

Effects of species extinction on ecosystems stability

Učinki izumrtja vrst na stabilnost ekosistema

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Abstract

The food web describes the feeding relations between species in the ecosystem and makes possible the modelling of the dynamics between species. Based on existing data, we attempt to identify important species in the food web by examining the dynamic response after the removal of different species one at a time and observing the number of extinct species. This gives us a measure that estimates whether an extinction of a species would greatly affect its surrounding ecosystem and possibly also an estimate of trophic levels in the ecosystem. We also compare this measure as the baseline to other centrality measures in an attempt to establish a good and cost-efficient alternative.

Keywords: Species importance, food web, ecosystem stability, population dynamics.

Izveček

Omrežje plenilec-plen opisuje prehranjevalne odnose med vrstami v ekosistemu in omogoča modeliranje dinamike med vrstami. V članku skušamo z uporabo obstoječih podatkov najti pomembne vrste v tovrstnem omrežju. Uvedemo mero, ki definira pomembnost posamezne vrste in opisuje, kako močno bi izumrtje posamezne vrste vplivalo na njeno okolico. Njeno vrednost dobimo z opazovanjem dinamičnega odziva po odstranitvi vrste in s spremljanjem števila izumrlih vrst, ki ga taka odstranitev povzroči. S takšno mero lahko dobimo tudi oceno o strukturi tropskih nivojev v ekosistemu. Dobljeno mero, ki služi kot osnova primerjamo z ostalimi merami središčnosti v upanju, da najdemo dobro in poceni alternativo.

Ključne besede: pomembnost vrst, omrežje plenilec-plen, stabilnost ekosistemov, populacijska dinamika

1. INTRODUCTION

An ecosystem of different species of flora and fauna can be described by the relations between these species, for example how they feed on each other. This information can be recorded by a network structure called a food-web. A food-web is a directed weighted network that describes relations between predators and their prey, where the weights are correlated to the intensity of the feeding relation between the predator and its prey. Food-webs are usually smaller networks consisting of 20 to 150 nodes. They also

come with the initial biomasses of the species in the system, which is usually given in kcal per square meter or weight per square meter.

Because food-webs give us a relation of how much one species feeds on another and what the size of each population is, we can use the data to define a population model, giving us a prediction on how each species population will change in time. Using existing food-web networks that describe how species interact and feed, we try to model their dynamics. Specifically, using a dynamic model, we test the system for weak

points. This information can tell us which species are most important for the stability of others, giving them a higher priority to preserve than other species that have a smaller impact on the system. The analysis can be done by simply removing a species from a stable network and observing how the system responds to the change, if any other species became extinct, or how many of them became extinct. Since this method takes some time for computations, we compare it to other centrality measures in hope of finding a method that gives similar results, but is also cheaper.

In the paper we first do a short review of related work dealing with similar problems. Then, in the methods section, we propose our methods of determining the importance of species. We also describe other centrality measures we test and approaches of comparing them to our methods. In the results section, we first show an example of population dynamic. Then, we show the results of our methods and other centrality measures on different food-webs and compare the results.

2. RELATED WORK

Gilljam et. al. (Gilljam, Curtsdotter, & Ebenman, 2015) dealt with similar extinctions that lead to instabilities, but expanding on this, evaluated what happens if the predators of the extinct species find a new prey or move to a prey that is less frequent in their diet, effectively making a link rewiring. First an observation was made that usually primary producers go extinct following by primary consumers and secondary consumers last. It has also been found that rewiring does not help the stability but only aggravates it. The negative effect was even stronger when predators were efficient in exploiting rare and new prey.

Williams and Martinez (Williams & Martinez, 2000) predicted different structural properties of some complex food webs from freshwater habitats, freshwater-marine interfaces and terrestrial habitats using random model, cascade model and niche model.

In the random model, any link among species occurs with the same probability. The cascade model assigns each species a random value drawn uniformly from the interval and each species has probability of consuming only species with values less than its own, where c_i denotes connectance level, l_i denotes number of actual links and L_i number of all possible links. 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 centre is less than the consumer's niche value.

The parameters of all models were set to synthesize webs with empirically observed species number and connectance level. They calculated normalized error as difference between empirical properties and a model's mean, predicted by Monte Carlo simulations, divided by the standard deviation of the property's simulated distribution. Results showed the niche model to be the most accurate, the cascade model was over an order of magnitude worse, while the random model was the worst. The random model's large errors show, that simply matching an empirical web's and does little to account for empirical food-web properties.

Palamara et. al. (Palamara, Zlatic, Scala, & Caldarelli, 2011) introduced weighted projection graphs that extend niche graphs by adding the possibility of weighted links. From comparing synthetic and real graphs properties they found some improvement. On top of this, they performed population dynamics evaluation described by the weights of the graphs, finding that the stability of the model decreases as its complexity increases.

Stouffer et. al (Stouffer, Sales-Pardo, Sirer, & Bascompte, 2012) measured species' roles and their dynamic importance when embedded in their community network. They introduced a definition of species' roles based around the concept of network motifs, which provide a mesoscale characterization of community structure. They focused on communities made out of 3 node motifs, composed of 30 unique positions. To take into account dynamics, they associate a benefit to each position across all motifs, determined by how much community persistence increases or decreases when single motif is added to the network. For each species they calculated how many times it appears in each position, where they also weighted positions with their benefits. They searched for species that exhibit statistically similar motif profiles. Across the 2468 empirical species and 32 webs, they observe 54 distinct empirical roles. They were also interested if this result reflects an intrinsic property of each species, so they compared the relative importance of 150 species that occur in at least 2 of the 10 different networks and found that if species is important in one web, it is also important in other webs in which it appears.

Allesina and Pascual (Allesina & Pascual, 2009), similarly to our method, tried to evaluate the most important species that their extinctions cause extinction cascades. First they introduced a »root« node to the food-web that points to the primary producers and defined that a species goes extinct if it severs its reachability to it. Next they introduce an algorithm that in each step, removes a species from the food web according to the measure of choice and removes species that became extinct. The iteration stops when all species go extinct or are removed. For the methods of choice the authors propose two measures based on PageRank (Sergey & Page, 1998) and compare them to more basic measures, namely, degree, closeness, betweenness centrality and a dominators measure where node dominates node if all the paths from »root« contain . They compared results with a proposed »extinction area« measure, which returned the area under the plot of proportion of extinct species related to the proportion of removed nodes. Their results show that the eigenvector measures proved to give the fastest extinction sequences, beating the other measures in all given food-webs.

3. METHODS

We denote as the biomass of species in time. The dynamics of species is modeled using the population equation

$$\frac{dx_i(t)}{dt} = x_i(t) \left(b_i + \sum_{j=1}^S a_{ij} x_j(t) \right), \quad (1)$$

where represents the number of species and denotes the linear rate with which the population of species is growing or dying regardless of its predators and prey.

This can be interpreted as contribution from natural death and fertility of the species. The parameter denotes the relation between species and , which can be positive if is prey of or negative and the relation is flipped. The sign is inferred from the direction of the link in the network. This part of the relation can be interpreted as a model of encounters. If there are more species of and , their encounters are more probable, so the one will feed on the other more often, driving the numbers of the prey down and the numbers of the predator up, since more food is a positive force to the fertility.

Before removing species and observing the response we want the initial network to be stable. To achieve this we specify the condition . This is done by simply correcting the parameters accordingly

$$b_i = - \sum_{j=1}^S a_{ij} x_j(0). \quad (2)$$

After we obtain a static system, we can start removing nodes to observe the response. We propose an algorithm which assesses the importance of a node, which we name *Ratio* (Algorithm 1).

The algorithm uses the Euler method to perform the integration in time, while the *count_dead* method just counts how many species biomass came under a certain threshold, which is a user set parameter that determines the lower bound, where the species is not yet extinct. We set the threshold to 1% of the initial biomass. Note that during the integration, we remove species that fall below the threshold, since, according to the population equation, they can still recover even if their biomass is unreasonably small.

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Data: Input food-web
Result: Dictionary of importances for each species
importance = {}
Initialize b_i so that dx/dt = 0
for i = 1...S do
    remove node i from the food-web
    new_x = integrate using the system of equations for a
              certain time and return final biomasses
    importance[i] = count_dead(new_x) / S
    add node i back into the food-web
return importance
    
```

Algorithm 1: **Computation of importance for every species/node.**

This counting technique might not be the best, since heavier species would die out when its biomass would go under a higher threshold, while lighter species such as plankton can still have high numbers even if its biomass is seemingly low.

The *Ratio* measure is likely to give the same result for multiple species, since multiple species can lead to the same number of extinctions. To give species more variance in their importance we introduce another measure, named *Area*. Here, instead of just counting how many species die after the integration, we use the time plot of the ratio of remaining species along the time axis (example in Figure 1). We then calculate the area under each curve, normalized to the area where no species came to extinction. A small area close to 0 indicates rapid extinction, making the species that cause it very important, while an area of 1 indicates no extinctions at all.

Our food-webs contain nodes »Input«, »Output« and »Respiration«, which we remove before we run our algorithms. The justification for this is that these three nodes serve as an external »force« on our system and it would be unreasonable to model the dynamics of external parameters. We also presume external forces just by the stability condition we specified by correcting parameters. This removal causes some other nodes to become isolated from the rest of the network. Since isolated nodes have no predators and no prey, their biomass would not change over time, so we removed them too.

We define our methods *Ratio* and *Area* as base methods, since they are the most theoretically sound.

We compare centrality measures *PageRank*, *betweenness*, *closeness centrality* and *clustering coefficient* with our proposed methods.

PageRank (Sergey & Page, 1998) first assigns an equal amount of importance to each node and then iteratively calculates *PageRank* for each node according to the equation

$$p_i = \alpha \sum_j A_{ij} \frac{p_j}{k_j^{out}} + \frac{1 - \alpha}{n}, \quad (3)$$

where p_i is the *PageRank* of the node i , A_{ij} is the adjacency matrix, k_j^{out} is the degree of out-going edges of node j , α is a damping parameter and n is the number of nodes in a network. The basic idea of the algorithm is that importance is propagated through the network where important nodes point to important nodes. We took the reversed graph when calculating *PageRank*, because species that »feed« others should be ranked higher so they should be successors of their predators, but in the case of food-webs the arcs are reversed. This can be better explained with a toy example where we have one prey/food source that, in the case of a food-web, points towards its predators that aren't connected to one another, essentially making a star-like structure. In this case the *PageRank* of the prey would be spread between its predators, making its rank the smallest. If we reverse the links, the opposite happens and the central node accumulates all of the *PageRank* from its predators, making it the most important, which it is, since if we remove it, all other species die out from the lack of a food source.

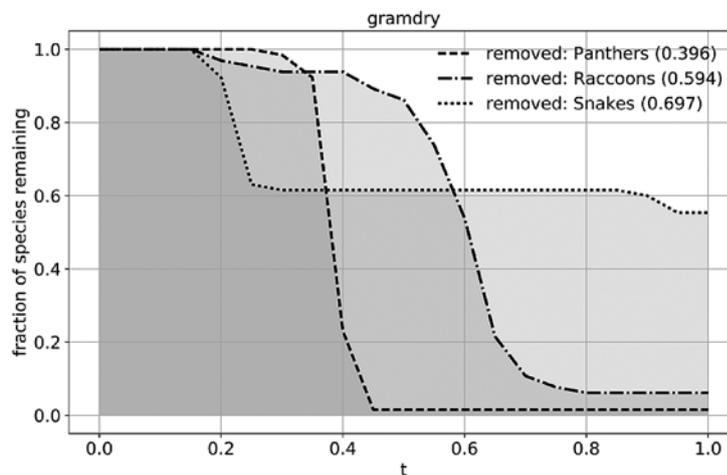


Figure 1: Plot of fraction of remaining species along the time of integration for the granddry food-web. The area under each curve is used to evaluate the belonging species. The legend shows area results for »Panthers«, »Raccoons« and »Snakes«.

Betweenness centrality (σ_i) gives a larger value to nodes that have a position such that they lay on a large number of shortest paths between other pairs of nodes in the graph. It is calculated using equation

$$\sigma_i = \frac{1}{n^2} \sum_{st} \frac{g_{st}^i}{g_{st}}, \quad (4)$$

where n is the total number of shortest paths from i to j and g_{st} is the number of paths going through i .

Closeness centrality (NetworkX, 2018) for a node is calculated by equation

$$c_i = \frac{n - 1}{\sum_j d(i, j)}, \quad (5)$$

where $d(i, j)$ is the length of the shortest path from node i to node j . Its justification is that a node should be more important if it is closer to the other nodes.

Clustering coefficient for a node gives an information about local density of a network around that node. More precisely it tells what fraction of pairs of neighbours of node are connected to each other. It is calculated by equation

$$c_i = \frac{t_i}{\binom{k_i}{2}}, \quad (6)$$

where k_i is the degree of node i , t_i is the number of all possible pairs of neighbours of node i , and $\binom{k_i}{2}$ represents the number of pairs of neighbours of node i that are connected. If a node has degree 0 or 1, it doesn't have any pairs of neighbours, so its clustering coefficient is 0.

We also compare our methods with two other measures, one that takes into account degrees of nodes and one that takes into account weights on links. The first one we calculated as degree of the node, normalized with number of all links in the network and the second one as sum of weights over all in-links and out-links of the node, normalized with sum of weights over all links in the network.

Finally, we calculate correlations between all measures and show a correlation coefficient matrix with the measures on the axis (Figure 5). The correlations were calculated using the Pearson product-moment correlation coefficients

$$C_{ij} = \frac{\sum_l (x_l^{(i)} - \bar{x}^{(i)})(x_l^{(j)} - \bar{x}^{(j)})}{\sqrt{\sum_l (x_l^{(i)} - \bar{x}^{(i)})^2} \sqrt{\sum_l (x_l^{(j)} - \bar{x}^{(j)})^2}}, \quad (7)$$

and the correlation coefficient matrix elements were calculated as

$$R_{ij} = \frac{C_{ij}}{\sqrt{C_{ii}C_{jj}}} \quad (8)$$

Note that when performing these calculations we inverted our *Area* measure as so that we didn't have to deal with anti-correlations when comparing it with our *Ratio* measure.

4. RESULTS

We found food-web data on the *pajek* website (Batagelj, 2004). For each food-web we analyzed, we first calculated to induce stability.

When testing the *Ratio* measure on the *CrystalC* food-web we found that whatever species we remove, it causes extinction of several other species. The most important species in this network is »blacktip shark«, removal of which causes 11 other species to die out and the least important is »silverside«, which causes extinction of 6 other species. After cleaning the network we ended up with 20 nodes, not including the initially extinct species the »blacktip shark«. For these 20 nodes we plotted time dependency of

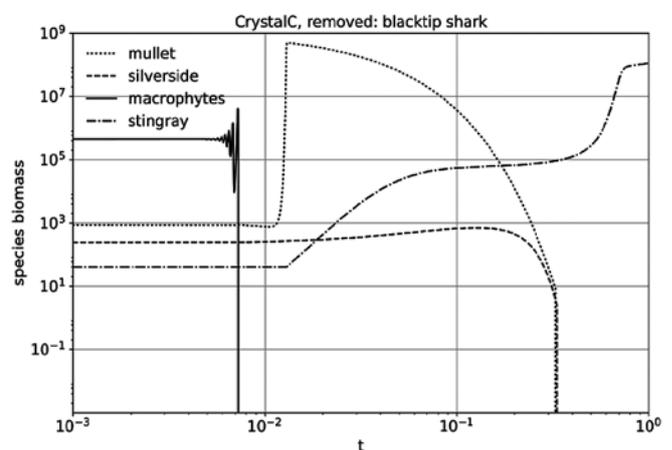


Figure 2: Changes of biomasses over time after removing node »blacktip shark« in the food-web *CrystalC*. Nodes »mullet« and »silverside« show how species die out over time, the same for »macrophytes«, which represents species that start oscillating too violently, while »stingray« demonstrates species that increases in size.

biomass changes and in Figure 2 showed the most interesting ones.

For already mentioned food-web *CrystalC* and for the food-web *gramdry*, we calculated values of importance for each species in the network by 8 different methods. The most significant results are shown in Table 1 and in Table 2.

Looking at the results for the *CrystalC* food-web, the *Ratio* measure gives an interesting observation. We can see that 5 groups of species form, each with the same rank. These groups roughly translate to the pyramidal structure of trophic levels of ecosystems, where we have apex predators, consumers, producers and decomposers. In our case, we have the »blacktip shark« as the apex predator, various fish as consumers, and plankton, invertebrates, microphytes and macrophytes forming a joint group of producers and decomposers. The last two groups feed on dead organic material called »detritus« which isn't a living organism, but can still be considered as the lowest level. Of course the ordering isn't perfect, for example the »goldspotted killifish« and similar small fish in the joint group with *Ratio* value of 0.45 should most likely belong to the consumers. Optimally, the joint group of producers and decomposers should also be split up. The »silverside« fish also belongs to the consumers and not in its separate and lowest level.

In the *Area* measure, a similar observation of groups can be made, only the values are more varied and the clusters aren't immediately apparent. To better show trophic levels, we do an agglomerative hierarchical clustering and show its results (Figure

3). The clustering on *Area* performs even better than *Ratio*. The pyramidal structure remained, and what's more, small fishes split from the joint producers/decomposers group. We only find a few stragglers in the results such as »mullet«, which shouldn't be at the top and the fish »silverside«, which shouldn't belong to the joint level, although now it is not strongly connected to it.

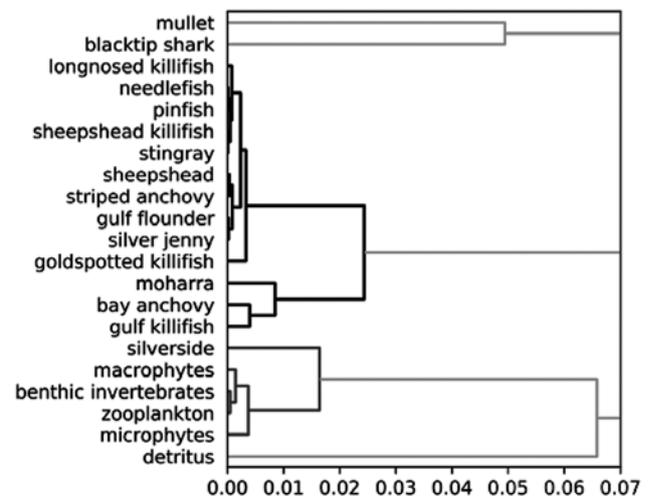


Figure 3: A dendrogram visualizing the agglomerative clustering on the *CrystalC* food-web, using the Ward measure. The dendrogram is not plotted fully since we are not interested in its top-most branches. The groups are shown with different shades of gray for the lines.

As for the other measures, we didn't see much correlation, they give »detritus« the largest score, since it has the most in-going edges.

Table 1: Species importance by different measures for the *CrystalC* food-web. Table shows all 21 species. The species are ordered by the results of our method using the *Ratio* score, while we also show what species placed in the first three places for other measures, including our score that uses the *Area* measure.

species	Ratio	Area	degree	weights	pagerank	betweenness	clustering	closeness
blacktip shark	0.60	0.606 (2)	0.024	0.000393	0.016	0.0000	0.000657	0.357
stingray	0.50	0.669	0.074	0.000111	0.016	0.0447	0.000037	0.465
striped anchovy	0.50	0.670	0.049	0.000023	0.016	0.0197	0.000094	0.540 (3)
needlefish	0.50	0.669	0.111	0.000244	0.016	0.0842	0.000066	0.487
sheepshead killifish	0.50	0.669	0.086	0.000272	0.017	0.0552	0.000155	0.540 (3)
longnosed killifish	0.50	0.668 (3)	0.049	0.000838	0.017	0.0000	0.000694 (2)	0.350
silver jenny	0.50	0.670	0.049	0.000021	0.016	0.0263	0.000124	0.540 (3)
sheepshead	0.50	0.669	0.037	0.000056	0.016	0.0236	0.000338	0.363
pinfish	0.50	0.669	0.123 (3)	0.000322	0.027	0.2500 (3)	0.000073	0.487
gulf flounder	0.50	0.670	0.061	0.000017	0.016	0.3236 (2)	0.000012	0.434
microphytes	0.45	0.719	0.061	0.053924	0.053	0.0000	0.001176 (1)	0.000

species	Ratio	Area	degree	weights	pagerank	betweenness	clustering	closeness
macrophytes	0.45	0.715	0.012	0.543455 (2)	0.173 (2)	0.0000	0.000000	0.000
zooplankton	0.45	0.716	0.098	0.025203	0.067	0.0000	0.000273	0.512
benthic invertebrates	0.45	0.716	0.172 (2)	0.368955 (3)	0.131 (3)	0.0973	0.000340	0.512
bay anchovy	0.45	0.681	0.098	0.000538	0.032	0.0210	0.000130	0.540 (3)
goldspotted killifish	0.45	0.672	0.098	0.000358	0.017	0.0763	0.000171	0.555 (2)
moharra	0.45	0.676	0.098	0.001093	0.022	0.0000	0.000271	0.540 (3)
mullet	0.45	0.556 (1)	0.086	0.006728	0.033	0.0500	0.000686 (3)	0.526
gulf killifish	0.40	0.685	0.123 (3)	0.001021	0.018	0.0078	0.000149	0.487
detritus	0.40	0.765	0.370 (1)	0.993402 (1)	0.237 (1)	0.7197 (1)	0.000235	1.000 (1)
silverside	0.30	0.703	0.111	0.003026	0.046	0.0000	0.000430	0.540 (3)

Table 2: Species importance by different measures for the grandry food-web. Table shows only the most significant species out of 66. The ordering is shown in the same way as in Table 1.

species	Ratio	Area	degree	weights	pagerank	betweenness	clustering	closeness
Panthers	0.984	0.396	0.0100	0.000000	0.0056	0.18870	0.000000	0.439
Nighthawks	0.984	0.394	0.0088	0.000000	0.0056	0.00000	0.000001	0.343
Tadpoles	0.969	0.374	0.0113	0.000000	0.0056	0.03966	0.000003	0.520
Mink	0.969	0.403	0.0592	0.000000	0.0056	0.15481	0.000000	0.714 (3)
Bobcat	0.969	0.404	0.0100	0.000000	0.0056	0.15336	0.000001	0.457
Ducks	0.969	0.403	0.0390	0.000000	0.0056	0.00000	0.000000	0.460
Sediment Carbon	0.969	0.149 (1)	0.0895 (2)	0.551595 (1)	0.0657 (3)	0.12981	0.000238	0.928 (2)
Labile Detritus	0.969	0.191 (2)	0.0327	0.393440 (3)	0.0665 (2)	0.01466	0.000876 (2)	0.361
Mesoinverts	0.953	0.245 (3)	0.0643 (3)	0.001846	0.0562	0.06010	0.000058	0.537
Other Small Fishes	0.953	0.409	0.0327	0.000000	0.0056	0.25481 (3)	0.000001	0.537
Otter	0.953	0.589	0.0390	0.000013	0.0056	0.00000	0.000002	0.515
Living Sediments	0.938	0.497	0.0327	0.142788	0.0631	0.00000	0.001198 (1)	0.485
Macrophytes	0.938	0.462	0.0252	0.039412	0.0572	0.00000	0.000099	0.000
Floating Veg.	0.938	0.461	0.0163	0.055918	0.0331	0.00000	0.000138	0.000
Large frogs	0.938	0.593	0.0264	0.000004	0.0056	0.00000	0.000002	0.424
Medium frogs	0.938	0.593	0.0239	0.000005	0.0063	0.00000	0.000002	0.398
Small frogs	0.938	0.594	0.0264	0.000001	0.0058	0.00048	0.000001	0.398
Alligators	0.938	0.594	0.0529	0.000004	0.0062	0.04976	0.000001	0.613
Rats&Mice	0.938	0.593	0.0176	0.000054	0.0061	0.01298	0.000023	0.419
Raccoons	0.938	0.594	0.0290	0.000018	0.0056	0.09976	0.000005	0.492
Opossum	0.938	0.567	0.0214	0.000138	0.0056	0.00000	0.000027	0.565
W-T Deer	0.923	0.589	0.0088	0.000030	0.0058	0.00000	0.000081	0.030
Turtles	0.907	0.603	0.0378	0.000020	0.0056	0.01418	0.000005	0.550
Periphyton	0.876	0.710	0.0239	0.316464	0.1704 (1)	0.00000	0.000497 (3)	0.000
Bitterns	0.784	0.530	0.0353	0.000000	0.0056	0.33317 (2)	0.000000	0.460
Refractory Detritus	0.784	0.499	0.1021 (1)	0.480765 (2)	0.0438	0.61995 (1)	0.000142	0.970 (1)
Freshwater Prawn	0.676	0.476	0.0428	0.000322	0.0222	0.00000	0.000039	0.371
Snakes	0.446	0.697	0.0378	0.000090	0.0062	0.00000	0.000010	0.477
Lizards	0.353	0.745	0.0126	0.000023	0.0066	0.00000	0.000027	0.365
Large Aquatic Insects	0.307	0.794	0.0504	0.000068	0.0095	0.03029	0.000007	0.363

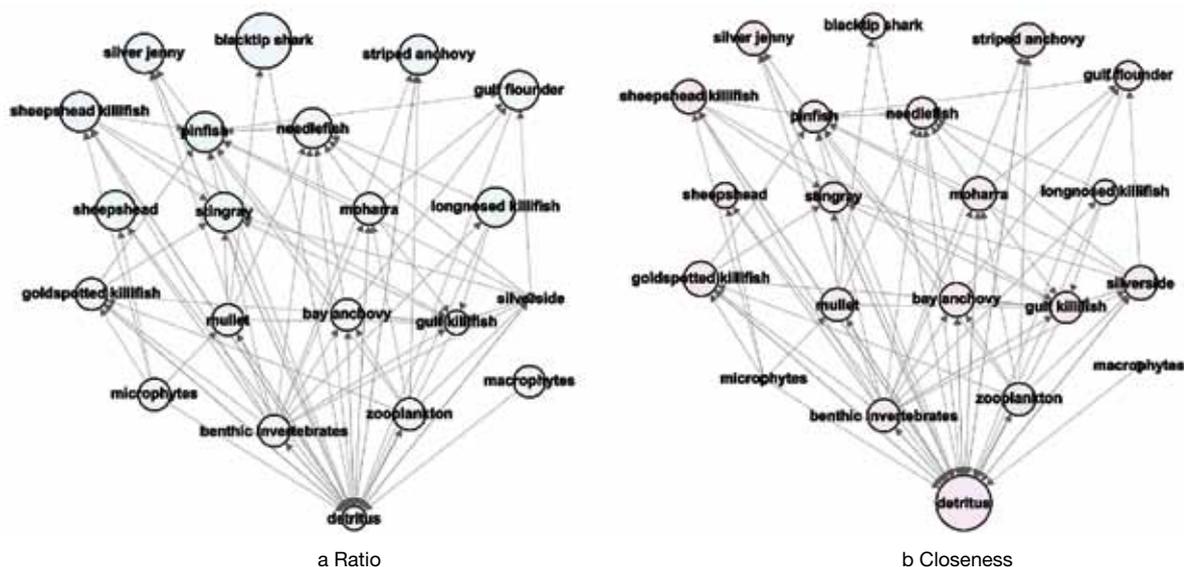


Figure 4: **Visualization of the CrystalC food-web, where nodes are positioned such that their locations roughly relate to their trophic levels. We use two metrics to adjust the node size, one is our algorithm using the Ratio metric and the other is closeness.**

Our methods also show promising, albeit not perfect, results in the *gramdry* food-web (Table 2). Again, using *Ratio*, the predators, such as »Panther«, »Bobcat« and »Nighthawks« proved to be most important, and smaller animals being less important. The biggest error in this web was with small organisms such as »Mesoinverts« and »Macrophytes« and with sediments like »Labile Detritus« and »Sediment Carbon«, which scored high, especially in the *Area* measure, but should be in the lowest trophic levels.

All other measures failed to predict the same importance of species as our methods did. This was the same both for *CrystalC* and *gramdry* food-web. The pyramidal structure of the trophic levels is also apparent only in our methods. We show the difference in Figure 4, where we visualize the *CrystalC* food-web, so that species are ordered in the pyramidal structure, with sediments and food source species at the bottom and predators at the top. We then make node size correlated with the specified measure. The visualization shows that *Area* brings clear differentiation into levels while *closeness* doesn't.

We also tried to remove »detritus« from *CrystalC*

in the preparation step, since it is not a living organism. Unfortunately this brought more problems than advantages, since the population dynamic behaved slower and the pyramidal structure broke.

Finally, we plot the correlation coefficient matrices, comparing correlations between the 8 measures. In Figure 5, we show results for two already discussed food-webs and also for *Florida* and *Narragan*. After cleaning, the *Florida* food-web has 125 species and *Narragan* has 32. Our two measures *Ratio* and *Area* are unsurprisingly correlated, since they are both derived from the same information on the population dynamics of species.

On the other hand, they are very uncorrelated to all other measures, showing that they aren't a viable choice of determining the importance of species. In the other methods of measuring importance, we also see some clustering. For example, in all cases *PageRank* and the *weights* measure are very correlated, while, interestingly, *degree* and *weights* aren't for these food-webs. This is because the weights for different edges differ so much that any correlation with degree is broken.

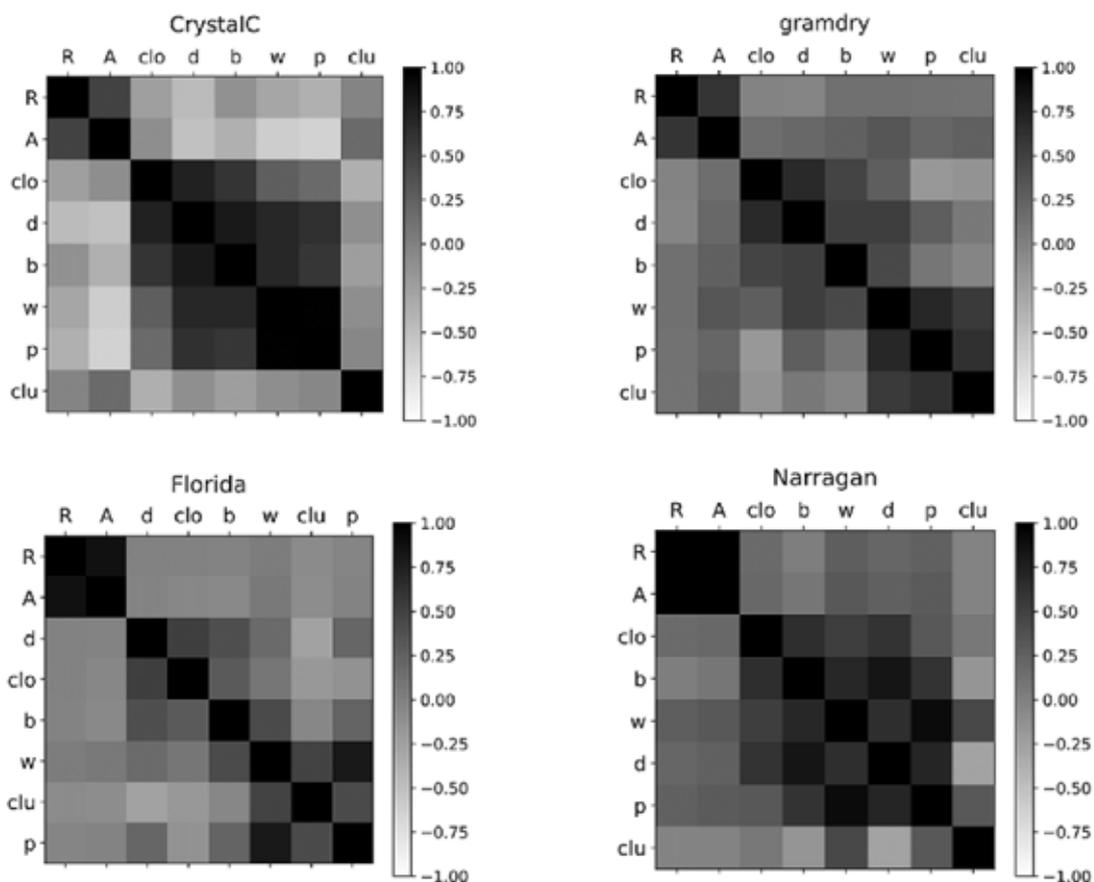


Figure 5: Correlation coefficient matrix depicting correlations between measures R: Ratio (ours), A: Area (ours), d: degree, w: weights, p: PageRank, b: betweenness, clu: clustering clo: closeness.

5. DISCUSSION

We have introduced an algorithm that uses food-web information about biomass flow to make a dynamic model of the population and gives two measures of importance to individual species, *Ratio* and *Area*. The *Ratio* measure is correlated with the importance of species and *Area* is anti-correlated. For both measures, species with higher importance would make a greater impact on the ecosystem if it would come to its extinction. The results are promising, especially since the results of *Ratio* and *Area* for *CrystalC* food-web show a clear pyramidal structure of the species, where *Area* is slightly better since it brings more differentiation inside clusters. These results indicate that the measures can be taken as a baseline for evaluating species importance. They can also be used for species clustering into different trophic levels. Similar pyramidal structure can be observed in the *gramdry* food-web, although not perfect, giving too much importance to microorganisms.

More work should be done on optimizing parameters of the methods, making the model as dynamic as possible, while keeping precision in the numerical computations, thus solving cases where no activity occurs because of a too small time step. Using an adaptive time step would also be helpful. Changing the time step as needed, instead of keeping a constant one, would help lower computational time for cases where no activity occurs for longer periods of time, since solving such cases with a small time step is very time consuming. Also, more thought should be put into determining the stopping criteria of the integration. If we achieve stability at the end of the integration, the results should improve too, moving singletons like »mullet« or »silverside« into more appropriate trophic levels.

The correlation matrices showed that finding a cheaper alternative to our measures was unsuccessful, which is disheartening since our method is very time consuming. A faster alternative is still quite needed.

ded, although improving parameters can also speed up computations.

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