

# Structure of interactions and different models of ecological network

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Food web structure or system can refer simply to the number of trophic levels in a food chain or can represent the linkages within a complex food web network. Food webs, through direct and indirect interactions, describe the energy flow through an ecosystem. By tracking the energy flow, you can derive where the energy from your last meal came from, and how many species contributed to the meal. Understanding food webs can also help predict how important any given species is, and how ecosystems change by adding a new species or removing a current species. Through the various interactions in a food web, energy gets transferred from one organism to another; we want to explore the complexity of food webs in mathematical terms using a physical model, called a directed graph (digraph), to map the interactions between organisms. This study aims to create the corresponding competition (niche, cascade) overlap graph, and projection graphs to determine the dimensions of a community's habitat. Moreover, this study also recognizes various relationships between organisms and looks for patterns in food webs.

## INTRODUCTION

For the past 50 years, ecologists', mathematicians, and conservationists' have been working on the food web, observing the situation based on their own position. They are constantly discovering new aspects of it. Generally, A food web represents various types of information such as the number of trophic levels, the route of energy flow, the biomass of organisms, and the most dynamically important linkages. Most of the Research on food webs measures the direct effects of multiple stressors and their interactions on biological endpoints. Food-web network analysis can be a powerful guide to the management, stability, and restoration of complex ecosystems. Due to poor datasets, prior to the mid-1980s, most webs published connectance in a simplistic manner where they contained few species and/or links. A new catalogue of better quality, data-rich food webs started to emerge in the mid-1980s, challenging the received wisdom that complexity was the exception rather than the rule. The newer webs are far more exhaustively sampled and better resolved taxonomically than many of the earlier webs. The reason for the transition from "early and simple" webs to the "recent and complex" webs is that species are generally more likely to be detected in the community than their food web linkages characterized adequately. In this study, we want to address the patterns resulting from species' feeding choices and species interaction density in a particular habitat with an enriched dataset.

## COLLECTING DATA

Our project focused on food webs with "prey-predator" boolean linkages, where an active link  $A_{ij} = 1$  indicates

a specific predation. In order to perform the food webs analysis, many different food webs datasets have been collected from the website web of life<sup>1</sup>. We chose most of the dataset from the east coast of the United State and others from southern America. The food web graph used for this analytical study is simple, unweighted, unipartite and directed. In this network, nodes are compartments (organisms and species or sources of energy in the food web) and edges represent energy flow (A directed edge from  $i$  to  $j$  means that carbon is transferred from  $i$  to  $j$  i.e. organism  $j$  eats organism  $i$ ). In addition, vertices are partitioned in different types as follows: 1 - Living/producing compartment 2 - another compartment 3 - Input 4 - Output 5 - Respiration. Included with this network data are group classification labels.

## NETWORK ANALYSIS

### Motif Analysis

In general, Motifs in a network are not independent. These are the over-represented sub-graphs in a directed unipartite network. So motif analysis is one of the standard tools of complex network science to analyze small recurrent substructures. The importance of network motifs relies largely on the observation that small subgraphs indicate specific patterns of interactions between network nodes and in this way they may carry a regulatory or dynamic function. The frequency distribution of small subgraphs in the network can be visualized in the form of a significance profile or motif spectrum. This study mainly focuses on the 3-node substructures and the representation of their significance profile. So it is a low-order motif analysis. Low-order motif calculations are not com-

plicated and do not consume a lot of time. Moreover, it also interprets the quantitative analysis of their local structure.

Z-score is the most classic and common indicator that reveals the network's frequency. It is one of the most fundamental tasks and a key parameter that reflects the importance of motifs. Z-score indicates how much a given value differs from the standard deviation. According to our project, we have found seven sets of data points for z-score analysis. The heading of each set is indicated by "G" and the data point is denoted by "S". So our total set ranges from G1-G7 and data points range from S1-S5. The formula for z-score analysis is  $Z = \text{Raw Score} - \text{Mean} / \text{Standard Deviation}$ . The positive values of the Z-scores interpret that they are above the mean, and negative Z-scores are from values below the mean. Additionally, one value is closer to zero which reveals that the closer the Z-score is to zero, the closer the value is to the mean.

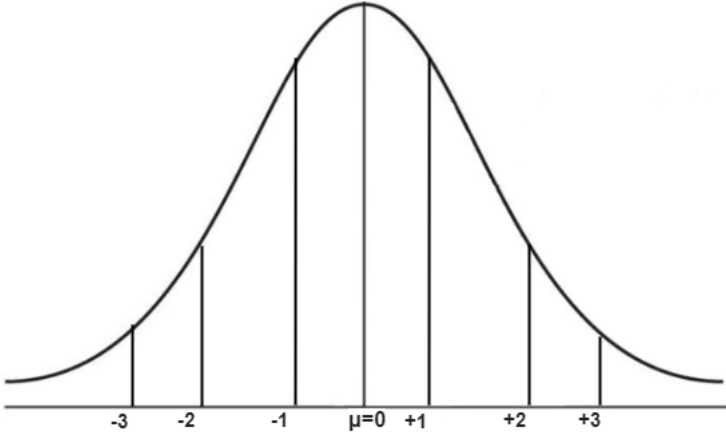


FIG. 1: Value distribution of Z-score.

### Centrality analysis

Degree centrality assigns an importance score based simply on the number of links held by each node. It tells us: How many direct, 'one hop' connections each node has to other nodes in the network. For finding very connected individuals, popular individuals, individuals who are likely to hold most information or individuals who can quickly connect with the wider network.

#### Degree centrality

A degree is a simple centrality measure that counts a node's neighbours. If the network is directed, we have

two versions of the measure: in-degree is the number of incoming links or the number of predecessor nodes; out-degree is the number of outgoing links or the number of successor nodes. Typically, we are interested in in-degree, since in-links are given by other nodes in the network, while out-links are determined by the node itself. Let  $A = (a_{i,j})$  be the adjacency matrix of a directed graph. The in-degree centrality  $x_i$  of node  $i$  is given by:  $x_i = \sum_k a_{k,i}$  or in matrix form (1 is a vector with all components equal to unity):  $x = 1A$ . The out-degree centrality  $y_i$  of node  $i$  is given by:  $y_i = \sum_k a_{i,k}$  or in matrix form:  $y = A1$ .

### Betweenness centrality

Betweenness centrality measures the extent to which a vertex lies on paths between other vertices. Vertices with high betweenness may have considerable influence within a network by virtue of their control over information passing between others. They are also the ones whose removal from the network will most disrupt communications between other vertices because they lie on the largest number of paths taken by messages.

Mathematically, let  $n_{s,t}^i$  be the number of geodesic paths from  $s$  to  $t$  that pass through  $i$  and let  $n_{s,t}$  be the total number of geodesic paths from  $s$  to  $t$ . Recall that a geodesic path is not necessarily unique and the geodesic paths between a pair of vertices need not be node-independent, meaning they may pass through some of the same vertices. Then the betweenness centrality of

vertex  $i$  is:  $b_i = \sum_{s,t} w_{s,t}^i = \sum_{s,t} \frac{n_{s,t}^i}{n_{s,t}}$  where by convention the ratio  $w_{s,t}^i = 0$  if  $n_{s,t} = 0$ . Notice that each pair of vertex  $s, t$  contribute to the sum for  $i$  with a weight  $w_{s,t}^i$  between 0 and 1 expressing the betweenness of  $i$  with respect to the pair  $s, t$ . Observed neighbours

1. The given definition counts the geodesic paths in either direction separately between each vertex pair. Since these paths are the same on an undirected graph this effectively counts each path twice;
2. The definition includes paths starting or ending with  $i$  ( $s$  can be equal to  $i$  or  $t$  can be equal to  $i$ ), as well as paths from a vertex to itself ( $s$  can be equal to  $t$ ). It seems reasonable to define a vertex to be on a path between itself and someone else, or between some vertex and itself since normally a vertex has control over information flowing from or to itself.

It makes little difference in practice to consider the alternative definitions since one is usually concerned only with the relative magnitudes of the centralities and not with their absolute values. The sum can be normalized by dividing by the total number of ordered pairs of nodes, which is  $n^2$ , so that betweenness lies strictly between 0 and 1.

### Closeness centrality

Closeness centrality measures the mean distance from a vertex to other vertices. Recall that a geodesic path is the shortest path through a network between two vertices. Suppose  $d_{i,j}$  is the length of a geodesic path from  $i$  to  $j$ , meaning the number of edges along the path. Then the mean geodesic distance for vertex  $i$  is:  $l_i = \frac{1}{n} \sum_j d_{i,j}$

This quantity takes low values for vertices that are separated from others by only a short geodesic distance on average. Such vertices might have better access to information at other vertices or more direct influence on other vertices. In a social network, for instance, a person with a lower mean distance from others might find that their opinions reach others in the community more quickly than the opinion of someone with a higher mean distance. Some authors exclude from the sum the term  $j = i$  for which  $d_{i,i} = 0$  and hence divide the sum for  $n - 1$  instead of  $n$ . The mean distance  $l_i$  is not a centrality measure in the sense of the previous ones, since it gives low values to more central nodes and high values to less central ones, which is the opposite of other centrality measures. In the social network literature, therefore, researchers commonly calculate its inverse, called closeness centrality:  $C_i = \frac{1}{l_i} = \frac{n}{\sum_j d_{i,j}}$

### Eigenvector centrality

A natural extension of degree centrality is eigenvector centrality. In-degree centrality awards one centrality point for every link a node receives. But not all vertices are equivalent: some are more relevant than others, and, reasonably, endorsements from important nodes count more. The eigenvector centrality thesis reads: A node is important if it is linked to by other important nodes. Eigenvector centrality differs from in-degree centrality: a node receiving many links does not necessarily have a high eigenvector centrality (it might be that all linkers have low or null eigenvector centrality). Moreover, a node with high eigenvector centrality is not necessarily highly linked (the node might have few but important linkers). Let  $A = (a_{i,j})$  be the adjacency matrix of a graph. The eigenvector centrality  $x_i$  of node  $i$  is given by:

$$x_i = \frac{1}{\lambda} \sum_k a_{k,i} x_k$$

where  $\lambda \neq 0$  is a constant. In matrix form we have:

$$\lambda x = xA$$

Hence the centrality vector  $x$  is the left-hand eigenvector of the adjacency matrix  $A$  associated with the eigenvalue

$\lambda$ . It is wise to choose  $\lambda$  as the largest eigenvalue in the absolute value of matrix  $A$ . By virtue of the Perron-Frobenius theorem, this choice guarantees the following desirable property: if matrix  $A$  is irreducible, or equivalently if the graph is (strongly) connected, then the eigenvector solution  $x$  is both unique and positive.

### Community detection and analysis

Structures formed by groups of multiple nodes can be analyzed by looking at what types of relationships the nodes (representing a species) are typically embedded in (e.g. competition, intraguild predation - intraguild predation is the killing and sometimes eating of potential competitors. This interaction represents a combination of predation and competition, because both species rely on the same prey resources and also benefit from preying upon one another), by determining if there are nodes found in dense clusters or non-overlapping compartments, forming modular communities or using motif distribution.

Louvain algorithm which optimizes the modularity to form communities is used on this network to form communities. 4 communities are formed with varying sizes. Interestingly, we don't get a clear distinction between each group through community detection. Many groups are evenly distributed in all the communities. This phenomenon presumably indicates that the roles of these species in the carbon exchange cannot be derived from the traditional divisions in a trivial manner. Community detection via Clique Conductance is one such algorithm which works well in this network and splits it into communities based on groups.

## FOOD WEBS MODELS

### Cascade model matrix

In the cascade model, species are ordered to form a hierarchy, and each species has a fixed probability of preying upon the preceding species. The produced networks do not contain cycles - although cycles are observed in empirical networks. In the cascade model, the species with the highest ranking functions as a top predator, while those with the lowest ranking function as a producer. Accordingly, the species with the highest ranking has a negative column and positive row, while the opposite is true for the species with the lowest ranking.

The cascade model assigns each species a random value drawn uniformly from the interval  $[0, 1]$  and each species has a probability  $P = 2CS/(S - 1)$  of consuming only species with values less than its own. This pecking order helps to explain species richness among trophic levels but

underestimates interspecific trophic similarity and overestimates food-chain length and number in larger webs.

### Niche model matrix

The niche model similarly assigns each species a randomly drawn "niche value". The species are then constrained to consume all prey species within one range of values whose randomly chosen center is less than the consumer's niche value. The single range adds a community-level contiguity of niche space to the cascade model by causing species with similar niche values to share consumers frequently within the community. The placement of the niche partially relaxes the cascade hierarchy by allowing up to half a consumer's range to include species with niche values higher than the consumer's value.

Each of  $S$  species (for example,  $S = 6$ , each shown as an inverted triangle) is assigned a 'niche value' parameter ( $\nu_i$ ) drawn uniformly from the interval  $[0,1]$ . Species  $i$  consumes all species falling in a range ( $r_i$ ) that is placed by uniformly drawing the centre of the range ( $c_i$ ) from  $[r_i/2, \nu_i]$ . This permits looping and cannibalism by allowing up to half of  $r_i$  to include values  $\leq \nu_i$ . The size of  $r_i$  is assigned by using a beta function to randomly draw values from  $[0,1]$  whose expected value is  $2C$  and then multiplying that value by  $\nu_i$  [expected  $E(\nu_i) = 0.5$ ] to obtain the desired  $C$ . A beta distribution with  $a = 1$  has the form  $f(x|1, \beta) = \beta(1-x)\beta^{-1}$ ,  $0, x, 1, 0$  otherwise, and  $E(X) = 1/(1 + \beta)$ . In this case,  $x = 1 - (1 - y)1/\beta$  is a random variable from the beta distribution if  $y$  is a uniform random variable and  $b$  is chosen to obtain the desired expected value. We chose this form because of its simplicity and ease of calculation. The fundamental generality of species  $i$  is measured by  $r_i$ . The number of species falling within  $r_i$  measures realized generality. Occasionally, model-generated webs contain completely disconnected species or trophically identical species. Such species are eliminated and replaced until the web is free of such species. The species with the smallest  $\nu_i$  has  $r_i = 0$  so that every web has at least one basal species.

### Nested hierarchy model matrix

This modeling framework gives each species a niche value and a range, exactly as in the Niche Model. However, instead of establishing links directly to species within the range, first the number of prey to be consumed by each species is determined, in proportion to the range,  $k_{in}^i \propto r_i$ , so as to generate an expected number of links  $L$ , if the resulting number exceeded  $S-1$ , we arbitrarily reduced it to  $S-1$ . These links are then attributed in the following way. The species with lowest niche value has no prey, while the one with the highest has no predators (so there is always at least one basal species and one apex



FIG. 2: Tropical networks (where the yellow and purple nodes are represent for predator and prey species respectively).

predator). Starting from the species with second smallest niche value and going up in order of  $n$ , we take each species  $i$  and apply the following rules to determine its  $k_{in}^i$  prey:

1. We choose a random species  $j$  already in the network (so  $n_j \leq n_i$ ) and set it as the first prey species of  $i$ .
2. If  $j$  has no predators other than  $i$ , we repeat 1 until either the chosen prey does have other predators, or we reach  $k_{in}^i$ . Else we go to 3.
3. We determine the set of species which are prey to the predators of  $j$ . We select, randomly, species from this set to become also the prey of  $i$  until we either complete  $k_{in}^i$ , or we go to 4.
4. We continue choosing prey species randomly from among those with lower niche values. If we still have not reached  $k_{in}^i$  when these run out, we continue choosing them randomly from those with higher niche values.

By creating groups of consumers, stage one (2) expresses the part in a food-web organization that is determined by phylogenetic constraints. Links attributed to species free of consumers, and links distributed randomly in the second stage, render the adaptation of consumers to new prey. In forcing consumers to form various trophic groups, our 'nested-hierarchy model' escapes the one-dimensional nature of former models, and better reflects the kind of hierarchies emanating from the phylogenetic structure of the community.

## RESULTS

### Empirical food webs analysis

The food webs are chosen vary a lot in the number of species, from 14 to 249 species. During the analysis, we found out that the number of species does not identify the structure of the food web except for its complexity. Furthermore, the connectance depends on the abundance of the species inside the network and the number of links respectively. The connectance ranges are between 0.107 and 0.526 and from the observation, it seems to be inversely proportional to the number of species.

### Motif analysis

The figure shows us that from all of 8 networks the numbers of 3-node cycle motif type do not exist or exist in a small number. The network will generally have cycles with path length more than 3. The second motif type is of the competition kind which is also has small amount compare to other motifs. We can conclude that species in our network mostly come from basal and top species, which can be seen in the graph that 4th and 5th type of motif are dominant.

We also found the G-score for each network. For G1, S1-199, S2-31, S3-03, S4-274 and S5-151 are the data points which we collect from the first set of motif analysis. In this case, the mean is 131.6 and the standard deviation is 101.83. By calculating the value of the z-score, we have found that  $Z1=0.66$ ,  $Z2 = -0.99$ ,  $Z3 = -1.26$ ,  $Z4= 1.39$  and  $Z5 = 0.19$ . Here we have obtained three positive values and two negative values.

For G2, S1-03, S2-04, S3-00, S4-12 and S5-06 are the data points which we collect from the second set of motif analysis. In this case, the mean is 5 and the standard deviation is 4. By calculating the value of the z-score, we have found that  $Z1=-0.5$ ,  $Z2 = -0.25$ ,  $Z3 = -1.25$ ,  $Z4= 1.75$  and  $Z5 = 0.25$ . Here we have availed three negative values and two positive values.

For G3, S1-112, S2-24, S3-07, S4-92 and S5-62 are the data points which we collect from the third set of motif analysis. In this case, the mean is 59.4 and the standard deviation is 39.58. By calculating the value of the z-score, we have found that  $Z1=1.32$ ,  $Z2 = -0.89$ ,  $Z3 = -1.32$ ,  $Z4= 0.82$  and  $Z5 = 0.06$ . Here we have earned three positive values and two negative values.

For G4, S1-81, S2-27, S3-00, S4-123 and S5-96 are the data points which we collect from the fourth set of motif analysis. In this case, the mean is 65.4 and the standard deviation is 45.27. By calculating the value of the z-score, we have found that  $Z1=0.34$ ,  $Z2 = -0.84$ ,  $Z3 = -1.44$ ,  $Z4= 0.27$  and  $Z5 = 0.67$ . Here we have acquired three positive values and two negative values.

For G5, S1-239, S2-113, S3-09, S4-289 and S5-202 are the data points which we collect from the fifth set of motif analysis. In this case, the mean is 170.4 and the standard deviation is 99.11. By calculating the value of the z-score, we have found that  $Z1=0.69$ ,  $Z2 = -0.57$ ,  $Z3 = -1.62$ ,  $Z4= 1.19$  and  $Z5 = 0.31$ . Here we have gathered three positive values and two negative values.

For G6, S1-166, S2-109, S3-10, S4-141 and S5-228 are the data points which we collect from the sixth set of motif analysis. In this case, the mean is 130.8 and the standard deviation is 71.91. By calculating the value of the z-score, we have found that  $Z1=0.48$ ,  $Z2 = -0.30$ ,  $Z3 = -1.67$ ,  $Z4= 0.14$  and  $Z5 = 1.35$ . Here we have captured three positive values and two negative values.

For G7, S1-241, S2-68, S3-02, S4-259 and S5-213 are

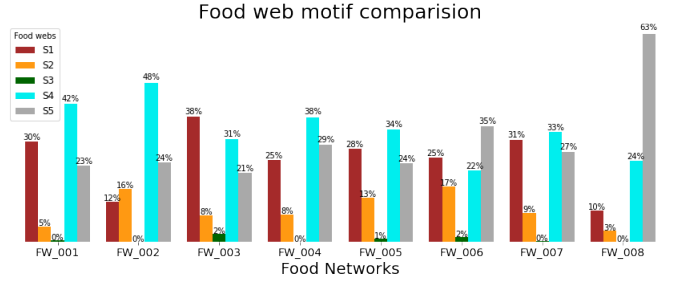


FIG. 3: Motif comparison of empirical networks.

the data points which we collect from the seventh set of motif analysis. In this case, the mean is 156.6 and the standard deviation is 102.50. By calculating the value of the z-score, we have found that  $Z1=0.82$ ,  $Z2 = -0.86$ ,  $Z3 = -1.50$ ,  $Z4= 0.99$  and  $Z5 = 0.55$ . Here we have received three positive values and two negative values.

Consequently, we have come to the point that we have two negative values on average in every set of our project and the remaining all are positive.

### Centralities analysis

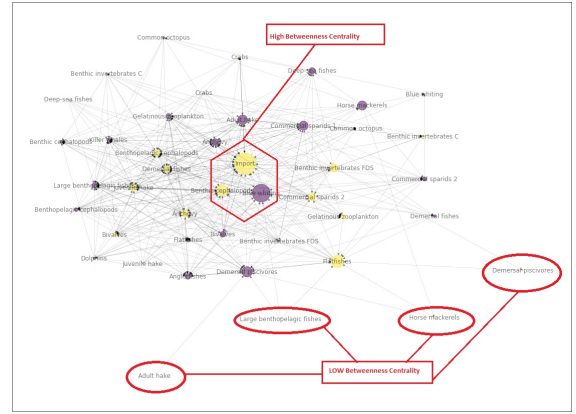


FIG. 4: Betweenness Centrality.

Centralities are used to identify possible keystone species in ecological networks. As Betweenness centrality is a way of detecting the amount of influence a node has over the flow of information in a graph, so if the influenced node is removed in any way then it will affect the entire network. From our project perspective, we have two types of sets of nodes; one set is denoted as "yellow" in color and the remaining one is "violet" in color. A total of 43 nodes have been identified in our project, with 20 yellow nodes and 23 violet nodes. One of the yellow nodes called import seems to be very influential because a lot of other nodes are pointing at it. One of the yellow nodes called import seems to be the most influential

Closeness centrality signifies how close a node is to all other nodes in the network. If we see the graph by making the yellow node number 38 is centre, we can recognise a balanced distribution of violet nodes throughout the graph. On the other hand, the yellow nodes are present in clusters of 3/4 separate sets. The most isolated nodes in the graph are 1, 30, 36, and 43 in the lower portion of the graph.

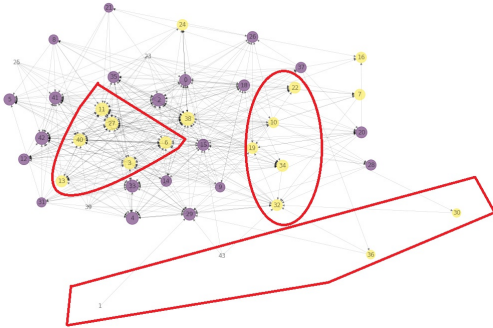


FIG. 5: Closeness Centrality.

Eigenvector Centrality is a measuring process for the transitive influence of nodes. A high eigenvector score conveys that a node is connected to many nodes that themselves have high scores. so our Eigenvector Centrality analysis motivation is, a node is important if it is linked to other important nodes. At that viewpoint, nodes called "Anchovy", "Benthopelagic cephalopods", "demersal fishes", "Large Benthopelagic fishes", and "Anglerfishes" hold the Eigenvector Centrality very nicely.

### Community detection

Structures formed by groups of multiple nodes can be analyzed by looking at what types of relationships the nodes (representing a species) are typically embedded in (e.g. competition, intraguild predation - intraguild predation is the killing and sometimes eating of potential competitors. This interaction represents a combination of predation and competition because both species rely on the same prey resources and also benefit from preying upon one another), by determining if there are

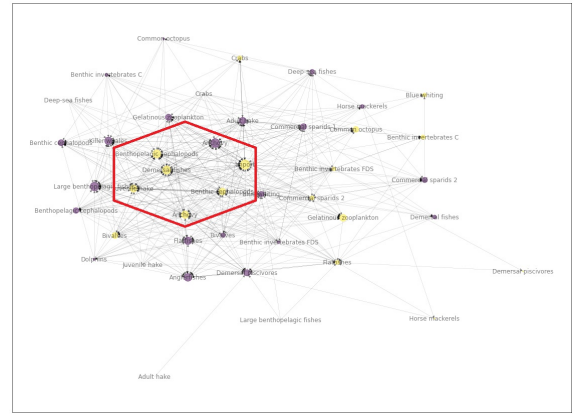


FIG. 6: Eigenvector Centrality.

nodes found in dense clusters or non-overlapping compartments, forming modular communities or using motif distribution. Louvain algorithm which optimizes the modularity to form communities is used on this network to form communities. 4 communities are formed with varying sizes. Interestingly, we don't get a clear distinction between each group through community detection. Many groups are evenly distributed in all the communities. This phenomenon presumably indicates that the roles of these species in the carbon exchange cannot be derived from the traditional divisions in a trivial manner. For example in FW005, though both are mammals, the killer whale and the dolphin have very different diverse diets. The dolphin feeds on small fishes and shrimps with diverse sources of food, the killer whale has fewer options for preying (larger basal species). Consequently, one would expect that the different and the dolphin play different roles in the carbon exchange. Community detection via Clique Conductance is one such algorithm which works well in this network and splits it into communities based on groups.

## Model food webs and comparison

During the analysis of top and basal species abundance, it had been noticed that there are differences between the papers' authors' choices: basal species are sometimes collapsed together and sometimes not. This difference influences many network properties, so when comparing these parameters it would be proper to consider only one of these groups. Given a real FW, a new one is generated from each model, using as parameters the number of species and connectance of the real FW. In this way, a dataset of five FWs will be obtained for each model. All three models predict a lower number of top predators than real networks. It happens because they have been thought in order to ensure in-link complexity. On the other hand, the fraction of basals does not de-



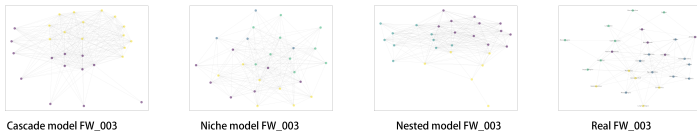


FIG. 7: Empirical network and model network comparison of FW\_003.

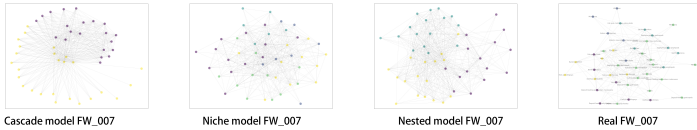


FIG. 8: Empirical network and model network comparison of FW\_007.

pend on the in-degree, and niche and nested models are able to reproduce that behaviour.

The cascade model creates an ordered hierarchy where the top species predate almost every other species: a single predator is on the top of an ordered ecological pyramid. As we can see in the FIG, the cascade model can predict the community and the network well with less number of species while with a high number of species, the shape of the network starts to become a vortex.

The niche model organizes the network in slightly interacting groups, called niches, it tries to reproduce the variety of connections inside the same niche as in a real FW. As we can see, the Niche model gives a phenomenal result in predicting the network and the number of communities compares with the empirical network.

The nested model is similar to the niche one in predicting trophic levels but instead of having independent niches, it tends to make them interact. It implies that many species could end up having the same diet. We can see in the figures, the nested model forms the number of species in the group and it gives a clear distinction between each group through community detection.

Overall niche model behaves pretty well together with nested in predicting observables but the niche model

produces trophic level distribution more similar to the expected ones. This makes the Niche model the best-performing of the three.

## CONCLUSION

Network science is a typical interdisciplinary subject, which focuses on the qualitative and quantitative laws of complex network systems. The scope of network science research is extensive. One of the most typical applications is to mine information in large-scale networks such as biological webs science. In this work, we started with the real food webs dataset, and analysis and were able to describe their properties. These observables are used to analyze the real data, highlighting how the author's choices may have a big impact on a food web structure and on the generality of obtained results. Another part of our work is to generate the model for our food webs. three different models are generated and compared to exploit these summaries:

The cascade model can describe the small ecological network in a good way;

The niche model is able to capture the biggest number of food webs observables and up to some extent it can create structures close to the realistic ones;

The nested model provides similar results to the niche model but is not able to reproduce properly the trophic structure observed in real data.

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