

Network analyses support the role of prey preferences in shaping resource use patterns within five animal populations

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Individual variation is an inherent aspect of animal populations and understanding the mechanisms shaping resource use patterns within populations is crucial to comprehend how individuals partition resources. Theory predicts that differences in prey preferences among consumers and/or differences in the likelihood of adding new resources to their diets are key mechanisms underlying intrapopulation variation in resource use. We developed network models based on optimal diet theory that simulate how individuals consume resources under varying scenarios of individual variation in prey preferences and in the willingness of consuming alternate resources. We then investigated how the structure of individual–resource networks generated under each model compared to the structure of observed networks representing five classical examples of individual diet variation. Our results support the notion that, for the studied populations, individual variation in prey preferences is the major factor explaining patterns in individual–resource networks. In contrast, variation in the willingness of adding prey does not seem to play an important role in shaping patterns of resource use. Individual differences in prey preferences in the studied populations may be generated by complex behavioral rules related to cognitive constraints and experience. Our approach provides a pathway for mapping foraging models into network patterns, which may allow determining the possible mechanisms leading to variation in resource use within populations.

Ecological theory is often based on the simplifying assumption that differences among individuals within populations can be ignored. However, individuals within animal populations can show substantial variation regarding many aspects of their ecology, life history, behavior and morphological traits (Bolnick et al. 2003). Age, sex, morphology and learning are important drivers of intrapopulation variation in resource use (Grant et al. 1976, Gustafsson 1988, Tinker et al. 2009, Masri et al. 2013). Intrapopulation variation in turn can affect ecological processes such as predation rates and the degree of intraspecific competition, which can scale up to alter ecological patterns at the community level (Hughes et al. 2008, Bolnick et al. 2011, Moleón et al. 2012). Individual variation in resource use is the raw material for evolution and may favor polymorphic populations which eventually, can contribute to diversification and speciation (Dieckmann and Doebeli 1999).

One way to examine the frequency and importance of intrapopulation variation is to investigate food niche variation among individuals. A theoretical framework used to explain individual variation is the optimal diet theory (ODT, Stephens and Krebs 1987). ODT predicts that an individual should maximize its energy gain given the costs and benefits of consuming a given food item, which are determined by

the energy content of the food item and the handling and search times associated with it. If individuals follow different rules in maximizing energy intake, they should differ in their rank preferences and hence differ in their prey choices (Tinker et al. 2009). There are several mechanisms that can lead individuals to differ in rank preferences and a good starting point for a better understanding of individual variation is to use simple models to address how such differences can emerge between individuals (Robinson and Wilson 1998). Two broad classes of mechanisms can lead to variation in prey choice. First, individuals can differ in their preference for prey, given differences in maximization rates associated with each prey species (Price 1987, Afik and Karasov 1995). Second, individuals can vary in their willingness to add a new food resource to their diets once their preferred resource becomes scarce (Schindler et al. 1997, Svanbäck and Persson 2004).

Svanbäck and Bolnick (2005) developed genetic-based models that explored how these two basic mechanisms can be used to describe individuals exploiting resources under different scenarios of intraspecific competition. These models of resource use assume a predator species with variation in resource use, in which the degree of intraspecific competition influences resource availability thus affecting resource

use. Individuals can 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 have different top-ranked prey (distinct preferences model) (Svanbäck and Bolnick 2005, Pires et al. 2011a). As intraspecific competition increases individuals are expected to add prey species to their diets according to their rank sequence. In this sense, each model presents a specific feeding strategy. A fundamental question is if these different feeding strategies are at some level encoded in particular patterns of resource use and niche partition within populations.

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 (Roughgarden 1972, Pianka 1974). When individuals within a population use resources differently, the degree to which two individuals overlap is variable (Bolnick et al. 2002). An informative way to quantitatively describe diet overlap is using a network approach (Araújo et al. 2008, 2010). When investigating patterns of resource use using networks, individuals are represented as one set of nodes and the types of resources they consume are represented as another set of nodes. A link between the two sets of nodes represents the feeding interaction between the individual and the resource (individual–resource networks – Pires et al. 2011a, Tinker et al. 2012). The structural patterns formed by individual–resource networks, such as nestedness and modularity, can reveal distinct aspects of how individuals share resources. Nestedness is a pattern found in networks representing different types of interactions, such as the interaction between mutualistic species and interactions between individuals and their resources within populations (Bascompte et al. 2003, Pires et al. 2011a). In individual–resource networks, a nested pattern is found when the diet of selective individuals is a subset of the diet of less selective individuals (Araújo et al. 2010, Pires et al. 2011a), indicating asymmetrical overlap in resource use among individuals. Modularity emerges when groups of individuals share similar diets but differ from other groups of individuals, forming subsets (modules) of individuals and resources (nodes) that are more connected to each other than with nodes outside the module (Tinker et al. 2012). A modular individual–resource network indicates that a population can be characterized by discrete groups and niche overlap is low among individuals belonging to different groups but high among individuals within groups (Araújo et al. 2008).

The structure of individual–resource networks can provide information about possible mechanisms generating the observed pattern. For instance, the structure of individual–resource networks has been associated with different models of resource use based on ODT or to combinations of these models (Tinker et al. 2012, Moleón et al. 2012). Nested networks in which the diets of selective individuals were nested subsets of the diets of less selective individuals have been associated with the predictions of the shared preferences model (Araújo et al. 2010, Pires et al. 2011a). Modular patterns characterized by semi-isolated groups of individuals in a population, each having a different top-ranked prey has been considered to be consistent with the distinct preferences

model (Araújo et al. 2008). Alternatively, modular networks may also indicate that the core prey selected by individuals is similar and alternative prey differed among individuals, a pattern consistent with the competitive refuge model (Tinker et al. 2012, Moleón et al. 2012).

So far, the relationship between ODT models and the overall structure of individual–resource networks has been established verbally, without a formal underlying quantitative framework. To unravel the role of the mechanisms associated with ODT in structuring resource use within populations we moved beyond the intuitive link between network structural patterns and ODT. Our main goal was to develop models that quantitatively associate each ODT model to network patterns. To derive predictions of network patterns emerging from ODT models, we developed an approach using rule-based models analogous to food-web models (Williams and Martinez 2000, Stouffer 2010). This class of models has been used to test hypotheses on the structure of food webs and mutualistic interactions (Pimm 2002, Pires et al. 2011b). The modeling approach presented here combines a set of possible feeding strategies, inspired in Svanbäck and Bolnick's (2005) models, with network rule-based models, allowing the investigation of potential mechanisms structuring resource use within populations and testing hypothesis on the structure of individual–resource networks.

We combined numerical simulations and tools originated from network theory, such as spectral analysis of complex networks, to derive theoretical predictions associated with each model. The predictions were confronted with empirical data of classical examples of animal populations showing compelling evidence for intrapopulation variation in resource use, in order to determine which model encompass the most likely mechanisms underlying the structure of intrapopulation variation.

Material and methods

Dataset

We used individual–resource networks describing qualitatively the patterns of resource use, i.e. presence absence of pairwise interactions of five populations from three animal species. The datasets used to build the networks in the present study are classic examples of populations with considerable amount of inter-individual diet variation, in which individuals within the population consistently use a subset of total population niche (Bolnick et al. 2003). In these populations, inter-individual variation is a striking pattern since it is not explained by individuals' age, sex, morphology, environmental heterogeneity or sampling biases (West 1986, 1988, Werner and Sherry 1987). Variation in resource use is also not associated to spatial heterogeneity, since there is compelling evidence showing that all individuals in these populations have access to the same resources (Bolnick et al. 2003). Therefore, the variation found among individuals in the datasets used is due to intrinsic differences across individuals.

The first network analyzed is from the species of finch *Pinaroloxias inornata* (Passeriformes, Thraupidae) from Cocos Island, Costa Rica (Werner and Sherry 1987). The

Pinaroloxias network comprised 21 sampled individuals that used seven different feeding strategies to acquire the resources they consume, leading to a connectance (C) – the proportion of interactions that do occur within a network given all possible interactions – of 0.34. The second and third networks analyzed are from two populations of the Californian predatory marine snail *Nucella emarginata* (Neogastropoda, Muricidae, West 1986). The *Nucella* A (site A) network comprised 20 sampled individuals that consumed seven resources ($C = 0.31$) and the *Nucella* B (site B) network comprised 31 sampled individuals consuming three resources ($C = 0.59$). The fourth and fifth networks analyzed are from two populations of the predatory marine snail from Panama *Vasula melones* (Neogastropoda, Muricidae, West 1988). The *Vasula* A (site A) network comprised 42 sampled individuals that consumed eight resources ($C = 0.29$) and the *Vasula* B (site B) network comprised 21 sampled individuals that consumed 14 resources ($C = 0.17$).

Resource-use network models

The network models introduced here 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). To adapt such models, they were simplified into minimal sets of simple rules defining the interactions between individuals and the resources it consumes, and generating individual–resource networks associated with feeding strategies. Each network model was used to generate an ensemble of theoretical networks based on real data (1000 theoretical networks for each empirical network). The empirical network can be described as a matrix \mathbf{A} in which rows represent individuals and columns represent resources. The matrix element $a_{ij} = 1$ when individual i consumes resource j and equals zero otherwise. A matrix \mathbf{T} , representing a theoretical network, is created with the same number of individuals (rows) and resources (columns) registered in the empirical network. The same number of interactions registered in the empirical network is distributed across elements of \mathbf{T} according to the set of rules associated with each model. To preserve basic aspects of network structure, the original number of individuals, resources and connectance from each empirical population is fixed for each simulation. By doing this, any structural differences encountered between the theoretical networks and the empirical network is a consequence of the varying rules of resource use in the different models and not a side effect of changing the number of sampled individuals, resources or the total number of interactions recorded between individuals and resources. Below we describe each model.

Shared preferences model

The shared preferences model states that individuals within a population show the same rank-sequence of prey species but differ in their willingness to add new resources to their diets (Svanbäck and Bolnick 2005). This model has been previously related to nested patterns found in individual–resource networks (Araújo et al. 2010, Pires et al. 2011a, Tinker et al. 2012). To create a theoretical matrix (\mathbf{T}) based on the

rules of the shared preferences model, all individuals (matrix rows) have an interaction with the top-ranked resource, represented by the first column in the theoretical matrix. Then, the remaining interactions are distributed according to the following steps: 1) an individual i is selected with probability (p_i) proportional to the number of different resources consumed by the individual in the empirical matrix:

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

where k_i is the number of resource types consumed by the individual i in the empirical matrix \mathbf{A} , k_m is the number of resource types consumed by the individual m in matrix \mathbf{A} and N is the total number of sampled individuals from the population. This procedure ensures that individuals consuming more resources in the empirical networks have a larger probability of adding a new resource to its diet; 2) a resource is added to the diet of the selected individual in a predictable order, determined by the column sequence. Resources (columns) in \mathbf{T} are sorted based on the number of individuals that consumed each resource, as indicated by the marginal sum of \mathbf{T} columns, so that the order of columns represent the population's rank-sequence for resources. The shared preferences model's key assumption is that all individuals share the same rank-sequence for resources, which is represented by column sequence in \mathbf{T} . The new item added to the diet of individual i will be represented by changing t_{ij} from zero to one, in which $j-1$ represent the food item previously added to the diet of individual i . It is worth noticing that the shared preferences model produces matrices that are as perfectly nested as possible given the recorded number of individuals, resources and interactions (perfect nestedness sensu Staniczenko et al. 2013), in which individuals that have the same degree (i.e. consume the same number of resources) share the same pattern of interaction, consuming the same resources. The same logic applies to resource types: resources with the same degree (i.e. consumed by the same number of individuals) are consumed by the same individuals. Having said that, variation in nestedness across populations will occur even if the populations follow the shared preferences model due to variation in the number of individuals, resources and interactions recorded in each population.

Competitive refuge model

The competitive refuge model assumes that individuals within a population share the same top-rank resource and differ in their alternative resources. For instance, the top-ranked resource can be a resource that provides sufficient energetic return, without demanding specific handling abilities or morphological adaptation for its consumption (Robinson and Wilson 1998). The use of alternative resources might involve tradeoffs and if there is variation in the way these tradeoffs operate among individuals, individuals will rely upon different secondary resources (Price 1987, Estes et al. 2003). The competitive refuge model has been associated with the pattern of resource use from different animal populations, such as threespine stickleback *Gasterosteus aculeatus*, Bonelli's eagle *Aquila fasciata* and southern sea otters *Enhydra lutris nereis* (Araújo et al. 2008, Moleón et al. 2012,

Tinker et al. 2012). To create a theoretical matrix (**T**) based on the competitive refuge rules, all individuals consume the top-ranked resource, represented by the first column. Then, the remaining interactions are distributed as following: 1) an individual i is selected with uniform probability; 2) a resource is selected with probability p_j , which decays with the number of individuals consuming that resource:

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

k_j is the number of individuals consuming resource j . The term $1 - \frac{k_j}{N}$ represents the proportion of individuals that are not consuming 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 recorded; and R represents the total number of resources consumed by the population.

Distinct preferences model

The distinct preferences model states that individuals within a population have different top-ranked resources. This model was related to the pattern of resource use in a population of threespine sticklebacks, in which two different diet groups of individuals were identified even when individuals were exposed to low intraspecific competition (Araújo et al. 2008). To create a theoretical matrix (**T**), individuals were assigned to 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 in the empirical network. Individuals that consumed the most eaten resource by the population were assigned to group one. Individuals that consumed the second most eaten resource by the population and that were not assigned to group one were assigned to group two and so on until all individuals were assigned to a group. A key assumption associated with this model is 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 1987, Araújo et al. 2008). In the theoretical matrix (**T**), each individual consumes the resource that defines its groups. The remaining interactions are distributed as following: 1) an individual is selected with uniform probability; and 2) a resource is selected with uniform probability.

Null models

Two different null models were used to generate theoretical networks in order to test whether the patterns encountered could be generated by a random assignment of interactions between sampled individuals and resources (Bascompte et al. 2003). In the first null model – a bipartite version of a Erdős–Renyi random graph – all interactions are equally probable and proportional to the size ($R \times N$) and connectance of the empirical network:

$$p_{ij} = \frac{C}{RN} \quad (3)$$

The second null model states that 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 and is given by:

$$p_{ij} = \left(\frac{K_i}{R} + \frac{K_j}{N} \right) \frac{1}{2} \quad (4)$$

in which K_i is the number of resources individual i consumes, and K_j is the number of individuals that consume resource j . Therefore, in addition to preserving the number of individuals, number of resources and connectance, the null model controls for the heterogeneity in the number of recorded resource types across individuals (and resources). Thus, these null models provide benchmarks, to investigate if the simple ODT models perform better in reproducing the observed patterns of overlap in resource use when compared to simply considering the effects of variation in the number of resources recorded for each individual in the field.

Caveats

The proposed models represent a simple way to build individual–resource networks given simple sets of rules thought to contribute to the observed patterns of interactions. Although the proposed models embrace possible mechanisms leading to variation in resource use, different mechanisms could lead to similar patterns and there might be other processes not investigated in the present study that could also generate such variation in network structure. The original models proposed by Svanbäck and Bolnick (2005) were models based on genotypic differences describing patterns of resource use of five resources by three types of individuals. The generalization proposed accounts for n individuals, m prey items and different populations, which leads to a simplification that do not consider the genetic basis of individual preference, which is difficult to estimate in natural populations (but see Thompson and Pellmyr 1991). Even though the rules used to build the theoretical networks are very simple, they can represent behavioral differences associated with resource use. Experimental and long-term observational data supports that differences in feeding patterns might be associated with complex behavioral rules (Svanbäck and Persson 2004, Tinker et al. 2009) that can be decomposed in combinations of the simple rules studied here. Since the models we developed are static models they do not include learning, which may introduce an additional layer of variation by changing rank preferences over time. Learning may generate mixed patterns of resource use by combining assembly rules (Tinker et al. 2012). We think network models that include learning may be the next logical step for exploring how individuals partition resources within populations. Finally, information on the feeding interaction between individuals and resources is qualitative, in a binary form, which takes into account the number of different resources a given individual consumes, without incorporating the proportion of each resource in an individual's diet. Although the frequency of resource use is very important for

a number of ecological processes, it is also very sensitive to sampling (Bolnick et al. 2002). Thus, we opted for a conservative approach by using binary networks.

Model reproducibility

The first step in analyzing model's performance is to determine if the theoretical networks produced by the models have similar features when compared with the 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 networks generated by each model. A confidence interval comprised 95% of the values from the theoretical distribution and a model was considered to reproduce a given structural property of an empirical network if the empirical value of the metric fell within the interval confidence.

Nestedness

A nested pattern of interaction indicates that the diet of selective individuals is a subset of the diet of less selective individuals (Pires et al. 2011a). We used the metric NODF to quantify nestedness (Almeida-Neto et al. 2008). NODF ranges from zero, when interactions show non-nested patterns such as extreme modularity, to 100, when interactions are perfectly nested. NODF was calculated using the program ANINHADO (Guimarães Jr and Guimarães 2006) and is defined as following:

$$\text{NODF} = \frac{\sum N_{\text{paired}}}{\left[\frac{N(N-1)}{2} \right] + \left[\frac{R(R-1)}{2} \right]} \quad (5)$$

where $\sum N_{\text{paired}}$ is the degree of nestedness calculated for all pairwise individuals and resources (Almeida-Neto et al. 2008).

Nestedness can also be assessed through the leading eigenvalue of a matrix (Staniczenko et al. 2013). When comparing matrices with the same dimensions and the same connectance, larger leading eigenvalues correspond to networks with higher nestedness (Staniczenko et al. 2013). Another advantage of using the leading eigenvalue when inferring nestedness is that eigenvalue distribution is an invariant property of a matrix and does not change with column or row permutation. To test the sensitivity of our results to the approach used for nestedness characterization, we repeated all analyses using this alternative technique of estimating nestedness (Supplementary material Appendix 1 Fig. A1). See section 'Spectral analysis' for a description of how eigenvalues were computed.

Modularity

Modules in individual–resource networks occur if individuals within a population consume resources in a similar fashion and if resource types share the same individual consumers. We used the metric M to assess modularity, calculated using the simulated annealing algorithm (Guimerà and Amaral 2005). M ranges from 0 (individuals and resources

are assigned to a single group) to 1 (individuals and resources form multiple and isolated modules). The metric M was calculated using NETCARTO (Guimerà and Amaral 2005) and is defined as:

$$M = \sum_{s=1}^{N_m} \left[\frac{I_s}{I} - \left(\frac{k_s}{2I} \right)^2 \right] \quad (6)$$

where N_m is the number of modules found by the algorithm, I_s is the number of interactions within the module s , I is the total number of interactions recorded and k_s is the sum of all interactions within module s . Although M calculates modularity considering the network to be unipartite, the null model we used retains the bipartite structure considering two sets of nodes and controlling for any effects this could have in modularity estimates.

Spectral analysis

In network analysis, there is a trade off between the amount of information used for pattern recognition and the interpretation of patterns. Network-level metrics such as degree of nestedness and modularity summarize information of network organization as single indexes, allowing easy recognition and interpretation of patterns in networks. However, the maximum amount of information in a matrix formed by n individuals and m resources is $n \times m$. Therefore, by summarizing network organization into a single index a lot of information is ignored. Finer-scale network organization can be accessed through matrix spectra, which is the eigenvalue distribution of the associated matrix. An individual–resource matrix has $n + m$ eigenvalues. In this sense, as a consequence of the inequality $I < n + m < n \times m$ in any system with more than one resource and one individual, the eigenvalue distribution provides a much more complete – although still incomplete – characterization of network organization than single indexes (Farkas et al. 2001, de Aguiar and Bar-Yam 2005, Pavlicev et al. 2009).

Matrix spectra can only be computed for square matrices, therefore, all matrices, empirical and theoretical, were converted into a square matrix with both individuals and resources depicted in rows and columns. We define a square matrix \mathbf{Q} in which the dimensions are $\mathbf{S} \times \mathbf{S}$, $S = n + m$. The first n rows (and columns) represent the n individuals and the rows (columns) $n + 1$ to $n + m$ represent the m resources. The equality $q(i, j) = q(j, i) = a(i, j - n)$ holds if $i \leq n$ and $n < j \leq n + m$. All additional elements in \mathbf{Q} are non-informative and zero by definition (individual–individual and resource–resource elements). Thus, it is worth noting that the new square matrix contains the very same information as the original matrices about the interactions between individuals and resources. The transformation to a square matrix allows the computation of eigenvalues, which are not defined for non-square matrices as the original individual–resource matrices. The distribution of eigenvalues is affected by matrix size, connectance, and the patterns of interaction of each individual and each resource. However, given that the empirical and theoretical matrices have the same dimensions and the same connectance, the number of eigenvalues describing the empirical matrix and its theoretical counterparts is the same and their differences cannot be associated with neither matrix size nor differences in the

number of links, but only with differences in network structure (see Pavlicev et al. 2009 for a similar approach in the study of the evolution of complex phenotypes). For each transformed squared matrix (**Q**) all eigenvalues were sorted in decreasing values. Eigenvalue deviation was computed between theoretical and empirical matrices as following:

$$\sigma = \frac{\sum_{Q=1}^G \sum_{i=1}^L (\lambda_{e_i} - \lambda_{Q_i})^2}{G} \tag{7}$$

where λ_{e_i} is the i_{th} eigenvalue of the square empirical matrix, λ_{Q_i} is the i_{th} eigenvalue of squared theoretical matrix, L is the number of eigenvalues of the matrices, and G is the number of simulated matrices generated in a simulation (which we set as 1000). The σ is a proxy for the goodness of fit from a given model. The model with the lowest σ is considered the model that generates matrices best resembling the observed distribution of links between individuals and resources in the empirical network.

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.2h1q2>> (Lemos-Costa et al. 2015).

Results

Nestedness was a recurrent pattern in all analyzed populations. All networks, except *Nucella* A network ($p > 0.999$), were significantly more nested than expected by both null models, which keeps the number of sampled individuals, the number of resources recorded and the number of observed interactions, but assigns interactions randomly (Fig. 1a). In contrast, all networks, except for *Nucella* A network (Fig. 1b), are less modular than expected according to both null models. Therefore, all analyzed populations, with exception of *Nucella* A, are characterized by considerable degree of asymmetrical overlap between diets of individuals (nestedness) and no evidence suggesting individuals form discrete groups based on feeding records (modularity).

The models strongly differ in their ability to reproduce the empirical patterns of nestedness. In general, the shared preferences model produced networks that were more nested than the empirical ones, only reproducing the nestedness of the second *Nucella* population (*Nucella* B; Fig. 1a, Supplementary material Appendix 1 Fig. A1). Similarly, the competitive refuge model generally produced networks that were more nested than the empirical ones and was able to reproduce the empirical NODF value of all but two populations,

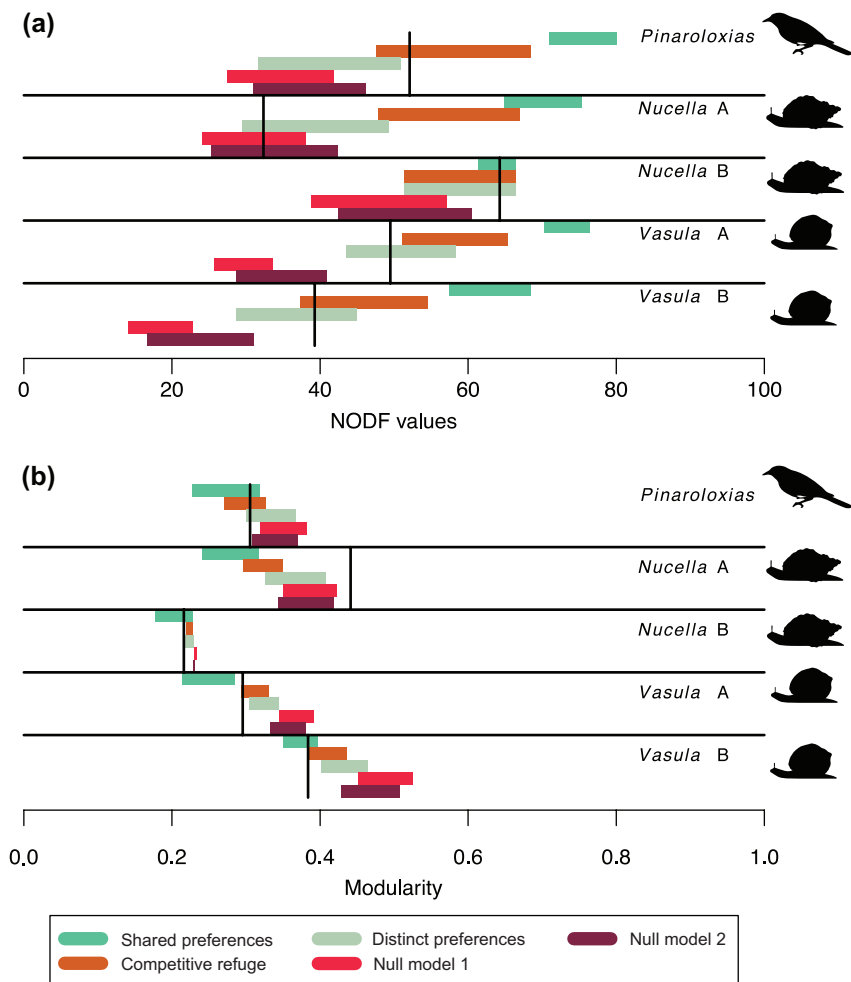


Figure 1. Model reproducibility of the five analyzed populations. The x-axis represents the values of network metrics. Vertical dashed lines represent empirical values of metrics estimated from empirical networks. Bar length indicate 95% confidence intervals. (a) Reproducibility of nestedness values. (b) reproducibility of modularity values.

Nucella A and *Vasula* A (Fig. 1a). When using the leading eigenvalue as nestedness estimator, the matrices produced by the competitive refuge model were more nested than the empirical ones for three populations (*Pinaroloxias*, *Nucella* A and *Vasula* A networks, Supplementary material Appendix 1 Fig. A1). Finally, the distinct preferences model produced theoretical networks that were able to reproduce the NODF value of all networks except for the network describing the interaction of *Pinaroloxias inornata* (Fig. 1a) and for nestedness estimated by the leading eigenvalue, the distinct preferences model could only reproduce the leading eigenvalue from *Nucella* A (Supplementary material Appendix 1 Fig. A1).

Regarding modularity, the shared preferences model produced networks that were on average less modular than the empirical ones, and was able to reproduce the empirical value of modularity of three analyzed networks: *Pinaroloxias*, *Nucella* B and *Vasula* B (Fig. 1b). The competitive refuge model reproduced the empirical value of modularity of *Pinaroloxias*, *Vasula* A and *Vasula* B networks (Fig. 1b). Finally, the distinct preferences model generally produced networks that were more modular than the empirical ones, except for *Nucella* A, and was able to reproduce the empirical modularity value from *Pinaroloxias* and *Nucella* B networks (Fig. 1b).

To sum up, all models were able to reproduce at least one feature of the empirical networks (Table 1), meaning that the models are capable of generating networks whose overall structure, assessed through nestedness and modularity, are similar to the empirical networks. For some populations a single candidate model could be associated with a given network pattern. For example, the pattern of resource use observed for *Pinaroloxias* is significantly nested and the competitive refuge model was the only model able to generate networks with nestedness degree (NODF and leading eigenvalue) similar to the empirical one (Fig. 1a, Table 1). Nevertheless, for most cases, different models were able to reproduce the same property, nestedness or modularity, of a given empirical network. For instance, for *Pinaroloxias*, all proposed models could generate theoretical networks with a degree of modularity similar to the one estimated for the empirical network (Fig. 1b, Table 1).

We used spectral analysis to explore the performance of the different models in greater detail. The three models proposed presented different performances for all but a single population (*Nucella* B) (Fig. 2). Matrix spectra revealed that the shared preferences model presented the worst performance among all models, having the highest eigenvalue deviation,

and hence producing networks whose structure deviates the most when compared with the empirical networks (Fig. 2). In fact, both null models performed better than the shared preferences model, but not as good as the competitive refuge and distinct preferences models in all populations but *Nucella* B. For all other populations, the competitive refuge model and the distinct preferences model had a similar performance, producing networks whose spectrum best resembled the spectrum of the empirical networks.

Discussion

Recent work based on network theory allowed the characterization of novel patterns of niche variation, which led to new hypotheses about intrapopulation niche organization (Araújo et al. 2008, 2010, Pires et al. 2011a, Tinker et al. 2012) and its consequences to ecological processes (Gómez et al. 2011, Cantor et al. 2013). In this work, we introduced network models of resource use to the study of niche variation within populations. These rule-based models were able to reproduce the structure of empirical individual–resource networks. These findings contribute to our understanding of intrapopulation variation in resource use in three different ways.

First, the approach developed here combining network models with structural and spectral analysis helped us to investigate the patterns resulting from intrapopulation variation in resource use. A modeling approach consisting of simple rule-based models allows quantitative predictions to be made in terms of network structure given a simple set of assumptions. This approach has been used to unravel the structure of food webs, its robustness against perturbations and investigate the possible outcomes resulting from different ecological and evolutionary processes (Williams and Martinez 2000, Stouffer 2010, Cohen et al. 2011). We suggest future work should focus on extending this approach to investigate the effects of incorporating foraging traits known to affect network structure on patterns of resource partitioning (Beckerman et al. 2006).

Our analysis of the network spectra highlights the usefulness of spectral analysis to describe and compare network organization more accurately. Nestedness and modularity are network-level patterns and, as we have shown, different sets of rules might lead to the same levels of nestedness and modularity. Spectral analysis is an approach largely used in physics to better understand patterns of connection among nodes along with dynamic behavior of different sorts of

Table 1. Summary of models reproducibility indicating network property reproduced by the networks generated by each model's sets of rules. Numbers indicate network size (individuals \times resources).

Network	Shared preferences	Competitive refuge	Distinct preferences	Null model 1	Null model 2
<i>Pinaroloxias</i> (21 \times 7)	modularity	nestedness modularity	modularity		
<i>Nucella</i> A (20 \times 7)			nestedness	nestedness	nestedness
<i>Nucella</i> B (31 \times 3)	nestedness modularity	nestedness	nestedness modularity		
<i>Vasula</i> A (42 \times 8)		nestedness modularity	nestedness		
<i>Vasula</i> B (21 \times 14)	modularity	nestedness modularity	nestedness		

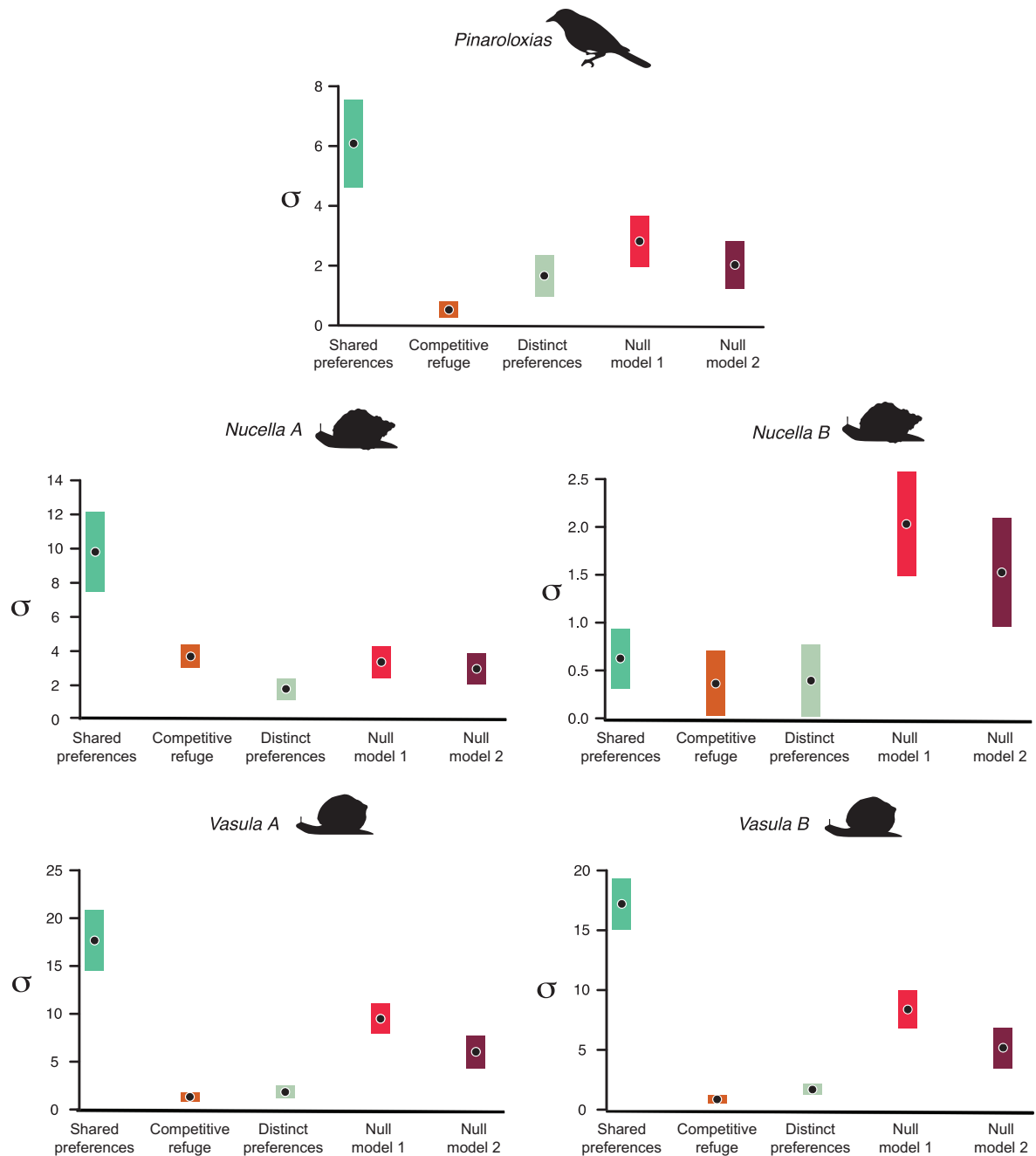


Figure 2. Eigenvalue deviation. σ is the mean value of the summed square deviation from the empirical eigenvalues and all the simulated eigenvalues of a given model and bars are the standard deviation. Smaller values indicate best model performance.

networks (de Aguiar and Bar-Yam 2005). In ecology it has been applied to understand the role of antagonistic and mutualistic interactions in the stability of networks and to characterize nestedness in mutualistic networks (Allesina and Tang 2012, Staniczenko et al. 2013). We used spectral analysis as an additional measure of nestedness in networks and to determine which of the candidate models produce networks better resembling the empirical networks. When investigating the structure of the networks at a finer scale, using network spectra, we were able to differentiate among candidate models. Specifically, spectral analysis revealed that the competitive refuge model and distinct preferences model,

which were the two models with the best fit, performed similarly. Additionally spectral analysis showed that even though the shared preferences model could generate networks that reproduced global aspects of the structure of empirical networks, this model performed worse than all other models, including both null models.

Second, our analyses provide further insights on how foraging strategies translate into non-intuitive patterns of niche overlap. By creating sets of rules that simulate possible mechanisms underlying intrapopulation variation, we showed that several routes could lead to a nested structure: a recurrent pattern in individual–resource networks (Araújo

et al. 2010, Pires et al. 2011a). The nested pattern in individual–resource has been related to the shared preferences model (Araújo et al. 2010). The shared preferences model assumes that all individuals in a population share the same rank preference. This assumption leads to a nested structure as the diet of more selective individuals, those that are less likely to consume low-ranked resources when preferred resources are limited, would be a subset of the diets of less selective individuals. Using network models that incorporate such rules we showed that theoretical networks generated under the shared preferences model do present a nested structure. However, this model often overestimates the degree of nestedness when compared with empirical networks (Fig. 1a). In contrast, alternative models – in which individuals share the same top-ranked prey and differ in their alternative prey choices (competitive refuge) – not only lead to nested structures in individual networks, but can reproduce the degree of nestedness observed in empirical networks (Fig. 1a). Moreover, these results bring forth the question if similar principles, at species level, could contribute to nested patterns in species networks (Bascompte et al. 2003). We hypothesize that the mechanisms embedded in the foraging models considered here, such as distinct preferences propelled by competitive interactions or differences in the willingness to consume alternative resources under resource limitation, could act at the species level generating nestedness in mutualistic (Bascompte et al. 2003) and antagonistic (Pires and Guimarães 2013) networks. In this sense, modeling approaches such as the one proposed here offer appropriate tools to go beyond pattern description and investigate possible rules underlying the patterns observed in nature.

Third, by connecting foraging models and network structure we can infer how behavioral constraints result in different resource use patterns for different populations. The interindividual variation in the populations studied has been discussed in terms of behavioral and cognitive differences between individuals (West 1986, 1988, Werner and Sherry 1987). For instance, in *Nucella emarginata* the distinct preferences model presented a better performance for population A. The distinct preferences model is consistent with individuals varying their hunting techniques associated with each prey, which has been proposed as the explanation for the interindividual variation in *N. emarginata* populations (West 1986). *Nucella emarginata* uses different techniques for consuming barnacles, limpets and mussels. These different techniques consist in differences regarding drilling location on prey shell. Assuming these techniques have a learning component, different individuals could specialize in different techniques during their lifetime, generating differences in resource use patterns. In the case of *Vasula melones*, we were not able to differentiate between the competitive refuge model and the distinct preferences model. This could be due to the fact that the rules embedded in each model are acting simultaneously in the natural populations (Tinker et al. 2012). False limpet (genus *Siphonaria*) and oyster (genus *Ostrea*) are the two prey species that are preferentially consumed by both populations of *V. melones*. In site B where preferred prey were less abundant, the population presented a broader range of prey species (West 1988). In this sense, the absence of a single pattern of prey selection for this species could indicate among-population differences in

the feeding rules when consuming preferred prey versus non-preferred prey (West 1988, Tinker et al. 2012). In the finch *Pinaroloxias inornata*, feeding patterns appear to involve complex behaviors, whereby individuals can vary from one to a few feeding strategies to acquire resources (Werner and Sherry 1987). For instance, individuals can glean branches and leaves for small insects, probe and glean dead leaves for crickets and cockroaches, probe flowers and feed upon extrafloral nectar. If some of these strategies were easier to master, most individuals would rely upon this particular strategy, leading to a structure consistent with the competitive refuge model. Additionally, mastering each feeding strategy appears to have an observational learning component, dependent on the interactions individuals established during their development (Werner and Sherry 1987). Juvenile individuals that followed adults using certain foraging strategies during development may have specialized in acquiring resources using the observed technique.

For all populations studied, feeding specialization appears to have an important learning component (West 1986, 1988, Werner and Sherry 1987), and these learning techniques, and consequently individuals' patterns of resource use, may involve individual differences in preference ranks between individuals. Learning behavior can also change the predictions associated with ODT, reducing mean searching time, when individuals learn to use clues to search for their preferred resources more effectively (Thompson and Pellmyr 1991) or master techniques associated with consumption of specific prey (Tinker et al. 2009). Here we explored static models, but dynamical models that include a learning component could use the models we propose here as a starting point. If learning is included in the models, individuals' ranks are not fixed and can change taking into account functional trade-offs, morphological constraints or cognitive experiences, generating mixed assembly rules (Araújo et al. 2008, Tinker et al. 2012). The challenge is to parameterize such models, as the rates of learning and the consequences learning has for foraging patterns are unknown for most populations. By now, our results support the notion that no single model accounts for resource use patterns across all populations. This suggests that even though resource use patterns can be remarkably consistent (Pires et al. 2011a), the underlying mechanisms generating these patterns can be highly context dependent (Tinker et al. 2012, Moleón et al. 2012).

The approach we introduced here is a first step towards quantitatively connecting foraging models and network structure. We expect future work will be able to benefit from this approach to study interindividual variation and resource use patterns in other populations. Moreover, further development of our network model approach may allow incorporating behavior and other traits more explicitly. In this sense, a natural follow up in the analysis of the underlying mechanisms shaping individual–resource networks is to explore how learning behavior is structured within populations and how learning and experience could affect the rank sequences within populations and hence patterns of resource use.

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Supplementary material (available online as Appendix oik-03006 at <www.oikosjournal.org/appendix/oik-03006>). Appendix 1.