Paula Lemos da Costa

Variação intrapopulacional no uso do recurso:
modelos teóricos e evidência empírica

Intrapopulation variation in resource use:
theoretical models and empiric evidence

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Aos meus pais, por serem
sempre uma inspiração magnífica

Epígrafe

“essentially, all models are wrong, but some are useful.”

George E. P. Box
(1919-2013)

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Introdução Geral

Tradicionalmente, a ecologia trata os indivíduos de uma mesma população como ecologicamente equivalentes em relação ao uso de recursos (Gustafsson 1988). Sendo assim, uma das suposições centrais de diferentes teorias ecológicas é que todos os indivíduos de uma população fazem uso dos mesmos tipos de recurso e em intensidade similar (Chase e Leibold 2003). O nicho populacional frequentemente é definido pelo uso médio dos recursos pelos indivíduos de determinada população. A noção de nichos individuais recebeu historicamente pouca atenção em ecologia, sob a suposição de que o nicho de um indivíduo é uma aproximação do nicho populacional, e as diferenças entre indivíduos seriam simplesmente desvios em relação ao nicho populacional (Pielou 1972). Variações encontradas entre diferentes populações de uma mesma espécie foram então atribuídas a diferenças entre os locais de ocorrência de cada população, e poderiam ser causadas, por exemplo, por diferenças entre micro-habitats encontrados em cada local (Patterson 1983). Dessa forma, variações intrapopulacionais seriam ocasionadas por fatores externos à população e eventuais variações no uso do recurso entre os indivíduos não seriam relevantes para a dinâmica ecológica (Estes *et al.* 2003). No entanto, ao desconsiderar as variações entre os indivíduos, é possível que se percam informações importantes para entender os mecanismos responsáveis pela dinâmica das populações. Assim, uma avaliação dessa perda de informação se torna fundamental para entendermos as implicações de uma abordagem que descreve indivíduos por meio de médias populacionais. Por exemplo, é possível que a variação intrapopulacional modifique as dinâmicas populacionais e evolutivas destes organismos (Bolnick *et al.* 2011). Ainda, a variação

intrapopulacional pode elucidar como decisões comportamentais e interações ecológicas, como a competição, influenciam o uso de recursos por indivíduos (Tinker *et al.* 2012).

A ausência de variação intrapopulacional no uso de recursos na maioria das teorias ecológicas foi uma simplificação que permitiu avanços significativos na construção e desenvolvimento da ecologia. Entretanto, a ocorrência de variação no uso de recursos entre indivíduos de uma mesma população tem sido descrita para uma ampla gama de espécies de animais (West 1986, Werner e Sherry 1987, Gustafsson 1988, Estes *et al.* 2003, Martins *et al.* 2008, Araújo *et al.* 2009a). Um crescente número de estudos teóricos tem mostrado que variação intrapopulacional pode influenciar substancialmente dinâmicas ecológicas e evolutivas quando incorporada em estudos de modelagem (Kondoh 2003, Svanbäck e Bolnick 2005, Okuyama 2008, Bolnick *et al.* 2011). Por exemplo, a incorporação de variação intrapopulacional no uso de recursos em modelos predador-presa e em estudos de teias tróficas, por exemplo, possui efeito de estabilizar a dinâmica de comunidades (Kondoh, 2003; Okuyama, 2008).

Diferentes fatores podem gerar a variação intrapopulacional. Por exemplo, no marsupial *Gracilinanus microtarsus* (Marsupialia: Didelphimorphia) a variação no uso dos recursos entre indivíduos é parcialmente explicada por diferenças entre os sexos (Martins *et al.* 2008). Ainda, indivíduos de uma mesma espécie em distintas fases do desenvolvimento podem usar recursos diferentemente, de acordo com suas necessidades metabólicas, ou ainda por restrições impostas pela idade (Gustafsson 1988). Por fim, a variação intrapopulacional pode ser causada por variação no uso do recurso que parece ser intrínseca ao indivíduo e que foi descrita como especialização individual (*sensu* Bolnick *et al.* 2003).

Especialização individual ocorre quando um indivíduo consome apenas parte dos recursos consumidos pela população, e essa variação não pode ser atribuída ao sexo, à idade, a fatores ambientais, à dificuldade de caracterizar a dieta do organismo ou à forma com que o organismo usa o ambiente (Bolnick *et al.* 2003). Por exemplo, a variação no comportamento alimentar dos indivíduos de uma população de tentilhões da ilha de Cocos, *Pinaroloxias inornata*, da Costa Rica (Passeriformes: Thraupidae) não parece estar associada a nenhum desses fatores (Werner e Sherry 1987). O mesmo padrão de variação no comportamento alimentar de indivíduos de uma mesma população foi observado para as lontras marinhas *Enhydra lutris* da costa oeste dos Estados Unidos (Carnivora: Mustelidae) (Estes *et al.* 2003). Uma das principais consequências da variação intra-populacional no uso de recurso é que a aptidão de um indivíduo pode ser influenciada não somente por efeitos dependentes de densidade, mas também por efeitos dependentes de frequência (Gustafsson 1988, Sargeant 2007).

Dependência de densidade ocorre quando o uso de recurso é influenciado simplesmente pela densidade populacional dos consumidores. Em baixas densidades populacionais, a teoria prediz que indivíduos tendem a utilizar os recursos que maximizam o ganho de energia e nutrientes fundamentais para o desenvolvimento. Em uma versão simplificada, o problema fundamental pode ser visto como a maximização do ganho energético por unidade de tempo (Stephens e Krebs 1986, Pierce e Ollason 1987). Em altas densidades populacionais, a competição intra-específica pelos recursos pode ser maior, levando alguns indivíduos a adicionarem novos itens alimentares em suas dietas. A dependência de frequência ocorre quando indivíduos dentro de uma população consomem recursos diferentemente, sendo o uso de um dado recurso determinado não somente pela densidade populacional total, mas

também pela frequência de indivíduos utilizando este recurso. Como consequência da dependência de frequência, o consumo de uma presa sub-ótima (e.g. que não apresenta alto teor calórico ou que é difícil de ser processada), pode ser benéfico para o indivíduo se apenas uma pequena parcela da população estiver utilizando este recurso. O consumo de um recurso sub-ótimo está atrelado a uma redução na intensidade de competição intraespecífica, o que compensa a qualidade inferior do recurso (Estes *et al.* 2003, Sargeant 2007). Tanto mecanismos dependentes de densidade quanto mecanismos dependentes de frequência podem levar à expansão do nicho populacional, levando à variação na dieta dos indivíduos (Svanbäck e Bolnick 2005).

A expansão do nicho populacional causada pela variação na dieta dos indivíduos dentro de uma população pode ser explicada à luz da teoria da dieta ótima (em inglês *Optimal Diet Theory* – (Stephens e Krebs 1986), segundo a qual os indivíduos consomem apenas parte dos recursos disponíveis, maximizando seus ganhos energéticos (Svanbäck e Bolnick 2005). Indivíduos podem apresentar dietas ótimas distintas de acordo com suas habilidades de procura, captura, processamento e digestibilidade de suas presas (Araújo *et al.* 2011). Três modelos distintos de variação na preferência por presas foram propostos como simplificações que ilustram regras de partilha de recursos bem distintas (Svanbäck e Bolnick 2005). O modelo de “preferências compartilhadas” supõe que todos os indivíduos apresentam a mesma ordem de preferências de suas presas, porém diferem em sua propensão à adição de novas presas em suas dietas. No modelo de “refúgio competitivo”, os indivíduos de uma mesma população possuem a mesma presa predileta, mas usam presas alternativas distintas. No modelo de “preferências distintas” os indivíduos de uma mesma população apresentam presas prediletas distintas (Svanbäck e Bolnick 2005).

Os diferentes modelos de dieta ótima descritos acima predizem padrões de uso de recurso distintos. Desta forma, cada modelo pode fornecer um catálogo de padrões esperados para diferentes aspectos da variação intra-populacional no uso de recurso (Pires *et al.* 2011a). Estas expectativas teóricas podem ser contrastadas com padrões observados em populações naturais. Neste contexto, a abordagem de redes complexas (Albert e Barabási 2002) permite a caracterização detalhada da estrutura das relações tróficas. Essa descrição das relações tróficas, por sua vez, permite a seleção entre diferentes modelos, com base na comparação entre os padrões estruturais emergentes dos modelos e os padrões estruturais empíricos (Pascual e Dunne 2005). Em tese, um modelo capaz de reproduzir os padrões estruturais observados em populações naturais inclui parte dos mecanismos fundamentais responsáveis por gerar tais padrões.

As interações tróficas entre presas e predadores podem ser descritas por uma rede, na qual presas e predadores são representados por pontos, e linhas conectando diferentes pontos descrevem interações tróficas (Pimm 2002). A estrutura das redes pode ser caracterizada por métricas originadas em diferentes campos da ciência, incluindo teoria de grafos, mecânica estatística e sociologia estrutural (Albert e Barabási 2002). Estas métricas tem sido usadas para caracterizar interações tróficas entre espécies (Bascompte e Melián 2005, Guimarães *et al.* 2007b, Pires *et al.* 2011a) e interações sociais entre indivíduos em uma população (Guimarães *et al.* 2007a, Lusseau *et al.* 2009, Cantor *et al.* 2012). A abordagem de redes é uma ferramenta útil para o estudo da variação intra-populacional no uso de recurso, permitindo investigar as estruturas que emergem no nível da população em decorrência da variação individual detectada em populações naturais. Além disso, a abordagem de redes permite inferir processos que geram os padrões

observados (Araújo *et al.* 2008, 2009b, Pires *et al.* 2011a, Tinker *et al.* 2012).

A abordagem de redes permitiu identificar o padrão de uso de recursos de algumas espécies de animais. Por exemplo, ao estudar a dieta de uma população de marsupiais (*Gracilinanus microtarsus*, Marsupialia: Didelphimorphia) constatou-se que essa população é composta por indivíduos mais seletivos e indivíduos menos seletivos (Araújo *et al.* 2009b). Foi observado que a dieta dos indivíduos mais seletivos era um subconjunto previsível e ordenado da dieta dos indivíduos menos seletivos, um padrão conhecido como aninhamento (Atmar e Patterson 1993). Este padrão foi associado ao modelo de preferências compartilhadas, no qual indivíduos dentro de uma população compartilham a mesma sequência de preferências por presas (Araújo *et al.* 2009b). Um padrão modular em uma rede, onde grupos de indivíduos dentro da população estão mais conectados entre si do que com indivíduos de outros módulos, estaria associado com o modelo de preferências distintas. Esses grupos de indivíduos representam indivíduos que compartilham preferências por espécies de presas, formando módulos dentro das populações (Araújo *et al.* 2008). Determinados padrões estruturais em redes de interação tem sido associados com os diferentes modelos de dieta ótima. No entanto, a investigação do tipo de padrão que poderia ser esperado dadas as premissas de cada modelo é um campo ainda em expansão. O próximo passo na análise da variação intrapopulacional é associar previsões, em termos de padrão estrutural de redes de interação, a modelos alternativos de uso de recurso. Neste sentido, uma das grandes vantagens da abordagem de redes complexas é a possibilidade de desenvolver modelos que consideram o contexto em que cada indivíduo está inserido, além de permitir o uso de diversas métricas para caracterizar as interações observadas na natureza. Desse

modo, é possível revelar padrões emergentes, que não são observados quando os indivíduos são considerados isoladamente, permitindo assim a diferenciação entre modelos (Lewinsohn *et al.* 2006; Allesina *et al.* 2008). A abordagem de redes complexas constitui uma ferramenta eficaz para a construção de modelos que visam gerar redes teóricas que reproduzam a estrutura de redes de interação empíricas segundo um conjunto de regras (Allesina *et al.* 2008). O conjunto de regras usado para gerar cada rede de interação teórica incorpora parte dos princípios considerados importantes na determinação dos padrões observados. Assim, esse tipo de abordagem permite fazer inferências embasadas em previsões quantitativas, o que possibilita ir além da associação intuitiva entre padrão observado e estrutura da rede de interação.

Objetivos gerais

A presente dissertação teve três objetivos principais. Em primeiro lugar, explorar as diferenças nas previsões de modelos de dieta ótima por meio da combinação de modelos matemáticos e a análise das diferenças topológicas das redes de uso de recursos alimentares. Em segundo lugar, testar as predições dos diferentes modelos em cinco populações naturais, de três espécies distintas, para as quais os dados de variação no uso de recurso estão disponíveis. Em terceiro lugar, determinar qual dos modelos foi capaz de gerar predições teóricas que mais se assemelhavam aos padrões observados na natureza.

Exploring underlying processes structuring individual-resource networks

Exploring underlying processes structuring individual-resource networks

Paula Lemos-Costa¹, Mathias M. Pires¹, Márcio S. Araújo², Paulo R. Guimarães Jr.¹

¹ Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil

² Departamento de Ecologia, Universidade Estadual Paulista “Júlio de Mesquita Filho”, Rio Claro, Brazil

Abstract

Intrapopulation variation in resource use is a common pattern found in animal populations. To explore distinct ways in which individuals vary in resource use individual-resource networks, which represent the feeding interaction between individuals and the resources they consume, are a useful tool. We investigated possible mechanisms generating variation among individuals in resource use. We used three models describing how individuals facing intraspecific competition could exploit resources: (i) individuals could share the same rank preference for prey but differ in their likelihood to add alternative resources to their diets (shared preferences model); (ii) individuals could share the same top-ranked resource and rely upon different alternative resources (competitive refuge model); (iii) individuals could have distinct top-ranked resources (distinct preferences model). For each model we performed a set of numerical simulations that generated quantitative predictions regarding the structure of individual-resource networks and compared them with empirical data describing variation in resource use in five populations from three different animal species. We compared each model's ability in reproducing features of empirical networks, and performed spectral analysis to assess models' fit. For most networks studied, the shared preferences model was the one with the worst performance, whereas the other two models investigated had a similar performance. Our approach highlights the importance of generating quantitative predictions in order to accurately define and differentiate possible mechanisms leading to variation in resource use. Our findings suggest, for the set of species we studied, that the rank sequence of prey items is more important in structuring the pattern of resource use within the population rather than the likelihood of adding new prey items.

Introduction

Individuals within a population can show substantial variation regarding many aspects of their ecology, life history and traits. Age stages, sex, morphology, and learning behavior are important drivers of intrapopulational variation (Grant *et al.* 1976, Gustafsson 1988, Tinker *et al.* 2009, Masri *et al.* 2013), which is a phenomenon found in many animal populations (Bolnick *et al.* 2003). Intrapopulational variation can affect ecological processes such as predation rates and the degree of intraspecific competition, which in turn can scale up to alter the patterns and the stability of interactions among species (Hughes *et al.* 2008, Araújo *et al.* 2011, Bolnick *et al.* 2011). Evolutionary dynamics are also affected by individual variation in resource use, which may lead to the emergence of stable polymorphisms and, eventually, speciation (Dieckmann and Doebeli 1999).

One way to examine the frequency and importance of intrapopulational variation is to investigate niche variation among individuals (Bolnick *et al.* 2002). A theoretical framework used to explain the basis of individual variation is optimal diet theory (ODT, Stephens and Krebs 1986). ODT predicts that an individual should maximize its energy gain given the prey's costs and benefits, which are related to the energy content of the prey and the handling and search time associated with the prey. If individuals follow different rules in maximizing prey items, they should differ in their prey choices and hence differ in rank preferences for different prey. There are several ways by which individuals can differ in their rank preferences and a good starting point is to use simple models to address how such differences can emerge between individuals.

Svanbäck and Bolnick (2005) developed genetically explicitly models that explored three different ways in which individuals exploit

resources, given the degree of intraspecific competition and resource availability. Individuals can either share the same rank preference for prey but differ in their willingness to add alternative prey to their diets (Shared Preferences Model); individuals can share the same top-ranked prey and differ in their alternative prey (Competitive Refuge Model); or individuals can differ in their top-ranked prey (Distinct Preferences Model). As intraspecific competition increases individuals are expected to add prey items to their diets according to their rank preferences (Svanbäck and Bolnick 2005). In this sense, each model presents a specific feeding strategy, which is associated with the individual's phenotype. As a consequence, each feeding strategy results in a specific pattern of resource use within the population (Figure 1).

Figure 1: Representation of the predictions associated with each model. Orange snail represents individuals' predators in the population. The four remaining columns represent diet items sorted following individuals' rank preferences. Resources on the left column are preferred over resources on the column to the right. **A** Shared Preferences Model, all individuals share the same rank sequence of prey items but differ in their willingness to add alternative prey; **B** Competitive Refuge Model, all individuals share the same top-ranked prey but differ in their secondary prey choices; and **C** Distinct Preferences Model, individuals have different top-ranked prey.

It is possible to investigate the patterns of resource use within a population by measuring diet overlap among individuals and between individuals and the population (Bolnick *et al.* 2002). When individuals use resources differently, they differ in their diet similarity and hence the degree in which two individuals overlap is always variable. An efficient way to describe diet overlap is using interaction networks (Araújo *et al.* 2008, 2009b). There are multiple metrics that allow the characterization of pairwise overlap among individuals (Bolnick *et al.* 2002). More recently, it was shown that the use of network approach to describe patterns of resource use allows new insights on the processes and implications of individual variation (Araújo *et al.* 2008). When investigating diet overlap nodes can represent individuals and links between pairs of nodes can represent pairwise diet overlap between individuals (individual-individual networks - Araújo *et al.* 2008). Another way to investigate diet overlap using networks is to represent individuals as one set of nodes and the preys they consume as another set of nodes. A link between the two sets of nodes will represent the feeding interaction between the individuals and their prey (individual-resource networks - Pires *et al.* 2011a, Tinker *et al.* 2012). Individual-individual networks are very useful when investigating pairwise overlap between individuals' diets, however when using this sort of networks, information regarding the resources that are consumed by a single individual is lost. In this sense, individual-resource networks can be more informative, because they content all information regarding the pattern of resource use within the population. The structural patterns formed by individual-resource interactions can be assessed using network metrics, such as nestedness and modularity, informing about distinct aspects of how individuals share resources.

Nestedness is a structural pattern found in networks representing different types of interactions, such as the interaction between mutualistic partners and predator-prey interactions (Bascompte *et al.* 2003, Pires *et al.* 2011a). In networks representing the feeding interaction between individuals and resources, a nested pattern is found when the diet of selective individuals is a predictable subset of the diet of less selective individuals (Araújo *et al.* 2009b). Modularity emerges when groups of individuals share similar diets but differ from other groups of individuals, forming subsets (modules) of nodes (individuals and resources) that are more connected to each other than other nodes within the network (Guimerà and Amaral 2005, Tinker *et al.* 2012).

The structure of individual networks can provide information about possible mechanisms generating the observed pattern. Studies investigating individual networks have associated the structure of these networks to each of the models of resource use (Araújo *et al.* 2008, 2009b, Pires *et al.* 2011a, Tinker *et al.* 2012). Networks in which the diets of selective individuals were nested subsets of the diets of less selective individuals were consistent with the Shared Preferences Model (Araújo *et al.* 2009b, Pires *et al.* 2011a). A structural pattern that identified groups of individuals in a population, each having a different top-ranked prey is consistent with the Distinct Preferences Model (Araújo *et al.* 2008). Networks indicating that the core prey selected by individuals were similar and alternative prey differ among individuals were consistent with the Competitive Refuge Model (Tinker *et al.* 2012).

So far, the overall structure of networks at the level of individuals has been associated with the expected patterns generated by the proposed mechanisms. The next step in unraveling the underlying mechanisms of the variation in patterns of resource use within populations is to move forward from the intuitive link between the models and the expected

structural patterns arising from each model, so that we can associate each mechanism to a specific pattern. To do so, we aim to generate quantitative predictions, regarding network structure, to be expected by each proposed mechanism. To derive such predictions we developed an approach using simple rule-based models. A simple model is used to build interaction networks given a set of simplistic rules that describe a certain process thought to be important in shaping the pattern of interaction (eg. Allesina *et al.* 2008). Similar models have been used in ecology to test hypotheses on the structure of food web and mutualistic interactions (Williams and Martinez 2000, Pimm 2002, Pires *et al.* 2011b). We used a similar approach to generate theoretical predictions associated with each of Svanbäck and Bolnick's (2005) models, considered possible mechanisms generating variation in resource use within populations.

We generalized models of resource use describing individuals with different feeding strategies preying upon five resources (Svanbäck and Bolnick 2005). In order to be able to generalize such models, we simplify them into minimal set of simple rules defining the interactions between i individuals and the j resources they consume. Each model is considered a hypothesis about how individuals within a population may partition the resources they consume. We combined numerical simulations and tools originated from network theory, such as spectral analysis of networks, to derive theoretical predictions associated with each model. We confronted these predictions with empirical data of well-studied animal populations in which evidence for intrapopulation variation is compelling in order to determine which model represents the most likely mechanism underlying the structure of intrapopulation variation.

Methods

Dataset

Our goal is to test the possible underlying mechanisms generating the patterns of resource use among individuals within a population. To do so, we compared models' ability in reproducing structural properties of real individual-resource networks (see below). We used 5 individual-resource binary networks describing feeding habits of five populations from 3 different animal species. The networks used in the present study are known to represent populations with considerable amount of individual diet variation, in which individuals within the population use a subset of total population niche, and this pattern is not explained by individuals' age, sex, morphology, environmental heterogeneity, or sampling biases (West 1986, 1988, Werner and Sherry 1987). Rather, the variation among individuals in the dataset used is intrinsic from each individual. This intrinsic variation allows exploring the putative role of rules of interaction in shaping individual variation without the influence of other effects that could affect the pattern of resource use, such as sex, age, morphology or environmental features.

The first network analyzed is from a population of Darwin's finch *Pinaroloxias inornata* (Passeriformes, Emberizidae) from Cocos Island, Costa Rica (Werner and Sherry 1987). The *Pinaroloxias* network comprised 21 sampled individuals that consumed 7 resources, leading to a connectance, the proportion of interactions that do occur within a network given all possible interactions, of $C = 0.34$. The second and third networks analyzed are from two populations of the Californian marine snail *Nucella emarginata* (Neogastropoda, Muricidae - West 1986). The *Nucella* A (site A) network comprised 20 sampled individuals that

consumed 7 resources ($C=0.31$) and the *Nucella B* (site B) network comprised 31 sampled individuals consuming 3 resources ($C=0.59$). The fourth and fifth networks analyzed are from two populations of the marine snail from Panama *Thais melones* (Neogastropoda, Muricidae - West 1988). The *Thais A* (site A) network comprised 42 sampled individuals that consumed 8 resources ($C=0.29$) and the *Thais B* (site B) network comprised 21 sampled individuals that consumed 14 resources ($C=0.17$).

The models

For each empirical network, 1000 simulated networks were generated according to each of the model of resource use's set of rules. We fixed the number of individuals, resources and connectance from each population for each simulation to preserve basic aspects of network structure. By doing this, we ensure that the structural differences encountered in the theoretical networks were a consequence of the contrasting rules of resource use from different models and not a side effect of changing the number of sampling individuals, resources or the total number of recorded interactions between individuals and resources.

The models are a generalization of models describing variation in resource use within a population in which an individual's diet is determined by its genotype and affected by intraspecific competition (Svanbäck and Bolnick 2005). The simple models developed here describe individual-resource networks and each model consists of a set of rules that generate a theoretical interaction network parameterized with the number of sampled individuals, resources and interactions recorded in an empirical network. Networks can be described as a matrix $\mathbf{A}$ in which rows represent individuals and columns represent resources. A matrix element $a_{ij} = 1$ when individual i consumes resource j and equals zero

otherwise. We begin by creating a matrix with the same dimensions as the empirical matrix (number of individuals and number of resources) and then proceed distributing the number of interactions registered in the empirical matrix according to each models' set of rules. The rank-sequence of prey items and the probability that an individual will add a prey item to its diet differs for each model. Below we describe the assumption of each model and the set of rules used to build matrices.

Shared Preferences Model

The shared preferences model states that individuals within a population show the same rank-sequence of preys but differ in their willingness to add new preys to their diets. This model has been previously related to nested patterns found in individual-resource networks (Araújo *et al.* 2009b, Pires *et al.* 2011a, Tinker *et al.* 2012). To create a theoretical matrix (**S**) based on the shared preferences rules, we first set that all individuals consume the same top-ranked prey, arbitrarily chosen to be represented by the first column. Then, we distribute the remaining interactions according to the following steps: (i) we select an individual i with probability proportional to the number of different prey species eaten by the individual in the empirical matrix:

$$p_i = \frac{k_i}{\sum_{m=1}^N k_m}, \quad (1)$$

where k_i (k_m) is the number of prey items eaten by the individual i (m) calculated from the empirical matrix and N is the total number of individuals in the population. By doing so we assure that individuals consuming more resources in the empirical network have a larger probability of adding a new resource to its diet; (ii) we add a prey to the diet of the selected individual in a predicted order, determined by the column sequence. We sorted the theoretical matrix columns using the

number of resources consumed, assuming that the column sequence represents the populations' rank preference. The new item added to the diet of individual i will be represented by changing s_{ij} from zero to one, in which $j-1$ represent the last food item previously added to the diet of individual i .

Competitive Refuge Model

The competitive refuge model states that individuals within a population share the same top-ranked prey and differ in their alternative prey. For instance, the top-ranked prey can be a prey species that provides sufficient energetic return, without demanding specific handling abilities or morphological adaptation for its consumption (Robinson and Wilson 1998). In this scenario, alternative prey species might require specific handling abilities involving trade-offs in resource use. As a consequence given that handling an alternative prey requires some sort of specialization, individuals can vary in their handling abilities and hence rely upon different secondary preys (Svanbäck and Bolnick 2005). This model has been related to the pattern of use of most consumed resources in sea otters, in which individuals share a top-ranked prey and differ in their alternative prey, which requires learning specific handling abilities to be able to process the prey (Tinker *et al.* 2012). To create a theoretical matrix (**S**) based on the competitive refuge rules, we first define that all individuals consume a top-ranked prey, represented by the first column. Then, the remaining interactions are distributed as following: (i) we select an individual i with uniform probability; (ii) we select a prey to be consumed with probability p_j . The probability that a given prey is selected decays with the number of individuals consuming that prey and is given by:

$$p_j = \frac{1 - \frac{k_j}{N}}{\sum_{n=1}^R \left(1 - \frac{k_n}{N}\right)}, \quad (2)$$

where k_j (k_n) is the number of individuals consuming prey j (n) and N is the total number of individuals in the population; the term $1 - \frac{k_j}{N}$ represents the proportion of individuals that are not consuming prey j ; $\sum_{n=1}^R \left(1 - \frac{k_n}{N}\right)$ represents all the possible interactions between individuals and resources that are not yet occurring; and R represents the total number of prey species.

Distinct Preferences Model

The distinct preferences model states that individuals within a population have different top-ranked preys. This model was related to the pattern of resource use in a population of sticklebacks, in which two different diet clusters of individuals were identified even when individuals were exposed to low intraspecific competition (Araújo *et al.* 2008). To create a theoretical matrix (**S**), first we need to assign individuals into groups defined by their pattern of resource use observed in the empirical matrix. Resources were ranked according to the number of individuals that consume each resource. Individuals that consumed the most eaten resource were assigned to group one. Individuals that consumed the second most eaten resource and that were not assigned to group one were assigned to group two and so on until all individuals were assigned to a group. Therefore, we assume that most consumed resources are the core resources defining groups in the population. This assumption is rooted on the prediction derived from ODT that preferred resources should be eaten whenever possible (Stephens and Krebs 1986, but see Araújo *et al.* 2008). In the theoretical matrix (**S**), all individuals consume the resource that defined their groups. The remaining

interactions are distributed as following: (i) an individual is selected with uniform probability; and (ii) a resource is selected with uniform probability.

Null Model

We performed also generated theoretical networks using a null model to test whether the patterns encountered could be generated by a random distribution of interactions between sampled individuals and resources. We selected a null model in which the probability that an interaction occurs between an individual and a resource (p_{ij}) is proportional to the number of resources eaten by an individual and the number of individuals that eat a certain resource (Bascompte *et al.* 2003) and is given by

$$p_{ij} = \left(\frac{k_i}{R} + \frac{k_j}{N} \right) \frac{1}{2}, \quad (3)$$

in which k_i is the number of preys individual i consumes, R is the number of preys eaten by the population, k_j is the number of individuals that eat prey j , and N is the total number of sampled individuals in the population. Therefore, in addition to preserving the number of individuals, number of resources and the connectance, this model controls for the heterogeneity of the number of interactions across individuals (and resources). Thus, it allowed us to investigate if the simple models based on OFT are reproducing patterns of overlap in resource use that goes beyond the effects of variation in the number of resources recorded for each individual.

Caveats

The proposed models represent a simple way to build interaction networks and investigate possible mechanisms thought to be drivers of

the observed patterns of interactions. However, we recognize that different processes might lead to the same patterns and our aim is to determine if the processes we investigate could lead to the observed patterns. The proposed models are possible mechanisms leading to variation in resource use, however, there might be other processes not investigated in the present study that can also generate such variation. In order to generalize the model to account for n individuals and m prey items, we simplified the rules that governed the pattern of interaction among individuals and resources. For instance, differently from Svanbäck and Bolnick (2005), our models do not consider the genetic basis of individual preference, which is a parameter difficult to estimate in nature (but see Thompson and Pellmyr 1991). Along the same lines, even the behavioral changes associated to resource availability are unknown for most of studied animal populations and therefore support for the proposed behavioral rules are mostly provided by theoretical studies (Svanbäck and Bolnick 2005) and observational data (Araújo *et al.* 2009b, Pires *et al.* 2011a, Tinker *et al.* 2012). In fact, experimental evidence supports that changes in feeding patterns might be associated with complex behavioral rules (Araújo *et al.* 2008) that, however, can be decomposed in combinations of the simple rules studied here. Finally, information on the feeding interaction between individuals and resources is qualitative, in a binary form, which takes into account the number of different prey species a given individual eats, without incorporating the proportion of each prey in an individual's diet. Binary matrices represents the overall pattern of resource use found in the population, whereas there is evidence that individuals can use core and periphery resources relying upon different behavioral rules (Tinker *et al.* 2012).

Performance Analysis

We tested model performance by investigating if models were able to reproduce the structure of empirical networks and if so how closely the models could reproduce the structure of the empirical networks. We used each model to generate a set of 1000 theoretical matrices based on each empirical matrix. In order to characterize the matrices simulated by each model, we computed metrics that capture the structure of the matrix and compare it with the empirical value computed for the empirical matrix.

Nestedness

Nestedness is a pattern found in distinct ecological systems and it was first described for species distributions across islands, in which the species found in islands with a small species richness were a subset of the species found in the richer islands (Patterson and Atmar 1986). In species networks, nestedness is found when specialized species interacts with a predictable subset of the interactions realized by generalized species (Bascompte *et al.* 2003). In the present study, a nested pattern of interaction indicates that the diet of selective individuals is a predicted subset of the diet of less selective individuals (Pires *et al.* 2011a). We used the metric NODF to assess nestedness values (Almeida-Neto *et al.* 2008). NODF values ranges from zero, when interactions within a network show other non-nested patterns such as extreme modularity (see below), to 100, when interactions are perfect nested. NODF was calculated using the program ANINHADO (Guimarães Jr. and Guimarães 2006) and is defined as following

$$NODF = \frac{\sum N_{paired}}{\left[\frac{n(n-1)}{2}\right] + \left[\frac{m(m-1)}{2}\right]}, \quad (4)$$

where N_{paired} is the degree of nestedness calculated for all pairwise individuals and resources; n is the number of individuals and m is the number of resources. For more information regarding nestedness analysis and NODF we refer readers to Almeida-Neto *et al* (2008).

Modularity

Modules in networks comprise nodes that are more connected to each other than to nodes outside the module (Guimerà and Amaral 2005). In the present study, modules are formed by individuals and preys and represent individuals that sharing the same preys choices. We used the metric M to assess modularity, calculated using the simulated annealing algorithm (Guimerà and Amaral 2005). M values ranges from 0, when individuals within a network do not form multiple modules, to 1, when individuals form multiple and isolated modules. The metric M was calculated using NETCARTO (Guimerà and Amaral 2005) and is defined as

$$M = \sum_{s=1}^{N_m} \left[\frac{I_s}{I} - \left(\frac{k_s}{2I} \right)^2 \right], \quad (5)$$

where N_m represents the number of modules found by the algorithm, I_s represents the number of interactions within the module s , I represents the total number of interactions recorded and k_s represents the sum of all interactions within module s . The modules represent individuals within the population that share similar preferences for prey species, and analogously the prey species that share the same individual predators.

Do models reproduce the structure of empirical networks?

To test the ability of each model in reproducing the structure of empirical networks we compared the empirical value of nestedness and modularity against the distribution of nestedness and modularity values

for the 1000 theoretical matrices generated under each model. We defined a confidence interval comprising 95% of the values from the distribution and we considered that a model could reproduce the structure of an empirical network if the empirical value of the metric relied within the confidence interval.

Model eligibility

After determining if models were able to reproduce the structure of empirical networks, we investigated each models' eligibility in producing networks with the same structure as the empirical networks. In order to maintain network structure, we defined *a priori* that the simulated matrix must have the same number of individuals as the empirical matrix. We guarantee this restriction by attributing a first interaction to all individuals. Each model attributes this first interaction in a different way, as described above. As the remaining interactions are distributed among individuals, some resources might end up not being consumed. When one or more resources were not consumed, a fundamental property of the empirical network (number of resources consumed) is not fulfilled and thus we considered this matrix as non-eligible and discarded it. As a consequence, we ensure that all matrices used in the analysis have the same size as the empirical matrix. We also estimated each models' eligibility, defined as the probability that a given model would generate a simulated matrix with the same fundamental properties as the empirical matrix (number of individuals, number of resources and connectance) by performing 1000 simulations and calculating the number of simulated matrices that were eligible for analysis.

Spectral analysis

Next, we performed a deviation analysis to determine model performance. To do so, we converted the matrices, empirical and theoretical, which represent bipartite networks, into a square matrix and then computed their eigenvalues (Figure 2). Eigenvalues have a broad application in ecology and have been used to infer the stability of food webs, persistence of species in a landscape and to model population dynamics in age-structured species (Leslie 1945, Hanski and Ovaskainen 2000, Allesina and Tang 2012). The number of eigenvalues in our square matrix is equal to the number of resources plus sampled individuals. Because eigenvalue distributions (i.e., the matrix spectra) is fundamentally related to the entries of the associated matrix, eigenvalues provide information on the structure of networks (de Aguiar and Bar-Yam 2005, Staniczenko *et al.* 2013). For each theoretical matrix ($\mathbf{S}$) we ordered all eigenvalues and subtracted the i_{th} empirical eigenvalue (λ_{e_i}) from the i_{th} theoretical eigenvalue (λ_{s_i}) and squared that difference $((\lambda_{e_i} - \lambda_{s_i})^2)$. We summed across all eigenvalues differences of a given matrix l . For each model we summed across all theoretical matrices and then normalized this value for the number of matrices as following:

$$\sigma = \frac{\sum_{s=1}^T \sum_{i=1}^L (\lambda_{e_i} - \lambda_{s_i})^2}{T} \quad (6)$$

where λ_{e_i} is the i_{th} eigenvalue of the empirical matrix, λ_{s_i} is the i_{th} eigenvalue of theoretical matrix $\mathbf{S}$, L is the number of eigenvalues of the matrix (which is equal to the number of rows or the number of columns in a squared matrix), and T is the number of simulated matrices generated in a simulation (which we set as 1000).

The σ value is a single normalized value that we considered as a proxy for the fit of a given model. The model with the lowest σ value is

considered the model that generates matrices whose structure best resembles the structure of the empirical matrix.

Figure 2: Matrix transformation. Matrix **A** is a hypothetical rectangular matrix, in which rows represent individuals within a population and columns represent the resources they consume. Matrix **B** is the square representation of matrix **A**, in which columns are added as rows and rows are added as columns. Note the same information is present in both matrices, but eigenvalues computation is only possible for squared matrices, such as **B**.

Results

Nestedness was a recurrent pattern in the analyzed populations. All networks, except the *Nucella A* network, were significantly more nested than expected by the number of sampled individuals, number of resources recorded and the heterogeneity in interactions across individuals and resources (null model analysis, Table 1, $p < 0.05$ for all other networks). In contrast, all networks are less modular than expected by the null model used, except for *Nucella A* network, which has a higher degree of modularity than expected by the null model (Table 2, $p < 0.05$).

In general, the Shared Preferences Model produced matrices that were more nested than the empirical matrices, being able to reproduce the

nestedness value calculated for the *Nucella B* network (Table 1). Similarly, the Competitive Refuge Model produced matrices that were more nested than empirical matrices in all but one empirical network, and was able to reproduce the nestedness values of all but two networks (Table 1). The Distinct Preferences Model had a more variable outcome and produced matrices that were more nested than the empirical matrices for *Nucella A* and *Thais A* networks (Table 1). For *Nucella B*, *Pinaroloxias* and *Thais B* networks, the Distinct Preferences Model produced networks that were less nested than the empirical networks. The Distinct Preferences model was able to reproduce the nestedness values of all networks except *Pinaroloxias* network.

Table 1: Mean value and standard deviation of NODF (nestedness) from one set of simulation (1000 matrices) under each model's set of rules. *empirical matrix is significantly nested.

Network	Empirical NODF	Shared Preferences	Competitive Refuge	Distinct Preferences	Null
<i>Pinaroloxias</i>	52.1*	76.81 ±2.47	59.70 ±5.81	41.36 ±4.87	38.38 ±3.94
<i>Nucella – A</i>	32.37	72.77 ±2.62	59.69 ±5.11	39.34 ±5.05	33.61 ±4.28
<i>Nucella – B</i>	64.26*	65.47 ±1.39	61.97 ±4.07	61.62 ±4.27	53.57 ±4.56
<i>Thais – A</i>	49.48*	74.69 ±1.57	59.55 ±3.79	51.68 ±3.84	34.33 ±3.10
<i>Thais – B</i>	39.27*	64.60 ±2.69	47.40 ±4.51	37.13 ±3.98	23.36 ±3.74

Regarding modularity, the Shared Preferences Model produced matrices that were less modular than the empirical matrices, except for *Nucella* B in which the simulated matrices had a similar value of modularity when compared with the empirical matrix (Table 2). The Competitive Refuge Model produced matrices that were more modular than the empirical matrices, except for the *Nucella* A and *Pinaroloxias* networks, in which case the Competitive Refuge Model produced matrices that were less modular than the empirical matrices (Table 2). The Distinct Preferences Model produced matrices that were more modular than the empirical matrices; except for the *Nucella* A network, which is more modular than the matrices produced by the model (Table 2).

All models were able to reproduce at least one feature of the empirical matrices (Table 3). For some populations, it was possible to associate a single candidate model to a given network pattern. For example, the nestedness analysis of *Thais* A network shows that the empirical matrix is significantly nested and the only model that was able to generate matrices that resemble the empirical matrix was the Distinct Preferences Model (Figure 3). The histograms showing the distribution of theoretical values of nestedness and modularity for all networks are provided in the Appendix. For some species, different models were able to reproduce the same property, nestedness or modularity, of the empirical network. For instance, using *Pinaroloxias* network as an example, all proposed models generate matrices that reproduced the modularity value of the empirical network (Table 3).

Table 2: Mean value and standard deviation of M (modularity) from one set of simulation (1000 matrices) under each model's set of rules. The empirical value estimated from the empirical networks is shown in the side of network name.
 *empirical matrix is significantly modular.

Network	Empirical M	Shared Preferences	Competitive Refuge	Distinct Preferences	Null
<i>Pinaroloxias</i>	0.3054	0.2745 ±0.0234	0.2967 ±0.0142	0.3307 ±0.0165	0.3382 ±0.0158
<i>Nucella – A</i>	0.4413*	0.2781 ±0.0209	0.3187 ±0.0137	0.3636 ±0.0198	0.3768 ±0.0188
<i>Nucella – B</i>	0.2160	0.2117 ±0.0114	0.2248 ±0.0027	0.2248 ±0.0034	0.2302 ±0.0023
<i>Thais – A</i>	0.2995	0.2445 ±0.0185	0.3097 ±0.0092	0.3238 ±0.0107	0.3550 ±0.0124
<i>Thais – B</i>	0.3838	0.3682 ±0.0143	0.4067 ±0.0135	0.4323 ±0.0163	0.4669 ±0.0199

Table 3: Summary of models reproducibility. Analysis if models were able to generate networks that reproduced nestedness (NODF) and modularity values of empirical networks.

Network	Shared Preferences	Competitive Refuge	Distinct Preferences	Null
<i>Pinaroloxias</i>	Modularity	NODF Modularity	Modularity	
<i>Nucella – A</i>			NODF	NODF
<i>Nucella – B</i>	NODF Modularity	NODF	NODF Modularity	
<i>Thais – A</i>		Modularity	NODF	
<i>Thais – B</i>	Modularity	NODF Modularity	NODF	

Thais melones – site A

Figure 3: Model reproducibility for *Thais A* network. Histogram showing distribution of nestedness (NODF) values from simulated networks generated according to each model (n=1000). Dashed lines represent confidence interval of 95% and bold line represents the NODF value estimated from the empirical network.

The analyses of model eligibility revealed that Shared Preferences Model and Null Model produced mostly non-eligible matrices, i.e., matrices whose fundamental properties differ from those found in the empirical matrices. In this sense, the rules from the Shared Preferences Model are less likely to generate matrices containing all resources recorded being consumed in the natural population. Meanwhile, the Competitive Refuge Model and Distinct Preferences Model produced mostly eligible matrices in a simulation. That pattern is consistent among all populations studied, except for *Thais B* network, in which all models produced mostly non-eligible matrices (Table 4), except for the Null Model. For the *Thais B* network, the only model that produced eligible matrices (89% of the simulated matrices) was the Null Model.

Along the same lines, spectral analysis revealed that Shared Preferences Model presented the worst performance among all models. Except for the *Nucella B* network, the Shared Preferences Model was the model that generated matrices whose structure was less similar to the structure the empirical matrices, evidenced by a higher eigenvalue deviation (Figure 4). For all other networks, the Competitive Refuge Model and the Distinct Preferences Model had a similar performance, producing matrices whose structural properties resembled the structure of empirical networks (Figure 4).

Table 4: Model eligibility. Percentage of matrices produced by each model that conserves the number of prey items consumed by the natural population (eligible matrices). The percentage indicates the percentage of matrices produced by each model that were eligible for analysis in a set of simulation. The higher percentages indicate the more eligible matrices the model produces. Each simulation generated a total of 1000 matrices.

Network	Shared Preferences Model	Competitive Refuge Model	Distinct Preferences Model	Null Model
<i>Pinaroloxias</i>	45.4%	98.5%	99.5%	18.1%
<i>Nucella A</i>	38%	93.5%	96.2%	16.2%
<i>Nucella B</i>	100%	100%	100%	74%
<i>Thais A</i>	61%	99.8%	100%	36%
<i>Thais B</i>	0%	29.7%	30%	89%

Figure 4: Eigenvalue deviation. σ is the normalized value of the summed square deviation from the empirical eigenvalues and the simulated eigenvalues of a given model, summed across all theoretical matrices generated by each model (equation 6). The error bars indicate the standard deviation calculated for the summed squared deviation from the empirical eigenvalues and the simulated eigenvalue for all matrices of a given model.

Discussion

The simple models of resource use we proposed are able to reproduce the structure of empirical networks and we show that different models can lead to similar structure in individual-resource networks. Overall, the Distinct Preferences Model and the Competitive Refuge Model performed better in reproducing the structure, degree of nestedness and modularity of empirical networks and both generated mostly eligible networks for analysis. When investigating the structure of the simulated networks in a finer scale, using spectral analysis, we found that the models producing networks in which the structure best resembles the structure of empirical networks was again the Competitive Refuge Model and the Distinct Preferences Model. The rules under the Shared Preferences Model are less likely to be producing the structure emerging from the patterns of interactions in the populations we studied. Our findings contribute to the theory of intrapopulation variation and the basis of individual-resource interactions in three different ways.

First, our modeling approach allows making accurate predictions regarding network structure given a simple set of rules used to build interaction networks. This sort of approach have been used to disentangle the structure of food webs, its robustness against perturbations and possible outcomes resulting from different ecological and evolutionary processes (Cohen *et al.* 1990). When using simple models it is possible to use the structure of simulated networks, which are built considering set of rules thought to be important in nature, and compare the structure of the simulated networks with the patterns observed in nature. This approach allows elucidating possible mechanisms shaping the patterns of interaction among individuals within a population and the resources they choose to consume.

Second, by creating a set of rules describing possible mechanisms generating intrapopulation variation, we showed that there are several routes leading to a nested structure in individual-resource networks. Nestedness is a common pattern found in many interaction matrices (Bascompte *et al.* 2003). In networks describing individuals in a population and the resources they consume, a nested pattern was expected under the shared preferences model (Araújo *et al.* 2009b) and it is apparently overrepresented in individual-resource networks analyzed so far (Pires *et al.* 2011a). Since this model assumes that all individuals in a population share the same rank preference, a nested structure is expected given that the diet of less selective individuals would be a proper subset of the diets of more selective individuals (Pires *et al.* 2011a). Although our version of the shared preferences model do generated nested networks it often overestimates the degree of nestedness of real networks. Our findings suggest alternative models in which individuals share the same top-ranked prey and differ in their alternative prey choices (Competitive Refuge Model), may also lead to a nested structure in individual networks. These unexpected results are a clear example of the difficulties encountered when inferring process based in pattern observation (Levin 1992). In this sense, simple model approach provides appropriate tools to go beyond pattern observation and carefully investigate possible rules underlying the patterns we found in nature. In addition, simple model approach allows investigating how different sets of rules might lead to the same patterns.

Nestedness and modularity are metrics describing global aspects of networks. Global metrics are used to describe the overall structure of networks, and as shown different sets of rules might lead to the same overall structure. Our results highlight the usefulness of spectral analysis as an accurate description of network topology. Spectral analysis is an

approach largely used in physics to understand dynamics of different sorts of networks (de Aguiar and Bar-Yam 2005). In ecology it has been applied to understand the role of species interactions in the stability of networks and to infer network stability in response to perturbations (Allesina and Tang 2012, Staniczenko *et al.* 2013). We used spectral analysis in order to determine which of our candidate models produces networks better resembling the structure of empirical networks. Even though the global structure of the empirical networks we studied was similar, when investigating the structure of the networks in a finer scale we were able to differentiate among the models and realize that it is less likely that individuals share the same rank sequence for prey. This highlights the importance of using an approach that describes networks structure more accurately when searching for evidence supporting competing models describing the organization of networks.

We found that different models might contain the possible rules underlying the structure of individual-resource networks. Nevertheless, we found that the Shared Preferences Models is the model that produces mostly non-eligible networks for analysis, and the networks produced by this model present a structure that deviates the most from the empirical networks. One way to move forward in our knowledge regarding intrapopulation variation in resource use and try to comprehend which rules possibly underlie the patterns of resource use in populations is to try to develop methods and experiments that would allow investigating the basis of different mechanism in the field. Integrating natural history with theory will help us get a better understanding of the mechanisms behind the patterns we observe in nature. In this sense, experiments aiming to reveal the principles underlying the way individuals add resources to their diets would be an important contribution in revealing the basis of individual differences in resource use.

Conclusões

O nicho ecológico é um conceito central para a ecologia (Schoener 2009). A teoria ecológica foi construída supondo que a variação individual no nicho poderia ser ignorada e as populações poderiam ser descritas por suas médias (Bolnick *et al.* 2003). A incorporação de variação intra-populacional em modelos ecológicos sugere que esta variação pode influenciar as dinâmicas ecológicas de populações e comunidades (Bolnick *et al.* 2011). Além disso, essa variação pode ter importantes implicações evolutivas, ao gerar seleção disruptiva dependente de frequência (Bolnick 2004, Bolnick e Lau 2008). Dada a potencial importância da variação intra-populacional para a organização da diversidade biológica, esta dissertação contribui de duas formas principais para a compreensão dos mecanismos que influenciam os padrões populacionais de uso de recurso.

Em primeiro lugar, identificamos quais padrões estruturais seriam esperados sob os diferentes modelos de uso de recurso em populações naturais por meio de previsões quantitativas com respeito a estrutura das redes de interação indivíduo-recurso. Para isso, foi investigado como a estrutura de redes de interação que descrevem o uso do recurso por indivíduos de uma população está relacionada a diferentes modelos de dieta ótima. A descrição dos padrões estruturais esperados sob cada modelo foi possível por meio do desenvolvimento de modelos simples baseados em regras que descrevem a interação entre indivíduos de uma população e as espécies de presas que eles consomem. Esses modelos simples são uma ferramenta eficaz para a compreensão das possíveis regras de organização do uso de recurso dentro de populações. Ao criarmos regras simples de montagem de matrizes, descrevendo cada um

dos modelos de uso de recurso de Svanbäck e Bolnick (2005), foi possível investigar quais padrões emergem sob cada um dos modelos. Essa abordagem permite a comparação entre o padrão específico esperado por cada modelo e o padrão observado na natureza e como consequência é possível inferir se os modelos de uso de recurso são capazes de reproduzir o padrão de interação encontrado na natureza. Ainda, a abordagem de modelos mínimos permite confrontar diversos modelos concorrentes. Como consequência esta parte do trabalho permitirá, no futuro, incorporar os efeitos da variação intra-populacional na estrutura de redes de interação entre indivíduos em modelos baseados em indivíduos (IBMs, Grimm e Railsback 2005) visando compreender a evolução de interações ecológicas.

Em segundo lugar, foi investigado se os modelos de dieta ótima reproduzem a estrutura observada em populações naturais. Dessa forma, foi possível testar pela primeira vez, em diferentes sistemas, algumas previsões dos modelos de dieta ótima de forma quantitativa, vinculando as previsões teóricas de cada modelo com a estrutura dos padrões de interação observados em populações naturais. Ao confrontar modelos distintos usando análise espectral foi possível determinar qual dos modelos concorrentes produziu redes de interação que mais se assemelhavam com as redes amostradas da natureza. Nesse sentido, a análise espectral fornece uma descrição acurada das redes de interação, que vai além da descrição dessa rede por meio de métricas globais, que sintetizam toda a estrutura desta rede em um único valor da métrica.

Essas duas contribuições, que resultaram da combinação de análises de dados empíricos, de métodos derivados da teoria de redes complexas e de modelagem, se inserem em um corpo teórico em construção que visa compreender a relação entre estrutura de redes de interação e a teoria do nicho ecológico. O desenvolvimento de modelos

simples de uso de recurso, e o uso da análise espectral permitiram separar de maneira acurada os padrões estruturais de cada um dos modelos. Por exemplo, um padrão aninhado em redes de interação, anteriormente estava associado com o modelo de Preferências Compartilhadas, porém com a abordagem adotada no presente trabalho mostramos que esse padrão estrutural também está associado com o modelo de Refúgio Competitivo. Ainda, encontramos que dentre os modelos de uso de recurso investigados, o modelo de Preferências Compartilhadas é o que gera redes de interação que menos se assemelham com as redes empíricas estudadas, pois superestima o valor de aninhamento, enquanto os modelos de Refúgio Competitivo e Preferências Distintas apresentaram resultados semelhantes para as populações estudadas. Futuramente, esses modelos de uso de recurso podem ser incorporados em estudos de dinâmica de redes. Investigar as consequências evolutivas de cada um desses modelos de uso de recurso dentro de um arcabouço teórico que considere a dinâmica evolutiva de populações permitiria inferir fatores que possam contribuir para a evolução de preferências em escalas acima do nível populacional.

Resumo

Tradicionalmente, nichos populacionais são descritos como a somatória de todos os recursos utilizados por uma população. Entretanto, diversos estudos mostram que indivíduos dentro de uma população podem usar recursos de forma distinta. Investigamos três maneiras pelas quais indivíduos podem variar quanto ao uso do recurso. Indivíduos podem apresentar a mesma preferência por presas, mas diferir na propensão à adição de novos itens alimentares em sua dieta (Preferências Compartilhadas); indivíduos podem apresentar a mesma presa preferida mas diferirem em suas presas alternativas (Refúgio Competitivo); ou indivíduos podem apresentar presas preferidas distintas (Preferências Distintas). Estudamos os padrões de interação que emergem sob os pressupostos de cada um dos modelos usando redes de interação entre indivíduos e os recursos que eles consomem. Dessa forma, para derivarmos as previsões de cada um dos modelos de uso de recurso, desenvolvemos modelos simples que geram redes de interação segundo regras que seguem os pressupostos dos modelos e confrontamos essas previsões com dados empíricos, comparando a estrutura dessa rede de interação. Encontramos que o modelo que menos se assemelha ao padrão de uso de recurso observado para as populações estudadas foi o modelo de Preferências Compartilhadas. Para as populações estudadas, a variação intrapopulacional na escolha de presas parece estar mais associada a diferenças nas sequências de preferências por presas entre indivíduos e não à propensão desses indivíduos em adicionarem novos recursos às suas dietas.

Abstract

Traditionally, a population's niche is described as the sum of all resources consumed by a population. However, several studies have highlighted that individuals within a population can use resources differently. We investigate three ways in which individuals can vary in their resource use. Individuals can show the same preference for prey, but differ in their likelihood of adding new prey to their diets (Shared Preferences); individuals can share the same top-ranked prey but differ in their alternative prey (Competitive Refuge); or individuals can have different top-ranked prey (Distinct Preferences). We studied the pattern of interaction that emerges under each model's assumption using interaction networks between individuals and the resources they consume. In this sense, to derive the predictions associated with each model of resource use, we developed simple models that generates interaction networks according to a set of rules that represent the assumptions of each model and then confronted these predictions with empirical data on interaction networks, by looking at the structure of these interaction networks. We found that the model that least resembles the pattern of resource use observed in the populations studied was the Shared Preferences model. For the studied populations, intrapopulation variation is not associated with individuals sharing the same rank sequence and differing in their willingness to add new resources to their diets. Instead, it seems that differences in the rank sequence of prey choice are more important in structuring the pattern of resource use in these populations.

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Anexos

Histogramas mostrando reproducibilidade dos modelos de uso de recurso para as redes de interações entre indivíduos e recursos investigadas no presente estudo. Os histogramas mostram a distribuição de valores das métricas de aninhamento e modularidade calculados para as redes teóricas simuladas de acordo com as regras de montagem de matrizes de cada um dos modelos. As linhas pontilhadas indicam o intervalo de confiança de 95% e a linha em negrito indica o valor da métrica calculado para a rede empírica.

Nucella emarginata – site A

Appendix 1: Model reproducibility for *Nucella A* network. Histogram showing distribution of modularity values from simulated networks generated according to each model (n=1000). Dashed lines represent confidence interval of 95% and bold line represents the modularity value estimated from the empirical network.

Nucella emarginata – site A

Appendix 2: Model reproducibility for *Nucella A* network. Histogram showing distribution of nestedness values (NODF) from simulated networks generated according to each model (n=1000). Dashed lines represent confidence interval of 95% and bold line represents the NODF value estimated from the empirical network.

Nucella emarginata – site B

Appendix 3: Model reproducibility for *Nucella B* network. Histogram showing distribution of modularity values from simulated networks generated according to each model (n=1000). Dashed lines represent confidence interval of 95% and bold line represents the modularity value estimated from the empirical network.

Nucella emarginata – site B

Appendix 4: Model reproducibility for *Nucella B* network. Histogram showing distribution of nestedness values (NODF) from simulated networks generated according to each model (n=1000). Dashed lines represent confidence interval of 95% and bold line represents the NODF value estimated from the empirical network.

Pinaroloxias inornata

Appendix 5: Model reproducibility for *Pinaroloxias* network. Histogram showing distribution of modularity values from simulated networks generated according to each model (n=1000). Dashed lines represent confidence interval of 95% and bold line represents the modularity value estimated from the empirical network.

Pinaroloxias inornata

Appendix 6: Model reproducibility for *Pinaroloxias* network. Histogram showing distribution of nestedness values (NODF) from simulated networks generated according to each model (n=1000). Dashed lines represent confidence interval of 95% and bold line represents the NODF value estimated from the empirical network.

Thais melones – site A

Appendix 7: Model reproducibility for *Thais A* network. Histogram showing distribution of nestedness values (NODF) from simulated networks generated according to each model (n=1000). Dashed lines represent confidence interval of 95% and bold line represents the NODF value estimated from the empirical network.

Thais melones – site B

Appendix 8: Model reproducibility for *Thais B* network. Histogram showing distribution of modularity values from simulated networks generated according to each model (n=1000). Dashed lines represent confidence interval of 95% and bold line represents the modularity value estimated from the empirical network.

Thais melones – site B

Appendix 9: Model reproducibility for *Thais B* network. Histogram showing distribution of nestedness values (NODF) from simulated networks generated according to each model (n=1000). Dashed lines represent confidence interval of 95% and bold line represents the NODF value estimated from the empirical network.