same species:

$$P_{Z_n^i} = \frac{W_{z_n^i}}{\sum_{i=1}^{N_2} W_{Z_n^i}}. \tag{2.7}$$

where $P_{Z_n^i}$ it 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. 2.7), and ΣW_{Z_n} 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 distribution:

$$P_{(\delta)} = \frac{1}{\sigma\sqrt{2\pi}} e^{\frac{-\delta^2}{2\sigma^2}}, \tag{2.8}$$

where $P_{(\delta)}$ is the probability of occurring a variation of magnitude δ, σ is the standard deviation, which can be distinct between trophic levels ($\sigma \in \{\sigma_X, \sigma_Y)\}$).

2.1.2 Simulation parameters

In all the simulations the number of species, the number of consumer and resource individuals per species, and the intensity of external stabilizing pressure were maintained constant ($M_X = M_Y = 50$; $N_X = N_Y = 100$, $\gamma = 1$, respectively). The traits favored by the stabilizing selection of the resource 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 favored by the external stabilizing selection. We have also investigated a situation where all favored traits were equal to zero and our qualitative conclusions showed to be robust to this modification (Supplementary material).

We ran simulations without active consumer choice under different intensities of interaction pressures (see values of α and β in Table 1) in order to verify the effects of this behavior on the coevolutionary dynamics. The model without this behavior is equivalent to the case where the interaction neighborhood is equal to a single resource individual and 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 two values correspond to intermediate values approached in the case without active choice. Also different sizes of the interaction neighborhoods 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 and to avoid transient effects, we only used the data for the last 4,000 generations, sampled at every 200 generations, resulting in 21 networks per simulation. In order to verify the model's sensitivity to random events,

Tabela 1: Parameters and variables used in the simulations

Parameter.variable	Value	Description
M_X, M_Y	50, 50	number of species of consumers and resources
N_X	100	number of resource individuals by species
N_Y	100	Number of consumer individuals by species
γ	1	Stabilizing pressure intensity
θ	$\theta \sim \mathcal{N}(0,1)$ for consumers and resources	phenotype favoured by stabilizing pressure
δ	0.02	Standard deviation used to calculate phenotypic variation due to reproduction
α	0.05, 0.1, 0.2, 0.4, 0.8, 1.6, 3.2, 6.4	Intensity of interaction pressure on the consumer
β	0.05, 0.1, 0.2, 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 random)

five replicates of each simulation were performed (146.491 networks in model with active choice and 5.145 in the model without active choice). The simulations were carried out in FORTRAN language both in the LCPAD - Central High Performance Processing Laboratory, Federal University of Paraná and through the Amazon web service.

2.2 Data analysis

2.2.1 Persistence of interactions over time

To investigate the persistence of interactions over time, we calculated the number of generations in which at least one interaction between the same pair of species was recorded. We created a matrix of temporal interactions for each simulation, with the number of times that an interaction between pairs of species occurred over time. To represent the persistence of interactions we use a color scheme, where white cells represent the absence of interactions at any time, blue colors represent low frequency of interactions over time and colors close to yellow represent high frequencies of interactions over time. That is, the interaction between species occurs in most generations of the simulation.

2.2.2 Interaction network structure

The characterization of the interaction networks that resulted from the simulations was evaluated using the following metrics: modularity (M)[38], specialization index (*H2'*)[39], connectivity (C) and Nestedness (NODF2)[40]. The measure of all the mentioned metrics was implemented through the bipartite package and performed in an R[41] environment. Modularity was measured using the DIRTLPAwb+ algorithm using the *computeModules* function[40]. This metric measures the degree to which species are organized into internally more connected groups when compared to other species in the network[38]. Specialization *H2'* was measured using the *H2fun* function, which uses quantitative matrices[40]. This metric measures the degree of selectivity of interactions between nodes in the networks. The connectance (C) was calculated in binary matrices and refers to the ratio between the number of occurrences of interactions between species by the maximum number of possible interactions[40]. NODF2 calculations were performed using the *nested* function (*NODF2* method)[40]. Basically it measures how species interactions are nested: the interactions of specialist species are subsets of the interactions of generalist species. In addition to these measures, we analyzed the consumer success rate (S), obtained by the ratio of the number of successful interactions among all individuals of all consumer species:

$$\boldsymbol{S} = \frac{\sum_{i=1}^{N_Y}\sum_{n=1}^{M_Y}\sum_{j=1}^{N_X}\sum_{m=1}^{M_X}\delta(P_{Y_n^i \to X_m^j})}{M_Y N_Y} \tag{2.9}$$

where $\delta(P_{Y_n^i \to X_m^j})$ equals to 1 if the interaction between the consumer i of the species n succeeded in interacting with individual j of the species m and $\delta(P_{Y_n^i \to X_m^j})$ equals 0 otherwise. The sums then add up all the successes of all consumers individuals. The term MyNy equals the total number of consumer individuals. As a consequence, S ranges between 0 and 1; a value of 1 indicates a situation in which all consumer individuals of all species had a successful interaction.

3. Results

In most cases, the nonrandom pattern of interactions generated by active consumer choice led to coevolutionary 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 (Fig.3, upper panel and Fig. S1). Smaller neighborhoods presented more extreme trait dynamics, with some average trait values reaching two-fold the amplitudes of larger neighborhoods (between 5 and 5 and -2.5 and 2.5, respectively) (Fig. 3, upper panel and Fig. S1). In the smaller neighborhoods, in most of the cases there was a high frequency of interactions between consumers and resources within each module (most interactions are colored in yellow). That is, all species interact with each other inside the modules in most generations. In larger neighborhoods, due to a higher opportunity of encounters with resources with greater trait matching, the frequency of interactions (over generations) between all species inside the module decreased (blue colors) (compare $\Phi = 4\%$ and $\Phi = 60\%$, for example, Figs. 3, bottom panel, S2). However, the presence of interactions highlight that a consumer species changes its choice of interaction over time, among the species in the same module. It occurs due to the phenotype small variation in a module: while the consumers interact with the prefered species, the unpreferred species evolves towards the optimum trait imposed by the stabilizing selection. However, this evolution goes towards the consumer's traits, making the previously unpreferred species as preferred (Fig. 3, bottom panel). This alternation is maintained over the generation but it is locked inside the module without breaking the unit of coevolution.

Stable coevolutionary units were not observed in scenarios without active consumer choice: the interactions occur between almost all species regardless of the interaction pressure (Fig. 4). The increase of interaction pressure makes species extinct instead of generating modules (Fig.S3).

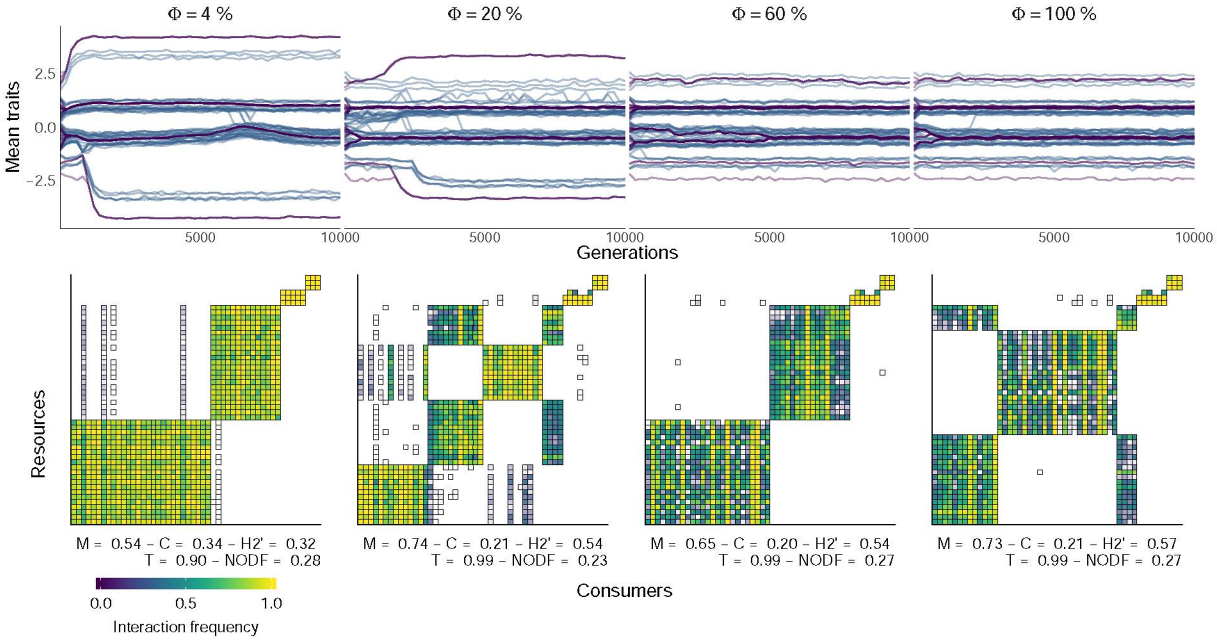

Fig.3|Coevolution under active consumer choice. Coevolutionary dynamics of traits (upper panel) and matrices of interactions between consumers and resources (lower panel) in different sizes of interaction neighborhoods. The average traits of consumer species are represented by the blue lines and resource species are represented by the purple lines. The color scale represents the frequency of interaction over time (from generation 4000 to 10000). The absence of interaction is represented by the color white. Network metrics represent the latest generation of each network. M = Modularity; C = Connectance; H2' Specialization; T = Consumer success rate; NODF = Nestedness. Note that for any value of ϕ species interactions are limited to subgroups, evidencing the stability of the evolutionary units.

With active choice the networks presented a wide range of metric values (modularity, from 0.14 to 0.77; H2', from 0.11 to 0.67; nestedness, from 14.45 to 76.91; connectivity, from 0.17 to 0.71; and consumer success rate, from 0.51 to 1). Most of networks with active consumer choice were more modular (96.8 %, 146,491 networks of a total of 141,827), more specialized (97.3%; 142,520 networks), less connected (94.4%, 138,256 networks), (36.0%; 52,659) and less nested (94.8%,138,963 networks) and more than a third presented a higher rate of consumer success (36.0%; 52,659) in relation to networks without the active choice behavior of the consumer(Fig. 5). Thus, with the resources options increasing, the networks became more modular and more specialized with greater success from consumers and less connected and nested. However, as neighborhoods increased, there is a transient time when all network metrics followed an opposite trend and became less modular and less specialized with lower success from consumers and more connected and nested. Also, some values of nestedness approaches the values produced by the null model. This indicates that the size of the interaction neighborhood results in a non-monotonic dynamic, generating two distinct topological patterns in the networks (Fig.5).

The increased pressure on the interaction maintained the high frequency of interactions mainly within the modules formed (Fig.4). On the other hand, the interactions between these modules ceased to exist or occurred less frequently. This generated modular, specialized networks, with less connectivity, less consumer success and less nestedness (Fig.4 - bottom panel, S4). The metrics of the networks showed a smaller range of values in relation to scenarios with active consumer choice: modularity: from 0.09 to 0.34; H2 'from 0.07 to 0.21; connectivity: from 0.39 to 0.82 and consumer success rate from 0.36 to 0.8 (Fig. 5, S5).

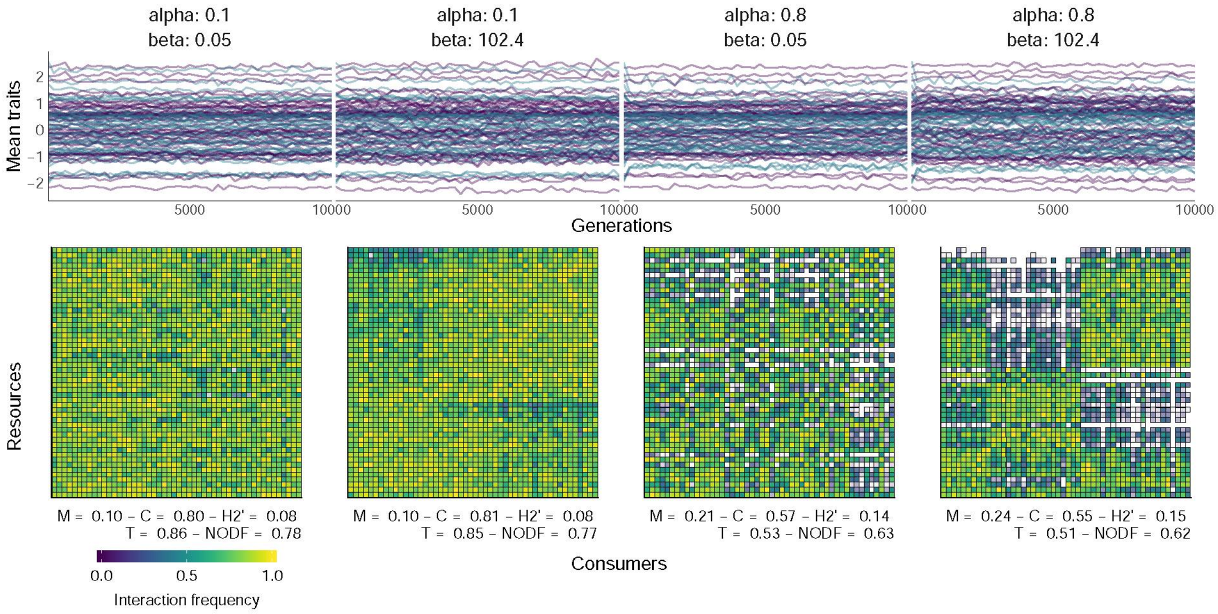

Fig.4| Coevolution without consumer active choice. Coevolutionary trait dynamics (top panel) and matrices of interactions between consumers and resources over time (bottom panel) under different intensities of pressure on interaction (α, β). The average traits of consumer species are represented by the blue lines and resource species are represented by the purple lines.The color scale and transparency represent the frequency of interaction over time. The absence of interaction is represented by the color white. Network metrics represent the latest generation of each network. M = Modularity; C = Connectance; H2' Specialization; T = Consumer success rate; NODF = Nestedness.

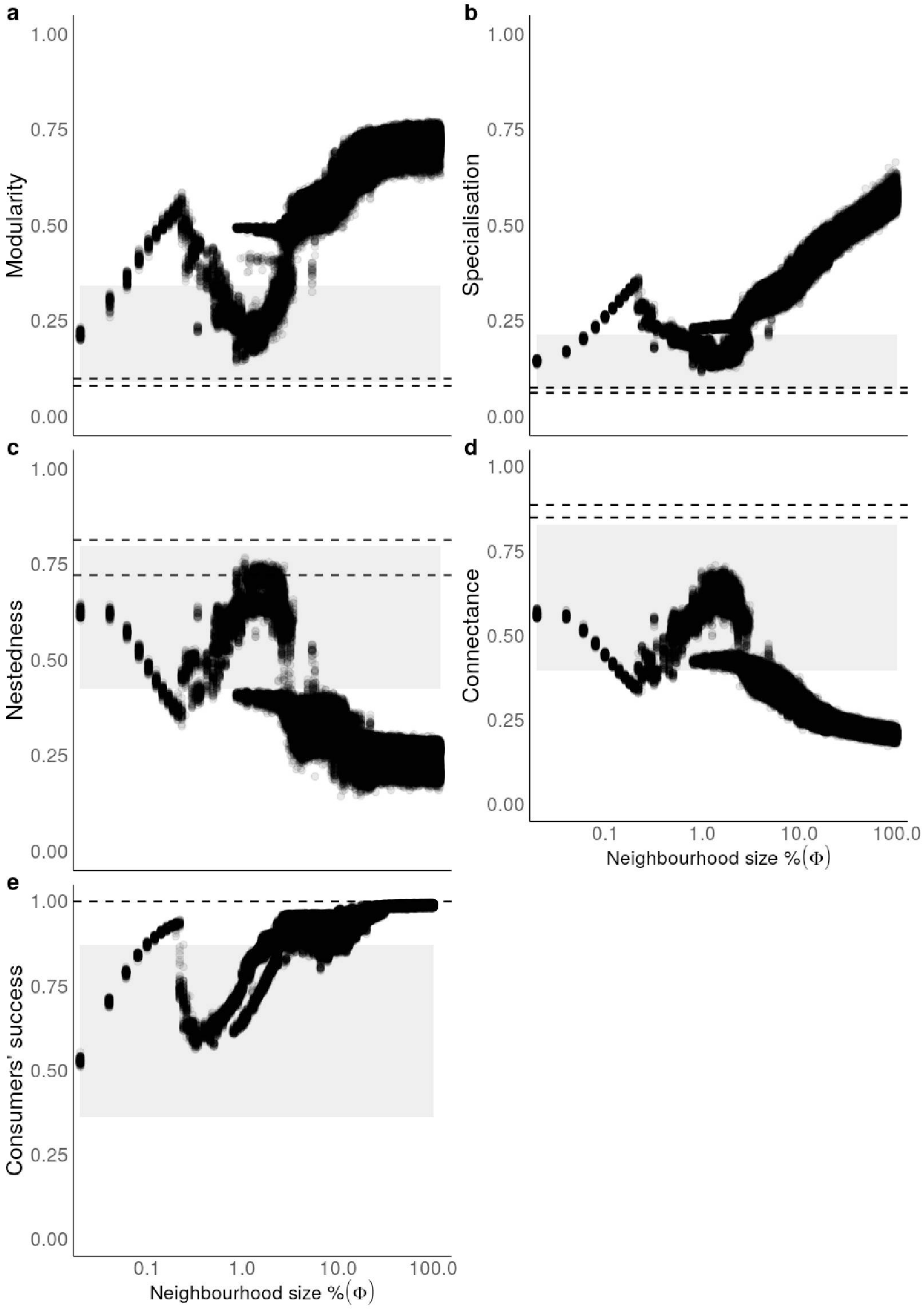

Fig.5|Network metrics in scenarios with active choice and without active consumer choice in relation to the size of the interaction neighborhood. (a) Modularity; (b) Specialization; (c) Nestedness; (d) Connectance and (e) Consumers' success. Each point represents a network of interactions for the case with active choice of the consumers, the grey bands represent the amplitude of the values of the metrics in the scenarios without the active choice, under different intensities of the pressure on the interaction. The dotted lines represent the amplitude of the metrics obtained in the null model (random interactions without any pressure). Observe that all network metrics did not follow a monotonous trend in relation to the size of the interaction neighborhoods: there are two trend inversions.

4. Discussion

We demonstrated that interactions given by consumer active choice behavior play an important role in eco-evolutionary dynamics. When interacting with resources that maximizes their fitness, the consumers preferentially link to the certain groups in the network. This non-random pattern of interaction reshapes the selective pressure regimes leading to trait convergence of both trophic levels. Thus, modules were formed by the coevolution on these groups and species composition in the modules are stable over time, characterizing coevolutionary units. Our study complements and extends a previous study, which shows that the explicit description in modeling of the mechanism of active consumer choice can change the eco-evolutionary dynamics between pairs of species[23]. Moreover, we show that higher intensities of pressure on the interaction is not a sufficient ingredient for the formation of well-defined modules or traits convergence. Also, we show that networks generated without any coevolutionary pressure can approach the value of metrics of networks with coevolutionary pressure.

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 of antagonistic networks. The species of consumers choose actively and track the resources that maximize their fitness inside a neighborhood and tend to interact tightly with them over time. They exert strong reciprocal selection on traits that converge and lock them inside the modules (Fig.3). As a consequence, the selective pressure, traits convergence and species composition inside the modules stay stable over time, characterizing a coevolutionary unit. The mechanism behind this is probably the same observed for two species interaction[23]. This study analytically showed that the active choice behaviour increases the probability of resource trait value keeping stable over time because any mutant resource that maximizes the consumer fitness will not go unnoticed by the consumer. In fact, our results show that in a module resource traits converge around an average value. The resources individuals are surrounded by consumer individuals in similar traits groups (Fig.3, upper panel). A small variation in a resource trait makes it a better resource choice by any of the surrounding consumers, reducing resource fitness. Also, the consumers may shift to other resource species inside the module over time. On the other hand, without active choice, the chance of a mutant consumer going unnoticed by the consumer increases and the stability of the module is generally broken (Fig. 4, upper panel). Thus, higher intensities of pressure on the interaction (α and β) is not a sufficient ingredient for the formation of well-defined modules or traits convergence.

It was suggested that modules are candidates for coevolutionary units once traits under convergent selection are often similar geographically[31]. The clearest evidence that supports this hypothesis is the registration of well-defined co-phylogenetic patterns and trait matching within modules in mutualistic networks[37]. However, in antagonistic interaction it is not expected trait convergence once the fitness benefit of a consumer implies in fitness prejudice of its resource. Under these conditions this is the first study to demonstrate the mechanism by which traits converge in antagonistic networks.

The fact that simulations with the same neighborhood size show different paths in eco-evolutionary dynamics reinforces the importance of random processes. Since species interactions may amplify the importance of initial random processes[42]. This is because the interactions between members of the neighborhood and the trade-offs of these interactions depend on the composition of the community[43]. We reinforce the idea that coevolution in these systems is not just a combination of pairwise interactions, rather, the set of differences in the community can generate different regimes selective pressures that influence trait evolution and diversification[44–48]. These results suggest that disturbances that cause loss of species and local homogenization of species attributes, such as current human disturbances, may result in changes in the eco-evolutionary[49,50].

In our model with active choice the increase of these discontinuities in dissimilarities between species are a product of coevolutionary dynamics. Although the modules are formed by species with similar θ_i (favored trait imposed stabilizing pressure), the convergence of traits is independent of this initial condition (see supplementary material Fig. S5 where $\theta_i = 0$ for all species and still allows the formation of modules), but depends on size of neighborhoods. Differently, in some models, the distribution of traits in order to maximize the dissimilarity between resources imposed a priori may lead to the formation of modules even without the explicit modelling of the active choice behavior, due to the impossibility of successful interactions occurring between individuals of different groups. Also, some studies adjust the traits distributions using information of empirical networks, that include implicitly that dissimilarity[22].

Considering that the increase in the neighborhood of interactions is a form of coevolutionary pressure, we also emphasize that the directionality of the metrics may not be directly correlated with the intensity of that pressure. At first glance, it is reasonable to expect that the increased interaction neighborhood will make the consumer more specialist in some resource, increasing modularity and specialization and reducing network nestedness. However, such a trend was not always observed; on an adaptive time scale, increasing the interaction neighborhood did not necessarily increase consumer success and network metrics can shift their trend (see Fig.5).

In this model, we were able to evaluate the effects of active choice behavior in eco-evolutionary dynamics using simplifications (see methods). We suggest that future studies include more ingredients in modelling to capture more information about this mechanism. For example, asexual inheritance can be a limitation for generalization of the model, although there are several types of antagonistic interactions in which the interacting species present asexual reproduction, as in interactions between bacteria - viruses[51–55] or bacteria - protists[56,57], bacteria - nematodes[58,59], daphnias - parasites[60,61]. The spatial homogeneity disregards the differences between landscapes, as well as the gene flow. Species could coevolve in some populations but not in others due to the geographic mosaic[31,62]. Finally, the equivalence between generations of consumers and resources that disregards the consumer and resource life cycle can be very different, including several generations of consumers in relation to a single generation of the resource, as in parasite-host relationships[34].

In conclusion, we show that the consumers' active choice for resources that maximize their fitness is a crucial element for the formation of coevolutionary units. That is, modules formed through the coevolutionary process. As far as we know, this work is the first to demonstrate the mechanism by which traits converge in antagonistic networks. Furthermore, the variation in the structure of the networks follows a non-monotonic dynamic, which may not be directly correlated with the intensity of the coevolutionary pressure imposed by the size of the neighborhoods or the trait's amplitude.

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Supplementary material

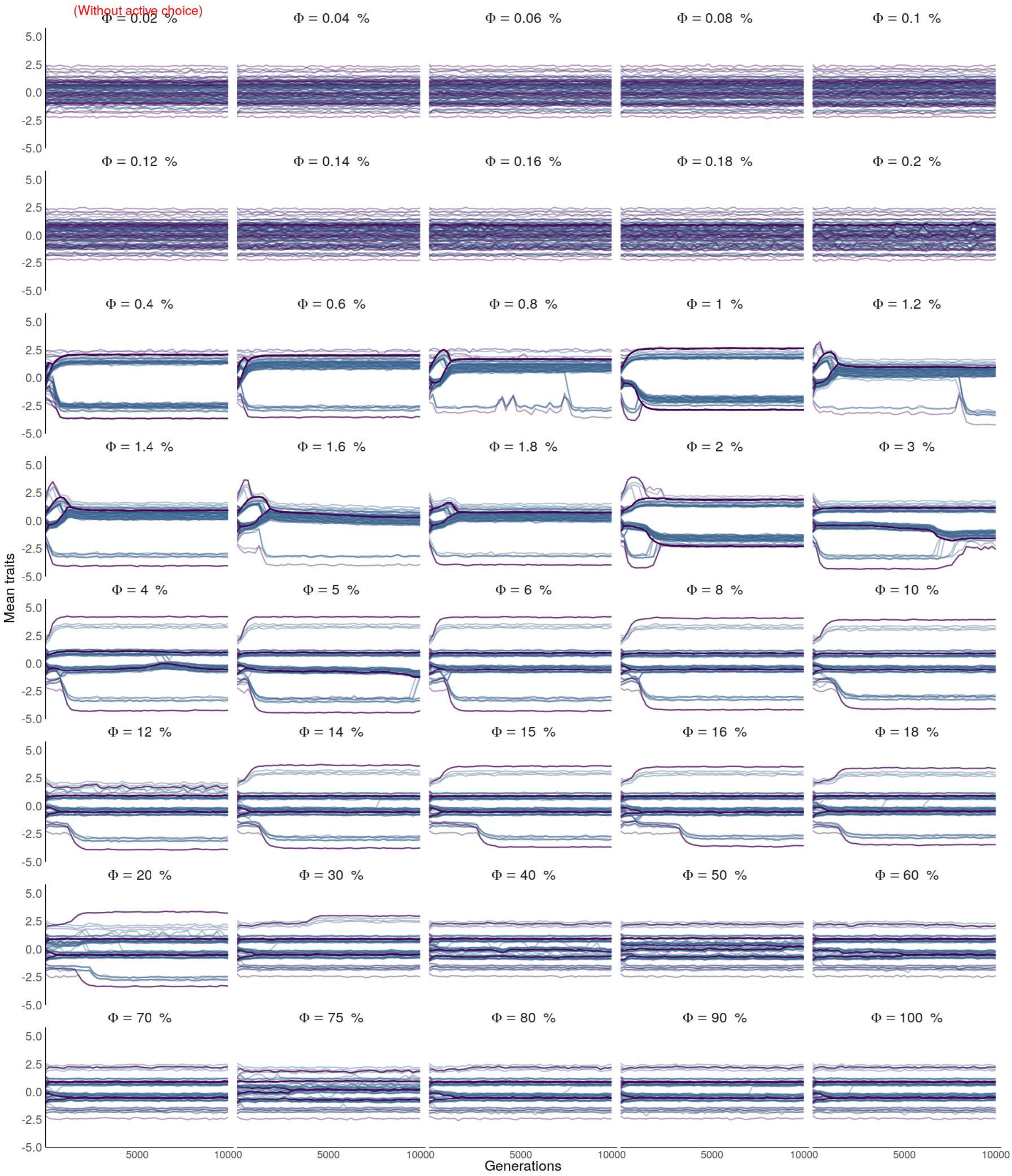

Fig.S1|Coevolutionary dynamics in different neighborhood sizes of interactions in the model with active choice. The average phenotypes of the consumer species are represented by the blue lines and the resource species are represented by the purple lines. Note that in intermediate values of Φ the phenotypes evolve to more extreme values. The active choice in conjunction with the size of the interaction neighborhood changed the coevolutionary dynamics. The dynamics were similar to the scenario without active choice in neighborhoods with sizes between $\Phi = 0.02\%$ and $\Phi = 0.2\%$. From that value of Φ, the phenotypes of the resources converged. These converging phenotypes evolved towards the ends of the phenotypic space, moving away from the optimal values imposed ((θ_i)) by the stabilizing selection. Consumers also showed a convergence of phenotypes (see $\Phi = 0.6\%$, for example). In even larger neighborhoods, resource phenotypes were trapped between consumer groups with similar phenotypes, forming coevolutionary units (see $\Phi = 100\%$, for example).

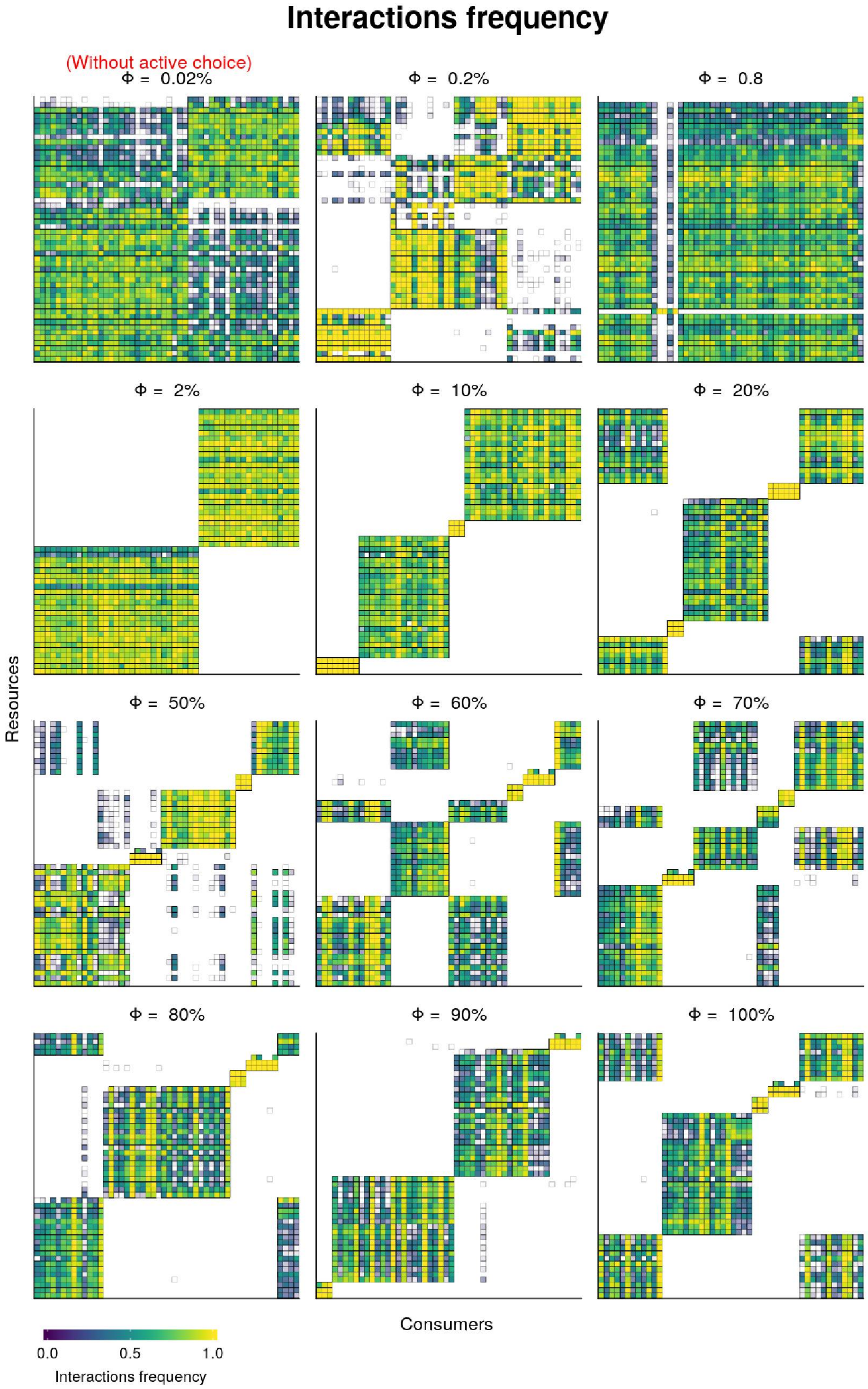

Fig.S2| The matrices represent the interactions performed in the last generation (10,000) of the coevolutionary dynamics shown in Fig. S1 for selected values of Φ. Colors represent the modules and transparency, the frequency of interactions. NODF = Nesting; M = Modularity; C = Connectivity; H2 '= Specialization; T = Consumer success rate.

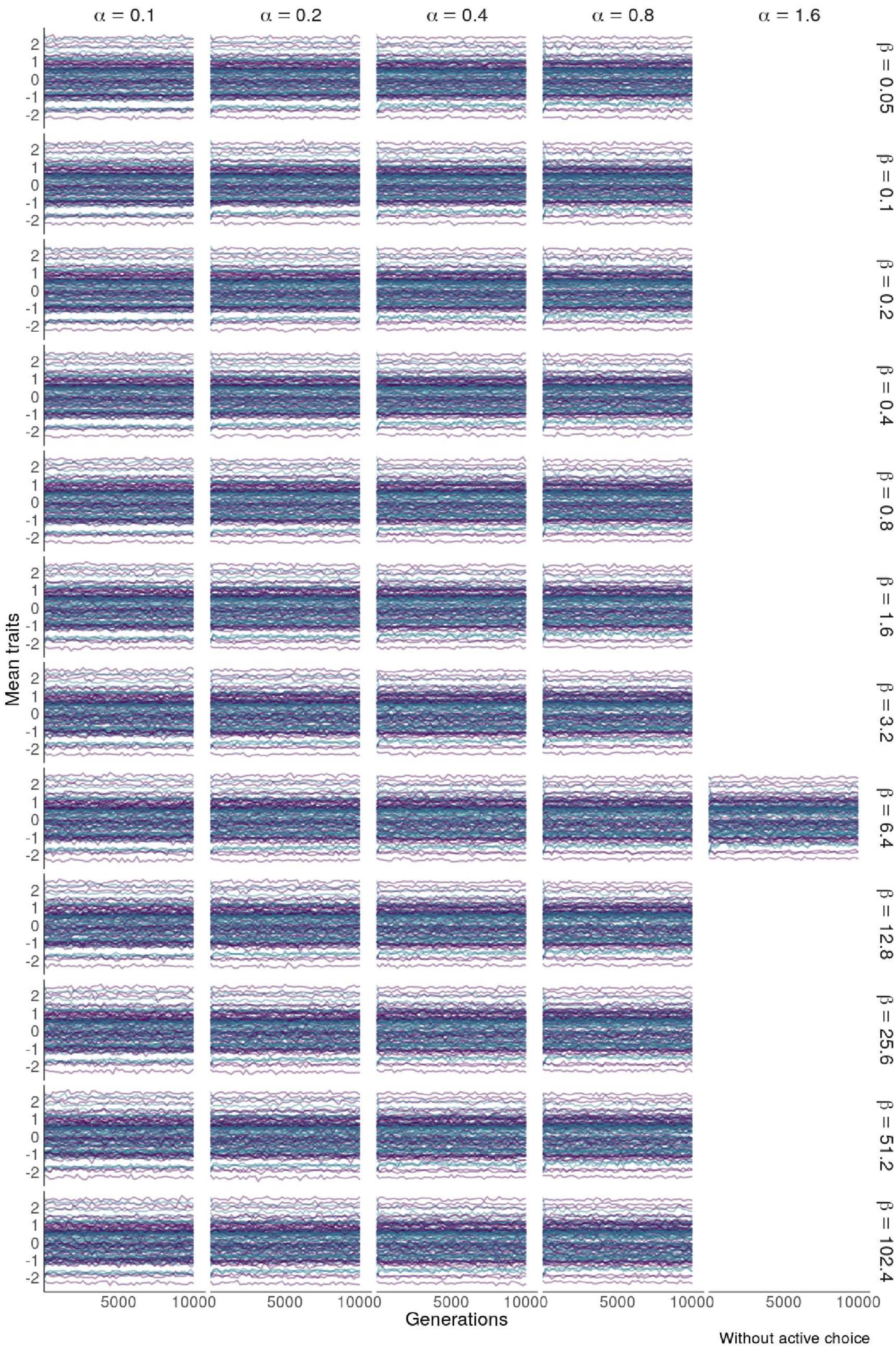

Fig.S3| Coevolutionary dynamics in different intensities of interaction pressure in the model without active choice. The average phenotypes of the consumer species are represented by the blue lines and the resource species are represented by the purple lines.

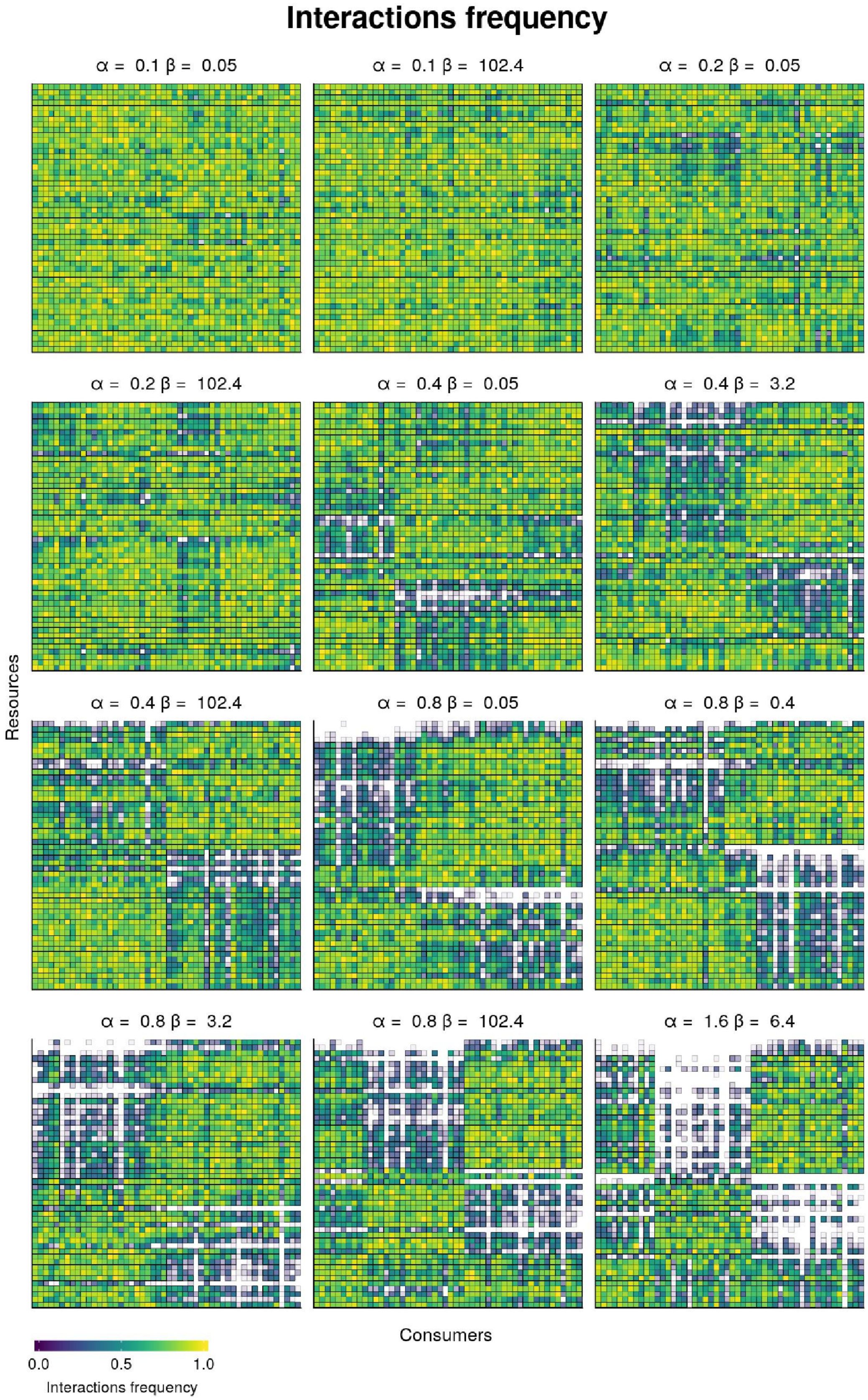

Fig.S4| The matrices represent the interactions performed in the last generation (10,000) of the coevolutionary dynamics shown in Fig. S3 for selected values of Φ. Colors represent the modules and transparency, the frequency of interactions. NODF = Nestedness; M = Modularity; C = Connectivity; H2 '= Specialization; T = Consumer success rate.

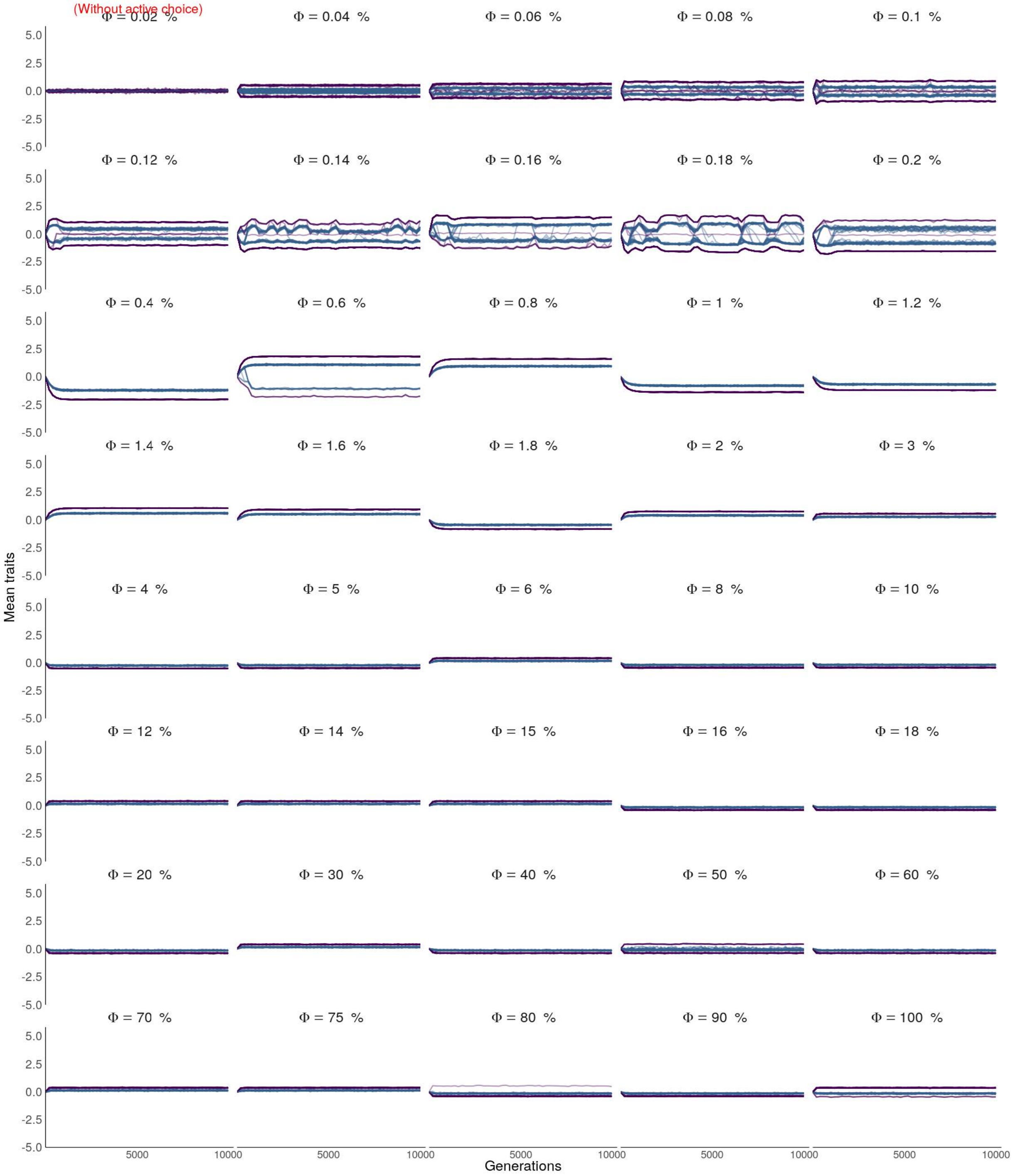

Fig.S5| Coevolutionary dynamics in different neighborhood sizes in the model considering $\theta_i = 0$. The average traits of the consumer species are represented by the blue lines and the resource species are represented by the purple lines. In general, the increase in the interaction neighborhood allows for greater convergence between the phenotypes of the species, on the other hand, a higher trait's amplitude occur when such a neighborhood of intermediate size. With these results we reinforce that the effect of the formation of coevolutionary units depends strongly on the consumers's active choice and does not depend on the initial distribution of the values of θ_i.

Empirical networks

In order to verify which model better describes the network metrics observed in real communities, we used the specialization *H2 '*[1] and the modularity M^2 to compare the networks obtained in simulations with empirical networks. These metrics were selected because they are less sensitive to variations in relation to network sizes, which allows the comparison between networks with different species numbers. We used 51 network interactions between parasites and hosts (fleas and mammals) analyzed in the study by Hadfield and collaborators (2014)[3] available in the database [Web-of-life] (http://www.web-of-life.es/). To compare network metrics we use the *Z-score* to standardize the metrics of each network:

$$Z = \frac{X_{obs} - \overline{X}_{sim}}{\sigma_{X_{sim}}} \tag{1.1}$$

where X_{obs} is the value of the metric of the empirical network, $\overline{X}_{sim}$ is the mean of simulated networks and $\sigma_{X_{sim}}$ is its standard deviation of the simulated networks. We considered two groups of simulated networks: (i) generated by the simulation with no active choice; (ii) generated by all values of Φ but, as mentioned before, keeping $\alpha = 0.8$ and $\beta = 0.2$. In this way, for each empirical network we had three *Z-score* values.

The specialization and modularity of the 51 empirical networks showed a wide range of variation: Specialization varied between 0.05 and 0.94 and modularity varied between 0.01 and 0.71. Empirical networks were best described by the model with active consumer choice (distance less than 2 standard deviations). The networks generated in the scenarios with active choice (considering all values of Φ and setting α and β) described the specialization of 33 networks (64.7%, Fig 6 a) and the modularity of 21 (41.17%, Fig. 6 b). On the other hand, the networks generated in the scenarios without active choice described the specialization of only three empirical networks (5.88%, Fig. 6 c) under different interaction pressures. Regarding modularity, 15 empirical networks were described (29.41%, Fig. 6 d) by both models.

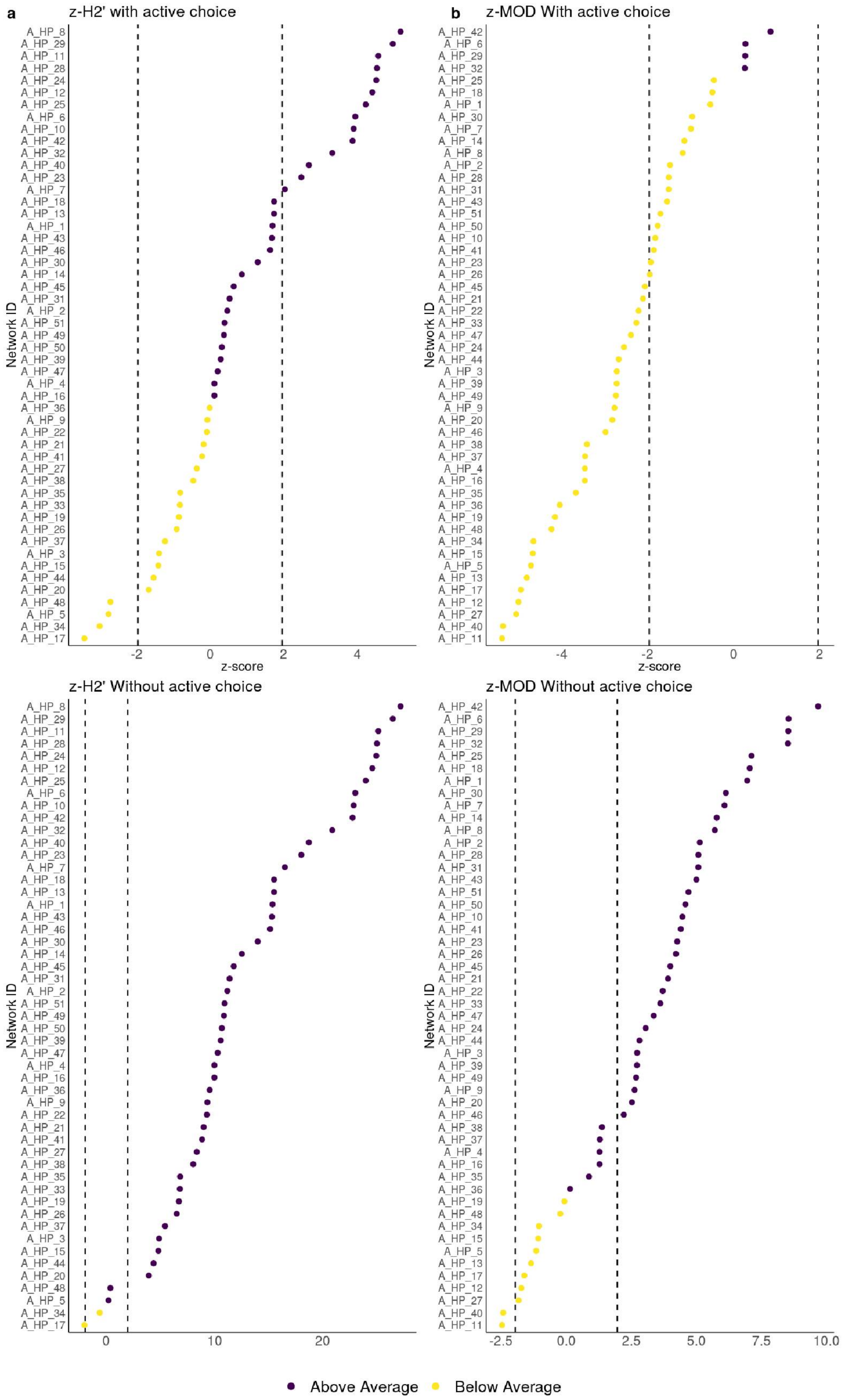

Fig.S6|Comparison between the Specialization and Modularity of empirical networks and the theoretical networks of scenarios with and without active choice. Figures (a) and (b) show how far the empirical metrics are from the predictions made by the model with active choice while (c) and (d) from the model without active choice. Dashed lines highlight the 95% of the modeled networks. Observe that the model with active choice better approaches most of the empirical networks when compared to the model without active choice.

Appendix S2| R-Packages

R-base [4] - knitr [5] - markdown [6] - here [7] - ggsci [8] - cowplot [9] - ggpubr [10] - reshape2 [11] - igraph [12] - grid [13] - gridExtra [13] - viridis [14] - tinytex [15] - bookdown [16] - bookdownplus [17] - citr [18] - ggforce [19] - kableExtra [20] - RColorBrewer [21] - foreach [22] - doMC [23] - bipartite [24] - scales [25] - ggthemes [26] - devtools [27] expss [28] - captioner [29] - tidyverse [30] - dplyr [31] - gmodels [32]

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