12-5-2022

Caribbean Reef-Building Coral-Symbiodiniaceae Network: Identifying Symbioses Critical for System Stability in a Changing Climate

Shaman Patel
Nova Southeastern University

NSUWorks Citation
Shaman Patel. 2022. *Caribbean Reef-Building Coral-Symbiodiniaceae Network: Identifying Symbioses Critical for System Stability in a Changing Climate.* Master's thesis. Nova Southeastern University. Retrieved from NSUWorks, . (116)
https://nsuworks.nova.edu/hcas_etd_all/116.

Thesis of
Shaman Patel

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science
Marine Science

Nova Southeastern University
Halmos College of Arts and Sciences

December 2022

Approved:
Thesis Committee

Committee Chair: Timothy Swain, Ph.D.

Committee Member: Robert Smith, Ph.D.

Committee Member: Joana Figueiredo, Ph.D.

HALMOS COLLEGE OF ARTS AND SCIENCES

Caribbean Reef-Building Coral-Symbiodiniaceae Network: Identifying Symbioses Critical for System Stability in a Changing Climate

Shaman Patel

Submitted to the Faculty of
Halmos College of Arts and Sciences
in partial fulfillment of the requirements for
the degree of Master of Science in Marine Science with a specialty in:

Marine Biology

Nova Southeastern University

December 2022

Abstract**:**

Increasing global ocean temperatures and frequency of marine heatwaves pose dire consequences for coral reefs. High temperatures often lead to disruptions in coral symbiosis resulting in coral bleaching, increasing the mortality of corals. However, corals can potentially avoid bleaching peril by associating with thermally tolerant symbionts. Here we provide a tool for understanding symbiosis network stability of Caribbean reef-building corals. We created a network of Caribbean hermatypic corals and their associated Symbiodiniaceae phylotypes. A bleaching model was applied to this network to test for resilience and robustness (R50) to thermal stress. It was also layered with trait data for coral life history strategy, conservation attention and population status, as well as network measures including betweenness and eigenvector centrality. We found that the Caribbean network exhibits a narrow window in which it can resist bleaching but that it remains relatively robust to thermal stress. We identified one coral, *Dichocoenia stokesii*, to be heat tolerant, network-critical, and in need of conservation attention. Additionally, we found potential evidence of phylogenetic inertia exhibited by *Madracis decactis* as well as evidence for high connectance of invasive Symbiodiniaceae phylotypes, D1 and D1-4, amongst Caribbean hermatypic corals. The latter of which poses potential for a trade-off in biological function for increased thermotolerance. The resilient, network stabilizing corals identified in this study should be the focus of continued restoration effort in the Caribbean. It is vital to future-proof Caribbean reefs to protect the economic, cultural, and biological value they provide.

Keywords: bleaching, ecological robustness, resistance, ecosystem-based management, network analysis, resilience

Acknowledgements:

I struggled more with writing this section of the paper than any other section and not because I couldn't think of who to thank for getting me to this point but because I didn't know where to stop. I will begin by thanking my advisor, Dr. Timothy Swain, for his patient guidance over the past two years. Through weekly meetings, Tim provided guidance and support unlike any other professional mentor I have had. It has been a pleasure learning from Tim and observing his brilliant approach to science. I wish you and your unequivocally bright family well and look forward to more opportunities to work together. Next, I would like to thank my committee, Dr. Joana Figueiredo and Dr. Robert Smith for their edits and comments on my work. I would be remiss if I did not mention Dr. Andrew "Andy" G. Bauman for his timely assistance in this project. I was medically restricted from participating in the field work to collect samples for this study, but Andy stepped up and helped push my plans through.

Additionally, I would like to thank Dr. José "Joe" Lopez for offering his genetic expertise and loaning us some vital materials in a time of crucial need. Dr. Sara Williams also stepped up and provided updated code for their bleaching model that greatly improved the analysis in this paper. Your contributions and willingness to help is greatly appreciated and I look forward to working together on future projects should the opportunity arise. Additionally, I would not have been able to sift through the vast amounts of literature regarding coral-symbiont associations without the help of three bright and eager undergraduate students; Brady Estrada, Nadia Abeido, and Mackenzie Magyar are all equally responsible for providing the womanpower needed to complete this project.

My time at NSU would feel empty without the amazingly supportive and jovial work environment created by my bosses Emma Brennan and Dr. Bernhard Riegl. Their supervision and advice throughout my time at NSU has been invaluable and surpassed the support I imagined I could receive at a workplace. Lindsey Scott, my backup QB, thanks for introducing me to your angel of a dog. Bubs kept me sane. Another key figure in my time here, who also brought a lovely dog into my life, is Kathryn Toth. You, literally, saved my life and have been the best COVID-19 study partner I could ask for. I am proud to be Mr. Mako's 'funcle'. I have made many friends at NSU and to all, you know who you are, I hope we stay close and continue to make memories as future leaders in marine science. I would like to thank, from the bottom of my heart, my baking partner and favorite adventure buddy, Gretchen Spencer, for all her care and support through my trials and tribulations this year. I couldn't have done it without you.

I am appreciative of the Banks Family, Marine Industries Association of South Florida, NSU Fishing tournament, and the Brian Keller Memorial Fellowship for providing the financial support needed to complete this project. I also want to thank Gregory Alan Isakov, Nujabes, Vivaldi, Kevin Parker, Jermaine Lamarr Cole, and Dominique Armani Jones for making music that kept me centered and focused through long nights behind my computer.

Finally, I want to thank my parents, Bijal Thakkar and Ross McKay, for their unconditional love and support. Without your sacrifices I would not have been able to pursue my dreams. I love you both tremendously and cannot express how proud I am to be your son.

Table of Contents

List of Figures:

List of Tables:

Introduction:

Corals are marine Cnidaria in the anthozoan sub-class Hexacorallia within order Scleractinia. These are commonly referred to as “stony corals” as they build hard skeletons. Corals can exist as solitary polyps living freely or as colonies. Coral colonies are comprised of clonal polyps that excrete a calcium carbonate exoskeleton beneath them. As corals grow and polyps multiply, the colony’s exoskeleton also grows. Corals are vital organisms for not only the marine realm, but also for the approximately one billion people who rely on coral reef ecosystem services. These services include food provisioning, coastal protection, income from tourism and fisheries, and cultural services (GCRMN et al. 2020). Coral reefs services are valued at 3.4 billion (USD) each year in the United States. There are many environmental pressures that affect coral health. These include, but are not limited to, temperature (Hoegh-Guldberg and Smith, 1989; Glynn, 1993, Coles and Fadlallah, 1991; Muscatine et al., 1991), pH (Marubini and Atkinson, 1999), dissolved oxygen, light (Yonge and Nicholls, 1931; Hoegh-Guldberg and Smith, 1989, Lesser et al., 1990; Kinzie, 1993), sedimentation, salinity (Goreau, 1964; Fang et al., 1995), and turbidity (Hoegh-Guldberg et al. 2017). These highly valuable animals are rapidly declining in population as threats from climate change, including, but not limited to, coral bleaching, intensify. To understand the threat to ecosystem services from the loss of corals we must first understand the degree to which coral communities will be impacted by climate change. Investigations on coral bleaching are abundant in scientific literature, however few have considered the community-level characteristics of resilience to thermal bleaching. It is therefore important to understand how the various coral species will react to these environmental pressures and how their reaction to rapid environmental change will consequently affect coral reef ecosystems.

Corals can be grouped based on their ecological role, including ability (or not) to build a reef and association (or not) with zooxanthellae. A coral is termed constructional if it forms an elevated durable carbonate structure in shallow or in deep water (Schuhmacher and Zibrowius, 1984). Corals that significantly contribute to framework of reefs are considered hermatypic. In this study, we will focus on hermatypic corals that are, by definition, constructional and zooxanthellate. These corals are the major contributors to building living coral reefs and, in addition to calcareous algae, also building reef framework; a reef framework is the physical ridge of material at or near the surface of the ocean (Goreau 1963; van Woesik and Done, 1997). Reefs build at rates dependent upon carbonate deposited by corals and other calcareous organisms. Building reef-framework occurs over geologic time and has exhibited varied rates of growth in the past (Perry and Smithers, 2011). Recent investigations have found that modern reef-growth rates are projected to keep pace with projections for sea level rise (Kench et al. 2022). While this is promising, the potential for future growth rates to maintain modern rates is unlikely as corals populations are diminishing. The implications of sea level rise overtaking reef growth rates include, but are not limited to, increased coastal flooding, loss of protective barriers for incident wave energy, and loss of culturally valuable sites. It is therefore crucial to embed resilience to thermal stress in coral reef ecosystems as a measure to protect against the projected consequences of sea level rise.

Corals can also be grouped as zooxanthellate or azooxanthellate (Schuhmacher and Zibrowius, 1984). The former describes corals that house dinoflagellates while the latter do not. These dinoflagellates, colloquially known as zooxanthellae, are photosynthetic and have a symbiotic relationship with corals. Zooxanthellae convert sunlight into the energy corals require to grow and provide up to 95% of coral fixed carbon requirements (Muscatine et al., 1984). In return, corals provide zooxanthellae with protection by sequestering them within their tissues and augment their growth with coral waste products (CO_2 & nitrogen). Loss of these symbionts due to physiological stressors is termed ‘coral bleaching’. This causes coral skeleton to be visible through the transparent coral tissues and appear white and often leads to increased mortality due to the disruption of energy intake provided by the zooxanthellae.

Zooxanthellae of the family Symbiodiniaceae are the most commonly occurring dinoflagellates in symbiosis with marine invertebrates including scleractinian corals (Trench 1979). Symbiodiniaceae typically contain one or more chloroplasts and can exist in either a vegetative cyst (coccoid form) or as a motile form (McLaughlin and Zahl 1959; Freudenthal 1962). The coccoid form is the most common form of zooxanthellae found within coral tissue (Schoenberg and Trench 1980). The coccoid form can reproduce, asexually, by binary fission to produce two or four daughter cells or, alternatively, form motile zoospores. Most symbiotic dinoflagellates were considered a single pandemic species, *Symbiodinium microadriaticum* based primarily on morphological classification (Taylor 1974). Since the 1970s, the advancement of molecular genetic techniques has led to the discovery of the immense diversity in symbiotic dinoflagellates. There are now consistently nine clades of Symbiodiniaceae with four genera *Symbiodinium* (formerly known as clade A, LaJeunesse et al., 2018), *Breviolum* (formerly known as clade B, LaJeunesse et al., 2018), *Cladocopium* (formerly known as clade C, LaJeunesse et al., 2018), and *Durusdinium* (formerly known as clade D, LaJeunesse et al., 2018) that are predominant within scleractinian corals (Baker 2003; Coffroth and Santos 2005; Stat et al. 2006). Pochon and Gates 2010). This delineation of genera was made possible through phylogenetic analysis of the internal transcribed spacers (ITS) 1 and 2, and small and large subunit (SSU and LSU) of ribosomal DNA (LaJeunesse et al., 2018). Each genus is further divided into subclades and phylotypes with the use of ITS2 DNA barcodes (LaJeunesse 2001). It is important to note that phylotypes are approximations of species-level distinctions and the precise taxonomic classification of symbionts is an ongoing effort. It is currently possible for multiple phylotypes to represent a single species and possible for single phylotypes to represent multiple species. Within these phylotypes, there is variation in capacity for photo acclimation as well as thermal tolerance both between and within cladal levels (Iglesias-Prieto and Trench 1994; Iglesias-Prieto and Trench 1997; Tchernov et al. 2004; Robison and Warner 2006; Hennige et al. 2009).

The combination of Symbiodiniaceae phylotypes with the unique traits of coral species can determine their vulnerability to thermal stress (Glynn et al. 2001, Berkelsman and van Oppen, 2006). It is therefore possible to predict a coral’s response to thermal stress based on their associations with either more or less tolerant phylotypes. It is also possible to inoculate corals used for restoring reefs with symbionts that are either naturally thermally tolerant or heat-evolved in lab (Buerger et al., 2020). This would allow for the manufacturing of thermally resilient corals through introduction of phylotypes or through direct modification of existing phylotypes which could potentially protect against projection for increased frequency of DHWs, a measure that shows how much heat stress has accumulated in an area over the past 12 weeks by adding up any temperature exceeding the bleaching threshold during that time period.

The delicate relationship between reef-building corals and their zooxanthellae has been severely impacted during the Anthropocene. Marine heatwaves have trended to become more frequent and more severe since 1980 and they are predicted under current models to become an annual event by mid-century (van Hooidonk 2015, Heron 2016, Castillo et al. 2019). Coral-

Symbiodiniaceae relationships can be disrupted during marine heating by coral bleaching, which leads to increased morbidity and mortality of coral hosts. The increased severity of marine heatwaves threatens to drive coral reefs to extinction and subsequently threatens the services humans derive from these ecosystems. The estimated global economic value of coral reefs is nearly 10 trillion (USD) per year (Constanza et al 2014). Disruption of Symbiodiniaceae symbiosis puts an estimated 800,000 species of reef fishes at risk from habitat loss (Fisher et al. 2015). Reefs protect coastlines in the tropics worldwide. Reefs protect an estimated 1.8 billion (USD) in damages in the United States annually, but the collapse of reefs in the United States would likely result in damages more than double that value (Beck et al. 2018, Storlazzi et al. 2019). Hard coral coverage on Caribbean reefs has decreased from 50% to 16% between 1970–2012 (Jackson et al. 2014). The worst global bleaching and mortality event on record occurred during 2014–2017 and the current status of coral coverage in the Caribbean as a whole is unknown. (Lough et al. 2018, Eakin et al. 2019, Claar 2020). However, decline in coral cover has been reported along the coast of South Florida from 2004-2018 with subsequent increases in macroalgae cover and relative increases in octocoral and sponge cover (Jones et al., 2022)

Both passive and active management strategies are being implemented to help mitigate the loss of coral reefs. There has been an increased use of active restoration strategies on coral reefs in the past couple of decades. However, there are some concerns associated with the current practice of coral restoration. Most projects appear to be short-term efforts that have limited post hoc ecological monitoring. Although a 60–70% survival rate is reported among restoration projects, it is likely this number is inflated due to the limited length and monitoring of projects (Boström-Einarsson et al. 2020). Boström-Einarsson et al. (2020) also found that 30% of restored corals are from a single genus; Acropora. Acropora are a fast-growing and rapidly declining genus and are therefore good candidates for preliminary research on restoration methods (Johnson et al. 2011). However, they might not be the most critical genera for the Caribbean network. Acroporids are particularly sensitive to thermal stress and may not be able to build reefs successfully as temperatures continue to rise. Although it is no replacement for significant action regarding climate change, restoration is still a valuable tool for helping ecosystems retain their function. Despite their room for improvement, restoration projects have served as a proof of concept that it is possible to successfully grow corals at a rate faster than is naturally observed (Forsman et al.

2015). It is important for restoration projects to transition from small-scale efforts to well-informed ecological scale efforts that epitomize reef resilience. To achieve this transition, management planning requires baseline data and tools for understanding and predicting how ecosystems will respond to perturbations and interventions.

Network science can conceptualize the complex system of coral-zooxanthellae associations and provides a means for determining the patterns of resistance to thermal stress and ecosystem stability during bleaching events for the Caribbean reef-building coral network. Networks achieve this by representing their components in the form of nodes; corals and Symbiodiniaceae phylotypes will make up the nodes of the network. These nodes are connected to each other by links, referred to as edges, to represent observed interactions. Coral-Symbiodiniaceae networks, like other natural world networks, have been shown to exhibit non-random organization (Swain 2021). These non-random networks have structure and topology that determine their ability to withstand perturbation (Albert et al. 2000, Allesina and Pascual 2008, Williams 2020). Common features of networks are that they exhibit power-law distributions where many nodes have a few connections with few nodes having many connections. This structuring allows for random removals of nodes to occur with little effect to the overall network. However, removals of highly connected nodes or within modules of nodes that are highly connected to each other can result in effects that threaten the stability of the overall network. Because real-world networks are particularly vulnerable to targeted attacks, there exists critical nodes and links that may affect overall network stability if lost. These network critical associations may create schisms in the network when lost or result in a network that is less robust to random loss of nodes. These critical associations and nodes may also allow us to identify how potential targeted attacks could disrupt network stability.

Here I present a network model that represents Caribbean hermatypic corals and their associated Symbiodiniaceae symbionts. This network is layered with metadata that includes population status, conservation status, phylogenetic relationships among hosts and symbionts, thermotolerance of hosts and symbionts (Swain 2016), and transmission mode of symbionts. The network consists of 38 hermatypic corals with referenced distributions in the Caribbean. The network includes Brazilian and South Floridian corals to reflect the most inclusive community of corals that could build reefs in the Caribbean region (Roberts 1997, Rippe et al. 2017). Coral-Symbiodiniaceae phylotype association data, determined using ITS2 phylotypes, were collected from literature for 32 of the 67 known corals in the Caribbean. Symbiont association data for the remaining six corals in this analysis were collected from a combination of existing literature and field samples.

The Caribbean network was tested for its resistance to perturbations by examining the temperature change needed to go from 10% of corals being bleached to 90% of corals bleached (Williams 2020). This was achieved by applying a model that assigns a bleaching threshold weight to links in the network (Williams 2020). This model accounts for thermotolerances of corals and their associated symbionts as well as mean monthly maximum sea surface temperature. This model provides weighted links that are removed when temperature exceeds the thermotolerance of the coral-symbiont association. The bleaching model combined with our network allows us to identify, first, the network critical coral-symbiont associations, and second, which of these critical species are best adapted for surviving inevitable marine heatwave events. Understanding this allows us to answer the following questions: 1) What corals or coral-symbiont associations are most vital to network stability in the Caribbean? 2) Which of these associations can be protected by increasing conservation effort on the coral hosts? 3) How resilient and how robust is the Caribbean network to thermal stress?

Methods:

Site selection:

Samples were collected from Belize near English Caye Light from two reef areas just south of the Lighthouse at 17.3162686°N, 88.0388308°W and 17.3162323°N, 88.0390834°W. This site was chosen due to its high density of hermatypic corals that are found throughout the rest of the Caribbean that lacked minimum symbiont association data for inclusion in the network analysis (Dinerstein et al. 1995).

Sample Collection:

Samples were collected on SCUBA within recreational diving limits (1–40m). All samples were collected between 1–20m. Coral fragments (1–5 cm^2) from living, non-bleached, nondiseased corals were collected from the top and bottom of each coral colony sampled: *Agaricia fragilis* (Dana, 1846), *Agaricia tenuifolia* (Dana, 1846), *Eusmilia fastigiata* (Pallas, 1766), *Manicina areolata* (Linnaeus, 1758), *Mussa angulosa* (Pallas, 1766), *Mycetophyllia ferox* (Wells, 1973), *Porites divaricata* (Le Sueur, 1820), and *Siderastrea stellata* (Verrill, 1868). Corals were identified based on morphology in the field by an experienced Caribbean coral researcher. Fragments were collected with a hammer and chisel and kept in individual plastic bags while underwater before being transferred to 5mL O-ring tubes and preserved in salt-saturated 20% DMSO. Colonies were sampled at least 5 metres apart from each other. Coral colonies were sampled until total records for each species reached the minimum 10 records required for inclusion in the network. All samples were kept at -80°C after collection until DNA extraction.

DNA Extraction and PCR:

Whole ITS region/ITS2 (phylotypes):

Symbiodiniaceae DNA was extracted from coral fragments using a cetyl trimethylammonium bromide (CTAB) extraction protocol (Supplemental D1) and diluted by adding 1µL of extraction with 49µL of molecular grade H_2O. PCR amplification of the complete ITS region, including ITS1, 5.8s, and ITS2, followed DNA extraction. Primers for the ITS region are as follows: ZooxITSAF (5' - GGG ATC CGT TTC CGT AGG TGA ACC TGC - 3') and ZooxITSbR (5' - GGG ATC CAT ATG CTT AAG TTC AGC GGG T - 3') (LaJeunesse 2001). Each PCR reaction required 1µL of extraction dilution, 12.5µL of DreamTaq MM(2X), 0.5µL of each primer, and 10.50 µL molecular grade H_2O. PCR was run under the following conditions: 95°C for 3 minutes, 38 cycles of 95°C for 45 seconds, 57°C for 60 seconds, and 72°C for 75 seconds, followed by a final 8-minute extension step at 72°C. All products were tested for successful amplification using gel electrophoresis. Successful amplifications were estimated to be around 700-800 base pairs (bp) long when compared to a 1000 bp DNA ladder. Failed amplifications were tried once again using the same PCR reaction above but with the addition of bovine serum albumen (BSA) as a general PCR enhancer to the reaction tube (Karunanathie et al. 2022). BSA was substituted in equal quantity for 1µL of molecular grade H_2O for four samples that failed initially. PCR products were transferred to a -80°C freezer for long-term storage.

Sample Purification and Sequencing:

PCR products were purified using the Illustra ExoProStar PCR and Sequence Reaction Clean-Up Kit following the Illustra recommended 1-step protocol. Purified samples were sent the Florida State University Biological Sciences DNA Sequencing Facility in Tallahassee, Florida for sequencing. Both forward and reverse sequences were obtained from sequencing. These were aligned in BioEdit using ClustalW multiple sequence alignment (Hall 1999). Consensus sequences were generated in BioEdit and inputted into The Basic Local Alignment Search Tool (BLAST) to generate phylotype matches.

Table 1. Caribbean Network Coral Species obtained from primary literature (see appendix for full reference list) with distributions located in the Western Atlantic. Corals from Florida, Brazil, Bermuda, the Gulf of Mexico, and the Caribbean Sea are included. Corals highlighted in light green are included in the network. Corals with insufficient symbiont association data are highlighted in orange.

🟩 *Acropora cervicornis*	🟧 *Leptoseris cailleti*	🟧 *Oculina diffusa*
🟩 *Acropora palmata*	🟧 *Madracis asperula*	🟧 *Oculina robusta*
🟩 *Agaricia agaricites*	🟧 *Madracis auretenra*	🟧 *Oculina tenella*
🟩 *Agaricia fragilis*	🟩 *Madracis decactis*	🟧 *Oculina valenciennesi*
🟩 *Agaricia grahamae*	🟩 *Madracis formosa*	🟧 *Oculina varicosa*
🟩 *Agaricia humilis*	🟩 *Madracis myriaster*	🟩 *Orbicella annularis*
🟩 *Agaricia lamarcki*	🟩 *Madracis pharensis*	🟩 *Orbicella faveolata*
🟩 *Agaricia tenuifolia*	🟩 *Madracis senaria*	🟩 *Orbicella franksi*
🟧 *Agaricia undata*	🟩 *Manicina areolata*	🟩 *Porites astreoides*
🟧 *Astrangia poculata*	🟧 *Meandrina brasiliensis*	🟧 *Porites branneri*
🟧 *Cladocora arbuscula*	🟧 *Meandrina jacksoni*	🟧 *Porites colonensis*
🟧 *Colpophyllia breviserialis*	🟩 *Meandrina meandrites*	🟩 *Porites divaricata*
🟩 *Colpophyllia natans*	🟩 *Montastraea cavernosa*	🟩 *Porites furcata*
🟧 *Dendrogyra cylindrus*	🟧 *Mussa angulosa*	🟩 *Porites porites*
🟩 *Dichocoenia stokesii*	🟧 *Mussismilia braziliensis*	🟩 *Pseudodiploria clivosa*
🟩 *Diploria labyrinthiformis*	🟧 *Mussismilia harttii*	🟩 *Siderastrea radians*
🟩 *Diploria strigosa*	🟧 *Mussismilia hispida*	🟩 *Siderastrea siderea*
🟩 *Eusmilia fastigiata*	🟧 *Mussismilia leptophylla*	🟩 *Siderastrea stellata*
🟩 *Favia fragum*	🟧 *Mycetophyllia aliciae*	🟧 *Solenastrea bournoni*

Favia gravida	*Mycetophyllia danaana*	*Solenastrea hyades*
Helioseris cucullata	*Mycetophyllia ferox*	*Stephanocoenia intersepta*
Isophyllia rigida	*Mycetophyllia lamarckiana*	
Isophyllia sinuosa	*Mycetophyllia reesi*	

Data analysis:

Network:

The natural network was constructed in R using the igraph package (Csárdi and Nepusz 2006). Two types of nodes, coral host species and Symbiodiniaceae phylotypes, will be connected by weighted links provided by the bleaching model described below (equation 1). The network is layered with metadata for each coral host node including symbiont transmission mode, EDGE (Evolutionarily Distinct and Globally Endangered) scores, and IUCN population status. Coral hosts were included if they met the sufficient data requirement of a minimum 10 phylotype association records. Network based analysis included measures for eigenvector centrality, which assigns value to a node based on how many connections the node's connected nodes have, and betweenness, which assigns value to a node based on the number of times it lies on the shortest path between other nodes. Eigenvector centrality measures how centrally connected a node is to the rest of the network, while betweenness identifies nodes that act as bridges between modules in the network. A node can be given a high betweenness value if it is located on the periphery of the network. These nodes were identified but not included in our analysis as they serve a less relevant role in the network. Both betweenness and eigenvector centrality were calculated using functions, betweenness and evcent, respectively, that are built into the R package igraph. Additionally, scores for Bleaching Response Index (BRI) values were obtained from Swain et al. 2016. Ranked EDGE scores and Shannon-Weiner Index values were also plotted on the network.

Bleaching model:

A model for bleaching (equation 1) susceptibility in response to temperature increase was applied to determine how the structure of the Caribbean network and the distribution of thermal tolerances might affect resistance to temperature stress (Williams 2020). The bleaching model from Williams (2020) was adapted to work in R by Sara Williams with igraph network types. The bleaching model is included below and provides weighted links based on the expectations that corals will bleach once temperatures exceed mean monthly maximum sea surface temperature and that there is an upper thermal limit for coral-symbiont association (Jokiel and Coles 1990, Fitt et al. 2001, Donner et al. 2005, Williams 2020).

$$W_{h.s} = T_{MMM(2005)} + \frac{T_{\Delta}(\tau_{symbiont}+\tau_{host})}{2} \qquad \text{(eq. 1)}$$

T_{MMM} represents the mean monthly maximum sea surface temperature from 2005 (Donner et al. 2005). The values for T_{MMM} were assigned to the Caribbean region by taking the average, 30.02°C, of all represented subregions (table 2). This was done to account for the noise present in coral host nodes that have an unequal distribution of association data from multiple regions. T_{Δ} represents the upper thermal limit for coral-symbiont association and values for $t_{symbiont}$ and t_{host} were obtained from Swain et al. 2017.

Table 2. Mean monthly maximum sea surface temperatures for the subregions of the Caribbean Coral Network (Donner et al. 2005).

Subregion	**$T_{MMM\ (2005)}$ (°C)**
Western Caribbean	29.72
Eastern Caribbean	29.63
Central Caribbean	29.94
Florida	30.25
Gulf of Mexico	30.54
Regional Average	30.02

Bleaching resistance metric:

The resistance of the Caribbean network was determined by calculating the required temperature for the network nodes to go from 10% to 90% bleached (Williams 2020). The required code and randomization tests needed to calculate and simulate this resistance metric was adapted from existing code (Williams 2020). This model ran 100 simulations for each distribution to obtain the change in temperature needed for 10% and 90% bleached corals for the natural network.

Ecological robustness:

Ecological robustness, unlike the resistance metric, is determined by finding an R50 value. The R50 value is the number of nodes or links needed to be removed until only 50% of the original nodes are remaining (Dunne et al. 2002, Dunne and Williams 2009, Williams 2020).

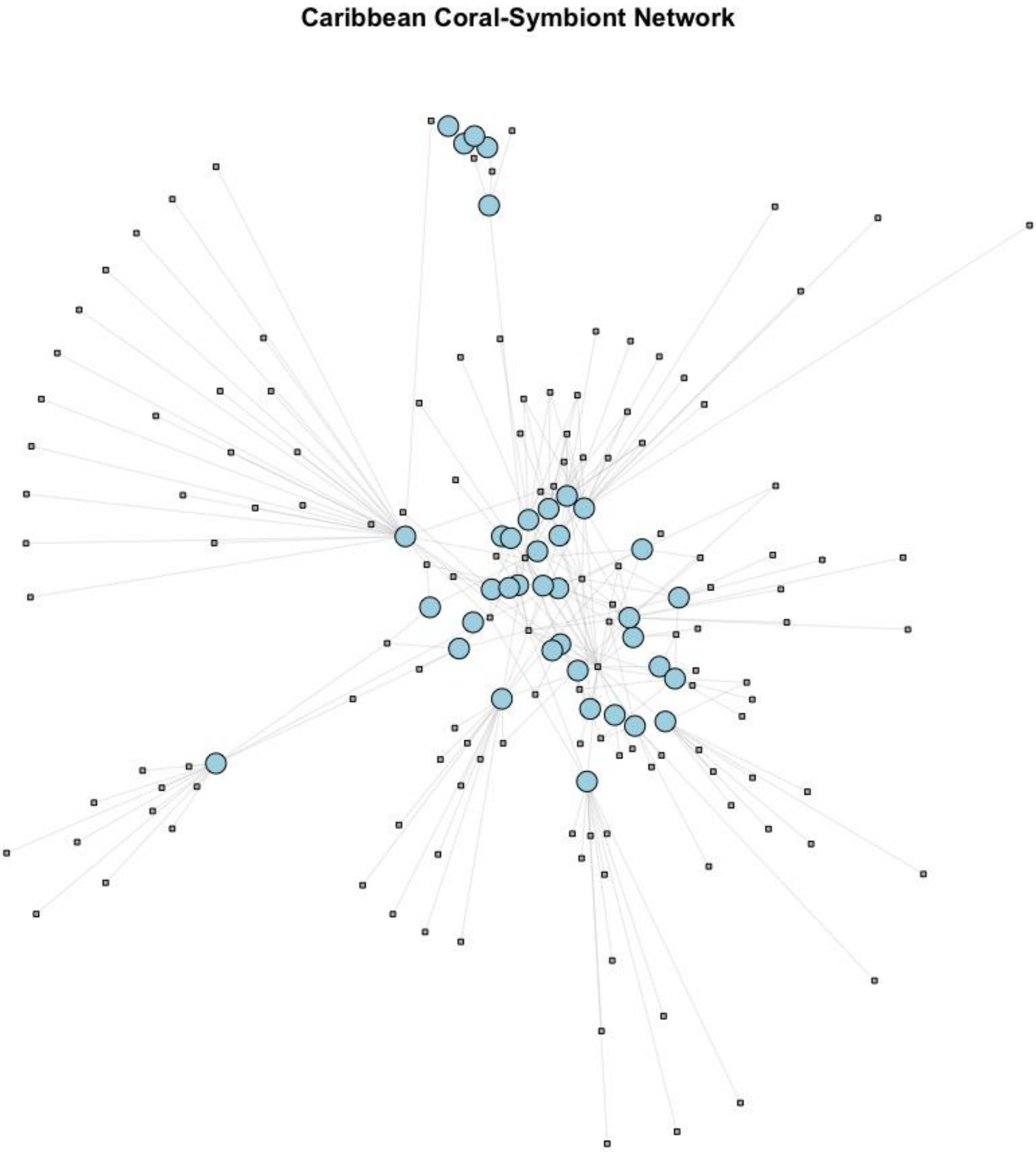
Conservation attention:

Coral nodes were labeled from low to high conservation status provided by EDGE (Evolutionarily Distinct and Globally Endangered) scores. EDGE scores are created by combining scores for both unique evolutionary history for each species as well as its global conservation (IUCN) status. These EDGE scores also include a measure for the conservation attention a species is receiving categorized as: good, medium, low, or very low.

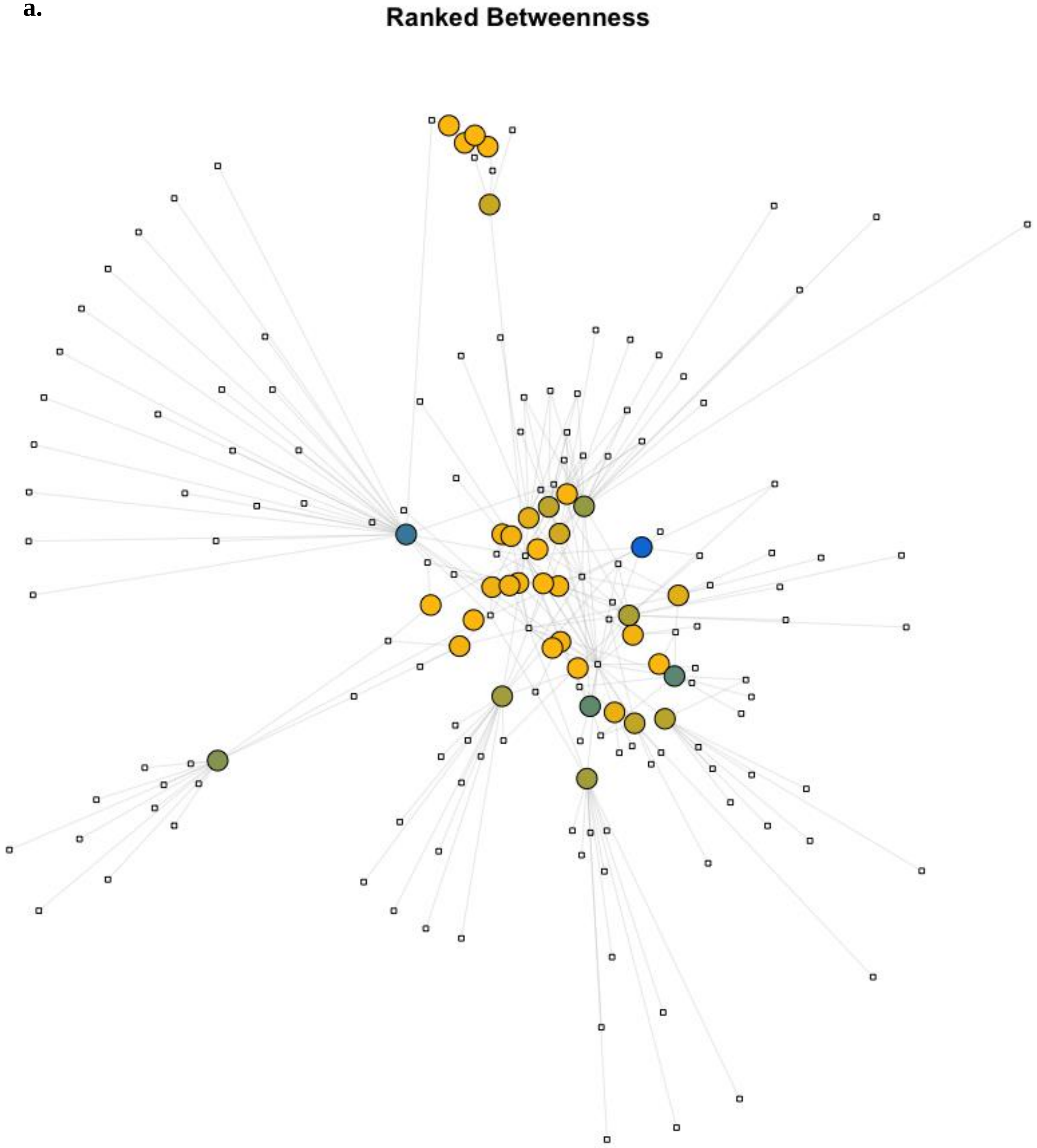
Results:

The initial database for this network, from Swain et al. (2021), consisted of 5,470 records of coral-Symbiodiniaceae phylotype associations in the Caribbean region. The database represented 32 coral hosts from 17 genera and 129 Symbiodiniaceae phylotypes from five clades. Six coral hosts and six phylotypes were added through association data collected from a further literature review and field samples. Total records of the database used for this analysis reached 5,539 records representing 38 coral hosts from 19 genera and 135 Symbiodiniaceae phylotypes from five clades (Supplemental T1). Additionally, new association records were added for three coral hosts for which sufficient data had already been included in the original dataset. Furthermore, metadata including transmission mode, sexual strategy, and reproductive system used by all 67 hermatypic corals in the Caribbean were included during literature search. Specific transmission mode for 62 corals, reproductive strategy for 64 corals, and sexual system for 53 corals were recorded (Supplemental T2).

Field samples were collected for eight coral hosts: *Agaricia fragilis* (Dana, 1846), *Agaricia tenuifolia* (Dana, 1846), *Eusmilia fastigiata* (Pallas, 1766), *Manicina areolata* (Linnaeus, 1758), *Mussa angulosa* (Pallas, 1766), *Mycetophyllia ferox* (Wells, 1973), *Porites divaricata* (Le Sueur, 1820), and *Siderastrea stellata* (Verrill, 1868). All ITS sequence reads were between 690–790 base pairs (bp) in length. ITS2 sequences were isolated from the complete ITS sequences using ITS2intfor2 and ITS2-reverse primers inputted into the primer alignment tool in BioEdit and resulted in sequence lengths between 190–250bp (Hall 1999, LaJeunesse 2002). BLAST (megablast) showed that all sequences collected from Belize contained the C1 phylotype with two exceptions: one sample of *Eusmilia fastigiata* associated with B1 and one sample of *Mycetophyllia ferox* contained phylotype C.2486705.



a.



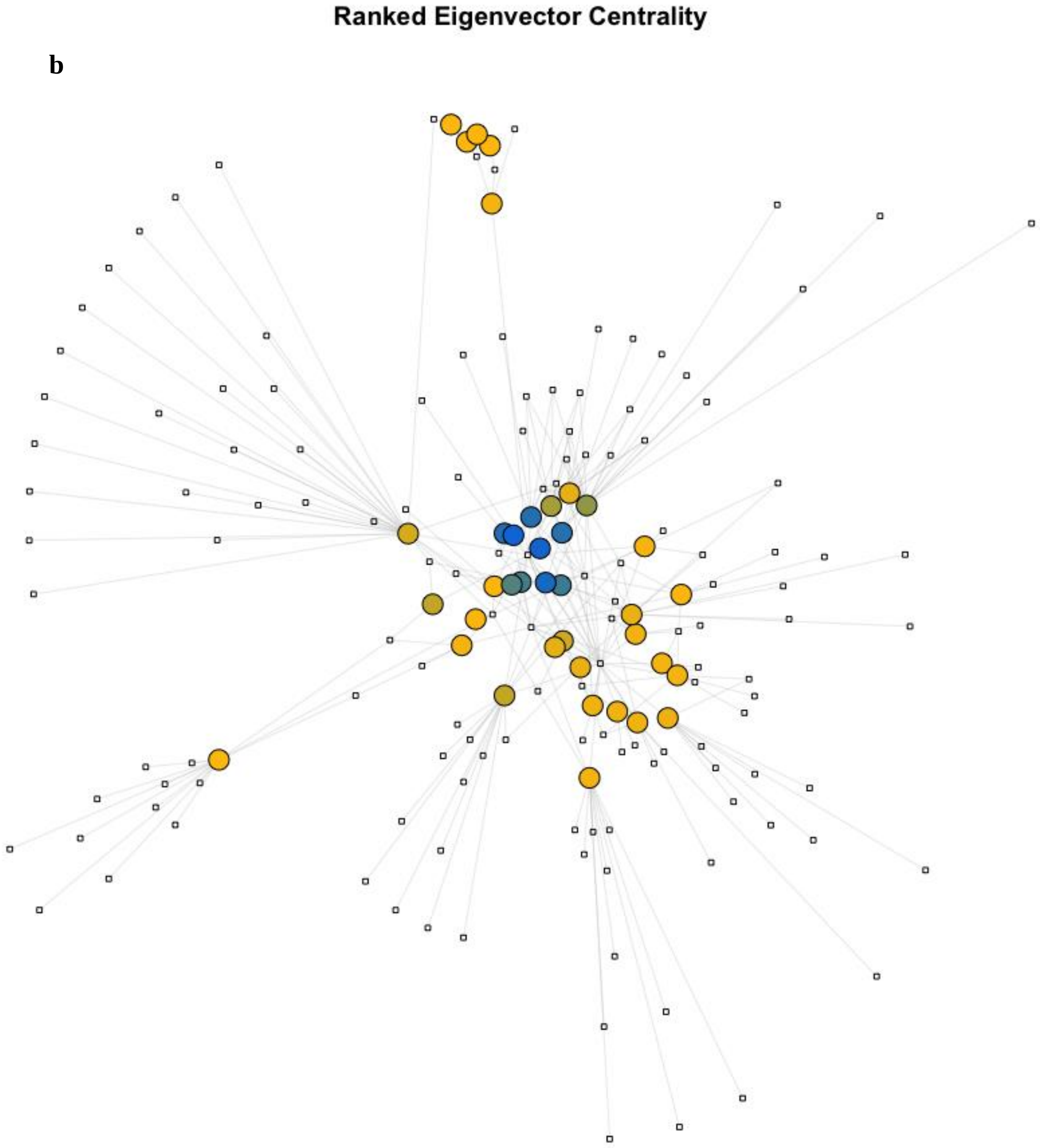
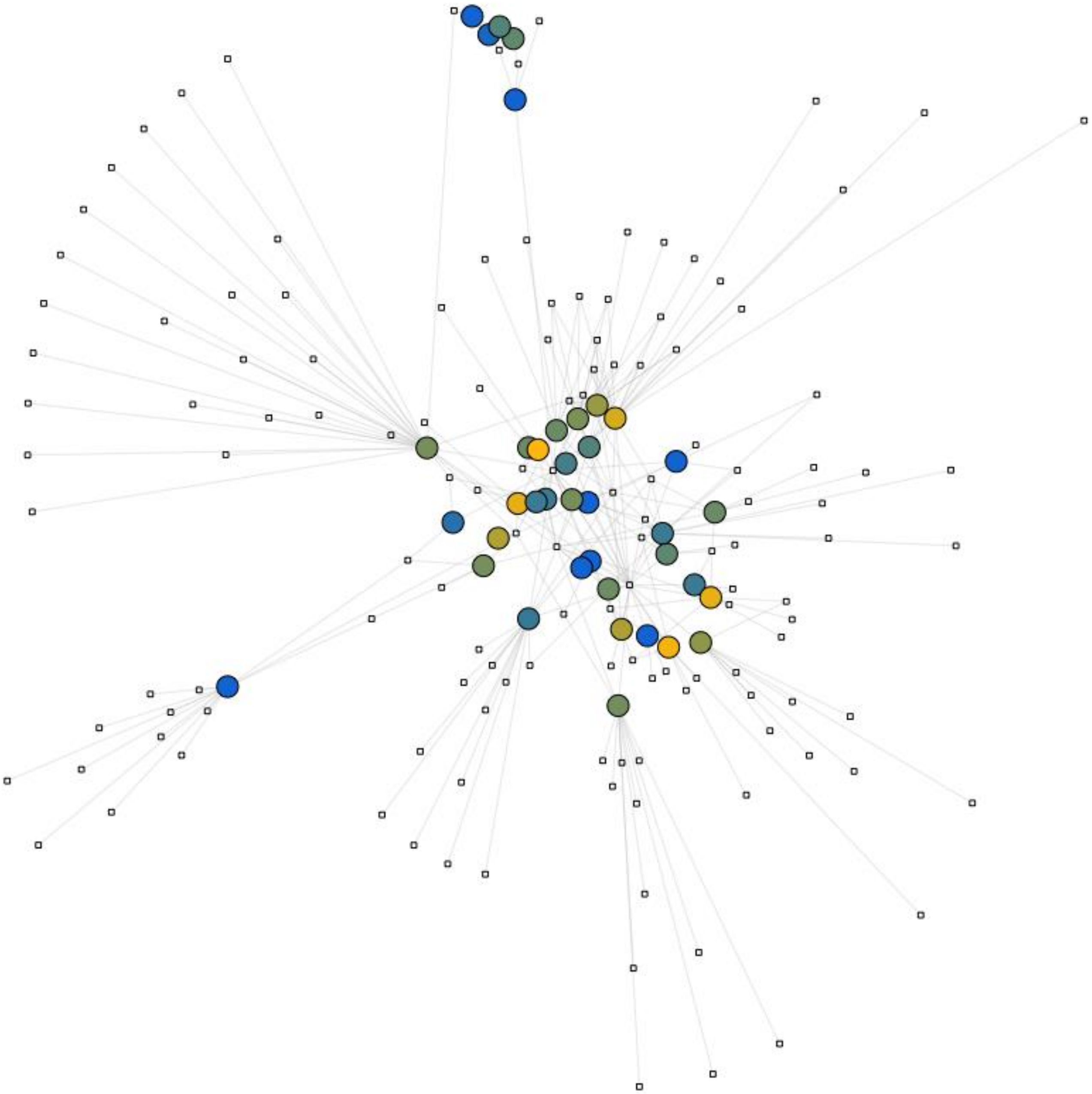


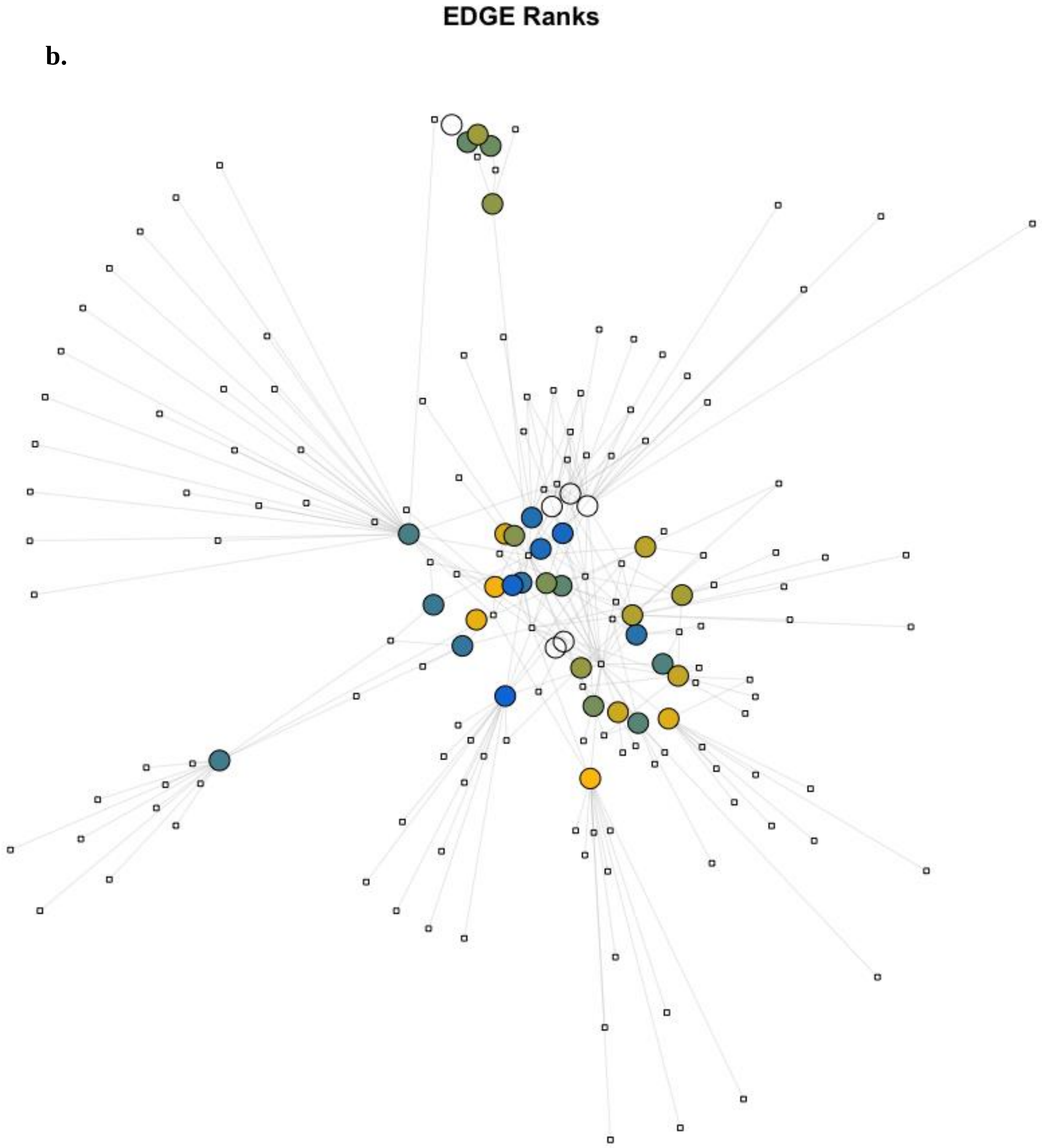
Figure 2: These networks visualize Caribbean network metrics for betweenness and eigenvector centrality. Plot a) indicates betweenness scores for coral hosts on a gradient color scale where blue represents the highest betweenness, yellow represents the lowest betweenness, and an intermediate between both ends of the gradient that produces a green color effect; b) indicates eigenvector centrality scores for coral hosts on a gradient color scale where blue represents the highest centrality, yellow represents the lowest centrality, and an intermediate between both ends of the gradient that produces a green color effect.

Ranked BRI

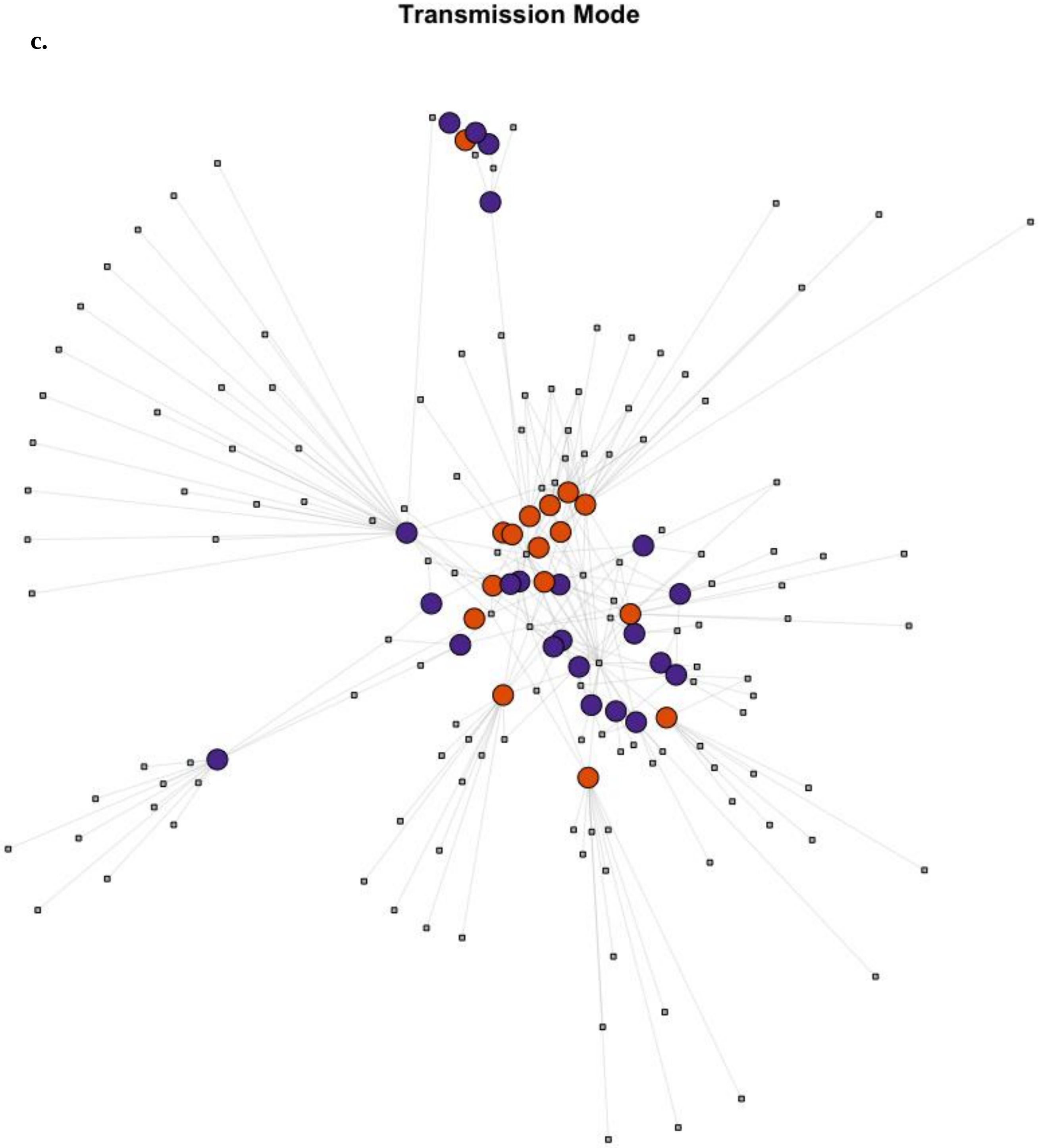
a.



b.



c.



d.

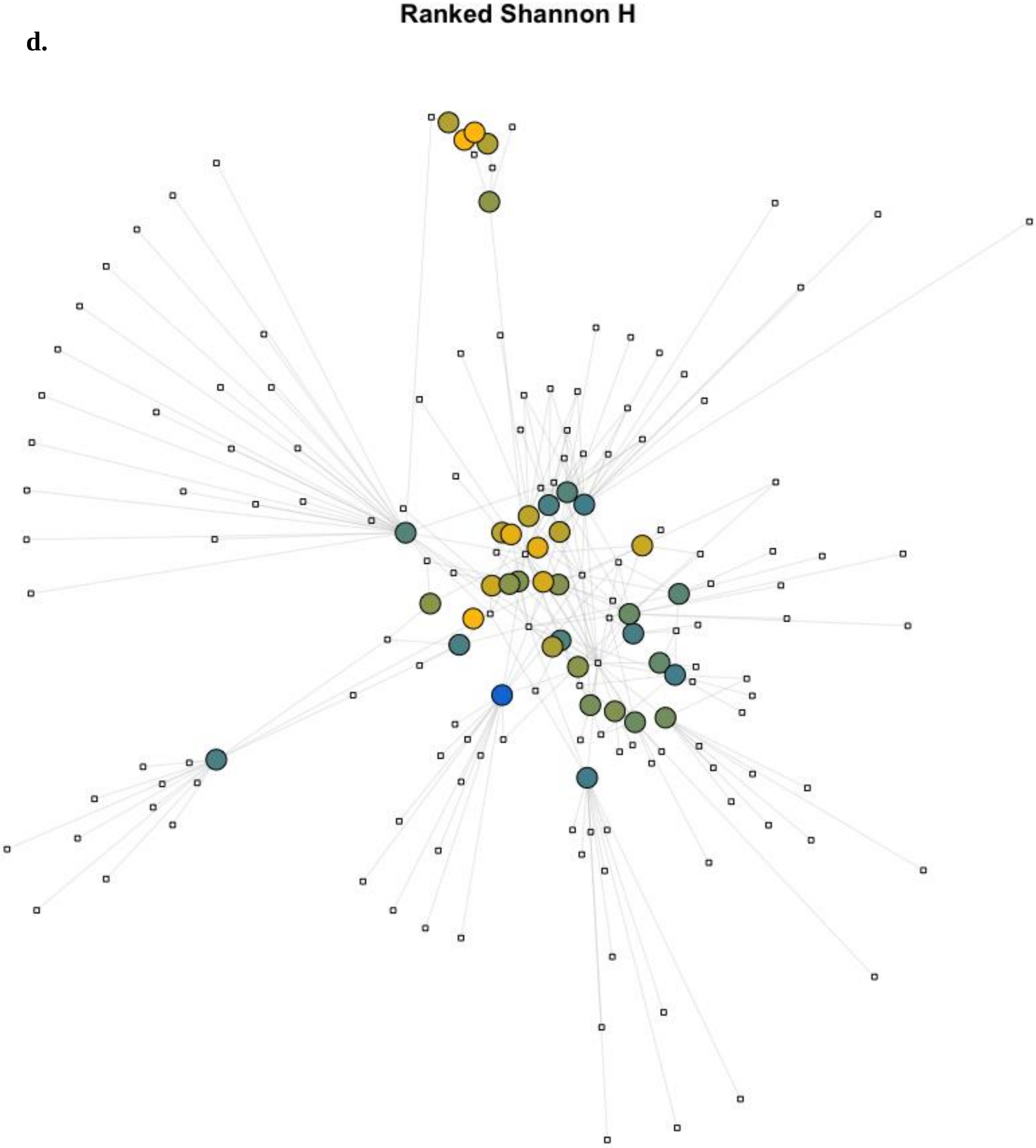


Figure 3: These plots represent metadata for coral host nodes: a) represents coral host BRI on a gradient color scale where blue represents corals with low BRI and yellow represents corals with high BRI that experience higher bleached tissue during bleaching events; b) EDGE ranks are plotted on a gradient where bluer nodes are less in need of conservation attention while yellow nodes are in greater need and white nodes are currently unranked or data deficient; c) visualizes transmission modes of coral hosts where purple indicates vertical transmission and orange indicates horizontal transmission of symbionts; d) plots the richness, based on the Shannon-Wiener H Index, of coral host associations with symbiont phylotypes.

Network plots enabled visualization of vital network parameters and ecologically and biologically relevant metadata. Nodes of interest for network betweenness (Figure 2a), which measures the number of times a node lies on the shortest path between other nodes, include: *Siderastrea radians* (Pallas 1766), *Siderastrea siderea* (Ellis & Solander, 1786), *Porites astreoides* (Lamarck, 1816), *Agaricia lamarcki* (Edwards & Haime, 1851), *Agaricia humilis* (Verrill, 1901), *Orbicella annularis* (Ellis & Solander, 1786), and *Colpophyllia natans* (Houttuyn, 1772). However, betweenness can have multiple interpretations in that a high betweenness value could indicate that a node holds authority over distinct clusters in a network, or just that they are on the periphery of one or more cluster. The following corals had high betweenness and were identified to be non-periphery, cluster-connecting nodes: *Siderastrea radians*, *Siderastrea siderea*, and *Orbicella annularis*. Nodes with high eigenvector centrality (Figure 2b), which measures a node's influence based on the number of links it has to other nodes in the network, and how well linked those other nodes are, include: *Manicina areolata* (Linnaeus, 1758), *Favia fragum* (Esper, 1793), *Meandrina meandrites* (Linnaeus, 1758), *Isophyllia sinuosa* (Ellis & Solander, 1786), *Diploria clivosa* (Ellis & Solander, 1786), *Diploria labyrinthiformis* (Linnaeus, 1758), *Diploria strigosa* (Dana 1846), *Eusmilia fastigiata*, and *Dichocoenia stokesii* (Milne-Edwards & Haime, 1849). Nodes with high BRI scores in the network (Figure 3a) include: *Acropora cervicornis* (Lamarck, 1816), *Acropora palmata* (Lamarck, 1816), *Eusmilia fastigiata*, *Orbicella annularis*, *Agaricia lamarcki*, *Agaricia agaricites* (Linnaeus, 1758), and *Agaricia humilis*. The nodes classified, according to EDGE scores (Figure 3b), as the most at risk and in need of conservation attention are, in order from most to least concern: *Stephanocoenia intersepta* (Esper, 1795), *Acropora cervicornis*, *Acropora palmata*, *Montastraea cavernosa* (Linnaeus, 1767), *Dichocoenia stokesii*, *Helioseris cucullata* (Ellis & Solander, 1786), and *Agaricia lamarcki*.

Combining corals with high values for betweenness and centrality that also have high BRI provides corals that are network critical and vulnerable to thermal stress. These corals included *Orbicella annularis* and *Eusmilia fastigiata*. Other coral hosts that were found to be both vulnerable based on BRI and deemed worthy of conservation attention, but were not network critical were: *Acropora cervicornis*, *Acropora palmata*, and *Agaricia lamarcki*. Alternatively, the most resilient corals, those with low BRI scores, that have the highest centrality scores for the network include: *Manicina areolata*, *Favia fragum*, *Meandrina meandrites*, *Isophylia sinuosa*, *Diploria clivosa*, *Diploria labyrinthiformis*, and *Diploria strigosa*. These corals are also considered lower priority in terms of EDGE ranking for conservation attention (figure 3b). *Siderastrea siderea* and *Siderastrea radians* were found to have high betweenness values and low BRI scores and are similarly not considered high conservation priority, nor were they considered central to the network. Finally, *Dichocoenia stokesii* had high eigenvector centrality, placed high in EDGE ranks, and is less sensitive to thermal stress with one of the lowest BRI values in the network.

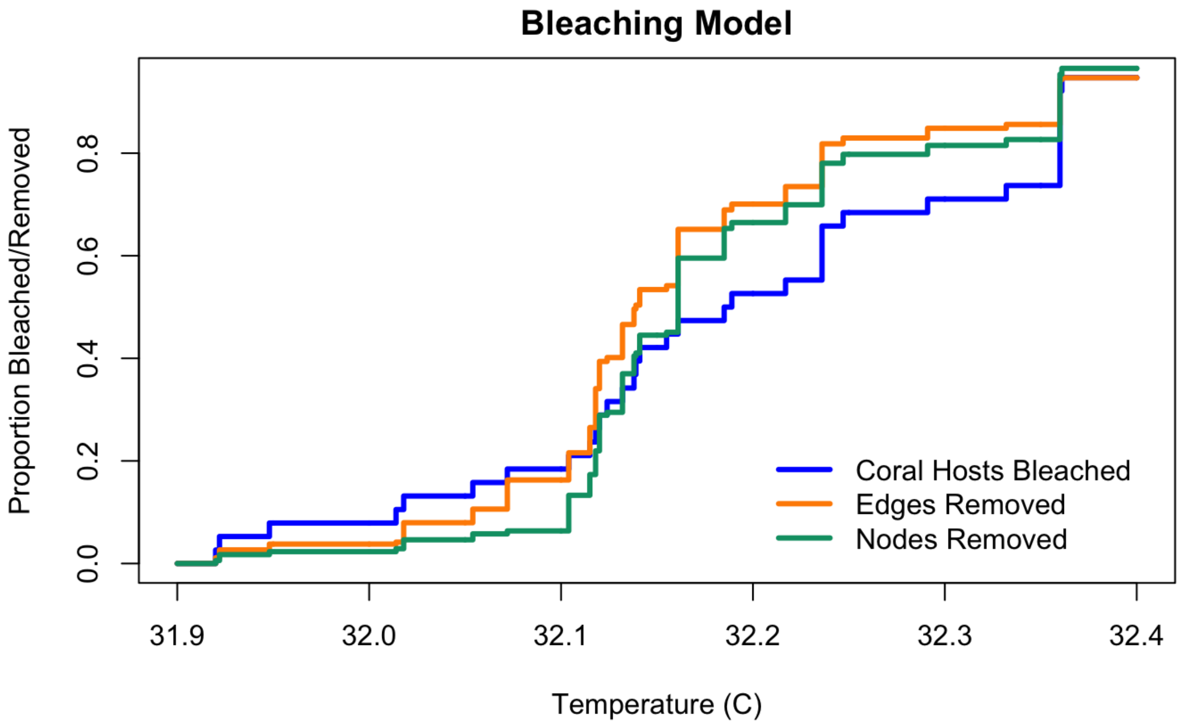


Figure 4: Bleaching model (equation 1) applied to the Caribbean network indicates bleaching starts at 31.9°C and affects 100% of corals at 32.37°C. The blue, orange, and green lines, respectively, tracks proportion coral hosts, edges, and nodes bleached or removed as temperature increases. The node category includes both coral hosts and symbiont phylotypes.

Resistance testing found it takes 0.115°C of temperature increase, after normalization due to model parameters, to go from 10% to 90% of corals bleached. This temperature increase occurs between 32°C and 32.4°C (figure 4). It is important to note that the temperature range is larger than the temperature required to meet resistance thresholds. This is explained by the need to normalize the resistance value by dividing by 3 to account for the upper thermal limit parameter,

T_Δ, from Williams (2020) bleaching model (equation 1). Robustness (R50) is calculated as a proportion where values closer to one indicate higher robustness. Robustness was found to be 0.65. This means 65% of combined nodes and edges were removed before 50% of the nodes in the network were removed.

Discussion:

The unique traits of coral species and Symbiodiniaceae phylotype combinations determine their vulnerability to thermal stress; therefore, the regional loss of coral species is potentially predictable. What is not yet predictable is how the loss of coral and their associated Symbiodiniaceae phylotypes will affect the remaining coral- Symbiodiniaceae symbiosis network. Loss of coral and/or phylotype nodes in the symbiosis network may destabilize the remaining links and further endanger species that are thought to be more resilient to climate change. The Caribbean network presented here provides a foundation for predicting how the loss of vulnerable Caribbean coral species will affect the stability of the network. We found *Orbicella annularis* and *Eusmilia fastigiata* to be network critical and vulnerable to the consequences of increasing severity and intensity of marine heatwaves. *Acropora cervicornis, Acropora palmata,* and *Agaricia lamarcki* were found to have poor tolerance to heat and but are not network-critical. *Manicina areolata, Favia fragum, Meandrina meandrites, Isophylia sinuosa, Diploria clivosa, Diploria labyrinthiformis,* and *Diploria strigosa* are the most connected corals and have the lowest bleaching response, thus are good candidates for maintaining a stable, heat-tolerant Caribbean coral network. *Dichocoenia stokesii* was found to be network critical, resistant to thermal stress, and in need of conservation attention. This combination makes *D. stokesii* an excellent candidate for smaller scale restoration efforts in the Caribbean to maximize resilience. Results of the bleaching model show that the Caribbean network increases from 10% to 90% coral hosts bleached within a narrow temperature range but remains relatively robust to bleaching. Additionally, *Madricis decactis* provided potential evidence of phylogenetic inertia among coral-symbiont associations. And finally, invasive symbiont phylotypes were found at the center of the network and could have potential to increase the resilience of the network at an uncertain physiological cost for coral hosts.

O. annularis and *E. fastigiata* were found to be network critical corals that should be given consideration in resilience-based management of Caribbean reefs despite their sensitivity to thermal stress. The following corals were identified as being network critical and vulnerable to the consequences of increasing severity and intensity of marine heatwaves: *Orbicella annularis* and *Eusmilia fastigiata*. These corals are relatively more vulnerable to thermal stress than the rest of the network and have high betweenness measures. This measure shows which nodes are "bridges" between nodes in a network. It does this by identifying all the shortest paths and then counting how many times each node falls on one of these shortest paths. Loss of these "bridge" corals would more likely result in schisms in the network than if another, lower ranked coral was to be lost. *Eusmilia fastigiata* is currently listed as "Least Concern" by the IUCN while *Orbicella annularis* is considered "endangered". It is important to note that these population statuses from the IUCN have not been updated since 2008 and would likely have changed dramatically considering the multiple large and small-scale bleaching events that have occurred in the Caribbean since 2008 (Eakin *et al.* 2019, Claar 2020). The unique combination of *O. annularis* and *E. fastigiata* as "bridge" corals that are also sensitive to thermal stress provides a dilemma for restoration priority. These coral populations are already depleted and are unlikely to survive the looming threat of marine heatwaves. However, as "bridge" corals they are considered important for network stability. While not the ideal targets for resilience-based restoration, *O. annularis* and *E. fastigiata* would be worth protecting as network critical corals.

Acropora cervicornis, Acropora palmata, and *Agaricia lamarcki* were found to have poor tolerance to heat and but are not network-critical. Coral with low tolerance to thermal stress in the Caribbean network reduce overall resistance to bleaching. These corals are valuable for maintaining diversity but may not be the most stable based on the network parameters measured here. The following coral were identified as having poor tolerance to heat and were also not found to be network-critical: *Acropora cervicornis, Acropora palmata,* and *Agaricia lamarcki.* These corals are more likely to face increased mortality as the Caribbean warms and marine heatwaves become more frequent and severe making them non-ideal targets for resilience-based restoration (Bove et al. 2022).

Manicina areolata, Favia fragum, Meandrina meandrites, Isophylia sinuosa, Diploria clivosa, Diploria labyrinthiformis, and *Diploria strigosa* are the most connected corals and have the lowest bleaching response, thus are good candidates for maintaining a stable, heat-tolerant Caribbean coral network. Corals that are centrally located, measured by eigenvector centrality are the most connected corals whose connections are also highly connected, loss of these corals would disrupt network structure and are more likely to create separate networks if lost. All corals, except for one which will be discussed later, with the highest centrality scores also have the lowest bleaching response: *Manicina areolata, Favia fragum, Meandrina meandrites, Isophylia sinuosa, Diploria clivosa, Diploria labyrinthiformis,* and *Diploria strigosa* all fit this category. These corals are network-critical and most resilient to thermal stress. Therefore, these corals are good candidates for maintaining a stable, heat-tolerant Caribbean coral network. Additionally, *Siderastrea siderea* and *Siderastrea radians* were found to have high betweenness scores and low BRI scores and would also be valuable in maintaining a stable network that is resilient to thermal stress. Finally, there was one network critical coral with high heat-tolerance and presently low conservation attention. *Dichocoenia stokesii* had high eigenvector centrality, placed high in EDGE ranks, and is less sensitive to thermal stress with one of the lowest BRI values in the network. This coral species requires increased attention and would serve well as a target for restoration projects. *D. stokesii* forms stable connection with symbionts that are shared throughout the network and is capable of withstanding thermal stress.

The Caribbean network increases from 10% to 90% coral hosts bleached within a narrow temperature range but remains relatively robust to bleaching. The bleaching model applied here provided metrics for resistance and robustness. Resistance measures the temperature range in which bleaching overtakes the coral network. Beyond 32°C, the Caribbean network is expected to rapidly bleach. This would require marine heatwaves to sustain temperatures in excess of 2°C above the Caribbean average mean monthly maximum, 30.02°C, in order for 90% of corals hosts to bleach. Corals that are not adapted to handle heat stress through individual characteristics or association with thermotolerant symbionts will likely be lost to predicted global climate change under climate change scenarios. RCP 8.5, inaccurately referred to as a "business as usual" model, is increasingly unlikely to occur and recent analysis of Caribbean warming predicts temperature rise closer to that in the RCP 4.5 model (Hausfather and Peters 2020, Bove et al. 2022). Under

RCP 4.5, global temperature is likely to increase 2-3°C by 2100. Sea surface temperatures will increase with global temperatures in the Caribbean by ~1.5°C on average by 2100 (Bove et al. 2022). This increase will not immediately cause corals to bleach in the Caribbean but will significantly reduce the heat required to initiate bleaching (Figure 4). As marine heatwaves trend to be more frequent and severe, the threshold for breaking the Caribbean coral network's resistance to bleaching will be more commonly surpassed. The toll of bleaching on coral mortality and growth will likely result in continued loss of coral cover in the Caribbean despite the robust nature of the network. However, the robustness of the network does provide hope that even as less thermotolerant corals bleach, the network has a chance of maintaining some stable connections between thermal tolerant hosts and symbionts.

Madricis decactis provides potential evidence of phylogenetic inertia among coral-symbiont associations (Figure 5). All other *Madracis* corals in the Caribbean utilize vertical transmission where symbionts are passed down from parents to offspring within coral propagules. However, *M. decactis* can acquire symbionts from the environment through a process known as horizontal transmission. Although *M. decactis* can acquire symbionts outside of the few symbionts typically associated with other *Madracis* corals (mostly clade B), *M. decactis* associates with the same symbiont types as others in its genus. This may be evidence of phylogenetic inertia. This refers to the limitations on evolutionary pathways imposed by previous adaptations (Huber 1939). While *M. decactis* acquires symbionts from the environment it most likely is constrained in acquiring the same symbionts with which the rest of the genus have evolved to use.

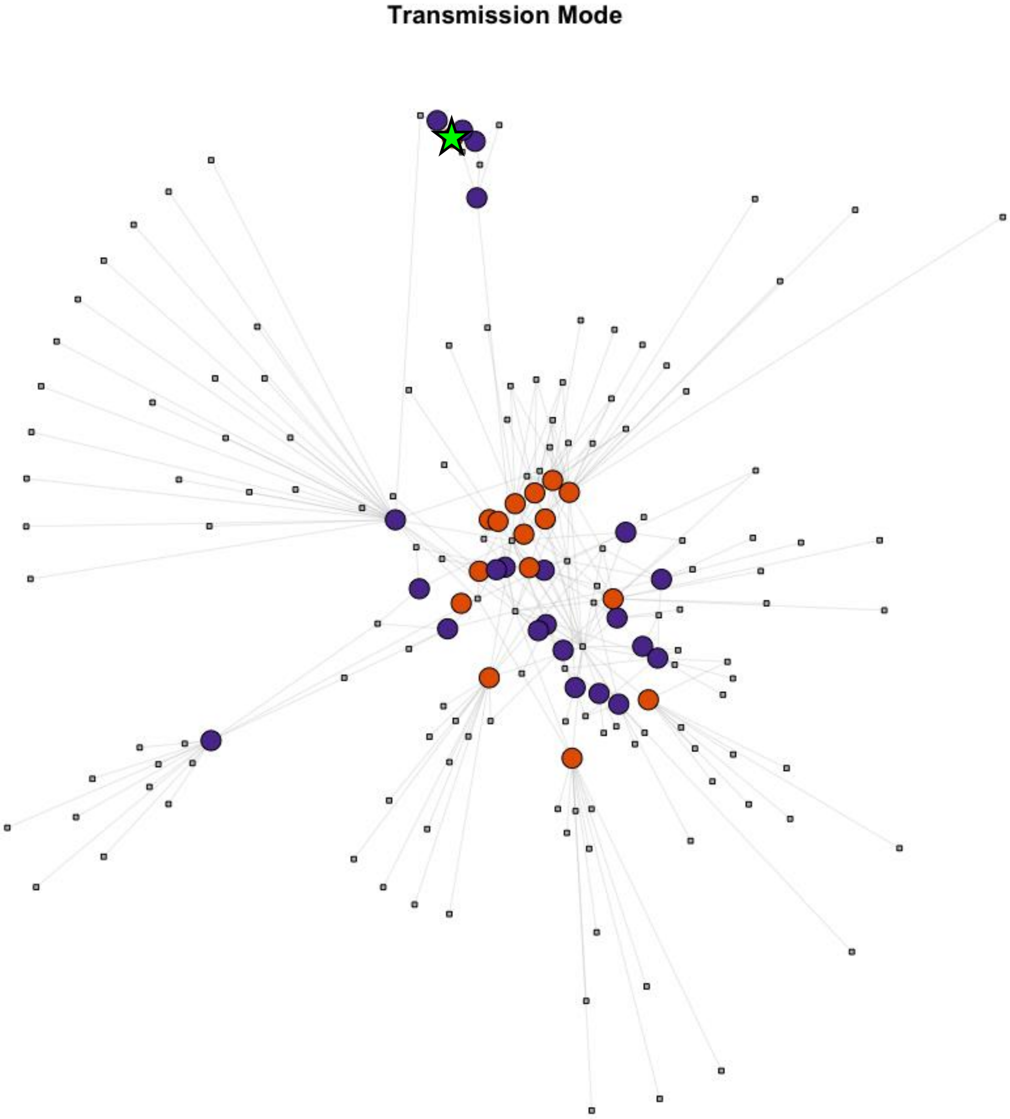


Figure 5: Transmission mode network with *Madracis decactis* labeled with a green star.

Invasive phylotypes, D1 and D1-4, were found at the center of the Caribbean network indicating their strong association with Caribbean hermatypic corals with added potential for increasing resilience to bleaching (Figure 6, Pettay et al., 2015). These phylotypes are both centrally located and form a hub of connected Caribbean corals without discrimination for phylogenetic relatedness, transmission mode, or geographic location. D1 and D1-4, now referred to as *Durusdinium trenchii* (LaJeunesse et al. 2014), are Indo-Pacific endosymbionts that are resistant to bleaching and present a biological issue for host corals. *D. trenchii* provides less nutrients and results in decreased growth and calcification rates in host corals (Pettay et al. 2015). Long term impacts of this includes decreased calcification rates across the region and decreased reef building. It was proposed that corals with flexible associations may have an ecological advantage by being able to acquire resistant symbiont types from the environment following bleaching events in a concept described as the ‘Adaptive Bleaching Hypothesis’ (Buddemeier and Fautin 1993). While it is unclear if thermally tolerant symbiont phylotypes like D1-4 are acquired from the environment after bleaching or if they were already present in low abundances and simply filled a vacant niche, there is evidence that symbiont community composition does change after bleaching (Kemp et al., 2014, Silverstein et al., 2014). While this has potential to benefit corals and the network by becoming more resilient through acquisition of resilient symbionts like *D. trenchii*, there would likely be physiological trade-offs that diminish coral functional performance (Pettay et al. 2015). However, there is some evidence to support that at higher ocean temperatures, this trade-off is eliminated and D. trenchii can enhance coral survival at little to no cost to the host (Cunning et al. 2015). There remains a need to better understand the ecological consequences of microbial invasions in Caribbean coral reefs.

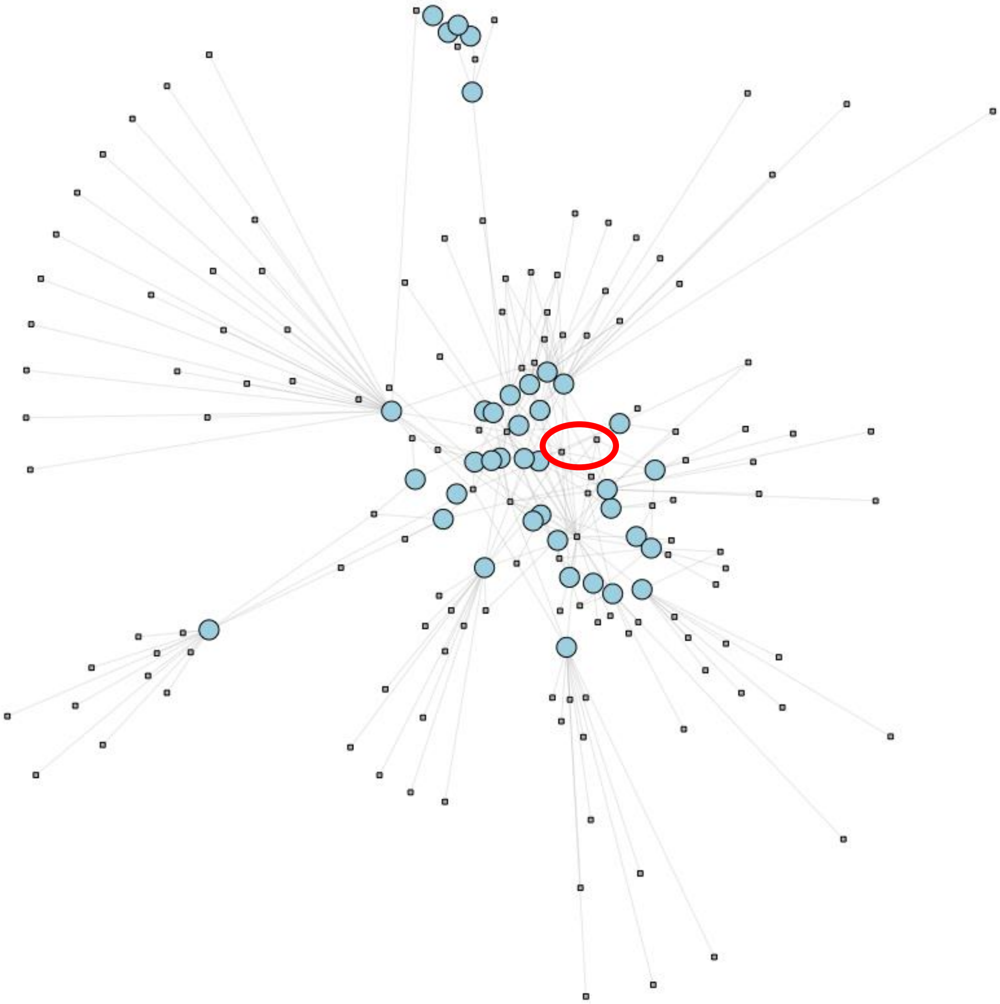


Figure 6: Caribbean network with Symbiodiniaceae phylotype D1 (left) and D1-4 (right) encased in a red oval.

This paper provides a referenced list of hermatypic corals with recorded distributions in the Caribbean as well as coral-Symbiodiniaceae phylotype association data for four corals which had no previous records. The resilient, network stabilizing corals identified in this study should be the focus of continued restoration effort in the Caribbean. Creating resilient coral reefs will help to future-proof Caribbean reefs and protect the economic, cultural, and biological value they provide. However, network measures alone are not enough to validate a coral host's value to the ecosystems, and it should be noted that inclusion of functional traits would improve the network. It is also important to note that while only 38 of the 67 known hermatypic corals were included in this analysis that distribution and population data for corals in the Caribbean is lacking. Most distribution records of corals found to create the complete list date back to the early or mid 2000s and IUCN population data hasn’t been published since 2008. There are likely fewer than 67 hermatypic corals with populations of ecological importance. There is also considerable noise involved with using ITS2 phylotypes of symbionts. These are not species level distinctions and true coral-host associations can be under or overestimated depending on the taxonomic classification used for Symbiodiniaceae phylotypes. Additionally, association data for unrepresented corals as well as functional traits for all corals in the Caribbean would greatly improve this analysis and provide a complete tool for determining network critical corals worthy of conservation attention.

References:

Albert, R., Jeong, H., & Barabási, A.-L. (2000) Error and attack tolerance of complex networks. *Nature* 406:378–382. https://arxiv.org/pdf/cond-mat/0008064.pdf

Allesina, S., & Pascual, M. (2008) Network structure, predator–prey modules, and stability in large food webs. *Theoretical Ecology* 1**,** 55–64. https://doi.org/10.1007/s12080-007-0007-8

Beck M.W., Losada I.J., Menéndez P., Reguero B.G., Díaz-Simal P., & Fernández F. (2018) The global flood protection savings provided by coral reefs. *Nature Communications,* 9, 2186. https://doi.org/10.1038/s41467-018-04568-z

Boström-Einarsson L., Babcock R.C., Bayraktarov E., Ceccarelli D., Cook N., Ferse S.C.A., Hancock, B., Harrison, P., Hein, M., Shaver, E., Smith, A., Suggett, D., Stewart-Sinclair, P.J., Vardi, T., & McLeod, I.M. (2020) Coral restoration – A systematic review of current methods, successes, failures and future directions. *PLoS ONE,* 15(1): e0226631.https://doi.org/10.1371/journal.pone.0226631

Bove CB, Mudge L, Bruno JF (2022) A century of warming on Caribbean reefs. *PLOS Climate* 1(3): e0000002. https://doi.org/10.1371/journal.pclm.0000002

Buddemeier RW, Fautin DG. (1993) Coral bleaching as an adaptive mechanism. *Bioscience*. 1993; 43:320–326. https://doi.org/10.2307/1312064

Buerger P et al (2020) Heat-evolved microalgal symbionts increase coral bleaching tolerance. *Science Advances* 6: eaba2498 https://doi.org/10.1126/sciadv.aba2498

C. Linardich, G. Ralph, K. Carpenter, N. Cox, D.R. Robertson, H. Harwell, A. Acero P., W. Anderson Jr., F. Barthelat, J.-L. Bouchereau, J. J. Brown, J. Buchanan, D. Buddo, B. Collette, M. Comeros-Raynal, M. Craig, M. Curtis, T. Defex, J. Dooley, W. Driggers III, C. Elfes Livsey, T. Fraser, R. Gilmore Jr., L. Grijalba Bendeck, A. Hines, R. Kishore, K. Lindeman, J.-P. Maréchal, J. McEachran, R. McManus, J. Moore, T. Munroe, H. Oxenford, F. Pezold, F. Pina Amargós, A. Polanco Fernandez, B. Polidoro, C. Pollock, R. Robins, B. Russell, C. Sayer, S. Singh-Renton, W. Smith-Vaniz, L. Tornabene, J. Van Tassell, J.-C. Vié, and J. T. Williams (2017). *The Conservation Status of Marine Bony Shorefishes of the Greater Caribbean*. Gland, Switzerland: IUCN. viii + 75 pp. http://dx.doi.org/10.2305/IUCN.CH.2017.RA.1.en

Claar, D.C., Starko, S., Tietjen, K.L., Epstein, H.E., Cunning, R., Cobb, K.M., Baker, A., Gates, R.B., & Baum, J.K. (2020) Dynamic symbioses reveal pathways to coral survival through prolonged heatwaves. *Nature Communication* 11**,** 6097. https://doi.org/10.1038/s41467-020-19169-y

Coles, S.L., and Fadlallah, Y.H. (1991). Reef coral survival and mortality at low temperatures in the Arabian Gulf: new species-specific lower temperature limits. *Coral Reefs* 9:231-237 https://doi.org/10.1007/BF00290427

Costanza R, de Groot R, Sutton P, van der Ploeg S, Anderson SJ, Kubiszewski I, Farber S, & Turner RK. (2014) Changes in the global value of ecosystem services. *Global Environmental Change* 26, p152-158. https://doi.org/10.1016/j.gloenvcha.2014.04.002

Csárdi, G., & Nepusz, T. (2006) The igraph software package for complex net- work research. *International Journal Complex Systems* 1695:1–9. Version 1.2.8. https://cran.r-project.org/web/packages/igraph/index.html

Cunning, R., Gillette, P., Capo, T. Galvez, K., Baker, A.C. (2015) Growth tradeoffs associated with thermotolerant symbionts in the coral *Pocillopora damicornis* are lost in warmer oceans. *Coral Reefs* **34**, 155–160. https://doi.org/10.1007/s00338-014-1216-4

Dana, J.D. (1846-1849). Zoophytes. United States Exploring Expedition during the years 1838-1842. *Lea and Blanchard, Philadelphia.* 7: 1-740, 61

Dinerstein, E., Olson, D. M., Graham, D. J., et al. (1995) A Conservation Assessment of the Terrestrial Ecoregions of Latin America and the Caribbean. World Bank, Washington DC. https://doi.org/10.1596/0-8213-3295-3

Donner, S. D., Skirving, W. J., Little, C. M., Oppenheimer, M., & Hoegh-Guldberg, O. (2005) Global assessment of coral bleaching and required rates of adaptation under climate change. *Global Change Biology* 11:2251–2265. https://doi.org/10.1111/j.1365-2486.2005.01073.x

Dunne, J. A., & Williams, R. J. (2009) Cascading extinctions and community collapse in model food webs. *Philosophical Transactions of the Royal Society B* 364:1711–1723. https://doi.org/10.1098/rstb.2008.0219

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

Eakin, C. M., Sweatman, H. P. A. & Brainard, R. E. (2019) The 2014–2017 global-scale coral bleaching event: insights and impacts. *Coral Reefs* 38, 539–545. https://doi.org/10.1007/s00338-019-01844-2

Ellis, J., Solander, D. (1786). The Natural History of many curious and uncommon Zoophytes, collected from various parts of the Globe. Systematically arranged and described by the late Daniel Solander. 4. *Benjamin White & Son: London*. 1-206, pls 1-63.

Esper, E.J.C. (1788-1830). Die Pflanzenthiere in Abbildungen nach der Natur mit Farben erleuchtet nebst Beschreibungen. Raspischen Buchhandlung, Nuremberg. 3 vols text, 2 vols pls.

Fang, L., Liao, C.W., and Lin, M.C. (1995). Pigment composition in different-colored scleractinian corals before and during the bleaching process. Zoological Studies 34:10-17

Fisher R., O'Leary R.A., Low-Choy S., Mengersen K., Knowlton N., Brainard R.E., & Caley M.J. (2015) Species richness on coral reefs and the pursuit of convergent global estimates. *Current Biology* 25, p500-505. https://doi.org/10.1016/j.cub.2014.12.022

Fitt, W. K., Brown, B. E., Warner, M. E., & Dunne, R. P. (2001) Coral bleaching: interpretation of thermal tolerance limits and thermal thresholds in tropical corals. *Coral Reefs* 20:51–65. https://doi.org/10.1007/s003380100146

Forsman Z.H., Page C.A., Toonen R.J., Vaughan D. (2015) Growing coral larger and faster: micro-colony-fusion as a strategy for accelerating coral cover. *PeerJ* 3:e1313 https://doi.org/10.7717/peerj.1313

Freudenthal HD (1962) Symbiodinium gen. nov. and Symbiodinium microadriaticum sp. nov., a zooxanthella: taxonomy, life cycle, and morphology. *Journal of Eukaryotic Microbiology* 9: 45-52. https://doi.org/10.1111/j.1550-7408.1962.tb02579.x

GCRMN, ICRI, AIMS, and UNEP (2020) Status of Coral Reefs of the World 2020. https://www.unep.org/resources/status-coral-reefs-world-2020

Glynn PW, Maté JL, Baker AC, Calderón M (2001) Coral bleaching and mortality in Panama and Ecuador during the 1997–1998 El Niño-Southern Oscillation event: spatial/temporal patterns and comparisons with the 1982–1983 event. *Bulletin of Marine Science* 69:79–109

Glynn, P.W. (1993). Coral-reef bleaching: Ecological perspectives. *Coral Reefs* 12:1-17. https://doi.org/10.1007/BF00303779

Goreau, T.F. (1963) Calcium carbonate deposition by coralline algae and corals in relation to their roles as reef-builders. *Annals of the New York Academy of Sciences.* May 31;109:127-67. https://doi.org/10.1111/j.1749-6632.1963.tb13465.x

Goreau, T.F. (1964). Mass expulsion of zooxanthellae from Jamaican reef communities after hurricane Flora. Science 145:383-386

Hall, T. A. (1999). BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. In *Nucleic acids symposium series* (Vol. 41, No. 41, pp. 95-98). [London]: Information Retrieval Ltd., c1979-c2000.

Hausfather, Z., & Peters, G. P. (2020). Emissions–the 'business as usual' story is misleading. *Nature* 577: 618-620. https://www.nature.com/articles/d41586-020-00177-3

Hennige S, Suggett D, Warner M, McDougall K, Smith D (2009) Photobiology of Symbiodinium revisited: bio-physical and bio-optical signatures. *Coral Reefs* 28: 179-195. https://doi.org/10.1007/s00338-008-0444-x

Heron, S. F., Maynard, J. A., van Hooidonk, R. & Eakin, C. M. (2016) Warming Trends and Bleaching Stress of the World's Coral Reefs 1985–2012. *Scientific Reports,* 6, Article #38402. https://doi.org/10.1038/srep38402

Hoegh-Guldberg, O., and Smith, G.J. (1989). The effect of sudden changes in temperature, light and salinity on the population density and export of zooxanthellae from the reef corals Stylophora pistillata Esper and Seriatopora hystrix Dana. *Journal of Experimental Marine Biology and Ecology* 129:279-304. https://doi.org/10.1016/0022-0981(89)90109-3

Hoegh-Guldberg, O., Poloczanska, E.S., Skirving W., Dove S. (2017) Coral Reef Ecosystems under Climate Change and Ocean Acidification. *Frontiers in Marine Science*. https://doi.org/10.3389/fmars.2017.0015

Houttuyn, M. (1772). Natuurlyke historie of uitvoerige beschryving der dieren, planten en mineralen, volgens het samenstel van den heer Linnaeus met naauwkeurige afbeelingen. *F. Houttuyn, Amsterdam.* 1 (17) 1-6, 1-614.

Huber, B (1939). "Siebrohrensystem unserer Baume und seine jahreszeitlichen Veranderungen". Jahrbücher für Wissenschaftliche Botanik. 88: 176–242.

Hume, B.C.C., Smith, E.G., Ziegler, M., Warrington, H.J.M., Burt, J.A., LaJeunesse, T.C., Wiedenmann, J., & Voolstra, C.R. (2019) SymPortal: a novel analytical framework and platform for coral algal symbiont next-generation sequencing ITS2 profiling. *Molecular Ecology Resources* 19:1063–1080. https://doi.org/10.1111/1755-0998.13004

Iglesias-Prieto R, Trench R (1994) Acclimation and adaptation to irradiance in symbiotic dinoflagellates. I. Responses of the photosynthetic unit to changes in photon flux density. *Marine Ecology Progress Series* 113: 163-175. https://doi.org/10.3354/meps113163

Jackson J.B.C., Donovan M.K., Cramer K.L., & Lam V.V. (2014) Status and Trends of Caribbean Coral Reefs: 1970-2012. *Global Coral Reef Monitoring Network, IUCN, Gland, Switzerland.* https://www.iucn.org/content/status-and-trends-caribbean-coral-reefs-1970-2012

Johnson, M.E., Lustic, C., Bartels, E., Baums, I., Gilliam, D., Larson, L., Lirman, D., Miller, M., Nedimyer, K., & Schopmeyer, S. (2011). Caribbean Acropora Restoration Guide: Best Practices for Propagation and Population Enhancement. *NSU Works, 1-64.* https://nsuworks.nova.edu/occ_facreports/71

Jokiel, P. L., & Coles, S. L. (1990) Response of Hawaiian and other Indo-Pacific reef corals to elevated temperature. *Coral Reefs* 8:155–162. https://doi.org/10.1007/BF00265006

Jones, N.P., Ruzicka, R.R., Colella, M.A. Pratchett, M.S., Gilliam, D.S. (2022) Frequent disturbances and chronic pressures constrain stony coral recovery on Florida’s Coral Reef. *Coral Reefs*. https://doi.org/10.1007/s00338-022-02313-z

Karunanathie, H, Kee, P.S., Ng, S.F. Kennedy, M.A., Wee Chua, E. (2022) PCR enhancers: Types, mechanisms, and applications in long-range PCR. *Biochimie*, Volume 197, Pages 130-143, ISSN 0300-9084, https://doi.org/10.1016/j.biochi.2022.02.009

Kemp D.W., Hernandez-Pech X., Iglesias-Prieto R., Fitt W.K., Schmidt G.W. (2014) Community dynamics and physiology of *Symbiodinium* spp. before, during, and after a coral beaching event. *Limnology and Oceanography*, **59**, 788–797. https://doi.org/10.4319/lo.2014.59.3.0788

Kench, P.S., Beetham, E.P., Turner, T., Morgan, K.M., Owen, S.D., and McLean, R.F. (2022) Sustained coral reef growth in the critical wave dissipation zone of a Maldivian atoll. *Communications Earth and Environment.* 3, 9 https://doi.org/10.1038/s43247-021-00338-w

Kinzie, R.A. III (1993). Effects of ambient levels of solar ultraviolet radiation on zooxanthellae and photosynthesis of the reef coral Montipora verrucosa. *Marine Biology* 116:319-327. https://doi.org/10.1007/BF00350022

Koumosu, A., Murase, K., Yoshida, A., Maruyama, H., Kikuchi, T. (2019) Improved 18s and 28s rDNA primer sets for NGS-based parasite detection. *Scientific Reports*, 9, 15789. https://doi.org/10.1038/s41598-019-52422-z

LaJeunesse T.C. (2002) Diversity and community structure of symbiotic dinoflagellates from Caribbean coral reefs. *Marine Biology*, 141, 387–400. https://doi-org.ezproxylocal.library.nova.edu/10.1007/s00227-002-0829-2

LaJeunesse T.C., & Trench R.K. (2000) Biogeography of two species of Symbiodinium (Freudenthal) inhabiting the intertidal sea anemone Anthopleura elegantissima (Brandt). *Biological Bulletin*, 199, 126–134. https://doi.org/10.2307/1542872

LaJeunesse, T. C.; Wham, D. C.; Pettay, D. T.; Parkinson, J. E.; Keshavmurthy, S.; Chen, C. A. (2014). Ecologically differentiated stress-tolerant endosymbionts in the dinoflagellate genus Symbiodinium(Dinophyceae) Clade D are different species. *Phycologia.* 53(4): 305-319. https://doi.org/10.2216/13-186.1

LaJeunesse, T.C. (2001) Investigating the biodiversity, ecology, and phylogeny of endosymbiotic dinoflagellates in the genus symbiodinium using the ITS region: in search of a “species” level marker. *Journal of Phycology*. 37: 866-880. https://doi.org/10.1046/j.1529-8817.2001.01031.x

LaJeunesse, T.C., Loh ,W.K.W., Van Woesik, R., Hoegh-Guldberg, O., Schmidt, G.W., & Fitt, W.K. (2003) Low symbiont diversity in southern Great Barrier Reef corals, relative to those of the Caribbean. *Limnology and Oceanography*, 48, 2046–2054. https://doi-org.ezproxylocal.library.nova.edu/10.4319/lo.2003.48.5.2046

LaJeunesse, T.C., Parkinson, J.E., Gabrielson, P.W., Jeong, H.J., Reimer, J.D., Voolstra, C.R., Santos, S.R. (2018) Systematic revision of symbiodiniaceae highlights the antiquity and diversity of coral endosymbionts. *Current Biology*, 28, pp. 2570-2580. https://doi.org/10.1016/j.cub.2018.07.008

LaJeunesse, T.C., Reyes Bonilla, H., Warner, M.E., Wills, M., Schmidt, G.W., & Fitt, W.K. (2008) Specificity and stability in high latitude eastern Pacific coral-algal symbioses.

Limnology and Oceanography, 53(2), p.719-727. https://doi-org.ezproxylocal.library.nova.edu/10.4319/lo.2008.53.2.0719

Lamarck, J.-B. M. de. (1816). Histoire naturelle des animaux sans vertèbres. Tome second. Paris: Verdière, 568 pp.

Le Sueur, C.A. (1820). Description de plusiers animaux appartenant aux polypiers lamellifères de M. le Chev. Lamarck. *Mémoires du Muséum d'Histoire Naturelle.* 7: 271-298, pls. 15-17.

Lesser, M.P., Stochaj, W.R., Tapley, D.W., and Shick, J.M. (1990). Bleaching in coral reef anthozoans: effects of irradiance, ultraviolet radiation, and temperature on the activities of protective enzymes against active oxygen. *Coral Reefs* 8:225-232. https://doi.org/10.1007/BF00265015

Linnaeus, C. (1758). Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. *Editio decima, reformata [10th revised edition], vol. 1: 824 pp. Laurentius Salvius: Holmiae*

Linnaeus, C. (1767). Systema naturae per regna tria naturae: secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Ed. 12. 1., Regnum Animale. 1 & 2. *Holmiae [Stockholm], Laurentii Salvii.* pp. 1-532 [1766] pp. 533-1327 [1767].

Loh, W.K.W., Loi, T., Carter, D., & Hoegh-Guldberg, O. (2001) Genetic variability of the symbiotic dinoflagellates from the wide-ranging coral species Seriatopora hystrix and Acropora longicyathus in the Indo-West Pacific. *Marine Ecology Progress Series*, 222, 97–107. https://doi.org/10.3354/meps222097

Lough, J. M., Anderson, K. D. & Hughes, T. P. (2018) Increasing thermal stress for tropical coral reefs: 1871-2017. *Scientific Reports* 8, 6079. https://doi.org/10.1038/s41598-018-24530-9

Lyman T (1859) On a new species of (Astraea decactis). Proceedings of the Boston Society of Natural History 6: 260-263.

Martin, K.J., Rygiewicz, P.T. (2005) Fungal-specific PCR primers developed for analysis of the ITS region of environmental DNA extracts. *BMC Microbiology* 5, 28 https://doi.org/10.1186/1471-2180-5-28

Marubini, F. and Atkinson, M.J. (1999) Effects of lowered pH and elevated nitrate on coral calcification. *Marine Ecology Progress Series* Vol. 188: 117-121

McLaughlin JJA, Zahl PA (1959) Axenic zooxanthellae from various invertebrate hosts. *Annals of the New York Academy of Sciences* 77: 55-72. https://doi.org/10.1111/j.1749-6632.1959.tb36892.x

Milne Edwards H, Haime J. (1849). Recherches sur les polypiers. Quatrième mémoire. Monographie des astréides(1). Tribu II. Astréens (Astreinae). *Annales des Sciences Naturelles, Série 3, Zoologie.* 11: 233–312.

Milne Edwards H, Haime J. (1851). Recherches sur les polypiers. Mémoire 6. Monographie des Fongides. *Annales des Sciences Naturelles, Zoologie, Series 3.* 15: 73-144.

Muñiz-Castillo, A.I., Rivera-Sosa, A., Chollett, I., Eakin, C. M., Andrade-Gomez, L., McField, M., & Arias-González, J.E. (2019) Three decades of heat stress exposure in Caribbean coral reefs: a new regional delineation to enhance conservation. *Scientific Reports*, 9, Article #11013. https://doi.org/10.1038/s41598-019-47307-0

Muscatine L., Falkowski P. G., Porter J. W. and Dubinsky Z. (1984) Fate of photosynthetic fixed carbon in light- and shade-adapted colonies of the symbiotic coral Stylophora pistillata. *Proceedings of the Royal Society B.*222181–202. https://doi.org/10.1098/rspb.1984.0058

Muscatine, L., Grossman, D., and Doino, J. (1991). Release of symbiotic algae by tropical sea-anemones and corals after cold shock. *Marine Ecology Progress Series* 77:233-243

Pallas, P. S. (1766). Elenchus zoophytorum sistens generum adumbrationes generaliores et specierum cognitarum succintas descriptiones, cum selectis auctorum synonymis. *[book]*. pp. 451, Fransiscum Varrentrapp, Hagae.

Perry, C.T. and Smithers, S.G. (2011) Cycles of coral reef 'turn-on', rapid growth and 'turn-off' over the past 8500 years: a context for understanding modern ecological states and trajectories. *Global Change Biology*, 17, 76– 86. http://doi.org/10.1111/j.1365-2486.2010.02181.x

Pettay, T.D., Wham, D.C., Smith, R.T., Iglesias-Prieto, R., & LaJeunesse, T.C. (2015) Microbial invasion of the Caribbean by an Indo-Pacific coral zooxanthella. *Ecology* 112 (24) p.7513-7518. https://doi.org/10.1073/pnas.1502283112

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

R. Berkelmans, M. J. H. van Oppen (2006) The role of zooxanthellae in the thermal tolerance of corals: A 'nugget of hope' for coral reefs in an era of climate change. *Proceedings of the Royal Society B.* **273**, 2305–2312. https://doi.org/10.1098/rspb.2006.3567

Rippe, J. P., Matz, M. V., Green, E. A., Medina, M., Khawaja, N. Z., Pongwarin, T., Pinzón C, J. H., Castillo, K. D., & Davies, S. W. (2017). Population structure and connectivity of the mountainous star coral, Orbicella faveolata, throughout the wider Caribbean region. *Ecology and Evolution*, *7*(22), 9234-9246. https://doi.org/10.1002/ece3.3448

Roberts, C.M. (1997) Connectivity and Management of Caribbean Coral Reefs. *Science* 278, 5342, pp. 1454-1457. https://doi.org/10.1126/science.278.5342.1454

Robison J, Warner M (2006) Differential impacts of photoacclimation and thermal stress on the photobiology of four different phylotypes of Symbiodinium (Pyrrhophyta). *Journal of Phycology* 42: 568-579. https://doi.org/10.1111/j.1529-8817.2006.00232.x

Sampayo, E.M., Dove, S. and LaJeunesse, T.C. (2009) Cohesive molecular genetic data delineate species diversity in the dinoflagellate genus Symbiodinium. *Molecular Ecology*, 18: 500-519. https://doi-org.ezproxylocal.library.nova.edu/10.1111/j.1365-294X.2008.04037.x

Santos, S.R., Taylor, D.J., Kinzie III, R.A., Hidaka, M., Sakai, K., & Coffroth, M.A. (2002) Molecular phylogeny of symbiotic dinoflagellates inferred from partial chloroplast large subunit (23s)-rDNA sequences. *Molecular Phylogenetics and Evolution.* 23(2), pp.97-111. https://doi.org/10.1016/S1055-7903(02)00010-6

Schoenberg DA, Trench RK (1980a) Genetic variation in Symbiodinium (=Gymnodinium) microadriaticum Freudenthal, and specificity in its symbiosis with marine invertebrates. I. Isoenzyme and soluble protein patterns of axenic cultures of Symbiodinium microadriaticum. *Proceedings of the Royal Society B.* 207: 405-427 https://doi.org/10.1098/rspb.1980.0031

Schuhmacher, H., Zibrowius, H. (1985) What is hermatypic? *Coral Reefs* 4, 1–9. https://doi.org/10.1007/BF00302198

Silverstein, R.N., Cunning, R. and Baker, A.C. (2015), Change in algal symbiont communities after bleaching, not prior heat exposure, increases heat tolerance of reef corals. *Global Change Biology*, 21: 236-249. https://doi-org.ezproxylocal.library.nova.edu/10.1111/gcb.12706

Storlazzi C.D., Reguero B.G., Cole A.D., Lowe E., Shope J.B., Gibbs A.E., Nickel B.A., McCall R.T., van Dongeren A.R., & Beck M.W. (2019) Rigorously Valuing the Role of U.S. Coral Reefs in Coastal Hazard Risk Reduction. *U.S. Geological Survey Open-File Report 2019*, 1027, pp. 42 https://doi.org/10.3133/ofr20191027

Swain, T.D, Vega-Perkins, J.B., Oestreich, W.K., Triebold, C., Dubois, E., Henss, J., Baird, A., Siple, M., Backman, V., & Marcelino, L. (2016) Coral bleaching response index: a new tool to standardize and compare susceptibility to thermal bleaching. *Global Change Biology* 22(7):2475-88. https://doi.org/10.1111/gcb.13276

Swain, T.D., Chandler, J., Backman, V., & Marcelino, L. (2017). Consensus thermotolerance ranking for 110 Symbiodinium phylotypes: an exemplar utilization of a novel iterative partial-rank aggregation tool with broad application potential. *Functional ecology, 31*, 172-183. https://doi.org/10.1111/1365-2435.12694

Swain, T.D., Lax, G.S., Backman, V., & Marcelino, L.A. (2021) A phylogeny-informed analysis of global coral-Symbiodiniaceae interaction network reveals that traits correlated with thermal bleaching are specific to symbiont transmission mode. *mSystems*, 6:e00266-21. https://doi.org/10.1128/mSystems.00266-21

Taylor DL (1974) Symbiotic marine algae: taxonomy and biological fitness. In: Vernberg WB (ed) Symbiosis in the Sea. University of South Carolina Press, South Carolina, pp 245-262

Tchernov D, Gorbunov M, de Vargas C, Narayan Yadav S, Milligan A, Haggblom M, Falkowski P (2004) Membrane lipids of symbiotic algae are diagnostic of sensitivity to thermal bleaching in corals. *Proceedings of National Academy of Science USA* 101: 13531-13535. https://doi.org/10.1073/pnas.0402907101

Trench RK (1979) The cell biology of plant-animal symbiosis. Annu Rev Plant Physiol 30: 485531 doi 10.1146/annurev.pp.30.060179.002413

Ushey, K., Allaire, J.J., Tang, Y., Eddelbuettel, D., Keydana, S., Lewis, B., Hafen, R., & Geelnard, M. (2021) Interface to 'Python': reticulate. R Package. Version 1.22 https://cran.r-project.org/web/packages/reticulate/index.html

van Hooidonk, R., Maynard, J. A., Liu, Y. & Lee, S. K. (2015) Downscaled projections of Caribbean coral bleaching that can inform conservation planning. *Global Change Biology*, 21, 3389–3401. https://doi.org/10.1111/gcb.12901

van Oppen, M.J.H., Mahiny A.J., & Done T.J. (2005) Geographic distribution of zooxanthella types in three coral species on the Great Barrier Reef sampled after the 2002 bleaching event. *Coral Reefs*, 24, 482–487. https://doi-org.ezproxylocal.library.nova.edu/10.1007/s00338-005-0487-1

van Woesik, R., Done, T. (1997) Coral communities and reef growth in the southern Great Barrier Reef. *Coral Reefs* 16, 103–115. https://doi.org/10.1007/s003380050064

Verrill AE. (1901). Comparisons of the Bermudian, West Indian, and Brazilian Coral Faunae. *Transactions of the Connecticut Academy of Arts and Sciences.* 11: 169-206, pls. 10-35.

Verrill, A.E. (1868). Notes on Radiata in the Museum of Yale College, with descriptions of new genera and species. No. 4. Notice of the corals and Echinoderms collected by Prof. C.F. Hartt, at the Abrolhos Reefs, Province of Bahia, Brazil, 1867. *Transactions of the Connecticut Academy of Arts and Sciences.* 1 (2): 351-376.

Wells J.W. (1973) New and old scleractinian corals from Jamaica. Bulletin of Marine Science 23: 16-58.

Williams, S. D., and M. R. Patterson. (2020) Resistance and robustness of the global coral–symbiont network. *Ecology* 101(5):e02990. https://doi.org/10.1002/ecy.2990

Yonge, C.M., and Nicholls, A.G. (1931). Studies on the physiology of corals, V: the effects of starvations in light and in darkness on the relationship between corals and zooxanthellae. *Scientific Reports / Great Barrier Reef Expedition* 1:176-211

Zardoya, R., Costas, E., Lopez-Rodas, V., Garrido-Pertierra, A., & Bautista, J.M. (1995) Revised dinoflagellate phylogeny inferred from molecular analysis of large subunit ribosomal RNA gene sequences. *Journal of Molecular Evolution*, 41, 637–645. https://doi-org.ezproxylocal.library.nova.edu/10.1007/BF00175822

Zhang, H., Bhattacharya, D., Lin, S. (2005) Phylogeny of dinoflagellates based on mitochondrial cytochrome b and nuclear small subunit rDNA sequence comparisons. *Journal of Phycology*, 41, 411–420. https://doi.org/10.1111/j.1529-8817.2005.04168.x