Coral Reef Dynamics as Complex Ecological Networks: Linking Structure to Resilience for Conservation

Introduction

Coral reefs are complex systems that vary in structure, species diversity, and ecological processes across space and time [1]. Globally, coral reef survival is increasingly tenuous: many coral reefs are declining in coral cover [2,3], have reduced function and resilience [4], and individual coral colonies have degraded health where intensive human influence is present [5,6]. Reef ecosystem function can be disrupted by single or cumulative stressors, direct or indirect effects, and feedbacks within the system [7,8]. Conservation of coral reef ecosystems that are subject to natural and anthropogenic disturbance will require that resilience parameters - the factors that either encourage or inhibit recovery from disturbance [9] - are identified and targeted for conservation. Although there is a high risk of continued reef loss on a global scale [10], there are variable responses to widespread stressors at local and regional scales. Some reefs are not exhibiting stress responses or are able to recover from disturbance [11] – these reefs are resilient. The secret to why some reefs seem to be irreversibly changed from disturbance and why some are able to bounce back is hidden in the complexity of a tangled web of interacting parts [8].

Theory

Network theory has identified structural properties of complex systems that reveal how individual parts of a network contribute to overall network function and behavior. Mapping the relationships (links) between components (nodes) in a system creates a network topology that contains information about the relative importance of each constituent part [12]. In the familiar example of information spreading through a social network, a small number of highly influential people are responsible for creating the structure of the information network [13]. **Figure 1** shows an example of betweenness centrality, one structural property of a network that illustrates why an individual would be highly influential as a propagator of information. This information agent is treated as a node in a network, and since it links two disparate clusters of nodes, it is more important for spreading information than other nodes.

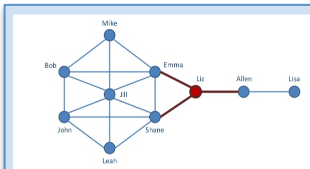

Figure 1. Betweenness centrality in a network. (*Source: Gašević 2014)*

This approach can be applied to a dynamical food web network where nodes represent species, links connect species that exchange energy, the links are weighted according to the interaction strength between each pair of nodes, and energy flow through the network changes over time [14, 15]. Some nodes in the web may be critically connected to others and have strong effects on the whole network, while others have weak effects on the whole [16]. The typical approach to ecology assumes that strong interactions are important systemically, but indirect and stabilizing effects from weak interactions can have a strong effect on system maintenance [17]. It is also often assumed that relationships between species are linear, however, relatively minor-seeming interactions can be non-linear, leading to feedback effects that propagate through network structure [18]. This suggests that an unknown number of 'influential' nodes and links that are critical indicators of reef resilience have likely not yet been identified nor strategically targeted for conservation.

Research Questions

In my Ph.D. research, I will investigate the following research questions using complex ecological network analysis:

Q1. Which species and species interactions in a coral reef ecosystem have the greatest influence on maintaining its community structure?
Q2. Which species and species interactions in a coral reef have the greatest influence on maintaining its ecosystem function and service provision?
Q3. Under what disturbance scenarios do these critical species and interactions gain or lose their influence on the larger reef system?

Methods

I will develop network models of the linkage structure of each reef (Q1) using a species list for each study site, and known species interactions between those organisms. The species are nodes and the interactions are links in the network. This allows me to first estimate the influence of each node on the community structure, using the topological properties of my reef network (e.g. density, size, path length, clustering, connectedness, etc.) and comparisons of these network properties between different reefs [12]. This static view of a structural network allows rapid comparisons of community structure.

Ecosystem function and services are process-based metrics of ecosystem 'health'; there is temporal change to data flowing through the network. To add these dynamics (Q2), I will develop a second model using energy exchange as a metric of ecosystem function. I will determine the relative strengths of interactions between each node pair from existing data and estimates that are derived from known relationships between organism size and metabolism [15]. These interaction strengths add weighting to each relationship in the network, and therefore energy is exchanged differentially, depending on the strength of that interaction [15]. These two component models will be hybridized into a probabilistic graphical niche model [19] that can be made more complex with the addition of various non-linear relationships between nodes if time permits. Probabilistic graphical models can be used to model both known and latent relationships, even under uncertainty about the nature of those relationships [20], and are thus a promising approach to this study. Simulations estimate the probability of an outcome (e.g. a phase shift or species recovery) given random starting values of energy input to the system, which is then propagated through the network via interactions between species [19]. The influence of each node and link on ecosystem function and service provision will be estimated with the same structural analysis above, by specifying a range of starting values that correspond to real world values for each node when the following conditions exist: high biodiversity, wave protection, and sustainable fisheries production. In this hybridized model, the network structure changes over time due to energy dynamics within the system.

I will use model manipulations and the methods above to estimate the effect of different disturbance conditions on high influence nodes and links (Q3). Disturbances are simulated by adding nodes (e.g. invasive species), removing nodes (e.g. geographic extinction), changing structural elements (e.g. changes to relationships), changing interaction strengths (e.g. change to nature of relationships), and specifying starting value ranges (proxy for environmental context of the network). These manipulations yield predictions of dynamic responses to environmental change, which can be validated by comparing the results to existing data on past reef system responses to change [12].

Program Collaboration
The Florida Keys National Marine Sanctuary (FKNMS) is uniquely suited to investigate these questions because: (1) its relatively low reef diversity has a simpler network structure, (2) human influence on its islands vary allowing for disturbance/protection comparisons between reefs and (3) the availability of long-term data. The large management effort and different zones of extraction regulations also offer real-world examples to validate network results. My work will yield three outcomes that support the Marine Zone Monitoring Program: Identifying the factors that control ecosystem structure, which is critical knowledge for how best to conserve ecosystem function with limited resources (Q1/Q2), understanding variability in system properties under different disturbance scenarios, which is essential to predicting vulnerability to human impacts (Q3), and lastly, developing methods to increase public engagement with the science of conservation (see *Broader Impacts)*. The models produced from this study will be provided to resource managers working in the FKNMS, and will be published online as a visualization template that can be applied to assess the sensitivity of any ecosystem to disturbance. In discussions with FKNMS, the sanctuary expressed strong interest in and support for this collaboration and stated that my proposed research aligns well with their science and information needs.

Broader Impacts
I am developing a citizen science training program that integrates past efforts by ReefCheck and REEF to engage recreational divers in the scientific process. Divers log more underwater observation hours in more locations than scientists can, are often highly knowledgeable about local natural history, and have large potential for meaningful scientific collaboration. For example, reef species interactions are poorly known, in part due to limited observation time. Dynamical reef models will improve substantially with more interaction records. The benefit of these collaborations is four-fold: science benefits from more data and new ideas, divers are enriched by contributing value to reef conservation, and management benefits by receiving better scientific information, as well as deeper and broader engagement by resource stakeholders. I have partnered with a software engineer (https://github.com/Juul) on our website, which teaches divers how to make observations, form hypotheses, collect data and build and interact with their own networks. The site community connects users to form collaborations, share data, ask questions and discuss ideas. This interactive network visualization tool will be the first open-source, open-access application of its kind, and can be used in any discipline.

Significance
This study will be the first to use a complex network approach for coral reef ecological dynamics. It is innovative within the field of complexity science by framing ecosystem dynamics based on their services, which yield non-trophic outcomes, and also by engaging the public in model improvement. This research will advance evidence-based coral reef conservation by deepening our understanding of the interdependence among reef components and by revealing the most influential mechanisms in the system under different projected disturbance scenarios, which can directly inform management action and management performance assessment. Therefore, this project aligns closely with both NOAA's and my own missions to improve our knowledge and ability to predict complex ocean ecosystem dynamics, to share this knowledge openly, and to use it to conserve our valuable resources.