# Abstract

Frequently, food web researchers need to aggregate the nodes in their network. For example, because they need to study really complex and large systems. This, however, might have repercussions on our capacity of finding what the most important species in a food web are. Here, we study how different aggregation methods change the relative importance of species in the network. In particular we investigated the effects of aggregation on 24 indices of importance. Our work was carried out on 76 aquatic food webs coming from the Ecopath with Ecosim database. We considered six main types of aggregation, according to the way that the nodes were clustered. These were (i) hierarchical clustering with Jaccard index, (ii) hierarchical clustering with REGE index, (iii) maximisation of directed modularity, (iv) maximisation of modularity according to modules in which species fed on the same prey, (v) maximisation of modularity according to modules in which species are fed upon by the same predator, and (vi) clustering through the group model.

What we found is that hierarchical clustering with Jaccard index and hierarchical clustering with REGE index outperformed the other four methods on maintaining the relative importance of species for all the indices of importance (except for the controstatus index). Jaccard index maintained better degree centrality, closeness centrality, betweenness centrality, topological importance, and species uniqueness. In contrast, REGE maintained better weighted degree centrality and weighted topological importance. The indices part of the status index family and of the keystone index family had mixed results. The choice between these two methods should follow our research question and the importance index we are interested in studying. In the future, it will be important to carry out this type of research taking into consideration dynamical indices and replicate the same results with larger food webs.

# Keywords

Keystone species, data aggregation, centrality indices, species role, ecological networks.

*Other possible keywords: structural equivalence, regular equivalence, group model, modularity, species importance, trophospecies, trophic role.*

Introduction

Trophic data management is something that ecologists always must deal with when working with food webs. Trophic interactions can be described among individuals, life stages, species, higher taxa, functional groups, and several other, appropriately defined nodes of food webs. Some kind of aggregation is unavoidable, even the most highly resoluted food webs contain big aggregates (e.g., “bacteria'', see Martinez (1991) ). At the same time, even the least resoluted food webs may contain species (e.g., “hake”, see Yodzis (1998)). Data aggregation can happen also at later stages, during data analysis, especially in large networks, where the study of hundreds of nodes would be unfeasible (Yodzis & Winemiller, 1999).

Data aggregation methods are problem dependent. Not considering this can bias the way by which we interpret the results of food web models (Hall & Raffaelli, 1993; Paine, 1988). For instance, various levels of aggregation at different trophic levels might bias our interpretation if we are trying to characterise the structure of a network (Yodzis & Winemiller, 1999). Both low- and high-resolution networks can be useful or useless, the key challenge is to properly match the problem, the data management, and the model construction. Even if this seems like a ubiquitous problem in food web ecology, standards for whether and how to aggregate data in a meaningful way does not exist yet.

The process of data aggregation assumes that there are nodes in the network that are similar enough that we can consider them functionally equivalent. For example, two fishes from the same genus might be aggregated into a node of the genus (e.g., *Poecilia sphenops* and *Poecilia reticulata* could be aggregated into *Poecilia*).

Similarity can be understood mathematically (equivalent network positions) and biologically (similar trophic habits). Yodzis & Winemiller (1999) and Luczkovich et al. (2003) tried to answer this question by borrowing two definitions from social networks. Yodzis & Winemiller (1999) borrowed the concept of structural equivalence – where two nodes are similar when sharing a high number of neighbours – and called the aggregation of structurally equivalent species” trophospecies”. Luczkovich et al. (2003) borrowed the concept of regular equivalence – where two nodes are similar when sharing a high number of similar but not necessarily the same neighbours. Nodes belonging to the same equivalence class share ecological roles.

Groups of nodes that have different neighbours but form dense subgraphs are called modules. Species in food web modules can play different roles (e.g., predator and prey), but they maintain well-defined multispecies processes (e.g., connecting benthic and pelagic organisms). Aggregating the modules of a food web has been suggested already by Allesina & Pascual (2009). The two most reliable ways of finding modules in food webs are through the group model and modularity maximisation. The group model was firstly developed by Allesina & Pascual (2009) and then extended by Sander, Wootton, & Allesina (2015). Modularity maximisation was firstly applied to food webs by Guimerà et al. (2010) following three definitions of modularity. The first one, which we will refer to as density-based modularity, is the degree to which nodes inside modules interact more among themselves than with nodes of other modules. The second one, which we call prey-based modularity, is the degree to which nodes inside modules tend to interact with the same predators. The third one, which we gave the name of predator-based modularity, is the degree to which nodes inside modules tend to interact with the same preys.

The positional importance of species differs in both highly aggregated and highly-resoluted networks. Central positions may be a proxy for functional importance and the community-wide distribution of either centrality values (Bauer, Jordán, & Podani, 2010) or hypothetical importance values (Mills, Doak, & Soulé, 1993) provide macroscopic descriptors of ecosystems.

In this paper, we investigate how these different aggregation methods maintain the relative importance of species according to 24 of the most used centrality indices. These centrality indices are the most widely used in keystone species research. Our investigation was carried out on 76 Ecopath with Ecosim food web models available on the EcoBase database (Colléter et al., 2013). By having been constructed with the same methodology (see Okey (2004)), they were easy to compare. The way we selected the food webs to be included in our analysis was the number of nodes: we selected only the food webs with at least 14 nodes. See a table of these food webs in the supporting information.

# Material and methods

## Clustering techniques

To cluster similar nodes, we used the following clustering techniques.

### Hierarchical clustering with Jaccard index

As a first clustering method, we clustered structurally equivalent nodes as in Yodzis & Winemiller (1999). We used the Jaccard similarity index (Jaccard P., 1912) as a measure of structural equivalence. See supporting information for the clustering algorithm.

### Hierarchical clustering with REGE index

Our second clustering method consisted of clustering regularly equivalent nodes as in Luczkovich et al., (2003). The measure of regular equivalence we used was the REGE index (Borgatti & Everett, 1993). See supporting information for the clustering algorithm.

### Clustering of density-based modules

As a third clustering method, we clustered the nodes inside the modules found by maximising the density modularity, as in Guimerà et al. (2010). This type of modularity is expressed as the number of extra links present within the modules compared to the ones expected by chance. For directed networks, it can be expressed through the following equation of Arenas, Duch, Fernández, & Gómez, (2007), which is a generalisation of the Newman-Girvan modularity (Newman, 2004)

where is the modularity of the network, is the number of links in the network, is the element of the adjacency matrix of the directed binary network (links go from to ), is the indegree of , is the outdegree of , is the module of , is the module of and is the Kronecker delta (Kozen & Timme, 2007).

The number and composition of the modules were found by using the Leiden algorithm of Traag, Waltman, & van Eck (2019). This algorithm is an extension of the Louvain algorithm (Blondel, Guillaume, Lambiotte, & Lefebvre, 2008). The latter is one of the best performing and fastest for community detection (Traag et al., 2019). However, it tends to produce communities that are arbitrarily poorly connected to each other and sometimes even disconnected. The Leiden algorithm not only solves this problem by producing better connected communities, but it is also faster. The code that we used was implemented in the igraph package (Csardi & Nepusz, 2006) for the statistical software R (R Development Core Team, 2013).

### Clustering of prey-based and predator-based modules

As the fourth and fifth clustering methods, we clustered the nodes of every module that was found by maximising the prey modularity and the predator modularity of the food web, as in Guimerà et al. (2010). In this case, the modularity of the food web is expressed as to how much different nodes connect to the same predators (for prey modularity) or preys (for predator modularity) than expected by chance. Mathematically, it can be expressed by the following equation (Roger Guimerà, Sales-Pardo, & Amaral, 2007) for prey modularity

or in the following one for predator modularity

where is the number of outgoing links that i and j have in common and is the number of incoming links that and have in common. We maximised this type of modules by using the rnetcarto package (Doulcier & Stouffer, 2015) for R. This finds the community structure of the network by using simulated annealing (Kirkpatrick, Gelatt, & Vecchi, 1983).

### Clustering of groups

As a sixth clustering method, we clustered the nodes inside the modules found by the group model of Allesina & Pascual (2009). This model finds the modules that maximise the probability of randomly retrieving the food web by generating a modular version of an Erdős-Rényi random graph. For an arbitrary number of groups k, the probability of retrieving the food web is:

where is the food web with number of nodes and number of links, is the vector containing the probabilities of a connection between and within clusters, is the probability that a node inside the group connects to another node inside the group , is the number of links connecting nodes belonging to the group to nodes belonging to the group , is the number of nodes in the cluster , and is the number of nodes in the cluster .

Because of the high number of possible module arrangements, it is not possible to explore them all. To find the best possible solution that our computation power allows us to find, we used the algorithm of Sander, Wootton, & Allesina, 2015. This relies on a Metropolis-Coupled Markov Chain Monte Carlo (), also known as parallel tempering (Geyer, 1991), with a Gibbs sampler (Yildirim, 2012). can be considered as a Markov chain Monte Carlo (MCMC) with multiple chains running all at once (Sander et al., 2015).

## Connecting the clusters and assigning interaction strength

The connection of the clusters followed a similar approach to the one described in Martinez (1991). We used five methods to decide whether there was a link between two clusters. The first method produces the maximum connectance and is known as maximum linkage (NMAX). Here, a cluster has a connection to another cluster if it has at least one link going from one of its nodes to the nodes of the second cluster. The second one produces the minimum connectance and is known as minimum linkage (NMIN). This time, a cluster is connected to another only if all its nodes have a connection to all the nodes of the other cluster. The other three methods produce an intermediate connectance. They consider a link from a cluster to the other only if at least 25%, 50%, or 75% of possible connections from the first cluster to the second are realised.

The weight of the link was then calculated in four different ways: as the minimum weight, the maximum weight, the mean weight, and the sum of the weights of the links going from the members of the first cluster to the ones of the second cluster.

## Centrality indices

For each food web, we calculated the centrality indices before and after the aggregation. The centrality index of a node after the aggregation process equalled the one of its cluster. Let’s consider the following example. Before the aggregation, the node "hake" has a degree centrality of 5. Through the aggregation process, this happens to be aggregated into a fish cluster. The degree centrality of this fish cluster is 8. The degree centrality of hake was 5 before the aggregation and 8 after the aggregation.

### Degree centrality (DC)

The degree centrality () of a node is the number of links it has (Wasserman & Faust, 1994)

where is the number of nodes in the food web, and is the element of the adjacency matrix, after the network has been transformed in a binary undirected one.

Another type of degree centrality that we considered was the weighted degree centrality (), often referred to as node strength. Its formula, as well as the formula of its normalised version, are the same as for the non-weighted degree centrality. This time, however, the adjacency matrix is of an undirected weighted network (Fornito, Zalesky, & Bullmore, 2016)

### Closeness centrality (CC)

The closeness centrality () of a node is the average distance of a node from all the others (Wasserman & Faust, 1994)

where is the shortest path between node and .

### Betweenness centrality (BC)

The betweenness centrality () of a node is the average number of times that it acts as a bridge along the shortest path between two other nodes. It can be mathematically expressed as follows (Wasserman & Faust, 1994)

where is the total number of shortest paths going from to and is the total number of these paths passing through .

### Status index (s)

The status index of a node is the sum of its distances from all the other nodes inside the network, calculated as their shortest paths following a bottom-up direction (Endrédi, Senánszky, Libralato, & Jordán, 2018)

It was first introduced to social networks, followed two years later by its application to food webs by Harary (1959, 1961). By following the same method but in a top-down direction we obtain the controstatus

The difference between the status and the controstatus is called the net status ()

The computation of the status index needs to be performed on a network without cycles. See supporting information for the algorithm we used to create such a network. ­­­­­

### Keystone index (K)

The keystone index was firstly introduced by Jordán, Takacs-Santa, & Molnar (1999) and inspired by the status index. As the status index family, the keystone index of a species () is calculated by considering the bottom-up and the top-down effects separately (Ferenc Jordán, Liu, & Davis, 2006)

where is its bottom-up keystone index of species and the top-down keystone index of species .

Unlike the status index, which only considers the distance between a node and all the other nodes, the keystone index takes into consideration how the size of a certain effect gets split between the different neighbours of a node. Every time the effect reaches a certain node connected to multiple nodes; the following nodes receive only a fraction of the total effect. For example, when considering the bottom-up effect, if the prey has two predators, the bottom-up effect received by each predator will be half. The bottom-up effect of a certain node is then calculated in the following way

where is a predator of , is the number of preys of , and is the fraction of bottom-up effects of that are caused by . The of top predators is set as 0. The top-down effect of a certain node is calculated exactly as , but with the direction of the links inverted. The bottom-up and the top-down effects can also be split into their direct and indirect component. The indirect component takes into consideration the bottom-up effects of the predator and the direct component does not

The direct and indirect components of the top-down effect are calculated in the same way, but with the direction of the links inverted. The direct and indirect keystone indices of a node are the sum of its direct/indirect bottom-up effects and its direct/indirect top-down effects

The keystone index not only is the sum of its top-down and bottom-up effects, but also the sum of its direct and indirect effects

The computation of the keystone index, as the status index, also needs to be performed on a network without cycles.

### Topological importance (TI)

The topological importance of a node represents its potential to create bottom-up effects on other species, up to a certain number of steps that we can set. It was first introduced to host-parasitoid networks by Müller, Adriaanse, Belshaw, & Godfray (1999) and then to food webs by Jordán, Liu, & van Veen (2003). The algorithm of its computation is reported in Appendix C (Jordán, 2009).

Topological importance can be also used for weighted networks - giving us weighted topological importance () – if instead of using the degree (), we use the weighted degree () (Scotti, Podani, & Jordán, 2007)

where is the element of the adjacency matrix of the weighted directed network.

### Trophic field overlap (TO) and species uniqueness (STO)

The trophic field overlap () represents how redundant the strong interactions of a node are. It was first introduced by Jordán, Liu, & Mike (2009). It is the number of times that it and another node interact strongly with the same predator. The algorithm for its computation can be found in Appendix D ( Jordán, Endrédi, Liu, & D’Alelio, 2018). Trophic field overlap can be also used for weighted networks – giving us weighted trophic field overlap () – if instead of using the degree () we use the weighted degree, (e.g., Xiao et al., (2019)).

To avoid having to choose a threshold, we chose multiple thresholds and summed the TO of a species i for each of these thresholds. This gave us the species uniqueness (STO), an index that was firstly introduced by Lai, Liu, & Jordán (2015).

### Trophic position (TP)

The trophic position of a node is the mean length connecting it to the producers of the ecological community (its energy source). It was firstly introduced by Levine (1980), as a generalization of the earlier use of integer trophic levels to include fractional positions. It can be calculated through the following formula

where is a certain path length and is the probability that species will reach the energy produced by the autotrophs via a path of length . equals 0 for producers, it equals 1 for herbivores and larger values for omnivores and carnivores.

## Statistical analysis

The combination of the six clustering techniques, five linkage methods and four ways of determining interaction strength produced 120 ways of aggregating food webs. For each of these aggregation methods, we studied their effects on 24 centrality indices. In particular, we studied the correlation between the ranking of the nodes before and after the aggregation. This correlation was calculated by using Kendall's tau b () - a version of Kendall's rank correlation coefficient that makes adjustments for ties (Agresti, 2012). For each combination of aggregation method and centrality index, we found the mean across all food webs. This required us to convert using the Fisher z-transformation (Fisher, 1915). For each fisher’s z mean, we found its 95% confidence interval by bootstrapping (DiCiccio & Efron, 1996). The fisher’s z means, and 95% confidence intervals were then back transformed to . and bootstrapping were implemented in the Statistics and Machine Learning Toolbox for MATLAB (Mathworks Inc., 2019).

# Results

## Size of the clusters produced

The 76 food webs we used had a median of 25.5 nodes (IQR = 16.0), with a minimum of 14 nodes and a maximum of 55 nodes. See Figure 1. The median size of the aggregated food web compared to the original one was 74.5% (IQR=10.8%) for the Jaccard index, 73% (IQR=7.2%) for the REGE index, 12.8% (IQR=6.5) for the density-based modules, 35.8% (IQR=21.3%) for the prey-based modules, 72.1% (IQR=29.6%) for the predator-based modules and 15.8% (IQR=6.5%) for the group model. See Figure 2 and 6.

## Correlation of centrality indices before and after the aggregation

The correlation between the ranking before and after the aggregation can be seen in Figure 3. If we focus only on the clustering method and we ignore the linkage method and the interaction strength method, we can select the best clustering for each combination of centrality indices and clustering methods. This would give us a clear explanation of what the best aggregation for each of the indices are. See Figure 4. If we now rank the clustering algorithms for each of the centrality indices, we get Table 1.

Density modularity always ranked as the worst clustering algorithm. Prey-based modules and group model were also always ranked as either fourth or fifth. The clustering through predator modules was ranked as the first algorithm sharing a tie with the REGE index for the controstatus index. Excluding controstatus, the Jaccard index and the REGE index were always ranked as the best clustering methods. Jaccard index was better than REGE for weighted and unweighted species uniqueness, unweighted topological importance, degree centrality, closeness centrality, and betweenness centrality. REGE was better for weighted topological importance and weighted degree centrality. Status index and keystone index were maintained better either by Jaccard or by REGE according to which index of those two families we considered.

# Discussion

To our knowledge, this is the first study quantitatively comparing different aggregation methods. ﻿Our results show that different aggregation methods maintain the relative importance of species in different ways. This means that different aggregation methods have the different potential of changing the keystone species of the food web. See Figure 5. Except for the controstatus index (), hierarchical clustering with the Jaccard index and hierarchical clustering with the REGE index outperformed the other methods. When choosing between these two methods, however, we need to consider that not all indices have the same power to predict keystone species. Gouveia (2019) looked at topological indices and how their findings correlated with the findings of the dynamical index keystoneness (Libralato, Christensen, & Pauly, 2006). She found that the most reliable topological index was the weighted degree (WDC). It could predict the most important species for dynamic processes 70.1% of the times. It was followed by the 5-step weighted topological importance (WI5). A combination of WDC and WI5 increased this percentage to 78.4%. In light of these findings, REGE might be considered the best clustering algorithm, as it maintains WDC and WI5 the best.

The choice of the aggregation algorithm, however, boils down to our research question. The particular index we are interested in might drive the choice between the Jaccard index and the REGE index. Or It might also depend on how much we need to aggregate and by the species role we are interested in. In case we might want to have higher aggregation, we might consider using the group model, which produces high aggregation, but performs way better than density-based modularity. See Figure 6. If we are interested in a particular species role, then we should aggregate according to that specific role. Of course, all these methods reveal important biological similarities between nodes, and we do not intend to criticize them.

Some limitations of our study should be noted. The downside of using food webs with the same type of interactions makes our research specific on only one type of interaction strength. Most of the topological indices, however, do not consider interaction strength. The ones that do are weighted degree centrality (WDC), weighted topological importance (WI) and weighted species uniqueness (wSTO). Another thing that should be noted is the small size of the food webs used in this study. It would be important in the future to repeat this type of analysis with larger food webs.

In our opinion, the next step in setting standards for data aggregation should be repeating the same study but with dynamical indices. For example, with the keystoneness index (Libralato et al., 2006) and eigenvector centrality (Allesina & Pascual, 2009b). In the end, what we are interested in is studying the dynamic processes happening inside the network. Food web structure and topological indices can be seen as a proxy for it. Furthermore, it would be important to study what the best linkage method is and what the best interaction strength method is.

In conclusion, we have shown that different aggregation methods maintain at different degrees the most important species in a food web. Hierarchical clustering with Jaccard index and hierarchical clustering with REGE index have been shown to be the best at doing this. The choice between these two algorithms should depend upon the type of importance index we are interested in maintaining. Future research should be carried out on larger food webs, dynamical indices and determining what the best linkage method and new interaction strength method are.

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# Supplementary material

The code used for this analysis is available at <https://github.com/Emanuele-Giacomuzzo/Data_aggregation>.

# References

Agresti, A. (2012). Analysis of Ordinal Categorical Data: Second Edition. In *Analysis of Ordinal Categorical Data: Second Edition*. https://doi.org/10.1002/9780470594001

Allesina, S., & Pascual, M. (2009a). Food web models: A plea for groups. *Ecology Letters*, *12*(7), 652–662. https://doi.org/10.1111/j.1461-0248.2009.01321.x

Allesina, S., & Pascual, M. (2009b). Googling food webs: Can an eigenvector measure species’ importance for coextinctions? *PLoS Computational Biology*, *5*(9). https://doi.org/10.1371/journal.pcbi.1000494

Arenas, A., Duch, J., Fernández, A., & Gómez, S. (2007). Size reduction of complex networks preserving modularity. *New Journal of Physics*, *9*(6), 176. https://doi.org/10.1088/1367-2630/9/6/176

Bauer, B., Jordán, F., & Podani, J. (2010). Node centrality indices in food webs: Rank orders versus distributions. *Ecological Complexity*, *7*(4), 471–477. https://doi.org/10.1016/j.ecocom.2009.11.006

Blondel, V. D., Guillaume, J. L., Lambiotte, R., & Lefebvre, E. (2008). Fast unfolding of communities in large networks. *Journal of Statistical Mechanics: Theory and Experiment*, *10*. https://doi.org/10.1088/1742-5468/2008/10/P10008

Borgatti, S. P., & Everett, M. G. (1993). Two algorithms for computing regular equivalence. *Social Networks*, *15*(4), 361–376. https://doi.org/10.1016/0378-8733(93)90012-A

Colléter, M., Valls, A., Guitton, J., Morissette, L., Arreguín-Sánchez, F., Christensen, V., … Pauly, D. (2013). EcoBase: A repository solution to gather and communicate information from EwE models. In *Fisheries Centre Research Reports*.

Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal Complex Systems*.

DiCiccio, T. J., & Efron, B. (1996). Bootstrap confidence intervals. *Statistical Science*, *11*(3), 189–228. https://doi.org/10.1214/ss/1032280214

Doulcier, G., & Stouffer, D. B. (2015). *Rnetcarto: Fast network modularity and roles computation by simulated annealing*.

Endrédi, A., Senánszky, V., Libralato, S., & Jordán, F. (2018). Food web dynamics in trophic hierarchies. *Ecological Modelling*, (368), 94–103. https://doi.org/10.1016/j.ecolmodel.2017.11.015

Fisher, R. A. (1915). Frequency Distribution of the Values of the Correlation Coefficient in Samples from an Indefinitely Large Population. *Biometrika*, *10*(4), 507–521. https://doi.org/10.2307/2331838

Fornito, A., Zalesky, A., & Bullmore, E. T. (2016). Fundamentals of Brain Network Analysis. In *Fundamentals of Brain Network Analysis*. https://doi.org/10.1016/C2012-0-06036-X

Geyer, C. J. (1991). *Markov chain Monte Carlo maximum likelihood*.

Gouveia, C. G. L. M. (2019). *Combination of Topological Indices in Network Analysis: A Computational Approach*. University of Lisbon, Portugal.

Guimerà, R., Stouffer, D. B., Sales-Pardo, M., Leicht, E. A., Newman, M. E. J., & Amaral, L. A. N. (2010). Origin of compartmentalization in food webs. *Ecology*, *91*(10), 2941–2951. https://doi.org/10.1890/09-1175.1

Guimerà, Roger, Sales-Pardo, M., & Amaral, L. A. N. (2007). Module identification in bipartite and directed networks. *Physical Review E - Statistical, Nonlinear, and Soft Matter Physics*, *76*(3), 1–8. https://doi.org/10.1103/PhysRevE.76.036102

Hall, S. J., & Raffaelli, D. G. (1993). Food Webs: Theory and Reality. In *Advances in Ecological Research* (Vol. 24). https://doi.org/10.1016/S0065-2504(08)60043-4

Harary, F. (1961). Who eats whom? *General Systems*, *6*, 41–44.

Harary, Frank. (1959). Status and Contrastatus. *Sociometry*, *22*(1), 23. https://doi.org/10.2307/2785610

Jaccard P. (1912). The distribution of the flora in the alpine zone. *New Phytologist*, *11*(2), 37–50.

Jordán, F., Liu, W. C., & van Veen, F. J. F. (2003). Quantifying the importance of species and their interactions in a host-parasitoid community. *Community Ecology*, *4*(1), 79–88. https://doi.org/10.1556/ComEc.4.2003.1.12

Jordán, Ferenc. (2009). Keystone species and food webs. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1524), 1733–1741. https://doi.org/10.1098/rstb.2008.0335

Jordán, Ferenc, Endrédi, A., Liu, W. C., & D’Alelio, D. (2018). Aggregating a plankton food web: Mathematical versus biological approaches. *Mathematics*, *6*(12), 336. https://doi.org/10.3390/math6120336

Jordán, Ferenc, Liu, W.-C., & Davis, A. J. (2006). Topological keystone species: measures of positional importance in food webs. *Oikos*, *112*(3), 535–546.

Jordán, Ferenc, Liu, W. C., & Mike, Á. (2009). Trophic field overlap: A new approach to quantify keystone species. *Ecological Modelling*, *220*(21), 2899–2907. https://doi.org/10.1016/j.ecolmodel.2008.12.003

Jordán, Ferenc, Takacs-Santa, A., & Molnar, I. (1999). A Reliability Theoretical Quest for Keystones. *Oikos*, *86*(3), 453. https://doi.org/10.2307/3546650

Kirkpatrick, S., Gelatt, C. D., & Vecchi, M. P. (1983). Optimization by simulated annealing. *Science*, *220*(4598), 671–680. https://doi.org/10.1126/science.220.4598.671

Kozen, D., & Timme, M. (2007). Indefinite summation and the Kronecker delta. *Ecommons.Cornell.Edu*.

Lai, S. M., Liu, W. C., & Jordán, F. (2015). A trophic overlap-based measure for species uniqueness in ecological networks. *Ecological Modelling*, *299*, 95–101. https://doi.org/10.1016/j.ecolmodel.2014.12.014

Levine, S. (1980). Several measures of trophic structure applicable to complex food webs. *Journal of Theoretical Biology*, *83*(2), 195–207. https://doi.org/10.1016/0022-5193(80)90288-X

Libralato, S., Christensen, V., & Pauly, D. (2006). A method for identifying keystone species in food web models. *Ecological Modelling*, *195*(3–4), 153–171. https://doi.org/10.1016/j.ecolmodel.2005.11.029

Luczkovich, J. J., Borgatti, S. P., Johnson, J. C., & Everett, M. G. (2003). Defining and measuring trophic role similarity in food webs using regular equivalence. *Journal of Theoretical Biology*, *220*(3), 303–321. https://doi.org/10.1006/jtbi.2003.3147

Martinez, N. D. (1991). Artifacts or Attributes ? Effects of Resolution on the Little Rock Lake Food Web. *Ecological Monographs*, *61*(4), 367–392.

Mathworks Inc. (2019). Matlab Statistics and Machine Learning Toolbox. Retrieved from 2015 website: https://www.mathworks.com/products/statistics.html

Mills, L. S., Doak, M. E., & Soulé, D. F. (1993). The keystone-species concept in ecology and conservation. *BioScience*, *43*(4), 219–224.

Müller, C. B., Adriaanse, I. C. T., Belshaw, R., & Godfray, H. C. J. (1999). The structure of an aphid-parasitoid community. *Journal of Animal Ecology*, *68*, 346–370. https://doi.org/10.1046/j.1365-2656.1999.00288.x

Newman, M. E. J. (2004). Fast algorithm for detecting community structure in networks. *Physical Review E - Statistical Physics, Plasmas, Fluids, and Related Interdisciplinary Topics*, *69*(6), 5. https://doi.org/10.1103/PhysRevE.69.066133

Okey, T. A. (2004). *Shifted community states in four marine ecosystems: some potential mechanisms*. University of British Columbia, Canada.

Paine, R. T. (1988). Road Maps of Interactions or Grist for Theoretical Development? *Ecology*, *69*(6), 1648–1654. https://doi.org/10.2307/1941141

R Development Core Team. (2013). *R: A Language and Environment for Statistical Computing*. https://doi.org/10.1007/978-3-540-74686-7

Sander, E. L., Wootton, J. T., & Allesina, S. (2015). What Can Interaction Webs Tell Us About Species Roles? *PLoS Computational Biology*, *11*(7), 1–22. https://doi.org/10.1371/journal.pcbi.1004330

Scotti, M., Podani, J., & Jordán, F. (2007). Weighting, scale dependence and indirect effects in ecological networks: A comparative study. *Ecological Complexity*, *4*(3), 148–159. https://doi.org/10.1016/j.ecocom.2007.05.002

Traag, V. A., Waltman, L., & van Eck, N. J. (2019). From Louvain to Leiden: guaranteeing well-connected communities. *Scientific Reports*, *9*(1), 1–12. https://doi.org/10.1038/s41598-019-41695-z

Wasserman, S., & Faust, K. (1994). *Social network analysis : methods and applications*. Cambridge University Press.

Xiao, Z., Wu, J., Xu, B., Zhang, C., Ren, Y., & Xue, Y. (2019). Uniqueness measure based on the weighted trophic field overlap of species in the food web. *Ecological Indicators*, *101*, 640–646. https://doi.org/10.1016/j.ecolind.2019.01.042

Yildirim, I. (2012). Bayesian Inference: Gibbs Sampling. *Technical Note, University of Rochester*. Retrieved from http://www.mit.edu/~ilkery/papers/GibbsSampling.pdf

Yodzis, P. (1998). Local trophodynamics and the interaction of marine mammals and fisheries in the Benguela ecosystem. *Journal of Animal Ecology*, *67*(4), 635–658. https://doi.org/10.1046/j.1365-2656.1998.00224.x

Yodzis, P., & Winemiller, K. O. (1999). In Search of Operational Trophospecies in a Tropical Aquatic Food Web. *Oikos*, *87*(2), 327–340.