Understanding the role of parasites in food webs using the group model

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Journal of Animal Ecology (2018)

Abstract

- 1. Parasites are ubiquitous and have been shown to influence macroscopic measures of ecological network structure, such as connectance and robustness, as well as local structure, such as subgraph frequencies. Nevertheless, they are often underrepresented in ecological studies due to their small size and often complex life cycles.
- 2. We consider whether or not parasites play structurally unique roles in ecological networks; that is, can we distinguish parasites from other species using network structure alone?
- 3. We partition the species in a community statistically using the group model, and we test whether or not parasites tend to cluster in their own groups, using a measure of "imbalance."
- 4. We find that parasites form highly imbalanced groups, and that concomitant predation, in which a predator consumes a prey and its parasites, but not the number of interactions, improves the group model's ability to distinguish parasites from non-parasites.
- 5. This work demonstrates that parasites and non-parasites interact in networks in statistically distinct ways, and that these differences are partly, but not entirely, due to the existence of concomitant predation.

Keywords:

community structure, degree, likelihood, motifs, species role, stochastic blockmodel

1 Introduction

Parasites are ecologically significant players in many communities, and several authors have urged the incorporation of these species into ecological networks (Marcogliese and Cone, 1997; Marcogliese, 2003; Lafferty et al., 2008). While many modern networks are well resolved with respect to most free living species, parasites are often excluded entirely. In networks which do incorporate parasites, these species affect several general aspects of food web structure; for example, increasing the proportion of possible links that are observed (connectance), the number of consumptive links between the highest and lowest trophic levels (trophic chain length), and, trivially, the number of species (richness) (Huxham et al., 1995; Thompson et al., 2005; Lafferty et al., 2006; Amundsen et al., 2009; Dunne et al., 2013b). Conversely, many parasite species may decrease network robustness—usually quantified as the proportion of species lost following a given number of primary extinctions (Dunne et al., 2002b)—because highly complex and specialized life cycles may make them prone to secondary extinction in response to host removal (Lafferty et al., 2008).

Parasites also affect local network structure. In a comprehensive analysis, Dunne et al. (2013b) show that parasites change the relative frequency of certain network subgraphs, and tend to have niches which are broader, but contain more gaps, than predators in aquatic food webs. The intimate connection between parasites and their hosts results in another major effect. Concomitant predation, wherein a predator consumes both the prey and its parasites, is sometimes a necessary part of parasitic life cycles, and may also be a relevant source of biomass for predators, given the high biomass of parasites in ecological communities (Kuris et al., 2008). These interactions increase the connectance of the network and affect the degree, *i.e.* the number of consumptive interactions a given species is involved in, of both parasites and their incidental predators.

There is some disagreement in the literature about how exactly parasite degree differs from that of free-living species. Parasites are often highly specialized (*e.g.* Althoff, 2003; Dyer et al., 2007), suggesting that parasites might have a lower in-degree (number of prey/hosts) than free-living predators. However, parasites have been found to increase overall connectance, depending on how the calculation is done (Lafferty et al., 2006). This would suggest that parasites have, on average, more interactions than their free-living predators and the out-degree (number of predators) of parasites. Taken together, these observations point toward degree as a structurally distinguishing feature of parasitic species, especially when in-degree and out-degree are considered separately.

Ecological networks often contain hundreds of species and thousands of consumer-resource interactions. To study these complex networks, it is useful to understand the general roles species play in the community. Species roles are sometimes classified based on phylogenetic (*e.g.* a terrestrial ungulate can be assumed to be herbivorous) or *a priori* trophic strategies (e.g. an herbivore consumes exclusively primary producers by definition), but they may also be identified statistically. *Ecologically equivalent* species (also known as trophic species) have the same set of predators and prey, and therefore play identical roles in the network structure (Luczkovich et al., 2003; Dunne et al., 2002a). This concept can be relaxed and generalized using the group model (Allesina and Pascual, 2009), which organizes species into groups, such that species in a group tend to eat and be eaten by members of the same other groups of species (Fig. 1). Equivalent to the stochastic blockmodel from the social science literature (Snijders and Krzysztof, 1997; Karrer and Newman, 2011), the group model uses network structure to form groups that often have straightforward ecological interpretations (Sander et al., 2015). Indeed the species roles defined by the group model are essentially functional groups, in that species within a group tend to interact with the same sets of species in the same way.

Using the group model, we consider the structural distinction between parasites and free-living predators. Whether or not parasites alter general network metrics, if the patterns of their interactions are structurally unique within the network (Cirtwill and Stouffer, 2015), then the groups identified by the model should reflect this distinction. For our study, we consider a set of large food webs that include information on both parasites and free-living species (Huxham et al., 1996; Hechinger et al., 2011; Mouritsen et al., 2011; Thieltges et al., 2011; Zander et al., 2011; Table S1), and we quantify how well the network's group structure matches broad trophic strategies. In general, it is difficult to identify the specific ecological drivers that contribute to the group structure. Here, we are able to isolate the effects of two ecological factors, degree and concomitant predation, which may influence group structure and how well it corresponds to the trophic strategies we expect. To examine the effect of degree, we compare the groupings found using a standard group model, and a variant of the model that removes the effect of degree on the group structure. To



Figure 1: Example of a group-model-produced grouping of an empirical adjacency matrix. The center matrix represents a subset of one of the empirical webs used in this analysis. To the right and left are the same subset, but with the rows/columns re-ordered to maximize the modularity (Newman, 2006) (left) or the group model (right). Both modularity and the group model attempt to condense the links into groups of species that are strongly connected, producing a pattern in which the matrix is divided into areas with either very high or very low connectance. Note that, though the links appear randomly distributed before sorting, applying a walk-trap algorithm to find modules partitions the matrix into four groups, with links concentrated within modules (in blocks along the diagonal). Applying the group model (unrestricted for number of groups) also finds four groups, but partitions the matrix differently, creating more strongly connected blocks that are often (though not necessarily) off the diagonal. In all cases, links are indicated by orange dots and groupings by black lines. The trophic species of each node is indicated with a colored box along the margins.

study concomitant predation, we compare groupings found when concomitant links are included and excluded.

We find that parasites perform unique roles in ecological communities, whether or not concomitant links are included and whether or not the model is corrected for degree. However, although the presence of concomitant links improves the model's ability to distinguish parasites from free-living species, degree heterogeneity does not.

2 Materials and methods

2.1 Data

We analyzed the seven well-resolved marine and estuarine food webs described in Hechinger et al. (2011), Zander et al. (2011), Mouritsen et al. (2011), Thieltges et al. (2011), and Huxham et al. (1996) (Dunne et al., 2013a). We analyzed two versions of each network: one which includes concomitant links, and one which excludes them. Concomitant interactions are inferred links based on the assumption that predators eat all parasite species of their prey Dunne et al. (2013b). For all webs, parasites with complex life-cycles had their various life-stages aggregated into a single node.

Species were classified into four trophic strategies: primary producer, herbivore, predator, or parasite. Primary producers were identified as any species with no prey. Herbivores were identified as species which consumed only primary producers. Parasites were identified based on Dunne et al.

(2013b). All other species were labeled as predators; therefore, this group contains both carnivores and omnivores.

2.2 Group Model

Metrics of categorizing network structure are common in analyses of ecological networks. One of the most popular of such metrics is modularity (Newman, 2006), which evaluates the presence of compartments within a community. These compartments contain individuals/species which interact more strongly with fellow members of their compartment than they do with members of other compartments (*e.g.* benthic versus pelagic species or flowers which bloom in the early versus late summer). This results in a structure of dense blocks along the diagonal of a matrix when properly ordered (Fig. 1). The group model can be thought of as a generalization of modularity, in which compartments are not defined exclusively by strong within-compartment connections, but rather by patterns of strong connections between compartments as well (*e.g.* between herbivores and primary producers). Note that the group model does not exclude the possibility of strong connections with one's own compartment, such that modularity is a subset of the possible groupings identified by the group model.

The group model provides a likelihood-based framework to calculate how well a specific grouping fits the observed network structure. High-likelihood groupings will tend to have groups which act as functional groups, that is, species within a group tend to eat and be eaten by the same other groups. Consider a food web with *S* species and *L* links, represented by directed adjacency matrix *A*. Modelling the network as an Erdős Rényi random graph with connectance (the proportion of possible links that are realized) c, the likelihood of obtaining *A* can be given by:

$$Pr(A(S,L)|c) = c^{L}(1-c)^{S^{2}-L}$$
(1)

The likelihood is maximized when $\hat{c} = \frac{L}{S^2}$, the observed connectance. Using a partition (grouping) *G* containing *g* groups, we can split the network into a series of blocks, where each block represents all of the interactions from group *r* to group *s*, and where the groups contain *S_r* and *S_s* species, respectively. A block has *L_{rs}* links and connectance *c_{rs}* (note that because the network is directed, block *rs* is distinct from block *sr*). Then the full likelihood can be calculated as the product of the likelihoods of each individual block, as follows:

$$Pr(A(S,L)|c_{rs}, r, s \in 1:g) = \prod_{r=1}^{g} \prod_{s=1}^{g} c_{rs}^{L_{rs}} (1-c_{rs})^{S_r S_s - L_{rs}}$$
(2)

which is maximized when $\hat{c}_{rs} = \frac{L_{rs}}{S_r S_s}$ for every *r*,*s*.

Model selection can be performed by calculating the Bayes factor, or, equivalently, by choosing the partition with the highest marginal likelihood, which can be calculated as:

$$Pr(A|G) = \prod_{r=1}^{g} \prod_{s=1}^{g} \frac{L_{rs}!(S_r S_s - L_{rs})!}{(1 + L_{rs})(1 + S_r S_s)!}$$
(3)

For a full derivation of the group model and the Bayes factor, see Eklöf et al. (2011) and Sander et al. (2015).

The group model may be extended to correct for degree. For this version of the model, the marginal likelihood may be calculated as:

$$Pr(A|G) = \left[\left(\frac{\beta^{\alpha}}{\Gamma(\alpha)} \right)^{g^{2}} \prod_{r=1}^{g} \prod_{s=1}^{g} (1+\beta)^{-(\alpha-L_{rs})} \Gamma(\alpha+L_{rs}) \right] \times \left[\prod_{r=1}^{g} \frac{\prod_{i=1}^{S_{r}} (k_{i}^{\text{in}})! (k_{i}^{\text{out}}!)}{\Gamma(S_{r})^{2} \Gamma\left(S_{r} + \sum_{i=1}^{S_{r}} k_{i}^{\text{in}}\right) \Gamma\left(S_{r} + \sum_{i=1}^{S_{r}} k_{i}^{\text{out}}\right)} \right]$$
(4)

where α and β are parameters on a Gamma prior ($\alpha = 1$ and $\beta = 1$ used in our analyses), and k_i^{in} and k_i^{out} are the in-degree (number of prey/hosts) and out-degree (number of predators/parasites) for species *i*, respectively. For a derivation of the likelihoods and Bayes factor for the degree-corrected model, see the Supplemental Information and Karrer and Newman (2011).

We searched for partitions that best fit the group model, one for each combination of the following variables: including/excluding concomitant predation, standard group model/degree corrected model, and maximum number of groups (2, 3, 5, 10, or 100). When up to 100 groups were allowed, the groupings collapsed down to a number that was more statistically parsimonious. Allowing for 100 groups gives the model the flexibility to find a truly optimal grouping, but constraining the number of groups makes the structure easier to visualize, understand, and interpret. In addition, it allows for a clear comparison between partitions with the same number of groups. Therefore, although we present results for all groupings, we focus on the 10 group case, which gives the model some flexibility, but is feasible to visualize and compare.

We used Metropolis-Coupled Markov Chain Monte Carlo (MC^3) with a Gibbs sampler to search for the partition of species into groups that maximizes the marginal likelihood (for details, see Supplemental Information and Sander et al., 2015). Since exhaustively searching all possible groupings is computationally infeasible, we performed 200 independent MC^3 runs for each grouping reported, with 10 chains and 200,000 steps. Differences from the true optimum are likely to be small, so finding the true optimum is unlikely to have a large effect on the results. For convenience, we refer to the best partitions found as "best groupings", although they are not guaranteed to be optimal.

We studied the effect of degree correction on the groupings by calculating the mutual information between degree-corrected and degree-uncorrected partitions. Mutual information is described in more detail in the section on Taxonomic Comparison.

2.3 Imbalance

Once the group structure was inferred, we evaluated how well these statistically defined groups correspond to ecologically relevant *a priori* partitions, such as those specifying general trophic strategies (*e.g.*, herbivores or parasites). We did this by characterizing the "imbalance" of the distribution of species employing a given strategy across the various groups specified by the group model. For instance, considering the distribution of species belonging to the dominant trophic strategy (*e.g.* parasites or non-parasites) in any given group:

$$\psi_i^{parasites} = \frac{max(\pi_i, \phi_i)}{\pi_i + \phi_i} \tag{5}$$

where π_i is the number of parasites in group *i* and ϕ_i is the number of free-living, *i.e.* non-parasitic, species. This index can range from $\frac{1}{2}$ in the case where both trophic strategies are present in equal

numbers, to 1 when all species in the group employ the same strategy. For a given network and partition, we can calculate the full imbalance for a given trophic strategy by taking the product across all groups in the partition:

$$\Psi^{parasites} = \prod_{i=1}^{g} \psi_i = \prod_{i=1}^{g} \frac{max(\pi_i, \phi_i)}{\pi_i + \phi_i}$$
(6)

We calculated imbalance in this way for all trophic strategies we considered: primary producers, herbivores, free-living predators, and parasites. We used a generalization of this measure to calculate the imbalance value for the full network (incorporating all strategies and groups simultaneously)¹:

$$\Psi^{All} = \prod_{i=1}^{g} \prod_{k=1}^{c} \psi_i^k = \prod_{i=1}^{g} \prod_{k=1}^{c} \frac{max(\chi_i^1, \chi_i^2, \dots, \chi_i^c)}{\sum_{k=1}^{c} \chi_i^k}$$
(7)

where g is the number of groups in the partition, c is the number of unique trophic strategies, and χ_i^k is the number of species with strategy k in group i. Note that $\left(\frac{1}{c}\right)^g \leq \Psi^{All} \leq 1$. To determine whether a given value for Ψ is higher than expected by chance, and therefore whether parasites significantly aggregate with other parasites in the partition, we wanted to associate Ψ with a p-value, measuring the probability of obtaining an equal or greater imbalance at random.

To get at this, we consider the following example. Suppose we partition *S* species into two groups (g = 2). The first group contains ϕ_1 free-living species and π_1 parasites, while the second group has ϕ_2 free-living species and π_2 parasites. Thus, the total number of parasites in the network is $P = \pi_1 + \pi_2 = \sum_{i=1}^{g} \pi_i$ and the total number of free-living species is $F = \phi_1 + \phi_2 = \sum_{i=1}^{g} \phi_i$. Clearly, S = P + F. The probability of obtaining exactly ϕ_1 , ϕ_2 , π_1 , π_2 at random can be computed using the hypergeometric distribution:

$$Pr(\phi_{1},\phi_{2},\pi_{1},\pi_{2}|\vec{\mathscr{P}},P,F) =$$

$$= \frac{\binom{P}{\pi_{1}}\binom{F}{\phi_{1}}}{\binom{P+F}{\pi_{1}+\phi_{1}}} \frac{\binom{P-\pi_{1}}{\pi_{2}}\binom{F-\phi_{1}}{\phi_{2}}}{\binom{P+F-\pi_{1}-\phi_{1}}{\pi_{2}+\phi_{2}}} = \frac{\binom{P}{\pi_{1}}\binom{F}{\phi_{1}}}{\binom{P+F}{\pi_{1}+\phi_{1}}} \cdot 1 = \frac{\binom{P}{\pi_{1}}\binom{F}{\phi_{1}}}{\binom{P+F}{\pi_{1}+\phi_{1}}}$$

$$= \frac{\binom{P}{\pi_{2}}\binom{F}{\phi_{2}}}{\binom{P+F}{\pi_{2}+\phi_{2}}} \frac{\binom{P-\pi_{2}}{\pi_{1}}\binom{F-\phi_{2}}{\phi_{1}}}{\binom{P+F-\pi_{2}-\phi_{2}}{\pi_{1}+\phi_{1}}} = \frac{\binom{P}{\pi_{2}}\binom{F}{\phi_{2}}}{\binom{P+F}{\pi_{2}+\phi_{2}}} \cdot 1 = \frac{\binom{P}{\pi_{2}}\binom{F}{\phi_{2}}}{\binom{P+F}{\pi_{2}+\phi_{2}}}$$

$$(8)$$

where $\vec{\mathscr{P}}$ is the partition structure (in this case there are only two groups, *i.e.*, $|\vec{\mathscr{P}}| = 2$) provided by the group model. Note that the probability is the same regardless of how we label the groups. Therefore, we can associate a probability of obtaining this result at random to each possible partition encompassing a given number of parasites and free-living species. The formula above can be generalized to an arbitrary number of groups $|\vec{\mathscr{P}}| = g$:

$$Pr(\vec{\phi}, \vec{\pi} | \vec{\mathscr{P}}, P, F) = \prod_{i=1}^{g} \frac{\binom{P - \sum_{j=0}^{j < i} \pi_j}{\pi_i} \binom{F - \sum_{j=0}^{j < i} \phi_j}{\phi_i}}{\binom{P + F - \sum_{j=0}^{j < i} (\pi_j + \phi_i)}{\pi_i + \phi_i}}$$
(9)

and trophic strategies c:

¹Note that in the case of just two strategies (*e.g.* parasites and non-parasites, this equation collapses into Eqn. 6 and is the same for both strategies.

$$Pr(\vec{\chi}^{1}, \vec{\chi}^{2}, \dots, \vec{\chi}^{c} | \vec{\mathscr{P}}, X^{1}, X^{2}, \dots, X^{c}) = \prod_{i=1}^{s} \frac{\prod_{k=1}^{c} \binom{X^{k} - \sum_{j=0}^{j < i} \chi_{j}^{k}}{\chi_{i}^{k}}}{\binom{S - \sum_{j=0}^{j < i} \sum_{k=1}^{c} \chi_{i}^{k}}{\sum_{k=1}^{c} \chi_{i}^{k}}}$$
(10)

where by definition $\phi_0 = \pi_0 = \chi_0 = 0$, $X^k = \sum_{i=1}^g \chi_i^k$ is the total number of species with strategy *k*, and, as above, $S = \sum_{k=1}^c X^k$ is the total number of species in the network. For a description of how to calculate *p*-values based on these probabilities, see Box 1.

All data and code needed to run the search algorithm and perform all analyses may be found at https://git.io/vXciH.

2.4 Taxonomic Comparison

In order to examine the biological relevance of the groupings found by the group model, we compared the group model results to a natural biological grouping by taxonomy. For this analysis, we utilized the Ythan network, which contained the most taxonomically detailed information about parasitic species, as a representative case-study. Taxonomic information to the family and order levels were gathered from the WoRMS database Horton et al. (2017), and compared the resulting partitions to the 10-group partitions identified by the group model. The 10-group partitions were chosen because the number of groups was most similar to the number of families and orders in the taxonomic grouping, and were therefore the most analagous partitions.

The similarity of the two partitions was determined using the information theoretic measure of mutual information (MI). MI measures the reduction in entropy of partition B when partition A is known, such that if the MI is 1, the two partitions contain identical information. It can be thought of as the intersection between the two entropies, and is calculated as follows:

$$MI_{AB} = H(A) + H(B) - H(A,B) = \sum_{a \in A} \sum_{b \in B} p(a,b) \ln \frac{p(a,b)}{p(a)p(b)}$$
(11)

where H(A) is the entropy of partition A, and H(A,B) is the joint entropy of partitions A and B. The significance of MI_{AB} was calculated using a randomization test. For more details, see (Sander et al., 2015).

2.5 Subgraph-Roles

We furthermore considered the usefulness of meso-scale network structures, such as subgraph participation, in distinguishing trophic roles. We tabulated the number of times each species participated in each of the thirty potential roles within the thirteen three-node subgraphs (Supplemental Information) and formed groups based on similarity of participation using a k-means algorithm. We then repeated the imbalance analysis described above using these alternative groupings and compared the results to those of the group model. **Box 1. Calculation of partition imbalance** *p***-values.** We are interested in the probability of observing an equal or larger value of imbalance at random. For networks with few groups and/or trophic strategies, we can compute this probability analytically by enumerating all possible cases and adding the probabilities of observing each imbalance value greater or equal to that observed. For example, take a network that is composed of 8 species (*S* = 8), of which 3 are parasites (*P* = 3) and 5 are free-living (*F* = 5). Suppose that when we use the group model to find the optimal partitioning into 3 groups we find that $\vec{\pi} = [1,0,2]$ and $\vec{\phi} = [0,4,1]$. The imbalance is $\Psi = \frac{2}{3}$. We can compute all the possible cases in which we arrange the *P* parasites and *F* free-living species into 3 boxes of sizes $\vec{\mathcal{P}} = [1,4,3]$, with each configuration having an associated imbalance value and probability of obtaining this configuration at random. We can then compute a *p*-value for the empirical distribution of trophic strategies across the partition produced by the group model by summing the probabilities associated with the configurations yielding imbalance equal or higher than that found in the partition produced by the group model (Fig. 2).

Though this brute-force method becomes infeasible for networks with many groups or trophic strategies, we can still calculate the *p*-value numerically by comparing the observed imbalance to a large number of randomized species strategy distributions sampled uniformly across the provided group structure, with fairly rapid convergence (Fig. S18).



Figure 2: Process for calculating the *p*-value for a hypothetical group model partition. Under "Configuration", we list all seven unique configurations for the three parasites (black circles) and five free-living species (grey circles) into three groups (boxes) whose sizes have been determined by the partition produced by the group model. π_1 , π_2 , and π_3 show the combinatorial tree to obtain these configurations. Using equation 6, we associate each configuration with an imbalance value ψ . Next, using equation 9, we compute the probability of obtaining each configuration at random. Finally we sum the probabilities for all configurations with equal or greater imbalance than the empirical partition (those in red boxes) to compute a *p*-value.

2.6 Life-Stages

Species, such as many parasites, which undergo complex life-cycles composed of stages with potentially distinct sets of interactions, face a dilemma in data organizations where ecological networks condense all interactions of a given species into the same node. We investigated the importance of this type of node resolution by defining nodes according to life-stages rather than species as in the previous analyses and broadening our trophic-strategy labels to incorporate this new information. We then repeated the grouping (using the group model) and imbalance analyses and compared the results to those found previously. Finally, using these same expanded networks, with separate nodes for each life-stage of the species involved, we repeated the imbalance analysis using simplified labels matching those used in the species-node case (*i.e.* the various life-stages of a given parasite species were still kept as separate nodes, but each stage had the same label of "parasite"). These results were then compared back to the original analysis as well as to the results of the life-stage-labeled imbalance values.

3 Results

Results were similar across networks. We report statistical results across all networks, but for simplicity we display figures and imbalance scores only for the largest network (Punta Banda) in the main text. Figures for the other six networks may be found in the Supplemental Information.

Concomitant Links	Degree Corrected	g	all	Herbivores	Parasites	Predators	1° Producers
		2/2	0.246***	0.737***	0.421	0.491***	0.895***
		3/3	0.120***	0.589	0.260	0.331***	0.826**
No	No	5/5	0.307***	0.551***	0.430***	0.628***	0.757***
		10/10	0.214***	0.448***	0.445***	0.439***	0.585*
		18/100	0.103***	0.441***	0.292***	0.494***	0.481**
		2/2	0.397***	0.692	0.449***	0.660***	0.874
		3/3	0.250***	0.565	0.521***	0.381***	0.815
No	Yes	5/5	0.109***	0.350	0.559***	0.289***	0.689
		10/10	0.027***	0.145	0.138***	0.244***	0.487
		43/100	0.000***	0.036***	0.005***	0.003***	0.162***
		2/2	0.555***	0.745***	0.555***	0.912***	0.898**
		3/3	0.370***	0.598	0.603***	0.835***	0.839**
Yes	No	5/5	0.327***	0.440*	0.710***	0.702***	0.731
		10/10	0.164***	0.284***	0.343***	0.582***	0.702***
		23/100	0.169***	0.253***	0.504***	0.590***	0.411***
		2/2	0.537***	0.709***	0.609***	0.812***	0.874
		3/3	0.282***	0.609***	0.515***	0.564***	0.833**
Yes	Yes	5/5	0.173***	0.360	0.506***	0.365***	0.716
		10/10	0.114***	0.198***	0.445***	0.364***	0.451
		54/100	0.000***	0.006***	0.024***	0.000***	0.148***

Table 1: Imbalance values for the Punta Banda network (with or without concomitant predation) found via uniform sampling of 10^6 possible distributions of trophic strategies across the partitionings found by the (degree-corrected or otherwise) group model with g groups. Significance is indicated by the trailing asterisks, with p < 0.05, p < 0.01, and p < 0.001, corresponding to *, **, and ***, respectively. Note that the lower bound for the imbalance varies with the number of groups, so it is only appropriate to compare raw imbalance scores when the number of groups is the same.

Partitions were significantly imbalanced in almost all cases, across different numbers of groups and all networks (Tables 1, S2-S7). Hence, the groupings maximizing the marginal likelihoods separated parasites (and other trophic strategies) from other strategies more than expected by chance alone. Results were significant whether or not the model corrected for degree, and whether or not concomitant predation was considered. The only exception was that producers and herbivores were often highly imbalanced, but not significantly so. Since these networks generally had few producers and herbivores, this could be due to the relatively low statistical power. It is fairly easy for trophic strategies with few species to appear in the same groups simply by chance; as a result, trophic strategies with few species tend to have higher imbalance, but lower significance. This is a common problem for permutation tests and other procedures involving discrete outcomes, such as in Fisher's exact test. Since raw imbalance scores depend both on the number of groups and the number of species in each trophic strategy, the scores alone can be misleading; for this reason, we focus our interpretation on the significance rather than the scores themselves. Producers did tend to group together, but these groups often contained non-producers as well. This could be because they were being consumed by a similar group of predators, *e.g.* by a group of omnivores. Parasites and predators in particular tended to form groups which were distinct from all other strategies (Fig. 3). Taking the network with the most resolved taxonomic information (Ythan), we found that the group model partitions shared a highly significant amount of information with the taxonomic partitions ($p \approx 0$ for all cases, see Table S21), demonstrating a strong overlap between the group model and a natural biological partition.



Figure 3: Condensed graph representation of the Punta Banda network using the best partitioning found by the group model. Each group is depicted by a pie-chart in which the fraction of nodes of each trophic strategy are indicated by the colored slices and the overall size is proportional to the number of nodes in the group. Number of links between (or within) groups is given by the thickness of each arrow and arrow direction of represents energy flow in the network; that is, arrows point to the consumer.

Average in- and out-degree varied across trophic strategies, whether or not concomitant predation was included (one-way ANOVA, p < .0001 for all four tests: in-degree without concomitant, F = 31.01; in-degree with conomitant, 126.2; out-degree without concomitant, F = 84.93; outdegree with concomitant, F = 174.5) (Fig. 4). Mean in-degree for predators was significantly higher than other trophic strategies (mean in-degree $\mu_{in} = 15.64$ without concomitant predation, $\mu_{in} = 30.54$ with concomitant predation), followed by parasites ($\mu_{in} = 12.80$ without concomitant, $\mu_{in} = 13.16$ with concomitant), followed by producers and herbivores, which were not statistically distinct ($\mu_{in} = 0$ and 1.65 for producers and herbivores, respectively, both with and without concomitant predation). Mean out-degree was highest for producers, herbivores, and predators without concomitant predation ($\mu_{out} = 14.71$, 13.73, and 13.25, respectively), with lower out degree for parasites ($\mu_{out} = 6.79$). When concomitant predation was added, the pattern flipped: outdegree for parasites was highest ($\mu_{out} = 31.00$), with the other trophic strategies significantly lower ($\mu_{out} = 14.71$, 13.88, and 13.25 for producers, herbivores, and predators, respectively). In all four cases, parasites were significantly different from free-living predators.

Despite the differences in degree between trophic strategies, the degree-corrected group model produced significantly more imbalanced groups overall (across webs, trophic strategies, and number of groups), both when concomitant predation was included (paired *t*-test, estimated difference: .12, p < .001) and excluded (estimated difference: .067, p < .001). Including concomitant links also produced more imbalanced groups, under both the degree-corrected (paired *t*-test, estimated difference: .034, p = .0049) and uncorrected (estimated difference: .085, p < .001) models.

In general, degree-corrected and uncorrected partitions contained similar information when allowed to form more than 3 groups (Table S20). The mutual information between corrected and uncorrected partitions increases as the number of groups increases. As expected, degree-corrected partitions tended to have fairly evenly sized groups (Karrer and Newman, 2011), whereas group size was significantly less even for uncorrected partitions, both with concomitant predation (paired *t* test, estimated difference in Pielou's evenness (Pielou, 1966): -.030, p = .031) and without (estimated difference: -.025, p = .001).

Considering the distribution of subgraph-roles across trophic strategies, we see little consistency without the inclusion of concomitant links (Figure S2). Though including concomitant links does reveal some trends (Figure S3), taking the additional step of applying our imbalance analysis to groupings of species informed by subgraph-role participation yielded less consistently significant imbalanced groups (compared to using the overall network structure as in the group model; Tables S8-S13), as did repeating the analysis for food webs in which nodes are defined by lifestage rather than by species for parasites (Tables S14-16). In this latter case, however, we still found significantly imbalanced groups with respect to particular life-stages in about half of the cases (*i.e.* combinations of concomitance, degree-correction, and number of groups) we considered. Re-labeling the life-stages with species-specific trophic strategies (*i.e.* labeling all life-stages of a parasite as just "parasite") yielded significant imbalances for these same groupings (Tables S17-S19).

4 Discussion

The group model can be used to find the coarse-grained ecological roles, similar to functional groups, that are present in a community. Here, we use the group model to identify general patterns in groupings across networks, to determine if parasites are structurally unique. Since groupings are based on the entire network structure, and the quality of a group depends on the quality of



Figure 4: Violin and boxplots of in-degree (number of prey) and out-degree (number of predators) for different trophic strategies in the Punta Banda network. Degree is plotted on a square root scale. Boxes indicate the traditional 25^{th} , 50^{th} and 75^{th} quartiles, with wiskers extending to 1.5 times the inter-quartile range. Above each violin are grouping letters as indicated by a Tukey's HSD (honest significant difference) test.

all other groups in the network, it is generally difficult to study how an ecologically relevant trait affects the group structure. In this study, we are able to consider the effect of two ecologically distinguishing features of parasites: concomitant predation and degree, by including or excluding concomitant links and by using a degree-corrected variant of the group model, respectively. We find that parasites are, in general, structurally distinct from free-living species, regardless of number of groups in the model, the inclusion or exclusion of concomitant predation, and whether or not the model corrects for degree. These findings contrast with those of Dunne et al. (2013b) on changes in local structure with the inclusion of parasites resulting mostly from the general increases in

diversity and complexity. This contrast is only apparent as it reflects a difference in focus; while Dunne et al. (2013b) addressed changes in the overall structure of the networks, we address here the position of parasites within this structure.

Concomitant predation tends to increase the distinction between parasites and free living species. This is not very surprising; concomitant interactions can create loops in the network, causing it to look less "cascade-like", that is, less like a network where species only consume species which are below them along some niche axis (Figs. S4-S10). In the absence of parasites, food webs tend to follow a largely cascade-like structure (Cohen and Newman, 1985), so the group model can easily use these interactions to distinguish parasitic species from free-living ones. Without concomitant links, parasites which have similar prey to free-living predators might end up in mixed groups of free-living and parasitic species; however, by including these links, parasitic species have additional predators that distinguish them from otherwise similar free-living species.

More surprising is the relationship we find with degree. Since parasites have different average in- and out-degree than free-living species, we might expect that degree would help the group model cluster parasites together. We found that the opposite was true: compensating for degree heterogeneity with the degree-corrected group model still produced more imbalanced groups. This suggests that degree is not the strongest structural signal that separates parasites from non-parasites. Indeed, although the mean degree is significantly different, the degree distribution of parasitic species overlaps considerably with the degree distributions of free-living categories. When uncorrected for degree, the group model tends to form a few groups with a small number of high-degree species. If the number of groups is constrained, as we have done here, this results in a few small groups and several larger groups. Thus, while the small groups may be highly imbalanced, the larger groups are often less imbalanced. The degree-corrected model counteracts this effect, producing groupings are significantly more even in size and even more strongly imbalanced. Relaxing the constraint on the number of groups improves the fit of the uncorrected model, and indeed, we see that the two models form more similar groupings as the number of groups increases (Table S20). This pattern suggests that the corrected and uncorrected models are identifying similar underlying structures, but that the uncorrected model "prioritizes" grouping of high-degree species over grouping species which are structurally similar. Put another way, the uncorrected model can be affected by high-degree outliers, especially when the number of groups is heavily constrained.

Finding little consolation in degree, one might think that the key to parasite structural uniqueness could be found in a slightly higher-order form of network structure, such as the local patterns of connectance termed "motifs" or subgraphs (Dunne et al., 2013b; Stouffer et al., 2012). Unfortunately, though some subgraph-roles are more associated with particular trophic strategies (Cirtwill and Stouffer, 2015; Supplemental Information), we found these trends to be less consistent than the group model at distinguishing strategies, such that groupings formed from species showing similarity in their subgraph-role participation were found to be less consistently significantly imbalanced and less strongly strongly significant on average when compared to those groupings found by the group model.

These results provide evidence that parasites are structurally distinguished, not by how many predators and hosts they have, but by who those predators and hosts are at a global scale. What are the ecological drivers of this difference? The groups identified by the group model do not lend themselves to easy interpretation in terms of one, or even a combination of several, node-specific properties of the network (*e.g.* degree, subgraph-role, taxonomy, body-size, trophic-level, centrality, *etc.*). Instead, the group model coalesces nodes that share similar roles within the network, *i.e.* species which interact with similar sets of other species in similar ways. Put another way, the group

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model acts upon the links between species, grouping links that go from and to similar species. Previous results have suggested that the group model is able to find more informative groupings than any one property alone (Staniczenko et al., 2014), but perhaps some combination of properties not investigated here could lend a more ecological explanation for the similarity of species within groups. In the Ythan network, we find that the group model partitions are closely related to an important biological property: evolutionary history, as captured by taxonomic partitions. The group model is able to capture taxonomic information using the results of the community's evolutionary history: the patterns of interaction between species.

One aspect of food web reporting that disproportionately affects parasites is the common practice of combining all life-stages of a species into a single node in the network. Parasites often have complex life-cycles, distinct stages of which might show wildly different patterns of interactions. The bulk of the results presented thus far consider food webs arranged in this way. To evaluate the effect of this data limitation on our results, for a subset of these networks we also looked at versions with these life-stages disaggregated. While we found the group model to be less consistent at distinguishing the various parasite life-stages from one another than it was at distinguishing species-aggregated trophic strategies, surprisingly, it still does fairly well at separating life-stages into different groups (Tables S14-16). More remarkably, if each life-stage is relabeled with the species-defined trophic strategies from before, we find even more consistently significantly imbalanced groupings than in the aggregated webs. This suggests that, when unable to distinguish between parasite life-stages, the group model tends to groups these various parasitic life-stages together, rather than lumping such stages in with another trophic strategy, and that the addition of this information on life-stages actually improves the group model's efficacy at grouping similar trophic strategies together at the species level.

Parasites constitute a very broad set of organisms. They can vary in many ways: size (from microscopic viruses to parasitic worms reaching a meter or longer; Randhawa and Poulin, 2009); life cycle complexity; level of specialization; presence of free living stages; and whether they live in or on their hosts. They are also extraordinarily phylogenetically diverse. Given these major differences, it is encouraging to see that a human-chosen categorization as parasite is indeed structurally relevant and statistically robust in food webs.

5 Conclusion

Network structure has been found to influence many important features of ecological systems, including robustness (Dunne et al., 2002c), stability (Allesina and Pascual, 2008), and resilience (Kéfi et al., 2016). General patterns of network structure are also used to develop structural (Cohen and Newman, 1985; Williams and Martinez, 2000; Petchey et al., 2008) and dynamic (Berlow et al., 2009; Haerter et al., 2016) models. However, many of these models were developed from data that excluded parasites, and parasites violate many of the patterns that they are based on. For example, concomitant predation creates loops that violate the cascade model, and allometric patterns which hold for free-living species (*e.g.*, Brose et al., 2006), such as predator:prey body mass ratios, are inverted for parasitic interactions (Romero-Romero et al., 2016). Models such as Allometric Diet Breadth Model (Petchey et al., 2008) and the Allometric Trophic Network (Berlow et al., 2009), which are based on body size data, are unlikely to capture parasites successfully.

Our finding that parasites have unique structural roles – in essence, form unique functional groups – suggests that existing food web models should be reevaluated to better fit these distinct structural patterns. This stands in contrast to previous work suggesting that parasites' effect on

network structure is mainly due to changes in connectance and diversity (Dunne et al., 2013b). Using the same set of networks, we instead find that parasites perform statistically distinct roles in networks, even when correcting for degree, and even when concomitant links are excluded. These results add to the growing evidence that parasites must be considered as we continue to study and model ecological networks.

6 Acknowledgements

Thanks to G Barabás, A Dobson, J Dunne, J Grilli, K Lafferty, and N Martinez for helpful discussions. ELS is supported by the NSF GRFP. MJM is supported by the U.S. Department of Education grant P200A150101. SA is supported by NSF DEB-1148867. This work was inspired by the Parasites and Food Webs Working Group supported by the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (DEB-0553768), the University of California, Santa Barbara and the State of California.

7 Authors' Contributions

All authors conceived the ideas and designed methodology; MJM and ELS analyzed the data, generated figures, and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

8 Data accessiblity

All food web data used in this project can be found in the Dryad Digital Repository: http://dx. doi.org/10.5061/dryad.b8r5c (Dunne et al., 2013a).

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Supplementary Information for:

Understanding parasites' roles in food webs using the group model

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S1 Group Model

The group model organizes species into groups such that species within a group tend to interact with other groups in the same way. Here, and throughout, we consider the directed case. The undirected case is mathematically very similar and is given a fuller treatment in (Karrer & Newman, 2011). In the most basic version of this model, it is possible to calculate the likelihood of obtaining the observed network A given the block structure or grouping G, where each block is treated as a separate Erdős-Rényi random graph. This likelihood is given as:

$$\mathcal{L}(A|G, c_{rs}; r, s \in 1, \dots, g) = \prod_{r=1}^{g} \prod_{s=1}^{g} c_{rs}^{L_{rs}} \left(1 - c_{rs}\right)^{S_r S_s - L_{rs}}$$
(1)

where c_{rs} is the connectance between groups r and s (note that, since the graph is directed, c_{rs} is not necessarily equal to c_{sr}), g is the number of groups, L_{rs} is the number of edges going from group r to group s, and S_r is the number of species in group r (Sander, Wootton & Allesina, 2015). Using a uniform prior, the Bayes factor can be calculated for model selection. For two groupings G_1 and G_2 , the Bayes factor is given by

$$B = \frac{P(A|G_1)}{P(A|G_2)}$$
(2)

where $P(A|G_1)$ is the marginal likelihood

$$\int_{0}^{1} \cdots \int_{0}^{1} P(c_{rs}; r, s \in 1, \dots, g) \mathcal{L}(A|G, c_{rs}, r, s \in 1:g) \, \mathrm{d}c_{11} \dots \, \mathrm{d}c_{gg}$$
(3)

which can be integrated to give

$$\prod_{r=1}^{g} \prod_{s=1}^{g} \frac{L_{rs}! \left(S_{r}S_{s} - L_{rs}\right)!}{\left(1 + L_{rs}\right) \left(1 + S_{r}S_{s}\right)!} \tag{4}$$

S2 Group Model for Multigraphs

Here we consider the group model for multigraphs, which is consistent with the degree-corrected case. For sparse networks such as ecological networks, the possibility of multiple edges between nodes does not significantly affect the results (Karrer & Newman, 2011). Using the multigraph group model, the number of interactions between a species from group r and a species from group s are drawn from a Poisson distribution with rate parameter ω_{rs} , such that $E[A_{ij}] = \omega_{rs}$ when $i \in r, j \in s$. Then the likelihood of the network A given the block structure G is:

$$\mathcal{L}(A|G,\omega_{rs};r,s\in 1,\ldots,g) = C\prod_{i=1}^{S}\prod_{j=1}^{S} \left(\omega_{g_ig_j}\right)^{A_{ij}} exp\left(-\omega_{g_ig_j}\right)$$
(5)

where

$$C = \prod_{i=1}^{S} \prod_{j=1}^{S} \left(A_{ij}! \right)^{-1}$$
(6)

The likelihood of a single block rs is then

$$\prod_{i \in r} \prod_{j \in s} (\omega_{g_i g_j})^{A_{ij}} exp(-\omega_{g_i g_j})$$
$$= (\omega_{rs})^{\sum_{i \in r} \sum_{j \in s} A_{ij}} exp(-\omega_{rs})$$
(7)

 $=\omega_{rs}^{L_{rs}}exp\left(-\omega_{rs}\right)$

Substituting this back into the likelihood for the full network, we get

$$\mathcal{L}(A|G,\omega_{rs};r,s\in 1,\ldots,g) = C\prod_{r=1}^{g}\prod_{s=1}^{g}\omega_{rs}^{L_{rs}}exp(-\omega_{rs})$$
(8)

Note that the fractional term C is constant with respect to the network structure, and therefore can be ignored when using Bayes factors for model selection on the same network. Note that C = 1 when the network is not a multigraph. Using equation 2 for the Bayes factor, we need to calculate the marginal likelihood. We can then use a Gamma distribution as a (conjugate) prior for the ω s, for the marginal likelihood

$$P(A|G_1) = C \int_0^\infty \cdots \int_0^\infty \prod_{r=1}^g \prod_{s=1}^g \frac{\beta^\alpha}{\Gamma(\alpha)} \omega_{rs}^{L_{rs}+\alpha-1} exp\left(-\omega_{rs}\left(1+\beta\right)\right) d\omega_{11} \dots d\omega_{gg}$$
(9)

Since the likelihood is a function, and the prior is the probability of that function, the quantity inside the integrals and products is an expectation. Since the expectation of the product is the product of expectations, this may be rewritten as

$$P(A|G_1) = C \prod_{r=1}^{g} \prod_{s=1}^{g} \int_0^\infty \cdots \int_0^\infty \frac{\beta^\alpha}{\Gamma(\alpha)} \omega_{rs}^{L_{rs}+\alpha-1} exp\left(-\omega_{rs}\left(1+\beta\right)\right) d\omega_{11} \dots d\omega_{gg}$$
(10)

which can be integrated to give

$$C\left(\frac{\beta^{\alpha}}{\Gamma(\alpha)}\right)^{g^2} (1+\beta)^{-\alpha g^2+L} \prod_{r=1}^g \prod_{s=1}^g \Gamma(\alpha+L_{rs})$$
(11)

where L is the total number of links in the network.

S3 Degree-Corrected Directed Group Model

Now to incorporate degree correction into the group model for multigraphs, consider parameters θ_i and ϕ_i , $i \in 1: S$, which control the expected in- and out-degree of vertex *i*, respectively. Then the expected number of edges going from species *j* to *i* is given by

$$E\left[A_{ij}\right] = \theta_i \phi_j \omega_{g_i g_j} \tag{12}$$

Then the likelihood may be written as

$$\mathcal{L}(A|G,\theta,\phi,\omega) = C \prod_{i=1}^{S} \prod_{j=1}^{S} \left(\theta_i \phi_j \omega_{g_i g_j}\right)^{A_{ij}} exp\left(-\theta_i \phi_j \omega_{g_i g_j}\right)$$
(13)

To normalize the θ s and ϕ s, we impose the following constraint for all groups r:

$$\sum_{i=1}^{S} \theta_i \delta_{g_i,r} = \sum_{i=1}^{S} \phi_i \delta_{g_i,r} = 1$$
(14)

where $\delta_{g_i,r}$ is the Kronecker delta. The likelihood can then be simplified, again by considering a single block rs:

$$\omega_{rs}^{L_{rs}} \prod_{i \in r} \prod_{j \in s} \left(\theta_i \phi_j \right)^{A_{ij}} exp\left(-\omega_{rs} \theta_i \phi_j \right) \tag{15}$$

$$=\omega_{rs}^{L_{rs}}exp\left[-\omega_{rs}\sum_{i\in r}\sum_{j\in s}\theta_{i}\phi_{j}\right]\prod_{i\in r}\prod_{j\in s}\theta_{i}^{A_{ij}}\phi_{j}^{A_{ij}}$$
(16)

$$=\omega_{rs}^{L_{rs}}exp\left[-\omega_{rs}\sum_{i\in r}\theta_{i}\sum_{j\in s}\phi_{j}\right]\prod_{i\in r}\theta_{i}^{\sum_{j\in s}A_{ij}}\prod_{j\in s}\phi_{j}^{\sum_{i\in r}A_{ij}}\tag{17}$$

then we can use the normalization constraints and plug this back into the likelihood for the full network to get

$$\mathcal{L}(A|G,\theta,\phi,\omega) = C \prod_{i=1}^{S} \theta_i^{k_i^{\text{out}}} \prod_{i=1}^{S} \phi_i^{k_i^{\text{in}}} \prod_{r=1}^{g} \prod_{s=1}^{g} \omega_{rs}^{L_{rs}} exp\left(-\omega_{rs}\right)$$
(18)

where k_i^{in} and k_i^{out} are the observed in- and out-degree of species *i*, respectively. Within each groups, the θ s and ϕ s are on a simplex (using the constraints in equation 14). Thus for each group *r*, we can set a prior of *Dirichlet*($\vec{1}$) over the θ s and ϕ s in each group to get a flat prior over the simplex. As before, we use a Gamma prior over each ω_{rs} , for the marginal likelihood

$$P(A|G_1) = C \int_0^\infty \cdots \int_0^\infty \prod_{r=1}^g \prod_{s=1}^g \frac{\beta^\alpha}{\Gamma(\alpha)} \omega_{rs}^{L_{rs}+\alpha-1} exp\left(-\omega_{rs}\left(1+\beta\right)\right) \mathrm{d}\omega_{11} \dots \mathrm{d}\omega_{gg} \times \int \cdots \int_{\Delta_r, r \in 1:g} \prod_{i \in r} \theta_i^{k_i^{\mathrm{out}}} \mathrm{d}\theta_1 \dots \mathrm{d}\theta_S \int \cdots \int_{\Delta_s, s \in 1:g} \prod_{j \in s} \phi_j^{k_j^{\mathrm{in}}} \mathrm{d}\phi_1 \dots \mathrm{d}\phi_S \quad (19)$$

Using the same technique as before, the products may be moved outside of the integrals, and the result may be integrated to give:

$$P(A|G_1) = C\left[\left(\frac{\beta^{\alpha}}{\Gamma(\alpha)}\right)^{g^2} \prod_{r=1}^g \prod_{s=1}^g (1+\beta)^{-(\alpha-L_{rs})} \Gamma(\alpha+L_{rs})\right] \times \left[\prod_{r=1}^g \frac{\prod_{i=1}^{S_r} \left(k_i^{\text{in}}\right)! \left(k_i^{\text{out}}!\right)}{\Gamma\left(S_r\right)^2 \Gamma\left(S_r + \sum_{i=1}^{S_r} k_i^{\text{in}}\right) \Gamma\left(S_r + \sum_{i=1}^{S_r} k_i^{\text{out}}\right)}\right]$$
(20)

S4 Search Algorithm

High-quality partitions were searched for using Metropolis-coupled Markov Chain Monte Carlo (MC^3) . This algorithm uses multiple MCMC chains, run in parallel at different temperatures, with occasional opportunities for chains to swap temperatures. The temperature parameter tunes the probability of accepting a "bad" move, that is, accepting a move that reduces the marginal likelihood. At low temperatures, the chain acts as a local search, only accepting steps which improve the marginal likelihood. At high temperatures, the chain acts more like a random walk, accepting many "bad" steps, in hopes of escaping local optima to find the globally optimal solution.

The algorithm was given a maximum number of groups g. Solutions were initialized by randomly assigning each species a group assignment between 1 and g. Throughout the search, partitions were allowed to collapse down to fewer than g groups (that is, some groups were allowed to be "empty"), but were never permitted to have more than g groups.

For further implementation details, see the main text and supplement of (Sander, Wootton & Allesina, 2015). The structure of the search algorithm used here is identical, but with the added constraint of a maximum number of groups.

S5 Subgraph Role Analysis

Here we investigate the usefulness of a species' subgraph contributions in classifying trophic strategies. In performing the following analyses, we utilize a subgraph-role naming convention which assigns a number to each of the thirteen non-isomorphic, three-node subgraphs (Milo *et al.*, 2002) and then distinguishes the roles within each subgraph by each node's degree distribution. For example, 1.2.0 corresponds to a node in subgraph 1 (apparent competition, see Figure S1), with an in-degree (number of prey) of 2 and an out-degree (number of predators) of 0 (*i.e.* the green node at the top). Likewise, the red nodes at the bottom share the same subgraph-role of 1.0.1 (subgraph 1, in-degree of 0, out-degree of 1). We start by enumerating how many of each of the thirty possible subgraph-role combinations each node of the network participates in.



Figure S1: A graphical portrayal of the thirteen unique, connected, three-node subgraph structures. The direction of the arrows represents energy flow in the network; that is, arrows point to the consumer. Some of these structures have been given names in the ecological literature, for instance subgraph 1 is often termed apparent competition while subgraph 5 can depict omnivory. Unique "roles" (*i.e.* unique degree distributions within the subgraph) are depicted by differing colors. There are thirty unique subgraph-role combinations in total across these subgraphs: two in the first subgraph (in-degree of 0, out-degree of 1 (red) and in-degree of 2, out-degree of 0 (green)), three in the second, *etc*.

Previous studies have indicated that the distribution of these subgraph-roles varies across trophic strategies. We see this as well (Figures S2 and S3), but without the inclusion of concomitant predation, no subgraph-role shows a consistent trend across all of the webs we looked at. With the inclusion of links depicting concomitant predation, however, several consistent trends emerge. For instance, Parasitism is consistently found to be enriched in subgraph-roles 3.1.1, 7.1.2, and 10.1.2 compared to other trophic strategies. These are all roles involving a bidirectional relationship with another species (*i.e.* the parasite both feeds on and is eaten by the same species). Similarly, predators are could to be consistently enriched in subgraph-roles 1.2.0, 4.1.0, 5.2.0, and 7.1.0. These are all roles without any out-degree (*i.e.* species which are not consumed by another species). Taken together, we can conclude that the addition of concomitant links better allows the separation of parasites from predators insofar as this inclusion adds loops (see discussion in main text) to the network while increasing the out-degree of parasites and the in-degree of predators (as was also suggested by examination of node degree; Section S16).

To investigate whether subgraph-role contribution could be used to distinguish trophic strategies more generally, these distributions (a vector of length 30 for each node in the network) were run through a principal component analysis to remove co-linearities and the resulting principal component coordinates were then clustered using a k-means algorithm into 2, 3, 5, or 10 groups in R to correspond to the number of groups found using the group model in other analyses. The k-means algorithm divides the data into a set number of groups (without the possibility of empty groups), thus it did not make sense to also repeat the g = 100 case in which we were looking for a natural upper-bound on the number of groups found by the group model.

The groupings found by the k-means algorithm were then evaluated for imbalance with respect to trophic

strategy as was done for the group model groupings. The results of this analysis are depicted in Section S8, in tables analogous to those for the group-model groupings in Section S7. Because this analysis is computationally intensive, we omitted the largest network (Punta Banda). In summary, we find these groupings to be less significantly imbalanced than those found by the group model. This is despite the trends observed in the subgraph distributions depicted in Figures S2 and S3 likely because of the substantial overlap in the distributions, even in the case of statistically distinct means.



Figure S2: Distribution of subgraph-roles across trophic strategies. Subgraph counts are plotted on a square root scale. Boxes indicate the traditional 25^{th} , 50^{th} , and 75^{th} quartiles, with whiskers extending to 1.5 times the inter-quartile range. Above each boxplot are grouping letters as indicated by a Tukeys HSD (honest significant difference) test. Note that, though some panels show a difference in subgraph role counts by trophic strategy, none of these trends are consistent across all webs listed.





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S6 Data

Table S1: Empirical food web data used in this paper. Each row corresponds to a different food web. Columns indicate, respectively, the name of the web, its number of species, number of links without (and with) including concomitant links, and a reference for the source of the original data.

Name	Species	Links (with concomitant predation)	Reference
Bahia Falsa	171	2234 (3720)	Hechinger et al. (2011)
Carpinteria Salt Marsh	165	2187 (3708)	Hechinger $et \ al. \ (2011)$
Flensburg Fjord	123	968~(1406)	Zander $et al.$ (2011)
Otago Harbor	142	1487(1844)	Mouritsen $et al.$ (2011)
Punta Banda	214	3334(5653)	Hechinger $et \ al. \ (2011)$
Sylt Tidal Basin	161	1950(3005)	Thieltges $et al.$ (2011)
Ythan Estuary	133	597 (1391)	Huxham, Beaney & Raffaelli (1996)

S7 Full Imbalance Results

Concomitant Links	Degree Corrected	g	all	Herbivores	Parasites	Predators	1° Producers
		2/2	0.191**	0.636^{***}	0.423	0.382	0.841**
		3/3	0.218^{***}	0.534^{***}	0.406^{***}	0.446^{***}	0.809^{***}
No	No	5/5	0.313^{***}	0.717^{***}	0.575^{***}	0.740^{***}	0.644^{*}
		10/10	0.202^{***}	0.480^{***}	0.459^{***}	0.655^{***}	0.439^{*}
		15/100	0.132^{***}	0.329^{***}	0.436^{***}	0.427^{***}	0.439^{***}
		2/2	0.309***	0.597^{*}	0.494*	0.679***	0.817
		3/3	0.326^{***}	0.452	0.576^{***}	0.646^{***}	0.737
No	Yes	5/5	0.221^{***}	0.544^{***}	0.403^{***}	0.568^{***}	0.587
		10/10	0.115^{***}	0.516^{***}	0.264^{***}	0.246^{***}	0.450^{***}
		38/100	0.001^{***}	0.015^{***}	0.021^{***}	0.012^{***}	0.131^{***}
		2/2	0.448***	0.649***	0.544^{***}	0.931***	0.845**
		3/3	0.541^{***}	0.580^{***}	0.798^{***}	0.906^{***}	0.754^{***}
Yes	No	5/5	0.588^{***}	0.625^{***}	0.897^{***}	0.882^{***}	0.734^{***}
		10/10	0.325^{***}	0.645^{***}	0.535^{***}	0.573^{***}	0.567^{***}
		19/100	0.358^{***}	0.704^{***}	0.425^{***}	1.000	0.842^{***}
		2/2	0.422***	0.612***	0.497^{*}	0.820***	0.819
		3/3	0.273^{***}	0.464^{*}	0.473^{***}	0.698^{***}	0.724
Yes	Yes	5/5	0.312^{***}	0.425^{***}	0.565^{***}	0.690^{***}	0.653^{***}
		10/10	0.091^{***}	0.241^{***}	0.553^{***}	0.325^{***}	0.321
		43/100	0.000***	0.013^{***}	0.067^{***}	1.000	0.100^{***}

Table S2: As Table 1 in main text, but for the Bahia Falsa network.

Table S3: As Table 1 in main text, but for the Carpinteria network.

Concomitant Links	Degree Corrected	g	all	Herbivores	Parasites	Predators	1° Producers
		2/2	0.198	0.735	0.418	0.438***	0.860
		3/3	0.195^{***}	0.685^{***}	0.353^{***}	0.465^{***}	0.836^{***}
No	No	5/5	0.346^{***}	0.539^{***}	0.576^{***}	0.625^{***}	0.685
		10/10	0.283^{***}	0.587^{***}	0.468^{***}	0.469^{***}	0.656^{***}
		14/100	0.234^{***}	0.730^{***}	0.312^{***}	0.494^{***}	0.510^{*}
		2/2	0.205	0.750^{***}	0.420	0.403***	0.865
		3/3	0.225^{***}	0.601	0.498^{***}	0.321^{***}	0.776
No	Yes	5/5	0.089^{***}	0.405	0.289^{***}	0.150^{***}	0.694
		10/10	0.041^{***}	0.282^{***}	0.146^{***}	0.147^{***}	0.367
		39/100	0.001^{***}	0.073^{***}	0.005^{***}	0.011^{***}	0.234^{***}
	No	2/2	0.236**	0.693	0.420	0.542***	0.840
		3/3	0.358^{***}	0.623	0.639^{***}	0.857^{***}	0.803
Yes		5/5	0.344^{***}	0.623^{***}	0.614^{***}	0.823^{***}	0.803^{***}
		10/10	0.259^{***}	0.529^{***}	0.500^{***}	0.552^{***}	0.769^{***}
		17/100	0.103^{***}	0.264^{***}	0.239^{***}	0.517^{***}	0.586^{***}
		2/2	0.535^{***}	0.743	0.608***	0.788^{***}	0.862
Yes		3/3	0.234^{***}	0.647	0.352^{***}	0.572^{***}	0.785
	Yes	5/5	0.160^{***}	0.401	0.502^{***}	0.318^{***}	0.632
		10/10	0.061^{***}	0.207	0.369^{***}	0.194^{***}	0.457
		47/100	0.002^{***}	0.055^{***}	0.072^{***}	0.010^{***}	0.315^{***}

Concomitant Links	Degree Corrected	g	all	Herbivores	Parasites	Predators	1° Producers
		2/2	0.425***	0.779	0.496***	0.567***	0.910
		3/3	0.281^{***}	0.730	0.404^{***}	0.358^{***}	0.818
No	No	5/5	0.312^{***}	0.642	0.461^{***}	0.470^{***}	0.750
		10/10	0.365^{***}	0.440	0.970^{***}	0.426^{***}	0.750
		13/100	0.478^{***}	0.674^{***}	0.827^{***}	0.557^{***}	0.750^{**}
		2/2	0.216	0.797	0.392	0.333	0.902
		3/3	0.433^{***}	0.622	0.728^{***}	0.492^{***}	0.888*
No	Yes	5/5	0.265^{***}	0.549	0.789^{***}	0.265^{***}	0.647
		10/10	0.117^{***}	0.347	0.404^{***}	0.268^{***}	0.500
		27/100	0.006^{***}	0.200^{***}	0.051^{***}	0.023***	0.200
		2/2	0.438***	0.876	0.562^{***}	0.619***	0.943
		3/3	0.291^{***}	0.829^{**}	0.470^{***}	0.423^{***}	0.921
Yes	No	5/5	0.300^{***}	0.690^{**}	0.525^{***}	0.315^{***}	0.857^{**}
		10/10	0.426^{***}	0.680^{***}	0.857^{***}	0.533^{***}	0.615
		14/100	0.486^{***}	0.700^{***}	0.814^{***}	0.567^{***}	0.750^{**}
		2/2	0.356***	0.742	0.561^{***}	0.387^{*}	0.854
		3/3	0.189^{***}	0.680	0.347^{***}	0.208	0.835
Yes	Yes	5/5	0.177^{***}	0.541	0.655^{***}	0.207^{***}	0.538
		10/10	0.237^{***}	0.477^{***}	0.909^{***}	0.276^{***}	0.500
		32/100	0.016^{***}	0.200^{***}	0.240^{***}	0.024^{***}	0.250

Table S4: As Table 1 in main text, but for the Flensburg network.

Table S5: As Table 1 in main text, but for the Otago network.

Concomitant Links	Degree Corrected	g	all	Herbivores	Parasites	Predators	1° Producers
		2/2	0.380***	0.517^{***}	0.756	0.504^{***}	0.931
		3/3	0.326^{***}	0.588^{***}	0.632	0.343^{***}	0.902
No	No	5/5	0.191^{***}	0.603^{***}	0.442	0.263^{***}	0.667
		10/10	0.281^{***}	0.527^{***}	0.533^{***}	0.351^{***}	0.800
		15/100	0.113^{***}	0.277^{***}	0.433^{***}	0.169^{***}	0.667
		2/2	0.278	0.464	0.748	0.278	0.941
		3/3	0.182^{**}	0.288	0.619	0.221^{*}	0.911
No	Yes	5/5	0.083^{***}	0.162	0.546^{***}	0.145^{***}	0.822
		10/10	0.024^{***}	0.105^{***}	0.412^{***}	0.063^{***}	0.577
		34/100	0.005^{***}	0.055^{***}	0.321^{***}	0.007^{***}	0.211
		2/2	0.452^{***}	0.538^{***}	0.786^{**}	0.690^{***}	0.956
		3/3	0.371^{***}	0.569^{***}	0.589	0.543^{***}	0.833
Yes	No	5/5	0.165^{***}	0.606^{***}	0.358	0.297^{***}	0.500
		10/10	0.373^{***}	0.401^{***}	0.794^{***}	0.465^{***}	1.000^{***}
		17/100	0.217^{***}	0.257^{***}	0.755^{***}	0.317^{***}	0.831^{*}
		2/2	0.294	0.491	0.740	0.294	0.945
Yes		3/3	0.178^{**}	0.354^{***}	0.613	0.178	0.920^{*}
	Yes	5/5	0.086^{***}	0.256^{***}	0.490	0.101^{*}	0.789
		10/10	0.052^{***}	0.193^{***}	0.572^{***}	0.052^{***}	0.562
		36/100	0.008^{***}	0.072^{***}	0.500^{***}	0.008^{***}	0.225

Concomitant Links	Degree Corrected	g	all	Herbivores	Parasites	Predators	1° Producers
		2/2	0.491	0.933*	0.579	0.491	0.933*
		3/3	0.347	0.871	0.493	0.347	0.842
No	No	5/5	0.487^{***}	0.879^{*}	0.660^{***}	0.487^{***}	0.870
		10/10	0.290^{***}	0.756	0.543^{***}	0.507^{***}	0.473
		15/100	0.191^{***}	0.633	0.514^{***}	0.280^{***}	0.510
		2/2	0.494	0.927	0.605	0.494	0.925
		3/3	0.603^{***}	0.896	0.688^{***}	0.692^{***}	0.871
No	Yes	5/5	0.335^{***}	0.809	0.470^{***}	0.396^{***}	0.820
		10/10	0.129^{***}	0.632	0.196^{***}	0.338^{***}	0.635
		36/100	0.007^{***}	0.268	0.064^{***}	0.018^{***}	0.169
		2/2	0.476	0.972	0.551	0.476	0.927
		3/3	0.767^{***}	0.959	0.812^{***}	0.849^{***}	0.899
Yes	No	5/5	0.554^{***}	0.947	0.718^{***}	0.554^{***}	0.829
		10/10	0.351^{***}	0.778	0.675^{***}	0.468^{***}	0.540
		15/100	0.231^{***}	0.771	0.452^{***}	0.309^{***}	0.540
		2/2	0.484	0.975	0.547	0.484	0.929
		3/3	0.707^{***}	0.964	0.728^{***}	0.831^{***}	0.878
Yes	Yes	5/5	0.468^{***}	0.915	0.644^{***}	0.504^{***}	0.758
		10/10	0.207^{***}	0.859	0.476^{***}	0.207^{***}	0.559
		43/100	0.003^{***}	0.500	0.042^{***}	0.007^{***}	0.213

Table S6: As Table 1 in main text, but for the Sylt network.

Table S7: As Table 1 in main text, but for the Ythan network.

Concomitant Links	Degree Corrected	g	all	Herbivores	Parasites	Predators	1° Producers
		2/2	0.248***	0.479	0.562^{***}	0.390	0.926
		3/3	0.373^{***}	0.533^{***}	0.538^{***}	0.611^{***}	0.899
No	No	5/5	0.371^{***}	0.476^{***}	0.778^{***}	0.412^{***}	0.912
		8/10	0.212^{***}	0.303^{***}	0.713^{***}	0.255^{***}	0.856
		8/100	0.212^{***}	0.303^{***}	0.713^{***}	0.255^{***}	0.856
		2/2	0.269***	0.514	0.470	0.479***	0.935
		3/3	0.550^{***}	0.754^{***}	0.733^{***}	0.611^{***}	0.914
No	Yes	5/5	0.344^{***}	0.740^{***}	0.452^{***}	0.426^{***}	0.846
		10/10	0.035^{***}	0.398^{***}	0.079^{***}	0.063^{***}	0.636
		27/100	0.000^{***}	0.007^{***}	0.001^{*}	0.004^{***}	0.480
		2/2	0.457^{***}	0.609^{***}	0.543^{***}	0.891^{***}	0.957
		3/3	0.426^{***}	0.483^{***}	0.604^{***}	0.753^{***}	0.929^{*}
Yes	No	5/5	0.312^{***}	0.476^{***}	0.374^{***}	0.745^{***}	0.819
		10/10	0.426^{***}	0.598^{***}	0.519^{***}	0.643^{***}	0.927^{**}
		13/100	0.276^{***}	0.326^{***}	0.455^{***}	0.651^{***}	0.874^{**}
		2/2	0.348***	0.497	0.448	0.706***	0.940
	Yes	3/3	0.197^{***}	0.394^{***}	0.304	0.593^{***}	0.909
Yes		5/5	0.350^{***}	0.492^{***}	0.445^{***}	0.699^{***}	0.853
		10/10	0.198^{***}	0.362^{***}	0.397^{***}	0.386^{***}	0.764
		34/100	0.001^{***}	0.013^{***}	0.064^{***}	0.004^{***}	0.338

S8 Subgraph Role Imbalance Results

Table S8: As Table 1 in main text, but for groupings based on k-means clustering of the subgraph-role contributions of each node of the Bahia Falsa network.

Concomitant Links	Degree Corrected	g	all	Herbivores	Parasites	Predators	1° Producers
		2	0.243*	0.748*	0.482	0.423	0.893
No	No	3	0.253^{***}	0.730^{**}	0.621^{***}	0.497^{**}	0.786
	NO	5	0.092^{***}	0.427^{**}	0.399^{***}	0.218^{**}	0.706
		10	0.015^{***}	0.407^{***}	0.071^{***}	0.028^{**}	0.394
Yes		2	0.128	0.560	0.517^{*}	0.440**	0.713
	No	3	0.201^{***}	0.442	0.441	0.407^{***}	0.809^{**}
	INO	5	0.096^{***}	0.362^{*}	0.208	0.330^{***}	0.590
		10	0.055^{***}	0.235^{**}	0.237^{***}	0.298^{***}	0.568

Table S9: As Table 1 in main text, but for groupings based on k-means clustering of the subgraph-role contributions of each node of the Carpinteria network.

Concomitant Links	Degree Corrected	g	all	Herbivores	Parasites	Predators	1° Producers
N		2	0.224	0.819**	0.369	0.303	0.906^{*}
	No	3	0.156^{**}	0.744^{***}	0.288	0.321^{**}	0.867^{***}
INO	NO	5	0.124^{***}	0.630^{*}	0.207^{*}	0.180^{**}	0.800
		10	0.008^{***}	0.276	0.040^{**}	0.029^{**}	0.648^{***}
		2	0.278^{***}	0.767	0.451*	0.469^{***}	0.892**
Voc	No	3	0.262^{**}	0.847	0.418	0.404^{*}	0.920
res	INO	5	0.205^{***}	0.441	0.350^{***}	0.586^{***}	0.797^{*}
		10	0.049^{***}	0.362	0.159^{***}	0.313^{***}	0.554

Table S10: As Table 1 in main text, but for groupings based on k-means clustering of the subgraph-role contributions of each node of the Flensburg network.

Concomitant Links	Degree Corrected	g	all	Herbivores	Parasites	Predators	1° Producers
		2	0.475	0.893	0.631	0.525	0.951
No	No	3	0.146	0.821^{*}	0.226	0.208	0.813
	NO	5	0.078^{**}	0.739^{***}	0.209^{**}	0.152^{**}	0.652
		10	0.094^{***}	0.548	0.286^{***}	0.172^{***}	0.364
		2	0.280	0.699	0.582**	0.336	0.815
Voc	No	3	0.298^{*}	0.670	0.513^{*}	0.459^{**}	0.730
res	NO	5	0.108^{*}	0.616	0.361^{***}	0.243^{**}	0.809
		10	0.134^{***}	0.528^{*}	0.324^{***}	0.202^{***}	0.604

Concomitant Links	Degree Corrected	g	all	Herbivores	Parasites	Predators	1° Producers
		2	0.525	0.688	0.865	0.525	0.972
Ne	No	3	0.139	0.392^{**}	0.469	0.249^{*}	0.924
INO	NO	5	0.172^{***}	0.392^{***}	0.459	0.244^{***}	0.934
		10	0.030^{*}	0.133^{*}	0.405	0.047^{*}	0.432
		2	0.272	0.691	0.583	0.272	0.815
Var	No	3	0.446^{**}	0.679^{*}	0.727	0.446^{*}	0.969
res	NO	5	0.228^{***}	0.478^{***}	0.558	0.241^{**}	0.963
		10	0.051^{***}	0.162^{**}	0.243	0.116^{***}	0.750

Table S11: As Table 1 in main text, but for groupings based on k-means clustering of the subgraph-role contributions of each node of the Otago network.

Table S12: As Table 1 in main text, but for groupings based on k-means clustering of the subgraph-role contributions of each node of the Sylt network.

Concomitant Links	Degree Corrected	g	all	Herbivores	Parasites	Predators	1° Producers
		2	0.477	0.923	0.600	0.477	0.917
No	No	3	0.398^{***}	0.897	0.534^{***}	0.398^{***}	0.880
NO	NO	5	0.149	0.897^{*}	0.311	0.186	0.458
		10	0.054	0.798	0.148	0.054	0.495
		2	0.599^{*}	0.964	0.682*	0.599^{*}	0.933
Voc	No	3	0.543^{**}	0.979	0.613	0.543^{**}	0.936^{*}
res	NO	5	0.171	0.873	0.376	0.214	0.632
		10	0.197^{***}	0.881	0.241^{**}	0.354^{***}	0.612

Table S13: As Table 1 in main text, but for groupings based on k-means clustering of the subgraph-role contributions of each node of the Ythan network.

Concomitant Links	Degree Corrected	g	all	Herbivores	Parasites	Predators	1° Producers
		2	0.379	0.727	0.682	0.621	0.970
No	No	3	0.232^{***}		0.382^{***}	0.290^{**}	0.909
INO	NO	5	0.144^{***}	0.387^{***}	0.410^{***}	0.204^{*}	0.789
		10	0.076^{***}	0.326^{***}	0.165^{***}	0.213^{***}	0.780
		2	0.278^{***}	0.582^{***}	0.506^{*}	0.572^{***}	0.955
Voc	No	3	0.129^{**}	0.576^{***}	0.226		0.953
res	NO	5	0.147^{***}	0.600^{***}	0.273	0.257^{**}	0.956
		10	0.050^{***}	0.735^{***}	0.074^{*}	0.062^{**}	

Concomitant Links	Degree Corrected	<i>5</i> 0	all	Herbivore	Parasite	Parasite cas-	Parasite	Parasite	Parasite	Predator	1°Producer	1°Producer
				detritivore		trator	nonfeeding	pathogen	trophictrans-			other
									mission			
		2/2	0.312^{***}	0.994	0.775^{**}	0.912	0.925	0.975	0.769**	0.688^{***}	0.975	0.988
		3/3	0.113^{***}	0.991	0.656^{***}	0.725	0.890^{**}	0.953	0.572*	0.449^{***}	0.963	0.982
Yes	No	5/5	0.124^{***}	0.982	0.568^{***}	0.731	0.786	0.924	0.439^{**}	0.351^{***}	0.929^{**}	0.964
		10/10	0.068^{***}	0.964	0.465^{***}	0.562	0.571	0.894^{**}	0.235^{***}	0.502^{***}	0.857	0.929
		14/100	0.042^{***}	0.800	0.453^{***}	0.562	0.556	0.896*	0.216^{***}	0.346^{***}	0.578	0.770
		2/2	0.194^{***}	0.982	0.712^{***}	0.888**	0.782	0.968	0.704^{***}	0.477^{***}	0.927	0.964
		3/3	0.061	0.979	0.563^{***}	0.702	0.745	0.945	0.514	0.259^{**}	0.915	0.957
γ_{es}	Yes	5/5	0.092^{***}	0.960	0.440^{***}	0.576	0.520	0.917	0.335	0.595^{***}	0.840	0.920
		10/10	0.024^{***}	0.957	0.211^{***}	0.331	0.522	0.797	0.128^{*}	0.267^{***}	0.826	0.913
		34/100	0.000^{***}	0.750	0.095^{***}	0.533^{***}	0.300^{***}	0.555	0.046^{***}	0.033^{***}	0.417	0.500
		2/2	0.321^{***}	0.994	0.778*	0.914	0.926	0.975	0.772*	0.679^{***}	0.975	0.988
		3/3	0.198^{***}	0.987	0.566	0.823	0.854	0.952	0.593^{*}	0.439^{***}	0.949	0.975
No	No	5/5	0.127^{***}	0.982	0.554^{***}	0.659	0.786	0.931	0.461^{**}	0.304^{***}	0.929	0.964
		10/10	0.044^{***}	0.964	0.483^{***}	0.583^{**}	0.571	0.885*	0.126	0.247^{***}	0.857	0.929
		14/100	0.034^{***}	0.800	0.405^{***}	0.700^{***}	0.556	0.877^{*}	0.169^{***}	0.193^{***}	0.578	0.770
		2/2	0.180^{***}	0.983	0.700^{***}	0.877*	0.800	0.967	0.677^{***}	0.430^{***}	0.933	0.967
		3/3	0.233^{***}	0.989	0.519	0.839^{***}	0.862^{***}	0.943	0.542	0.499^{***}	0.954	770.0
No	Yes	5/5	0.085^{***}	0.960	0.418^{***}	0.576	0.520	0.916	0.331	0.538^{***}	0.840	0.920
		10/10	0.024^{***}	0.952	0.268^{***}	0.389	0.571	0.877*	0.177^{***}	0.132^{***}	0.714	0.905
		34/100	0.000^{***}	0.800	0.050^{***}	0.500^{***}	0.333^{***}	0.476	0.026^{***}	0.023^{***}	0.420	0.400

S9 Disaggregated Life-cycles—Node-specific Trophic Strategies
1°Producer	0.966 0.965 0.923 0.500 0.250	$\begin{array}{c} 0.965\\ 0.955*\\ 0.897\\ 0.625\\ 0.188\end{array}$	0.966 0.963 0.919 0.600 0.600	0.965 0.956 0.900 0.625 0.281	
Predator	$\begin{array}{c} 0.505^{***} \\ 0.331^{***} \\ 0.277^{***} \\ 0.371^{***} \\ 0.156^{***} \end{array}$	$\begin{array}{c} 0.433 \\ 0.313*** \\ 0.536*** \\ 0.166*** \\ 0.003*** \end{array}$	$\begin{array}{c} 0.509^{***}\\ 0.366^{***}\\ 0.257^{***}\\ 0.335^{***}\\ 0.166^{***}\end{array}$	$\begin{array}{c} 0.435\\ 0.307^{***}\\ 0.574^{***}\\ 0.189^{***}\\ 0.002^{***}\end{array}$	
Parasite trophictrans- mission	0.879** 0.818*** 0.750** 0.472 0.273	$\begin{array}{c} 0.842^{*} \\ 0.757 \\ 0.676 \\ 0.358 \\ 0.152^{***} \end{array}$	$\begin{array}{c} 0.880^{**}\\ 0.809^{**}\\ 0.733^{*}\\ 1.000\\ 0.352 \end{array}$	$\begin{array}{c} 0.843*\ 0.745\ 0.639\ 0.367\ 0.141***\end{array}$	
Parasite nonfeeding	$\begin{array}{c} 0.903^{**}\\ 0.791\\ 0.814^{***}\\ 0.620\\ 0.375\end{array}$	$\begin{array}{c} 0.860\\ 0.818^{*}\\ 0.586\\ 0.586\\ 0.602^{***}\\ 0.250^{***}\end{array}$	$\begin{array}{c} 0.904*\\ 0.804\\ 0.785*\\ 1.000\\ 0.417\end{array}$	$\begin{array}{c} 0.859 \\ 0.824^{**} \\ 0.600 \\ 0.602^{***} \\ 0.250^{***} \end{array}$	
Parasite cas- trator	$\begin{array}{c} 0.895**\\ 0.845***\\ 0.802***\\ 0.626*\\ 0.612***\end{array}$	$\begin{array}{c} 0.862 \\ 0.783 \\ 0.695 \\ 0.400 \\ 0.306^{***} \end{array}$	$\begin{array}{c} 0.896**\\ 0.832**\\ 0.768*\\ 1.000\\ 0.627***\end{array}$	$\begin{array}{c} 0.863^{**} \\ 0.783 \\ 0.666 \\ 0.459 \\ 0.260^{***} \end{array}$	he Otorie notine
Parasite	$\begin{array}{c} 0.863^{**}\\ 0.710\\ 0.644\\ 0.551^{**}\\ 0.577^{***}\end{array}$	$\begin{array}{c} 0.819\\ 0.707\\ 0.499\\ 0.750^{***}\\ 0.238^{***}\end{array}$	0.864^{**} 0.720 0.706^{**} 0.268^{***} 0.577^{***}	$\begin{array}{c} 0.821 \\ 0.693 \\ 0.492 \\ 0.761^{***} \\ 0.190^{***} \end{array}$	1 - C1 4 1 5 1
Herbivore detritivore	$\begin{array}{c} 0.982\\ 0.988\\ 0.974\\ 0.833\\ 0.833\\ 0.500 \end{array}$	0.988 0.985 0.966 0.875 0.800	0.982 0.988 0.973 0.800 0.800	0.988 0.985 0.967 0.875 0.800	E - 150 -
all	$\begin{array}{c} 0.505^{***} \\ 0.297 \\ 0.224^{***} \\ 0.072^{***} \\ 0.024^{***} \end{array}$	0.433 0.262 0.148** 0.046*** 0.001***	0.509*** 0.288 0.215*** 0.088***	0.435 0.254 0.134 0.045^{***} 0.000^{***}	Ē
60	2/2 3/3 5/5 10/10 16/100	2/2 3/3 5/5 10/10 38/100	2/2 3/3 5/5 10/10 16/100	2/2 3/3 5/5 10/10 38/100	
Degree Corrected	No	Yes	No	Yes	
Concomitant Links	Yes	Yes	No	Νο	

Concomitant Links	Degree Corrected	60	all	Herbivore	Parasite	Parasite cas-	Parasite	Parasite	Predator	1°Producer
				detritivore		trator	nonfeeding	trophictrans-		
								mission		
		2/2	0.376^{***}	0.994	0.826^{***}	0.848^{***}	0.893^{**}	0.837^{***}	0.624^{***}	0.978
		3/3	0.166^{**}	0.991	0.712^{***}	0.697	0.821^{***}	0.688	0.362^{***}	0.959
Yes	No	5/5	0.106^{***}	0.962	0.455	0.671^{***}	0.684	0.613^{***}	0.349^{***}	0.846
		10/10	0.082^{***}	0.955	0.490^{***}	0.442^{***}	0.797^{***}	0.278	0.446^{***}	0.862
		18/100	0.041^{***}	0.800	0.502^{***}	0.450^{***}	0.776^{***}	0.216^{**}	0.282^{***}	0.564
		2/2	0.277	0.989	0.777^{***}	0.806^{***}	0.791	0.788***	0.449^{***}	0.960
		3/3	0.140	0.982	0.648	0.713^{**}	0.670	0.695^{***}	0.259^{***}	0.940
\mathbf{Yes}	Y_{es}	5/5	0.180^{***}	0.978	0.430	0.539	0.597	0.509	0.628^{***}	0.919
		10/10	0.057^{***}	0.938	0.614^{***}	0.540^{***}	0.792^{***}	0.239	0.182^{***}	0.782
		44/100	0.000^{***}	0.667	0.141^{***}	0.050^{***}	0.370^{***}	0.016^{***}	0.005^{***}	0.400
		2/2	0.373^{***}	0.994	0.825^{***}	0.847^{***}	0.893^{**}	0.836^{***}	0.627^{***}	0.977
		3/3	0.167^{**}	0.991	0.716^{***}	0.695	0.824^{***}	0.686	0.352^{***}	0.959
No	No	5/5	0.100^{***}	0.962	0.469	0.665^{***}	0.684	0.611^{***}	0.348^{***}	0.846
		10/10	0.090^{***}	0.955	0.460^{***}	0.493^{***}	0.800^{***}	0.311	0.309^{***}	0.869
		18/100	0.026^{***}	0.800	0.413^{***}	0.375^{***}	0.770^{***}	0.220^{***}	0.151^{***}	0.556
		2/2	0.278^{*}	0.989	0.777^{***}	0.800^{***}	0.796	0.788^{***}	0.425^{***}	0.960
		3/3	0.139	0.982	0.660	0.708^{**}	0.671	0.677	0.221^{**}	0.942
No	Yes	5/5	0.184^{***}	0.978	0.430	0.539	0.597	0.509	0.655^{***}	0.919
		10/10	0.110^{***}	1.000	0.229^{***}	1.000	0.791^{***}	1.000	0.239^{***}	0.864^{**}
		44/100	0.000^{***}	1.000	0.007^{***}	1.000	0.476^{***}	1.000	0.016^{***}	0.360

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S10 Disaggregated Life-cycles—Species-specific Trophic Strategies

Concomitant Links	Degree Corrected	g	all	Herbivore	Parasite	Predator	1°Producer
		2/2	0.644^{***}	0.994	0.644^{***}	0.688^{***}	0.962
		3/3	0.409^{***}	0.991	0.409^{***}	0.449^{***}	0.945^{*}
Yes	No	5/5	0.351^{***}	0.982	0.431^{***}	0.351^{***}	0.893
		10/10	0.317^{***}	0.964	0.422^{***}	0.502^{***}	0.786
		14/100	0.257^{***}	0.800	0.370^{***}	0.346^{***}	0.741
		2/2	0.477***	0.982	0.569^{***}	0.477***	0.891
		3/3	0.259^{***}	0.979	0.328^{***}	0.259^{**}	0.872
Yes	Yes	5/5	0.375^{***}	0.960	0.407^{***}	0.595^{***}	0.760
		10/10	0.169^{***}	0.957	0.169^{***}	0.267^{***}	0.739
		34/100	0.022^{***}	0.750	0.133^{***}	0.033^{***}	0.185
		2/2	0.636***	0.994	0.636***	0.679^{***}	0.963
		3/3	0.368^{***}	0.987	0.439^{***}	0.439^{***}	0.924
No	No	5/5	0.304^{***}	0.982	0.373^{***}	0.304^{***}	0.893
		10/10	0.156^{***}	0.964	0.208^{***}	0.247^{***}	0.786
		14/100	0.144^{***}	0.800	0.207^{***}	0.193^{***}	0.741
		2/2	0.430***	0.983	0.514^{***}	0.430***	0.900
		3/3	0.426^{***}	0.989	0.478^{***}	0.499^{***}	0.931^{*}
No	Yes	5/5	0.340^{***}	0.960	0.368^{***}	0.538^{***}	0.760
		10/10	0.088^{***}	0.952	0.110^{***}	0.132^{***}	0.635
		34/100	0.005^{***}	0.800	0.032^{***}	0.023^{***}	0.158

Table S17: As Table S15 (*i.e.* using the disaggregated food web), but labeling nodes with the trophic strategy of their aggregated node from the prior analyses.

Table S18: As Table S15 (*i.e.* using the disaggregated food web), but labeling nodes with the trophic strategy of their aggregated node from the prior analyses.

Concomitant Links	Degree Corrected	g	all	Herbivore	Parasite	Predator	1°Producer
		2/2	0.505***	0.982	0.540***	0.505^{***}	0.966
		3/3	0.331^{***}	0.988	0.356^{**}	0.331^{***}	0.965
Yes	No	5/5	0.277^{***}	0.974	0.313^{***}	0.277^{***}	0.923
		10/10	0.186^{***}	0.833	0.247^{***}	0.371^{***}	0.500
		16/100	0.039^{***}	0.500	0.078^{***}	0.156^{***}	0.250
		2/2	0.433	0.988	0.459	0.433	0.965
		3/3	0.313^{***}	0.985	0.339^{***}	0.313^{***}	0.955^{*}
Yes	Yes	5/5	0.462^{***}	0.966	0.462^{***}	0.536^{***}	0.897
		10/10	0.083^{***}	0.875	0.166^{***}	0.166^{***}	0.625
		38/100	0.003^{***}	0.800	0.021^{***}	0.003^{***}	0.188
		2/2	0.509^{***}	0.982	0.544^{***}	0.509^{***}	0.966
		3/3	0.366^{***}	0.988	0.394^{***}	0.366^{***}	0.963
No	No	5/5	0.257^{***}	0.973	0.291^{***}	0.257^{***}	0.919
		10/10	0.201^{***}	0.800	0.268^{***}	0.335^{***}	0.600
		16/100	0.099^{***}	0.800	0.132^{***}	0.166^{***}	0.600
		2/2	0.435	0.988	0.461	0.435	0.965
		3/3	0.307^{***}	0.985	0.333^{***}	0.307^{***}	0.956
No	Yes	5/5	0.497^{***}	0.967	0.492	0.574^{***}	0.900
		10/10	0.095^{***}	0.875	0.189^{***}	0.189^{***}	0.625
		38/100	0.002^{***}	0.800	0.011^{***}	0.002^{***}	0.281

Concomitant Links	Degree Corrected	g	all	Herbivore	Parasite	Predator	1°Producer
		2/2	0.596^{***}	0.994	0.596^{***}	0.624^{***}	0.978
		3/3	0.350^{***}	0.991	0.369^{***}	0.362^{***}	0.959
Yes	No	5/5	0.280^{***}	0.962	0.280^{***}	0.349^{***}	0.846
		10/10	0.382^{***}	0.955	0.408^{***}	0.446^{***}	0.862
		18/100	0.141^{***}	0.800	0.306^{***}	0.282^{***}	0.564
		2/2	0.444***	0.989	0.470***	0.449^{***}	0.960
		3/3	0.259^{***}	0.982	0.292^{***}	0.259^{***}	0.940
Yes	Yes	5/5	0.585^{***}	0.978	0.609^{***}	0.628^{***}	0.919
		10/10	0.136^{***}	0.938	0.214^{***}	0.182^{***}	0.782
		44/100	0.001^{***}	0.667	0.005^{***}	0.005^{***}	0.400
		2/2	0.599^{***}	0.994	0.599^{***}	0.627***	0.977
		3/3	0.340^{***}	0.991	0.358^{***}	0.352^{***}	0.959
No	No	5/5	0.279^{***}	0.962	0.279^{***}	0.348^{***}	0.846
		10/10	0.265^{***}	0.955	0.285^{***}	0.309^{***}	0.869
		18/100	0.076^{***}	0.800	0.173^{***}	0.151^{***}	0.556
		2/2	0.420***	0.989	0.446^{***}	0.425^{***}	0.960
		3/3	0.221^{**}	0.982	0.250^{***}	0.221^{**}	0.942
No	Yes	5/5	0.610^{***}	0.978	0.635^{***}	0.655^{***}	0.919
		10/10	0.212^{***}	0.963	0.229^{***}	0.239^{***}	0.864^{**}
		44/100	0.002^{***}	0.667	0.007^{***}	0.016^{***}	0.360

Table S19: As Table S15 (*i.e.* using the disaggregated food web), but labeling nodes with the trophic strategy of their aggregated node from the prior analyses.

Web	Concomitant	G	H(Uncorrected)	H(Corrected)	MI	
Flensburg	Yes	2	0.42	0.64	0.19***	
Flensburg	Yes	3	0.92	1.09	0.36***	
Flensburg	Yes	5	1.43	1.58	0.78***	
Flensburg	Yes	10	2.14	2.26	1.71***	
Flensburg	No	2	0.69	0.69	0.012	
Flensburg	No	3	1.08	1.06	0.23***	
Flensburg	No	5	1.45	1.58	0.85***	
Flensburg	No	10	2.02	2.26	1.50***	
Carpinteria	Yes	2	0.69	0.69	0.073***	
Carpinteria	Yes	3	1.08	1.09	0.39***	
Carpinteria	Yes	5	1.49	1.58	0.93***	
Carpinteria	Yes	10	2.06	2.27	1.49***	
Carpinteria	No	2	0.69	0.69	0.03**	
Carpinteria	No	3	1.07	1.08	0.37***	
Carpinteria	No	5	1.58	1.60	0.83***	
Carpinteria	No	10	2.11	2.28	1.30***	

S11 Mutual Information Between Group Models

Otago	Yes	2	0.65	0.69	0.0021	
Otago	Yes	3	1.02	1.10	0.14^{***}	
Otago	Yes	5	1.42	1.59	0.72***	
Otago	Yes	10	2.07	2.25	1.48***	
Otago	No	2	0.65	0.69	0.0055	
Otago	No	3	1.06	1.10	0.21***	
Otago	No	5	1.40	1.59	0.59***	
Otago	No	10	2.04	2.26	1.34***	
Bahia Falsa	Yes	2	0.64	0.67	0.46***	\bigcirc
Bahia Falsa	Yes	3	1.08	1.08	0.43***	
Bahia Falsa	Yes	5	1.50	1.57	1.07***	
Bahia Falsa	Yes	10	2.16	2.25	1.51***	
Bahia Falsa	No	2	0.65	0.68	0.024**	
Bahia Falsa	No	3	1.00	1.09	0.27***	
Bahia Falsa	No	5	1.53	1.58	0.79***	
Bahia Falsa	No	10	2.12	2.27	1.54***	

Ythan	Yes	2	0.62	0.69	0.30***	
Ythan	Yes	3	1.08	1.10	0.25***	
Ythan	Yes	5	1.52	1.61	0.86***	
Ythan	Yes	10	1.93	2.28	1.22***	
Ythan	No	2	0.59	0.69	0.0017	
Ythan	No	3	0.96	1.10	0.46***	
Ythan	No	5	1.33	1.58	0.68***	
Ythan	No	10	1.72	2.28	1.02***	
Punta Banda	Yes	2	0.65	0.69	0.44***	\bigcirc
Punta Banda	Yes	3	1.07	1.08	0.44***	
Punta Banda	Yes	5	1.57	1.59	0.82***	
Punta Banda	Yes	10	2.18	2.28	1.62^{***}	
Punta Banda	No	2	0.66	0.69	0.059***	
Punta Banda	No	3	1.09	1.10	0.066***	
Punta Banda	No	5	1.58	1.59	0.67***	
Punta Banda	No	10	2.18	2.28	1.41***	
Sylt	Yes	2	0.64	0.69	0.018^{*}	

Sylt	Yes	3	0.95	1.08	0.34***	
Sylt	Yes	5	1.59	1.57	0.74***	
Sylt	Yes	10	2.12	2.28	1.46***	
Sylt	No	2	0.69	0.69	0.01	
Sylt	No	3	1.06	1.06	0.16***	
Sylt	No	5	1.51	1.59	0.74***	
Sylt	No	10	2.02	2.28	1.30***	

Table S20: Overlap between partitions that are corrected for degree and those that are not. Columns list the food web (Web), whether or not concomitant predation is included (Concomitant), the maximum number of groups the network is split into (G), the entropy of the degree-corrected and non-degree-corrected partitions (H(Corrected) and H(Uncorrected)), the mutual information shared by the two partitions (MI), and the overlap represented as a Venn diagram. The left (purple) circle corresponds to the partition found by the group model without degree correction, and the right (green) circle corresponds to the partition found by the degree-corrected model. The area of each circle is proportional to the corresponding entropy, and the area of overlap between the circles is proportional to the mutual information. Stars next to the mutual information values correspond to the level of significance (< .05, < .01, < .001), as calculated by a randomization test Sander, Wootton & Allesina (2015). As the number of groups increases, the entropy also increases, but the two partitions become increasingly similar. Corrected and uncorrected partitions become very similar when the network is partitioned into 10 groups, although there is always some distinct information in each.

S12 Mutual Information between Ythan Taxonomy and Group Model

Table S21: Overlap between taxonomic partition and 10-group group model partition for the Ythan network. Columns list whether or not concomitant predation is included (Concomitant Links), whether or not the model is corrected for degree (Degree Correction), taxonomic rank (Rank), entropy of the group model partition (H(Group)), entropy of the taxonomic partition (H(Taxonomic)), and mutual information (MI), with the significance from a randomization test marked in asterisks.

Concomitant Links	Degree Correction	Rank	H(Group)	H(Taxonomi	c) MI
No	No	Family	1.75	4.02	1.57^{***}
INO	NO	Order	1.76	3.11	1.39^{***}
No	Voc	Family	2.27	4.02	2.00***
NO I	Tes	Order	2.27	3.11	1.58^{***}
Voc	No	Family	1.98	4.02	1.64^{***}
ies	NO	Order	1.98	3.11	1.30^{***}
Voc	Voc	Family	2.28	4.02	2.08***
ies	res	Order	2.29	3.11	1.67^{***}



S13 Empirical Network Adjacency Matrices – Grouped by Trophic Strategy

Figure S4: Punta Banda network structure with (top) and without (bottom) concomitant predation and species grouped by trophic strategy. Colored squares represent trophic strategy (green for primary producers, blue for herbivores, red for parasites, and yellow for other predators), and dots represent feeding interactions wherein the column species consumes the row species. Note the addition of concomitant links increases the number of consumer-resource interactions from predators to parasites and decreases the cascade-like structure seen in the top matrix.

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Figure S5: As Figure S4, but showing the Bahia Falsa network.

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Figure S6: As Figure S4, but showing the Carpinteria network.

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Figure S7: As Figure S4, but showing the Flensburg network.

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Figure S8: As Figure S4, but showing the Otago network.



Figure S9: As Figure S4, but showing the Sylt network.

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Figure S10: As Figure S4, but showing the Ythan network.



S14 Empirical Network Adjacency Matrices – Grouped by Model

Figure S11: Group model results for uncorrected group model and either including concomitant links (bottom) or not (top) for the Punta Banda network.



Figure S12: As Figure 1 in main text. Group model results for uncorrected group model and either including concomitant links (bottom) or not (top) for the Bahia Falsa network.



Figure S13: As Figure 1 in main text. Group model results for uncorrected group model and either including concomitant links (bottom) or not (top) for the Carpinteria network.

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Figure S14: As Figure 1 in main text. Group model results for uncorrected group model and either including concomitant links (bottom) or not (top) for the Flensburg network.

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Figure S15: As Figure 1 in main text. Group model results for uncorrected group model and either including concomitant links (bottom) or not (top) for the Otago network. 37



Figure S16: As Figure 1 in main text. Group model results for uncorrected group model and either including concomitant links (bottom) or not (top) for the Sylt network.

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Figure S17: As Figure 1 in main text. Group model results for uncorrected group model and either including concomitant links (bottom) or not (top) for the Ythan network.

S15 Imbalance Sampling Convergence



Figure S18: continued on next page



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Figure S18: Convergence of sampling routine to analytically calculated *p*-values. Horizontal red line is the analytical value, while the black lines are the sampled value as the number of samples increases. Blank plots indicate computationally infeasible analytical values.
S16 Degree Violin Plots



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 75^{th} quartiles, with whiskers extending to 1.5 times the inter-quartile range. Above each violin are grouping letters as indicated by a Tukeys HSD (honest significant difference) test. Figure S19: Violin and boxplots of in-degree (number of prey) and out-degree (number of predators) for different trophic strategies in all networks excluding concomitant predation. Degree is plotted on a square root scale. Boxes indicate the traditional 25^{th} , 50^{th} , and



Figure S20: As Figure S19 but for networks *including* concomitant predation.



S17 Condensed Network Diagrams

Figure S21: As Figure 3 in main text, but for the Bahia Falsa network and g = 2.



Figure S22: As Figure 3 in main text, but for the Bahia Falsa network and g = 3.



Figure S23: As Figure 3 in main text, but for the Bahia Falsa network and g = 5.



Figure S24: As Figure 3 in main text, but for the Bahia Falsa network and g = 10.



Figure S25: As Figure 3 in main text, but for the Carpinteria network and g = 2.



Figure S26: As Figure 3 in main text, but for the Carpinteria network and g = 3.



Figure S27: As Figure 3 in main text, but for the Carpinteria network and g = 5.



Figure S28: As Figure 3 in main text, but for the Carpinteria network and g = 10.



Figure S29: As Figure 3 in main text, but for the Flensburg network and g = 2.



Figure S30: As Figure 3 in main text, but for the Flensburg network and g = 3.



Figure S31: As Figure 3 in main text, but for the Flensburg network and g = 5.



Figure S32: As Figure 3 in main text, but for the Flensburg network and g = 10.



Figure S33: As Figure 3 in main text, but for the Otago network and g = 2.



Figure S34: As Figure 3 in main text, but for the Otago network and g = 3.



Figure S35: As Figure 3 in main text, but for the Otago network and g = 5.



Figure S36: As Figure 3 in main text, but for the Otago network and g = 10.



Figure S37: As Figure 3 in main text, but for the Punta Banda network and g = 2.



Figure S38: As Figure 3 in main text, but for the Punta Banda network and g = 3.



Figure S39: As Figure 3 in main text, but for the Punta Banda network and g = 5.



Figure S40: As Figure 3 in main text, but for the Punta Banda network and g = 10.



Figure S41: As Figure 3 in main text, but for the Sylt network and g = 2.



Figure S42: As Figure 3 in main text, but for the Sylt network and g = 3.



Figure S43: As Figure 3 in main text, but for the Sylt network and g = 5.



Figure S44: As Figure 3 in main text, but for the Sylt network and g = 10.



Figure S45: As Figure 3 in main text, but for the Ythan network and g = 2.



Figure S46: As Figure 3 in main text, but for the Ythan network and g = 3.



Figure S47: As Figure 3 in main text, but for the Ythan network and g = 5.



Figure S48: As Figure 3 in main text, but for the Ythan network and g = 10. Note that the group model without degree correction found that 8 groups outperforms 10 for the Ythan web without concomitant predation. This has the effect of making the nodes for this network disproportionately large and thus uncomparable to the condensed graphs with 10 nodes.