Network Analysis of the Everglades Graminoids and the Florida Bay Ecosystems

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I. Introduction

All ecosystems need a variety of species in order to thrive. However, not all species within the same ecosystem are equally important. For instance, in many ecosystems, beavers play a role that is crucial to the entire ecosystem. They are often called "ecosystem engineers" by ecologists because they alter their habitats by cutting down trees, building dams, digging canals and building lodges, which provide stable environments for many other species.

In these ecosystems, beavers are what ecologists call a "keystone species". A keystone species is a plant or animal that plays a unique and crucial role in the way an ecosystem functions. In the ecosystems where a key stone species is present, protecting that species is essential in order to preserve the entire ecosystem. It is therefore important to identify these species for conservation purposes.

However, keystone species do not exist in many ecosystems around the world, since it is far more common for several species to appear on the same trophic level and play similar roles in the system. In these intricate and well-connected ecosystems, it is harder to identify important species by simply looking at food chains. Nonetheless, species in an ecosystem have different importance levels, which contain important messages about their preservation. Learning about different importance levels of certain groups of animals and inorganic matters in various ecosystems can also help us understand their differences.

The purpose of our project is to find the most important species within specific ecosystems by applying network analysis measures to two different food webs in Florida: the Everglades Graminoids (wetlands) and the Florida Bay (aquatic) ecosystems. As will be explained in the methodology section, we will be applying and comparing PageRank centrality and KPPneg index to our datasets.

II. Related Work

The fact that the predator-prey interaction between two species can mainly be characterized as a directed link and the complexity of connections within an ecosystem suggest that network analysis is a potentially effective way to determine the importance of different species within an ecosystem. In order to conduct network researches, ecosystems are documented using a system called "food webs", where the nodes are all elements (living and nonliving) within the ecosystem, and the links represent relationship between elements in terms of consumption. Food webs are directed networks, where the direction of edges represents the flow of energy, meaning that the edge will point from the prey to the predator (eg: rat to fox). Self-loops are allowed since some species perform cannibalism. Larger food web networks often demonstrate hierarchical properties because elements can be organized into different trophy levels (how far away they are from primary producers).

Through analysis across a number of food webs, scholars have determined that they are valid objects for network analysis, since most of them demonstrate similar properties to common network models. A study in 2002[1] suggests that the degree distributions of food webs appear similar to other real-world networks. In terms of degree distribution, food webs deviate from random networks and most of them demonstrate exponential distributions. Properties such as preferential attachment are also observed within food web networks.

A few past researches studied species importance in food webs through application of different centrality measures. Different measures, including degree centrality, betweenness centrality, closeness centrality and eigenvector centrality shared some concordances when determining the most important species[2], showing that they share a good deal of information regarding species in food webs. It has also been found that different measures are best used when different questions are asked. Degree centrality shows basic qualities of the network, and the use of betweenness centrality and closeness centrality are suggested in cases when the question is how a focal species transmits effects[2]. When determining the important overall species, eigenvectors have been shown to be reliable measures of the most important producers or predators of a food web[3]; additionally, two new algorithms named KPPpos and KPPneg were proposed in 2006 by Stephen P. Borgatti[4] to find keystone species, as defined the species that is either most important (KPPpos) or the most indispensable (KPPneg) element in the network.

III. Data Sets

For the purpose of our study, we used four datasets from two different ecosystems: dry and wet season food webs of the Everglades Graminoids, as well as dry and wet season food webs of the Florida Bay ecosystem, both collected in a study by Ulanowicz, R.E., J.J. Heymans, and M.S.

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[1] Dunne, Jennifer A.; Williams, Richard J.; and Martinez, Neo D. "Food-web structure and network theory: The role of connectance and size", *Proceedings of the National Academy of Sciences of the United States of America*:99, July 2002

[2] Jordán, Ferenc; Liu, Wei-chung; Davis, Andrew J., "Topological keystone species: measures of positional importance in food webs", *OIKOS*: 112, 3 pp535-546, March 2006

[3] Allesina, Stefano; Pascual, Mercedes, "Googling Food Webs: Can an Eigenvector Measure Species' Importance for Coextinctions",PLoS Comput Biol 5(9): e1000494, 2009

[4] Borgatti, Stephen P., Identifying sets of key players in a social network, *Comput Math Organiz Theor* 12: 21–34, 2006

Egnotovich in 2000. The Graminoids data sets contain 69 vertices, which are divided into 8 sub-categories: living microbial compartments, primary producers, invertebrates, fishes, reptiles and amphibians, mammals, birds, and detritus compartments. The Florida Bay data sets contains 128 vertices, which fall into 8 categories: primary producers, invertebrates, fishes, birds, reptiles, mammals, and detrital compartments. All four food webs are weighted networks, with weight representing the amount of energy flow from prey to the predator.

IV. Methodology

We obtained our data files in Pajek format. The networkX package in Python was used to transform them into weighted multigraphs. Visualization was done using Python and Frutchterman Reingold layout in Gephi.

Past studies on centralities advised that eigenvector and KPP indices are best measurements of species importance within food webs. We also learned that PageRank centrality, developed by Google, provides a similar algorithm to eigenvector, but is more reliable when the network is directed. Since we are interested in learning about the generally important species, as well as the most indispensable species in our food webs, we will be applying and comparing PageRank centrality and KPPneg index to our datasets.

The PageRank centrality measures how important a node is by looking at if it is pointed to by other important nodes. In the case of a food web, it looks for important destinations of energy, which translate to most important predators. In order to find the most important preys / producers, which are often more important because they provide the foundation of the food web, we reversed the edges and ran PageRank again. We applied PageRank function in Python's networkX package, which implemented the following algorithm:

$$R(u) = d \sum_{v \in B_v} \frac{R(u)}{N_v} + e$$

which measures the PageRank of A by dividing the PageRank of all incoming nodes by its number of outgoing nodes. *d* is a normalization factor, taking value of 0.85 in general, and *e* = (1-*d*)/N.

The KPPneg index, on the other hand, measures how important a node is by looking at how much the network depends on the node to be cohesive. It measures the level of connectivity of the network when the target node is removed. We implemented the following algorithm in python:

$$F = 1 - \frac{2 \sum_i \sum_{j<i} r_{ij}}{n(n-1)}$$

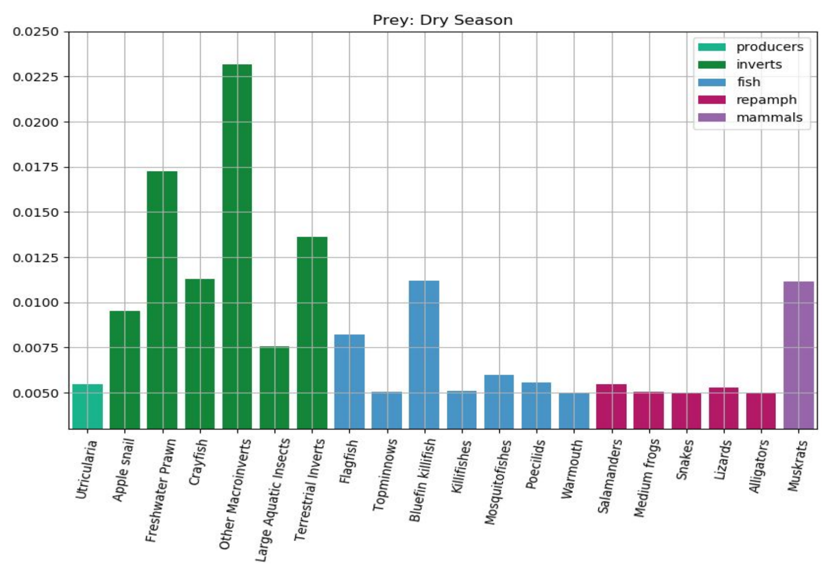
where r_{ij} is an indicator of whether i and j are connected; and n is the total number of nodes in the network.

The KPPneg index has limitations when implemented in our food webs because a number of nodes will share the same index since the food webs are relatively well-connected. But it is still an effective tool when looking for indispensable links in food webs.

V. Results and Analysis

Everglades Graminoids

Organisms with high pagerank centrality are ones which have high in-degrees and have highly weighted incoming edges from organisms with high in-degrees. Consumers with high pagerank centralities consume a wide variety of species or consume other consumers with high pagerank centralities. Similarly, prey with high pagerank centralities feed a wide variety of species or serve as food for prey with high pagerank centralities. Although the technical definition of high-value pagerank organisms is similar for consumers and prey, the ecological meanings are quite different. We interpret predator centrality as predator versatility, while we interpret prey centrality as importance of prey as the base of an ecosystem. From our graphs, we see that versatile, high-level consumers in the Graminoids are reptiles/amphibians and producers, and important base prey are invertebrates and fish (and muskrats).



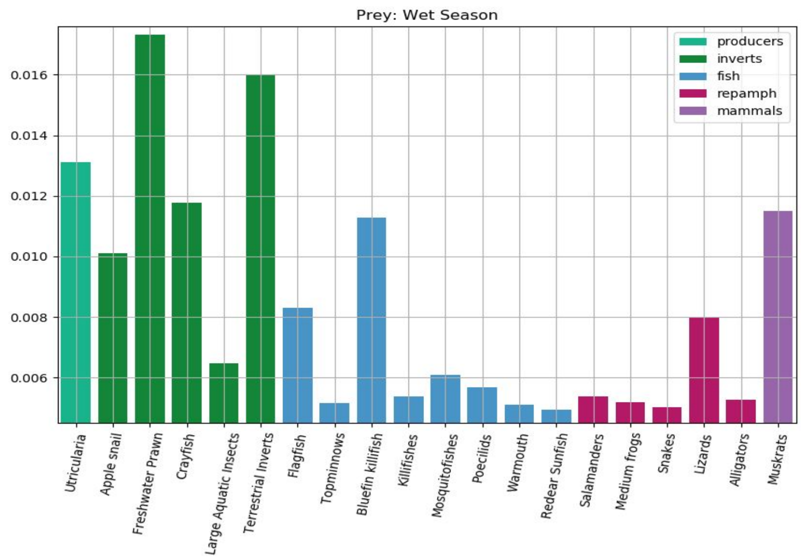
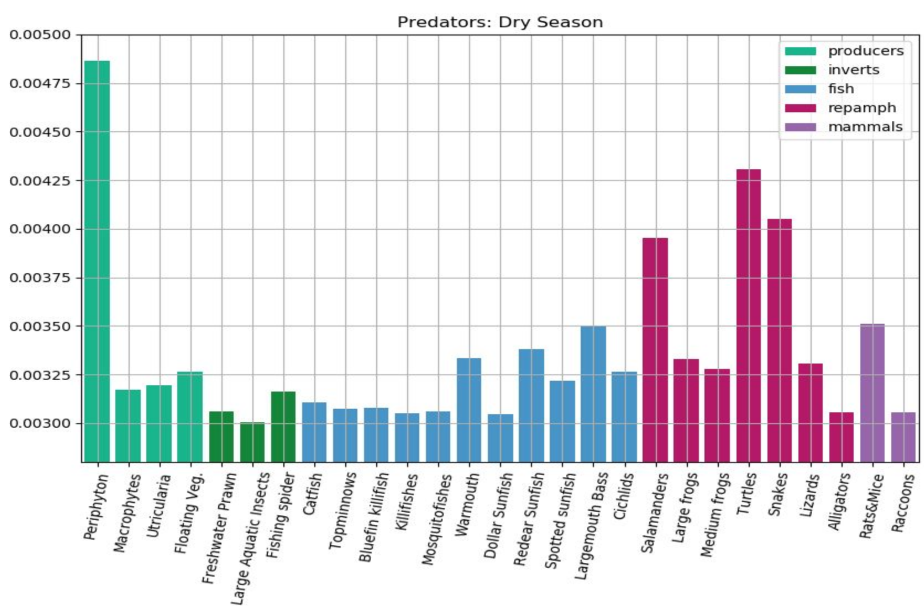


Figure A: Comparison of prey pagerank centrality by season. Note that prey species are relatively stable compared to predator species of the same region; exceptions include that general macroinvertebrates are central in the dry season but not wet and that Ultricularia, terrestrial invertebrate, and lizard centralities increase correspondingly during the wet season.



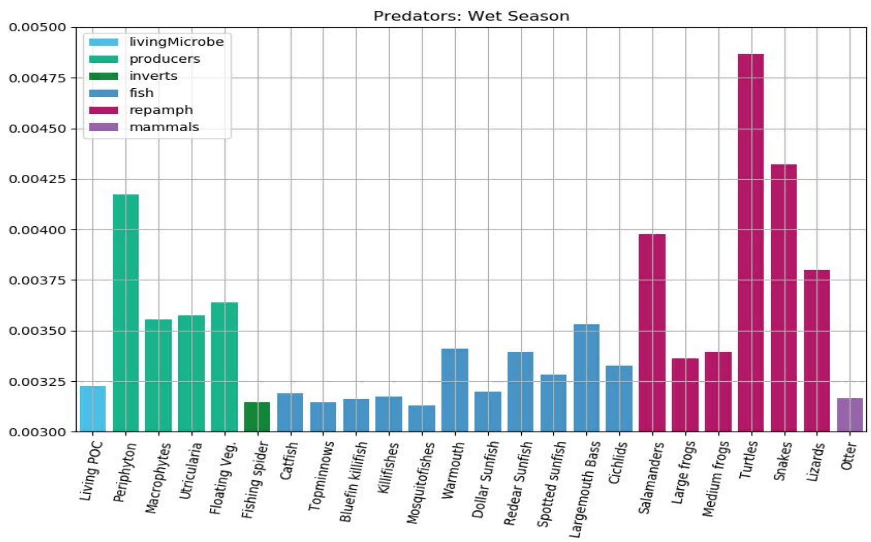


Figure B. The consumer pagerank distribution is noticeably different during the wet and dry seasons. Not only do the importance values change, but some important consumers change drastically. For example, rats/mice and raccoons replace otters during the dry season as important predatory mammals. However, note that consumers in the wet season are still mostly a subset of consumers in the dry season.

During the dry season, the most important prey are macroinvertebrates, freshwater prawn, terrestrial invertebrates, bluefin killifish, crayfish, and muskrats. The dry season's most important consumers are periphython, turtles, snakes, salamanders, rats/mice, and largemouth bass. Native rats and mice depend on aquatic animals, but live in dry areas, and largemouth bass are top predators in the ponds which form during dry season.

For the wet season, important prey are freshwater prawn, terrestrial invertebrates, Ultricularia, crayfish, muskrats, and bluefin killifish. The sudden importance of Ultricularia is due to its life cycle; it is dormant during the colder dry season and requires waterlogged soil to properly feed. It propagates quickly during the wet season and is eaten by herbivorous animals such as muskrats and turtles. During this time, the most important consumers are turtles, snakes, periphyton, salamanders, lizards, and floating vegetation. We notice that both top prey and consumer organisms look similar between seasons (though more so for prey).

This is expected because species in the Graminoids are not migratory (other than birds, which don't appear as top consumers or prey). Due to the drastically different natures of wet and dry season, most organisms which thrive have adapted to do well in both. The similarities between wet and dry season prey in particular is understandable because we'd expect that all stable food webs have stable bases. There needs to be a constant, reliable source of food at lower trophic levels for the whole ecosystem to survive.

Species	KPP-neg Index
Meso Invertebrates	0.2025
Sediment Carbon	0.1896
Terrestrial Invertebrates	0.1896
Mode	*0.1762*

Figure C. KPP-neg Indices of the Everglades Graminoids Food Web

The KPP-neg indices reveal that meso invertebrates, sediment carbon and terrestrial invertebrates are indispensable links in the Everglades Graminoids ecosystem, which is understandable since they represent entire levels of elements in the system. Most other species share the same KPP-neg indices, suggesting that the Graminoids is a relatively stable ecosystem and that the loss of one single species has limited effect on the survival of the ecosystem.

Florida Bay Ecosystem

Historically the bay has been described as varying between a positively functioning estuary and a tropical, hypersaline lagoon, depending up the season: a positively functioning estuary during periods of high rainfall (summer); a hypersaline lagoon when evaporation exceeds upland runoff and oceanic exchange (winter). On the other hand**,** the graminoid marsh is essentially a two-dimensional system, with reduced diversity of primary producers, and a more focused dependency of higher trophic levels on one particular primary producer, the periphyton

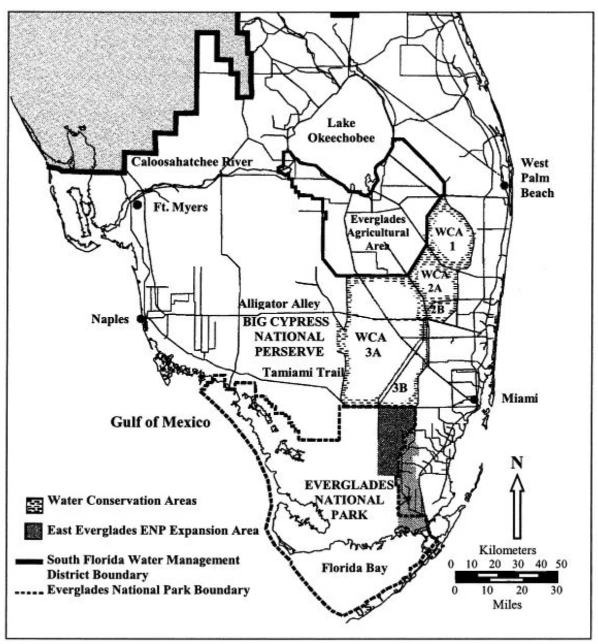


Figure D. The Florida Bay Ecosystem.

We applied the same network analysis on the Florida bay ecosystem. We were curious on how the change in the ecosystem would change the nature of our results. the graminoids being a wet marshland has different dynamics between its wet and dry seasons in comparison to the shallows of the Florida bay ecosystem. As presented by the graphs we were able to observe the following:

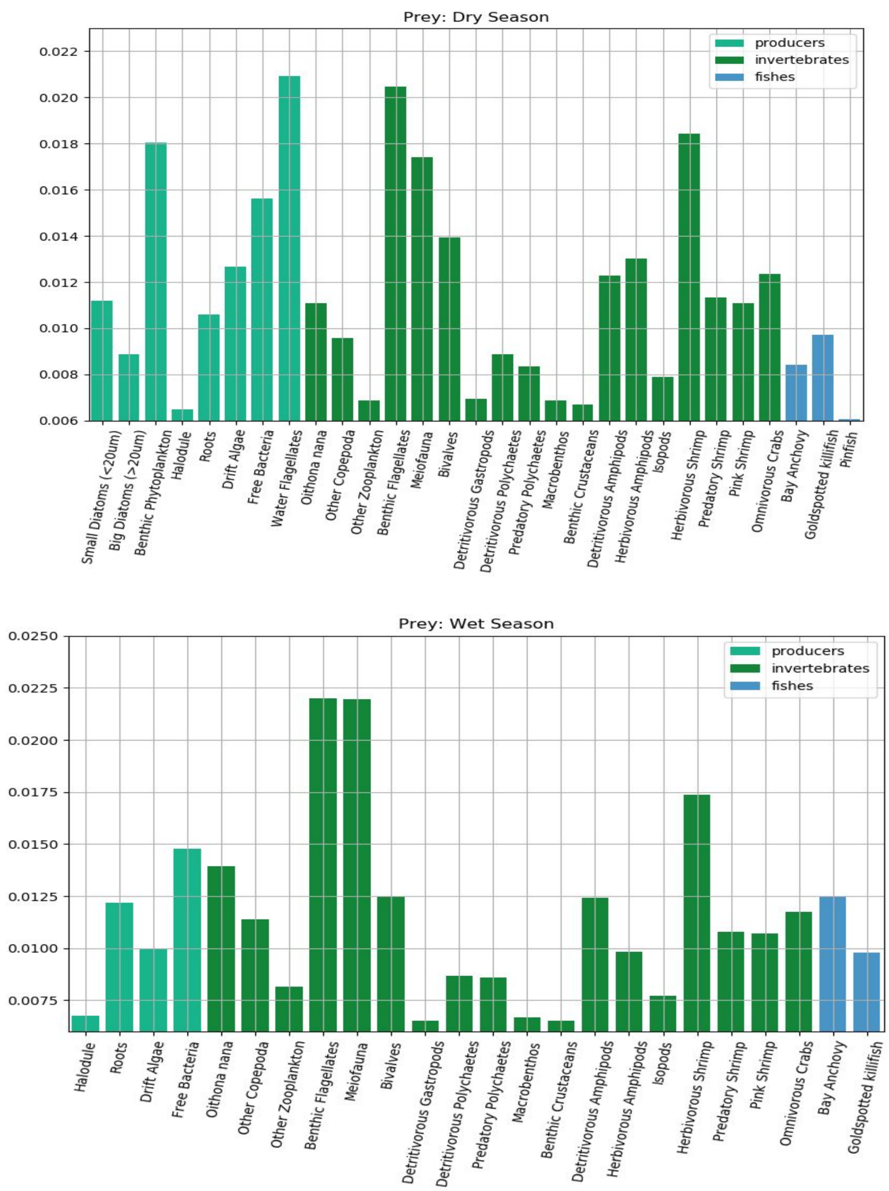


Figure E: Seasonal Comparison of Eigenvectors of the Original Florida Bay Network

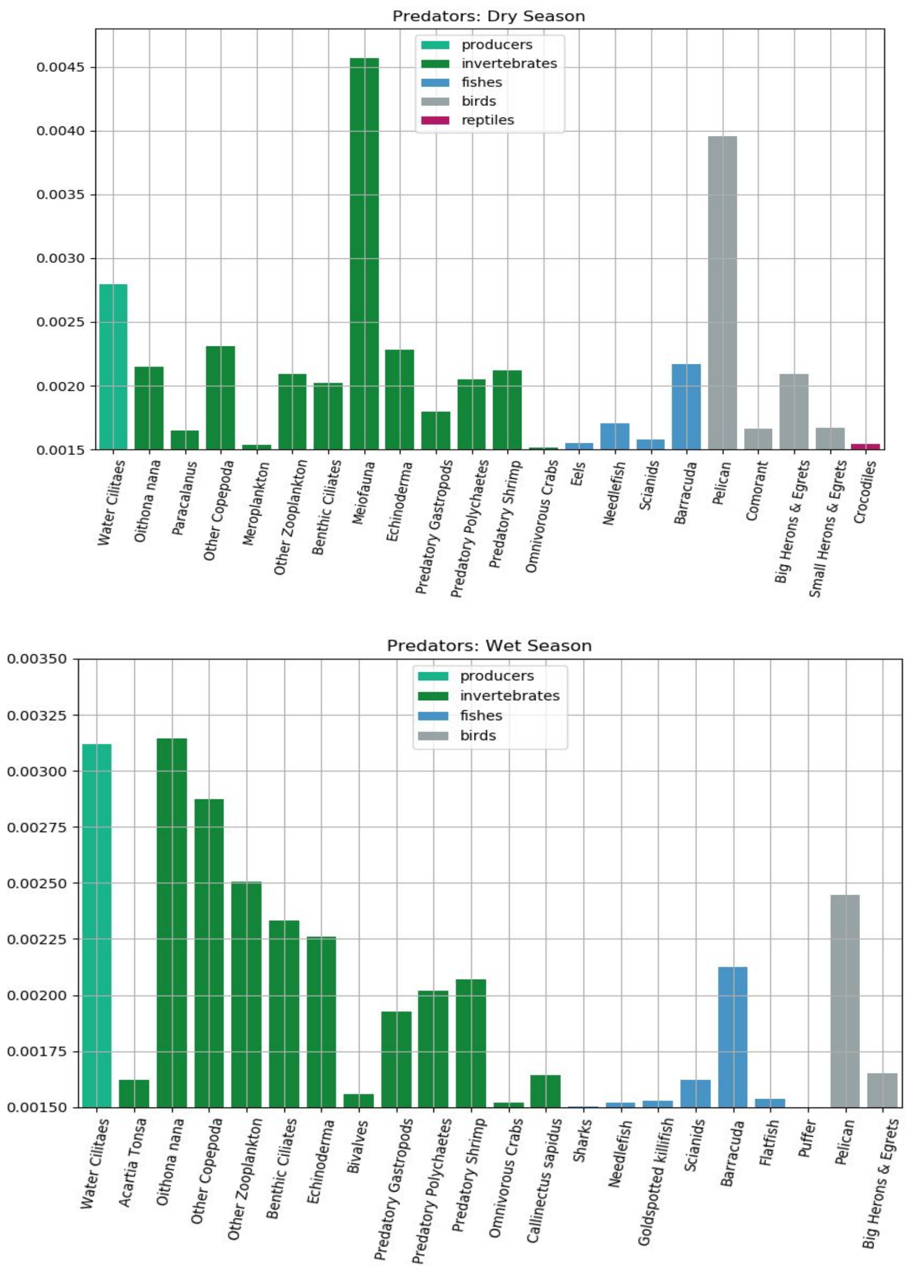


Figure F: Seasonal Comparison of Eigenvectors of the Reversed Florida Bay Network

Invertebrates are the primary ‘consumers’ in both the wet and dry seasons of the Florida bay ecosystem. At least 50% of the consumers in both seasons belong to the invertebrate category. In the wet season however, water ciliates which belong to the producer clan, compete with the oithona nana for most important consumer. In the dry season the importance of meiofauna is uncontested; their significance as a consumer in the dry season is at least twice that of water ciliates and almost 25% over that of the pelican. The pelican appears to be a more central consumer in the dry season; almost doubling its significance in the dry season. It appears that birds become more significant consumers in the dry season with the appearance of small herons and the cormorant, birds whose significance is unfelt in the wet season. Such a rise in the significance of birds at the turn of the season is expected because birds tend to favor the dry season for nesting since the dry season create more accessible feeding grounds. When the water dries up, the fish are moved into a much smaller area of space making it easier for the birds to to catch food (fish, crustaceans, and insects). Also, during the dry season birds come from all over the United States to get away from the cold and to nest around the Freshwater Slough in the pond apple trees.

It is also clear that most of the producers thrive in deeper waters. For example the Oithona nana are not as significant in the dry season, as well as the Copepoda, the Zooplankton and the Benthic Ciliates. It has been noted in previous research that the change in Ph over the seasons affects the abundance of these invertebrates. This could therefore explain the dip in their centrality on the onset of the dry season, since the dry season is characterised by a major change in salinity of the bay waters.

The KPPneg analysis of the Florida Bay ecosystem suggests that it cannot survive without Particulate Organic Carbon (both water and benthic), which is an obvious conclusion. The rest of the species share the same index, showing that it is also a stable and robust ecosystem.

Comparison between the Everglades Graminoids and Florida Bay Networks

From the PageRank centrality rankings of prey importance across both seasons, we were able to observe that invertebrates are the most important preys in the Everglades Graminoids ecosystem. On the other hand, the Florida Bay ecosystem is supported primarily by primary producers in the dry season, with invertebrates playing a bigger role in the wet season. These primary producers include water ciliates in the wet season and the likes of flagellates, free bacteria and phytoplankton in the dry season. Therefore, we can conclude that the more terrestrial an ecosystem is, the more important invertebrates become to the entire system. This seem to support the seasonal difference in the Florida Bay ecosystem. We hypothesize that during wet season, there will be more input from terrestrial ecosystems, which leads to the higher importance of invertebrates.

On the overall level, we noticed that the Everglades Graminoids system has higher predator and prey centralities in general compared to the Florida Bay ecosystem. The fact that all species are more important to the ecosystem suggests that the Everglades Graminoids has less biodiversity compared to the Bay ecosystem. This conclusion is supported by the number of nodes of the Florida Bay Ecosystem (128) to the number of nodes in the Everglades Graminoids (69).

Comparing dry/wet season changes in both ecosystems, we observed the Bay ecosystem centrality changes are more drastic than that of Graminoids. This finding suggests that aquatic ecosystems are surprisingly more heavily influenced by rainfalls. The reason behind this conclusion may be that aquatic ecosystems provide more flexibility for predators to travel, changing their levels of importance more drastically.

Prey versus predator comparison from both ecosystems reveals that prey importances are more stable than predator importances across seasons. Similarly, this suggests that predators are in general more free to travel, whereras preys are more confined within an ecosystem.

KPPneg indices are in general higher in the Florida Bay system, suggesting that it is more unstable and vulnerable to species extinctions, despite having more biodiversity. This seemingly contradictory conclusion was supported by a number of scholarly researches concluding that ecosystems are more robust if the overall connectance is higher, regardless of the number of species or biodiversity[5].

VI. Conclusion

Network analysis is a valid and informative tools to gather information from food webs. In our project, we applied PageRank centrality and KPP-neg index to the Everglades Graminoids and the Florida Bay ecosystems to identify species important to the respective ecosystem. From our analysis, we found that snakes, lizards, killifishes and mosquito fishes are important species within the Everglades Graminoids since they are both important preys and predators. A number of shrimps are the most central species to the Florida Bay ecosystem. We also found that cross-comparison of indices across ecosystems reveal intriguing differences between ecosystems. For instance, aquatic ecosystems are more affected by seasonal changes. Lastly, we also found evidence supporting the argument that biodiversity and robustness of ecosystems are not correlated.

[5] Dunne, J. A. , Williams, R. J. and Martinez, N. D. (2002), Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters*, 5: 558–567. doi:10.1046/j.1461-0248.2002.00354.x

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