The role of foundation species in shaping the biodiversity of mangrove islands

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To my niece Danka and nephew Aleksandar whom we welcomed into our hearts and to the many loved ones who passed on over these past five years. You are loved forever and always.

Danka, age 3, exploring the mangrove forests at home.

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Abstract

Tropical mangrove forests are considered one of the world's most threatened ecosystems due to anthropogenic impacts, including conversion to aquaculture and agriculture, urbanization, exploitation of resources, and pollution. The loss of mangroves may have severe effects on local biodiversity because mangroves are foundation species recognized for supporting diverse epibiont communities on their roots, including corals for which mangroves may serve as a refuge. The overall goal of this dissertation is to understand the role that habitat forming organisms such as mangroves can have in shaping biodiversity by buffering environmental stress and interacting with co-occurring foundation species. I used field experiments, surveys, and extensive reviews of the emerging literature to improve our understanding of the influence that foundation species have on the distribution and composition of associated organisms. First, I described four types of coexisting mangrove and coral (CMC) habitats that occur worldwide and provided global tallies of the coral species occupying these habitats. I then identified biotic and abiotic characteristics common to CMC systems based on field data and previous reports and used a GIS model to suggest where additional systems may occur globally. Second, I delved into the mechanisms of interactions among co-occurring foundation species to understand how mangroves are facilitating coral condition and survival. Using field surveys and a reciprocal transplant experiment, I tested the effects of light and habitat (e.g., reef or mangrove) on coral community structure and condition. I found that mangroves provide an alternative habitat for corals with greater coral species richness and diversity than on the adjacent shallow reef. Experimental manipulation of light in mangrove and reef habitats suggests that light intensity is a key factor mediating coral bleaching and survival, with mangrove habitats providing a refuge from the light stress experienced on nearby shallow reefs. Third, I manipulated physical attributes of mangroves using living and non-living mangrove roots, as well as root mimics, to determine how traits of foundation species such as mangroves affect the composition of associated communities. Overall substrate composition (i.e., root material) had effects on community composition, including species richness, abundance, and structural complexity, with the direction and strength varying among treatments. I found that root mimics are functionally similar to living mangrove roots, and the epibiont community was similar between living and non-living mangrove roots until non-living mangrove roots deteriorated and were no longer viable substrate for epibiont occupancy. Finally, I addressed how environmental factors shape mangrove associated epibiont communities. I did so by examining the effects of wave energy on root epibiont community composition. Specifically, I found that epibiont community varied as a function of wave energy, and I then tested whether this was due to effects of wave energy on initial community establishment or later growth and persistence. I found that epibiont communities of root mimics reciprocally transplanted became similar to the surrounding root communities. Together, these studies provide critical insight into the context dependence of foundation species' role in shaping associated community biodiversity in relation to environmental stress, foundation species traits, and wave energy, with important implications for restoration and conservation of these biogenic habitats.

Résumé

Les forêts de mangroves tropicales sont considérées comme l’un des écosystèmes les plus menacés au monde en raison des impacts anthropiques. La disparition des mangroves peut avoir des effets graves sur la biodiversité locale, car les mangroves sont des espèces fondatrices reconnues soutenant diverses communautés d'épibiontes sur leurs racines, comme les coraux, qui peuvent se servir des mangroves comme refuge. L'objectif de cette thèse est de comprendre le rôle de ses organismes formant des habitats, comme les mangroves, peuvent jouer dans la formation de la biodiversité en amortissant le stress environnemental et en interagissant avec les espèces fondatrices concourantes. J'ai utilisé des expériences de terrain, d'échantillonnage et des revues de la littérature émergente pour améliorer notre compréhension de l'influence des espèces fondatrices sur la distribution et la composition des organismes associés. Premièrement, j'ai décrit quatre types d'habitats de mangrove et de corail coexistants (CMC) existant mondialement et fourni des dénombrements mondiaux des espèces de corail occupant ces habitats. J'ai ensuite identifié les caractéristiques biotiques et abiotiques communes aux systèmes de CMC sur la base de données de terrain et de rapports précédents et utilisé un modèle SIG pour suggérer où des systèmes supplémentaires pourraient se rencontrer mondialement. Ensuite, j'ai exploré les mécanismes des interactions entre les espèces fondatrices concourantes pour comprendre comment les mangroves facilitent l'état et la survie des coraux. À l'aide d’échantillonnage sur le terrain et d'une expérience de transplantation réciproque, j'ai testé les effets de la lumière et de l'habitat sur l’état des coraux et sur la structure de la communauté corallienne. J'ai trouvé que les mangroves offrent un habitat alternatif aux coraux et possèdent une richesse et diversité d'espèces coralliennes plus grande que sur le récif peu profond adjacent. Des manipulations expérimentales suggèrent que l'intensité lumineuse est un facteur clé de blanchiment et de survie des coraux, et que les habitats de mangrove offrant un refuge contre le stress léger subis par les récifs peu profonds et proches. De plus, j'ai manipulé les attributs physiques des mangroves en utilisant des racines de mangroves vivantes et non vivantes, ainsi que des racines artificielles, pour déterminer comment les traits des espèces fondatrices telles que les mangroves, affectent la composition des communautés associées. La composition globale du substrat avait des effets sur la composition de la communauté (la richesse en espèces, l'abondance et la complexité structurelle), avec la direction et la force des effets variant selon les traitements. J'ai trouvé que les racines artificielles sont fonctionnellement similaires aux racines de mangroves vivantes et que la communauté d'épibiontes était similaire entre les racines de mangroves vivantes et non vivantes, jusqu'à ce que les racines de mangroves non vivantes se détériorent et ne soient plus un substrat viable. Enfin, j'ai abordé la manière dont les facteurs environnementaux façonnent les communautés d'épibiontes associées aux mangroves. J'ai découvert que la communauté d'épibiontes variait en fonction de l'énergie des vagues, donc j'ai testé si cela était dû aux effets de l'énergie des vagues sur l'établissement initial de la communauté ou à la croissance et à la persistance ultérieures. J'ai trouvé que les communautés épibiontes de racines artificielles transplantées réciproquement sont devenues similaires aux communautés de racines environnantes. En tout, ces études fournissent un aperçu critique du contexte de dépendance du rôle des espèces fondatrices dans la formation de la biodiversité communautaire associée en relation avec le stress environnemental, les caractéristiques des espèces fondatrices et l'énergie des vagues, avec des implications importantes pour la restauration et la conservation de ces habitats biogéniques.

Resumen

Los bosques de manglar se consideran uno de los ecosistemas más amenazados del mundo debido a impactos antropogénicos que incluyen la conversión a la acuicultura y la agricultura, la urbanización, la explotación del recurso y la contaminación. La pérdida de manglares puede tener efectos negativos sobre la biodiversidad local ya que los manglares son especies fundacionales que sustentan comunidades de epibiontes en sus raíces, incluidos los corales, y para los cuales los manglares pueden servir como refugio. El objetivo de esta disertación es dilucidar el papel que tienen los manglares en la configuración de la biodiversidad asociada a sus raíces por medio de la disminución del estrés ambiental y la interacción de estos bosques con las especies que en el coexisten. La metodología consistió en llevar a cabo experimentos de campo, encuestas y revisiones de la literatura con el objeto de mejorar el conocimiento de la influencia que tienen los manglares en la distribución y composición de sus organismos asociados. Inicialmente describí cuatro tipos de hábitats coexistentes entre los manglares y los corales (CMC) que ocurren alrededor del mundo, proporcionando recuentos globales de las especies de coral que pueden ocupar los mismos. Luego identifiqué características bióticas y abióticas comunes a los sistemas CMC con base en datos de campo e informes previos, y utilicé un modelo de SIG para sugerir dónde podrían ocurrir sistemas similares alrededor del mundo. También estudié los mecanismos de interacción entre las especies para entender cómo los manglares están facilitando la supervivencia de los corales. Utilizando estudios de campo y un experimento de trasplante recíproco, investigué los efectos de la luz y del hábitat en la estructura y estado de la comunidad coralina. Mis resultados indican que los manglares proporcionan un hábitat alterno para los corales con una mayor riqueza y diversidad de especies de coral cuando se comparan con arrecifes de poca profundidad adyacente. Usando manipulación experimental de la luz en los manglares y en los arrecifes, encontré que la intensidad de la luz es un factor clave que afecta el blanqueamiento y la supervivencia de los corales, y los manglares proporcionan un refugio del estrés lumínico que prevalece en arrecifes aledaños. Seguidamente, manipulé los atributos físicos de los manglares utilizando raíces de manglares vivas, no vivas y artificiales para determinar cómo se afecta la composición de las comunidades asociadas. La composición del sustrato (es decir, el tipo de raíz) tuvo efectos sobre la composición de la comunidad, incluida la riqueza de especies, la abundancia y la complejidad estructural. También encontré que las raíces muertas son funcionalmente similares a las raíces de

mangle vivas y la comunidad de epibiontes fue similar entre raíces de mangle vivas y no vivas hasta que las raíces de manglares sin vida se deterioraron y dejaron de ser un sustrato viable para la ocupación de epibiontes. Finalmente, menciono como los factores ambientales afectan las comunidades de epibiontes asociadas a los manglares. Esta última parte la realicé examinando los efectos que la energía de las olas tiene sobre la composición de la comunidad de epibiontes asociada a las raíces. Específicamente, encontré que la comunidad de epibiontes varía en función de la energía de las olas y luego examiné si esto se debía a los efectos de la energía de las olas en el establecimiento inicial de la comunidad o en el crecimiento y la persistencia posteriores. Encontré que las comunidades de epibiontes en raíces artificiales trasplantadas recíprocamente se vuelven similares a las comunidades de las raíces aledañas. En conjunto, estos estudios brindan información crítica sobre el papel de las especies fundacionales en la configuración de la biodiversidad comunitaria asociada con relación al estrés ambiental, los rasgos de las especies fundacionales y la energía de las olas, con importantes implicaciones para la restauración y conservación de estos hábitats biogénicos.

Preface

Thesis format

This thesis is presented in manuscript-based format, with each chapter (1-4) consisting of an individual manuscript published or intended for publication in a peer-reviewed, academic journal, with myself as the lead author. Chapters are linked by brief statements (prefaces) that summarize the key findings of the previous chapter and introduce concepts and questions explored in the subsequent chapter. This thesis starts with a general introductory section before the first chapter and closes after the last chapter with a general conclusion section that summarizes the main contributions of this work and suggests productive avenues for future research. Four appendices provide supplementary information for each chapter. I followed the referencing format of the journal *Ecosphere* for all chapters. The citations for the chapters are as follows:

<u>Chapter 1</u> Stewart, H.A., J.L. Wright, M. Carrigan, A.H. Altieri, D.I. Kline, and R.J. Araújo. Coexisting mangrove-coral habitats: What we have learned in the past 60 years and directions for the future. In preparation for *PNAS*.

<u>Chapter 2</u> Stewart, H.A., D.I. Kline, L.J. Chapman, and A.H. Altieri. 2021. Caribbean mangrove forests act as coral refugia by reducing light stress and increasing coral richness. *Ecosphere* 12:e03413.

<u>Chapter 3</u> Stewart, H.A., D.S. Janiak, D.A.G.A. Hunt, J.L. Wright, A. Carmona Cortes, K.T. Powell, L.J. Chapman, and A.H. Altieri. Cascading effects of mangroves on assembly of epibiont communities are contingent on root characteristics. In revision for *Marine Ecology Progress Series*.

<u>Chapter 4</u> Stewart, H.A. and A.H. Altieri. Context dependence of wave exposure in shaping mangrove epibiont community composition. In preparation

Statement of originality

This dissertation blends field surveys, field experiments, and a literature review to examine the role that foundation species play in shaping biodiversity of mangrove islands across a range of spatial scales. Chapter 1 examines interactions between mangroves and corals at a global scale by identifying factors that define habits where corals co-exist with mangroves in nested assemblages. Chapter 2 explores mechanisms driving coexisting mangrove-coral (CMC) community structure by focusing on the scale of an island fringe (mangrove canopy and adjacent shallow reef) in Caribbean Panama to test whether mangroves reduce solar irradiance and/or temperature stress to corals. Chapter 3 examines how foundation species traits can mediate diversity at the scale of individual mangrove roots (2 m between neighboring roots). Finally, Chapter 4 takes a landscape approach, exploring the effects of wave exposure on the epibiont community composition and diversity within (100-250 m) and between mangrove islands (2-12 km). Together, these four chapters provide critical insights into how the functions of foundation species such as mangroves are likely to respond to factors such as environmental stress, foundation species traits, and wave energy, with important implications for restoration and conservation of these biogenic habitats in a global change context.

Chapter 1 provides the first systematic review of scientific literature identifying the presence of corals living within mangrove habitats and reveals that CMC habitats occur in virtually every tropical region of the world. The rapid increase in observations of CMC habitats in the literature may reflect increased interest in these systems and/or a shifting pattern of co-occurring foundation species assemblages. This chapter was also the first to report a zonation pattern of coral species and colony size within the mangrove forest and the first to demonstrate that corals have sustained, rapid growth within the canopy. By integrating a scientific review of CMC habitats with a new field survey conducted in Panama, I identified characteristics that define these co-existing mangrove-coral habitats and developed criteria for predicting where further nested assemblages are likely to occur.

Using a reciprocal transplant experiment and field survey, Chapter 2 tests the hypothesis that light and temperature are environmental factors affecting coral condition and survivorship on the shallow reef and within the mangrove canopy. This is the first study to experimentally explore the interactive effects of shade and habitat on coral bleaching and survival. Higher coral species richness and diversity in the mangrove canopy than the adjacent shallow reef with similar live coral cover combined with corals generally faring better when transplanted to lower light levels suggest that mangroves are serving as long-term coral refugia.

Chapter 3 contributes to the growing literature exploring the role of mangrove root traits in determining associated epibiont communities. Previous work has quantified effects of root complexity (Nagelkerken et al. 2010, Vorsatz et al. 2021), root contact with the ground (Schutte and Byers 2017), and root density (Nanjo et al. 2014). My study is the first to experimentally test effects of root substrate composition and root health (alive or dead) on epibiont communities. This study is unique it that it attempts to address whether mobile invertebrate community assemblage is directly affected by mangrove root traits or indirectly affected through a facilitation cascade of secondary foundation species (e.g., sponges, bivalves). I did not find evidence for nutrient exchange or other biotic controls shaping the associated community, nor did I find that species of wood substrate influenced epibiont colonization and assemblage. However, I did find that non-living roots quickly deteriorated and became shorter or were lost altogether, and as result had a reduced capacity to support a diverse community.

Chapter 4 provides novel contributions to our understanding of the effect abiotic forces, such as wave energy, exert on mangrove root assemblages by quantifying consequences of landscape position (high versus low wave exposure) on both initial establishment of mangrove root epibiont communities (year 1) and subsequent persistence (year 2). Use of reciprocal transplants allowed me to test whether transplanted communities became similar to neighboring roots in their new setting as a function of their new environmental context or remained the same as a function of initial establishment in their original setting, an approach that yielded novel insights on the interactions between abiotic and biotic drivers of epibiont assemblage structure.

Contribution of Authors

Chapter 1

- Heather A. Stewart conceived, designed, and performed the surveys, conducted the review, analyzed the data, and led writing of the manuscript.
- Jennifer L. Wright assisted with and contributed to the design of the surveys, conducted GIS analyses, and provided approval for submission for publication.
- Matthew Carrigan assisted with and contributed to the design of the surveys and provided approval for submission for publication.
- Andrew H. Altieri contributed to drafts of the manuscript and provided approval for submission for publication.
- David I. Kline contributed to drafts of the manuscript and provided approval for submission for publication.
- Rafael J. Araújo contributed to the conceptual design of the paper and drafts of the manuscript and provided approval for submission for publication.

Chapter 2

- Heather A. Stewart conceived and designed the reciprocal transplant experiment and surveys, performed the surveys, conducted the experiment, analyzed the data, and led writing of the manuscript.
- David I. Kline contributed to the design of the surveys and contributed to drafts of the manuscript and provided final approval for publication.
- Lauren J. Chapman contributed to drafts of the manuscript and provided final approval for publication.
- Andrew H. Altieri contributed to the design of the reciprocal transplant experiment and surveys and contributed to drafts of the manuscript and provided final approval for publication.

Chapter 3

- Heather A. Stewart conceived, designed, and performed the surveys, laboratory sampling and taxonomic identification of epibionts, analyzed the data, and led writing of the manuscript.

- Dean S. Janiak contributed to the design, helped with taxonomic identification of epibionts and statistical analyses, contributed to drafts of the manuscript.
- Jennifer L. Wright assisted with surveys, laboratory sampling and taxonomic identification of epibionts.
- David A.G.A. Hunt contributed to statistical analyses.
- Andrea Carmona Cortes assisted with surveys, laboratory sampling and taxonomic identification of epibionts.
- Krystyna T. Powell contributed to the experimental design and assisted with surveys.
- Lauren J. Chapman contributed to drafts of the manuscript.
- Andrew H. Altieri contributed to the design of the experiment and drafts of the manuscript.

Chapter 4

- Heather A. Stewart conceived, designed, and performed the surveys, analyzed the data, and led writing of the manuscript.
- Andrew H. Altieri contributed to the design of the experiment and drafts of the manuscript.

Ethics statement

All research included in this thesis was conducted following approval of the Republic of Panama Ministry of the Environment (MiAmbiente) and in compliance with the Smithsonian Tropical Research Institute's animal care policies (Animal Care and Use protocol 2017-0218-2020). Scientific permits used for data collection and exportation of samples were #SE/A-34-17, SE/AP-13-17, SE/PO-2-18, and SE/AP-21-19.

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Introduction

Global environmental changes due to anthropogenic disturbances and climate change are unraveling ecosystems and degrading their functioning by altering species composition and threatening species persistence (Chapin III et al. 1997, Loreau et al. 2001, Dinerstein et al. 2019). This has led to a global biodiversity crisis with half a million species at risk of extinction in the coming decades (Alongi 2015, Mokany et al. 2020) and made conservation of remaining natural habitats critical to mitigate extinctions (Johnson et al. 2017, Mokany et al. 2020). Maintenance of biodiversity in the face of environmental change is critical because species loss can have negative effects on ecosystem functioning including resilience and productivity (Bond and Chase 2002, Emmett Duffy 2009, Johnson et al. 2017).

Nearly half of the world's population lives within 150 km of coasts, and as the human population continues to grow, unprecedented environmental pressures for land and resources pose great challenges to marine conservation (Miloslavich et al. 2010, Turschwell et al. 2020, Worthington et al. 2020). Conservation and management of coastal habitats must consider interactions between terrestrial and marine habitats, because these adjacent and connected habitats can buffer one another in the face of disturbance (Nagelkerken 2009). In tropical regions, coastal ecosystems often consist of a network (seascape) of adjacent habitats including coral reefs, mangroves, and seagrass beds (Boström et al. 2011, Davis et al. 2014, Guannel et al. 2016, Berkström et al. 2020). If one habitat degrades, the others can help compensate or assist in recovery. For example, when the structural complexity of reefs is lost or a coral reef degrades, mangroves can support fisheries equal to or greater than that of complex reefs without mangroves (Rogers and Mumby 2019). However, the concurrent loss and degradation of multiple coastal habitats may overwhelm the resilience of these complex systems, which is why in 2016 the International Union for Conservation of Nature (IUCN) called for the full protection of >30% of global marine habitat by 2030 at the World Conservation Congress (Zhao et al. 2020) to protect biodiversity and mitigate climate change impacts. This dissertation focuses on two adjacent and potentially interacting coastal habitats that are rich in biodiversity, provide important ecosystem services, and are highly threatened by multiple anthropogenic stressors including climate change: mangroves and coral reefs.

Mangroves serve as biodiversity reservoirs, provide coastal protection (e.g., reduce waves and storm surges, defend against flooding and erosion), sequester 16% of the ocean's carbon, and have the potential to keep pace with sea-level-rise through vertical accretion (Menéndez et al. 2020, Luo et al. 2021). Each year mangroves protect >15 million people and reduce property damage by >65 billion USD (Menéndez et al. 2020), yet tropical mangrove forests are considered one of the world's most threatened ecosystems due to anthropogenic impacts, including conversion to aquaculture and agriculture, urbanization, exploitation of resources, and pollution (Thomas et al. 2017, Turschwell et al. 2020, Worthington et al. 2020). By the end of the 20th century, mangrove area had declined by 35% globally, and continued to be lost at a rate of 1-3% per year through the 2000s (Valiela et al. 2001, Friess et al. 2019). Although deforestation of mangroves declined to 0.2-0.7% between 2000 and 2012, the synergistic interactions of natural (e.g., sea level rise, climate change) and anthropogenic stressors has led to rapid and large-scale mangrove die-offs globally (Feller et al. 2017).

Tropical coral reefs harboring an estimated one third of all described marine species (Knowlton et al. 2010) are also one of the most sensitive ecosystems to climate change (Van Hooidonk et al. 2013). Human activities also have negative local impacts on coral reefs through sedimentation, nutrient runoff, pollution, and overfishing (Hughes et al. 2003, Carpenter et al. 2008), potentially reducing the resilience of corals to global stressors such as ocean warming and acidification (Carpenter et al. 2008). A combination of these local and global factors has led to global mass bleaching events becoming increasingly frequent and severe, typically followed by reduced coral growth rates, decreased fecundity and recruitment, and high coral mortality (Hoegh-Guldberg 1999, Hughes et al. 2003). Of global coral reef systems, the Caribbean coral reefs make up 10% of the cover but account for 45% of endemic fish species and 25% endemic coral species (UNEP-CEP 2020). These are among the most threatened reefs in the world, having suffered an estimated 80% reduction in live coral cover from 1975 to 2000 (Gardner et al. 2003, Guzmán 2003, Côté et al. 2005, Contreras-Silva et al. 2020) with current cover of live coral averaging just 10-13% (Schutte et al. 2010, Jackson et al. 2014, Tkachenko 2017).

As foundation species, the loss of either mangroves or coral reefs may have severe effects on local biodiversity. The overall goal of this dissertation is to understand the role that habitat forming organisms such as mangroves can have in shaping biodiversity by buffering environmental stress, providing refuge for corals, and interacting with other foundation species. Below I review the importance of foundation species and their potential cascading effects on associated community assemblages through their interactions, introduce my study systems, and provide an overview of the dissertation chapters.

Foundation species

Foundation species are organisms that play a dominant role in structuring communities through habitat creation and have been recognized as an integral driver of ecosystem processes (Dayton 1972, Ellison et al. 2005). The degree to which environmental stress or disturbance are influenced by the foundation species (e.g., positively or negatively) may reflect variation in foundation species traits such as structural complexity (e.g., density), age, and patch size, which in turn affect the composition of associated communities (Irving and Bertness 2009, Angelini et al. 2011). For example, the links between traits and functions have been observed in intertidal cordgrass, where variation in the density and height of cordgrass can alter the sediment accretion and wave energy functions of the cordgrass, and its ability to sustain diverse associated communities (Bruno et al. 2003, Irving and Bertness 2009). The concept of foundation species and recognition of their ecological role has been around since the 1970s (Dayton 1972). There is extensive literature related to direct (e.g., competition, top-down control) and indirect effects (e.g., facilitation) foundation species are known to have on associated assemblages (Altieri and Van De Koppel 2013, Ellison 2019), however, there are still significant gaps in our understanding. The use of field experiments that manipulate physical attributes (e.g., mimic/artificial structures) or the presence of foundation species can improve our understanding of the influence foundation species have on the distribution and composition of associated organisms and help to identify traits that may drive the assemblage structure (Angelini et al., 2011).

Facilitation cascades

Facilitation theory, in the 2000s (Bruno and Bertness 2001, Bruno et al. 2003) emphasized the basic principles such as how positive interactions by a foundation species could expand the realized niche to improve predictions of species occurrence on the landscape. We now recognize that communities can be structured by single or multiple foundation species that influence habitat complexity, resource availability, environmental conditions, diversity, and community organization (Angelini et al. 2011). Ecosystems composed of multiple coexisting foundation species may occur in either nested assemblages, where a stress-tolerant primary foundation species colonizes a habitat enabling a secondary foundation species to establish, or as adjacent assemblages, where foundation species create discrete competitively determined zones (Angelini et al. 2011, Gillis et al. 2014, Igulu et al. 2014). In either type of assemblage, secondary foundation species further augment the quantity and/or quality of habitat available by providing complementary levels of complexity to support diverse species assemblages in a chain of positive interactions known as a facilitation cascade (sensu Altieri et al. 2007). Facilitation cascades exist in both terrestrial and marine ecosystems and may function to reduce predation pressure, provide protection from abiotic stress, modify nutrient availability, and alter the physical environment (Angelini et al. 2011). The resilience of ecosystems to these disturbances largely depends on the response and interactions of foundation species and their ability to mitigate stress for the associated community.

Mangrove-coral interactions

Corals and mangroves are foundation species recognized for their adjacent assemblages within the seascape (Gillis et al. 2014). In these adjacent assemblages, mangroves are recognized for having positive effects on corals of nearby reefs through long-distance positive interactions (e.g., reducing sediment flux and retaining nutrients), while coral reefs dissipate wave energy, creating calm conditions that allow mangroves to thrive (Harborne et al. 2006, Gillis et al. 2014, van de Koppel et al. 2015). However, there has been an increasing frequency of observations of mangrove-coral nested assemblages over the past decade, with corals establishing extensive communities within mangrove habitats (Rogers 2009, Rogers and Herlan 2012, Yates et al. 2014). It remains unclear whether mangroves are having a positive effect on corals growing within these nested assemblages and whether the increase in observations is due to changing environmental conditions. Given that the shallow reef environment (typically ≤ 3 m deep) typically has extremes in temperature and light conditions (Spalding et al. 2001) that may be getting more stressful due to global change, it has been suggested that mangrove habitats, by providing shade, may serve as crucial refugia (Rogers and Herlan 2012, Yates et al. 2014, Camp et al. 2019). We define refugia here as habitats where species may retreat to and persist in under changing and/or unfavorable environmental conditions and may serve as a potential source population to expand from (Keppel and Wardell-Johnson 2012, Cacciapaglia and van Woesik 2015). Refuge sites can ameliorate both acute environmental stress such as short-term thermal anomalies and more chronic stressors such as ocean acidification (Oliveira 2020).

Mangroves of the Caribbean

In this dissertation, I use the red mangrove (*Rhizophora mangle* L.) as a model organism to study the role of foundation species in shaping biodiversity. Mangroves are woody plants found at the intersection of land and sea in tropical and subtropical regions, and they span over 118 countries with a global coverage of 137,600 km^2 (Kathiresan and Bingham 2001, Bunting et al. 2018). There are 73 mangrove species worldwide (Spalding et al. 2010), and their defining characteristics are their ability to survive in waterlogged, high salinity, and anaerobic soils, enabling them to grow in rather unstable and harsh environments (Spalding et al. 2010, Hogarth 2015). I chose red mangroves as the focal foundation species of this thesis due to their global distribution, importance to humans, and the characteristic aerial roots recognized for the diverse community they support. The roots of the red mangrove, which originate from branches or stems, grow down towards to the substrate to stabilize the tree and the substrate. These aerial roots provide gas exchange that allows mangroves to live in anaerobic environments (Kathiresan and Bingham 2001). A prominent feature of mangrove prop roots is that they form complex, living submerged habitats encrusted in diverse epibiont communities composed of many different plants, animals, fungi, and bacteria (Kathiresan and Bingham 2001).

Epibiont communities

The epibiont community on mangrove roots varies in relation to the geographic region of the mangrove and suitability of environmental factors (e.g., wave energy, water flow, water depth, tidal patterns, light) (Rützler 1995, Diaz et al. 2004, Schutte and Byers 2017), but it is unclear how these factors, and traits of the roots (e.g., root length, living versus non-living roots) influence species richness, diversity, and abundance of the epibiont community (Guerra-Castro and Cruz-Motta 2014, Janiak et al. 2018). Sponges and bivalves are dominant groups found on subtidal mangrove roots within the Caribbean (Guerra-Castro and Cruz-Motta 2018) and are often considered secondary foundation species (Bishop et al. 2012, Altieri and Van De Koppel 2013, Aquino-Thomas and Proffitt 2014, Vozzo and Bishop 2019, Aquino-Thomas 2020) because of the structural complexity they add to the mangrove system that provides refuge to a speciose invertebrate community (Henkel and Pawlik 2011, Rebolledo et al. 2014). In this thesis the epibiont communities I examined commonly consisted of algae, anemones, tubeworms, bivalves, barnacles, tunicates, sponges, and corals. Of these taxonomic groups, I focused on corals, sponges, and bivalves as nested secondary foundation species within the mangrove habitat to address mechanisms mediating patterns of biodiversity in association with primary and secondary foundation species and their associated communities.

Thesis overview

The chapters of my dissertation applied the concepts of co-occurring foundation species and facilitation cascades to understand the role that foundation species play in shaping biodiversity. Mangroves are the primary foundation species studied in every chapter and were chosen as a model system because of their wide distribution, diverse epibiont communities, and importance to human well-being through the ecosystem services they provide. In Chapters 1 and 2, I focused on the organization of foundation species (mangroves as primary and corals as secondary) in nested assemblages and the implications for biodiversity, and in Chapters 3 and 4, I tested factors including foundation species traits and environmental context in mediating patterns of biodiversity in association with primary and secondary foundation species.

Thesis structure

In Chapter 1, I integrated a scientific review and field data to address how the association between two foundation species, mangroves and coral reefs, varies globally as nested and adjacent assemblage types. I distinguished nested mangrove-coral assemblages from adjacent coral reef and mangrove forests, and I provided appropriate terminology and criteria to categorize four types of coexisting mangrove-coral (CMC) habitats: lagoon, channel, edge, and canopy, to aid in distinguishing these habitats within the scientific literature and in future studies. I used roving surveys to demonstrate that this nested assemblage within Caribbean Panama is not an isolated phenomenon and provided the first description of a canopy CMC habitat of Bocas del Toro, Panama. I then provided a global perspective of these CMC habitats by identifying biotic and abiotic characteristics common to CMC systems and used a GIS model to suggest where additional systems may occur.

In Chapter 2, I delved into the mechanisms driving community structure of the CMC system, focusing on CMC canopy sites in Bocas del Toro, Panama to test whether mangroves reduce solar irradiance and/or temperature stress on corals. I conducted field surveys to compare the coral community structure (i.e., coral species richness, abundance, and diversity) between the reef and mangrove habitats within the archipelago, and I used a reciprocal transplant experiment to quantify effects of light and habitat (e.g., reef or mangrove) on condition (i.e., level of bleaching, tissue loss, and mortality) of multiple coral species.

In Chapter 3, I tested for links between characteristics of mangrove prop roots and associated community assemblages to better understand the relationship between foundation species traits and the biodiversity of associated organisms. I compared sessile species richness, diversity, abundance, and community composition on living, non-living, and artificial roots mimics after 14 months of community development. I then examined how these root characteristics indirectly affected the mobile invertebrate community (i.e., species richness, diversity, and abundance) by examining the relationship between secondary foundation species (e.g., sponges, bivalves) and biodiversity of the mobile species within the epibiont community.

In Chapter 4 I tested how environmental factors impact the associated community assemblage of mangrove roots. Specifically, I explored the effect of wave energy on the epibiont community composition of mangrove islands by comparing these communities between areas with intense wave action and sheltered areas. Through a reciprocal transplant experiment, I tested whether variation in the epibiont community was due to effects of wave energy on initial community establishment or later growth and persistence. I end the dissertation by summarizing the key findings of each chapter and highlighting both theoretical and applied aspects of the dissertation, as well as potential areas for future study.

Chapter 1: Coexisting mangrove-coral habitats: a synthesis of research, classification, and directions for the future

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1.1 Abstract

Marine ecosystems are structured by coexisting foundation species occurring in adjacent or nested assemblages. Mangroves and corals are typically observed in adjacent assemblages (i.e., mangrove forests and coral reefs) but are increasingly reported in nested mangrove-coral assemblages (i.e., corals living within mangrove habitats). Here we define these nested assemblages as "coexisting mangrove-coral" (CMC) habitats, and we review the scientific literature to date to formalize a baseline understanding of these ecosystems and create a foundation for future in-depth studies. Our scientific literature review revealed 96 species of corals living within mangrove habitats across 12 locations spanning the Caribbean Sea, Red Sea, Indian Ocean, and South Pacific. This included our field study of a canopy CMC habitat type located in Bocas del Toro, Panama, the second most coral rich CMC habitat reported in the world with 34 species of corals growing on and/or among submerged red mangrove prop roots. Based on our literature review and field data, we identified biotic and abiotic characteristics common to CMC systems and created a classification framework of CMC habitat categories: Lagoon, Inlet, Edge, and Canopy. We then used the compiled data to create a GIS model to suggest where additional systems may occur globally. In a time where many ecosystems are at risk of disappearing, discovery, and description of alternative habitats for species of critical concern are of utmost importance for their conservation and management.

1.2 Introduction

Many communities are structured by foundation species interactions which influence habitat complexity, diversity, and community organization (Dayton 1972, Ellison et al. 2005, Altieri and van de Koppel 2013). Coexisting foundation species occur in either nested assemblages, where a stress-tolerant primary foundation species colonizes a habitat enabling a secondary foundation species to establish through a facilitation cascade providing complementary levels of complexity, or as adjacent assemblages where foundation species create discrete zones (Angelini et al. 2011) linked through long-distance interactions mediated by exchanges of nutrients/organic matter, movement of organisms, and modification of the environment (Huijbers et al. 2008, Granek et al. 2009, Ooi and Chong 2011, Gillis et al. 2014, Igulu et al. 2014, van de Koppel et al. 2015, Shideler et al. 2017).

Corals and mangroves are foundation species that often co-occur in tropical coastal environments, and the scientific literature contains occasional observations of corals growing on or between mangrove roots in general biodiversity surveys (Fishelson 1971, Loya 1976, Farnsworth and Ellison 1996, Macintyre et al. 2000, 2009, Rützler et al. 2000, 2004, de la Guardia et al. 2004) or as a dying coral reef is overgrown by mangrove forest with sea-level fall (Almy and Carrion-Torres 1963, Fujimoto and Miyagi 1993, Alongi et al. 2008, Fujimoto et al. 2015). Recently, however, there have increasingly been specific empirical studies that document nested mangrove-coral assemblages with corals establishing long-term and extensive communities within mangrove habitats (Rogers 2009, Rogers and Herlan 2012, Yates et al. 2014) including locations in the Caribbean (Hernández-Fernández 2015, Rogers 2017, Bengtsson et al. 2019, Buob 2019, Wright 2019, Kellogg et al. 2020, Scavo Lord et al. 2020a, 2020b Stewart et al. 2021 [Chapter 2]), Australia's Great Barrier Reef (Camp et al. 2019), New Caledonia (Camp et al. 2017), Seychelles and Sulawesi (Camp et al. 2016). These nested mangrove-coral assemblages may be of evolutionary importance as potential genetic reservoirs under climate change, and of ecological importance for identifying stress tolerant populations in climate refugia and unique habitats created jointly by corals and mangroves.

In this study conducted in the Bocas del Toro Archipelago of Panama, we report on one of the most extensive nested mangrove-coral assemblages observed, with many coral species growing on and among mangrove roots from the forest fringe extending up to 19 m into the mangrove canopy. In these habitats we found differences in coral community composition and morphology, as well as significant differences in abiotic conditions, among the mangrove canopy (≥2 m into mangrove canopy), mangrove edge (<2 m into mangrove canopy), and shallow reef. These observations, along with prior published reports, led us to conclude that these habitats are ecologically distinct and thus in need of appropriate terminology to organize their study and identify general trends in their ecology. Moreover, because mangroves and corals are frequently referenced together in the literature (for example, searches of "mangrove AND coral" and "mangrove-coral" in Scopus yielded 16,131 and 176 hits respectively), we propose the term "coexisting mangrove-coral" (CMC) habitats to distinguish nested mangrove-coral assemblages from the adjacent coral reef and mangrove habitats that have been the focus of conventional work on these communities.

To provide a baseline for further research on CMC systems, we systematically reviewed the existing literature on co-occurrences of mangroves and corals, and added new data collected from our study system in Panama. With these data we address four major goals: (1) describe a newly documented CMC system in Bocas del Toro; (2) use field data and the existing literature to identify characteristics and conditions necessary for CMC habitats to occur; (3) use these data to characterize different CMC habitat types to provide an easy-to-use classification system; and (4) predict where additional CMC habitats could occur worldwide.

1.3 Methods

Systematic review on CMC habitats

We conducted a systematic review of mangrove-coral studies using Web of Science, Scopus, and Google Scholar using search parameters calibrated on 14 known articles (Table 1.1) on the mangrove-coral system ("original papers"), to discover how widespread CMC systems are reported in the literature. The most parsimonious search term which resulted in successfully detecting our 14 test articles were "mangrove* AND coral* AND scleractinian AND root". Web of Science generated a list of 114 results, 4 of which were the original papers. Scopus detected 125 results, 5 of which were the original papers. Of all databases searched, only Google Scholar captured the full original target list and produced the most comprehensive results returning 1,920 candidate papers, which resulted in 966 after duplicates and citations were removed through the software Publish or Perish. In addition, we searched the references of all papers produced by the literature search. The last search date was January 3, 2021. HAS examined search results to exclude publications that were not relevant or simply referencing another paper that described mangrove-coral habitats. The papers remaining after this selection process were sorted into three categories: (1) papers that referenced corals growing in the mangrove habitat but did not quantify the community, (2) papers that described the coral community within the mangrove but did not include abiotic factors, or (3) papers that correlated and/or tested coral species presence in the mangrove habitat in relation to abiotic factors. Only 26 of the candidate papers met our criteria for inclusion in the review. We added 10 publications from scientific reports, theses, and non-English literature based on our expert knowledge and communication with specialists for a total of 36 publications (Table 1.1). Information extracted from the studies were: (1) location of observed mangrove-coral habitat, (2) type of mangrove-coral habitat (i.e., where the corals were found growing in relation to the mangroves), (3) mangrove species, (4) coral species, and (5) abiotic factors such as depth, pH, temperature, dissolved oxygen, salinity, turbidity, chlorophyll, alkalinity, pCO_2, HCO_3, CO_3^{2-}, Ω_{arg}, and DIC. From these data, we compiled a table of the coral species observed growing in CMC habitats, separated by CMC type (Table A1) and a table with CMC habitats characterized by region, type, mangrove species, and number of coral species observed (Table 1.2). We intended on conducting a meta-analysis of existing literature to test whether our CMC habitat typologies fit within published research, which would allow us to identify the conditions necessary for corals to thrive within mangrove habitats and to predict where additional CMC systems may exist. However, we found a lack of environmental data in the CMC literature prior to 2014, so we summarized the existing data (Tables A2 & A3).

Panama CMC description

Bocas del Toro CMC habitat description

The Bocas del Toro Archipelago of the Caribbean coast of Panama encompasses two large bays (Almirante Bay and the Chiriquí Lagoon), six large islands, a vast network of small mangrove cays, and mainland peninsulas fringed by mangroves. The area has an estimated total mangrove cover of 28 km^2, which is half of the total mangroves on the Caribbean coast of Panama (Guzmán 2003, Lovelock et al. 2005). The vegetated fringe surrounding most islands of the archipelago is best characterized as a dwarf forest, dominated by red mangroves *Rhizophora mangle* rarely exceeding 2 m in height (Araújo 2018). The islands of Bocas del Toro are surrounded by fringing coral reefs (<20 m deep) and shallow reef patches. Eighty-seven percent of the scleractinian coral species reported in Caribbean Panama are found in this area (Guzmán 2003, Guzmán et al. 2005). Bocas del Toro has a characteristic zonation pattern of corals with

Porites furcata dominating shallow areas, followed by *Agaricia agaricites* and *A. tenuifolia*, then massive corals like *Siderastrea siderea*, *Montastraea cavernosa*, *Orbicella franksi*, *Colpophyllia* spp., and *Stephanocoenia intercepta* on the reef slope (Guzmán 2003).

Bocas del Toro roving site assessments

Field observations in March 2017 suggested that common features of CMC habitats within Bocas del Toro were: mangrove forest height ≤2 m, water inundation >1 m into canopy, water depth <2 m, open patches or channels within the mangrove canopy, high levels of water circulation, limited freshwater flow, clear water, and nearby reefs (within 5 m). Based on these observations, we conducted roving site assessments across the Bocas del Toro Archipelago in January 2018 and March 2019 to determine how common CMC habitats were in this region and to evaluate how well these features correlated with coral richness of CMC habitats. Each roving site assessment covered approximately 100 m^2, which took ~25-40 minutes depending on accessibility limitations due to root density in the mangrove habitat. During each survey we recorded the number of coral species observed within the mangrove canopy, mangrove edge, and adjacent reef flat. At each site we recorded relative water clarity (e.g., visual distance), proximity to land development, freshwater inflow, and signs of pollution (e.g., garbage).

Canopy coexisting mangrove-coral map

In June 2018, we selected one of the CMC canopy sites with high coral richness (Fuego) on the eastern side of Bastimentos Island (N 09°16′23.1″, W 082°07′53.1″) to construct a 10 × 14 m grid by laying strings 2 m inland from the fringe/outermost aerial root, which was long enough to capture the distance to which corals extend into the mangroves. This site was characterized by Holocene sediments (Coates et al. 2005), and a 50–500 m wide swath of mangrove forest around the edge of the island transitioning to tropical rainforest in upland areas. Moving offshore, the mangrove forest is adjacent to gradually sloping fringe reef (0.5–3 m depth). Due to the curvature of the island and mangrove canopy, we used 2 × 2 m parallelograms as cells within the grid to maintain the same distance (2 m) from the open water (Figure 1.1B). Within each grid cell we recorded coral species richness, coral abundance (i.e., number and size of colonies), coral growth form (e.g., plating, mounding, encrusting), substrate on which coral colonies were growing, root density (quantified as the number of mangrove prop roots including bifurcation per m^2), and water depth to establish zonation patterns. For comparison, we recorded coral richness, root density, and water depth on the adjacent mangrove edge and coral richness on the adjacent reef flat along a 50 m transect. To construct the mangrove canopy coral map, we measured and mapped the location all colonies > 5 cm diameter within the grid. The GPS location of all four corners of the quadrat were taken in the field, uploaded to ArcGIS Pro v2.4.1 (ESRI 2019), and subsequently connected by drawing polylines in a newly created feature class in order to recreate the 10 × 14 m string grid. Next, a second feature class was created, and each coral was drawn as an additional polygon within that feature class.

Mangrove canopy coral monitoring and growth

Within the mapped grid, 17 of the largest coral colonies were tagged and numbered for further monitoring to determine growth and survivorship. All colonies were measured using a fabric measuring tape and reference measurement points. We returned to the study site 15 months later (September 2019) to measure growth (i.e., change in surface area) and survivorship of the tagged coral colonies from 2018. The area for most coral colonies was calculated as ellipses, but some were triangles.

Environmental measurements

At the Fuego site we recorded water temperature and light every 15 min in the mangrove canopy (2–14 m from the fringe), mangrove fringe, and on the reef flat from mid-June to mid-July 2018 with data loggers (HOBO Pendant® Temperature/Light 64K Data Logger). We also measured light as photosynthetically active radiation (PAR) using a pair of spherical underwater quantum sensors (Li-cor LI-193) to take readings within the mangrove canopy and reef habitats simultaneously in July 2018 and September 2019. We deployed YSI EXO2 multiparameter sondes a fixed point for each habitat: mangrove canopy, mangrove fringe, reef flat, and reef slope in September 2019. These sondes recorded depth, water temperature, pH, turbidity, dissolved oxygen (ODO), salinity, specific conductivity, total dissolved solids (TDS), fluorescent dissolved organic matter (fDOM), and total chlorophyll (chlorophyll *a* and *b*) every minute from 10:30 am to 5 pm.

Coexisting mangrove-coral habitat definitions

We categorized CMC habitat types described in the literature and observed in our study into lagoon, channel, edge, and canopy types based on physical setting and coral location in relation to the mangrove forest from our literature review and field observations. We created generalized diagrams to illustrate these habitat types using graphics created with vector files from Tracey Saxby, Dieter Tracey, and Joanna Woerner Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/).

Global mapping of CMC habitats

To identify areas where CMC habitats could potentially occur globally, we explored the overlap between the global distributions of coral reefs (30 m spatial resolution) (UNEP-WCMC et al. 2018) and mangroves (25 m spatial resolution) (Bunting et al. 2018) using GIS. All files were uploaded to ArcGIS Pro v2.4.1 (ESRI 2019) as shapefiles using the World Behrmann Projected Coordinate System. Due to the large sizes of the datasets, all analyses were performed for 9 separate global regions, and then the merge and dissolve tools were used to combine these regions into one global extent. To find the greatest potential CMC habitat extent, we combined two global mangrove distributions (Spalding et al. 2010, Bunting et al. 2018). The mangrove extent from Spalding et al. (2010) and the coral reef shapefile were both created using data from 1999–2003. The mangrove data from Bunting et al. (2018) were available for 1996 and 2007, so we used the intersect tool in GIS to find the area that remained the same for these two time periods, resulting in mangrove extent for the time period of 1999–2003. Then, the erase, append, and dissolve tools were used to combine the Spalding et al. (2010) and Bunting et al. (2018) mangrove extents into one global shapefile. After creating the new mangrove extent, the overlap between the mangrove and coral shapefiles was analyzed using the intersect tool, resulting in a shapefile with potential CMC habitat extent. It is possible that some of these polygons overlapped with one another, resulting in duplicate CMC habitat area. To remove this potential issue, the dissolve tool was used to dissolve the boundaries between any adjacent or overlapping CMC habitat polygons. To show how the model predictions aligned with locations of CMC observations, stars were added to Figure 1.5B as reference points. The Human Footprint Dataset (Wildlife Conservation Society 2005) was used to show the percentage of relative human influence on the biome, ranging from 0 (least influenced) to 100 (most influenced) on these potential CMC sites to highlight areas under potential threat of loss.

All reported CMC habitats in the literature to date occur at a depth <2 m. We therefore narrowed down the potential mangrove-coral habitat by areas with a tidal amplitude of ≤2 m (microtidal), since a greater tidal amplitude would lead to prolonged air exposure of corals in this area. We hypothesized that areas with larger tidal amplitudes (e.g., Pacific coast of Panama, Mozambique Channel) have mangroves that are only periodically inundated with water, therefore limiting coral settlement and growth on/among the mangrove roots. We obtained global tide variables (Matthias Obst 2017) and reclassified the raster file into two categories: ≤ 2 m and > 2 m. This reclassified raster was converted into a shapefile and the >2 m polygon was deleted from the shapefile, leaving only area with ≤2 m tidal amplitude. Finally, the clip tool was used on the overlap shapefile to obtain only the overlapping mangrove-coral extent that was within areas with ≤ 2 m tidal amplitude. For ground truthing our observation of lower coral richness with proximity to freshwater input, we used the intermittent creeks shapefile from Panama's Hydrology Network (STRI GIS Laboratory 2013) in ArcGIS Pro to measure the distance of each CMC habitat site to the nearest creek endpoint.

Analyses

All data were analyzed with R version 3.6.3 (R Core Team 2020). To summarize and visualize the multivariate environmental data collected in the mangrove canopy, mangrove fringe, reef flat, and reef slope, we used Principal Component Analysis (PCA) with the *ggfortify* and *factoextra* packages. To analyze 2018 temperature and light data, we first checked for normality using qqnorm, then used two separate GLMs to test for main effects of position within CMC habitat (reef flat, mangrove fringe, and 2, 6, 8, 12, and 14 m into the mangrove canopy), time of day, and the interaction between position and time. If an interaction was found over 24 hours, a second GLM was run at mid-day when temperature and light intensity were the greatest. If no interaction was found but significant differences were detected in one or more of the main effects, a Tukey post-hoc test was used for pairwise comparisons. All data generated or analyzed during this study are included in the tables or supplementary information files. References are provided for all studies from which data were drawn within the legend of tables. Detailed methodological information for these studies can be found within the corresponding papers.

1.4 Results

Systematic review on CMC habitats

There has been a rapid increase in the publication rate on CMC habitats, with 26 of the 36 relevant publications published since 2000 (Table 1.1). The oldest reference, that we detected, to corals growing on mangrove roots was from the Great Barrier Reef Expedition 1928-1929 (Stephenson et al. 1931), demonstrating this is not a new phenomenon. Many of these older references are difficult to obtain electronically and often are not detected in online searches, as was the case with Stephenson et al. 1931. This reference was found indirectly, through a citation within another paper that was detected with our search terms. Our search revealed that CMC habitats occur in virtually every tropical region of the world, with the highest documented number of coral species in locations in the Caribbean Sea and Australia's Great Barrier Reef (Table 1.2). There were 94 unique species of corals described as living in these CMC habitats, including results from our surveys. The most described coral genera in decreasing order are *Porites*, *Siderastrea*, *Favia*, *Manicina*, *Millepora*, *Agaricia*, and *Montastraea* (Table A1). As for mangroves, New World locations were associated with *Rhizophora mangle*, while Old World localities had a greater variety of species within the genera *Rhizophora*, *Bruguiera*, *Lumnitzera*, and *Avicennia*.

The first studies including extensive abiotic data were published in 2014, and in the time since, abiotic data have been published for only half of the locations where CMC habitats had been documented. A qualitative assessment of the limited data from the existing literature suggests that CMC habitats require (1) a connection to the open ocean/open patches or channels within mangrove stands, (2) submergence through all stages of the tidal cycle, (3) limited quantity or frequency of freshwater inputs, and (4) clear water (Yates et al. 2014, Bengtsson et al. 2019, Kellogg et al. 2020). Observed qualitative differences among mangrove sites with varying coral richness and diversity suggest that water flow and current are major determinants of mangrove suitability for corals (Bengtsson et al. 2019, Kellogg et al. 2020), but lack of quantitative measurements limit further characterization of this variable. For example, Bengtsson et al. (2019) compared abundance of coral colonies among three contiguous bodies of water (a high-flow channel, a moderate-flow creek, and a low-flow mangrove pond) and found that coral species richness was positively associated with relative differences in flow, but flow was characterized based on stillness of water and effort needed by snorkelers to maintain their position. We have compiled a summary of the current abiotic data reported for CMC systems to serve as a reference for future studies (Tables A2 & A3).

Description of CMC habitats in Panama

Roving site assessments

We observed corals growing within mangrove habitats at 29 sites across the Bocas del Toro archipelago, with coral species richness within the mangrove canopy varying by site: ≥10 species at 7 sites, 5–9 species at 5 sites, and 2–4 species at 17 sites (Figure 1.1A). Overall, we recorded 32 species of hermatypic scleractinian corals within the mangroves, with 29 species occurring under the mangrove canopy and 20 species on the mangrove edge. Two milleporid coral species were also found in both mangrove habitats. Comparatively, we observed 24 scleractinian species and 1 milleporid coral species on shallow, adjacent reef, 13 scleractinian species on reef flat (<1 m depth) and 22 scleractinian species on reef slope (>1.5 m depth) (Tables 1.3 & A1). However, only a subset of those species was found in each respective habitat at a given site. Most observed corals were shallow (≤1 m), and the furthest inland corals were found growing was 19 m into the mangrove canopy. Coral richness tended to be higher in areas with high water clarity and greater mangrove area and lower in areas close to freshwater inflow, land development, and pollution. We observed a decrease in coral species richness at multiple CMC sites between 2017 and 2019 at resampled sites, following nearby land development and the associated increase in sedimentation covering the mangrove roots (personal observation). Of the 29 CMC sites in Bocas del Toro, 4 were within 1.2 km of freshwater input (1 site off Colon Island, 1 site off Popa Island, 2 sites off Bastimentos Island), and all four sites were in the lowest species richness category. All sites with greater than 4 coral species were at least 1.8 km away from freshwater input.

Canopy coexisting mangrove-coral map

Detailed mapping of 140 m^2 of mangrove canopy shows 14 coral species growing in water depth ranging from 27 to 74 cm with high root density (31–105 roots m^{-2}) (Figure 1.1B). The nearby mangrove edge had 15 coral species in slightly deeper water (56–79 cm) and similar root density (15 to 129 roots m^{-2}). In contrast, only six coral species were observed in the adjacent reef flat. At this site, corals were observed 15 m inland from the mangrove edge. The detailed map shows a zonation pattern of smaller corals (<10 cm) growing densely along the mangrove edge (0–2 m inland) with the occasional large colony (≥1 m diameter), followed by patches of corals with varying diversity and size further into the canopy (3–7 m inland), then transitioning into a zone with the greatest coral density, dominated by large (average surface area 1.3 m^2), visibly healthy *Siderastrea siderea* colonies (8–12 m inland), and smaller, infrequent coral colonies more than 12 m inland (Figure 1.1B). Within the mangrove habitat, corals grew on varied substrates (e.g., mangrove roots, bottom between roots, on other corals) and displayed variation in coloration and growth form. On the mangrove edge both mounding and plating growth forms were observed, and coral colony colors resembled those of the adjacent reef. In the canopy encrusting and plating growth forms were predominant and there was more variation in colony coloration within species (Figure 1.1C).

Mangrove canopy coral monitoring and growth

Of the 17 individual coral colonies monitored for growth from June 2018 to September 2019, all showed sustained growth, except for a *Porites astreoides* colony, which decreased in area, and a *Colpophyllia natans* colony, which went missing (Table 1.4).

Environmental measurements

We found an interactive effect of distance from the reef and time of day on average water temperature ($P < 0.001$) with diel water temperature range increasing in variability with distance from the reef flat and peak separation in temperatures between 09:00 and 12:00 (mid-day) (Figure 1.2A). To better understand this interaction, we ran a second GLM on average mid-day temperatures and found no difference between the mangrove edge and reef flat nor the mangrove edge and 2 m into the mangrove canopy. The reef flat and mangrove edge were warmer than waters >2 m within the mangrove canopy (Table A4). Maximum temperatures recorded were 31.2 °C, 30.9 °C, and 31.0 °C on the reef flat, mangrove edge, and within the mangrove canopy (all positions averaged), respectively. There was a similar interactive effect of distance from the reef on average light ($P < 0.001$) with the greatest diel range being on the reef flat and peak light intensity across areas occurring between 10:00 and 16:00. Unlike temperature, light intensity did not follow a clear pattern. The reef flat had both the greatest mean and maximum light levels, but light within the mangrove canopy was extremely patchy and readings were not consistent with distance from the reef (Figure 1.2B). Mean photosynthetically active radiation (PAR) measurements recorded at midday (11 am–1 pm) from 2018 and 2019 showed PAR levels to be 3.5–5.5 times greater on the reef flat than within the mangrove canopy (Table A2).

PCA analysis indicated that within the CMC habitat, the mangrove edge and mangrove canopy separated based on pH, dissolved oxygen, turbidity, chlorophyll and fluorescent dissolved organic matter; meanwhile, the mangrove edge and reef flat were similar to each other (Figure 1.3). The mangrove canopy had the shallowest depth, and lowest levels of dissolved oxygen, pH, temperature, and salinity (Table A2), but the greatest average levels of chlorophyll and fluorescent dissolved organic matter. The proportion of variance explained by PCA1 was

55.52% and 26.11% by PCA2, with a cumulative proportion of variance explained of 81.63% (Figure 1.3).

Coexisting mangrove-coral habitat types and definitions

We identified the following CMC habitat types which we characterized based on physical setting and location of coral relative to the mangrove forest:

> *(1) Non-CMC habitat:* Adjacent assemblage of coral reefs and mangrove forests where these ecosystems create discrete zones (Figure 1.4A). A non-CMC habitat corresponds to the classic zonation pattern in which mangroves are near, but not overlapping with, a coral reef, oftentimes with seagrasses in between them.
>
> *(2) Lagoon CMC habitat:* Corals grow within lagoons that are semi-enclosed by mangroves. The corals are close to the mangroves, but outside the shade of the mangrove canopy (Figure 1.4B).
>
> *(3) Inlet CMC habitat:* Corals grow along mangrove channels or creeks (e.g., between mangrove islands or cays, boat channels) partially or fully under the shade of the mangrove canopy (Figure 1.4C).
>
> *(4) Edge CMC habitat:* Corals grow on and around the mangrove roots along the fringe of the mangroves partially or completely under the shade of their canopy. Edge CMC habitats are more connected with adjacent reef than other CMC habitats as they are not semi enclosed by mangroves as in Lagoon CMC habitats nor have mangrove on opposite shore as in Inlet CMC habitats. This category may include portions of fringe reefs where corals are growing under the shade of mangrove canopies (Figure 1.4D).
>
> *(5) Canopy CMC habitat:* Corals grow on and around mangrove roots, completely under the mangrove canopy and have less connection with the open ocean (e.g., water flow reduced by prop roots) than Edge or Channel CMC habitats. The interior nature of this habitat contributes to the lowest light and temperature among the various CMC habitats (Figure 1.4E).

A visualization of CMC habitats is shown in Figure 1.4F. From the scientific literature review and our surveys, a global tally of 31 coral species were identified within Canopy, 42 within Edge, 19 within Channel, and 61 within Lagoon CMC habitats (Table A1) with edge and lagoon habitats being most extensively studied at this time (Rogers and Herlan 2012, Yates et al. 2014, Camp et al. 2016, 2017, 2019).

Global mapping of CMC habitats

The intersection of mangrove habitat and coral reef distribution resulted in an overlapping global area of 805 km^2 (Figure 1.5A). 710 km^2 of this overlapping area corresponded to microtidal regimes (i.e., ≤2 m annual average) that allow mangrove aerial roots to be fully submerged through most tidal cycles so corals may grow with minimal air exposure (Figure 1.5B). Our study sites in Bocas del Toro are in the Caribbean, where only 6.6% of the potential CMC habitat extent is found; the four locations with the greatest proportion of the potential CMC habitat are the South Pacific (44.8%), Red Sea (16.8%), North Pacific (13.8%), and South China Sea (10.8%, Table 1.5).

From our systematic review and personal observations, we compiled a list of 30 CMC habitat locations throughout Bocas del Toro (Figure 1.5C). Of these 30 sites, 23 sites (77%) were within 1 km of the overlap model output. Three sites (10%) were not captured by the model around Isla Pastores because there was no mangrove coverage reported for that island, as well as no coral reef extent for the southwestern portion of the island. An additional 4 sites (13%)—two on Colon Island and two on Bastimentos Island—were not captured by the model although the two habitat layers contained mangroves and nearby coral reefs in those locations.

1.5 Discussion

In our review, we found that studies from the Caribbean show that mangrove forests are serving as critical habitat for many coral species (Yates et al. 2014, Bengtsson et al. 2019, Stewart et al. 2021), but in other regions of the world, mangroves are considered an extreme habitat, with low pH and highly variable temperature range, that selects for stress tolerant corals (Camp et al. 2016, 2017, 2018, 2019, 2020). Further research is needed to identify whether these differences in the habitat function provided by mangroves may be due to the difference between regions in the dominant CMC habitat type stress regime, or habitat requirements among coral taxa. The most commonly observed coral genera found in CMC habitats are considered stress tolerant (*Siderastrea*, *Montastraea*, *Favia*) or weedy (*Porites*, *Manicina*, *Millepora*, *Agaricia*) coral taxa (Darling et al. 2012, Courtney et al. 2020), which have been observed replacing more stress-sensitive but competitively dominant, branching coral genera on degrading reefs (Cramer et al. 2012, Darling et al. 2012). While coral reefs decrease in architectural complexity with the shifts from competitively dominant species (e.g., acroporid corals) to stress tolerant and weedy taxa with simpler morphologies, CMC habitats may compensate for complexity lost on the reef.

Since corals are dependent on areal coverage of suitable substrate, the occupation of space by mangrove roots within CMC habitats may necessitate corals to utilize compound plate and encrusting morphologies to persist (Figure 1.1C), subsequently enhancing the mangrove habitat for fishes and invertebrates (Wright 2019). Due to worldwide differences in mangrove composition and structure, it is important for future studies to collect data both on coral community abundance, richness, health, and survival as well as measure biogeochemical conditions within CMC habitats (e.g., diurnal and seasonal variations in water flow, seawater chemistry, salinity, PAR, and temperature) so that meta-analyses can be used to improve our understanding of the origin of these systems and how CMC habitats may impact conservation of coral reefs. Stewart et al. (2021) found that CMC habitats supported greater coral species richness and diversity than the adjacent shallow reef, with no difference in the amount of live coral cover (30–36%) between the two habitats (Stewart et al. 2021). Additionally, of six coral species experimentally transplanted into mangrove habitats from the reef in that study, the majority of species thrived in their new environment, demonstrating that these systems are an important habitat for corals particularly as the reef environment degrades.

The Bocas del Toro CMC habitats are primarily characterized by fringe forests in which *Rhizophora mangle* dominates (Araújo 2018), consistent with other locations throughout the Caribbean (Yates et al. 2014, Hernández-Fernández 2015, Bengtsson et al. 2019, Kellogg et al. 2020). We show that the nested mangrove-coral assemblages commonly occur across the archipelago and support many coral species. The current study is the first to show that corals will occur far into the mangrove forest, having been commonly found 8-19 m inland of the mangrove fringe. The dominant compound plate and encrusting growth forms of corals within the mangrove canopy as well as the vast color variation of colonies suggest plasticity in growth form and photophysiology in response to the complexity of mangrove architecture where average light does not decrease with distance into the canopy and instead is patchy due to variation in canopy structure (e.g., sunflecks) and forest density. Since coral distribution within mangroves can be patchy (Bengtsson et al. 2019, Camp et al. 2019, Stewart et al. 2021), we questioned whether it may be more closely related to light than temperature limitations. Darker pigment and flattened morphologies of corals are common in mesophotic reefs (Dustan 1979, Kühlmann 1983, Kahng et al. 2010) as a physiological adaptation to low light conditions. These adaptations which maximize light captured by increasing light-harvesting pigments and reducing the ratio of tissue to projected area for increased light capture efficiency (Stambler and Dubinsky 2005, Cohen and Dubinsky 2015, Kahng et al. 2019), and could be utilized in the mangrove for the same purpose. Further, flattened morphologies may be a response of coral colonies to grow through lateral expansion rather than upward to avoid exposure at low tide (Stewart et al. 2021). However, the thin plate and cup forms of coral colonies may also limit growth within the mangrove habitat as these corals are extremely fragile and have been observed to break with root movement (e.g., swaying from boat wake). Based on our monitoring of mangrove corals, we found more successful growth types, based on growth rate and survival, to be those that wrap around multiple mangrove roots or cement the root to the ground for stabilization.

With an increasing rate of research emerging on nested mangrove-coral assemblages, consistent terminology is required to distinguish these systems from traditional adjacent coral reef and mangrove forest ecotones. We believe the terminology proposed here will help to identify the system being studied and aid in meaningful geographic comparisons, as has been done separately for coral reefs or mangrove forests (Lugo and Snedaker 1974, Spalding et al. 2001). While we highlight the commonalities and distinctive characteristics of nested mangrove-coral assemblages, we are aware that we lack data on the health and functioning of CMC habitats in most parts of the world that may reveal important information about future trends of these mangrove-coral associations.

The field of studying CMC systems is new and rapidly developing due to its potential importance for marine conservation. Despite observations of corals growing on mangrove roots found in the scientific literature going back 90 years, there remains little known about the ecological parameters that define where these habitats exist. It is time for these natural history observations to be compiled with the quantitative data to date to help describe these systems and understand their global importance. Potential positive controls, suggested from our systematic review and field observations, are a connection to the open ocean/open patches or channels within mangrove canopy, submergence through all stages of the tidal cycle, and close proximity (~5 m) to coral reef/source. Meanwhile, potential negative controls identified were land development, pollution, sedimentation, and freshwater in flow. We observed that land development, pollution, and sedimentation were negatively correlated with the number of coral species present in CMC habitats and frequently completely limited coral presence or survival. Freshwater inflow (e.g., proximity to a creek) seemed to consistently limit coral presence in our surveys. CMC habitats from the literature were described as being without freshwater influence other than rain and subsoil water (Bengtsson et al. 2019). While some studies mentioned the importance of water flow and current (Bengtsson et al. 2019, Kellogg et al. 2020), we did not find consistency in ranges that could be used as a criterion. In Panama we observed greater coral richness and abundance in windward mangrove areas relative to leeward sites (Chapter 4), suggesting the potential importance of wave exposure. However, corals could be found in both habitats. The current literature is regionally biased, with most published studies restricted the Caribbean region. Until there is greater global representation, the current criteria we established should be viewed as an evolving framework to inform potential metrics and to build from. For example, in the Caribbean, corals in CMC habitats may need to be submerged through all stages of the tidal cycle, whereas in the Pacific where corals are more commonly exposed to air, tidal submergence may not be such a limiting factor.

Our GIS simulation based on tidal regime and mangrove/coral distribution suggested that the global extent of CMC communities could be substantial throughout the tropics. Although more knowledge is needed to refine global models, models such as ours creates a baseline for the field to progress by suggesting which geographic locations should be the target of future studies. Given the global threats to mangrove habitats and coral reefs, we wanted to reference where these unique CMC habitats may be occurring relative to the human footprint in those areas. This is important to highlight potential areas in need of future exploration and protection. The majority of current CMC literature is focused on Caribbean locations (Almy and Carrion-Torres 1963, Rogers and Herlan 2012, Yates et al. 2014, Hernández-Fernández 2015, Bengtsson et al. 2019, Kellogg et al. 2020, Scavo Lord et al. 2020b, Stewart et al. 2021), an area representing 6.6% of the potential global extent in our GIS analysis. If further exploration is conducted in the South and North Pacific (where 58.6% of the area is potentially suitable CMC habitat), we could perhaps better understand CMC ecosystem variability and the environmental conditions driving it. Improving our understanding of how coral and mangrove ecosystems interact is essential to determine the significance of CMC habitats for coral survival in the face of climate change and other anthropogenic impacts so that we can identify how to best conserve and protect these unique ecosystems.

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1.7 References

Almy, C. C., and C. Carrion-Torres. 1963. Shallow-water stony corals of Puerto Rico. Pages 1-44 Institute of Caribbean Studies.

Alongi, D. M., L. A. Trott, Rachmansyah, F. Tirendi, A. D. McKinnon, and M. C. Undu. 2008. Growth and development of mangrove forests overlying smothered coral reefs, Sulawesi and Sumatra, Indonesia. Marine Ecology Progress Series 370:97–109.

Angelini, C., A. H. Altieri, B. R. Silliman, and M. D. Bertness. 2011. Interactions among foundation species and their consequences for community organization, biodiversity, and conservation. BioScience 61:782–789.

Araújo, R. J. 2018. Mangrove forests of Bocas del Toro Province and the Ngöbe-Buglé Comarca, Panama: Structural description and comparision to neotropical forests. Pages 182–207 *in* D. O. Suman and A. K. Spalding, editors. Coastal resources of Bocas del Toro, Panama: Tourism and development pressures and the quest for sustainability. University of Miami, Coral Glables, FL.

Altieri, A. H., and J. Van De Koppel. 2013. Foundation species in marine ecosystems. Pages 37-56 in M. D. Bertness, J. F. Bruno, B. R. Silliman, and J. J. Stachowicz, editors. Marine Community Ecology and Conservation. Sinauer Associates, Sunderland, Massachusetts.

Bengtsson, Z. A., K. M. Kuhn, A. T. Battaglino, A. S. Li, M. N. Talbot, M. Wafapoor, C. J. Atta, S. P. Margolis, E. A. Rar, E. M. Burmester, K. C. Lesneski, K. S. Lord, L. Kaufman, M. B. Kowalski, S. P. Margolis, E. A. Rar, E. M. Burmester, K. C. Lesneski, K. Scavo, L. Kaufman, N. L. Stewart, and J. R. Finnerty. 2019. *Porites divaricata* is a locally abundant component of the epibiont community on mangrove prop roots at Calabash Caye, Turneffe Atoll, Belize. Caribbean Naturalist 67:1–16.

Bunting, P., A. Rosenqvist, R. M. Lucas, L. M. Rebelo, L. Hilarides, N. Thomas, A. Hardy, T. Itoh, M. Shimada, and C. M. Finlayson. 2018. The global mangrove watch - A new 2010 global baseline of mangrove extent. Remote Sensing 10.

Buob, A. M. 2019. Characterization of red mangrove proproot epibiont communities of St. Johns USVI. Montclair State University. MSc Thesis.

Camp, E. F., T. Kahlke, M. R. Nitschke, D. Varkey, N. L. Fisher, L. Fujise, S. Goyen, D. J. Hughes, C. A. Lawson, M. Ros, S. Woodcock, K. Xiao, W. Leggat, and D. J. Suggett. 2020. Revealing changes in the microbiome of Symbiodiniaceae under thermal stress. Environmental Microbiology 22:1294–1309.

Camp, E. F., J. Edmondson, A. Doheny, J. Rumney, A. J. Grima, A. Huete, and D. J. Suggett. 2019. Mangrove lagoons of the Great Barrier Reef support coral populations persisting under extreme environmental conditions. Marine Ecology Progress Series 625:1–14.

Camp, E. F., V. Schoepf, P. J. Mumby, L. A. Hardtke, R. Rodolfo-Metalpa, D. J. Smith, and D. J. Suggett. 2018. The future of coral reefs subject to rapid climate change: Lessons from natural extreme environments. Frontiers in Marine Science 5:1–21.

Camp, E. F., M. R. Nitschke, R. Rodolfo-Metalpa, F. Houlbreque, S. G. Gardner, D. J. Smith, M. Zampighi, and D. J. Suggett. 2017. Reef-building corals thrive within hot-acidified and deoxygenated waters. Scientific Reports 7:1–9.

Camp, E. F., D. J. Suggett, G. Gendron, J. Jompa, C. Manfrino, and D. J. Smith. 2016. Mangrove and seagrass beds provide different biogeochemical services for corals threatened by climate change. Frontiers in Marine Science 3:1–16.

Coates, A. G., D. F. McNeill, M. P. Aubry, W. A. Berggren, and L. S. Collins. 2005. An introduction to the geology of the Bocas del Toro Archipelago, Panama. Caribbean Journal of Science 41:374–391.

Cohen, I., and Z. Dubinsky. 2015. Long term photoacclimation responses of the coral *Stylophora pistillata* to reciprocal deep to shallow transplantation: photosynthesis and calcification. Frontiers in Marine Science 2:1–13.

Cramer, K. L., J. B. C. Jackson, C. V. Angioletti, J. Leonard-Pingel, and T. P. Guilderson. 2012. Anthropogenic mortality on coral reefs in Caribbean Panama predates coral disease and bleaching. Ecology Letters 15:561–567.

Dayton, P. K. 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos of McMurdo Sound, Antarctica. Pages 81-95 in B. C. Parker, editor. Proceedings of the Colloquium on Conservation Problems in Antarctica. Allen Press, Lawrence, KS.

Dustan, P. 1979. Distribution of zooxanthellae and photosynthetic chloroplast pigments of the reef-building coral *Montastrea*. Bulletin of Marine Science 29:79–95.

Eagleson, R. 2019. Spatial distribution of benthic habitats and ecological patterns of the Mustard Hill Coral (*Porites astreoides*) in the nearshore waters of Grenada. The University of Guelph. MSc Thesis.

Ellison, A., M. Bank, B. Clinton, E. Colburn, K. Elliot, C. Ford, D. Foster, B. Kloeppel, J. Knoepp, G. Lovett, J. Mohan, D. Orwig, J. Thompson, B. Von Holle, and J. Webster. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 3:479-486.

ESRI. 2019. ArcGIS Pro: Release 2.4.1. Redlands, CA: Environmental Systems Research Institute.

Farnsworth, E. J., and A. M. Ellison. 1996. Scale-dependent spatial and temporal variability in biogeography of mangrove root epibiont communities. Ecological Monographs 66:45–66.

Fishelson, L. 1971. Ecology and distribution of the benthic fauna in the shallow waters of the Red Sea. Marine Biology: International Journal on Life in Oceans and Coastal Waters 10:113–133.

Fujimoto, K., and T. Miyagi. 1993. Development process of tidal-flat type mangrove habitats and their zonation in the Pacific Ocean. Vegetatio 106:137–146.

Fujimoto, K., Y. Mochida, T. Kikuchi, R. Tabuchi, Y. Hirata, and S. Lihpai. 2015. The relationships among community type, peat layer thickness, belowground carbon storage and habitat age of mangrove forests in Pohnpei Island, Micronesia. Open Journal of Forestry 5:48–56.

Gillis, L. G., T. J. Bouma, C. G. Jones, M. M. Van Katwijk, I. Nagelkerken, C. J. L. Jeuken, P. M. J. Herman, and A. D. Ziegler. 2014. Potential for landscape-scale positive interactions among tropical marine ecosystems. Marine Ecology Progress Series 503:289–303.

Granek, E. F., J. E. Compton, and D. L. Phillips. 2009. Mangrove-exported nutrient incorporation by sessile coral reef invertebrates. Ecosystems 12:462–472.

Guzmán, H. M. 2003. Caribbean coral reefs of Panama: Present status and future perspectives. Pages 241–274 *in* J. Cortés, editor. Latin American Coral Reefs. Elsevier Science B.V., Amsterdam, The Netherlands.

Guzmán, H. M., P. A. G. Barnes, C. E. Lovelock, and I. C. Feller. 2005. A site description of the CARICOMP mangrove, seagrass and coral reef sites in Bocas del Toro, Panama. Caribbean Journal of Science 41:430–440.

Hernández-Fernández, L. 2015. Corales petreos sobre raices sumergidas de *Rhizophora mangle* L. del Parque Nacional Jardines de la Reina, Cuba. Revista Investigaciones Marinas 35:16–20.

Huijbers, C. M., E. M. Mollee, and I. Nagelkerken. 2008. Post-larval French grunts (*Haemulon flavolineatum*) distinguish between seagrass, mangrove and coral reef water: Implications for recognition of potential nursery habitats. Journal of Experimental Marine Biology and Ecology 357:134–139.

Igulu, M. M., I. Nagelkerken, M. Dorenbosch, M. G. G. Grol, A. R. Harborne, I. A. Kimirei, P. J. Mumby, A. D. Olds, and Y. D. Mgaya. 2014. Mangrove habitat use by juvenile reef fish: Meta-analysis reveals that tidal regime matters more than biogeographic region. PLoS ONE 9.

Kahng, S. E., D. Akkaynak, T. Shlesinger, E. J. Hochberg, J. Wiedenmann, R. Tamir, and D. Tchernov. 2019. Light, temperature, photosynthesis, heterotrophy, and the lower depth limits of mesophotic coral ecosystems. Pages 801–828 *in* Y. Loya, K. A. Puglise, and T. Bridge, editors. Coral Reefs of the World. Springer Nature Switzerland AG, Cham, Switzerland.

Kahng, S. E., J. R. Garcia-Sais, H. L. Spalding, E. Brokovich, D. Wagner, E. Weil, L. Hinderstein, and R. J. Toonen. 2010. Community ecology of mesophotic coral reef ecosystems. Coral Reefs 29:255–275.

Kellogg, C. A., R. P. Moyer, M. Jacobsen, and K. K. Yates. 2020. Identifying mangrove-coral habitats in the Florida Keys. PeerJ 8.

Kühlmann, D. H. H. 1983. Composition and ecology of deep-water coral associations. Helgoländer Meeresuntersuchungen 36:183–204.

de la Guardia, E., J. A. Gaspar González-Sansón, C. Aguilar, and P. González-Díaz. 2004. Biodiversidad en la zona de buceo del Parque Nacional de Punta Francés, Isla de la Juventud, Cuba. Revista Investigaciones Marinas 25:90–102.

Lovelock, C. E., I. C. Feller, K. L. McKee, and R. Thompson. 2005. Variation in mangrove forest structure and sediment characteristics in Bocas del Toro, Panama. Caribbean Journal of Science 41:456–464.

Loya, Y. 1976. The Red Sea coral *Stylophora pistillata* is an r strategist. Nature 259:478–480.

Lugo, A. E., and S. C. Snedaker. 1974. The ecology of mangroves. Annual Review of Ecology and Systematics 5:39–64.

Macintyre, I. G., I. Goodbody, K. Rützler, D. S. Littler, and M. M. Littler. 2000. A general biological and geological survey of the rims of ponds in the major mangrove islands of the Pelican Cays, Belize. Atoll Research Bulletin 467.

Macintyre, I. G., M. A. Toscano, I. C. Feller, and M. A. Faust. 2009. Decimating mangrove forests for commercial development in the Pelican Cays, Belize: Long-term ecological loss for short-term gain? Smithsonian Contributions to the Marine Sciences:281–290.

Matthias Obst. 2017. Global tidal variables. Version 1.0 University of Gothenburg, Department of Marine Sciences. Swedish national data service.

Ooi, A. L., and V. C. Chong. 2011. Larval fish assemblages in a tropical mangrove estuary and adjacent coastal waters: Offshore-inshore flux of marine and estuarine species. Continental Shelf Research 31:1599–1610.

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Rogers, C. S. 2009. High diversity and abundance of scleractinian corals growing on and near mangrove prop roots, St. John, US Virgin Islands. Coral Reefs 28:909.

Rogers, C. S. 2017. A unique coral community in the mangroves of Hurricane Hole, St. John, US

Virgin Islands. Diversity 9.

Rogers, C. S., and J. J. Herlan. 2012. Life on the edge: corals in mangroves and climate change. Pages 9–13 Proceedings of the 12th International Coral Reef Symposium. Cairns, Australia.

Rützler, K., M. C. Diaz, R. W. M. Van Soest, S. Zea, K. P. Smith, B. Alvarez, and J. L. Wulff. 2000. Diversity of sponge fauna in mangrove ponds, Pelican Cays, Belize. Atoll Research Bulletin 476.

Rützler, K., I. Goodbody, M. C. Diaz, I. C. Feller, and I. G. Macintyre. 2004. The aquatic environment of Twin Cays, Belize. Washington, D.C.

Scavo Lord, K., K. C. Lesneski, Z. A. Bengtsson, K. M. Kuhn, J. Madin, B. Cheung, R. Ewa, J. F. Taylor, E. M. Burmester, J. Morey, L. Kaufman, and J. R. Finnerty. 2020. Multi-year viability of a reef coral population living on mangrove roots suggests an important role for mangroves in the broader habitat mosaic of corals. Frontiers in Marine Science 7:1–16.

Scavo Lord, K., A. Barcala, H. E. Aichelman, N. G. Kriefall, C. Brown, L. Knasin, and R. Secor. 2021. Distinct phenotypes associated with mangrove and lagoon habitats in two widespread Caribbean corals, Porites astreoides and Porites divaricata. Biology Bulletin 240.

Shideler, G. S., R. J. Araujo, B. K. Walker, J. Blondeau, and J. E. Serafy. 2017. Non-linear thresholds characterize the relationship between reef fishes and mangrove habitat. Ecosphere 8:1–18.

Spalding, M., M. D. Spalding, C. Ravilious, and E. P. Green. 2001. World Atlas of Coral Reefs. University of California Press, London, England.

Spalding, M. D., M. Kainuma, and L. Collins. 2010. World Atlas of Mangroves. Earthscan, London, UK.

Stambler, N., and Z. Dubinsky. 2005. Corals as light collectors: An integrating sphere approach. Coral Reefs 24:1–9.

Stephenson, T. A., A. Stephenson, G. Tandy, and M. Spender. 1931. The structure and ecology of low isles and other reefs. Great Barrier Reef Expedition 1928-29 Vol. III, No. 2.

Stewart, H. A., D. I. Kline, L. J. Chapman, and A. H. Altieri. 2021. Caribbean mangrove forests act as coral refugia by reducing light stress and increasing coral richness. Ecosphere 12:e03413.

UNEP-WCMC, W. Centre, WRI, and TNC. 2018. Global distribution of warm-water coral reefs, compiled from multiple sources including the Millennium Coral Reef Mapping Project. Version 4.0 Includes contributions from IMaRS-USF and IRD (2005), IMaRS-UF (2005) and Spalding et al. (2001). Cambridge (UK): UN Environment World Conservation Monitoring Centre.

van de Koppel, J., T. van der Heide, A. H. Altieri, B. K. Eriksson, T. J. Bouma, H. Olff, and B. R. Silliman. 2015. Long-distance interactions regulate the structure and resilience of coastal ecosystems. Annual Review of Marine Science 7:139-158.

Wildlife Conservation Society. 2005. WCS, and Center for International Earth Science Information Network - CIESIN - Columbia University. Last of the Wild Project, Version 2, 2005 (LWP-2): Global Human Footprint Dataset (Geographic). Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC). https://doi.org/10.7927/H4M61H5F. Accessed 9 May, 2021.

Wright, J. L. 2019. The effects of coral presence among Red Mangrove (*Rhizophora mangle*) prop roots on Caribbean fish communities. University of Miami.

Yates, K. K., C. S. Rogers, J. J. Herlan, G. R. Brooks, N. A. Smiley, and R. A. Larson. 2014. Diverse coral communities in mangrove habitats suggest a novel refuge from climate change. Biogeosciences 11:4321–4337.

Yunus, M. Z. M., F. S. Ahmad, and N. Ibrahim. 2018. Mangrove vulnerability index using GIS. AIP Conference Proceedings 1930.

1.8 Tables

Table 1.1 Results of systematic review on coexisting mangrove-coral (CMC) literature. Publications in bold were the original papers that the search parameters were based around.

Appeared in search?	Location	Publication
Reference coexisting mangrove-coral (CMC) habitats but do not quantify		
Yes	Puerto Rico	Almy & Carrion-Torres 1963
Yes	U.S. Virgin Islands	**Rogers et al. 2008, Rogers 2009,** Rogers 2019
Yes	Belize	**Macintyre et al. 2000, 2009**
Yes	Panama	Granek et al. 2009, MacDonald and Weis 2013
Yes	Grenada	Eagleson 2019
Yes	Northern Red Sea	Fishelson 1971, Loya 1976
No	Belize	Rützler et al. 1969, **2000,** 2004, Rützler and Macintyre 1982, Farnsworth and Ellison 1996
No	Cuba	de la Guardia et al. 2004
Describe CMC coral community but do not include abiotic factors		
Yes	Cuba	**Hernández-Fernández 2015**
Yes	U.S. Virgin Islands	**Rogers 2017**
Yes	Belize	**Bengtsson et al. 2019,** Scavo Lord et al. 2020
No	U.S. Virgin Islands	Buob 2019
Include both CMC coral community and abiotic data		
Yes	Florida	Kellogg et al. 2020
Yes	U.S. Virgin Islands	**Rogers & Herlan 2012, Yates et al. 2014**
Yes	Belize	Scavo Lord et al. 2021
Yes	Panama	**Wright 2019,** Stewart et al. 2021
Yes	Northern Red Sea	Por et al. 1977
Yes	Seychelles	**Camp et al. 2016**
Yes	Sulawesi	**Camp et al. 2016**
Yes	Great Barrier Reef	**Camp et al. 2019**
Yes	New Caledonia	**Camp et al. 2017,** Camp et al. 2020
No	Great Barrier Reef	Stephenson et al. 1931
No	Northern Red Sea	Por and Dor 1975

Table 1.2 Coexisting mangrove-coral (CMC) habitats by region. Coexisting mangrove-coral (CMC) habitats reported in existing literature and our study, indicating location of observations, type of CMC habitat, family of mangrove corals were found growing within, number of coral species observed, and the source from which the information was obtained. [1] This study and Stewart et al. 2021, [2] Granek et al. 2009, [3] Hernández-Fernández 2015, [4] de la Guardia et al. 2004, [5] Almy et al. 1963, [6] Kellogg et al 2020, [7] Rogers 2009, [8] Rogers 2017, [9] Rogers and Herlan 2012, [10] Buob 2019, [11] Yates et al. 2014, [12] Rützler et al 2004, [13] Macintyre et al 2000, [14] Bengtsson et al. 2019, [15] Lord et al 2020, [16] Por and Dor 1975, [17] Loya 1976, [18] Por et al. 1977, [19] Fishelson 1971, [20] Camp et al. 2016, [21] Stephenson et al. 1931, [22] Camp et al. 2017, [23] Camp et al. 2019.

Region	**CMC Type**	**Mangrove Species**	**Coral Richness**
Caribbean Panama	Canopy[1] and Edge[1-2]	*Rhizophora mangle*	34
Cuba	Edge[3] and Channel[4]	*Rhizophora mangle*	13
Puerto Rico	Edge[5]	*Rhizophora mangle*	3
Florida Keys	Edge[6] and Channel[6]	*Rhizophora mangle*	6
U.S. Virgin Islands	Edge[7-11]	*Rhizophora mangle*	37
Belize	Edge[12-13], Channel[12,14-15], and Lagoon[13]	*Rhizophora mangle*	22
Northern Red Sea	Lagoon[16-19]	*Avicennia marina*	1
Seychelles	Lagoon[19]	*Rhizophora mucronata, Lumnitzera racemosa, Bruguiera gymnorhiza,* and *Avicennia marina*	8
Sulawesi	Lagoon[19]	*Rhizophora stylosa*	9
New Caledonia	Lagoon[20]	species not listed	19
Great Barrier Reef	Edge[21], Channel[21] and Lagoon[21-23]	*Rhizophora mucronata*	35

Table 1.3 Mangrove and reef coral species. Coral species observed growing within coexisting mangrove-coral (CMC) habitats and adjacent reef in Bocas del Toro, Panama.

Coral Species	Edge CMC	Canopy CMC	Overall Mangrove	Reef Flat	Reef Slope	Overall Reef
Agaricia agaricites	X	X	X	X	X	X
Agaricia fragilis	X	X	X	X	X	X
Agaricia humilis		X	X		X	X
Agaricia lamarcki	X	X	X	X	X	X
Agaricia tenuifolia	X	X	X	X	X	X
Colpophyllia natans	X	X	X	X	X	X
Diploria labyrinthiformis		X	X		X	X
Dichocoenia stokesi		X	X		X	X
Eusmilia fastigiata	X	X	X	X		X
Favia fragum		X	X			
Helioseris cucullata		X	X			
Isophyllia sinuosa		X	X			
Isophyllia rigida		X	X			
Madracis auretenra					X	X
Manicina areolata	X	X	X	X	X	X
Meandrina meandrites					X	X
Millepora alcicornis	X	X	X	X	X	X
Millepora complanata	X	X	X			
Montastraea cavernosa	X	X	X	X	X	X
Mussa angulosa	X	X	X		X	X
Mycetophyllia aliciae		X	X			
Orbicella annularis	X		X		X	X
Orbicella faveolata	X	X	X		X	X
Orbicella franksi	X		X			
Phyllangia americana	X	X	X			
Porites astreoides	X	X	X	X	X	X
Porites divaricata		X	X	X		X
Porites furcata	X	X	X	X	X	X
Porites porites	X		X	X	X	X
Pseudodiploria clivosa	X	X	X		X	X
Pseudodiploria strigosa		X	X			
Scolymia cubensis	X	X	X		X	X
Scolymia lacera		X	X			
Siderastrea radians	X	X	X			
Siderastrea siderea	X	X	X	X	X	X
Solenastrea bournoni					X	X
Stephanocoenia intersepta		X	X			
Total species observed:	**22**	**31**	**34**	**14**	**23**	**25**

Table 1.4 Mangrove canopy coral colony growth. Tagged coral colonies monitored from June 2018 to September 2019. All corals monitored over 15 months, except for one *Porites astreoides* colony (decrease in area) and the *Colpophyllia natans* colony (missing in 2019), showed sustained growth.

Coral ID	Distance into Mangrove Canopy	Coral Species	Initial Area (cm^2)	Change in Area (cm^2)	Change in Area (%)
990	6-8 m	*Agaricia fragilis*	1925	1550	80
989	2-4 m	*Colpophyllia natans*	57	NA	NA
997	6-8 m	*Porites astreoides*	580	-10	-2
992	8-10 m	*Porites astreoides*	186	56	30
988	2-4 m	*Pseudodiploria clivosa*	90	119	132
985	6-8 m	*Pseudodiploria clivosa*	1785	112	6
998	6-10 m	*Pseudodiploria clivosa*	1655	89	5
986	8-10 m	*Pseudodiploria clivosa*	663	111	17
1000	4-6 m	*Pseudodiploria strigosa*	297	122	41
999	6-8 m	*Pseudodiploria strigosa*	971	135	14
991	6-8 m	*Siderastrea siderea*	15056	2046	14
996	8-10 m	*Siderastrea siderea*	8445	609	7
993	8-10 m	*Siderastrea siderea*	7106	1324	19
983	8-12 m	*Siderastrea siderea*	12417	1021	8
984	10-12 m	*Siderastrea siderea*	10295	227	2
994	10-14 m	*Siderastrea siderea*	12648	2241	18
995	12-14 m	*Siderastrea siderea*	16713	55	0

Table 1.5 Potential global extent of coexisting mangrove-coral habitats. Potential extent of mangrove and coral reef habitat overlap (within ≤2 m tidal amplitude; displayed in Figure 1.5B), based on GIS analysis, divided into 9 global regions.

Region	Global Overlap (km^2)	Global Overlap (%)
Red Sea	119.10	16.8%
Persian Gulf	0.44	0.1%
Indian Ocean	48.74	6.9%
South China Sea	76.76	10.8%
North Pacific	98.37	13.8%
South Pacific	317.89	44.8%
Caribbean	47.23	6.6%
North Atlantic	0.01	0.0%
South Atlantic	1.66	0.2%
Total	**710.20**	**100%**

1.9 Figures

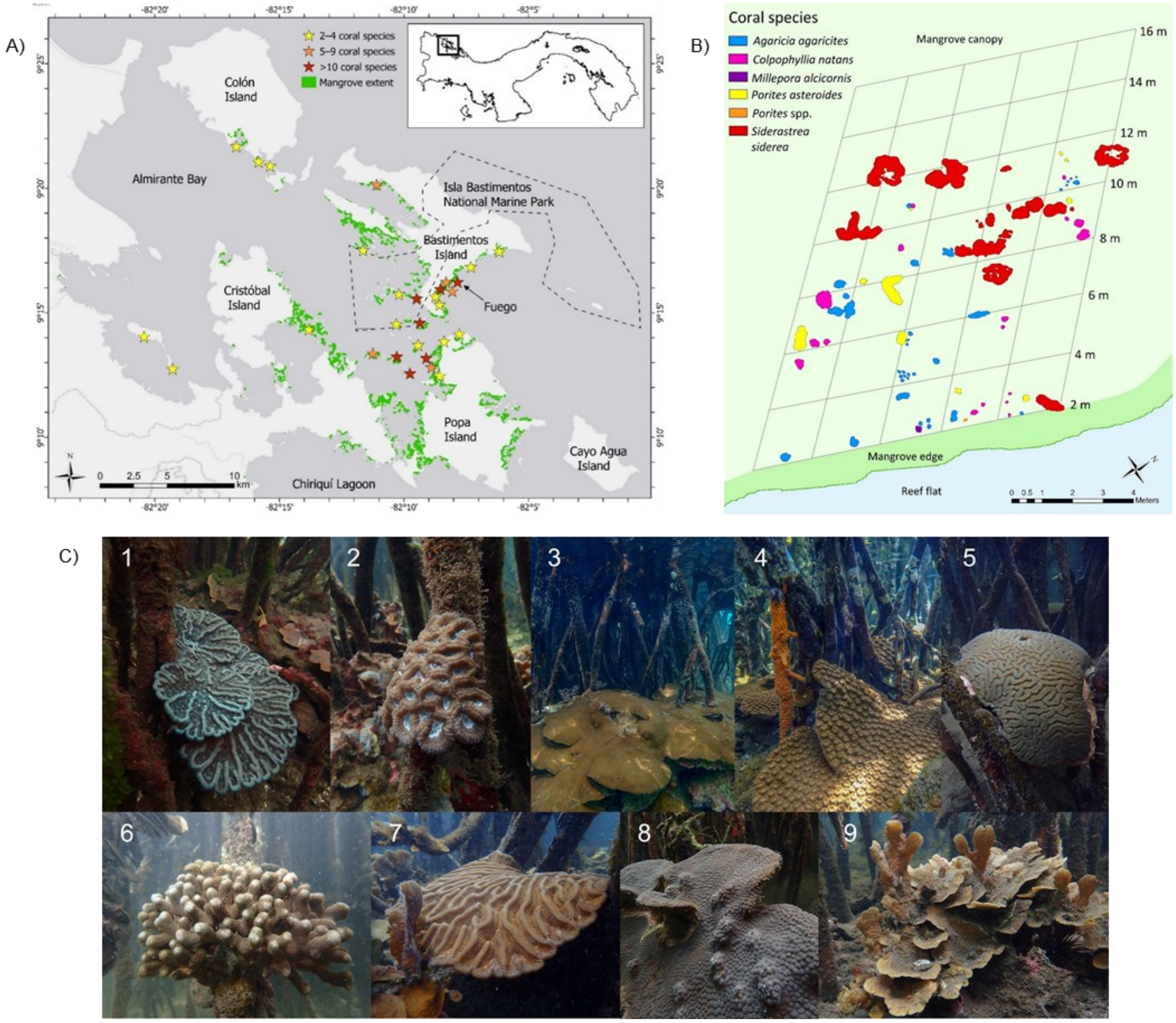

Figure 1.1 Coexisting mangrove-coral habitats of Bocas del Toro, Panama. (A) Confirmed coexisting mangrove-coral sites of Bocas del Toro with coral species richness, mangrove extent, and marine protected area (Isla Bastimentos National Marine Park). (B) mangrove canopy zonation map of coral colonies >5×5 cm at Fuego site. *Porites* spp. are branching species (*Porites porites*, *P. furcata*, or *P. divaricata*). (C) Mangrove coral growth forms and strategies (e.g., growing on or between roots). Coral species: 1) *Mycetophyllia aliciae* 2) *Isophyllia rigida,* 3) *Siderastrea siderea,* 4) *Montastraea cavernosa,* 5) *Diploria labyrinthiformis,* 6) *P. furcata,* 7) *Colpophyllia natans,* 8) *Orbicella faveolata,* 9) *Agaricia tenuifolia*.

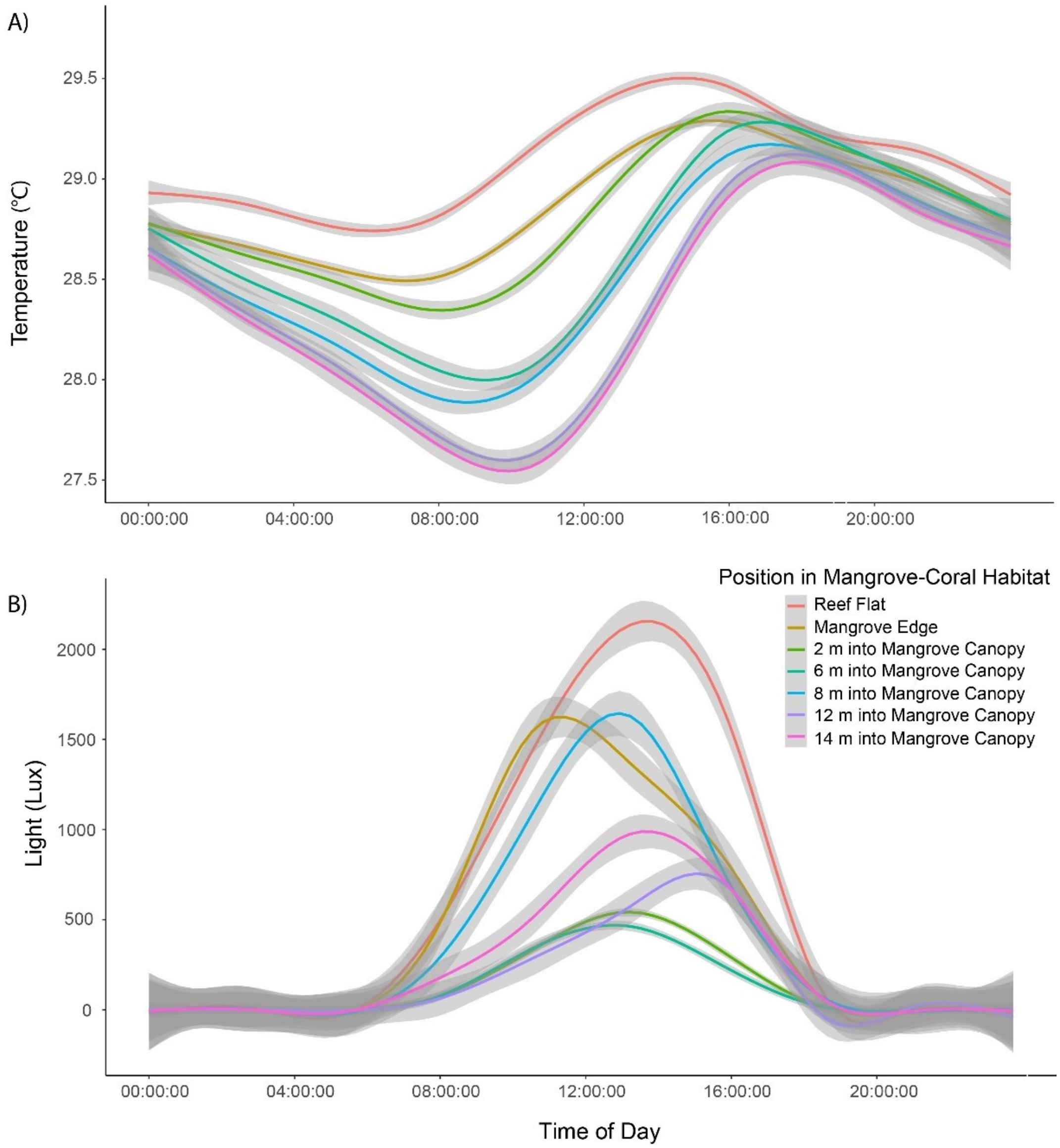

Figure 1.2 Daily A) mean temperature and B) mean light profiles. Data collected from June-July 2018 with 95% confidence interval (gray) of positions within mangrove-coral habitat on the reef flat (red), mangrove edge (gold), and mangrove canopy increasing every 2 m into the canopy from 2 m (green), 6 m (teal), 8 m (blue), 12 m (purple) to 14 m (magenta). Average water temperature was greatest on the reef flat and progressively decreased with depth into the mangrove canopy.

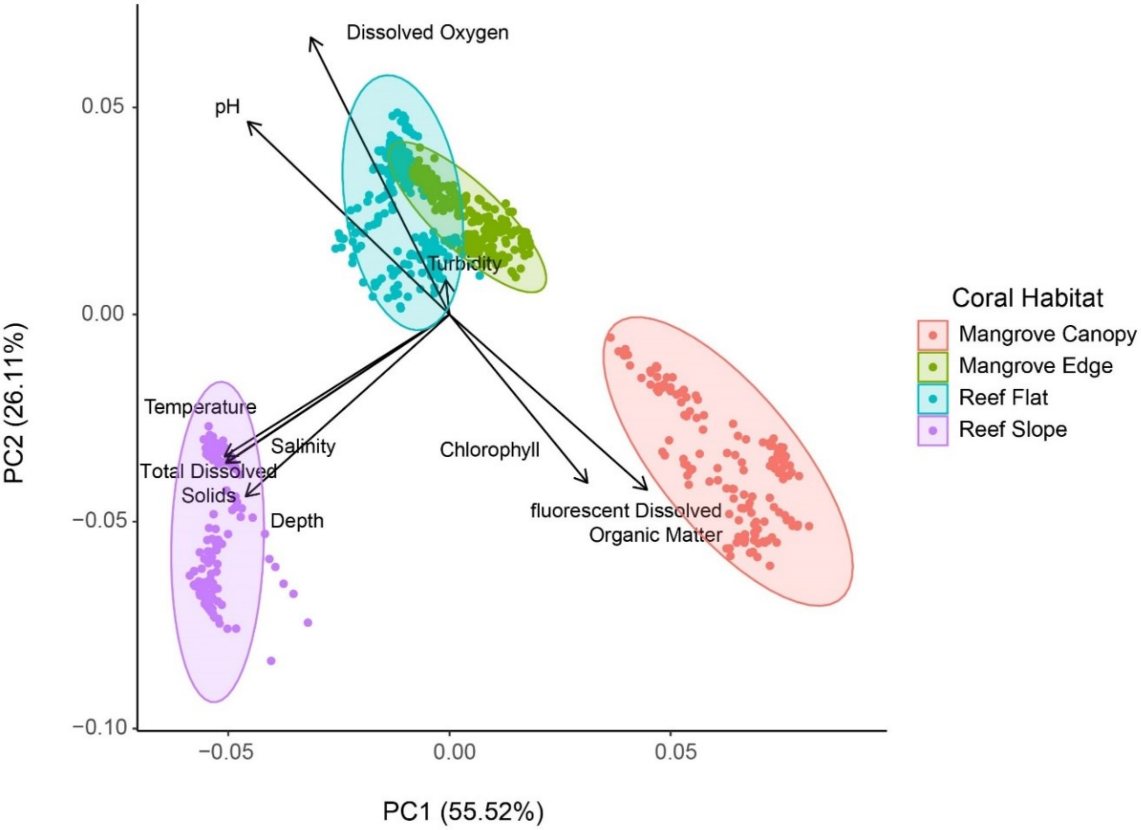

Figure 1.3 Abiotic distinction of coral habitats in Bocas del Toro, Panama. Principal Component Analysis of chlorophyll, fluorescent dissolved organic matter (fDOM), temperature, salinity, total dissolved solids (TDS), dissolved oxygen (ODO), and pH over four coral habitats. Points are the raw data and color represents the habitat those data correspond to.

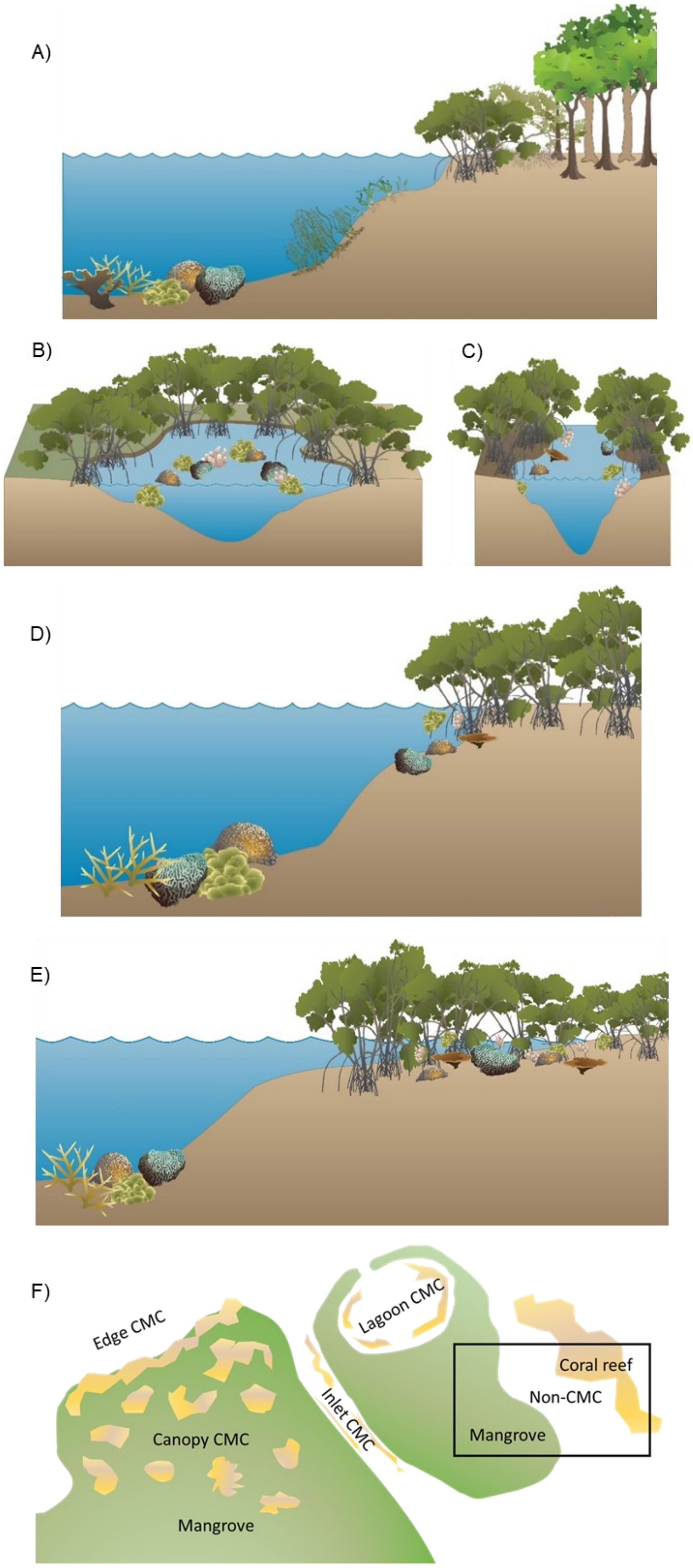
A)
B)
C)
D)
E)
F)
Edge CMC
Lagoon CMC
Coral reef
Non-CMC
Inlet CMC
Canopy CMC
Mangrove
Mangrove

Figure 1.4 Coexisting mangrove-coral (CMC) assemblage types. (A) *Non-CMC*: discrete adjacent assemblage of coral reefs and mangrove forests. (B) *Lagoon CMC*: corals along semi-enclosed mangrove lagoons outside the shade of the mangrove canopy, but close enough for biogeochemical influence. (C) *Inlet CMC*: corals along mangrove channels partially under shade. (D) *Edge CMC*: partially or completely shaded corals grow on and around mangrove roots along the fringe of the mangrove. (E) *Canopy CMC*: corals grow completely under the mangrove canopy with the lowest light among CMC habitats. (F) CMC habitats relative to each other. Graphics created with vector files from ian.umces.edu/imagelibrary/.

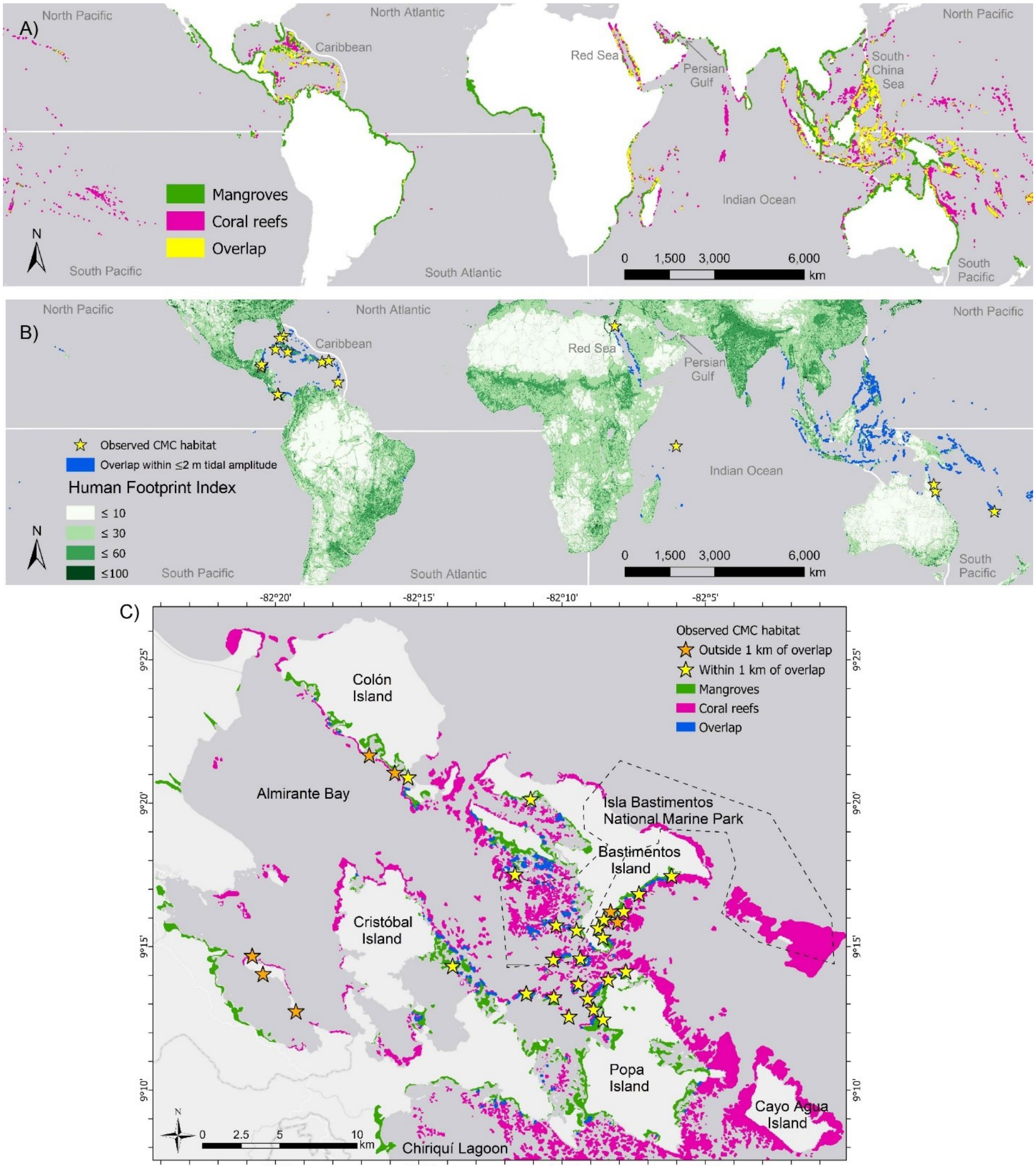

Figure 1.5 Potential global extent of coexisting mangrove-coral (CMC) habitats. (A) Global distribution of mangroves (green) and coral reefs (pink), showing overlap (up to 10 m annual average tidal amplitude) of their extents (yellow). (B) Microtidal overlap (≤2 m annual average tidal amplitude) wherein mangrove roots are fully submerged at all tidal cycles. Stars represent CMC habitat locations obtained from literature review to show how the model predictions

compares to observed CMC sites. The Human Footprint Index (Wildlife Conservation Society 2005) is a percentage of relative human influence on the biome, ranging from 0 (least influenced) to 100 (most influenced). (C) Ground-truthing of CMC model to validate accuracy based on crosschecking the output with known CMC habitat locations in the Bocas del Toro Archipelago. The model was able to predict 77% of our known CMC habitats within 1 km of the overlap shapefile.

Preface to Chapter 2

In Chapter 1 I introduced how the association between two foundation species, mangroves and coral reefs, vary globally as nested and adjacent assemblage types. By integrating a scientific review of these unique assemblages and field data collected in Panama, I identified characteristics that define these habitats and conditions that may facilitate coral growth and developed criteria for predicting where further nested assemblages are likely to occur. Based on my field surveys, I described a zonation pattern of coral species and colony size within the mangrove forest and hypothesized that light may be more of a driving factor in coral growth and development than temperature given the patchy distribution of colonies observed within the mangrove canopy. I also conducted long-term monitoring of corals within the mangrove canopy, and demonstrated that corals have sustained, rapid growth, within the mangrove. This is consistent with the hypothesis that mangroves may serve as an alternative to reefs as a coral habitat.

In Chapter 2 I delve deeper into the hypothesis generated in Chapter 1 by experimentally testing the effects of shade within the mangrove habitat on coral condition and survival at one of the Bocas del Toro CMC sites. This site was selected due to its high coral diversity and abundance of healthy coral colonies to separate the effects of shade provided by mangroves from other aspects of the habitat in a representative site. I created four experimental treatments: reef natural light (reef control), mangrove natural light (mangrove control), mangrove high light created by pulling back the mangrove canopy, and reef low light created by installing a shade cloth over reef habitat. I then conducted a reciprocal transplant experiment using these treatments with multiple coral species commonly found in the mangrove canopy and on the adjacent shallow reef based on surveys of multiple islands in Bocas del Toro. I measured temperature and light conditions while monitoring coral condition and survival over time. The results from this chapter will increase our understanding of why coral zonation within the mangrove canopy exists and what it means for the future of corals living in nested assemblages with mangroves.

Chapter 2: Caribbean mangrove forests act as coral refugia by reducing light stress and increasing coral richness

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2.1 Abstract

Foundation species structure communities by creating habitat and modifying environmental conditions, and there is increasing interest in how foundation species, such as corals and mangroves, interact with one another as these interactions can have cascading effects on diversity and abundance of associated organisms. Given recent reports of corals living on or between mangrove roots under the canopy, we hypothesized that mangroves can serve as a refuge for corals from stresses such as high solar irradiance and temperatures that are associated with the adjacent shallow reef. Using field surveys and a reciprocal transplant experiment, we tested the effects of light and habitat (e.g., reef or mangrove) on coral community structure (i.e., coral species richness, abundance, and diversity) and condition (i.e., level of bleaching, tissue loss, and mortality). The surveys revealed higher coral richness in mangroves than on the adjacent reef, indicating that mangroves can serve as refugia for numerous coral species. Our experimental manipulation of light in mangrove and reef habitats indicated that light intensity is a key environmental parameter mediating coral bleaching and survival, with mangrove habitats providing a refuge from the light stress experienced on nearby shallow reefs. Moreover, our experiment revealed that reef corals bleached less than mangrove corals following transplantation, regardless of whether they were transplanted into mangrove or reef habitats. We suggest that the lower coral richness of the shallow reef is the result of the extreme environmental conditions that select for a subset of coral species able to tolerate these conditions. The facilitative interactions that allow mangroves to act as coral refugia by reducing environmental stress will likely become increasingly important with global climate change.

2.2 Introduction

Tropical coral reefs are the most biodiverse marine ecosystems, harboring an estimated one third of all described marine species (Knowlton et al. 2010). Coral reefs are also one of the most sensitive ecosystems to climate change (Van Hooidonk et al. 2013) with global mass bleaching events becoming increasingly frequent and severe, typically followed by reduced coral growth rates, decreased fecundity and recruitment, and high coral mortality (Hoegh-Guldberg 1999, Hughes et al. 2003). Human activities can have negative local impacts on reefs through sedimentation, nutrient runoff, pollution, and overfishing (Hughes et al. 2003, Carpenter et al. 2008), potentially reducing the resilience of corals to global stressors such as ocean warming and acidification (Carpenter et al. 2008). A combination of these local and global factors have made Caribbean coral reefs among the most threatened reefs in the world, having suffered an estimated 80% reduction in live coral cover from 1975 to 2000 (Gardner et al. 2003, Guzmán 2003, Côté et al. 2005, Contreras-Silva et al. 2020) with current cover of live coral averaging just 10-13% (Schutte et al. 2010, Jackson et al. 2014, Tkachenko 2017). Therefore, understanding mechanisms of coral resilience, including positive species interactions that can ameliorate stressors, is of utmost importance (Bulleri 2009).

Among coral reef habitats, the shallow reef (typically ≤ 3 m deep) is typically an extreme reef environment with high temperature and light conditions (Spalding et al. 2001). For this reason, shallow reefs are a sentinel system for how corals are likely to respond to anthropogenic stressors, with low coral diversity and corals adapted to extreme environmental conditions (Camp et al. 2018). However, the future success of shallow reef corals under global climate change is dependent on both coral adaptations to increasingly challenging environmental conditions and the availability of refuge habitats that can maintain coral diversity (Wild et al. 2011). Coral habitats adjacent to shallow reefs, such as intermediate (4-29 m) and mesophotic (≥30 m) reefs (Aronson et al. 2004, Bongaerts et al. 2015, Camp et al. 2018) and mangroves (Rogers and Herlan 2012, Yates et al. 2014, Camp et al. 2019) may serve as crucial refugia for corals increasingly exposed to stressful environmental conditions. We define refugia here as habitats where species may retreat to and persist in under changing and/or unfavorable environmental conditions and may serve as a potential source population to expand from (Keppel and Wardell-Johnson 2012, Cacciapaglia and van Woesik 2015). Refuge sites can ameliorate both acute environmental stress such as short-term thermal anomalies and more chronic stressors such as ocean acidification (Oliveira 2020). The use of these habitats could be a key survival mechanism for corals (Camp et al. 2018). Persistence in refugia may be enhanced by acclimatization to the unique conditions of refuge habitats initially through phenotypic plasticity, or in the long-term through adaptation to the refugia conditions over multiple generations (Torda et al. 2017).

Red mangroves (*Rhizophora mangle*) frequently occur in close proximity to reefs, and there are a few studies documenting the occurrence of corals growing among and near the mangrove roots such as in the saltwater ponds and channels of Belize (Macintyre et al. 2000, Rützleret al. 2000, Bengtsson et al. 2019, Scavo Lord et al. 2020a, 2020b), bays of the U.S. Virgin Islands (Rogers 2009, Rogers and Herlan 2012, Yates et al. 2014), and the Florida Keys (Kellogg et al. 2020). These observational studies suggest that mangroves can serve as an alternative habitat for corals and perhaps a refugium in the face of continued reef degradation. In Bocas del Toro on the Caribbean coast of Panamá, we observed the mangrove-coral association extending past the mangrove fringe (i.e., edge where mangrove forests meets open water) to several meters into the mangrove forests with corals growing both on and between the prop roots (Figure 2.1). This overlapping distribution makes it an ideal system to experimentally test the nature of mangrove-coral interactions.

Most ecosystems are structured by multiple foundation species that influence the community by creating habitat and modifying environmental conditions. Coral reefs are an example of an ecosystem composed of multiple foundation species (e.g., corals) where multiple clonal organisms form complex structures that promote species diversity (Angelini et al. 2011). Coexisting foundation species occur in either 1) nested assemblages where a facilitation cascade allows the first foundation species to colonize a habitat and then facilitate another foundation species or 2) adjacent assemblages where foundation species compete for space and create discrete competitively determined zones (Angelini et al. 2011). Traditionally, corals and mangroves would be considered adjacent assemblages, but corals thriving within the mangrove canopy could serve as an example of a nested assemblage. Mangroves can have positive effects on scleractinian corals of nearby reefs at the seascape scale through long-distance positive interactions (e.g., reducing sediment flux and retaining nutrients) (Gillis et al. 2014, van de Koppel et al. 2015), but it remains unclear whether corals growing on and between the mangrove roots benefit from an association with mangrove habitats. Mangrove forests are typically thought to be unsuitable habitat for coral recruitment and growth (Yates et al. 2014) yet increasing reports of overlapping coral and mangrove habitats suggest there could be positive interactions between these foundation species. Where foundation species co-occur, their interactions can have cascading effects on diversity and abundance of associated organisms (Angelini et al. 2011, Thomsen et al. 2018) so understanding these interactions can provide insights into the entire community. We hypothesize that overlapping zonation occurs where corals benefit from a close association with mangroves due to amelioration of high light and temperature stress, creating suitable conditions for the corals to thrive. For example, large (1 m across) scleractinian corals within mangroves of the U.S. Virgin Islands are believed to have survived bleaching events that caused high mortality on the adjacent reef (Rogers and Herlan 2012). Experimental shading on reefs has been shown to be a local mitigation tool for coral bleaching (Coelho et al. 2017), suggesting that shading by the mangrove canopy may be a mechanism of local scale facilitation of corals. While observational data are highly suggestive of coral facilitation by mangroves, no study has tested whether light intensity in mangroves influences coral survival relative to adjacent reefs. Further, no study has compared the ability of different coral species to survive in the mangrove habitat. Identifying local-scale positive associations between corals and mangroves, i.e. interactions in the area of distributional overlap of corals on and within the mangroves, that drive their co-occurrence would change the view on what determines the relative distribution of mangroves and corals, and would have significant implications for predicting the importance of refuge habitats where corals might persist with increasing climate change stress.

In this study, we examined the effects of light and habitat (i.e., reef or mangrove) on coral bleaching, tissue loss, and survival using field surveys and a reciprocal coral transplant experiment. In the transplant experiment, we tested the effects of light conditions by increasing light levels in the mangrove habitat with canopy removals and by decreasing light levels on the reef with shade cloths. To determine whether mangroves can act as coral refugia, we used the results of our surveys and experiment to answer three questions: (1) Are some coral species better able to survive and persist in the mangroves than others? (2) Is refuge from the high light levels found on adjacent shallow reefs one of the main local-scale advantages of mangrove habitats for corals? (3) Are corals from the reef or mangroves better able to acclimate to new environments?

2.3 Methods

Reciprocal transplant experimental design

To study the importance of light and habitat, we ran a reciprocal transplant experiment at the site Fuego off of the Island of Bastimentos in the Bocas del Toro archipelago on the Caribbean coast of Panamá from June to September 2019 (Figure 2.2a). We created four experimental treatments with 10 replicate plots each: reef natural light (reef control), mangrove natural light (mangrove control), mangrove high light created by pulling back canopy, and reef low light created by installing a shade cloth (Figure 2.2b-c). In June 2019 we identified six coral species to transplant into each experimental plot from an initial qualitative roving site assessment: two that more commonly occurred in mangroves (*Montastraea cavernosa* and *Pseudodiploria clivosa*), two that more commonly occurred on the reef (*Diploria labyrinthiformis* and *Porites astreoides*), and two that were observed in similar frequency in both habitats (*Colpophyllia natans* and *Orbicella faveolata*). *Colpophyllia natans* and *Orbicella faveolata* were collected from both mangrove and reef habitats to test for evidence of intraspecific variation in coral bleaching and mortality related to source habitat.

One colony was selected per coral species as the source of experimental fragments, except for *C. natans* and *O. faveolata* where a colony was collected from both mangrove and reef habitats. We opted to select one colony per species rather than multiple colonies to minimize impact on this undescribed system of mangrove-coral habitat. Each colony was divided into 40 fragments of 2-3 cm diameter, mounted to 3 cm diameter ceramic plugs (Oceans Wonders) with reef glue (Seachem Cyanoacrylate Gel), and secured in a random order to weighted rigid eggcrate. Only healthy colonies without signs of bleaching or disease were used in the transplant experiment. Since abruptly transplanting coral fragments, particularly to higher light levels, can initially cause bleaching (Richier et al. 2008, Forrester et al. 2012, Cohen and Dubinsky 2015), all corals were placed in the intermediate fringe habitat between the reef and mangrove canopy and allowed to recover for a week. Since all the experimental corals experienced the same level of handling stress, we did not test the effects of transplant directly again on non-transplanted controls, rather we compared corals that were transplanted back to their source habitat to corals that were transplanted to the other habitat. For the reef low light treatment, 1 x 1 m shades were created from a double layer of 40% sunblock shade cloth (Agfabric UV stabilized High Density Polyethylene), held in place 65 cm above the plot by a PVC frame, to mimic the light levels found within the mangrove canopy. All plots where transplant corals were placed had corals currently growing within them, indicating it should be a suitable environment for corals. Mangrove high light treatments were created by pulling back mangrove branches with plastic locking tree ties (Dimex EasyFlex), so that at midday no shadows were cast upon a 1 x 1 m plot area. In total, nine coral fragments were removed from analyses as a result of being dislodged or bleached during the first two days of the experiment (i.e., evidence of transplantation shock) including seven mangrove sourced corals (4 *C. natans*, 1 *M. cavernosa*, 2 *P. clivosa*) and two reef sourced corals (1 *C. natans*, 1 *D. labyrinthiformis*). No signs of disease were observed during the acclimation period or throughout the experiment.

Light and temperature measurements

Light, recorded as photosynthetically active radiation (PAR), was measured during the experiment to quantify relative differences in the light level of each plot. Prior to setting up the experiment, we measured the average peak midday PAR levels, that were over 3.5x higher on the reef (729 ± 118 μmol s^{-1} m^{-2}, mean ± SE) than in the mangrove canopy (203 ± 80 μmol s^{-1} m^{-2}). These data were used to determine the amount of shading needed on the reef to approximately match light levels within the mangrove canopy. During the experiment, light measurements were made between 11:00-13:00 on a cloud-free day in September 2019. We used a pair of spherical underwater quantum sensors (Licor LI-193s) to take our readings within mangrove canopy and reef habitats simultaneously. The light measurements used in analyses were an average of three PAR readings per plot. To quantify variation in temperature among treatments, we deployed five data loggers (HOBO Pendant® 64K Data Logger) per treatment to record a week-long water temperature profile.

Coral condition and mortality

Coral condition was scored visually on an index of: 5 = completely healthy corals/no visible bleaching/no tissue loss, 4 = <50% bleaching, 3 = >50% bleaching, 2 = visible tissue loss, or 1 = dead (Figure 2.2d). We observed algal overgrowth only after the coral died, so those corals remained in category 1. None of the coral fragments showed visual signs of disease so disease was not included in our index. Coral condition was scored one week after the treatments were established and again three months later at the end of the experiment. Plots were visited weekly to clean the shades and maintain canopy restraints.

Coral community surveys

The coral community in Bocas del Toro is diverse, containing 87% of the scleractinian coral species reported in Caribbean Panamá (Guzmán 2003, Guzmán et al. 2005). To characterize the coral community in the mangrove canopy and adjacent shallow reef, and to show that the association between corals and mangroves appeared similar at multiple sites, we conducted surveys in March 2020, expanding from the initial site (Fuego) where the reciprocal transplant experiment ran to two additional sites (Figure 2.2a). In these surveys we quantified live coral species richness, abundance (percent cover), and diversity. Criteria for site selection were area (needed to be large enough to run our transects, ≥60 m long), distance from one another (> 5 km apart to allow ecological independence), and proximity of mangroves and shallow reef (<2 m apart). Although many mangrove islands in the archipelago have corals growing within them, mangrove-coral areas can be patchy due to development, deforestation, and freshwater inflow, so we avoided such locations in our study. Since we were interested in contrasting corals within mangroves and reefs to examine potential factors driving use of refugia habitat, we selected sites with established coral communities both on the reef and in the mangrove canopy. At each site, we placed 16 to 24 replicate 1-m^2 quadrats at semi-regular intervals (> 2 m apart) along a mangrove and a reef transect placed parallel to one another. Each transect was 4 m apart (2 m from the mangrove fringe in both directions). If root density prevented placement of the quadrat in the mangrove habitat, we moved to a position 1-2 m adjacent to that spot. Each quadrat was divided into a grid with 25 points, and we identified the benthic substrate or organism that was dominant under each point. Water depth was recorded in each quadrat, and the average depth relative to mean lower low water (MLLW) was 0.5-1 m. Mangrove-coral areas had corals growing from the fringe of the mangrove to >7 m into the canopy. Corals grew both on and between the mangrove roots. Corals growing between roots were typically found on substrates including coral rubble, shells, or peat.

Analyses

All data were analyzed with R version 3.6.3 (R Core Team 2020). Since light (PAR) was recorded in all 40 plots and there was overlap in the PAR values among treatments, we treated light as a continuous variable independent of habitat in our experimental analyses. Light and mean temperature were positively correlated ($p < 0.001$, t-test = 10.577, df = 145, correlation coefficient = 0.660; Figure B1), so temperature was excluded from the overall model to avoid confounding effects from multicollinearity. As coral condition was measured with an index (ordinal data), we used an ordinal logistic regression model to test for effects of habitat (i.e., plot location in mangrove or reef), light, source (i.e., coral collection site in mangrove or reef), coral species, depth, interaction terms (source x habitat, source x light, and species x light), and a random effect of plot. We were unable to include the interaction term of species x habitat due to limitations in sample size. Models were fit using the polr function from the *MASS* package. We tested the proportional odds assumption and checked for multi-collinearity with the *GGally* package. We used the ANOVA function from the *car* package and summary functions to perform a Type II sum of squares to look at the main effects and compare coefficients. The *lsmeans* package was used to run pairwise comparisons when interaction terms were significant. We used ggpredict from the *ggeffects* package to obtain predicted probabilities to plot modeled data.

We analyzed complete mortality separate from the coral condition analysis to provide further resolution on the effects of predictor variables on coral survivorship by fitting a binomial generalized linear mixed-effects model (GLMM) using the glmer function with the effects of habitat, light, source, coral species, interaction term of source x light, and a random effect of plot. Light used in the binominal model was treated as high (reef control and mangrove high light treatments) or low (mangrove control and reef low light treatments) within a given habitat because the model failed to converge using PAR measurements. We used a chi-squared likelihood ratio test of our model fit and performed residual diagnostics with the *DHARMa* package.

For the surveys, coral species diversity (Shannon-Wiener and Simpson indices) and richness were calculated from the percent cover of live coral using the *vegan* package. Effects of habitat type (reef vs mangrove) and site on diversity and richness were analyzed using linear models and two-way ANOVAs.

2.4 Results

Light and temperature measurements

Although we succeeded in creating a mangrove high light treatment (571 ± 43, 333.4-952.2 µmol s^{-1} m^{-2}, mean ± SE, range) that overlapped with the reef control (1341 ± 67, 869.1-1833 µmol s^{-1} m^{-2}) and whose range was outside of the mangrove control treatment (193 ± 16, 101.3-322.7 µmol s^{-1} m^{-2}), we could not further increase light in the mangroves, likely because of colored dissolved organic matter (CDOM) in the water and the trees circling the experimental plot that blocked indirect sunlight. Our reef low light treatment (276 ± 15, 109.9-468.5 µmol s^{-1} m^{-2}) aligned well with the mangrove control, but also overlapped with the mangrove high light treatment. Both reef treatments had greater average temperatures and depths than mangrove treatments, but mangroves had a larger diel temperature range (28.1-33.0 °C) and less variance in depth (Table B2, Figure B2).

Coral condition and mortality

Corals from the reef had significantly higher condition scores than corals sourced from mangroves across treatments ($p < 0.001$, $t = 3.643$, PrChisq < 0.001) (Figure 2.3a-b). This trend was evident both across species and within the two species (*C. natans* and *O. faveolata*) sourced from both habitats. Reef-sourced *C. natans* and *O. faveolata* did better on the reef than those same species when sourced from mangrove habitat (Figure 3a-b). Even though there was no significant interaction between source and light ($p = 0.786$, $t = 0.271$, PrChisq $= 0.815$) on coral condition, there was an interaction between species and light (PrChisq $= 0.018$), where condition was negatively correlated with light for all coral species, except *D. labyrinthiformis* where it was positively correlated (Figure 2.3c). When light was held at a mean level of 529 µmol s^{-1} m^{-2} in the model, coral condition significantly differed between species in 10 of the 14 pairwise comparisons, with *D. labyrinthiformis* consistently showing worse condition than all other coral species. Mangrove-sourced *O. faveolata* had the highest condition in the mangrove control, then mangrove high light, reef low light, and finally reef control (the only treatment with *O. faveolata* death). *C. natans* and *O. faveolata* had the least visible bleaching and 100% survival, regardless of source, in the reef shade treatment. There was no effect of habitat ($p = 0.398$, $t = -0.845$, PrChisq $= 0.786$) or depth ($p = 0.694$, $t = 0.393$, PrChisq $= 0.695$), and no significant habitat by source interaction ($p = 0.087$, $t = 1.710$, PrChisq $= 0.081$) on coral condition.

Across all treatments and coral species, only 25 coral fragments of the original 311 died during the experiment (5% placed on the reef and 12% placed in the mangroves). There was a significant interactive effect of the source of corals and light on mortality ($p = 0.005$, F value $=$ 7.997, PrChisq $= 0.005$) with corals sourced from the reef having lower levels of mortality under higher experimental light levels than corals sourced from the mangroves. Complete mortality experiment-wide differed among species (PrChisq < 0.001, F value $= 2.867$) with *D. labyrinthiformis* having significantly greater levels of mortality ($p < 0.001$) compared to the other coral species. Mortality did not significantly differ among the other coral species (Table B3). The habitat that corals were transplanted into also significantly affected mortality (p = 0.026, F value = 2.548, PrChisq = 0.026).

Coral community surveys

We recorded a total of 23 scleractinian coral species and 2 milleporid coral species (colonial hydrozoans) in our surveys: 22 scleractinian species were found in the mangrove habitats and 10 on the adjacent shallow reef, although only a subset of those species were found in the respective habitat at a given site. Both milleporid coral species were found in both habitat types (Table B1). Nine of the scleractinian species were observed in both habitat types, whereas 13 were found exclusively in mangroves and one exclusively on reefs (Appendix S1: Table S1). Our reef sites had an average depth of 89 ± 2 cm (mean ± SE), and our mangrove canopy sites had an average depth of 68 ± 2 cm. Live coral had the highest average percent cover of all benthic groups across habitats and sites (32-36%), followed by dead coral (10-21%) (Figure 2.4a) with the exception of Cayo Ramirez reef which had 30% live coral and 37% dead coral cover (Table 2.1). There was no significant difference in live coral cover (PrChisq = 0.923) or dead coral cover (PrChisq = 0.193) between habitats. Although it was not possible to determine the cause of coral mortality in these surveys, it could have been due to bleaching events in 2005, 2010 and 2015, hypoxia events, or subsequent disease outbreaks (Neal et al. 2017). However, based on observations in the area of phase shifts to algae and increased land clearing activities, it is likely to be linked to land-based runoff and algal overgrowth. Observed elevated sea surface temperatures, increased nutrients, and overexploitation of herbivorous reef fishes in the area could all promote algal growth (Cramer et al. 2020).

There was no interactive effect of habitat x site on coral richness (PrF = 0.482) or Shannon-Wiener (PrF = 0.231) or Simpson's diversity indices (PrF = 0.107). Coral species richness (p = 0.004, t = -2.916, PrF < 0.001), Shannon-Wiener Diversity index (p < 0.001, t = -3.735, PrF < 0.001) and Simpson's Diversity index (p < 0.001, t = -4.096, PrF < 0.001) were significantly higher in mangroves than in the reef habitat. There was a site effect, with coral species richness (PrF = 0.009), Shannon-Wiener Diversity index (PrF = 0.012), and Simpson Diversity index (PrF = 0.019) significantly lower at Cayo Ramirez than at the other two sites. Of the live coral observed in the surveys, the most abundant species in the reef community were *Millepora alcicornis* (22-57%) and *Porites furcata* (18-68%). In contrast, within the mangrove canopy *Siderastrea siderea* (15-51%), *Agaricia tenuifolia* (6-31%), and *Porites astreoides* (3-17%) were the most abundant species (Figure 2.4b).

2.5 Discussion

Given the high diversity of the corals observed in the mangrove habitat, the presence of several large colonies within the mangrove canopy, and the fact that the majority of the corals survived transplantation into the mangrove, it is reasonable to speculate that mangroves could serve as long-term coral refugia. We found that corals generally fared better when transplanted to lower light levels, and that shade from the mangrove canopy had a positive effect on coral condition and survivorship by ameliorating stressful light conditions that limited coral success on shallow reefs. Therefore, we conclude that refuge from high light levels of the adjacent shallow reef is an advantage of the mangrove habitat. If mangroves are able to provide refuge from bleaching stress, they may also reduce coral disease incidence, which has been shown to increase following a bleaching event (Miller et al. 2009). By providing a refuge for coral species not able to survive on the harsh shallow reef environment, we found mangroves host coral communities with higher species richness and diversity than the adjacent shallow reef with similar live coral cover. Our surveys detected 24 coral species within the mangrove habitat, a coral refuge community only surpassed by a study in the U.S. Virgin Islands that observed > 30 coral species (Yates et al. 2014), although notably that record was prior to extensive hurricane damage (Rogers 2019). Bocas del Toro lies outside the hurricane belt, primarily receiving the associated rainfall (Lovelock et al. 2005), and thus the mangrove forests and coral reefs are not subjected to the same stress as many other parts of the Caribbean. Since our surveys revealed twice as many coral species in the mangrove compared to the adjacent shallow reef, it is possible that the source of the mangrove corals could be larvae from deeper corals.

Our study is the first to quantitatively measure coral richness within the mangrove habitat compared to the adjacent shallow reef, setting a baseline for future studies. In our reciprocal transplant experiment, corals sourced from the reef had less bleaching and mortality than corals sourced from the mangrove canopy whether transplanted to reef or mangrove habitats, suggesting that corals from the reef are better able to acclimate to new environments. This finding is consistent with previous tests of refugia habitats that found the subset of corals species living on the reef to be physiologically adapted to high irradiance levels and the more diverse community of corals in dimly lit areas (e.g., mesophotic reefs) to be adapted to low light (Cohen and Dubinsky 2015). Although it is known that shading can protect corals from UV radiation (Coelho et al. 2017), light availability influences coral calcification and photosynthesis rates and lower light availability can increase some coral species susceptibility to ocean acidification (Suggett et al. 2013), so it was previously unclear whether shading by mangroves was beneficial or detrimental to corals in this system. Our study was the first to test bleaching thresholds of corals growing within the mangrove habitat compared to that on the shallow reef.

Corals living in low light environments have adaptations that may be shared by corals living in mangroves. Within mangroves, the majority of corals we observed had flattened tri-dimensional morphologies as described in mesophotic coral reef ecosystems (Dustan 1979, 1982, Kühlmann 1983, Kahng et al. 2010). This morphology is typically an adaptation to low light conditions as it reduces the ratio of tissue to projected area needing to be sustained by light (Stambler and Dubinsky 2005), reduces self-shading, and maximizes light captured by increasing light-harvesting pigments (Kahng et al. 2012, 2019). This growth form may also be a response to shallow water conditions within the mangrove (~0.5 m depth on average), as the coral colony grows laterally to avoid air exposure. Corals from low light habitats such as mesophotic reefs have also been shown to host different species of *Symbiodiniaceae* than those in high light environments (Iglesias-Prieto et al. 2004), and to have mono-layered zooxanthellae packaging to increase photosynthetic efficiency (Dustan 1982, Kahng et al. 2010, 2012). Whether corals in mangrove habitats have such adaptations is yet to be explored.

We propose that a reason why mangrove-sourced corals in our study did not fare as well as reef-sourced corals when transplanted onto the reef is related to the differences in their levels of mycosporine-like amino acids (MAAs). Reef corals are known to have greater concentrations of MAAs in response to the increased UV radiation as these compounds protect the host and their symbionts (Corredor et al. 2000). Furthermore, it has been demonstrated that MAA concentrations in corals decrease with increasing depth and decreasing UV levels (Corredor et al. 2000, Lesser 2000). We expect MAA concentrations to be lower in corals originating from the mangrove canopy than corals that originated on the reef, as the mangrove canopy attenuates light intensity while CDOM and suspended sediments in the water absorb light and UV (Maie et al. 2008). Without this additional UV protection, the mangrove corals could be at greater risk of UV damage and physiological shock when transplanted to the reef where they are exposed to high light and UV. This may indicate that long-term exposure to mangrove habitat reduces the stress tolerance of corals to reef conditions. Alternatively, corals sourced from the mangroves may need a more gradual transplant process. Cohen and Dubinsky (2015) found that when incrementally transplanting corals between shallow and deep reefs, with 10-day intervals between transplanting to the next shallower depth, coral bleaching and mortality from light stress was minimal. Mangrove-sourced corals in our study were transplanted across a similar magnitude light gradient from mangrove to reef but only provided with one intermediate habitat, the mangrove fringe, to acclimate to prior to the start of the experiment. The relatively poor condition of mangrove corals in the high light environment of the reef indicates that either a one-week acclimation period on the mangrove fringe was not sufficient for induced protective traits, an incremental acclimation with more stages would be necessary to decrease transplant stress, and/or traits underlying stress tolerances are fixed in populations of the respective habitats. Additionally, outside of *Siderastrea siderea*, the majority of coral species (abundance and diversity) in the mangroves were brooding species. The community structure of many Caribbean reefs have been shifting from a dominance of long-lived broadcast spawning species to brooding corals with shorter lifespans and resilient life history strategies (Vermeij et al. 2011). Studies comparing broadcast spawning corals to brooding corals suggest that larvae produced by deeper water colonies may be more susceptible to UV radiation than those produced by colonies from shallow water (Gleason et al. 2006). Further, coral larvae behaviorally avoid damaging UV radiation during planktonic dispersal and subsequent settlement (Gleason et al. 2006); therefore, coral larvae from deeper water may be selecting for the mangrove habitat rather than the shallow reef to reduce UV exposure.

The aforementioned mechanisms (e.g., alternate morphologies, changing zooxanthellae packaging, hosting different species of *Symbiodiniaceae*, differences in MAA levels) that allow corals to specialize in high-light or low-light settings could explain the variation in condition and mortality within and among species across light, habitat, and source revealed in our experiment, but were not quantified in this study. We tested for evidence of intraspecific variation in coral condition related to source habitat with *C. natans* and *O. faveolata*. Reef *O. faveolata* had less bleaching than mangrove *O. faveolata*, which could be related to the adaptations of corals on the shallow reef to extreme environmental conditions that increase coral resilience to variation in light conditions. Further, it has been shown that corals have a smaller physiological response when moved from high light to low light than vice versa, as observed in reciprocal transplantation of coral fragments between deep and shallow reef depths (Richier et al. 2008, Cohen and Dubinsky 2015). However, the only bleaching that did occur within reef-sourced *O. faveolata* was in the reef control treatment, suggesting that prior exposure to higher levels of irradiance does not necessarily pre-empt a stress response to subsequent exposure to higher light levels in *O. faveolata*. Our finding that *C. natans* and *O. faveolata*, regardless of coral source, had the least bleaching and no mortality in the reef low light treatment indicates that shallow reef high light conditions are challenging even for coral species that routinely live on the reef. When controlling for source and habitat, and modelling only light, the patterns of how different coral species perform in relation to light is clearer. Nearly all coral species declined in health with increasing light intensity. This supports the conclusions that the shallow reef represents a stressful environment and that most species of corals, with the rare exception, can take advantage of mangroves as an alternative habitat. The only coral that had improved condition with increasing light was *D. labyrinthiformis*, which notably was also the only coral never seen in the mangrove habitat in Panamá. However, *D. labyrinthiformis* is one of the most abundant mangrove corals in other parts of the Caribbean (Yates et al. 2014). In bleaching censuses of *D. labyrinthiformis* and *C. natans* colonies in the U.S. Virgin Islands, *C. natans* only bleached 2-5% where *D. labyrinthiformis* bleached 17-59% (Rogers and Herlan 2012) at the same sites over the same time frame. These data in combination with our own findings suggest that *C. natans* is more of a generalist species, resistant to variation in environmental factors, compared to *D. labyrinthiformis,* which is more sensitive to fluctuations and extremes in temperature and light (Rogers and Herlan 2012). Differences in environmental conditions of these sites could explain the regional variation in *D. labyrinthiformis* abundance within mangroves of the Caribbean. Although both *D. labyrinthiformis* and *C. natans* are broadcast spawning corals, the timing of gamete release by *D. labyrinthiformis* differs among locations throughout the Caribbean with one versus multiple spawning events per year (Chamberland et al. 2017). These differences in reproductive timing are not related to latitude nor sea temperature, and the cause of spatial differences is suspected to be linked to other environmental cues (e.g., photoperiod, monthly rainfall, internal rhythms inherited from ancestral populations) (Chamberland et al. 2017). It should be noted that colony identity may have contributed to differences we observed since replicates for a given species were sourced from the same colony. This study found that some coral species are better able to survive in the mangroves than others and sets the foundation for future studies to examine why, which should expand to exploring genotypic variation in the responses that we observed.

Shading has been proposed as a mechanism by which mangroves serve as refugia for corals by ameliorating stresses associated with shallow reef environments such as solar radiation, which alone or in combination with temperature, can induce bleaching in corals (Siebeck 1988, Gleason and Wellington 1993, Lesser and Farrell 2004). Reducing irradiance during periods of thermal stress can prevent bleaching (Coelho et al. 2017), and corals found growing in mangroves with >70% attenuation of incident PAR were able to thrive in higher temperatures than corals in nearby reef habitat (Yates et al. 2014). We found that reduction of solar radiation minimized the impact of stress-induced bleaching from transplantation into a new environment. Since temperature and light values were highly correlated, we could not separate the effects of each in this study. However, mean PAR readings were seven times greater in the reef control than in the mangrove control even with reef plots being twice as deep as mangrove plots, whereas temperature varied little between treatments, with a maximum temperature in the mangrove high light treatment of 33 °C compared to 32 °C for all other treatments, and all mean and minimum temperatures of the various treatments falling within the error range of the data loggers (±0.53 °C) (Table B2). The temperature difference between mangrove canopy treatments (high light, low light) may be a product of minimal water circulation and shallow depths of the mangrove habitat that rapidly warms the water without the shade provided by the mangrove canopy. We acknowledge that additional abiotic factors will vary between the mangrove and reef, however a spot check of salinity and turbidity of these habitats at our experiment site showed little difference in average values. We measured salinity in the mangrove and shallow reef habitats as 33.67 ± 0.01 ppm mean ± SE and 33.83 ± 0.01 ppm, respectively. Turbidity was 0.598 ± 0.026 FNU and 0.572 ± 0.007 FNU in the mangrove and shallow reef habitats, respectively. Further research is needed to explore additional abiotic factors and the influence they have on the corals within these habitats. This is especially important since the environmental conditions that may preclude coral settlement and growth on the reef may be different (average, minimum, maximum) within the mangrove habitat and are potentially species specific. As this study used coral fragments, it did not test whether mangroves can serve as a source population to recolonize disturbed areas. In order to address this, recruitment rates and survival of propagules would need to be quantified, however, the response of coral fragments following transplantation can be used to determine whether mangroves could be used in coral restoration efforts.

The importance of mangroves as refugia for corals is likely to increase as ocean warming makes coral bleaching events more frequent and severe. As ocean conditions (e.g., temperature, light, pH and O_2) change and the shallow reef environment degrades, alternative habitats may become relatively more beneficial to corals (Yates et al. 2014). For example, some have suggested that deep reefs, such as mesophotic reefs may serve as a refugium and/or refuge for shallow reef corals as they experience less stress (Holstein et al. 2015, Semmler et al. 2017, Lesser et al. 2018), although others have questioned the generality of their effectiveness (Bongaerts et al. 2010, Smith et al. 2016, Rocha et al. 2018). Some regions, including our study area of Bocas del Toro, Panamá, do not have mesophotic reefs (Guzmán et al. 2005), making alternative refugia all the more important. Although both coral reefs and mangroves are threatened by climate change, the greatest threat to mangrove survival is local anthropogenic stressors (e.g., land conversion for aquaculture, palm oil plantations, coastal development, and pollution) and pending rates of deforestation, mangroves are predicted to survive into the foreseeable future even with global temperatures, atmospheric CO_2 concentrations, and sea levels continuing to rise (Alongi 2015, Friess et al. 2019). At a global scale, hurricanes and associated extreme weather events are predicted to increase with climate change and the high energy winds, destructive waves and storm surges can cause severe damage to mangrove habitats (Walcker et al. 2019). However, under natural conditions, mangroves are resilient and storm damage is rarely persistent. It is when anthropogenic stressors degrade the mangrove ecosystem and alter flow regimes that mangroves are unable to recover (Walcker et al. 2019). If mangroves can be protected from human destruction, they may serve as refugia for corals under climate change and a global strategy for coral reef persistence. Although the field of overlapping mangrove-coral systems is in its infancy, studies are showing that when these foundation species co-occur, they alter ecological functioning. Mangroves with corals had greater fish species richness compared to mangroves without corals, however, adding artificial corals to mangroves only increased fish abundance (Wright 2019). There is still much to understand about this ecosystem and how it functions, but at least in the Caribbean it has been found to be beneficial to corals. We suggest that the shading by mangroves buffers corals, and that impact is not limited to this region, so there should be a global effort to protect mangroves, especially in locations where mangroves and corals co-occur, and further explore the ecological functioning of these systems.

Significance

Our study revealed that mangroves provide habitat for a diverse assemblage of coral species, and that transplanted corals generally fared better in lower light levels, suggesting that mangroves can serve as a refuge from the light stress associated with shallow reef environments. Additionally, increased light levels were more harmful to shade-acclimated corals, thus removal of mangroves or their canopy from mangrove-coral systems could induce coral bleaching and mortality. Positive interactions between mangroves and corals where they co-occur could play an increasingly important role as solar irradiance and thermal stress continue to negatively affect shallow reefs with climate change. This research highlights the importance of habitats with overlapping foundation species such as mangrove-coral systems, which currently do not have special protection status and should be prioritized in conservation efforts.

2.6 Acknowledgements

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2.7 References

Alongi, D. M. 2015. The impact of climate change on mangrove forests. Current Climate Change Reports 1:30–39.

Angelini, C., A. H. Altieri, B. R. Silliman, and M. D. Bertness. 2011. Interactions among foundation species and their consequences for community organization, biodiversity, and conservation. BioScience 61:782–789.

Aronson, R. B., I. G. Macintyre, C. M. Wapnick, and M. W. O'Neill. 2004. Phase shifts, alternative states, and the unprecedented convergence of two reef systems. Ecology 85:1876–1891.

Bengtsson, Z. A., K. M. Kuhn, A. T. Battaglino, A. S. Li, M. N. Talbot, M. Wafapoor, C. J. Atta, S. P. Margolis, E. A. Rar, E. M. Burmester, K. C. Lesneski, K. S. Lord, L. Kaufman, M. B. Kowalski, S. P. Margolis, E. A. Rar, E. M. Burmester, K. C. Lesneski, K. Scavo, L. Kaufman, N. L. Stewart, and J. R. Finnerty. 2019. *Porites divaricata* is a locally abundant component of the epibiont community on mangrove prop roots at Calabash Caye, Turneffe Atoll, Belize. Caribbean Naturalist:1–16.

Bongaerts, P., P. R. Frade, K. B. Hay, N. Englebert, K. R. W. Latijnhouwers, R. P. M. Bak, M. J. A. Vermeij, and O. Hoegh-Guldberg. 2015. Deep down on a Caribbean reef: Lower mesophotic depths harbor a specialized coral-endosymbiont community. Scientific Reports 5:1–9.

Bongaerts, P., T. Ridgway, E. M. Sampayo, and O. Hoegh-Guldberg. 2010. Assessing the "deep reef refugia" hypothesis: Focus on Caribbean reefs. Coral Reefs 29:1–19.

Bulleri, F. 2009. Facilitation research in marine systems: State of the art, emerging patterns and insights for future developments. Journal of Ecology 97:1121–1130.

Cacciapaglia, C., and R. van Woesik. 2015. Reef-coral refugia in a rapidly changing ocean. Global Change Biology 21:2272–2282.

Camp, E. F., J. Edmondson, A. Doheny, J. Rumney, A. J. Grima, A. Huete, and D. J. Suggett. 2019. Mangrove lagoons of the Great Barrier Reef support coral populations persisting under extreme environmental conditions. Marine Ecology Progress Series 625:1–14.

Camp, E. F., V. Schoepf, P. J. Mumby, L. A. Hardtke, R. Rodolfo-Metalpa, D. J. Smith, and D. J. Suggett. 2018. The future of coral reefs subject to rapid climate change: Lessons from natural extreme environments. Frontiers in Marine Science 5:1–21.

Carpenter, K. E., M. Abrar, G. Aeby, R. B. Aronson, S. Banks, A. Bruckner, A. Chiriboga, J. Cortés, J. C. Delbeek, L. DeVantier, G. J. Edgar, A. J. Edwards, D. Fenner, H. M. Guzmán, B. W. Hoeksema, G. Hodgson, O. Johan, W. Y. Licuanan, S. R. Livingstone, E. R. Lovell, J. A. Moore, D. O. Obura, D. Ochavillo, B. A. Polidoro, W. F. Precht, M. C. Quibilan, C. Reboton, Z. T. Richards, A. D. Rogers, J. Sanciangco, A. Sheppard, C. Sheppard, J. Smith, S. Stuart, E. Turak, J. E. N. Veron, C. Wallace, E. Weil, and E. Wood. 2008. One-third of reef-building corals face elevated extinction risk from climate change and local impacts. Science 321:560–563.

Chamberland, V. F., S. Snowden, K. L. Marhaver, D. Petersen, and M. J. A. Vermeij. 2017. The reproductive biology and early life ecology of a common Caribbean brain coral, *Diploria labyrinthiformis* (Scleractinia: Faviinae). Coral Reefs 36:83–94.

Coelho, V. R., D. Fenner, C. Caruso, B. R. Bayles, Y. Huang, and C. Birkeland. 2017. Shading as a mitigation tool for coral bleaching in three common Indo-Pacific species. Journal of Experimental Marine Biology and Ecology 497:152–163.

Cohen, I., and Z. Dubinsky. 2015. Long term photoacclimation responses of the coral *Stylophora pistillata* to reciprocal deep to shallow transplantation: photosynthesis and calcification. Frontiers in Marine Science 2:1–13.

Contreras-Silva, A. I., A. Tilstra, V. Migani, A. Thiel, E. Pérez-Cervantes, N. Estrada-Saldívar, X. Elias-Ilosvay, C. Mott, L. Alvarez-Filip, and C. Wild. 2020. A meta-analysis to assess long-term spatiotemporal changes of benthic coral and macroalgae cover in the Mexican Caribbean. Scientific Reports 10:1–12.

Corredor, J. E., A. W. Bruckner, Z. Muszynski, R. A. Armstrong, R. García, and J. M. Morell. 2000. UV-absorbing compounds in three species of Caribbean zooxanthellate corals: depth distribution and spectral response. Bulletin of Marine Science 67:821–830.

Côté, I. M., J. A. Gill, T. A. Gardner, and A. R. Watkinson. 2005. Measuring coral reef decline through meta-analyses. Philosophical Transactions of the Royal Society B: Biological Sciences 360:385–395.

Cramer, K. L., A. O'Dea, J. S. Leonard-Pingel, and R. D. Norris. 2020. Millennial-scale change in the structure of a Caribbean reef ecosystem and the role of human and natural disturbance. Ecography 43:283–293.

Dustan, P. 1979. Distribution of zooxanthellae and photosynthetic chloroplast pigments of the reef-building coral Montastrea. Bulletin of Marine Science 29:79–95.

Dustan, P. 1982. Depth-dependent photoadaption by zooxanthellae of the reef coral *Montastrea annularis*. Marine Biology 68:253–264.

Forrester, G. E., A. Maynard, S. Schofield, and K. Taylor. 2012. Evaluating causes of transplant stress in fragments of *Acropora palmata* used for coral reef restoration. Bulletin of Marine Science 88:1099–1113.

Friess, D. A., K. Rogers, C. E. Lovelock, K. W. Krauss, S. E. Hamilton, S. Y. Lee, R. Lucas, J. Primavera, A. Rajkaran, and S. Shi. 2019. The state of the world's mangrove forests: past, present, and future. Annual Review of Environmental and Resources 44:1–27.

Gardner, T. A., I. M. Côté, J. A. Gill, A. Grant, A. R. Watkinson, G. Paredes, R. R. Warner, J. B. C. Jackson, J. M. Pandolfi, R. H. Bradbury, E. Sala, T. P. Hughes, K. A. Bjorndal, R. G. Cooke, D. McArdle, L. McClenachan, and M. J. H. Newman. 2003. Long-term region-wide declines in Caribbean corals. Science 301:958–960.

Gillis, L. G., T. J. Bouma, C. G. Jones, M. M. Van Katwijk, I. Nagelkerken, C. J. L. Jeuken, P. M. J. Herman, and A. D. Ziegler. 2014. Potential for landscape-scale positive interactions among tropical marine ecosystems. Marine Ecology Progress Series 503:289–303.

Gleason, D. F., P. J. Edmunds, and R. D. Gates. 2006. Ultraviolet radiation effects on the behavior and recruitment of larvae from the reef coral *Porites astreoides*. Marine Biology 148:503–512.

Gleason, D. F., and G. M. Wellington. 1993. Ultraviolet radiation and coral bleaching. Nature 365:836–838.

Guzmán, H. M. 2003. Caribbean coral reefs of Panama: Present status and future perspectives. Pages 241–274 *in* J. Cortés, editor. Latin American Coral Reefs. Elsevier Science B.V., Amsterdam, The Netherlands.

Guzmán, H. M., P. A. G. Barnes, C. E. Lovelock, and I. C. Feller. 2005. A site description of the CARICOMP mangrove, seagrass and coral reef sites in Bocas del Toro, Panama. Caribbean Journal of Science 41:430–440.

Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. Marine and Freshwater Research 50:839–866.

Holstein, D. M., T. B. Smith, J. Gyory, and C. B. Paris. 2015. Fertile fathoms: Deep reproductive refugia for threatened shallow corals. Scientific Reports 5:1–12.

Van Hooidonk, R., J. A. Maynard, and S. Planes. 2013. Temporary refugia for coral reefs in a warming world. Nature Climate Change 3:508–511.

Hughes, T. P., A. H. Baird, D. R. Bellwood, M. Card, S. R. Connolly, C. Folke, R. Grosberg, O. Hoegh-Guldberg, J. B. C. Jackson, J. Kleypas, J. M. Lough, P. Marshall, M. Nyström, S. R. Palumbi, J. M. Pandolfi, B. Rosen, and J. Roughgarden. 2003. Climate change, human impacts, and the resilience of coral reefs. Science 301:929–933.

Iglesias-Prieto, R., V. H. Beltra, T. C. Lajeunesse, H. Reyes-Bonilla, and P. E. Thome. 2004. Different algal symbionts explain the vertical distribution of dominant reef corals in the eastern Pacific. Proceedings of the Royal Society B: Biological Sciences 271:1757–1763.

Jackson, J., M. Donovan, K. Cramer, and V. Lam, editors. 2014. Status and Trends of Caribbean Coral Reefs: 1970-2012. Global Coral Reef Monitoring Network, IUCN, Gland, Switzerland.

Kahng, S. E., D. Akkaynak, T. Shlesinger, E. J. Hochberg, J. Wiedenmann, R. Tamir, and D. Tchernov. 2019. Light, temperature, photosynthesis, heterotrophy, and the lower depth limits of mesophotic coral ecosystems. Pages 801–828 *in* Y. et al. Loya, editor. Coral Reefs of the World. Springer Nature Switzerland AG.

Kahng, S. E., J. R. Garcia-Sais, H. L. Spalding, E. Brokovich, D. Wagner, E. Weil, L. Hinderstein, and R. J. Toonen. 2010. Community ecology of mesophotic coral reef ecosystems. Coral Reefs 29:255–275.

Kahng, S. E., E. J. Hochberg, A. Apprill, D. Wagner, D. G. Luck, D. Perez, and R. R. Bidigare. 2012. Efficient light harvesting in deep-water zooxanthellate corals. Marine Ecology Progress Series 455:65–77.

Kellogg, C. A., R. P. Moyer, M. Jacobsen, K. K. Yates, U. S. G. Survey, F. Fish, W. C. Commission, and C. A. Kellogg. 2020. Identifying mangrove-coral habitats in the Florida Keys. PeerJ 8.

Keppel, G., and G. W. Wardell-Johnson. 2012. Refugia: keys to climate change management. Global Change Biology 18:2389–2391.

Knowlton, N., R. E. Brainard, R. Fisher, M. Moews, L. Plaisance, and M. J. Caley. 2010. Coral reef biodiversity. Pages 65–77 *in* A. D. McIntyre, editor. Life in the World's Oceans. Blackwell Publishing Ltd.

van de Koppel, J., T. van der Heide, A. H. Altieri, B. K. Eriksson, T. J. Bouma, H. Olff, and B.

R. Silliman. 2015. Long-distance interactions regulate the structure and resilience of coastal ecosystems. Annual Review of Marine Science 7:139–158.

Kühlmann, D. H. H. 1983. Composition and ecology of deep-water coral associations. Helgoländer Meeresuntersuchungen 36:183–204.

Lesser, M. P. 2000. Depth-dependent photoacclimatization to solar ultraviolet radiation in the Caribbean coral *Montastraea faveolata*. Marine Ecology Progress Series 192:137–151.

Lesser, M. P., and J. H. Farrell. 2004. Exposure to solar radiation increases damage to both host tissues and algal symbionts of corals during thermal stress. Coral Reefs 23:367–377.

Lesser, M. P., M. Slattery, and C. D. Mobley. 2018. Biodiversity and functional ecology of mesophotic coral reefs. Annual Review of Ecology, Evolution, and Systematics 49:49–71.

Lovelock, C. E., I. C. Feller, K. L. McKee, and R. Thompson. 2005. Variation in mangrove forest structure and sediment characteristics in Bocas del Toro, Panama. Caribbean Journal of Science 41:456–464.

Macintyre, I. G., I. Goodbody, K. Rützler, D. S. Littler, and M. M. Littler. 2000. A general biological and geological survey of the rims of ponds in the major mangrove islands of the Pelican Cays, Belize. Atoll Research Bulletin 467.

Maie, N., O. Pisani, and R. Jaffé. 2008. Mangrove tannins in aquatic ecosystems: Their fate and possible influence on dissolved organic carbon and nitrogen cycling. Limnology and Oceanography 53:160–171.

Miller, J., E. Muller, C. S. Rogers, R. Waara, A. Atkinson, K. R. T. Whelan, M. Patterson, and B. Witcher. 2009. Coral disease following massive bleaching in 2005 causes 60% decline in coral cover on reefs in the US Virgin Islands. Coral Reefs 28:925–937.

Neal, B. P., A. Khen, T. Treibitz, O. Beijbom, G. O'Connor, M. A. Coffroth, N. Knowlton, D. Kriegman, B. G. Mitchell, and D. I. Kline. 2017. Caribbean massive corals not recovering from repeated thermal stress events during 2005–2013. Ecology and Evolution 7:1339–1353.

Oliveira, M. De. 2020. Marginal reef paradox: A possible refuge from environmental changes? Ocean and Coastal Management 185:1–8.

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Richier, S., J.-M. Cottalorda, M. M. M. Guillaume, C. Fernandez, D. Allemand, and P. Furla.

2008. Depth-dependant response to light of the reef building coral, *Pocillopora verrucosa*: Implication of oxidative stress. Journal of Experimental Marine Biology and Ecology 357:48–56.

Rocha, L. A., H. T. Pinheiro, B. Shepherd, Y. P. Papastamatiou, O. J. Luiz, R. L. Pyle, and P. Bongaerts. 2018. Mesophotic coral ecosystems are threatened and ecologically distinct from shallow water reefs. Science 361:281–284.

Rogers, C. S. 2009. High diversity and abundance of scleractinian corals growing on and near mangrove prop roots, St. John, US Virgin Islands. Coral Reefs 28:909.

Rogers, C. S. 2019. Immediate effects of hurricanes on a diverse coral/mangrove ecosystem in the U.S. Virgin Islands and the potential for recovery. Diversity 11(8):130.

Rogers, C. S., and J. J. Herlan. 2012. Life on the edge: corals in mangroves and climate change. Pages 9–13 Proceedings of the 12th International Coral Reef Symposium. Cairns, Australia.

Rützler, K., M. C. Diaz, R. W. M. Van Soest, S. Zea, K. P. Smith, B. Alvarez, and J. L. Wulff. 2000. Diversity of sponge fauna in mangrove ponds, Pelican Cays, Belize. Atoll Research Bulletin 476.

Scavo Lord, K., K. C. Lesneski, Z. A. Bengtsson, K. M. Kuhn, J. Madin, B. Cheung, R. Ewa, J. F. Taylor, E. M. Burmester, J. Morey, L. Kaufman, and J. R. Finnerty. 2020. Multi-year viability of a reef coral population living on mangrove roots suggests an important role for mangroves in the broader habitat mosaic of corals. Frontiers in Marine Science 7:1–16.

Schutte, V. G. W., E. R. Selig, and J. F. Bruno. 2010. Regional spatio-temporal trends in Caribbean coral reef benthic communities. Marine Ecology Progress Series 402:115–122.

Semmler, R. F., W. C. Hoot, and M. L. Reaka. 2017. Are mesophotic coral ecosystems distinct communities and can they serve as refugia for shallow reefs? Coral Reefs 36:433–444.

Siebeck, O. 1988. Experimental investigation of UV tolerance in hermatypic corals (Scleractinia). Marine Ecology Progress Series 43:95–103.

Smith, T. B., J. Gyory, M. E. Brandt, W. J. Miller, J. Jossart, and R. S. Nemeth. 2016. Caribbean mesophotic coral ecosystems are unlikely climate change refugia. Global change biology 22:2756–2765.

Spalding, M., M. D. Spalding, C. Ravilious, and E. P. Green. 2001. World Atlas of Coral Reefs. University of California Press.

Stambler, N., and Z. Dubinsky. 2005. Corals as light collectors: An integrating sphere approach.

Coral Reefs 24:1–9.

Suggett, D. J., L. F. Dong, T. Lawson, E. Lawrenz, L. Torres, and D. J. Smith. 2013. Light availability determines susceptibility of reef building corals to ocean acidification. Coral Reefs 32:327–337.

Thomsen, M. S., A. H. Altieri, C. Angelini, M. J. Bishop, P. E. Gribben, G. Lear, Q. He, D. R. Schiel, B. R. Silliman, P. M. South, D. M. Watson, T. Wernberg, and G. Zotz. 2018. Secondary foundation species enhance biodiversity. Nature Ecology and Evolution 2:634–639.

Tkachenko, K. S. 2017. Coral reefs in the face of ecological threats of the 21st century. Biology Bulletin Reviews 7:64–83.

Torda, G., J. M. Donelson, M. Aranda, D. J. Barshis, L. Bay, M. L. Berumen, D. G. Bourne, N. Cantin, S. Foret, M. Matz, D. J. Miller, A. Moya, H. M. Putnam, T. Ravasi, M. J. H. van Oppen, R. V. Thurber, J. Vidal-Dupiol, C. R. Voolstra, S.-A. Watson, E. Whitelaw, B. L. Willis, and P. L. Munday. 2017. Rapid adaptive responses to climate change in corals. Nature Climate Change 7:627–636.

Vermeij, M. J. A., J. Bakker, N. van der Hal, and R. P. M. Bak. 2011. Juvenile coral abundance has decreased by more than 50% in only three decades on a small Caribbean Island. Diversity 3:296–307.

Walcker, R., C. Laplanche, M. Herteman, L. Lambs, and F. Fromard. 2019. Damages caused by hurricane Irma in the human-degraded mangroves of Saint Martin (Caribbean). Scientific Reports 9:1–11.

Wild, C., O. Hoegh-Guldberg, M. S. Naumann, M. F. Colombo-Pallotta, M. Ateweberhan, W. K. Fitt, R. Iglesias-Prieto, C. Palmer, J. C. Bythell, J. C. Ortiz, Y. Loya, and R. Van Woesik. 2011. Climate change impedes scleractinian corals as primary reef ecosystem engineers. Marine and Freshwater Research 62:205–215.

Wright, J. L. 2019. The effects of coral presence among Red Mangrove (*Rhizophora mangle*) prop roots on Caribbean fish communities. Thesis. University of Miami, Coral Gables, Florida, United States of America.

Yates, K. K., C. S. Rogers, J. J. Herlan, G. R. Brooks, N. A. Smiley, and R. A. Larson. 2014. Diverse coral communities in mangrove habitats suggest a novel refuge from climate change. Biogeosciences 11:4321–4337.

2.8 Tables

Table 2.1 Coral richness, abundance and diversity of mangrove and reef habitats. Average ± SE richness, abundance (percent cover that was comprised of live or dead coral), and diversity (Shannon-Wiener and Simpson indices) of live coral from surveys within the mangrove canopy and on the adjacent reef at three sites and combined by habitat type in bold.

	Richness	Live Coral % Cover	Dead Coral % Cover	Shannon Diversity	Simpson Diversity
Cayo Ramirez Mangrove	12	32 ± 0.75	10 ± 0.02	0.88 ± 0.11	0.50 ± 0.06
Cayo Ramirez Reef	8	30 ± 0.92	37 ± 0.03	0.29 ± 0.09	0.17 ± 0.05
Fuego Mangrove	17	35 ± 0.66	20 ± 0.03	1.03 ± 0.11	0.55 ± 0.05
Fuego Reef	11	36 ± 0.67	21 ± 0.03	0.74 ± 0.10	0.41 ± 0.05
Sunny Mangrove	11	35 ± 0.81	14 ± 0.03	1.00 ± 0.08	0.57 ± 0.03
Sunny Reef	6	36 ± 0.87	17 ± 0.03	0.42 ± 0.10	0.26 ± 0.06
Combined Mangrove	**24**	**34 ± 0.01**	**14 ± 0.03**	**0.97 ± 0.06**	**0.54 ± 0.03**
Combined Reef	**12**	**34 ± 0.02**	**25 ± 0.06**	**0.52 ± 0.06**	**0.30 ± 0.04**

2.9 Figures

Figure 2.1 Coral species growing within the mangrove habitat of Bocas del Toro, Panamá.

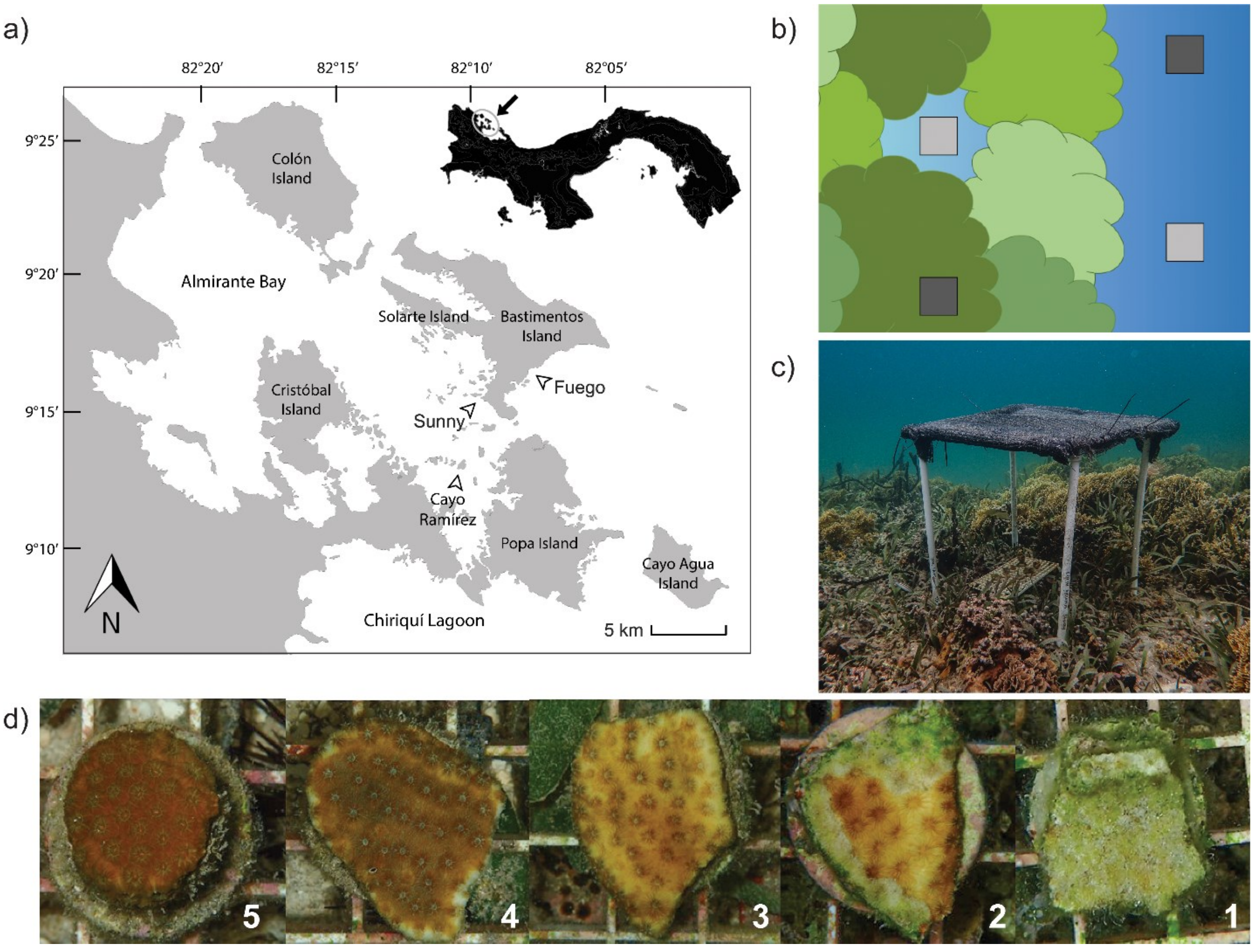

Figure 2.2 Coral transplant experimental design. (a) Map of Bocas del Toro coral survey sites marked with open arrow heads (Fuego, Sunny, and Cayo Ramirez). The Fuego site was used for the reciprocal transplant experiment. Inset, Archipelago of Bocas del Toro, Panamá circled and indicated with the arrow. (b) Four experimental treatments with 10 replicate plots each: reef control (natural light), mangrove control (natural light), mangrove high light created by pulling back canopy, and reef low light created by installing a shade. Dark gray indicates lower light treatments while light gray indicates higher light treatments. (c) Coral fragments were placed on rigid eggcrate, seen here under shade in reef low light treatments. (d) Corals during the experiment were scored on a coral condition index according to the follow criteria: (5) completely healthy corals, (4) <50% bleaching, (3) >50% bleaching, (2) visible tissue loss, or (1) dead. These scores are shown from left to right, respectively, with *O. faveolata.*

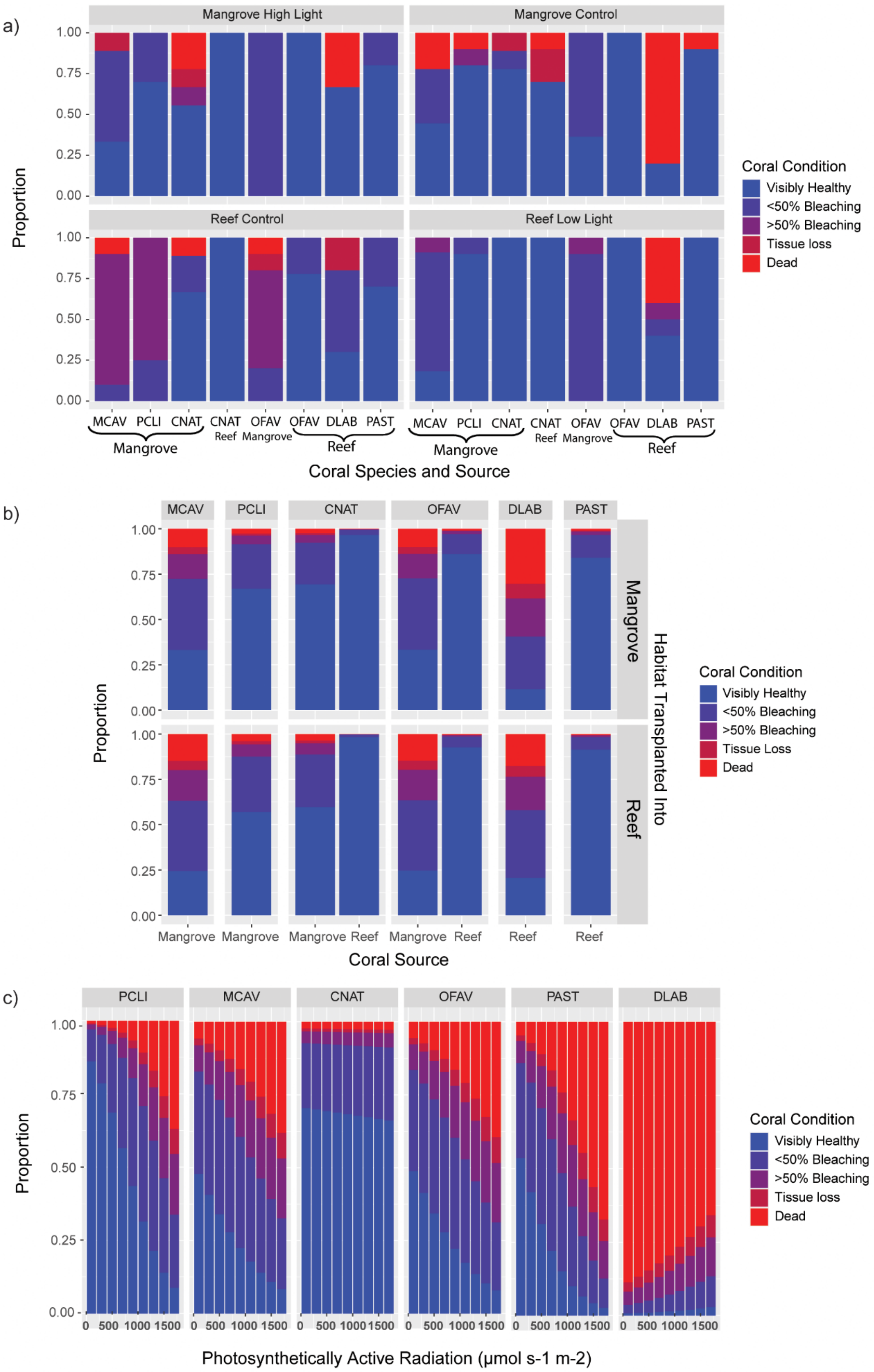
a)
Mangrove High Light
Mangrove Control
Reef Control
Reef Low Light
Proportion
1.00
0.75
0.50
0.25
0.00
MCAV PCLI CNAT CNAT OFAV OFAV DLAB PAST
Reef Mangrove
Mangrove
Reef
Coral Species and Source
Coral Condition
Visibly Healthy
<50% Bleaching
>50% Bleaching
Tissue loss
Dead
b)
MCAV
PCLI
CNAT
OFAV
DLAB
PAST
Mangrove
Reef
Habitat Transplanted Into
Proportion
Mangrove Mangrove Mangrove Reef Mangrove Reef Reef Reef
Coral Source
Coral Condition
Visibly Healthy
<50% Bleaching
>50% Bleaching
Tissue Loss
Dead
c)
PCLI
MCAV
CNAT
OFAV
PAST
DLAB
Proportion
0 500 1000 1500
Photosynthetically Active Radiation (μmol s-1 m-2)
Coral Condition
Visibly Healthy
<50% Bleaching
>50% Bleaching
Tissue loss
Dead

Figure 2.3 Modeled coral condition. (a) Raw data of coral condition scores from which we used ggpredict to obtain predicted probabilities to plot modeled data. (b) Modeled coral health data with the main effects of coral source ($p < 0.001$), habitat corals were transplanted into, and species ($p < 0.001$), at the mean light level (pooled PAR values). MCAV = *Montastraea cavernosa*, PCLI = *Pseudodiploria clivosa*, CNAT = *Colpophyllia natans*, OFAV = *Orbicella faveolata*, DLAB = *Diploria labyrinthiformis*, PAST = *Porites astreoides*. (c) Coral condition with the significant interaction of coral species and light ($p = 0.008$) plotted across a light gradient using the PAR values measured in the field ranging from 116-1783 μmol s^{-1} m^{-2}.

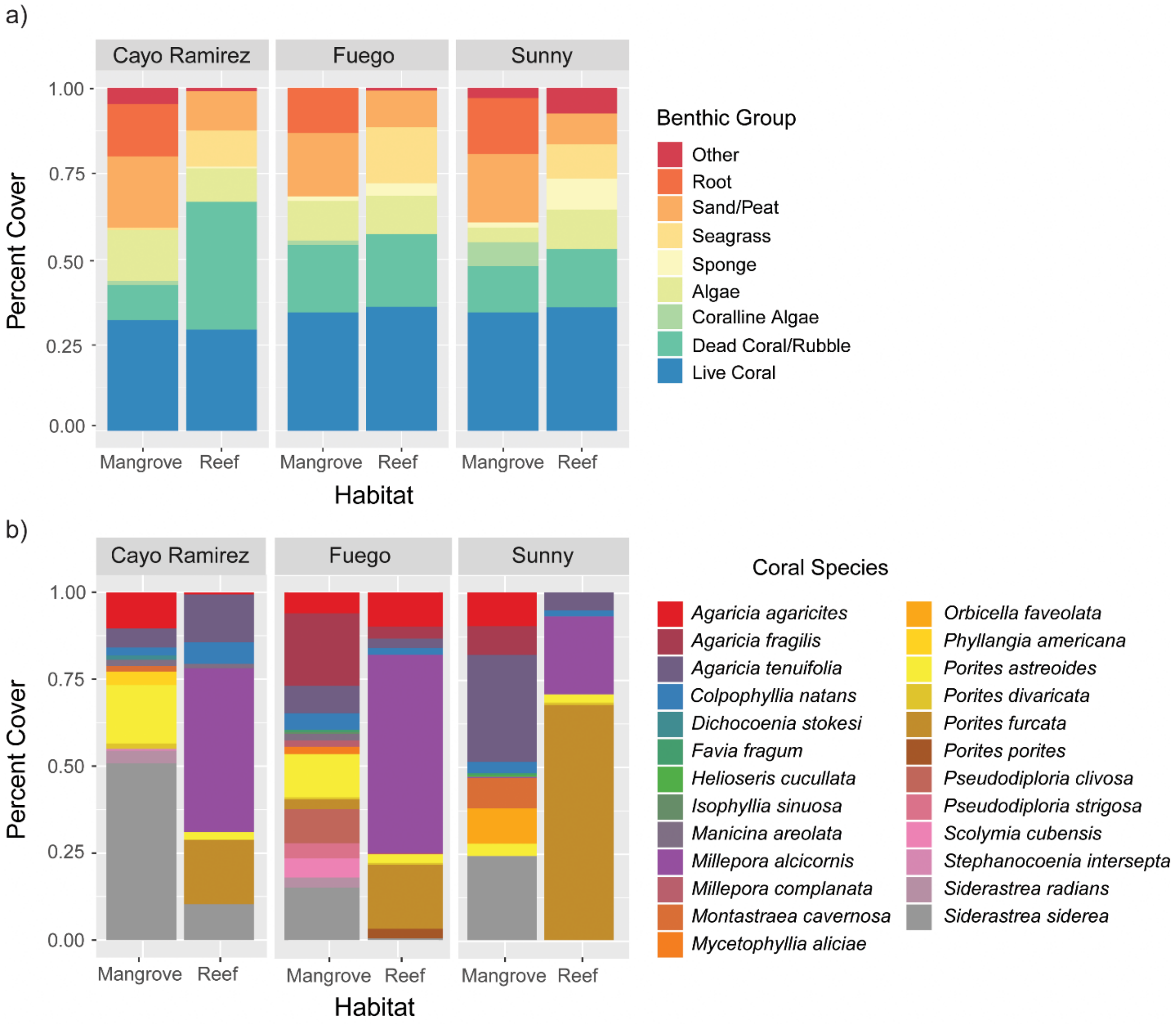

Figure 2.4 Percent cover of benthic groups and coral species between mangrove and reef habitats. (a) Percent cover of 1-m^2 quadrats (pooled per habitat type by site) surveyed on the reef and mangrove canopy, at each of three sites. (b) The proportion of each coral species that make up the live coral category from panel a.

Preface to Chapter 3

In Chapter 2, I examined how mangroves function as foundation species, modifying environmental factors influencing the condition and survival of associated organisms (e.g., corals). I found that mangroves facilitate coral community structure and survival within the canopy by ameliorating thermal and photic stress commonly experienced in shallow conditions. Foundation species traits such as surface area, age, and patch size determine the degree to which conditions are modified (e.g., amount of shade mangroves provide corals) and how the associated organisms will be impacted (e.g., positively or negatively).

In Chapter 3, I test for links between foundation species traits and associated biodiversity to better understand the mechanisms that determine community assemblage in this speciose and functionally diverse system. Using red mangrove as my model foundation species, I identified structure and substrate composition as traits of the mangrove prop roots to test for links to epibiont community composition and facilitation cascades. Since structure is a complex trait involving substrate composition (e.g., material and biological activity) and can be linked to available area (i.e., root length), I compared epibiont communities among living and non-living mangrove roots and non-living root mimics (i.e., wood and PVC) after 14 months of colonization and development. I also tested how these traits indirectly affected the mobile fauna community (i.e., species richness and diversity) because of their potential reliance on secondary foundation species (e.g., sponges, bivalves) that are directly affected by traits of mangrove roots.

Chapter 3: Cascading effects of mangroves on assembly of epibiont communities are contingent on root characteristics

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3.1 Abstract

Foundation species traits that structure communities are rarely experimentally examined, thus, a predictive understanding of their functions lags behind patterns of observed species associations. Red mangrove (*Rhizophora mangle*) roots form complex living habitats that support diverse epibiont communities, making them a model system for testing links between variation in foundation species traits and associated biodiversity. Here we compared epibiont community composition between living and non-living mangrove roots, as well as root mimics, to test how foundation species traits affect community structure. We also quantified the community structure of associated mobile invertebrates to examine their relationship with secondary foundation species (e.g., sponges, bivalves) that grow on the roots. After 14 months of colonization and succession, substrate composition (i.e., mangrove, wood, PVC) did not have a large effect on epibiont communities, however, non-living roots were five times more likely to deteriorate, and consequently had the lowest epibiont diversity and abundance. We found strong positive relationships between mobile invertebrate richness and the abundance, diversity, and complexity of sponges and bivalves, suggesting that variation among roots in secondary foundation species play an important role in mediating the diversity of mobile invertebrates. This study highlights the functional role of habitat structure, and how rapidly that function can be lost without biogenic maintenance. Our results indicate the importance of facilitation cascades in fostering diverse mobile invertebrate communities and highlight both advantages and limitations in using artificial structures for application to restoration programs.

3.2 Introduction

Foundation species (sensu Dayton 1972) play a disproportionately important role in structuring communities by creating biogenic habitat, modifying environmental conditions, and altering resource availability and species interactions (Dayton 1972, Ellison et al. 2005, Angelini et al. 2011, Altieri and Van De Koppel 2013). Variation in traits of foundation species such as structural complexity, age, and patch size can determine the strength of facilitation, defined here as the degree to which environmental conditions are modified or stress is ameliorated, and the subsequent effects on associated species composition and interactions (Irving and Bertness 2009, Bishop et al. 2013, Schutte and Byers 2017). For example, variability in the density and structural complexity of foundation species (e.g., seagrass, marsh grass, macroalgae, coral) can modify water flow velocity, turbulence, and sediment characteristics, as well as reduce predation intensity, which affects growth rates, survivorship, body size, and population density of associated species (Bruno and Bertness 2001, Bruno et al. 2003).

In a facilitation cascade (sensu Altieri et al. 2007), the primary foundation species enables the colonization of a secondary foundation species, thereby providing complementary facilitative functions to support diverse species assemblages. These types of assemblages can exist in both terrestrial and marine ecosystems and function through a suite of positive interactions such as reducing predation pressure by increasing habitat complexity, altering the physical environment to provide protection from abiotic stress (e.g., canopy shading), and modifying nutrient availability (Angelini et al. 2011, Hughes et al. 2014, Thomsen et al. 2018). One way to study the relationship between primary and secondary foundation species and their associated organisms is by isolating primary foundation species traits with the use of mimics to experimentally identify which traits impact community composition of associated organisms (Angelini et al. 2011). Understanding links between foundation species traits and their associated assemblages is also important in the context of recovery and restoration efforts that involve artificial substrates that mimic foundation species.

In coastal systems, hard infrastructures such as artificial reefs, seawalls, and breakwaters are increasingly used for coastal protection and to mitigate other repercussions of lost foundation species (Gittman et al. 2015). A mechanistic understanding of the effectiveness of such hard infrastructures, including their cascading effects on the ecosystem, is needed for effective design and planning of coastal resource management (Dafforn et al. 2012, 2015, Morris et al. 2018, Vozzo et al. 2021). Experimental studies examining foundation species mimics as hard infrastructure can inform habitat restoration and enhancement efforts because they allow for traits of foundation species to be isolated to assess their impact on associated biodiversity. For example, the physical structure of a mimic may be more durable under stressful conditions (e.g., high wave energy) that would deteriorate or erode foundation species (e.g., break mangrove roots or topple coral colonies), allowing habitat structure to persist in the system. On the other hand, artificial infrastructure may lack important characteristics, such as chemical cues that are important for inducing recruitment of the desired species assemblage or contain additives that inhibit settlement (Dennis et al. 2018). As a consequence, differences in communities have also been observed between foundation species and hard infrastructure, including a greater presence of non-indigenous species on hard infrastructure than on foundation species (Ellison et al. 1996, Chapman 2003, Bulleri and Airoldi 2005, Glasby et al. 2007, Tyrrell and Byers 2007, Mineur et al. 2012, Airoldi et al. 2015). In this study, we examine how those differences can arise from variation in traits of foundation species and associated facilitation cascades.

We used red mangrove (*Rhizophora mangle*) as a model system for testing links between traits of foundation species and associated biodiversity. Mangrove aerial roots form living subtidal habitats recognized for their diverse fish and epibiont communities, with aerial roots providing a complex habitat and hard, stable settlement surface in an otherwise simple and unstable sedimentary environment (Farnsworth and Ellison 1996, MacDonald and Weis 2013). Most studies on mangroves and their associated biodiversity have been observational studies focused on the association between mangrove root traits and fish communities (Nagelkerken et al. 2010), relationships between epibionts and fishes (MacDonald et al. 2008, MacDonald and Weis 2013), or comparisons of epibiont communities between natural mangrove roots and either mangrove root mimics (e.g., PVC, wooden stakes) or hard infrastructure (e.g., concrete dock pilings, seawalls) (Guerra-Castro and Cruz-Motta 2014, Janiak et al. 2018). These previous studies using root mimics or hard infrastructure have demonstrated that they have distinct communities from natural mangrove roots, at both the local and regional scale (Guerra-Castro and Cruz-Motta 2014, 2018). However, there remains a lack of experimental tests addressing how root traits predict their function in shaping the composition of associated organisms. Sponges and bivalves are dominant groups found on subtidal mangrove roots within the Caribbean (Guerra-Castro and Cruz-Motta 2018) and often considered secondary foundation species (Bishop et al. 2012, Altieri and Van De Koppel 2013, Aquino-Thomas and Proffitt 2014, Vozzo and Bishop 2019, Aquino-Thomas 2020) because of the structural complexity they add to the mangrove system, which can provide refuge to a speciose invertebrate community (Henkel and Pawlik 2011, Rebolledo et al. 2014). However, few studies have quantified the importance of these secondary foundation species on associated mobile community structure within mangrove roots.

The objective of this study was to test for links between foundation species traits and associated biodiversity to better understand the mechanisms that determine community assemblage in a speciose and functionally diverse system. Our study expands the growing literature on mangrove root traits including root complexity (Nagelkerken et al. 2010, Vorsatz et al. 2021), root contact with the ground (Schutte and Byers 2017), and root density (Nanjo et al. 2014) by focusing on substrate composition and whether roots were alive or dead. By tracking community development after 14 months on living and non-living mangrove roots and non-living root mimics (i.e., wood and PVC), we were also able to examine the importance of other factors that came to vary among root treatments, including root length and the presence of secondary foundation (e.g., sponges, bivalves), in determining community structure. To address our objectives, we examined the following questions: (1) Are epibionts more likely to grow on living or non-living mangrove roots?, (2) Are root mimics functionally similar to living mangrove roots?, (3) Does wood type (mangrove root vs commercially available hardwood) matter for epibiont community structure?, (4) If the epibiont community is removed from mangrove roots, is 14 months sufficient for the community to recover?, and (5) Are there links between secondary foundation species (bivalves and sponges) and the mobile invertebrate community? Through these comparisons, we can isolate complex foundation species traits to understand what is important in influencing community composition and what that means for conservation and management of these dynamic environments.

3.3 Methods

Study site

We conducted our field experiment in the fringe red mangrove (*Rhizophora mangle*) forest on Solarte island in the Bocas del Toro Archipelago on the Caribbean coast of Panamá from April 2017 to May 2018. We selected two mangrove sites (Coco and Corales) with an average depth of 1.2 m and where aerial roots hanging from the branches were permanently inundated and encrusted with rich epibiont communities. Each site was in a cove facing Almirante Bay and protected by islets and reef from wave exposure (Figure 3.1).

Experimental design and mangrove root treatments

At each site, five root treatments with 10 replicates each, were assigned in a random order >2 m apart. Treatments consisted of: 1) an unmanipulated mangrove root control, 2) a mangrove root cleared of epibionts at the beginning of the experiment, 3) a cleared mangrove root that was cut from the tree, dried for three weeks, and reattached to a mangrove branch, 4) an untreated wooden dowel (poplar), and 5) a PVC pipe. We refer to treatments as follows: natural, scraped, cut, wood, and PVC, respectively. Roots and mimics of all treatments were similar in diameter. Pairwise comparisons between subsets of treatments allowed us to test our specific research questions for a variety of response variables (see Table 3.1). The two root mimic treatments consisting of wood (Eston et al. 1992, MacDonald et al. 2008, Guerra-Castro and Cruz-Motta 2014, 2018) and PVC (Eston et al. 1992, Verweij et al. 2006, Nagelkerken et al. 2010) have been used in previous mangrove studies and allow for a direct comparison of common materials assumed to be surrogates for natural mangrove roots. To minimize potential differences caused by root complexity, we only selected non-bifurcated mangrove roots for the natural, scraped, and cut treatments. The wooden rods had a weight added to their tip as ballast to maintain a vertical orientation. PVC pipes were lightly sanded to roughen their surface and partially closed at the ends to prevent predators (e.g., crabs) from residing inside while allowing water to enter to mitigate effects of buoyancy on root orientation. To control for potential variation in access by walk-on predators from below (Guerra-Castro and Cruz-Motta 2018), none of the roots were in contact with the sediment or other roots. We were able to control the length of the cut and mimic root treatments, but not the length of the scraped or natural mangrove roots without damaging the root itself. Therefore, we selected roots of a similar length to other treatments and then recorded initial root length to use as a covariate in analyses. We labeled each root with a numbered tag and marked the mean higher high water (MHHW) level with a horizontal-colored nylon cable tie to denote the top of the sampled portion of each root. We attached roots to branches using cable ties so that the root tip was 60 cm below MHHW, which was the average submerged length of non-bifurcated mangrove roots in the area. Roots were monitored monthly to re-secure cable ties and to record any roots that rotted away above the MHHW. In both *in situ* and laboratory sampling only the area below the MHHW was sampled.

Root growth and deterioration

To account for growth and deterioration of the roots over the course of the experiment, we measured the final root length *in situ*, which by necessity included the epibiont community growing on the roots (because overgrowth made it impossible to locate the end of root without disturbing the epibionts). The initial length was subtracted from final length to calculate the change in root length. This is important in quantifying available substrate for epibionts to colonize and measuring how the roots were affected by degradation due to boring invertebrates such as the isopod, *Spaeroma terebrans,* or shipworms (marine bivalves in the family Teredinidae). We recorded signs of boring (e.g., openings from S. *terebrans* or calcareous burrows of shipworms) as present or absent when roots were sampled in the laboratory. Because of the loss of some roots to deterioration, only 73 of the original 100 roots were sampled destructively. Since community composition can be linked to available area (i.e., root length) and root treatments may have differed in final length, we examined how change in root length and survival of roots differed among treatments and the relationship between final root length and community composition.

In situ percent cover

Prior to collection of roots at the end of the 14-month experiment, we conducted *in situ* surveys of sessile epibiont percent cover. *In situ* surveys are commonly used in the mangrove habitat to study epibiont communities (Ellison and Farnsworth 1990, MacDonald et al. 2008, Guerra-Castro and Cruz-Motta 2018, Janiak et al. 2018) and allow for evaluation of encrusting species, which may be difficult to accurately quantify through destructive sampling. We first recorded the total length of each root to account for growth or deterioration of non-PVC roots treatments. We then used a ruler to measure the proportion of space on the root dominated by each of the following 13 categories: empty space, barnacle, bivalve, green algae, red algae, crustose coralline algae, cyanobacteria, sponge, tunicate, tube worm, hydroid, anemone, and bryozoan. Where there were overlapping epibionts, the outermost layer of epibionts was used for the percent cover score. The percent cover of both sides of the roots (i.e., facing ocean, facing island) were measured, but no significant difference was found; therefore, the side facing the ocean was used in analyses.

Sessile community richness, diversity, biomass and composition

At the end of the experiment, the roots and mimics were collected (at a rate of ~4 randomly selected roots/sampling day). For collection, we enclosed each root in a large fabric bag with zip ties to retain all epibionts. Roots were transported to the laboratory in a cooler filled with aerated seawater. Once in the laboratory, the root epibionts were removed and identified to the lowest possible taxonomic level, henceforth referred to as morphospecies. We recorded individual and total wet mass for each morphospecies to obtain total biomass of all epibionts per replicate. However, the weights of encrusting taxa (e.g., encrusting bryozoans, crustose coralline algae, hydroids) were excluded due to their lack of structural integrity upon removal. The following metrics were quantified for the epibiota of each root: species richness, Shannon-Wiener diversity, biomass, and community composition. We employed destructive sampling in addition to the *in situ* percent cover to provide a more in-depth understanding of community assemblage as it accounts for the complex multi-layered epibiont community and allows for mobile invertebrate species to be quantified.

Mobile community richness, diversity, and abundance

To explore the effects of primary (mangrove root treatment) and secondary foundation species (epifaunal sponges and bivalves) on the associated mobile fauna of the roots, mobile invertebrates were collected and identified to the lowest possible taxonomic level. During destructive root sampling, visible mobile invertebrates were removed from the sessile epibionts and kept in separate aerated tanks to prevent predation. After all sessile epibionts were removed from the root, the epibionts and root were rinsed, and the water was sieved to collect mobile invertebrates that may have been missed previously. We quantified richness of the mobile community as the number of morphospecies per treatment and site. We calculated diversity (Shannon-Wiener index) from the number of individuals per mobile morphospecies and abundance of mobile fauna as count data.

Secondary foundation species and structural complexity

Based on our visual estimates of percent cover, sponges and bivalves were dominant and therefore, to examine whether they functioned as secondary foundation species on mangrove roots and root mimics, we tested whether root treatment or site affected their biomass and richness. To quantify the structural complexity of the epibiont community, we measured the circumference of the epibionts at 10-cm intervals along each root before denuding, and then used the standard deviation of these measurements for each root as a measure of structural complexity.

Analyses

Root growth and deterioration

All data were analyzed with R version 3.6.3 (R Core Team 2020). To examine how treatment affected change in root length (difference between initial and final root length), we fit generalized linear models (GLM) using the glm function with the main effects of root treatment and site and the response variable of change in root length. Roots that completely deteriorated were included as a final root length value of zero, for a change in root length of -100%. A subsequent binominal GLM on all treatments excluding PVC was used to examine the main effects of root treatment and site on presence of boring invertebrates. Overall significance of each factor in the model was assessed by a Wald test with a Chi-Square error distribution using the Anova() function from the package *car* with a type III sum of squares. If differences were detected, Tukey post-hoc multiple comparisons of means with the glht function of the *multcomp* package were used for pairwise comparisons. To examine the effect of final root length (as a proxy for available area on root) on sessile and mobile community composition (e.g., richness, diversity, and biomass) within each treatment, we used the ggscatter function within the *ggpubr* package to plot linear regressions with 95% confidence intervals and to calculate a Pearson's r correlation coefficient within each treatment.

In situ percent cover

We conducted a permutational multivariate analysis of variance (PERMANOVA) using the adonis2 function from the *vegan* package to test for differences in community composition with the main effects of root treatment and site and a covariate of initial root length, to account for variation within natural (average root length = 73.2 ± 2.4 cm, SE) and scraped roots (74.8 ± 2.6 cm). For *in situ* surveys, the abundance of taxa was estimated as percent cover of major taxonomic groups. Post-hoc pairwise comparisons were made using the pairwise.adonis function of the *pairwiseAdonis* package.

Sessile community richness, diversity, biomass, and composition

For sessile community data from collected roots, we used GLMs with main effects root treatment and site and a covariate of initial root length, to detect effects on species richness, Shannon-Wiener diversity, and biomass. Gaussian distribution was used in all regression models except for species richness for which we used the Poisson distribution. We then used the Anova function from the *car* package with a Type III sum of squares to run a Wald test with a Chi-square error distribution to test for the significance of the main effects and their interaction, and to compare coefficients.

To examine treatment differences in community composition data based on destructive sampling of collected roots, we created a Bray-Curtis dissimilarity matrix using root treatment and site as main effects. A square root transformation was used to improve normality and homogeneity of variances. The functions permutest and betadisper were used to analyze the multivariate homogeneity of group dispersion as a multivariate analogue of Levene's test for homogeneity of variances. We then conducted a second PERMANOVA using biomass of each of the 86 sessile epibiont morphospecies identified from destructive sampling as a representation of abundance. For the same sessile community data, similarity percentage analyses (SIMPER) were used to determine which taxonomic groups and species had the greatest contribution to dissimilarity in the community composition. The first SIMPER compared 10 major taxonomic groups (i.e., bivalve, sponge, tunicate, barnacle, red algae, green algae, cyanobacteria, hydroid, tubeworm, and sea anemone), whereas the second SIMPER compared all 86 morphospecies.

Mobile community richness, diversity, and abundance

For the mobile community, three response variables (morphospecies richness, diversity, and abundance) were assessed using GLMs with main effects root treatment and site and a covariate of initial root length. We then tested how root treatment indirectly affected the mobile community through secondary foundation species interactions. We used GLMs with main effects sponge and bivalve richness and biomass to assess response variables richness and diversity of mobile invertebrates.

Secondary foundation species and structural complexity

Variation in secondary foundation species (i.e., sponges and bivalves) richness and biomass among root treatments was assessed using GLMs, with main effects of root treatment and site, and a covariate of initial root length. Structural complexity of the sessile community was assessed using a GLM with Gaussian distribution and main effects of root treatment and site and a covariate of initial root length. To examine the effect of structural complexity on mobile community richness and diversity, we plotted linear regressions with 95% confidence intervals and Pearson's r correlation coefficient within each treatment.

3.4 Results

Root growth and deterioration

We found an effect of root treatment ($p < 0.001$, Chi-square test) but not site ($p = 0.748$) on change in root length (e.g., growth or deterioration). Cut roots were the shortest of all treatments by the end of the experiment, and post-hoc pairwise comparisons of root treatments indicated that cut roots had significantly greater decrease in root length compared to other treatments. Scraped and wood treatments had similar decreases in root length to each other and were significantly shorter than PVC. (Table C1). During the experiment there were noticeable signs of deterioration (e.g., rotting and/or boring by invertebrates) starting in month 8. By the end of the experiment, 70% of the cut mangrove roots had completely deteriorated, which was nearly five times more than the living mangrove treatments, while only one wood root completely deteriorated (Figure 3.2). Since we monitored the roots over time, we observed that roots were lost from progressive deterioration rather than other factors such as sudden dislodgment in storms. We found a significant effect of root treatment ($p<0.001$) on presence of boring, but no effect of site ($p = 0.228$) or the interaction of treatment and site ($p = 0.259$). Boring was observed at greater frequency in wood compared to the cut, scraped, and natural mangrove root treatments. Initial root length was used as a covariate in all analyses but never had a significant effect and is not reported for subsequent analyses.

In situ percent cover

The PERMANOVA revealed that root treatment ($p = 0.005$) and site ($p = 0.005$) had significant effects on community composition, and their interaction did not ($p = 0.195$). The dominant sessile epibiont groups were sponge and red algae, which together with empty space contributed to the most dissimilarity between root treatments. The post-hoc analysis revealed that epibiont composition differed between PVC and natural treatments (pairwise comparisons, $p = 0.020$, Figure 3.3A) with sponge, red algae, and green algae contributing the most to dissimilarity, PVC and cut mangrove roots ($p = 0.020$) with empty space, sponge, and cyanobacteria being the biggest contributors to dissimilarity, PVC and wood ($p = 0.030$) with sponge, empty space, and red algae contributing the most to dissimilarity, and wood and natural mangrove roots ($p = 0.020$) with sponge, empty space, and red algae being the largest contributors to dissimilarity.

Sessile community richness, diversity, biomass, and composition

A total of 86 sessile morphospecies were observed on the roots representing the classes of Demospongiae (sponge), Ascidiacea (tunicate), Bivalvia (bivalve), Polychaeta (tubeworm), Cyanophyceae (cyanobacteria), Hexanauplia (barnacle), Hydrozoa (hydroid), and Anthozoa (sea anemone) and the phyla Chlorophyta (green algae), Rhodophyta (red algae), and Bryozoa (bryozoan). No taxa were present on all roots. The sessile morphospecies detected on >50% of all roots, henceforth referred to as "common", were the barnacle *Amphibalanus spp.* and the oyster *Ostrea stentina*, which were found on every PVC root, and the ascidian *Eudistoma olivaceum* which was found on every natural and cut mangrove root (Table C2). The most common sponges included *Tedania ignis, Haliclona piscaderaensis, Haliclona manglaris*, and *Mycale microsigmatosa*. Morphospecies with the greatest biomass across all treatments were *Tedania ignis*, *Tedania klausi*, *Haplosclerida spp.*, *Ostrea stentina*, *Pinctada imbricata*, *Niphates erecta*, in order of biomass, respectively.

There was a significant effect of root treatment ($p<0.001$, Chi-square test), but no effect of site ($p = 0.760$) on sessile epibiont morphospecies richness. Natural mangrove roots and PVC had greater richness than all other treatments but did not differ from one another (Figure 3.4A). We found a significant positive correlation between sessile epibiont richness and final root length within scraped and wood treatments (Figure C1).

Shannon diversity of sessile organisms differed among treatments ($p < 0.001$), but there was no effect of site ($p = 0.343$). Natural mangrove roots had greater diversity than scraped ($p = 0.031$) and cut ($p = 0.010$). PVC also had greater diversity than scraped ($p = 0.046$) and cut ($p = 0.004$). There was no difference between natural mangrove roots and PVC. There were positive correlations between sessile epibiont diversity and final root length within scraped and wood treatments (Figure C2).

Total sessile epibiont biomass (i.e., wet weight) differed among root treatments ($p<0.001$) and sites ($p = 0.013$). Pairwise comparisons showed that natural roots had significantly greater biomass than all other treatments, with no differences found between the other treatments at the end of the experimental period (Figure 3.3B). Of the two sites, Corales had greater overall biomass than Coco, with generally more sponges and bivalves. Within scraped mangrove root and wood treatments there were positive correlations between total sessile epibiont community biomass and final root length (Figure C3).

The PERMANOVA revealed that community composition differed by root treatment ($p = 0.005$) and site ($p = 0.005$, Figure 3.3B), and their interaction was not significant ($p = 0.680$). Natural mangrove roots and PVC were different from all other treatments as well as each other (Table 3.2). The first SIMPER analysis on the same broad taxonomic epibiont categories used in the *in situ* surveys, excluding empty space, revealed that bivalves and sponges had the greatest contribution to the dissimilarity of community composition across all pairwise comparisons of treatments making up 71-85% of the cumulative contribution (Table 3.3). Bivalves accounted for 44-59% of the dissimilarity, and sponges accounted for 19-34% followed by tunicates 3-11% and barnacles 1-19%. Barnacles had a greater contribution to community composition in root mimic treatments than mangrove roots, living or non-living. In comparison, tunicates had a greater contribution to community composition in living mangrove roots than other treatments. Of the two sites, bivalves, barnacles, and sponges had a greater contribution to community composition in Corales than in Coco (Figure 3.3).

Using a second SIMPER analysis on morphospecies, we found 17 of the 86 taxa that accounted for the largest dissimilarities among treatment in sessile epibiont communities (Table 3.3). Of those, there were five bivalves: *Ostrea stentina, Pinctada imbricata, Crassostrea rhizophorae, Dendostrea frons,* and *Isognomon alatus*, all of which were also among the most commonly found species, detected on >50% of roots (Table C2). Eight sponges were among the taxa with the largest percent contribution to dissimilarity, of which two were common species, *Tedania ignis* and *Mycale microsigmatosa*. Barnacles, two species of tunicates (*Phallusia nigra and Herdmania pallida)* and the green algae, *Caulerpa verticillata*, were also among the taxon with the largest percent contribution to dissimilarity.

Mobile community richness, diversity, and abundance

The richness of mobile invertebrates differed among root treatments ($p < 0.001$, Chi-square test) and site ($p < 0.001$) with cut roots having the lowest mean richness (Figure 3.4B). Within scraped mangrove root and wood treatments, mobile richness was positively correlated with final root length (Figure C1). Looking at indirect effects of treatment through secondary foundation species richness and biomass, bivalve biomass ($p < 0.001$) and sponge biomass ($p =$

0.006) had positive effects on mobile community richness (Figure C4). The most frequently detected mobile invertebrates were the shrimp *Cuapetes americanus* (found on every natural mangrove root and over 85% of scraped mangrove and PVC treatments), polychaete worms of the family Nereididae (found on every PVC root and 94% of the natural roots), amphipods (found on every PVC and natural root), isopods from the genus *Paracerceis* (found on over 85% of natural, scraped and PVC roots), and the snapping shrimp *Synalpheus apioceros* (found on over 80% of natural mangrove roots, Table C3). Mobile community diversity differed by root treatment ($p = 0.011$) and site ($p = 0.025$) with PVC having greater mobile community diversity than wood ($p = 0.037$). There were no effects of bivalve or sponge richness or biomass on mobile community diversity. Mean mobile community abundance differed by root treatment ($p <0.001$) and site ($p = 0.009$). Corales had greater abundance of mobile fauna than Coco, but the trend of natural roots having greater abundance than scraped ($p = 0.016$) and cut roots ($p < 0.001$) was consistent across sites (Figure 3.5).

Secondary foundation species and structural complexity

The SIMPER analysis indicated that bivalves and sponges had the greatest influence on differences in sessile epibiont community structure, and therefore we explored how these taxa were affected by root treatments. There were significant effects of root treatment on sponge and bivalve richness and biomass. Site only influenced bivalve biomass (Table C4). Natural mangrove roots had greater sponge biomass than the other root treatments and greater bivalve biomass than scraped, cut, and wood treatments (Figure 3.6). The Corales site had greater bivalve biomass than Coco. Scraped mangrove roots had lower sponge richness than natural roots ($p = 0.034$, z test), and wood had lower sponge richness than natural roots ($p = 0.029$) and PVC ($p = 0.019$). Wood ($p<0.001$) and cut mangrove roots ($p<0.001$) had lower bivalve richness than natural roots.

There was an effect of root treatment ($p < 0.001$) on epibiont structural complexity (estimated as the variability of epibiont circumference along the root), but no effect of site ($p = 0.067$). Natural mangrove roots had greater complexity than all other treatments. Structural complexity of the sessile community had a positive correlation with richness of the mobile community within all treatments aside from PVC (Figure C5). Structural complexity of the sessile community was positively correlated with mobile community diversity in the wood ($p = 0.002$) and cut treatments ($p = 0.005$, Figure C5). Sponge biomass had a positive correlation with structural complexity across all treatments, and bivalve biomass had a positive correlation with structural complexity only in natural and scraped roots (Figure C6).

3.5 Discussion

Foundation species play an important role in ecosystems, but little is known regarding how foundation species traits shape the associated community composition. Our treatments represented variation in both substrate composition and whether the foundation species was alive or dead, allowing us to answer a series of complementary questions about mangrove traits and community structure of epibionts (Table 3.1). We compared non-living mangrove roots (i.e., cut treatments) to living mangrove roots (i.e., natural and scraped treatments) and wood root mimics and did not find evidence for biotic controls as would be exerted by living roots (e.g., nutrient exchange) shaping the associated community, nor did we find that species of wood substrate influenced epibiont colonization and assemblage. However, we found that non-living roots quickly deteriorated and became shorter or were lost altogether, and as result they had a reduced capacity to support a diverse community. We also established an unmanipulated living mangrove root control (i.e., natural treatment) for comparison to scraped mangrove roots, and found that 14 months was only sufficient for full development of certain metrics of epibiont community (e.g., percent cover of sessile community, mobile diversity, bivalve richness). This indicates which criteria are useful for determining whether the community recovers at various temporal scales. Over the course of the study, we found root mimics functioned similarly to living mangrove roots in some important metrics with wood mimics being more similar to mangrove roots than PVC.

Are epibionts more likely to grow on living or non-living mangrove roots?

We tested whether epibionts were more likely to grow on living scraped mangrove roots compared to non-living, cut mangrove roots, and the lack of difference suggests that nutrient exchange or other such mechanisms are relatively unimportant in how mangrove roots mediate epibiont community assemblage (Table 3.1). However, the rapid deterioration of non-living mangrove roots, and the correlation between root length and diversity, implies a limited time following death during which roots can serve as viable habitat for epibionts. Further, our study clearly shows high levels of root loss (10%) in the sampled mangrove stands over the course of our 14-month study, a pattern that could potentially be amplified in stands under stress. Stress to mangrove stands is compounded in many regions of the world with increasing frequency and magnitude of hurricanes combined with urban and aquacultural/agricultural encroachment preventing mangroves from expanding landward to recover and/or by altering hydrology of the area minimizing suitable refuge, which results in large stands of dead mangroves (Duke et al. 2017, Feller et al. 2017, Krauss et al. 2020, Radabaugh et al. 2020, Svejkovsky et al. 2020). Understanding the mechanisms influencing root length, including death and deterioration of roots, is important since root length determines the habitable area of roots, and length appeared to be the biggest difference between living and non-living roots in terms of influence on the biodiversity of epibiont communities. The sample size of non-living mangrove roots by the end of the study was limited, with only 6 roots remaining, and large variability within the cut root treatment makes it hard to know if there is a true non-effect, or if it is an artifact of the sample size and variability, warranting further exploration.

Given the roles that epibionts can play in biofiltration, bioremediation, bioturbation, habitat modification, and as food sources for fishes and humans (Ellison 2008, MacDonald et al. 2008, MacDonald and Weis 2013, Carrasquilla-Henao and Juanes 2017, Aguirre-Rubí et al. 2018, Seemann et al. 2018, Vaughn and Hoellein 2018), it is important for conservation and management purposes to understand how root damage/death affects the epibiont community. This is beneficial information for mangrove conservation and management, because findings suggest that following death of mangrove trees, the roots and associated epibiont community start to deteriorate within months. However, new mangroves should be restored to the area as soon as possible given that the persistence of habitat provision function by mangroves is relatively temporary compared to the time for mangrove regrowth.

Are root mimics similar functionally to living mangrove roots?

To explore the potential of root mimics in developing epibiont communities, we directly compared root mimic treatments to determine the usefulness of hard infrastructure as surrogates. One of the most commonly used root mimic materials in mangrove studies is PVC (Cocheret De La Moriniere et al. 2004, Nagelkerken et al. 2010, Hunting et al. 2013, Janiak et al. 2018) despite there being few studies that examine whether manufactured root mimics function similarly to living mangrove roots. Previous sponge studies found species specific differences in growth on mangrove roots compared to PVC with reef-associated sponge species growing faster when attached to PVC and mangrove-associate sponge species growing faster when attached to mangrove roots (Ellison et al. 1996, Wulff 2005). In this study, we also found a difference in the sponge species growing on mangrove roots compared to root mimics, however, sessile community richness, diversity, and community composition were greater in PVC than scraped treatments. Further, PVC functioned similarly to both natural and scraped living mangrove roots in terms of mobile community diversity and richness, structural complexity, and richness and biomass of secondary foundation species (Table 3.1). These results support the findings of Janiak et al. (2018) which showed higher epibiont percent cover, richness, and diversity on artificial structure (e.g., PVC colonization panels) compared to mangrove roots.

Although root mimics support general community patterns similar to live mangrove roots, we found differences in individual epibiont species and bias towards some taxa (e.g., barnacles), which warrants caution when describing species level implications for mangroves if using root mimics. We found that both PVC and wood root mimics had a greater abundance of barnacles, measured as both percent cover and biomass, and a smaller abundance of tunicates compared to living mangrove roots. Barnacles are common fouling species, especially on PVC (Janiak et al. 2018). These differences between treatments could be linked to biogeochemical compounds emitted from the roots that could alter induction or inhibition settlement cues. A previous study by Guerra-Castro and Cruz-Motta (2014) using pine wood as an artificial root treatment found greater abundance of barnacles on the pine compared to mangrove roots. The authors hypothesized that the dominant oyster *Crassostrea rhizophorae* may outcompete barnacles on natural roots and/or barnacle larvae select settlement habitats not previously colonized by oysters. Competitive exclusion is unlikely to be the cause of the lower abundance of barnacles on the mangrove treatments relative to root mimics in our study since mangrove roots had greater empty space than mimics indicating that available space was not limited. Further, no relationship between barnacle and oyster biomass was detected. Extensive barnacle coverage of mangrove roots can be detrimental to the tree as barnacles can interfere with root aeration and can reduce root growth by 30%, thus negatively impacting net production (Perry 1988). Thus, it is possible that the mangrove itself creates chemical cues to inhibit barnacle settling, which could explain the lower abundance of barnacles on roots than mimics.

The results of this study suggest that non-living wood and PVC root mimics may be useful in sustaining epibionts when mangrove roots are not available (e.g., mangrove dieback) or in ecological experiments that require manipulation not possible with living roots. We found no difference in the sessile epibiont diversity or total epibiont biomass between the two root mimic treatments. However, PVC had greater sessile richness than wood, which may be due to wood treatments deteriorating, since root length was positively correlated with richness. These differences being acknowledged, typical conditions of the mangrove environment (e.g., turbulent water, salinity, and UV radiation) increase leaching of harmful additives (e.g., BPA, phthalates) that threatens marine life from plasticized polyvinylchloride (PVC) into the marine environment (Suhrhoff and Scholz-Böttcher 2016). Therefore, plastic materials (e.g., PVC) should not be employed in large scale programs and wood mimics could be a safer alternative despite having lower epibiont diversity and their potential for deterioration.

Does wood type affect epibiont community composition?

We compared non-living mangrove roots to manufactured wood dowels to test whether wood type influenced epibiont assemblage, either directly by altering colonization or indirectly through difference in rate of deterioration. We found no differences in epibiont community composition between these two treatments (Table 3.1). Since the epibiont communities were similar between wood types (e.g., tree species), and the poplar wood treatment deteriorated more slowly, outplanting of wood root mimics could be used as a surrogate to sustain the epibiont community in mangrove habitats to reduce the loss of biodiversity, until damaged trees can recover, or new mangrove trees can establish. Our study did not explore characteristics of the wood treatments that may account for their effects on epibionts, but this may relate to variation in physical and chemical properties such as hardness, moisture content, and density. The observed difference in rates of boring by shipworms, which were observed in every root of the wood treatment but in only one root in each of the mangrove treatments (i.e., natural, scraped, and cut) may be explained by a difference in relative hardness of wood; the Janka hardness value for yellow poplar is 368 compared to red mangrove at 2760 (Wilkinson 2004, Uzcategui et al. 2020). Wood hardness is known to affect burrowing by the isopod *Spaeroma terebrans* in red mangroves (Wilkinson 2004). Further investigation of which commercially available wood dowels perform best is warranted.

Is 14 months sufficient for the epibiont community of living mangrove roots to recover to after epibiont removal?

It is important for management and conservation purposes to know how long it takes epibiont communities to recover after being disturbed by storms, anoxic events, wave action, or pollution (e.g., oil spills) (Orihuela et al. 1991, Burns et al. 1993, Wulff 2012, 2013). In this study we tested whether 14 months was sufficient for the epibiont community of scraped living mangrove roots to attain a community similar to unmanipulated roots. Scraped living mangrove roots had similar percent cover, mobile diversity, and bivalve richness to unmanipulated ("natural") mangrove roots by the end of the experiment, but the other measures of community structure, such as sessile richness, diversity, biomass and structural complexity, did not converge with control epibiont communities on this temporal scale (Table 3.1). The discrepancies in community composition of these living mangrove roots may be due to a difference in initial recruited epibiont community, which can determine patterns in epibiont distribution (Farnsworth and Ellison 1996) or possible disturbance to the integrity of the mangrove roots from the process of scraping, although care was taken to minimize negative effects. Although a final stage of specific dominate epibiont species cannot be determined, Guerra-Castro and Cruz-Motta (2018) proposed that patterns can be forecasted using broader taxonomic or functional groups. Their study of small-scale spatial variability in epibionts of mangrove roots found that roots are first colonized by hydroids, bryozoans, and algae, followed by tunicates, oysters, and encrusting sponges with final stages of succession being dominated by massive sponges and more tunicates (Guerra-Castro & Cruz-Motta 2018). Given the similar bivalve richness of scraped and natural mangrove roots, scraped roots may be in this intermediate phase where sponge biomass is drastically different between scraped and natural roots.

Links between secondary foundation species and the mobile invertebrate community

Despite the growing interest in facilitation cascades, few studies have examined the impact of secondary foundation species richness and abundance on inhabitant community richness and diversity. In our study, we observed similar mobile community richness among scraped, cut, and wood treatments at the Coco site, but scraped and wood treatments had greater mobile richness than cut at the Corales site. Secondary foundation species biomass may help explain these differences. Sponge and bivalve biomass were found to positively have a positive relationship with mobile community richness, and bivalve biomass was 2-3 times greater at the Corales site than Coco. Sponge biomass was approximately 1.5 times greater at Corales than Coco. Further, we found that while sponge and bivalve biomass have a positive effect on mobile community richness, no effect of secondary foundation species richness or biomass was detected on mobile community diversity. These results are consistent with previous work that observed a positive relationship between sessile biomass and mobile fauna abundance in mangrove root communities of Florida (Janiak et al. 2020). The greater influence of secondary foundation species biomass than richness may be due to the primary importance structural complexity that massive sponges and bivalves may offer as substrate. We propose that the stronger and more consistent positive correlation between sessile community structural complexity and sponge and bivalve biomass than richness supports this.

In our study we found that root treatment had significant effects on bivalve and sponge biomass and richness, and these factors were in turn correlated with the community structure of mobile epifauna, implying that root characteristics have an indirect effect on mobile organisms through a facilitation cascade. However, we did not directly manipulate sponge or bivalve richness or abundance on the roots, so we cannot conclusively establish the relative importance of primary (e.g., mangrove) vs secondary (e.g., sponge, bivalve) species on the mobile community. Given the known association of mobile invertebrates with structurally complex sponges and bivalve aggregations (Koukouras et al. 1992), and that many of the mobile species that we documented are known to be obligately or commonly associated with those secondary foundation species, we suggest that mangrove root communities are a strong model system for further exploration of the facilitation cascade concept. Prior studies using mangrove ecosystems have found that traits of primary and secondary foundation species are important in facilitating cascades (Bishop et al. 2012, 2013, Schutte and Byers 2017), and our findings indicate that the diversity of secondary foundation species could be an important factor in mediating this relationship.

Significance

This study has important conceptual and applied implications for mangrove management and biodiversity conservation by providing insight on how foundation species traits shape community assemblage of associated organisms. By comparing living and non-living mangrove roots with root mimics, we were able to identify the properties of mangrove roots needed to sustain driver communities of epibionts; and our results suggest that root mimics could be used to temporary support mangrove-associated communities while mangrove stands recover. Further, anthropogenic perturbations can alter mangrove root traits (e.g., death and deterioration of roots) that affect epibionts, so it is important to understand and predict how these disturbances are likely to affect the structure of mangroves and the complex communities that they support.

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3.7 References

Aguirre-Rubí, J., A. Luna-Acosta, M. Ortiz-Zarragoitia, B. Zaldibar, U. Izagirre, M. J. Ahrens, L. Villamil, and I. Marigómez. 2018. Assessment of ecosystem health disturbance in mangrove-lined Caribbean coastal systems using the oyster *Crassostrea rhizophorae* as sentinel species. Science of the Total Environment 618:718–735.

Airoldi, L., X. Turon, S. Perkol-Finkel, and M. Rius. 2015. Corridors for aliens but not for natives: Effects of marine urban sprawl at a regional scale. Diversity and Distributions 21:755–768.

Altieri, A. H., and J. Van De Koppel. 2013. Foundation species in marine ecosystems. Pages 37–56 *in* M. D. Bertness, J. F. Bruno, B. R. Silliman, and J. J. Stachowicz, editors. Marine Community Ecology and Conservation 2. Sinauer Associates, Sunderland, Massachusetts.

Angelini, C., A. H. Altieri, B. R. Silliman, and M. D. Bertness. 2011. Interactions among foundation species and their consequences for community organization, biodiversity, and conservation. BioScience 61:782–789.

Aquino-Thomas, J. 2020. The critical role of interactions between ecological foundation species in structuring a mangrove community. Florida Atlantic University, Boca Raton, Florida, United States of America.

Aquino-Thomas, J., and C. E. Proffitt. 2014. Oysters *Crassostrea virginica* on red mangrove *Rhizophora mangle* prop roots: Facilitation of one foundation species by another. Marine Ecology Progress Series 503:177–194.

Bishop, M. J., J. E. Byers, B. J. Marcek, and P. E. Gribben. 2012. Density-dependent facilitation cascades determine epifaunal community structure in temperate Australian mangroves. Ecology 93:1388–1401.

Bishop, M. J., J. Fraser, and P. E. Gribben. 2013. Morphological traits and density of foundation species modulate a facilitation cascade in Australian mangroves. Ecology 94:1927–1936.

Bruno, J. F., and M. D. Bertness. 2001. Habitat modification and facilitation in benthic marine communities. Pages 201–218 Marine Community Ecology. Sinauer Associates, Inc., Sunderland, Massachusetts.

Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. Trends in Ecology and Evolution 18:119–125.

Bulleri, F., and L. Airoldi. 2005. Artificial marine structures facilitate the spread of a nonindigenous green alga, *Codium fragile* ssp. tomentosoides, in the north Adriatic Sea. Journal of Applied Ecology 42:1063–1072.

Burns, K. A., S. D. Garrity, and S. C. Levings. 1993. How many years until mangrove ecosystems recover from catastrophic oil spills? Marine Pollution Bulletin 26:239–248.

Carrasquilla-Henao, M., and F. Juanes. 2017. Mangroves enhance local fisheries catches: a global meta-analysis. Fish and Fisheries 18:79–93.

Chapman, M. G. 2003. Paucity of mobile species on constructed seawalls: Effects of urbanization on biodiversity. Marine Ecology Progress Series 264:21–29.

Cocheret De La Moriniere, E., I. Nagelkerken, H. Van Der Meij, and G. Van Der Velde. 2004. What attracts juvenile coral reef fish to mangroves: Habitat complexity or shade? Marine Biology 144:139–145.

Dafforn, K. A., T. M. Glasby, L. Airoldi, N. K. Rivero, M. Mayer-Pinto, and E. L. Johnston. 2015. Marine urbanization: An ecological framework for designing multifunctional artificial structures. Frontiers in Ecology and the Environment 13:82–90.

Dafforn, K. A., T. M. Glasby, and E. L. Johnston. 2012. Comparing the invasibility of experimental "reefs" with field observations of natural reefs and artificial structures. PLoS ONE 7:1–16.

Dayton, P. K. 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos. Pages 81–95 *in* B. C. Parker, editor. Proceedings of the Colloquium on Conservation Problems in Antarctica. Allen Press, Lawrence, Kansas.

Dennis, H. D., A. J. Evans, A. J. Banner, and P. J. Moore. 2018. Reefcrete: Reducing the environmental footprint of concretes for eco-engineering marine structures. Ecological Engineering 120:668–678.

Duke, N. C., J. Kovacs, A. Griffiths, L. Preece, D. Hill, P. van Oosterzee, J. Mackenzie, H. Morning, and D. Burrows. 2017. Large-scale dieback of mangroves in Australia's Gulf of Carpentaria: a severe ecosystem response, coincidental with an unusually extreme weather event. Marine and Freshwater Research:1816–1829.

Ellison, A. M. 2008. Managing mangroves with benthic biodiversity in mind: Moving beyond roving banditry. Journal of Sea Research 59:2–15.

Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliott, C. R. Ford, D. R. Foster, B. D. Kloeppel, J. D. Knoepp, G. M. Lovett, J. Mohan, D. A. Orwig, N. L. Rodenhouse, V.

Sobczak, William, K. A. Stinson, J. K. Stone, C. M. Swan, J. Thompson, B. Von Holle, and J. R. Webster. 2005. Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 3:479–486.

Ellison, A. M., and E. J. Farnsworth. 1990. The ecology of Belizean mangrove-root fouling communities. I. Epibenthic fauna are barriers to isopod attack of red mangrove roots. Journal of Experimental Marine Biology and Ecology 142:91–104.

Ellison, A. M., E. J. Farnsworth, and R. R. Twilley. 1996. Facultative mutualism between red mangroves and root-fouling sponges in Belizean mangal. Ecology 77:2431–2444.

Eston, V. R., M. Rosario, A. Braga, M. Cordeiro-Marino, M. T. Fujii, and N. S. Yokoya. 1992. Macroalgal colonization patterns on artificial substrates inside southeastern Brazilian mangroves. Aquatic Botany 42:315–325.

Farnsworth, E. J., and A. M. Ellison. 1996. Scale-dependent spatial and temporal variability in biogeography of mangrove root epibiont communities. Ecological Monographs 66:45–66.

Feller, I. C., D. A. Friess, K. W. Krauss, and R. R. Lewis III. 2017. The state of the world's mangroves in the 21st century under climate change. Hydrobiologia 803:1–12.

Gittman, R. K., F. J. Fodrie, A. M. Popowich, D. A. Keller, J. F. Bruno, C. A. Currin, C. H. Peterson, and M. F. Piehler. 2015. Engineering away our natural defenses: An analysis of shoreline hardening in the US. Frontiers in Ecology and the Environment 13:301–307.

Glasby, T. M., S. D. Connell, M. G. Holloway, and C. L. Hewitt. 2007. Nonindigenous biota on artificial structures: Could habitat creation facilitate biological invasions? Marine Biology 151:887–895.

Guerra-Castro, E. J., and J. J. Cruz-Motta. 2014. Ecology of fouling assemblages associated with mangrove's roots: An artificial substrate for manipulative experiments. Journal of Experimental Marine Biology and Ecology 457:31–40.

Guerra-Castro, E. J., and J. J. Cruz-Motta. 2018. Colonization and succession as drivers of small-scale spatial variability in epibionts on mangrove roots in the Southern Caribbean. Marine Ecology Progress Series 588:15–27.

Henkel, T. P., and J. R. Pawlik. 2011. Host specialization of an obligate sponge-dwelling brittlestar. Aquatic Biology 12:37–46.

Hughes, A. R., P. E. Gribben, D. L. Kimbro, and M. J. Bishop. 2014. Additive and site-specific effects of two foundation species on invertebrate community structure. Marine Ecology

Progress Series 508:129–138.

Hunting, E. R., O. Franken, F. Knopperts, M. H. S. Kraak, R. Vargas, W. F. M. Röling, and H. G. Van Der Geest. 2013. Substrate as a driver of sponge distributions in mangrove ecosystems. Marine Ecology Progress Series 486:133–141.

Irving, A. D., and M. D. Bertness. 2009. Trait-dependent modification of facilitation on cobble beaches. Ecology 90:3042–3050.

Janiak, D. S., C. J. Freeman, J. Seemann, J. E. Campbell, V. J. Paul, and J. E. Duffy. 2020. Spatial variation in the effects of predator exclusion on epifaunal community development in seagrass beds. Marine Ecology Progress Series 649:21–33.

Janiak, D. S., R. W. Osman, C. J. Freeman, V. J. Paul, Q. Sites, and Q. Samples. 2018. Artificial structures versus mangrove prop roots: a general comparison of epifaunal communities within the Indian River Lagoon, Florida, USA. Marine Ecology Progress Series 607:85–98.

Koukouras, A., A. Russo, E. Voultsiadou-Koukoura, C. Dounas, and C. Chintiroglou. 1992. Relationship of sponge macrofauna with the morphology of their hosts in the North Aegean Sea. Internationale Revue der gesamten Hydrobiologie und Hydrographie 77:609–619.

Krauss, K. W., A. S. From, C. S. Rogers, K. R. T. Whelan, K. W. Grimes, R. C. Dobbs, and T. Kelley. 2020. Structural impacts, carbon losses, and regeneration in mangrove wetlands after two hurricanes on St. John, U. S. Virgin Islands. Wetlands and Climate Change 40:2397–2412.

MacDonald, J. A., T. Glover, and J. S. Weis. 2008. The impact of mangrove prop-root epibionts on juvenile reef fishes: A field experiment using artificial roots and epifauna. Estuaries and Coasts 31:981–993.

MacDonald, J. A., and J. S. Weis. 2013. Fish community features correlate with prop root epibionts in Caribbean mangroves. Journal of Experimental Marine Biology and Ecology 441:90–98.

Mineur, F., E. J. Cook, D. Minchin, K. Bohn, A. Macleod, and C. A. Maggs. 2012. Changing coasts: Marine aliens and artificial structures. Oceanography and Marine Biology: An Annual Review 50:189–234.

Morris, R. L., T. M. Konlechner, M. Ghisalberti, and S. E. Swearer. 2018. From grey to green: Efficacy of eco-engineering solutions for nature-based coastal defence. Global Change Biology 24:1827–1842.

Nagelkerken, I., A. M. De Schryver, M. C. Verweij, F. Dahdouh-Guebas, G. van der Velde, and N. Koedam. 2010. Differences in root architecture influence attraction of fishes to mangroves: A field experiment mimicking roots of different length, orientation, and complexity. Journal of Experimental Marine Biology and Ecology 396:27–34.

Nanjo, K., H. Kohno, Y. Nakamura, M. Horinouchi, and M. Sano. 2014. Effects of mangrove structure on fish distribution patterns and predation risks. Journal of Experimental Marine Biology and Ecology 461:216-225.

Orihuela, B., H. Diaz, and J. E. Conde. 1991. Mass mortality in a mangrove roots fouling community in a hypersaline tropical lagoon. Biotropica 23:592–601.

Perry, D. M. 1988. Effects of associated fauna on growth and productivity in the red mangrove. Ecology 69:1064–1075.

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Radabaugh, K. R., R. P. Moyer, A. R. Chappel, E. E. Dontis, C. E. Russo, K. M. Joyse, M. W. Bownik, A. H. Goeckner, and N. S. Khan. 2020. Mangrove damage, delayed mortality, and early recovery following Hurricane Irma at two landfall sites in Southwest Florida, USA. Estuaries and Coasts 43:1104–1118.

Rebolledo, A. P., I. S. Wehrtmann, D. L. Felder, and F. L. Mantelatto. 2014. Embryo production in the sponge-dwelling snapping shrimp *Synalpheus apioceros* (Decapoda, Alpheidae) from Bocas del Toro, Panama. ZooKeys 457:227–238.

Schutte, V., and J. Byers. 2017. Variation in a simple trait of mangrove roots governs predator access to, and assemblage composition of, epibiotic sponges. Marine Ecology Progress Series 573:15–23.

Seemann, J., A. Yingst, R. D. Stuart-Smith, G. J. Edgar, and A. H. Altieri. 2018. The importance of sponges and mangroves in supporting fish communities on degraded coral reefs in Caribbean Panama. PeerJ 2018:1–22.

Suhrhoff, T. J., and B. M. Scholz-Böttcher. 2016. Qualitative impact of salinity, UV radiation and turbulence on leaching of organic plastic additives from four common plastics - A lab experiment. Marine Pollution Bulletin 102:84–94.

Svejkovsky, J., D. E. Ogurcak, M. S. Ross, and A. Arkowitz. 2020. Satellite image-based time series observations of vegetation response to Hurricane Irma in the lower Florida keys.

Estuaries and Coasts 43:1058–1069.

Thomsen, M. S., A. H. Altieri, C. Angelini, M. J. Bishop, P. E. Gribben, G. Lear, Q. He, D. R. Schiel, B. R. Silliman, P. M. South, D. M. Watson, T. Wernberg, and G. Zotz. 2018. Secondary foundation species enhance biodiversity. Nature Ecology and Evolution 2:634–639.

Tyrrell, M. C., and J. E. Byers. 2007. Do artificial substrates favor nonindigenous fouling species over native species? Journal of Experimental Marine Biology and Ecology 342:54–60.

Uzcategui, M. G. C., R. D. Seale, and F. J. N. França. 2020. Physical and mechanical properties of hard maple (*Acer saccharum*) and yellow poplar (*Liriodendron tulipifera*). Forest Products Journal 70:326–334.

Vaughn, C. C., and T. J. Hoellein. 2018. Bivalve impacts in freshwater and marine ecosystems. Annual Review of Ecology, Evolution, and Systematics 49:183–208.

Verweij, M. C., I. Nagelkerken, S. L. J. Wartenbergh, I. R. Pen, and G. Van Der Velde. 2006. Caribbean mangroves and seagrass beds as daytime feeding habitats for juvenile French grunts, *Haemulon flavolineatum*. Marine Biology 149:1291–1299.

Vorsatz, L. D., P. Pattrick, and F. Porri. 2021. Quantifying the in situ 3-dimensional structural complexity of mangrove tree root systems: Biotic and abiotic implications at the microhabitat scale. Ecological Indicators 121:107154.

Vozzo, M. L., and M. J. Bishop. 2019. Co-occurring secondary foundation species have distinct effects on the recruitment and survival of associated organisms. Marine Ecology Progress Series 608:61–72.

Vozzo, M. L., M. Mayer-Pinto, M. J. Bishop, V. R. Cumbo, A. B. Bugnot, K. A. Dafforn, E. L. Johnston, P. D. Steinberg, and E. M. A. Strain. 2021. Making seawalls multifunctional: the positive effects of seeded bivalves and habitat structure on species diversity and filtration rates. Marine Environmental Research 165:105243.

Wilkinson, L. L. 2004. The biology of *Spaeroma terebrans* in Lake Pontchartrain, Louisiana with emphasis on burrowing. University of New Orleans.

Wulff, J. 2012. Ecological interactions and the distribution, abundance, and diversity of sponges. Pages 273–344 Advances in Marine Biology. First edition. Elsevier Ltd.

Wulff, J. 2013. Recovery of sponges after extreme mortality events: Morphological and taxonomic patterns in regeneration versus recruitment. Integrative and Comparative Biology

53:512–523.

Wulff, J. L. 2005. Trade-offs in resistance to competitors and predators, and their effects on the diversity of tropical marine sponges. Journal of Animal Ecology 74:313–321.

3.8 Tables

Table 3.1 Community analyses results. Results of multiple community analyses to address the four research questions regarding the role of foundation species traits in shaping community assemblage. All response variables in this table were significantly affected by root treatment. How results from pairwise comparisons in post-hoc analyses address the question (No vs Yes) are indicated after each question.

Root A	Root B	Question	Sessile Richness/ Diversity	Sessile Community Composition (% Cover/ Biomass)	Sessile Structural Complexity	Mobile Richness/ Diversity	Sponge Biomass/ Richness	Bivalve Biomass/ Richness
Scraped	Cut	Are epibionts more likely to grow on living or non-living mangrove roots? ($p < 0.05$ = Yes)	No/No	No/No	No	No/No	No/No	No/No
Scraped	PVC	Are root mimics functionally similar to living mangrove roots? ($p < 0.05$ = No)	No/No	Yes/No	Yes	Yes/Yes	Yes/Yes	Yes/Yes
Scraped	Wood		Yes/Yes	Yes/Yes	Yes	Yes/Yes	Yes/Yes	Yes/Yes
Cut	Wood	Does wood type matter for epibiont community structure? ($p < 0.05$ = Yes)	No/No	No/No	No	No/No	No/No	No/No
Natural	Scraped	If the epibiont community is removed from mangrove roots is 14 months sufficient for the community to recover? ($p < 0.05$ = No)	No/No	Yes/No	No	No/Yes	No/No	No/Yes

Table 3.2 Differences in mangrove epibiont communities among root treatments. Pairwise comparisons of root treatments from PERMANOVA using a Bray-Curtis dissimilarity matrix on square-root transformed data to test for differences in mangrove root communities. This analysis is based on species biomass data collected from the laboratory. Significant p-values are in bold.

Pairs	Df	Sum of Squares	F Model	R^2	Adjusted P value
Natural vs Scraped	1	0.783	3.037	0.101	**0.020**
Natural vs Cut	1	1.260	5.131	0.204	**0.010**
Natural vs PVC	1	0.739	3.916	0.106	**0.010**
Natural vs Wood	1	0.924	3.464	0.095	**0.010**
Scraped vs Cut	1	0.524	1.885	0.100	0.340
Scraped vs PVC	1	0.750	3.722	0.110	**0.010**
Scraped vs Wood	1	0.366	1.275	0.041	1.00
Cut vs PVC	1	1.438	8.275	0.265	**0.010**
Cut vs Wood	1	0.760	2.659	0.104	0.080
PVC vs Wood	1	0.587	2.676	0.069	**0.040**

Table 3.3 Percent contributions of most influential taxa to dissimilarity of community composition based on pairwise comparisons of root treatments. Results from similarity percentage analyses (SIMPER) ran on biomass data from root collections. Epibiont categories are denoted in gray and morphospecies in white. Bold indicates species found on >50% of the roots in multiple treatments. Bivalves and sponges had the greatest contribution in community biomass regardless of treatment, making up 71-87% of the composition.

Class	Taxa	Natural vs Scraped	Natural vs Cut	Natural vs PVC	Natural vs Wood	Scraped vs Cut	Scraped vs PVC	Scraped vs Wood	Cut vs PVC	Cut vs Wood	PVC vs Wood
Bivalvia	All species	43.69	48.31	42.78	42.16	48.99	49.71	45.35	56.67	46.85	50.47
(Bivalves)	***Ostrea stentina***	21.08	24.20	20.44	20.57	19.62	31.46	19.69	38.45	20.94	32.52
	Pinctada imbricata	7.21	6.09	5.96	6.46	8.30	8.29	9.87	6.85	6.82	8.02
	Crassostrea rhizophorae	4.85	6.37	3.10	5.34	10.36	3.77	8.34	3.50	13.11	3.87
	Dendostrea frons	4.73	4.26	4.41	4.12	9.79	5.71	7.25	5.01	2.78	5.40
	Isognomon alatus	2.43	2.33		2.38	2.58		2.26		2.77	
Demospongiae	All species	40.65	38.87	38.01	38.82	30.64	23.75	25.44	20.24	29.30	23.35
(Sponges)	***Tedania ignis***	17.13	18.31	18.07	18.63	10.18	4.55	9.21	5.73	15.75	7.41
	Tedania klausi	3.59	3.53	5.14	3.68		2.62		2.77		2.80
	Haliclona spp.	2.75				8.67	3.57	5.29			
	Haplosclerida			5.79	2.41		6.48		7.03	1.60	6.68
	Mycale microsigmatosa				2.53	5.23		5.43	2.27	4.81	3.62

	Halichondria magniconulosa	2.46	3.30							2.56	
	Haliclona implexiformis		2.43	2.13							
	Niphates erecta			2.17							
Cirripedia	All species	2.01	0.98	7.79	8.11	3.78	13.44	16.50	13.74	19.27	16.46
(Barnacles)	***Amphibalanus spp.***			6.13	7.11	3.49	11.13	14.54	12.94	17.52	13.43
Ascidiacea	All species	9.26	7.42	7.75	7.11	10.29	10.16	8.32	7.05	2.93	7.04
(Tunicates)	*Phallusia nigra*						2.55		2.79		2.55
	Herdmania pallida					2.96		2.39			
Chlorophyta	All species	3.20	3.76	2.10	2.87	2.22	0.52	1.31	0.24	0.18	0.27
(Green alga)	*Caulerpa verticillata*	2.62	3.34								

3.9 Figures

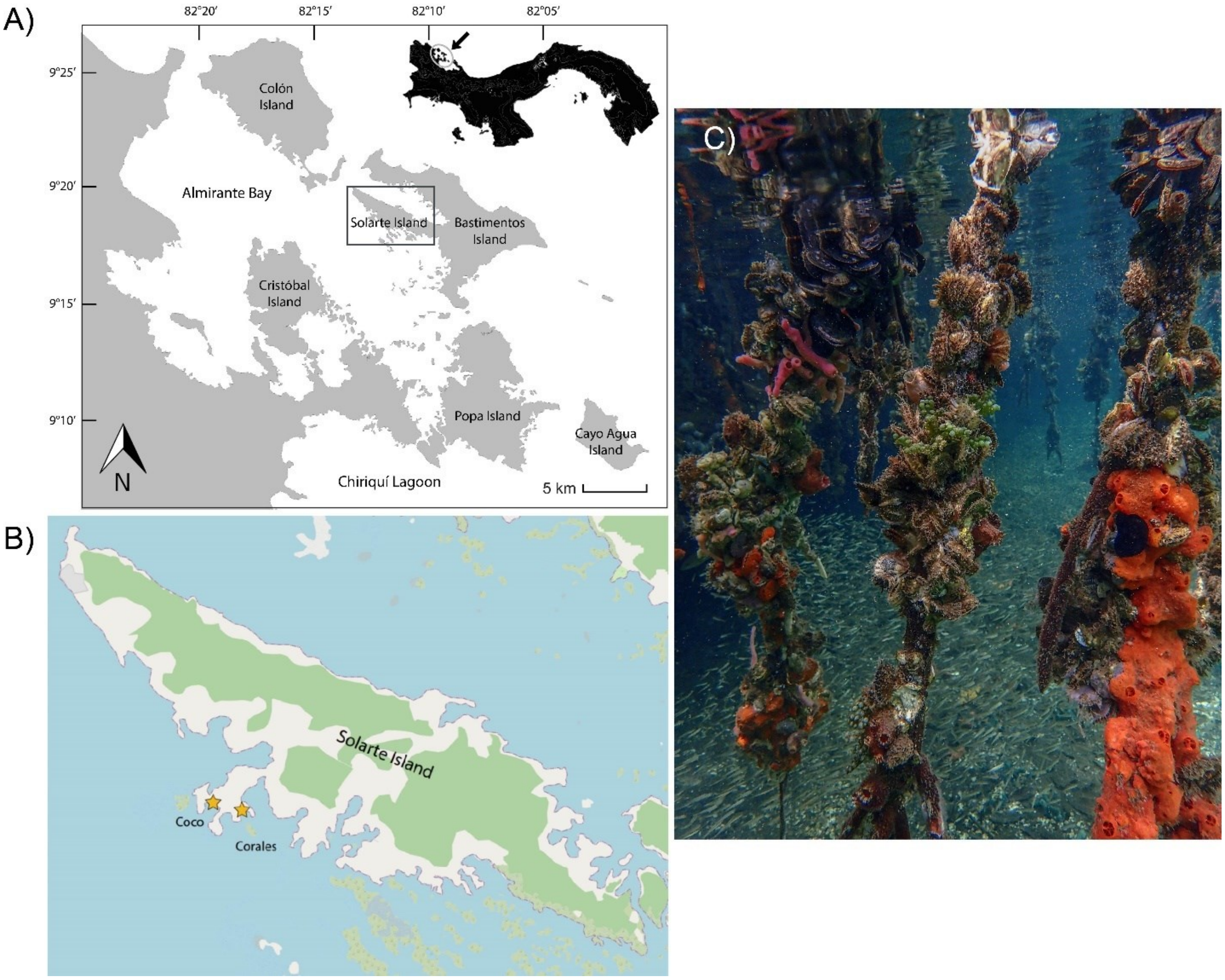

Figure 3.1 Experimental study sites. This research was conducted on A) Solarte Island (black box) of the Bocas del Toro Archipelago on the Caribbean coast of Panama. B) The two mangrove sites (Coco and Corales, marked with yellow stars) were selected because of their similar, rich epibiont communities seen in (C) to test for links between traits of foundation species and associated epibiont biodiversity.

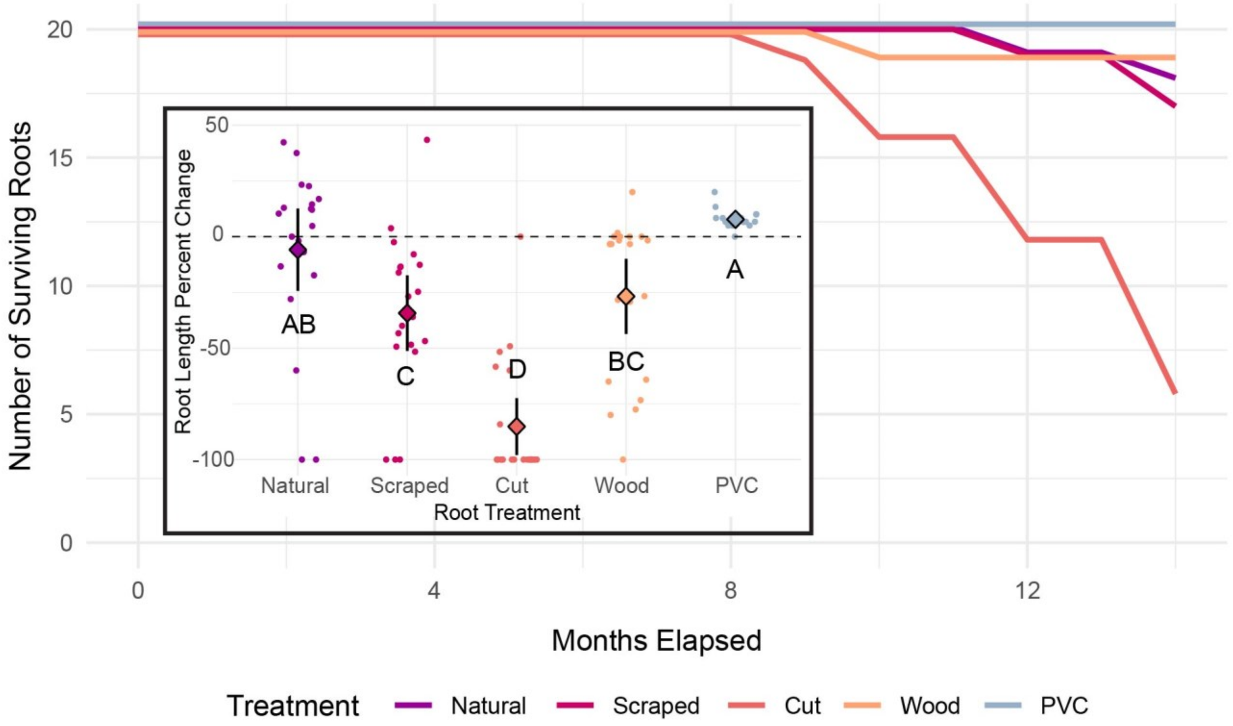

Figure 3.2 Root treatment survival and change in root length. Survival curve of total roots for both sites combined over the experiment duration based on complete loss of roots, with inset of root length percent change. Center diamond representing mean root length percent change, bars for 95% confidence interval, and points being individual roots. Lost roots are those that deteriorate away completely or to the mean higher high-water level, such that they could not be sampled. Lost roots were included in the root length change calculations as 100% reduction in length. Change in root length includes added length of epibionts at the tip, which explains why there was apparent increase in length for the PVC and some wood replicates. Treatments labeled with different letters were found to differ in the post-hoc analyses.

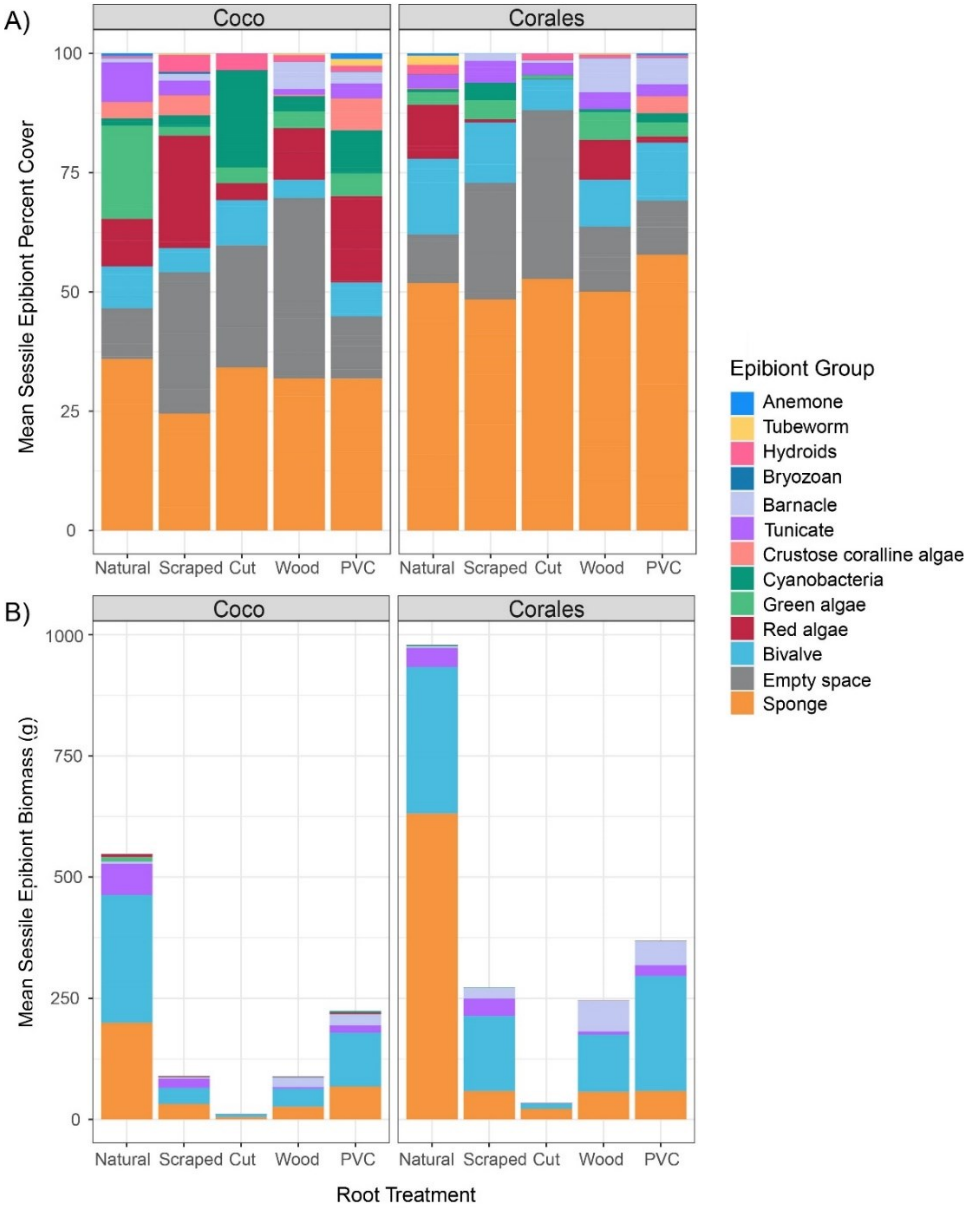

Figure 3.3 Community composition among root treatments. Community composition comparisons of mean A) percent cover of sessile epibionts and empty space and B) sessile epibiont biomass of five root treatments across two sites (Coco and Corales). Root treatment consisted of natural mangrove root control, scraped living mangrove root, cut and scraped non-living mangrove root, and two root mimics of wooden rod and PVC pipe. Percent cover differed among treatments and sites with pairwise comparisons revealing significant differences between PVC and natural and PVC and cut mangrove roots. Composition of sessile epibiont biomass differed among treatments and sites with pairwise comparisons revealing differences between natural mangrove roots and PVC from all other treatments as well as each other.

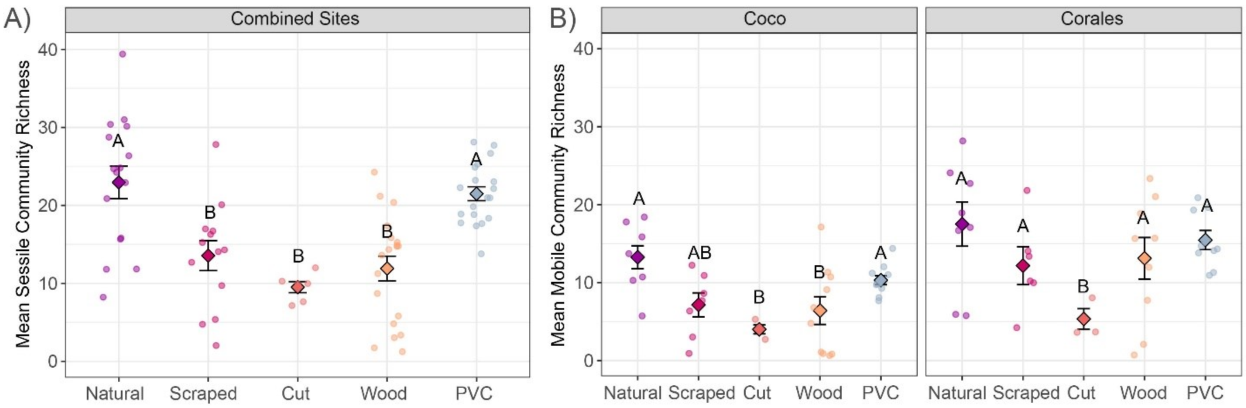

Figure 3.4 Community richness among root treatments. Mean A) sessile epibiont community richness by root treatment and B) mobile community richness by root treatment and site. Error bars represent standard error. Treatments within each plot that had different letters were found to differ in the post-hoc analyses. The dots represent the data from each sampled root.

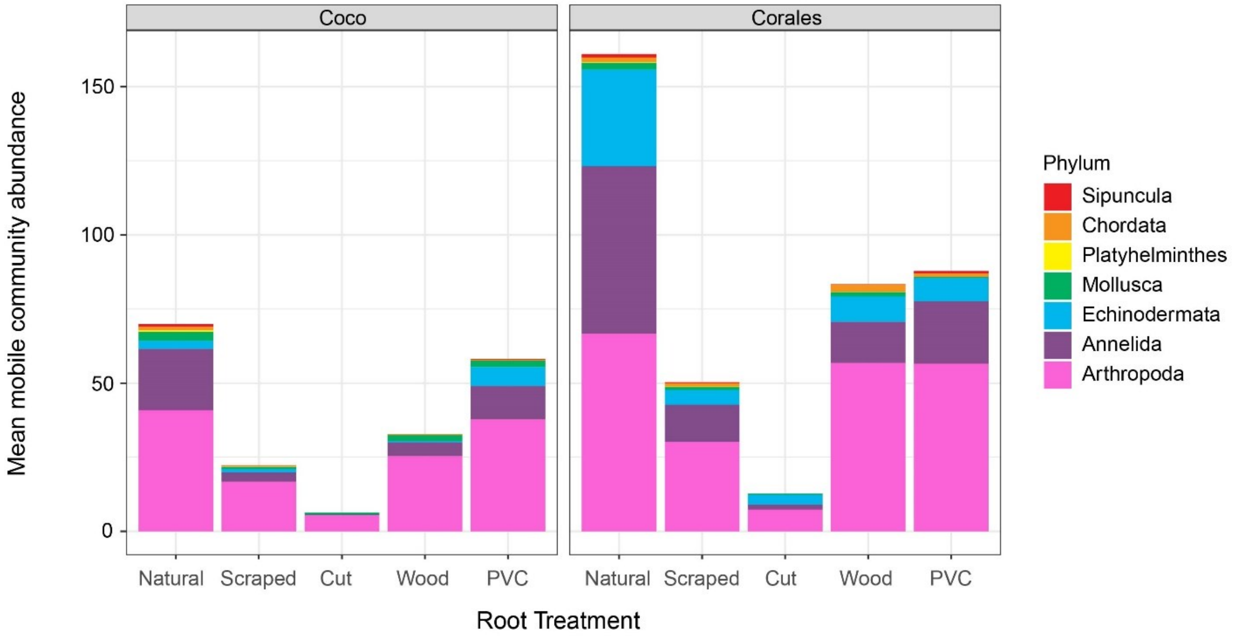

Figure 3.5 Mean mobile community abundance by treatment, averaged across roots. Root treatment had a significant effect on mean mobile community abundance, with natural roots having greater abundance than scraped roots and cut roots. Site also had a significant effect on mean mobile community abundance.

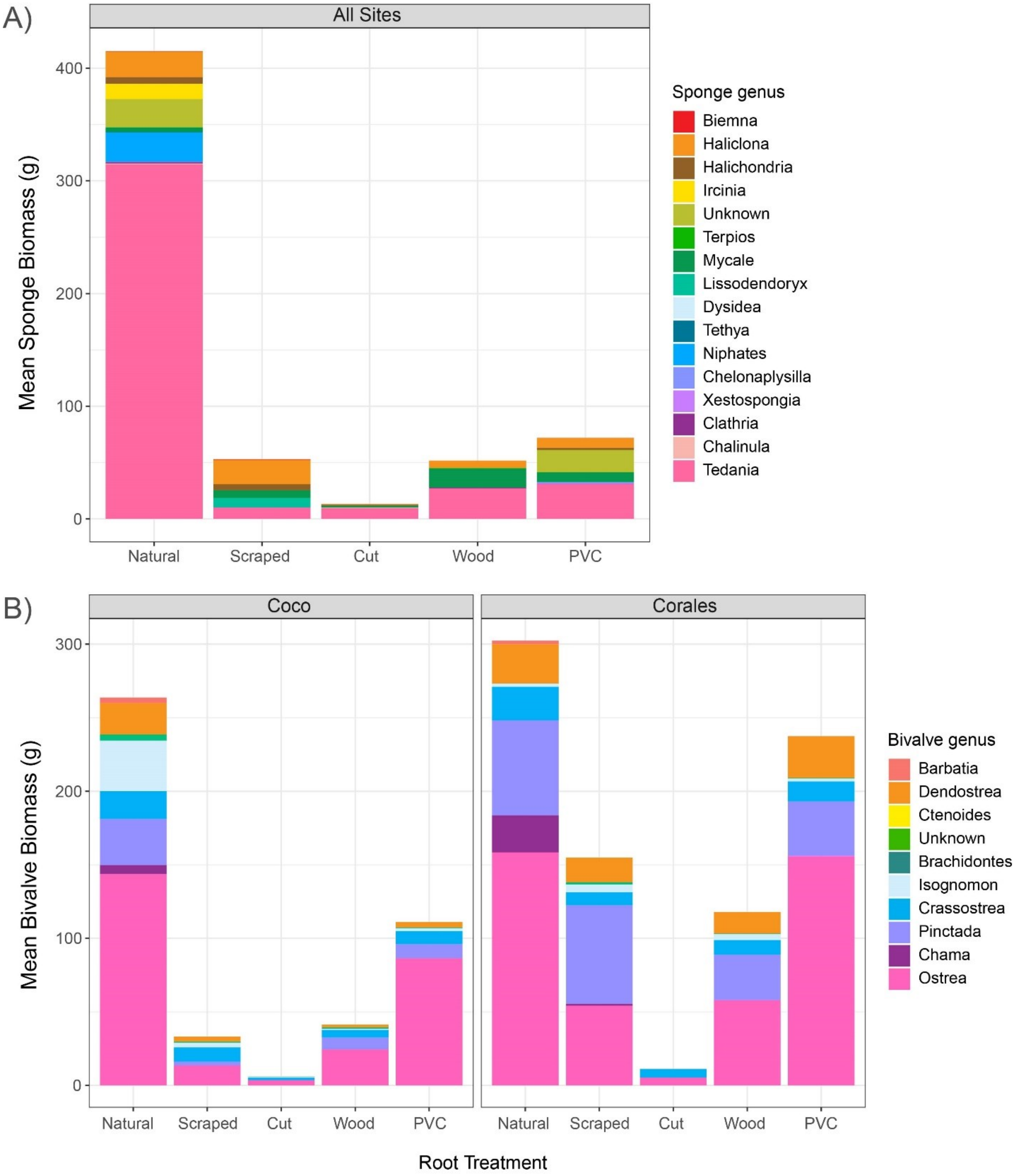

Figure 3.6 Mean biomass of A) sponge and B) bivalve species by root treatment and site. Root treatment had a significant effect on sponge biomass, with natural mangrove roots having the greater biomass than the other root treatments. Root treatment and site influenced bivalve biomass, with natural mangrove roots having greater biomass than scraped, cut, and wood treatments and Corales having greater bivalve biomass than Coco.

Preface to Chapter 4

In Chapter 3 I examined how mangrove traits drive community assemblage and biodiversity by comparing living and non-living mangrove roots to root mimics. I found that substrate composition and root length are important traits of mangrove roots affecting epibiont communities and that non-living wood root mimics may be useful in sustaining epibionts when mangrove roots are not available. I also found that sessile community richness, diversity, and community composition were greater in PVC root mimics than scraped mangroves roots and that PVC functioned similarly to living mangrove roots in terms of mobile community diversity and richness, structural complexity, and richness and biomass of secondary foundation species, which in turn were associated with variation in mobile epifauna. The results from Chapter 3 provided the basis for using PVC root mimics in a larger scale study in Chapter 4.

In Chapter 4, I build upon Chapter 3, which focused on how foundation species traits affect associated community diversity, to explore how environmental factors impact community assemblage in the same study system. I had qualitatively observed strong differences in epibiont communities between areas with intense wave action compared to sheltered areas and wanted to test the hypothesis that environmental context in the form of wave energy shapes epibiont communities. To do this, I placed PVC root mimics among scraped and natural mangrove roots on windward (high wave energy) and leeward (low wave energy) sides of nine islands and compared the epibiont community composition of these roots after a year to test the role of wave energy in shaping community composition pre-settlement. To test whether community was a constant function of the environmental setting or deterministic by the initial established community composition in windward and leeward areas is a function of community assembly or persistence, I conducted a reciprocal transplant experiment using the PVC root mimics.

Chapter 4: Context dependence of wave exposure in shaping mangrove epibiont community composition

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4.1 Abstract

Biotic and abiotic forces structure communities, however, there is debate over whether community development is stochastic in nature or deterministic. Initial communities can be shaped by factors influencing seed or larval supply, settlement cues, and recruitment, while subsequent persistence of community structure is often attributed to factors such as disturbance, competition, and predation. In marine systems, water flow has to the potential to act on both the establishment and persistence of communities through these factors. This study experimentally examined how wave exposure shapes the composition of epibiont communities associated with red mangrove (*Rhizophora mangle*) roots, which have been a model system for examining drivers of diversity in tropical marine systems. We compared root epibiont communities between the windward (high wave exposure) and leeward (low wave exposure) sides of mangrove islands after 1 year of assemblage development. After 1 year, roots in windward areas were dominated by turf algae with greater percent cover of barnacle, crustose coralline algae, and red macroalgae than leeward areas, while roots in leeward areas were dominated by sponges with greater percent cover of tunicates and green macroalgae than windward areas. We then conducted a reciprocal transplant experiment between high and low wave exposure sides of islands to ask whether the epibiont community after the transplant period resembled the roots from their source site or converged on the community composition of roots on their recipient site. Communities on root mimics transplanted from windward to leeward areas became similar to leeward control roots, but epibionts on roots transplanted from leeward to windward sides remained distinct from resident roots, suggesting that initial community structure has a stronger role in determining subsequent communities than abiotic factors in windward areas than leeward areas. Although mangroves are recognized for supporting biodiverse communities through their provision of habitat and amelioration of abiotic and biotic stressors, we found that wave exposure affects epibiont community development, but only determines epibiont community composition under certain contexts such as leeward areas.

4.2 Introduction

Biotic and abiotic forces structure communities, however, there is debate over whether community development is stochastic in nature or deterministic (Greene and Schoener 1982, Pulsford et al. 2016). Although successional studies originated, and have been most prolific, in terrestrial environments (Cowles 1899, Clements 1916, Drury and Nisbet 1973), the long temporal scales of community development in many plant communities such as forests limit the ability to test various hypotheses; whereas marine environments have rapid community development and thus offer practical advantages for testing mechanisms underlying patterns (Sousa 1979a, Greene and Schoener 1982). Studies of intertidal mussel beds (Levin and Paine 1974), rocky intertidal zones (Dayton 1971, Sousa 1979a, 1979b), coral reefs (Jackson and Buss 1975, River and Edmunds 2001, Cameron and Harrison 2020), and mangrove root communities (Bingham and Young 1995, Ross 2001, Bosire et al. 2004, Guerra-Castro and Cruz-Motta 2018) have examined drivers of community structure such as environmental factors and initial species arrivals. Initial communities are believed to be shaped by factors influencing seed or larval supply, settlement cues, and recruitment, while persistence and composition of the established community are often attributed to factors such as disturbance, competition, and predation (Bingham 1992, Rodríguez et al. 1993, Bingham and Young 1995, Farnsworth and Ellison 1996, Todd 1998, Ross 2001). Environmental drivers of community composition can act on both pre- and post-settlement processes. Abiotic factors such as water flow, air currents, and fire are essential to making seeds or larvae available to establish the initial community but can also shape post-settlement community by altering nutrient availability and disturbances that open areas to colonization (Sousa 1984, Bingham 1992, Bingham and Young 1995, Nathan and Muller-Landau 2000, Ames et al. 2016).

Foundation species are organisms which change community structure and function of the associated community by modifying environmental conditions (Dayton 1972, Ellison et al. 2005, Zarnetske et al. 2017). However, the role foundation species play in determining associated community composition is context dependent (Pinsky et al. 2013, Lajoie and Vellend 2015) where the foundation species may set the framework for the potential niche and associated community composition, but the realized niche and resulting community is dependent on processes at a larger spatial scale (Grabowski et al. 2005, Hughes et al. 2014). For example, in manipulative experiments of oysters and associated invertebrate assemblages across a wave exposure gradient, Vozzo and colleagues (2021) found that oysters supported richer and more abundant associated communities at sites sheltered from wave exposure than at high wave energy sites, which they attributed to differences in foundation species traits across the gradient.

Red mangroves (*Rhizophora mangle*) are a model system to explore the effects of abiotic factors driving community assembly and composition, because epibiont organisms quickly colonize submerged roots, and the roots can easily be manipulated experimentally. Previous studies on mangroves have shown that epibiont community composition is relatively deterministic based on abiotic conditions, but also found evidence for stochasticity due to the species that happened to make up the initial inhabitants; however, few studies have examined how these forces interact to shape the established community assembly (Wulff 2010, Guerra-Castro et al. 2016). Small-scale variation in epibiont community composition (e.g., between neighboring roots) has been shown to relate to successional changes due to temporal variation in larval availability (Bingham 1992, Farnsworth and Ellison 1996, Guerra-Castro and Cruz-Motta 2018). That is, the identity and abundance of larvae present at the time a substrate becomes available may determine the initial community, and the competitive strategies of initial inhabitants to tolerate or inhibit later species may impact subsequent community composition. This can explain the large variability of species richness, abundance, and composition between neighboring roots (Guerra-Castro and Cruz-Motta 2018). On a landscape scale, wind and wave exposure are dominant physical processes influencing shoreline community structure, and wave exposure has been cited as one of the most reliable predictors of sessile epibiont community composition of mangrove roots because it can act on both larval supply and disturbance regime (Jones and Demetropoulos 1968, Levin and Paine 1974, Farnsworth and Ellison 1996, Gaylord 1999, Burton et al. 2002, Sundblad et al. 2014). However, there is still a need to reconcile the importance of the initial epibiont assemblage structure and wave exposure in determining the composition of established epibiont communities.

The overall goal of this study was to test whether wave exposure acts by determining community development and/or continues to mediate the structure of the established assemblage. To meet this goal, we used two experiments. First, we compared natural mangrove roots (controls) to scraped roots and root mimics (PVC) on windward (high wave exposure) and leeward (low wave exposure) areas of mangrove islands after 1 year of assemblage development. This addressed the relative importance of wave exposure in epibiont community development.

We then used a reciprocal transplant experiment whereby PVC roots mimics were moved after 1 year of epibiont growth from windward to leeward sides of islands and vice versa and left for an additional year. This manipulation addressed whether initial community composition or wave exposure have a stronger role in shaping subsequent community composition. After 2 years, we also compared epibiont communities among natural, scraped, and PVC treatments to ask whether there is predictability of functional groups between windward and leeward areas over multiple years.

4.3 Methods

Study site selection

In June 2017, we selected 10 red mangrove (*Rhizophora mangle*) islands spanning the Bocas del Toro archipelago of Panamá (Figure 4.1) to study effects of wave exposure and water flow on epibiont assemblage and community structure. These islands were chosen because they varied in area, and each had a windward and leeward side defined by the prevailing winds that could be used to examine the effects of high and low wave exposure, respectively (Figure 4.2). We selected mangrove islands that were uninhabited by humans and large enough to accommodate the experiment under both wave regimes.

Characterization of wave exposure

To characterize the sites, we collected data on abiotic factors that may vary with wave action such as water depth, temperature, and flow on both sides of all selected islands. Wind speed and direction were measured periodically July 5, 2017-January 25, 2018 using a handheld digital anemometer (Holdpeak 566B) and compass. Data on overall prevailing wind direction, temperature, and rainfall for the archipelago over the duration of the study was obtained from the Bocas del Toro Research Station meteorological tower (Paton 2019). To characterize water flow through dissolution rates, we conducted a three-day deployment of dissolution blocks on July 18, 2017 (Jokiel and Morrissey 1993, Thompson and Glenn 1994). We also quantified the average submerged length and water depth of twenty roots per site.

Experimental design

To quantify epibiont community assembly and persistence on windward and leeward sides of islands, we conducted an experiment with three root treatments: unmanipulated mangrove root, mangrove root scraped free of epibionts, and a root mimic of polyvinylchloride

(PVC) pipe. At each site (windward or leeward side of island), there were 10 replicates per root treatments in a randomly assigned order spaced ~2 m apart. I selected PVC as a root mimic, so that after an epibiont community had established, we were able to transplant those “roots” to sites with different wave action to test how wave exposure mediates the structure of an established community. The PVC pipes were of similar length and diameter to the mangrove roots and were lightly sanded to roughen their surface, then partially closed at the ends to prevent occupancy by burrow dwelling organisms (see Chapter 3). Natural mangrove roots served as an unmanipulated control and were compared to other treatments over time to examine the degree to which the community that established in the other treatments resembled that of the established community. Scraped mangrove roots were carefully cleaned by removing mobile organisms by hand to avoid causing structural damage, and then using a plastic spatula and scouring pads to remove all remaining epibionts from the root. These roots were used to represent natural mangrove roots prior to colonization by epibionts, so that they would go through colonization on the same timeline as the root mimic treatment. PVC was used for a reciprocal transplant (described below) to address the effects of wave exposure on established communities because cut roots will not persist for the timescale necessary in this project. To minimize differences caused by root complexity and walk-on predators, we only selected non-bifurcated mangrove roots that were not in contact with the sediment or other roots (Schutte and Byers 2017, Guerra-Castro and Cruz-Motta 2018). Each root was tagged with a unique number, and the mean higher high water (MHHW) was marked with a horizontal-colored nylon cable tie to denote the intertidal portion of the root and the upper extent of the sampled epibiont community. We attached the PVC to branches using zip ties so that the root tip was 60 cm below MHHW, which was the average length of non-bifurcated mangrove roots in the area.

We initiated the experiment on June 27, 2017 but one site was later excluded from the study due to human tampering and removal of our study roots, resulting in nine islands for the final analyses. On July 20, 2018, after a little over year of colonization and epibiont growth, half of the PVC (n = 5) from a site (leeward or windward side of an island), was moved and reattached within the same site as a procedural control, while the other half was transplanted to the opposite side of the same island. This procedural control was used to detect any effects that moving may have had on epibiont communities so that our control could be directly compared to the transplant treatment. This created four root mimic treatments on each island for the second year of the experiment: windward control (PVC originally placed on the windward side and remained there), windward to leeward (moved from windward to leeward), leeward to windward (moved from leeward to windward), and leeward control (PVC originally placed on the leeward side and remained there). Natural and scraped mangrove roots remained in their original location. Following transplantation, all roots were left an additional year to allow for changes in epibiont community composition.

In-situ percent cover

To visually estimate the percent cover of space on each root dominated by bare space and each sessile epibiont taxa, we measured the length of root occupied by each, and then divided by the total length of the root and multiplied this proportion by 100. Because data were collected nondestructively in the field, which prevented detailed taxonomic identification, epibionts were classified into one of the following 14 categories: barnacle, bivalve, crustose coralline algae (CCA), cyanobacteria, turf algae, green macroalgae, red macroalgae, sponge, tunicate, tube worm, hydroid, anemone, bryozoan, and coral. Any measured unoccupied space was denoted as bare space. In-situ percent cover data were collected for year 1 on July 20, 2018 and for year 2 on June 19, 2019.

Statistical Analysis

All data were analyzed with R version 3.6.3 (R Core Team 2020). To examine how water flow, measured as dissolution rate (continuous variable calculated from deployed flow blocks), varied with wave exposure among islands, I fit two generalized linear models (GLM) using the glm function. The first GLM examined whether wave exposure interacted with island replicate to affect water flow with the main effects of wave exposure (i.e., categorical windward and leeward), island replicate, and their interaction. The second GLM examined whether any detected island differences were influenced by island area or distance between sampled windward and leeward sites. The main effects of the second GLM were wave exposure, island size, distance between sampled windward and leeward sites, and the interactions between wave exposure and island size and wave exposure and distance between sampled sites.

For percent cover data collected at the end of year 1 (prior to the reciprocal transplant), we conducted a permutational multivariate analysis of variance (PERMANOVA) using the adonis function from the *vegan* package to characterize patterns of epibiont community structure of mangrove roots and root mimics under conditions of low and high wave exposure with the main effects of root treatment (i.e., natural mangrove control, scraped mangrove root, and root mimic), wave exposure, and the interaction of root treatment and wave exposure, and with island replicate as a random effect. To account for overlap of water flow of leeward sides of some islands with the windward side of other islands, we ran a second PERMANOVA with the effects of root treatment, dissolution rate, and the interaction of root treatment and dissolution rate (continuous variable), and with island replicate as a random effect.

At the end of year 2, a year after the reciprocal transplant treatment was established, we conducted a PERMANOVA to test whether the initial wave exposure vs final wave exposure had a stronger role in shaping subsequent community composition with the main effect of root mimic treatment (i.e., windward control, windward to leeward transplant, leeward to windward transplant, leeward control) with island replicate as a random effect. We then conducted a second PERMANOVA to test wave exposure's continual role in shaping patterns of epibiont community structure of mangrove roots and a root mimic with the main effects of root treatment (i.e., natural mangrove control, scraped mangrove root, and root mimic control), wave exposure, and the interaction of root treatment and wave exposure with island replicate as a random effect. Similarity percentage analyses (SIMPER) were used on both year 1 and year 2 data to determine which taxonomic groups had the greatest contribution to dissimilarity in the community composition.

4.4 Results

Characterization of wave exposure

There was a significant interaction of wave exposure (categorical) and island replicate on dissolution rate ($p<0.001$, Chi-square test, Figure 4.2). The second GLM which looked at island area and distance between sites within an island to decipher island replicate affects found that dissolution rate was significantly affected by the interaction of wave exposure and the distance between sampled windward and leeward sites ($p = 0.037$) but not the interaction between wave exposure and island area ($p = 0.864$). However, island area ($p<0.001$) and wave exposure ($p = 0.008$) separately did effect dissolution rate. The prevailing winds in Bocas del Toro were consistently from the north-northwest (15 months) or northwest (remaining 9 months) throughout the experiment (Paton 2019). On average, wind speed, based on anemometer readings collected at each island, was 3.1 m/s for windward sites and 1.5 m/s for leeward sites

(Table 4.1). Although average water depth at windward sites was 85 m and 138 m at leeward sites (Table 4.1), average mangrove root length at windward sites was 74 cm and 80 cm at leeward sites.

Year 1 in-situ comparison of sessile epibiont community composition

The first PERMANOVA revealed that wave exposure ($p = 0.001$, F test) and root treatment ($p = 0.001$) had significant effects on community composition, and there was no significant interaction between wave exposure and root treatment ($p = 0.177$). Post-hoc pairwise comparisons revealed that both scraped and natural root treatments differed from the root mimic but did not differ from one another (Table 4.2, Table D1). The second PERMANOVA using dissolution rate as a metric for water flow revealed that dissolution rate ($p = 0.001$) and root treatment ($p = 0.001$) had significant effects on community composition, and the interaction of dissolution rate and root treatment did not ($p = 0.268$, Table D1). Turf algae, sponges, and bivalves contributed to over 60% of the dissimilarity between windward and leeward communities, with empty space, CCA, barnacles following in rank of importance. Windward areas had greater percent coverage of turf algae, CCA, and barnacles than leeward areas; while leeward areas had greater percent coverage of sponges and bivalves than windward areas across all treatments (Figure 4.3A). After 1 year, root mimics had similar cover of empty space (uncolonized area) in windward and leeward sites (25% and 23%, respectively). In contrast scraped and natural mangrove roots in windward areas were characterized by a greater amount of uncolonized space than leeward areas (average of 24% and 14%, respectively).

Year 2 in-situ comparison of sessile epibiont community composition

Community composition data of the root mimic treatment following year 2 were used to address the question of whether the epibiont assemblages of transplanted root mimics would converge with control root mimics that remained within the same wave exposure as the previous year. The PERMANOVA revealed that the root mimic treatment (i.e., windward control, windward to leeward, leeward to windward, and leeward control PVC) affected community composition ($p = 0.001$). The epibiont communities of root mimics reciprocally transplanted from windward to leeward areas became very similar to communities that had remained in leeward areas, but the leeward to windward transplants did not fully converge on windward controls (Table 4.3, Figure 4.4). The leeward to windward transplant did more closely resembled root mimics at windward sites (transplanted site) than the leeward sites (original site), but the convergence was less pronounced than in the windward to leeward transplants. Primary differences between the leeward to windward transplants and the windward controls were with a greater percent covers of green macroalgae, bivalves and anemones and lower percent cover of other algal groups (i.e., turf algae, CCA, and red macroalgae) and barnacles in the leeward to windward transplants. The sessile epibiont groups that contributed to over 50% of the dissimilarity between root mimic treatments year 2 were sponges and bivalves, together with turf alga (windward control), green alga (leeward to windward), and tunicates (windward to leeward).

Community composition data of the root mimic control treatments (those which were not transplanted) and the two mangrove root treatments (i.e., scraped and natural) following year 2, were used to test temporal variation of wave exposure effects in shaping patterns of epibiont community assemblage. The PERMANOVA revealed that wave exposure ($p = 0.001$) and root treatment ($p = 0.001$) had significant effects on community composition, but the interaction of wave exposure and root treatment was not significant ($p = 0.558$). In post-hoc pairwise comparisons, we found natural and scraped mangrove roots had similar community composition to one another, but both differed from the root mimic ($p = 0.003$, Table 4.2). Patterns of greater percent coverage of turf algae, CCA, and barnacle in windward areas than leeward areas continued in year 2. Leeward areas also continued to have greater percent coverage of sponge than windward areas (Figure 4.3B), but percent coverage of bivalve equalized and differences in empty space diminished between windward and leeward areas. For root mimics, empty space decreased by 5% by year 2, while in the scraped and natural mangrove roots available empty space decreased by 9% in windward areas and 7% in leeward areas.

4.5 Discussion

Overall, this study showed a strong effect of wave exposure in determining initial epibiont community structure of mangrove roots and interacting forces of wave exposure and initial community composition in subsequently driving the structure of the established community (year 2). By transplanting root mimics between areas with opposing wave exposure, we demonstrated that epibiont communities initiated in leeward areas are less likely to fully converge with neighboring roots after a year of growth and succession in windward areas than epibiont communities transplanted from windward areas to leeward areas. This suggests that initial community structure has a stronger role in determining subsequent communities than abiotic factors in windward areas than leeward areas.

Although mangrove roots may provide habitat for myriad of epibiont organisms, wave exposure is a fundamental force that influences the established epibiont communities. After one year of establishment, windward areas subjected to high water flow and wave exposure were characterized by epibiont communities dominated by filamentous turf algae with a greater percent cover of CCA and barnacles than leeward root communities, regardless of whether the roots were mimics or natural roots. Leeward roots were dominated by sponges. After two years, windward and leeward community patterns observed the previous year remained relatively stable, with a few notable shifts in assemblage. In particular, tunicates and green macroalgae became more prevalent in leeward areas, and red macroalgae increased coverage in windward areas. Farnsworth and Ellison (1996) studied mangrove epibiont communities on leeward and windward shores of four cays in Belize over a year. Although, the overall patterns they observed showed some similarities to my study, they found fleshy (macro) algae and small hydroids were most prevalent in the Belizean windward sites in addition to filamentous (turf) algae, while leeward areas were dominated by tunicates and anemones in addition to sponges (Farnsworth and Ellison 1996). Although roots in windward areas of the current study had a greater percent cover of hydroids and lower percent cover of anemones than leeward areas similar to their observations, neither group contributed much to the dissimilarity between wave exposure regimes in either year. In comparison, we found that sponges and turf algae were important in shaping dissimilarity between windward and leeward sides in year 1, followed by bivalves, empty space, CCA, and barnacles. In the Farnsworth and Ellison (1996) study, bivalves and barnacles were uncommon and corallines (CCA and coral) occupied low proportions of root space across all communities, resulting in little relative importance of these groups. The differences between these studies may reflect regional-scale variability, differences in frequency and intensity of disturbances or stochastic events, disparities in larval availability, temporal-scale (30-year difference) and/or a combination of these factors (Bingham 1992, Bingham and Young 1995, Farnsworth and Ellison 1996, Guerra-Castro et al. 2016, Guerra-Castro and Cruz-Motta 2018). Since the Farnsworth and Ellison study sampled roots along a transect but did not resample the identical roots, that too may have led to the differences in community composition observed between studies. Despite decades of studying mangrove root epibiont communities of the Caribbean, there is still much we do not understand about scale-dependent variability. The current study fills some of those gaps and further explores the intricacies of this system, by comparing established communities (natural mangrove roots) to newly colonized communities (scraped mangrove roots) and root mimics (PVC) over multiple years.

Some epibiont organisms have biotic processes that allow them to adapt to specific abiotic conditions, while others are more opportunistic and thrive under the frequent disturbances and variability of the mangrove root environment. Turf algae on windward roots and sponges on leeward roots were the two epibiont taxa groups with the greatest percent cover, respectively, and greatest differences between windward and leeward sites. Turf algae are algal assemblages that form persistent, low-laying, dense patches of filaments and branches (Connell et al. 2014). The reason why turf algae were so prolific in windward areas may reflect their resilience to disturbance. Turf algae are frequently the first colonists of open space in tropical reef systems, and their dense matrix forms settlement barriers making them a strong competitor (O'Brien and Scheibling 2018). Additionally, turf algae have been shown to use allelopathic chemical cues to deter other epibionts from settling and can exude photosynthate, which can increase the abundance of pathogens and decrease dissolved oxygen facilitating their dominance (Dixson et al 2014). Turf algae are more likely to thrive under windward conditions than larger epibionts due to their low profile, which may reduce drag dislodgment. Further, turf algae can have suppressed growth when shaded caused by other epibionts (O'Brien and Scheibling 2018), which is more likely in leeward areas. Barnacles and red algae (CCA and red macroalgae) were more prevalent in windward areas in the current study and are frequent colonizers of intertidal portions of mangrove roots (Ellison and Farnsworth 1992). Roots in windward areas undergo more frequent air exposure because the amplitude of the waves is much greater creating a larger intertidal section of these roots, which may account for the greater abundance of these taxa in windward than leeward areas.

Leeward epibiont communities develop under lower hydrodynamic forces. This may benefit large organisms that are prone to breakage (e.g., green macroalgae, massive sponges and tunicates) and observed to be more abundant on leeward sites. Algae morphology is largely determined by water flow, wave exposure, and currents as these abiotic factors can lead to dislodgment, which is usually fatal for algae (Anderson et al. 2006). Green macroalgae most likely had greater percent cover in leeward areas because there was less dislodgment occurring.

Physical disturbance by current-induced abrasion frequently results in fragmentation or complete loss of massive sponges; thus, water flow can have a strong influence in structuring the sponge-dominated communities of leeward areas (Bingham and Young 1995). Mangrove roots of windward areas of islands frequently have a mix of reef and mangrove sponge species, whereas leeward areas are dominated by mangrove sponge species (Wulff 2005). This may be related to windward areas being near coral reefs and having a greater presence of spongivores (e.g., parrotfish, sea stars) than leeward areas (Dunlap and Pawlik 1998, Wulff 2005, Lesser and Slattery 2013). Mangrove sponges are more readily consumed by spongivores (Wulff 2005), which may explain the difference in percent cover of sponges between windward and leeward areas of the current study. For example, the sponges on the windward areas may be reef species, which are slower growing and less competitive than mangrove species of leeward roots. In addition to competing with each other, sponges often outcompete other epibiont and benthic taxa such as tunicates (Goodbody 2000, Wulff 2005). Tunicates are known to be less abundant in windward mangrove areas relative to leeward areas and absent in localities with strong wave action (Goodbody 2000). In areas with high biodiversity, tunicates compete with one another and sometimes colonial tunicates will use solitary tunicates as secondary space to grow and develop (Goodbody 2000).

We transplanted root mimics (i.e., PVC) to test whether the initial community assemblage would shape subsequent community composition following a move to another wave regime, or whether the abiotic factors have an overriding effect that determines the subsequent epibiont community composition. If abiotic factors (e.g., wave exposure, wind, water flow) were the primary determining force of epibiont community composition, the community of root mimic transplants would be similar to the neighboring roots in the area to which they were moved. We found this to be the case for only one side of the reciprocal transplant. While the epibiont communities of root mimics transplanted between windward to leeward areas converged with communities in leeward areas (leeward mimic control), root mimics transplanted from leeward to windward areas showed less convergence. Given these findings, we propose that epibiont community assemblage is dependent on both the initial community assemblage and abiotic factors, with the relative importance of initial community assemblage varying across an abiotic gradient (e.g., wave exposure). Epibionts in windward areas must withstand abiotic factors associated with higher wave exposure and are characterized by encrusting organisms (e.g., CCA, barnacles) and persistent, low-laying algal assemblages, generally referred to as turf algae, that can withstand wave exposure and are difficult to dislodge. It may seem counterintuitive that these initial communities would have less of an effect on subsequent community composition than those that developed without physical disturbances (e.g., waves). The leeward to windward transplants in this study had reduced percent cover of sponges and tunicates than the leeward control, but similar percent cover to the windward control, which may be a result of greater potential for physical disturbances in windward areas. The percent cover of barnacles in the leeward to windward transplant treatment was more similar to the leeward control and less than windward, which may be due to barnacles use of settlement cues from adults and conspecifics (Satumanatpan and Keough 2001). Therefore, the initial leeward community of the transplant roots may be indicative of reduced recruitment. We found that certain epibiont groups in leeward to windward transplants, such as green macroalgae and bivalves, more closely resembled leeward controls than windward controls. This suggests that these groups, once established, may be able to outcompete turf algae, CCA, and barnacles, which are otherwise dominant on windward sides or resist dislodgement. For example, many macroalgae species utilize holdfast(s) to anchor themselves in sediment (e.g., mangrove detritus) (Anderson et al. 2006). The reason why the leeward to windward transplant treatment had greater percent cover of green macroalgae than either control may be due to the algae developing strong anchorage the first year in the leeward area and then being able to spread as the percent cover of sponges were reduced. Differences in predation could also explain these patterns (e.g., reduced herbivory in windward areas). Since the percent cover of CCA, red macroalgae, and turf algae of the leeward to windward transplants fell between the percent cover of these groups in the two controls, another possibility is that the community is still converging. The root mimic transplants suggest that the initial community, and the competitive strategies of initial inhabitants to tolerate or inhibit later species may impact subsequent community composition despite abiotic conditions.

The differences in community composition within root treatment between years suggests some annual fluctuations in epibiont community assemblage. These differences may be linked to the higher average annual temperature and decreased average annual rainfall and windspeed in year 2 compared to year 1 (Paton 2019). Reduced percent cover of turf algae in year 2 compared to year 1 could be due to the decreased efficiency of turf algae productivity as biomass increases (Tebbett and Bellwood 2021). Since tunicates prefer shaded areas (Goodbody 2000), the greater percent cover of tunicates in year 2 could be due to the epibiont community being more developed and perhaps providing more shade. The community composition of root mimics (e.g., all root mimics in year 1, root mimic controls in year 2) was dissimilar to natural and scraped mangrove root treatments in both years of the study, with root mimics having a greater percent cover of barnacles and CCA and lower turf algae relative to the mangrove roots across wave exposure regimes and years. Further, in leeward areas, the root mimic control had a lower percent cover of green macroalgae. When applying the results from mangrove root mimics transplanted between wave exposure sites, it is important to note that these root mimics were all PVC, so while general trends are applicable to natural mangrove roots, we would expect some differences in community composition between mangrove roots and root mimics. Notably, we found the percent cover of barnacles and CCA to be lower on natural mangrove roots than on PVC in the root treatment comparison of this study and in the experiments in Chapter 3. Chapter 3 results also suggest that sponge species composition and biomass differ between PVC and natural roots. Although the percent cover of turf algae and green macroalgae is likely to be different based on results from this study and Chapter 3, turf and green macroalgae algal cover fluctuates between sites and years, making it difficult to draw general conclusions.

In this study we selected islands of varying size to test whether patterns in epibiont community composition varied predictably as a function of island size. We found that island size did not directly affect dissolution rate but had indirect effects due to shorter distance between sampled windward and leeward sites leading to overlap of water flow patterns in smaller islands (e.g., Daphnia and Tapir). There was still a gradient in dissolution rate across island replicates within windward or leeward treatments and community composition analyses were based on wave exposure (categorical) rather than water flow (continuous). However, we used dissolution rates as a factor in some of our analyses and the general patterns were similar.

Epibiont communities of mangrove roots are complex with layers of organisms growing on top of each other, each with its own adaptation to colonize and persist making them excellent models of scale, succession and competition theory (Farnsworth and Ellison 1996, Guerra-Castro et al. 2016). In this study, we experimentally examine how abiotic factors shape initial community establishment and subsequent persistence, by quantifying effects of wave exposure on community assemblages associated with an important foundation species, the red mangrove (*Rhizophora mangle).* This study highlights some of the differences in epibiont groups between mangrove roots in windward and leeward areas and demonstrates that community structure is more deterministic in leeward areas and stochastic in windward areas. Although epibionts are frequently overlooked as important to the mangrove ecosystem due to much of mangrove fauna not being considered host-specific (Ellison and Farnsworth 1992), some of these taxa (e.g., algal turfs, sponges, bivalves) have been documented to have major contributions to benthic productivity, fuel trophic pathways, and play key functional roles in tropical marine systems (Wulff 2005, Tebbett and Bellwood 2021). This study sheds light on the applicability of classical models of ecological succession (e.g., facilitation inhibition, tolerance/competitive) within the mangrove habitat, demonstrating how abiotic forces alter successional dynamics and shape biodiversity, which can drive important ecosystem functions in mangrove ecosystems. Community differences between windward and leeward areas, and the transplantation of root mimics, reveals how these epibiont communities are likely to respond to changes in wind and wave energy, which can be impacted by humans and climate change. It is also important to note that these abiotic regimes can also be modified by human activities, such as through boat wakes, which cause aerial roots of red mangroves to collide, weakening the sessile community and leading to dislodgement of root epibionts (Goodbody 2000).

4.6 Acknowledgements

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4.7 References

Ames, G. M., S. M. Anderson, and J. P. Wright. 2016. Multiple environmental drivers structure plant traits at the community level in a pyrogenic ecosystem. Functional Ecology 30:789–798.

Anderson, K., L. Close, R. E. DeWreede, B. J. Lynch, C. Ormond, and M. Walker. 2006. Biomechanical properties and holdfast morphology of coenocytic algae (Halimedales, Chlorophyta) in Bocas del Toro, Panama. Journal of Experimental Marine Biology and Ecology 328:155–167.

Bingham, B. L. 1992. Life histories in an epifaunal community: Coupling of adult and larval processes. Ecology 73:2244–2259.

Bingham, B. L., and C. M. Young. 1995. Stochastic events and dynamics of a mangrove root epifaunal community. Marine Ecology 16:145–163.

Bosire, J. O., F. Dahdouh-Guebas, J. G. Kairo, S. Cannicci, and N. Koedam. 2004. Spatial variations in macrobenthic fauna recolonisation in a tropical mangrove bay. Biodiversity and Conservation 13:1059–1074.

Burton, T. M., C. A. Stricker, and D. G. Uzarski. 2002. Effects of plant community composition and exposure to wave action on invertebrate habitat use of Lake Huron coastal wetlands. Lakes and Reservoirs: Research and Management 7:255–269.

Cameron, K. A., and P. L. Harrison. 2020. Density of coral larvae can influence settlement, post-settlement colony abundance and coral cover in larval restoration. Scientific Reports 10:1–11.

Clements, F. E. 1916. Plant succession: an analysis of the development of vegetation. Carnegie Institution of Washington 242.

Connell, S. D., M. S. Foster, and L. Airoldi. 2014. What are algal turfs? Towards a better description of turfs. Marine Ecology Progress Series 495:299–307.

Cowles, H. C. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. The Botanical Gazette 27:95–117, 167–202, 281–308, 361–391.

Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs 41:351–389.

Dayton, P. K. 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos. Pages 81–95 *in* B. C. Parker, editor. Proceedings of the Colloquium on Conservation Problems in Antarctica. Allen Press, Lawrence, Kansas.

Drury, W. H., and I. C. T. Nisbet. 1973. Succession. Journal of the Arnold Arboretum 54:331–368.

Dunlap, M., and J. R. Pawlik. 1998. Spongivory by parrotfish in Florida mangrove and reef habitats. Marine Ecology 19:325–337.

Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliott, C. R. Ford, D. R. Foster, B. D. Kloeppel, J. D. Knoepp, G. M. Lovett, J. Mohan, D. A. Orwig, N. L. Rodenhouse, V. Sobczak, William, K. A. Stinson, J. K. Stone, C. M. Swan, J. Thompson, B. Von Holle, and J. R. Webster. 2005. Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 3:479–486.

Ellison, A. M., and E. J. Farnsworth. 1992. The ecology of Belizean mangrove-root fouling communities: patterns of epibiont distribution and abundance, and effects on root growth. Hydrobiologia 247:87–98.

Farnsworth, E. J., and A. M. Ellison. 1996. Scale-dependent spatial and temporal variability in biogeography of mangrove root epibiont communities. Ecological Monographs 66:45–66.

Gaylord, B. 1999. Detailing agents of physical disturbance: Wave-induced velocities and accelerations on a rocky shore. Journal of Experimental Marine Biology and Ecology 239:85–124.

Goodbody, I. 2000. Diversity and distribution of ascidians (Tunicata) in the Pelican Cays, Belize. Page Atoll Research Bulletin. Washington, D.C.

Grabowski, J. H., A. R. Hughes, D. L. Kimbro, and M. A. Dolan. 2005. How habitat setting influences restored oyster reef communities. Ecology 86:1926–1935.

Greene, C. H., and A. Schoener. 1982. Succession on marine hard substrata: a fixed lottery. Oecologia 55:289–297.

Guerra-Castro, E. J., J. E. Conde, and J. J. Cruz-Motta. 2016. Scales of spatial variation in tropical benthic assemblages and their ecological relevance: Epibionts on Caribbean mangrove roots as a model system. Marine Ecology Progress Series 548:97–110.

Guerra-Castro, E. J., and J. J. Cruz-Motta. 2018. Colonization and succession as drivers of small-scale spatial variability in epibionts on mangrove roots in the Southern Caribbean. Marine Ecology Progress Series 588:15–27.

Hughes, A. R., P. E. Gribben, D. L. Kimbro, and M. J. Bishop. 2014. Additive and site-specific effects of two foundation species on invertebrate community structure. Marine Ecology Progress Series 508:129–138.

Jackson, J. B. C., and L. Buss. 1975. Alleopathy and spatial competition among coral reef invertebrates. Proceedings of the National Academy of Sciences 72:5160–5163.

Jokiel, P. L., and J. I. Morrissey. 1993. Water motion on coral reefs: evaluation of the “clod card” technique. Marine Ecology Progress Series 93:175–181.

Jones, W. E., and A. Demetropoulos. 1968. Exposure to wave action: Measurements of an important ecological parameter on rocky shores on Anglesey. Journal of Experimental Marine Biology and Ecology 2:46–63.

Lajoie, G., and Vellend. 2015. Understanding context dependence in the contribution of intraspecific variation to community trait – environment matching. Ecology 96:2912–2922.

Lesser, M. P., and M. Slattery. 2013. Ecology of caribbean sponges: Are top-down or bottom-up processes more important? PLoS ONE 8:1–9.

Levin, S. A., and R. T. Paine. 1974. Disturbance, patch formation, and community structure. Proceedings of the National Academy of Sciences 71:2744–2747.

Nathan, R., and H. C. Muller-landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology and Evolution 15:278–285.

O’Brien, J. M., and R. E. Scheibling. 2018. Turf wars: Competition between foundation and turf-forming species on temperate and tropical reefs and its role in regime shifts. Marine Ecology Progress Series 590:1–17.

Paton, S. 2019. Monthly summary_Bocas Station.

Pinsky, M. L., G. Guannel, and K. K. Arkema. 2013. Quantifying wave attenuation to inform coastal habitat conservation. Ecosphere 4:1–16.

Pulsford, S. A., D. B. Lindenmayer, and D. A. Driscoll. 2016. A succession of theories: Purging redundancy from disturbance theory. Biological Reviews 91:148–167.

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

River, G. F., and P. J. Edmunds. 2001. Mechanisms of interaction between macroalgae and scleractinians on a coral reef in Jamaica. Journal of Experimental Marine Biology and Ecology 261:159–172.

Rodríguez, S. R., F. P. Ojeda, and N. C. Inestrosa. 1993. Settlement of benthic marine invertebrates. Marine Ecology Progress Series 97:193–207.

Ross, P. M. 2001. Larval supply, settlement and survival of barnacles in a temperate mangrove forest. Marine Ecology Progress Series 215:237–249.

Satumanatpan, S., and M. J. Keough. 2001. Roles of larval supply and behavior in determining settlement of barnacles in a temperate mangrove forest. Journal of Experimental Marine Biology and Ecology 260:133–153.

Schutte, V., and J. Byers. 2017. Variation in a simple trait of mangrove roots governs predator access to, and assemblage composition of, epibiotic sponges. Marine Ecology Progress Series 573:15–23.

Sousa, W. P. 1979a. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecological Monographs 49:227–254.

Sousa, W. P. 1979b. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. Ecology 60:1225–1239.

Sousa, W. P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics. Vol. 15 15:353–391.

Sundblad, G., T. Bekkby, M. Isæus, A. Nikolopoulos, K. M. Norderhaug, and E. Rinde. 2014. Comparing the ecological relevance of four wave exposure models. Estuarine, Coastal and Shelf Science 140:7–13.

Tebbett, S. B., and D. R. Bellwood. 2021. Algal turf productivity on coral reefs: A meta-analysis. Marine Environmental Research 168:105311.

Thompson, T. L., and E. P. Glenn. 1994. Plaster standards to measure water motion. Limnology and Oceanography 39:1768–1779.

Todd, C. D. 1998. Larval supply and recruitment of benthic invertebrates: do larvae always disperse as much as we believe? Hydrobiologia 375/376:1–21.

Wulff, J. L. 2005. Trade-offs in resistance to competitors and predators, and their effects on the diversity of tropical marine sponges. Journal of Animal Ecology 74:313–321.

Wulff, J. L. 2010. Sponge community dynamics on Caribbean mangrove roots: significance of species idiosyncrasies. Pages 501–514 *in* M. A. Lang, I. G. Macintyre, and K. Rützler, editors. Proceedings of the Smithsonian Marine Science Symposium. Smithsonian Institution, Washington, D.C.

Zarnetske, P. L., B. Baiser, A. Strecker, S. Record, J. Belmaker, and M.-N. Tuanmu. 2017. The interplay between landscape structure and biotic interactions. Current Landscape Ecology Reports 2:12–29.

4.8 Tables

Table 4.1 Characteristics of study sites. Island size (perimeter), average ± SE dissolution rate (a relative measure of water flow), windspeed, and water depth of leeward and windward areas of study islands. Dissolution rate is measured as the difference in weight of flow blocks before and after deployment divided by the total hours the blocks were deployed for.

Island	Island Area (m^2)	Distance between Sites (m)	Wave Exposure	Average Dissolution Rate ± SE (n = 8)	Average Windspeed (m/s) ± SE (n = 5)	Average Water Depth (cm) ± SE (n = 30)
Tapir	7,392	142	Leeward	0.16 ± 0.02	1.43 ± 0.54	173.60 ± 5.37
Nudibranch	12,1339	228	Leeward	0.05 ± 0.01	2.10 ± 0.70	115.23 ± 2.30
Daphnia	14,289	103	Leeward	0.11 ± 0.02	1.36 ± 0.17	130.00 ± 5.91
Gragger	39,550	180	Leeward	0.13 ± 0.01	2.13 ± 0.32	125.17 ± 3.72
Seahorse	45,182	234	Leeward	0.08 ± 0.01	2.65 ± 0.43	98.07 ± 2.91
Orca	51,685	153	Leeward	0.07 ± 0.01	1.20 ± 0.20	133.17 ± 4.01
Sid	75,631	183	Leeward	0.06 ± 0.00	0.90 ± 0.33	144.97 ± 5.02
Cougar	145,130	261	Leeward	0.04 ± 0.01	1.03 ± 0.24	175.30 ± 2.37
Elephant	401,698	162	Leeward	0.04 ± 0.01	1.10 ± 0.18	146.00 ± 5.02
	Combined Average Leeward Areas			0.08 ± 0.01	1.51 ± 0.14	137.94 ± 2.02
Tapir	7,392	142	Windward	0.25 ± 0.02	3.90 ± 0.56	91.37 ± 1.67
Nudibranch	12,1339	228	Windward	0.23 ± 0.02	3.10 ± 0.30	88.17 ± 1.52
Daphnia	14,289	103	Windward	0.20 ± 0.01	3.88 ± 0.68	92.67 ± 2.56
Gragger	39,550	180	Windward	0.29 ± 0.02	1.26 ± 0.52	95.43 ± 1.56
Seahorse	45,182	234	Windward	0.26 ± 0.02	4.08 ± 0.83	71.27 ± 0.90
Orca	51,685	153	Windward	0.28 ± 0.02	3.70 ± 1.45	93.07 ± 1.07
Sid	75,631	183	Windward	0.27 ± 0.02	4.03 ± 0.32	69.83 ± 0.86
Cougar	145,130	261	Windward	0.20 ± 0.02	3.33 ± 0.56	85.43 ± 2.71
Elephant	401,698	162	Windward	0.19 ± 0.01	1.15 ± 0.22	81.47 ± 1.04
	Combined Average Windward			0.24 ± 0.01	3.09 ± 0.29	85.41 ± 0.77

Table 4.2 Pairwise comparisons of natural and scraped mangrove roots and root mimic (PVC) control treatments after year 1 and 2 of epibiont assemblage development. PERMANOVA using a Bray-Curtis dissimilarity matrix on square-root transformed data was used to test for differences in mangrove root mimic communities between low and high wave exposures (leeward versus windward sides of mangrove islands). Significant p-values are in bold.

Pairs	Df	Sum of Squares	F Model	R^2	Adjusted P value
Year 1					
Natural mangrove root vs PVC	1	0.757	5.523	0.018	**0.003**
Scraped mangrove root vs PVC	1	1.010	7.628	0.024	**0.003**
Natural vs Scraped mangrove root	1	0.432	3.085	0.010	0.051
Year 2					
Natural mangrove root vs PVC	1	0.720	4.914	0.022	**0.003**
Scraped mangrove root vs PVC	1	1.028	7.198	0.032	**0.003**
Natural vs Scraped mangrove root	1	0.120	0.772	0.003	1.000

Table 4.3 Pairwise comparisons of the epibiont communities on root mimic (PVC) treatments one year following transplanting from windward to leeward sites and vice versa. PERMANOVA using a Bray-Curtis dissimilarity matrix on square-root transformed data were used to test for differences in mangrove root mimic communities between low and high wave exposures (windward and leeward sides of mangrove islands). Significant p-values are in bold.

Pairs	Df	Sum of Squares	F Model	R^2	Adjusted P value
Windward control vs windward to leeward	1	0.473	4.703	0.063	**0.006**
Windward control vs leeward control	1	0.908	8.114	0.104	**0.006**
Windward control vs leeward to windward	1	0.341	3.121	0.045	**0.030**
Windward to leeward vs leeward control	1	0.113	1.089	0.014	1.000
Windward to leeward vs leeward to windward	1	0.428	4.229	0.055	**0.006**
Leeward control vs leeward to windward	1	0.636	5.670	0.072	**0.006**

4.9 Figures

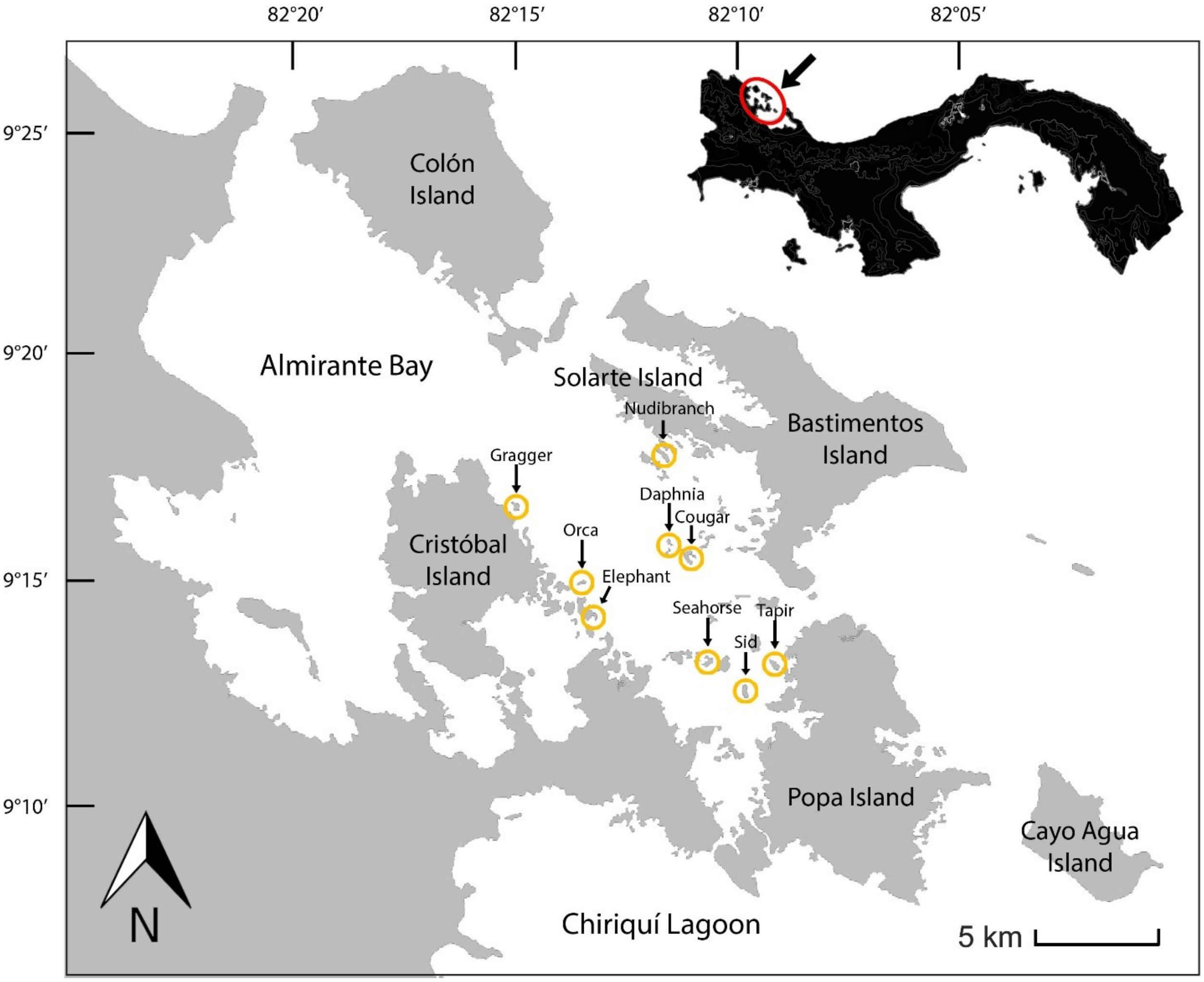

Figure 4.1 Wave exposure study sites. Yellow circled islands indicate the location of mangrove islands of the Bocas del Toro archipelago included for in-situ surveys. The red circled area shows where the Bocas del Toro archipelago is located within Panama.

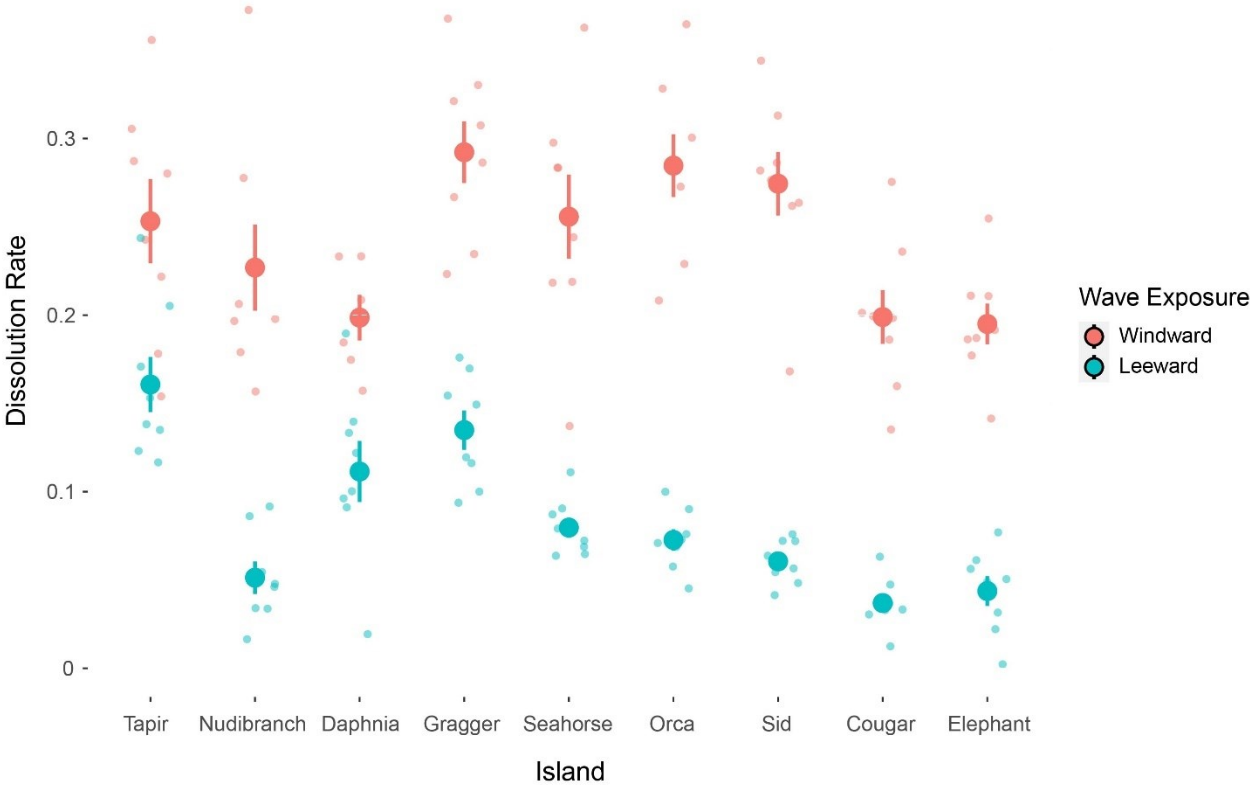

Figure 4.2 Dissolution rates among islands between windward and leeward sites. Mean (large circle) and standard error (bar) of dissolution rates from flow blocks deployed at the windward and leeward sides of mangrove islands in order from smallest area (left) to largest area (right). Raw data points given as small, faded dots. Dissolution rate is measured as the difference in weight of flow blocks before and after deployment divided by the total hours the blocks were deployed for.

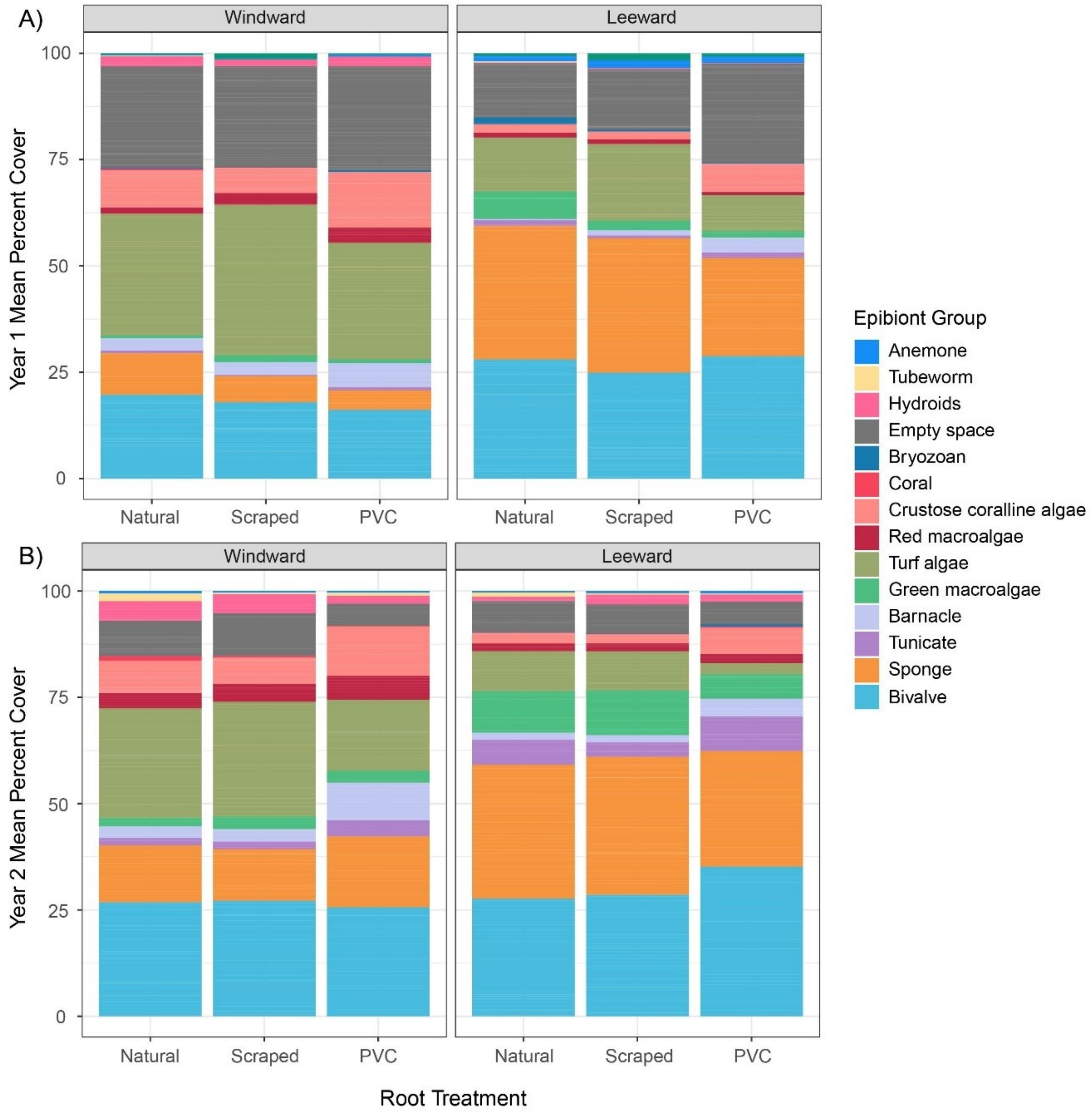

Figure 4.3 Epibiont percent cover among mangrove roots and root mimic treatment between windward and leeward sites. Percent cover of sessile epibionts and empty space averaged across islands after A) year 1 and B) year 2 of settlement across three treatments: Natural mangrove control (unmanipulated), scraped mangrove root, and root mimic (PVC) in windward and leeward areas (wave exposure) among nine islands. Root treatment (p = 0.001) and wave exposure (p = 0.001) had significant effects on epibiont community both years.

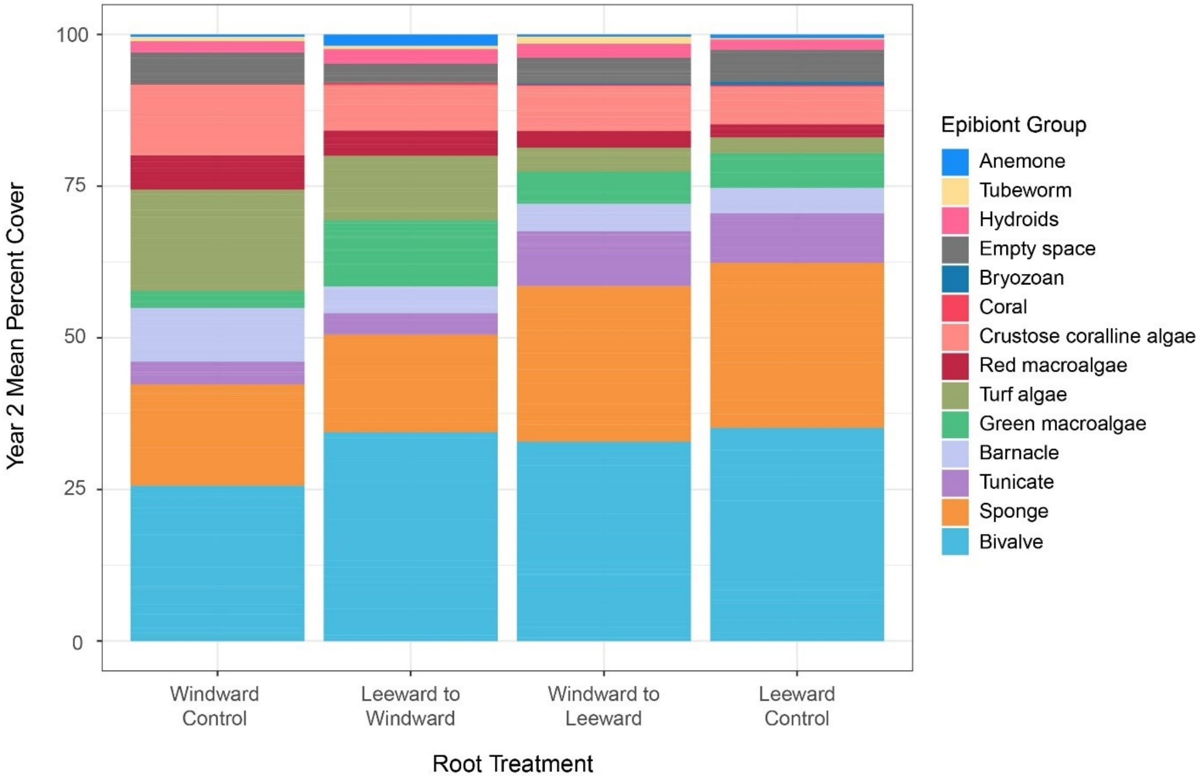

Figure 4.4 Epibiont percent cover of transplanted and control root mimic treatments. Mean percent cover of sessile epibionts and empty space across nine islands for each of the four root mimic treatments: Windward control (PVC originally placed on the windward side of an island that remained there), windward to leeward (moved from the windward to leeward side of an island), leeward to windward (moved from leeward to windward side of an island), and leeward control (PVC originally placed on the leeward side of an island that remained there). Treatment ($p = 0.001$) had significant effects on epibiont community composition with differences being detected among all treatments except transplanted PVC from windward to leeward sites, which became similar to the surrounding root communities in the leeward area.

General Discussion

This dissertation examined the role that foundation species play in shaping biodiversity of mangrove islands through multiple spatial-scale lenses. By blending field experiments, field surveys and a review of existing literature on coral—mangrove interactions, I addressed the importance of mangroves in buffering environmental stress, providing refuge for corals, and interacting with other foundation species to drive epibiont assemblage structure. Red mangroves of the Caribbean function as primary foundation species, and abiotic factors such as light, temperature, wind, wave exposure and water flow affect the interactions between co-existing foundation species, which has cascading effects on the associated sessile and mobile community composition. By examining mangrove communities from a global scale down to a scale of individual roots, this dissertation provides novel insights on the interactions between abiotic and biotic drivers of epibiont assemblage structure. The ability to understand and predict epibiont community composition and the relative importance of concurrent abiotic forces and biotic interactions has important implications for restoration and conservation of these biogenic habitats.

Role of abiotic factors in structuring mangrove epibiont communities

Coexisting foundation species can provide complementary levels of complexity to support diverse species assemblages in a chain of positive interactions known as a facilitation cascade (sensu Altieri et al. 2007). In mangrove islands, mangroves function as primary foundation species and may coexist with other secondary foundation species such as corals, sponges, and bivalves. However, abiotic factors are important in determining which species will inhabit these mangrove ecosystems and the spatial configuration of co-occurring foundation species (e.g., nested or adjacent assemblages). In Chapter 1, my field surveys and review of the scientific literature demonstrate that a connection to the open ocean/open patches or channels within mangrove canopy, submergence through all stages of the tidal cycle, limited freshwater inflow, clear water, water flow and current are key factors determining whether corals can live within the mangrove habitat. In Chapter 4, I moved from a global to landscape scale, quantifying consequences of landscape-scale variation in wave exposure on both initial establishment of mangrove root epibiont communities (year 1) and subsequent persistence (year 2). I demonstrated how mangrove epibiont communities of windward areas are distinctively different from leeward areas even though they may occur only 100-250 meters away from one another.

Windward areas, characterized by stronger wind, increasing wave energy, water flow, and turbidity relative to leeward areas, were dominated by encrusting sessile epibiont communities including turf algae, calcifying organisms (crustose coralline algae and coral), and barnacles, which can withstand physical disturbance of dislodgement and current-induced abrasion. Sheltered roots in leeward areas, on the other hand, were dominated by massive sponges and tunicates. In Chapter 2, I examined the importance of shading and habitat (e.g., mangrove or reef) in determining coral community structure (i.e., coral species richness, abundance, and diversity) and condition (i.e., level of bleaching, tissue loss, and mortality). My field surveys and reciprocal transplant experiment demonstrated that mangrove habitats provide a refuge to corals, with higher coral richness in mangroves than on the adjacent reef and that light intensity is a key environmental parameter mediating coral bleaching and survival. Previous studies hypothesized that shading from the mangrove canopy reduces temperature and UV radiation stress that can lead to coral colony bleaching and subsequent disease outbreaks, but these studies used correlations between number of coral colonies that bleached and whether they had been shaded or not to test this theory (Rogers and Herlan 2012, Yates et al. 2014). My reciprocal transplant experiment was the first the manipulate shading to test its role in coral bleaching and survival, confirming that shade provided by the mangrove canopy does reduce the light stress experienced on nearby shallow reefs. These facilitative interactions allow mangroves to act as coral refugia by reducing environmental stress; and these interactions will likely become increasingly important with global climate change.

The results of this dissertation highlight how responsive mangrove epibiont communities are to external forces. Chapter 4 demonstrated that abiotic forces are important drivers of both the initial epibiont assemblage that develops on mangrove roots (after 1 year) but also the assemblage that persists after 2 years. I found that sessile epibiont communities that were transplanted from leeward to windward areas were influenced by the initial community composition that developed in the leeward habitat so that after a year of living in their new windward area, they had not converged with neighboring roots. However, the community composition of roots in the reciprocal transplant from windward to leeward did converge on that of the leeward communities, which suggests that initial community establishment may be a stronger determinant of later composition on leeward areas, whereas physical forcing by waves may play a more important role in determining community structure on windward shorelines.

Importance of root traits for epibiont assemblage composition

Foundation species are organisms that play a dominant role in structuring communities through habitat creation, and they are integral drivers of ecosystem processes (Dayton 1972, Ellison et al. 2005). Variation in the traits of foundation species can affect these functions by determining the degree to which environmental stress or disturbance is influenced (e.g., positively or negatively) (Irving and Bertness 2009, Angelini et al. 2011). In Chapter 3, I manipulated physical attributes of mangroves using living and non-living mangrove roots, as well as root mimics, to determine how traits of foundation species such as mangroves affect the composition of associated communities. Previous work has quantified effects of root complexity (Nagelkerken et al. 2010, Vorsatz et al. 2021), whether roots are suspended or touch the ground (Schutte and Byers 2017), and root density (Nanjo et al. 2014). My study was the first to experimentally test effects of root substrate composition and root health (alive or dead) on epibiont communities. By tracking community development over a year among living and non-living mangrove roots and non-living root mimics (i.e., wood and PVC), I was able to examine the importance of these characteristics and explain how they affected community structure through variation in root length and the presence of secondary foundation (e.g., sponges, bivalves). I did not find evidence for nutrient exchange or other biotic controls from living mangrove roots shaping the associated community. However, non-living mangrove roots quickly deteriorated and became shorter or were lost altogether, and as result had a reduced capacity to support a diverse community. I found that, overall, root mimics function similarly to living mangrove roots, although wood mimics were more similar to living roots than PVC. Additionally, I found that sponge and bivalve biomass had a positive effect on mobile community richness, which I hypothesize is due to the structural complexity that massive sponges and bivalves offer as substrate, providing refuge to a speciose invertebrate community (Henkel and Pawlik 2011, Rebolledo et al. 2014). Since root treatment had significant effects on bivalve and sponge biomass, which in turn correlated with the community structure of mobile epifauna, root characteristics appear have an indirect effect on mobile organisms through a facilitation cascade.

Implications for conservation and restoration of mangrove habitat

In a time where global environmental changes and anthropogenic disturbances are unraveling ecosystems and degrading their functioning, it is important for conservation and management purposes to understand what forces are at play in structuring community and the resilience of these communities. As we move forward towards the International Union for Conservation of Nature (IUCN) goal of full protection of >30% of global marine habitat by 2030 (Zhao et al. 2020), we need to carefully consider what areas we protect by examining how those ecosystems are modified by abiotic factors, and what biodiversity they support. I suggest that management of mangrove ecosystems needs to prioritize how abiotic factors influence the types of communities that mangroves can support and what this means for mangrove-associated assemblages. For example, my dissertation demonstrates the important role of wave exposure on the composition of mangrove root communities. If the goal is to conserve mangroves to support sponges and bivalves, which have important roles in biofiltration, bioremediation, bioturbation, habitat provision, and as food sources for fishes and humans (Ellison 2008, MacDonald et al. 2008, MacDonald and Weis 2013, Carrasquilla-Henao and Juanes 2017, Aguirre-Rubí et al. 2018, Seemann et al. 2018, Vaughn and Hoellein 2018, Wright 2019), then leeward mangrove areas should be prioritized for protection. Regulation of boat traffic should also be considered, since the wake from boats may make the community of leeward areas resembled that of windward areas and cause significant bank erosion (Ellison and Farnsworth 1996). If managers are interested in transplanting corals into mangroves to reduce losses due to bleaching, coral species need to be selected to match the abiotic conditions. For example, in Chapter 1, I identified coral species zonation patterns within the mangrove canopy in Panama and in Chapter 2 I provide a model demonstrating the proportion of corals from six species to bleach under different levels of photosynthetically active radiation.

Globally, 75% of all coral reefs are at risk of partial or complete degradation due to natural and human-induced stressors (Tkachenko 2017, Clements et al. 2018). And Caribbean coral reefs are among the most threatened reefs in the world with live coral cover averaging just 10-13% (Gardner et al. 2003, Tkachenko 2017). Evidence suggests that corals are responding to stressors in four primary ways: 1) a shift in age structure towards a dominance by juveniles, 2) stress resistant taxa replacing sensitive taxa, 3) a shift in coral phenotypes through plastic or genetic change, and 4) phase shifts where reef-building corals are replaced by other benthic organisms such as turf algae and fleshy macroalgae (Tkachenko 2017). Little is known about coral interactions within mangrove habitats or their resilience. The results of my dissertation research suggest that mangroves mitigate stressful conditions that can cause bleaching of corals on the reef and subsequent competition with algae. Further, evidence of several large (1 m across) scleractinian corals 7-13 m into the mangrove canopy with positive annual growth rates suggests that corals are persisting in the mangrove habitat. Although this dissertation was unable to measure coral competition with algae within the reef compared to the mangrove habitat, I observed a period in 2019 of extensive algal growth within the mangrove canopy where algae were beginning to overgrow coral colonies living among the mangrove roots, but within days spotted sea hares (*Aplysia dactylomela*) arrived and grazed the algae until it was gone while algae mats remained on the reef for over a month. Future research should address how invertebrate interactions in these CMC systems impact resilience of community composition. While wave exposure is believed to be a driving force in reef communities, with windward reefs more frequently dominated by macroalgae than corals due to wave action limiting urchin grazing and density (Sangil and Guzman 2016), in the mangrove habitat we more frequently observed corals and crustose coralline algae in windward areas than leeward. Turf algae, which is known to compete with corallines, was also more frequent in windward areas but green macroalgae was more frequently observed in leeward areas of mangrove islands. These differences in algal composition within the mangrove habitats relative to the reefs along their respective wave exposure gradients could suggest that wave action has a lesser effect on sessile invertebrates (e.g., urchins) in mangroves, possibly due to the increased habitat complexity of mangrove roots dampening wave energy.

Final conclusion

Mangroves and coral reefs represent two adjacent and potentially interacting coastal habitats that are rich in biodiversity, provide important ecosystem services, and are highly threatened by multiple anthropogenic stressors including climate change. This dissertation focused on the organization of foundation species in nested assemblages (mangroves as primary and corals as secondary) and the implications of factors including foundation species traits and environmental context in mediating patterns of biodiversity in association with primary and secondary foundation species. The results of this body of work provide important insights into the forces that drive variation in mangrove root community assemblages and the role of mangroves as refuge for corals, a role that may be increasingly important as climate change continues to affect coral ecosystems. We highlight research areas in need of further exploration and suggest how this knowledge can be applied for conservation and management purposes.

Further, we demonstrate the usefulness of mangrove islands as a model system to explore concepts related to ecological succession and facilitation cascades.

General References

Aguirre-Rubí, J., A. Luna-Acosta, M. Ortiz-Zarragoitia, B. Zaldibar, U. Izagirre, M. J. Ahrens, L. Villamil, and I. Marigómez. 2018. Assessment of ecosystem health disturbance in mangrove-lined Caribbean coastal systems using the oyster *Crassostrea rhizophorae* as sentinel species. Science of the Total Environment 618:718–735.

Alongi, D. M. 2015. The impact of climate change on mangrove forests. Current Climate Change Reports 1:30–39.

Altieri, A. H., and J. Van De Koppel. 2013. Foundation species in marine ecosystems. Pages 37–56 *in* M. D. Bertness, J. F. Bruno, B. R. Silliman, and J. J. Stachowicz, editors. Marine Community Ecology and Conservation 2. Sinauer Associates, Sunderland, Massachusetts.

Altieri, A. H., B. R. Silliman, and M. D. Bertness. 2007. Hierarchical organization via a facilitation cascade in intertidal cordgrass bed communities. American Naturalist 169:195–206.

Angelini, C., A. H. Altieri, B. R. Silliman, and M. D. Bertness. 2011. Interactions among foundation species and their consequences for community organization, biodiversity, and conservation. BioScience 61:782–789.

Aquino-Thomas, J. 2020. The critical role of interactions between ecological foundation species in structuring a mangrove community. Florida Atlantic University, Boca Raton, Florida, United States of America.

Aquino-Thomas, J., and C. E. Proffitt. 2014. Oysters *Crassostrea virginica* on red mangrove *Rhizophora mangle* prop roots: Facilitation of one foundation species by another. Marine Ecology Progress Series 503:177–194.

Berkström, C., L. Eggertsen, W. Goodell, C. A. M. M. Cordeiro, M. B. Lucena, R. Gustafsson, S. Bandeira, N. Jiddawi, and C. E. L. Ferreira. 2020. Thresholds in seascape connectivity: the spatial arrangement of nursery habitats structure fish communities on nearby reefs. Ecography 43:882–896.

Bishop, M. J., J. E. Byers, B. J. Marcek, and P. E. Gribben. 2012. Density-dependent facilitation cascades determine epifaunal community structure in temperate Australian mangroves. Ecology 93:1388–1401.

Bond, E. M., and J. M. Chase. 2002. Biodiversity and ecosystem functioning at local and regional spatial scales. Ecology Letters 5:467–470.

Boström, C., S. J. Pittman, C. Simenstad, and R. T. Kneib. 2011. Seascape ecology of coastal biogenic habitats: Advances , gaps, and challenges. Marine Ecology Progress Series 427:191–217.

Bruno, J. F., and M. D. Bertness. 2001. Habitat modification and facilitation in benthic marine communities. Pages 201–218 in M. D. Bertness, S. D. Gaines, and M. E. Hay, editors. Marine Community Ecology. Sinauer Associates, Inc., Sunderland, Massachusetts.

Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. Trends in Ecology and Evolution 18:119–125.

Bunting, P., A. Rosenqvist, R. M. Lucas, L. M. Rebelo, L. Hilarides, N. Thomas, A. Hardy, T. Itoh, M. Shimada, and C. M. Finlayson. 2018. The global mangrove watch - A new 2010 global baseline of mangrove extent. Remote Sensing 10:1669.

Cacciapaglia, C., and R. van Woesik. 2015. Reef-coral refugia in a rapidly changing ocean. Global Change Biology 21:2272–2282.

Camp, E. F., J. Edmondson, A. Doheny, J. Rumney, A. J. Grima, A. Huete, and D. J. Suggett. 2019. Mangrove lagoons of the Great Barrier Reef support coral populations persisting under extreme environmental conditions. Marine Ecology Progress Series 625:1–14.

Carpenter, K. E., M. Abrar, G. Aeby, R. B. Aronson, S. Banks, A. Bruckner, A. Chiriboga, J. Cortés, J. C. Delbeek, L. DeVantier, G. J. Edgar, A. J. Edwards, D. Fenner, H. M. Guzmán, B. W. Hoeksema, G. Hodgson, O. Johan, W. Y. Licuanan, S. R. Livingstone, E. R. Lovell, J. A. Moore, D. O. Obura, D. Ochavillo, B. A. Polidoro, W. F. Precht, M. C. Quibilan, C. Reboton, Z. T. Richards, A. D. Rogers, J. Sanciangco, A. Sheppard, C. Sheppard, J. Smith, S. Stuart, E. Turak, J. E. N. Veron, C. Wallace, E. Weil, and E. Wood. 2008. One-third of reef-building corals face elevated extinction risk from climate change and local impacts. Science 321:560–563.

Carrasquilla-Henao, M., and F. Juanes. 2017. Mangroves enhance local fisheries catches: a global meta-analysis. Fish and Fisheries 18:79–93.

Chapin III, F. S., B. H. Walker, R. J. Hobbs, D. U. Hooper, J. H. Lawton, O. E. Sala, and D. Tilman. 1997. Biotic control over the functioning of ecosystems. Science 277:500–504.

Clements, C. S., D. B. Rasher, A. S. Hoey, V. E. Bonito, and M. E. Hay. 2018. Spatial and temporal limits of coral-macroalgal competition: the negative impacts of macroalgal density, proximity, and history of contact. Marine Ecology Progress Series 586:11–20.

Contreras-Silva, A. I., A. Tilstra, V. Migani, A. Thiel, E. Pérez-Cervantes, N. Estrada-Saldívar, X. Elias-Ilosvay, C. Mott, L. Alvarez-Filip, and C. Wild. 2020. A meta-analysis to assess long-term spatiotemporal changes of benthic coral and macroalgae cover in the Mexican Caribbean. Scientific Reports 10:1–12.

Côté, I. M., J. A. Gill, T. A. Gardner, and A. R. Watkinson. 2005. Measuring coral reef decline through meta-analyses. Philosophical Transactions of the Royal Society B: Biological Sciences 360:385–395.

Davis, J. P., K. A. Pitt, B. Fry, A. D. Olds, and R. M. Connolly. 2014. Seascape-scale trophic links for fish on inshore coral reefs. Coral Reefs 33:897–907.

Dayton, P. K. 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos. Pages 81–95 *in* B. C. Parker, editor. Proceedings of the Colloquium on Conservation Problems in Antarctica. Allen Press, Lawrence, Kansas.

Diaz, M. C., K. P. Smith, and K. Rützler. 2004. Sponge species richness and abundance as indicators of mangrove epibenthic community health. Page Atoll Research Bulletin. Washington, DC.

Dinerstein, E., C. Vynne, E. Sala, A. R. Joshi, S. Fernando, T. E. Lovejoy, J. Mayorga, D. Olson, G. P. Asner, J. E. M. Baillie, N. D. Burgess, K. Burkart, R. F. Noss, Y. P. Zhang, A. Baccini, T. Birch, N. Hahn, L. N. Joppa, and E. Wikramanayake. 2019. A global deal for nature: Guiding principles, milestones, and targets. Science Advances 5:1–18.

Ellison, A. M. 2008. Managing mangroves with benthic biodiversity in mind: Moving beyond roving banditry. Journal of Sea Research 59:2–15.

Ellison, A. M. 2019. Foundation species, non-trophic interactions, and the value of being common. iScience 13:254–268.

Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliott, C. R. Ford, D. R. Foster, B. D. Kloeppel, J. D. Knoepp, G. M. Lovett, J. Mohan, D. A. Orwig, N. L. Rodenhouse, V. Sobczak, William, K. A. Stinson, J. K. Stone, C. M. Swan, J. Thompson, B. Von Holle, and J. R. Webster. 2005. Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 3:479–486.

Ellison, A. M., and E. J. Farnsworth. 1996. Anthropogenic disturbance of Caribbean mangrove ecosystems: Past impacts, present trends, and future predictions. Biotropica 28:549–565.

Emmett Duffy, J. 2009. Why biodiversity is important to the functioning of real-world ecosystems. Frontiers in Ecology and the Environment 7:437–444.

Feller, I. C., D. A. Friess, K. W. Krauss, and R. R. Lewis. 2017. The state of the world's mangroves in the 21st century under climate change. Hydrobiologia.

Friess, D. A., K. Rogers, C. E. Lovelock, K. W. Krauss, S. E. Hamilton, S. Y. Lee, R. Lucas, J. Primavera, A. Rajkaran, and S. Shi. 2019. The state of the world's mangrove forests: past, present, and future. Annual Review of Environmental and Resources 44:1–27.

Gardner, T. A., I. M. Côté, J. A. Gill, A. Grant, A. R. Watkinson, G. Paredes, R. R. Warner, J. B. C. Jackson, J. M. Pandolfi, R. H. Bradbury, E. Sala, T. P. Hughes, K. A. Bjorndal, R. G. Cooke, D. McArdle, L. McClenachan, and M. J. H. Newman. 2003. Long-term region-wide declines in Caribbean corals. Science 301:958–960.

Gillis, L. G., T. J. Bouma, C. G. Jones, M. M. Van Katwijk, I. Nagelkerken, C. J. L. Jeuken, P. M. J. Herman, and A. D. Ziegler. 2014. Potential for landscape-scale positive interactions among tropical marine ecosystems. Marine Ecology Progress Series 503:289–303.

Guannel, G., K. Arkema, P. Ruggiero, and G. Verutes. 2016. The power of three: Coral reefs, seagrasses and mangroves protect coastal regions and increase their resilience. PLoS ONE 11:e0158094.

Guerra-Castro, E. J., and J. J. Cruz-Motta. 2014. Ecology of fouling assemblages associated with mangrove's roots: An artificial substrate for manipulative experiments. Journal of Experimental Marine Biology and Ecology 457:31–40.

Guerra-Castro, E. J., and J. J. Cruz-Motta. 2018. Colonization and succession as drivers of small-scale spatial variability in epibionts on mangrove roots in the Southern Caribbean. Marine Ecology Progress Series 588:15–27.

Guzmán, H. M. 2003. Caribbean coral reefs of Panama: Present status and future perspectives. Pages 241–274 *in* J. Cortés, editor. Latin American Coral Reefs. Elsevier Science B.V., Amsterdam, The Netherlands.

Harborne, A. R., P. J. Mumby, F. Micheli, C. T. Perry, C. P. Dahlgren, K. E. Holmes, and D. R. Brumbaugh. 2006. The functional value of Caribbean coral reef, seagrass and mangrove habitats to ecosystem processes. Advances in Marine Biology, 50, 57–189.

Henkel, T. P., and J. R. Pawlik. 2011. Host specialization of an obligate sponge-dwelling brittlestar. Aquatic Biology 12:37–46.

Hoegh-Guldberg, O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. Marine and Freshwater Research 50:839–866.

Hogarth, P. 2015. The Biology of Mangroves and Seagrasses. Third edit. Oxford University Press, Oxford.

Van Hooidonk, R., J. A. Maynard, and S. Planes. 2013. Temporary refugia for coral reefs in a warming world. Nature Climate Change 3:508–511.

Hughes, T. P., A. H. Baird, D. R. Bellwood, M. Card, S. R. Connolly, C. Folke, R. Grosberg, O. Hoegh-Guldberg, J. B. C. Jackson, J. Kleypas, J. M. Lough, P. Marshall, M. Nyström, S. R. Palumbi, J. M. Pandolfi, B. Rosen, and J. Roughgarden. 2003. Climate change, human impacts, and the resilience of coral reefs. Science 301:929–933.

Igulu, M. M., I. Nagelkerken, M. Dorenbosch, M. G. G. Grol, A. R. Harborne, I. A. Kimirei, P. J. Mumby, A. D. Olds, and Y. D. Mgaya. 2014. Mangrove habitat use by juvenile reef fish: Meta-analysis reveals that tidal regime matters more than biogeographic region. PLoS ONE 9(12):e114715.

Irving, A. D., and M. D. Bertness. 2009. Trait-dependent modification of facilitation on cobble beaches. Ecology 90:3042–3050.

Jackson, J., M. Donovan, K. Cramer, and V. Lam, editors. 2014. Status and Trends of Caribbean Coral Reefs: 1970-2012. Global Coral Reef Monitoring Network, IUCN, Gland, Switzerland.

Janiak, D. S., R. W. Osman, C. J. Freeman, V. J. Paul, Q. Sites, and Q. Samples. 2018. Artificial structures versus mangrove prop roots: a general comparison of epifaunal communities within the Indian River Lagoon, Florida, USA. Marine Ecology Progress Series 607:85–98.

Johnson, C. N., A. Balmford, B. W. Brook, J. C. Buettel, M. Galetti, L. Guangchun, and J. M. Wilmshurst. 2017. Biodiversity losses and conservation responses in the Anthropocene. Science 356:270–275.

Kathiresan, K., and B. L. Bingham. 2001. Biology of mangroves and mangrove ecosystems. Advances in Marine Biology 40:81–251.

Keppel, G., and G. W. Wardell-Johnson. 2012. Refugia: keys to climate change management. Global Change Biology 18:2389–2391.

Knowlton, N., R. E. Brainard, R. Fisher, M. Moews, L. Plaisance, and M. J. Caley. 2010. Coral reef biodiversity. Pages 65–78 *in* A. D. McIntyre, editor. Life in the World's Oceans: Diversity, Distribution, and Abundance. Blackwell Publishing Ltd, West Sussex, United Kingdom.

van de Koppel, J., T. van der Heide, A. H. Altieri, B. K. Eriksson, T. J. Bouma, H. Olff, and B. R. Silliman. 2015. Long-distance interactions regulate the structure and resilience of coastal ecosystems. Annual Review of Marine Science 7:139–158.

Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D. A. Wardle. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science (New York, N.Y.) 294:804–8.

Luo, Y. Y., C. Not, and S. Cannicci. 2021. Mangroves as unique but understudied traps for anthropogenic marine debris: A review of present information and the way forward. Environmental Pollution 271:116291.

MacDonald, J. A., T. Glover, and J. S. Weis. 2008. The impact of mangrove prop-root epibionts on juvenile reef fishes: A field experiment using artificial roots and epifauna. Estuaries and Coasts 31:981–993.

MacDonald, J. A., and J. S. Weis. 2013. Fish community features correlate with prop root epibionts in Caribbean mangroves. Journal of Experimental Marine Biology and Ecology 441:90–98.

Menéndez, P., I. J. Losada, S. Torres-Ortega, S. Narayan, and M. W. Beck. 2020. The global flood protection benefits of mangroves. Scientific Reports 10:1–11.

Miloslavich, P., J. M. Díaz, E. Klein, J. J. Alvarado, C. Díaz, J. Gobin, E. Escobar-Briones, J. J. Cruz-Motta, E. Weil, J. Cortés, A. C. Bastidas, R. Robertson, F. Zapata, A. Martín, J. Castillo, A. Kazandjian, and M. Ortiz. 2010. Marine biodiversity in the caribbean: Regional estimates and distribution patterns. PLoS ONE 5(8):e11916.

Mokany, K., S. Ferrier, T. D. Harwood, C. Ware, M. Di Marco, H. S. Grantham, O. Venter, A. J. Hoskins, and J. E. M. Watson. 2020. Reconciling global priorities for conserving biodiversity habitat. Proceedings of the National Academy of Sciences of the United States of America 117:9906–9911.

Nagelkerken, I., editor. 2009. Ecological Connectivity among Tropical Coastal Ecosystems. Springer, Dordrecht.

Nagelkerken, I., A. M. De Schryver, M. C. Verweij, F. Dahdouh-Guebas, G. van der Velde, and N. Koedam. 2010. Differences in root architecture influence attraction of fishes to mangroves: A field experiment mimicking roots of different length, orientation, and complexity. Journal of Experimental Marine Biology and Ecology 396:27–34.

Nanjo, K., H. Kohno, Y. Nakamura, M. Horinouchi, and M. Sano. 2014. Effects of mangrove structure on fish distribution patterns and predation risks. Journal of Experimental Marine Biology and Ecology 461:216-225.

Oliveira, M. De. 2020. Marginal reef paradox: A possible refuge from environmental changes? Ocean and Coastal Management 185:1–8.

Rebolledo, A. P., I. S. Wehrtmann, D. L. Felder, and F. L. Mantelatto. 2014. Embryo production in the sponge-dwelling snapping shrimp *Synalpheus apioceros* (Decapoda, Alpheidae) from Bocas del Toro, Panama. ZooKeys 238:227–238.

Rogers, A., and P. J. Mumby. 2019. Mangroves reduce the vulnerability of coral reef fisheries to habitat degradation. PLOS Biology 17:e3000510.

Rogers, C. S. 2009. High diversity and abundance of scleractinian corals growing on and near mangrove prop roots, St. John, US Virgin Islands. Coral Reefs 28:909.

Rogers, C. S., and J. J. Herlan. 2012. Life on the edge: corals in mangroves and climate change. Pages 9–13 Proceedings of the 12th International Coral Reef Symposium. Cairns, Australia.

Rützler, K. 1995. Low-tide exposure of sponges in a Caribbean mangrove community. Marine Ecology 16:165–179.

Sangil, C., and H. M. Guzman. 2016. Macroalgal communities on multi-stressed coral reefs in the Caribbean: Long-term changes, spatial variations, and relationships with environmental variables. Journal of Sea Research 117:7–19.

Schutte, V., and J. Byers. 2017. Variation in a simple trait of mangrove roots governs predator access to, and assemblage composition of, epibiotic sponges. Marine Ecology Progress Series 573:15–23.

Schutte, V. G. W., E. R. Selig, and J. F. Bruno. 2010. Regional spatio-temporal trends in Caribbean coral reef benthic communities. Marine Ecology Progress Series 402:115–122.

Seemann, J., A. Yingst, R. D. Stuart-Smith, G. J. Edgar, and A. H. Altieri. 2018. The importance of sponges and mangroves in supporting fish communities on degraded coral reefs in Caribbean Panama. PeerJ 2018:1–22.

Spalding, M. D., M. Kainuma, and L. Collins. 2010. World Atlas of Mangroves. Taylor & Francis Group.

Spalding, M., M. D. Spalding, C. Ravilious, and E. P. Green. 2001. World Atlas of Coral Reefs. University of California Press, London, England.

Thomas, N., R. Lucas, P. Bunting, A. Hardy, A. Rosenqvist, and M. Simard. 2017. Distribution and drivers of global mangrove forest change, 1996-2010. PLoS ONE 12.

Tkachenko, K. S. 2017. Coral reefs in the face of ecological threats of the 21st century. Biology Bulletin Reviews 7:64–83.

Turschwell, M. P., V. J. D. Tulloch, M. Sievers, R. M. Pearson, D. A. Andradi-brown, G. N. Ahmadia, R. M. Connolly, D. Bryan-brown, S. Lopez-marcano, M. Fernanda, and C. J. Brown. 2020. Multi-scale estimation of the effects of pressures and drivers on mangrove forest loss globally. Biological Conservation 247:108637.

UNEP-CEP. 2020. Regional strategy and action plan for the valuation, protection and/or restoration of key marine habitats in the wider Caribbean 2021 – 2030. Technical Report:1–73.

Valiela, I., J. L. Bowen, and J. K. York. 2001. Mangrove forests: One of the world's threatened major tropical environments. BioScience 51:807–815.

Vaughn, C. C., and T. J. Hoellein. 2018. Bivalve impacts in freshwater and marine ecosystems. Annual Review of Ecology, Evolution, and Systematics 49:183–208.

Vorsatz, L. D., P. Pattrick, and F. Porri. 2021. Quantifying the in situ 3-dimensional structural complexity of mangrove tree root systems: Biotic and abiotic implications at the microhabitat scale. Ecological Indicators 121:107154.

Vozzo, M. L., and M. J. Bishop. 2019. Co-occurring secondary foundation species have distinct effects on the recruitment and survival of associated organisms. Marine Ecology Progress Series 608:61–72.

Worthington, T. A., D. A. Andradi-Brown, R. Bhargava, C. Buelow, P. Bunting, C. Duncan, L. Fatoyinbo, D. A. Friess, L. Goldberg, L. Hilarides, D. Lagomasino, E. Landis, K. Longley-

Wood, C. E. Lovelock, N. J. Murray, S. Narayan, A. Rosenqvist, M. Sievers, M. Simard, N. Thomas, P. van Eijk, C. Zganjar, and M. Spalding. 2020. Harnessing big data to support the conservation and rehabilitation of mangrove forests globally. One Earth 2:429–443.

Wright, J. L. 2019. The effects of coral presence among Red Mangrove (*Rhizophora mangle*) prop roots on Caribbean fish communities. Thesis. University of Miami, Coral Gables, Florida, United States of America.

Yates, K. K., C. S. Rogers, J. J. Herlan, G. R. Brooks, N. A. Smiley, and R. A. Larson. 2014. Diverse coral communities in mangrove habitats suggest a novel refuge from climate change. Biogeosciences 11:4321–4337.

Zhao, Q., F. Stephenson, C. Lundquist, K. Kaschner, D. Jayathilake, and M. J. Costello. 2020. Where marine protected areas would best represent 30% of ocean biodiversity. Biological Conservation 244:108536.

Appendix A: Supplementary materials for Chapter 1

A.1 Supplementary tables

Table A1 Coral species observed growing within coexisting mangrove-coral (CMC) habitats. Bolded coral species are the most reported in the literature, having been reported in 5-7 studies at this point. [1] Panama, [2] Cuba, [3] Puerto Rico, [4] Florida, [5] U.S. Virgin Islands, [6] Belize, [7] Northern Red Sea, [8] Seychelles, [9] Sulawesi [10] New Caledonia, [11] Australia. *recorded as *Acropora formosa* prior to name change.

Coral Species	Canopy[1]	Edge[1-6]	Channel[2,4,6,11]	Lagoon[6-11]
Acropora aspera				X
Acropora austera				X
Acropora cervicornis		X		X
Acropora cf. _nobilis_				X
Acropora cf. _pulchra_				X
Acropora cf. _valida_				X
Acropora cytherea				X
Acropora gemmifera				X
Acropora humilis				X
Acropora intermedia				X
Acropora kirstyae				X
Acropora microphthalma				X
Acropora millepora				X
Acropora muricata*				X
Acropora palmata		X		
Acropora spp.				X
Acropora tenuis				X
Acropora vaughani				X
Agaricia agaricites	X	X		
Agaricia fragilis	X	X		
Agaricia grahamae		X		
Agaricia humilis	X			
Agaricia lamarcki	X	X		

***Agaricia* spp.**		X		
Agaricia tenuifolia	X	X		X
Astreopora gracilis				X
Cladocora arbuscula		X		
Coelastrea aspera				X
Colpophyllia natans	X	X		
***Cyphastrea* spp.**			X	X
Dendrogyra cylindrus		X		
Dichocoenia stokesi	X	X	X	
Diploria labyrinthiformis	X	X		
Euphyllia cristata				X
Eusmilia fastigiata	X	X		
Favia fragum	X	X	X	
***Favia* spp.**				X
Favites abdita				
***Favites* spp.**				X
Fungia danai				X
Fungia fungites				X
***Fungia* spp.**				X
Galaxea fascicularis				X
Goniastrea edwardsi				X
Goniastrea favulus				X
***Goniastrea* spp.**				X
Helioseris cucullata	X			
Heliopora spp.				X
Isophyllia rigida	X			
Isophyllia sinuosa	X			
***Leptastrea* spp.**			X	
Lobophyllia* cf. *hemprichii				X
Lobophyllia corymbosa				X
Madracis auretenra			X	

Manicina areolata	X	X		X
Meandrina meandrites		X		
Millepora alcicornis	X	X		X
Millepora complanata	X	X		X
***Millepora* spp.**		X		X
Montastraea cavernosa	X	X	X	X
Montipora digitata				X
Montipora turtlensis				X
Mussa angulosa	X	X		
Mycetophyllia aliciae	X			
***Mycetophyllia* spp.**		X	X	
Oculina diffusa		X		
Orbicella annularis		X		X
Orbicella faveolata	X	X	X	
Orbicella franksi		X		
***Oulophyllia* spp.**				X
Pavona* cf. *duerdeni				X
Pavona decussata				X
***Pavona* spp.**				X
Pavona varians				X
Phyllangia americana	X	X		
Platygyra sinensis				X
Pocillopora acuta				X
Pocillopora bulbosa				X
Pocillopora damicornis				X
Pocillopora verrucosa				X
Porites astreoides	X	X	X	X
Porites attenuata				X
Porites colonensis			X	
Porites cylindrica				X
Porites divaricata	X	X	X	

Porites furcata	X	X	X	
Porites lobata				X
Porites lutea				X
Porites porites		X	X	X
Pseudodiploria clivosa	X	X		
Pseudodiploria strigosa	X	X	X	
Scolymia cubensis	X	X		
Scolymia lacera	X	X		
***Seriatopora* spp.**				X
Siderastrea radians	X	X	X	
Siderastrea siderea	X	X	X	
Solenastrea bournoni		X	X	
Stephanocoenia intersepta	X	X	X	
***Stephanocoenia* spp.**			X	
Stylophora pistilata				X
Tubastrea aurea		X		
Tubastrea coccinea		X		
Turbinaria mesenterina				X
Turbinaria reniformis				X
Coral species observed by CMC habitat	**31**	**42**	**19**	**62**

Table A2 Mangrove-coral and adjacent reef habitats with corresponding coral richness and characteristic abiotic data. Values given as mean ± SE except pH which is mean and range values and photosynthetically active radiation (PAR) which is mean ± SE and maximum value between peak daylight hours 11 am to 1 pm. NR = not reported. *estimated from figure in text †reported as daily light integral. Superscript number by the habitat type indicates which study these data correspond to: [1] This current study, [2] Kellogg et al. 2020, [3] Yates et al. 2014, [4] Camp et al. 2019, [5] Camp et al. 2016, [6] Camp et al. 2017.

Habitat type	Location	Date	Coral richness	Water depth (m)	pH (mean, range)	Temperature (°C)	PAR (µmol m-2 s-1)	Dissolved oxygen (mg/L)	Salinity (PSU)
Canopy CMC[1]	Bocas del Toro, Panama	September 2019	31	0.30 ± 0.00	7.81, 7.74-7.93	28.46 ± 0.01	NR	3.74 ± 0.03	33.20 ± 0.01
Canopy CMC[1]	Bocas del Toro, Panama	July 2018	31	NR	NR	28.6 ± 0.01	NR	NR	NR
Channel CMC[2]	Upper Keys, Florida	October 2019	4	1.48	7.89, 7.78-7.93	28	NR	4.54	36.39
Channel CMC[2]	Lower Keys, Florida	January 2020	1	0.39	8.25, 8.09-8.40	20	NR	5.37	36.34
Edge CMC[2]	Upper Keys, Florida	October 2019	2	0.44	7.98, 7.96-8.00	27.77	NR	5.71	36.84
Edge CMC[2]	Lower Keys, Florida	January 2020	3	0.13	8.41, 8.07-8.70	22.04	NR	7.22	36.39
Edge CMC[1]	Bocas del Toro, Panama	July 2018	22	NR	NR	28.8 ± 0.01	203 ± 80, 838	NR	NR
Edge CMC[1]	Bocas del Toro, Panama	September 2019	22	0.50 ± 0.00	8.10, 8.04-8.17	28.71 ± 0.00	225 ± 28, 323	5.33 ± 0.01	33.67 ± 0.01
Edge CMC[3]	Otter Creek, USVI	November 2010	30	1 m	8.04, 8.01-8.05	27.89 ± 0.05	117 ± 7, 221	5.98 ± 0.1	32.87 ± 0.02
Edge CMC[3]	Water Creek, USVI	November 2010	26	1 m	8.00, 7.97-8.02	27.34 ± 0.09	120 ± 11, 930	6.12 ± 0.12	32.16 ± 0.1

Edge CMC[3]	Princess Bay, USVI	November 2010	19	1 m	7.99, 7.96-8.02	27.4 ± 0.12	NR	5.57 ± 0.32	32.8 ± 0.59
Edge CMC[3]	Otter Creek, USVI	July 2011	30	1 m	7.97, 7.95-7.98	27.89 ± 0.05	436 ± 25, 1221	5.98 ± 0.08	35.7 ± 0.05
Edge CMC[3]	Water Creek, USVI	July 2011	26	1 m	7.97, 7.92-7.99	29.1 ± 0.12	466 ± 30, 1713	6.05 ± 0.11	35.44 ± 0.07
Edge CMC[3]	Princess Bay, USVI	July 2011	19	1 m	7.98, 7.97-7.99	29.45 ± 0.05	NR	5.61 ± 0.06	35.6 ± 0.6
Edge CMC[3]	Otter Creek, USVI	July 2012	30	1 m	8.07, 8.05-8.08	29.35 ± 0.06	533 ± 35, 1143	6.22 ± 0.04	33.77 ± 0.14
Edge CMC[3]	Water Creek, USVI	July 2012	26	1 m	8.06,8.04-8.08	29.5 ± 0.25	NR	NR	34.74 ± 0.02
Edge CMC[3]	Princess Bay, USVI	July 2012	19	1 m	8.02*	29.64 ± 0.21	NR	6.2 ± 0.13	34.61 ± 0.01
Lagoon CMC[4]	Woody Isles, Great Barrier Reef	June 2017	12	1 m	7.879, 7.68-8.08	22.6 ± 0.008	NR	3.91 ± 0.015	33.9 ± 0.013
Lagoon CMC[4]	Howick Island, Great Barrier Reef	June 2017	29	NR	7.84	23.5 ± 0.014	NR	4.07 ± 0.015	35.3 ± 0.018
Lagoon CMC[4]	Woody Isles, Great Barrier Reef	Feb-April 2018	NR	1 m	7.76, 7.48-7.98	28.3 ± 0.006	NR	3.02 ± 0.007	32.5 ± 0.015
Lagoon CMC[5]	Hoga, Indonesia	August 2014	9	2-4 m range	8.06 ± 0.03	27.5 ± 0.09	17 ± 0.12†	NR	34.5 ± 0.15
Lagoon CMC[5]	Curieuse, Seychelles	April 2014	7	2-4 m range	8.00 ± 0.01	30.7 ± 0.16	17 ± 0.07†	NR	35.5 ± 0.05
Lagoon CMC[6]	Bourake, New Caledonia	February 2016	18	1-2 m range	7.62, 7.24-7.91	30.9 ± 0.90	NR	4.38 ± 0.08	36.2 ± 0.07
Lagoon CMC[6]	Bourake, New Caledonia	March 2016	18	1-2 m range	7.55, 7.31-7.87	28.4 ± 0.06	NR	4.47 ± 0.06	34.4 ± 0.02

Lagoon CMC[6]	Inner bay, Bourake, New Caledonia	May 2016	NR	1 m	7.76, 7.44-8.01	NR	NR	NR	NR
Lagoon CMC[6]	Lagoon entrance, Bourake, New Caledonia	May 2016	NR	1 m	7.73, 7.45-7.73	NR	NR	NR	NR
Mangrove without coral[3]	Otter Creek, USVI	November 2010	0	1 m	8.03, 8.00-8.09	27.79 ± 0.1	144 ± 11, 693	5.97 ± 0.07	32.9 ± 0
Mangrove without coral[3]	Water Creek, USVI	November 2010	0	1 m	7.96, 7.89-8.03	27.47 ± 0.18	NR	5.58 ± 0.24	32.17 ± 0.11
Mangrove without coral[3]	Princess Bay, USVI	November 2010	0	1 m	7.97, 7.95-8.02	27.41 ± 0.15	NR	5.33 ± 0.27	32.93 ± 0.49
Mangrove without coral[3]	Otter Creek, USVI	July 2011	0	1 m	7.96, 7.92-7.99	27.79 ± 0.1	148 ± 5, 647	5.82 ± 0.23	35.7 ± 0.09
Mangrove without coral[3]	Water Creek, USVI	July 2011	0	1 m	7.92, 7.77-7.98	28.87 ± 0.21	NR	5.67 ± 0.23	35.4 ± 0.13
Mangrove without coral[3]	Princess Bay, USVI	July 2011	0	1 m	7.95, 7.92-7.98	29.94 ± 0.3	NR	5.6 ± 0.19	36.03 ± 0.17
Mangrove without coral[3]	Otter Creek, USVI	July 2012	0	1 m	8.04, 8.01-8.07	29.31 ± 0.09	229 ± 12, 650	6.13 ± 0.06	33.8 ± 0.14
Mangrove without coral[3]	Water Creek, USVI	July 2012	0	1 m	8.02, 7.99-8.04	28.9 ± 0.26	NR	NR	34.86 ± 0.03
Mangrove without coral[3]	Princess Bay, USVI	July 2012	0	1 m	7.99*	29.63 ± 0.31	NR	5.87 ± 0.16	34.67 ± 0.02
Reef[4]	Woody Isles, Great Barrier Reef	June 2017	NR	NR	8.08	22.3 ± 0.036	NR	6.51 ± 0.018	35.3 ± 0.020
Reef[5]	Hoga, Indonesia	August 2014	NR	NR	8.121 ± 0.01	27.4 ± 0.02	21.18 ± 0.27†	6.83 ± 0.017	35.0 ± 0.02
Reef[5]	Curieuse, Seychelles	April 2014	NR	NR	8.122 ± 0.01	29.2 ± 0.02	20.79 ± 0.17†	NR	35.5 ± 0.03

Reef[6]	Bourake, New Caledonia	February 2016	46	1-3 m range	8.03, 7.97-8.08	29.0 ± 0.03	NR	6.48 ± 0.04	35.4 ± 0.02
Reef[6]	Bourake, New Caledonia	March 2016	46	1-3 m range	7.94, 7.79-8.05	28.1 ± 0.03	NR	6.38 ± 0.04	34.2 ± 0.03
Reef[3]	Otter Creek, USVI	November 2010	NR	1 m	8.05, 8.03-8.11	27.84 ± 0.1	1293 ± 77, 2230	6.11 ± 0.04	32.87 ± 0.02
Reef[3]	Otter Creek, USVI	July 2011	NR	1 m	7.97, 7.94-8.00	27.84 ± 0.1	1651 ± 65, 2520	5.85 ± 0.14	35.77 ± 0.02
Reef[3]	Otter Creek, USVI	July 2012	NR	1 m	8.07, 8.07-8.09	29.41 ± 0.06	1975 ± 46, 3131	6.28 ± 0.04	33.77 ± 0.14
Reef[1]	Bocas del Toro, Panama Reef Flat	July 2018	NR	NR	NR	29.2 ± 0.01	729 ± 118, 1311	NR	NR
Reef[1]	Bocas del Toro, Panama Reef Flat	September 2019	14	0.74 ± 0.00	8.12, 8.06-8.16	28.83 ± 0.01	1205 ± 104, 1833	5.56 ± 0.01	33.83 ± 0.01
Reef[1]	Bocas del Toro, Panama Reef Slope	September 2019	23	2.07 ± 0.00	8.09, 8.02-8.12	29.43 ± 0.01		4.73 ± 0.03	35.03 ± 0.02

Table A3 Summary of water chemistry for coexisting mangrove-coral (CMC) habitats and adjacent reefs from current literature. All values given as mean ± SE except. pCO$_2$ = partial pressure of carbon dioxide HCO$_3$ = bicarbonate, CO$_3^{2-}$ = carbonate ion, Ω_{arg} = aragonite mineral saturation state, and DIC = dissolved inorganic carbon. NR = not reported. Superscript number by the habitat type indicates which study these data correspond to: [1] Yates et al. 2014, [2] Camp et al. 2019, [3] Camp et al. 2016, [4] Camp et al. 2017.

Habitat type	Location	Date	Alkalinity	pCO2	HCO3-	CO32-	Ωarg	DIC [¬µmol/kg]
Edge CMC[1]	Otter Creek, USVI	November 2010	2280.27 ± 2.9	417.61 ± 5.75	NR	223.86 ± 1.93	3.66 ± 0.04	1958.66 ± 5.87
Edge CMC[1]	Water Creek, USVI	November 2010	2233.27 ± 4.99	459.73 ± 10.96	NR	199.07 ± 3.55	3.24 ± 0.06	1962.93 ± 11.46
Edge CMC[1]	Princess Bay, USVI	November 2010	2219.79 ± 36.05	467.31 ± 14.84	NR	196.79 ± 4.91	3.19 ± 0.07	1937.89 ± 26.53
Edge CMC[1]	Otter Creek, USVI	July 2011	2325.93 ± 2.97	476.41 ± 8.86	NR	211.23 ± 2.48	3.4 ± 0.04	2026.7 ± 3.53
Edge CMC[1]	Water Creek, USVI	July 2011	2318.11 ± 2.37	494.99 ± 12.14	NR	211.04 ± 3.38	3.41 ± 0.06	2026.04 ± 6.46
Edge CMC[1]	Princess Bay, USVI	July 2011	2327.25 ± 5.15	477.3 ± 9	NR	219.4 ± 5.1	3.55 ± 0.05	2007.55 ± 0.55
Edge CMC[1]	Otter Creek, USVI	July 2012	2283.17 ± 0.77	406.07 ± 2.17	NR	229.5 ± 0.62	3.75 ± 0.01	1961.54 ± 1.29
Edge CMC[1]	Water Creek, USVI	July 2012	2284.3 ± 0.85	417.07 ± 5.62	NR	229.2 ± 2.29	3.74 ± 0.04	1961.33 ± 3.93
Edge CMC[1]	Princess Bay, USVI	July 2012	2283.91 ± 1.95	418.87 ± 3.93	NR	229 ± 2.11	3.76 ± 0.04	1961.51 ± 5.1
Lagoon CMC[2]	Woody Isles, Great Barrier Reef	June 2017	2279.0 ± 11.1	655.6 ± 75.3	1913.0 ± 28.1	147.4 ± 13.3	2.3 ± 0.2	NR

Lagoon CMC[2]	Howick Island, Great Barrier Reef	June 2017	NR	NR	NR	NR	NR	NR
Lagoon CMC[2]	Woody Isles, Great Barrier Reef	Feb-April 2018	2148.6 ± 14.9	860.0 ± 0.2	1796.0 ± 16.9	141.4 ± 10.3	2.3 ± 0.2	NR
Lagoon CMC[3]	Hoga, Indonesia	August 2014	2093.9 ± 0.04	333 ± 12.07	NR	NR	3.6 ± 0.06	NR
Lagoon CMC[4]	Bourake, New Caledonia	February 2016	2268 ± 5.48	1399 ± 67.89	1398 ± 10.58	124 ± 4.27	2.02 ± 0.07	NR
Lagoon CMC[4]	Bourake, New Caledonia	March 2016	2272 ± 7.41	1531 ± 23.59	2048 ± 3.10	91 ± 1.25	1.47 ± 0.02	NR
Lagoon CMC[4]	Bourake, New Caledonia	May 2016	2312.3 ± 30.20	947 ± 31.4	1980.4 ± 12.51	135.7 ± 2.95	2.1 ± 0.05	NR
Lagoon CMC[4]	Bourake, New Caledonia	May 2016	2297.6 ± 29.07	1010 ± 32.90	1982.2 ± 12.51	126.03 ± 2.95	1.98 ± 0.04	NR
Lagoon CMC[3]	Curieuse, Seychelles	April 2014	1955.7 ± 1.14	372 ± 19.30	NR	NR	3.3 ± 0.13	NR
Non-CMC[1]	Otter Creek, USVI	November 2010	2285.64 ± 3.59	419.07 ± 12.68	NR	224.04 ± 4.32	3.64 ± 0.07	1977.9 ± 8.16
Non-CMC[1]	Water Creek, USVI	November 2010	2232.94 ± 14.97	514 ± 27.74	NR	186.8 ± 6.25	3.04 ± 0.1	1963.31 ± 21.59
Non-CMC[1]	Princess Bay, USVI	November 2010	2209.57 ± 48.89	484.16 ± 13.26	NR	191.36 ± 7.22	3.11 ± 0.12	1939.54 ± 36.66
Non-CMC[1]	Otter Creek, USVI	July 2011	2329.89 ± 3.07	516.4 ± 18.25	NR	201.06 ± 4.9	3.23 ± 0.08	2050.14 ± 7.66
Non-CMC[1]	Water Creek, USVI	July 2011	2331.73 ± 3.61	569.36 ± 45.37	NR	195.96 ± 8.79	3.16 ± 0.14	2051.27 ± 13.53
Non-CMC[1]	Princess Bay, USVI	July 2011	2343.19 ± 6.21	523.01 ± 12.87	NR	213.57 ± 4.63	3.46 ± 0.08	2027.21 ± 10.26
Non-CMC[1]	Otter Creek, USVI	July 2012	2284.37 ± 0.81	428.69 ± 3.51	NR	222.07 ± 1.15	3.63 ± 0.02	1974.23 ± 2.09

Non-CMC[1]	Water Creek, USVI	July 2012	2291.41 ± 2.46	462.01 ± 13.09	NR	213.7 ± 3.87	3.47 ± 0.07	1992.67 ± 8.5
Non-CMC[1]	Princess Bay, USVI	July 2012	2291.11 ± 3.63	479.5 ± 16.26	NR	212.49 ± 5.51	3.44 ± 0.09	1994.91 ± 8.4
Reef[4]	Bourake, New Caledonia	February 2016	2306 ± 7.13	413 ± 2.91	1730 ± 2.85	233 ± 1.14	3.76 ± 0.02	NR
Reef[4]	Bourake, New Caledonia	March 2016	2246 ± 5.84	527 ± 3.51	1788 ± 2.26	185 ± 0.90	2.99 ± 0.02	NR

Table A4 Multiple comparisons of means of average mid-day temperature among distances from the reef. Estimate gives the difference between each treatment in the comparison. Significant p-values are in bold.

Distance from Reef Comparison	Estimate	Standard Error	z value	P value
Mangrove edge - Reef flat	-0.443	0.218	-2.033	0.394
Mangrove canopy 2m - Reef flat	-0.846	0.218	-3.881	**0.002**
Mangrove canopy 6m - Reef flat	-1.133	0.218	-5.201	< **0.001**
Mangrove canopy 8m - Reef flat	-1.436	0.218	-6.591	< **0.001**
Mangrove canopy 12m - Reef flat	-1.347	0.218	-6.182	< **0.001**
Mangrove canopy 14m - Reef flat	-1.355	0.218	-6.218	< **0.001**
Mangrove canopy 2m - Mangrove edge	-0.403	0.218	-1.848	0.515
Mangrove canopy 6m - Mangrove edge	-0.690	0.218	-3.169	**0.026**
Mangrove canopy 8m - Mangrove edge	-0.993	0.218	-4.559	< **0.001**
Mangrove canopy 12m - Mangrove edge	-0.904	0.218	-4.149	< **0.001**
Mangrove canopy 14m - Mangrove edge	-0.912	0.218	-4.185	< **0.001**
Mangrove canopy 6m - Mangrove canopy 2m	-0.288	0.218	-1.320	0.843
Mangrove canopy 8m - Mangrove canopy 2m	-0.591	0.218	-2.711	0.096
Mangrove canopy 12m - Mangrove canopy 2m	-0.501	0.218	-2.301	0.244
Mangrove canopy 14m - Mangrove canopy 2m	-0.509	0.218	-2.337	0.226
Mangrove canopy 8m - Mangrove canopy 6m	-0.303	0.218	-1.390	0.807
Mangrove canopy 12m - Mangrove canopy 6m	-0.214	0.218	-0.981	0.958
Mangrove canopy 14m - Mangrove canopy 6m	-0.222	0.218	-1.017	0.950
Mangrove canopy 12m - Mangrove canopy 8m	0.089	0.218	0.410	1.000
Mangrove canopy 14m - Mangrove canopy 8m	0.081	0.218	0.373	1.000
Mangrove canopy 14m - Mangrove canopy 12m	-0.008	0.218	-0.036	1.000

Appendix B: Supplementary materials for Chapter 2

B.1 Supplementary tables

Table B1 Coral species observed during mangrove and adjacent reef flat surveys in Bocas del Toro, Panama. Bolded species are found in both habitats.

Coral Species	Fuego Mangrove	Fuego Reef Flat	Sunny Mangrove	Sunny Reef Flat	Cayo Ramirez Mangrove	Cayo Ramirez Reef Flat	Combined Mangrove	Combined Reef Flat
Agaricia agaricites	**X**	**X**	X		**X**	**X**	**X**	**X**
Agaricia fragilis	**X**	**X**	X				**X**	**X**
Agaricia tenuifolia	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**
Colpophyllia natans	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**
Dichocoenia stokesi					X		X	
Favia fragum	X		X				X	
Helioseris cucullata			X				X	
Isophyllia sinuosa	X						X	
Manicina areolata	X				**X**	**X**	**X**	**X**
Millepora alcicornis		X	**X**	**X**		X	**X**	**X**
Millepora complanata	**X**	**X**					**X**	**X**
Montastraea cavernosa			X		X		X	
Mycetophyllia aliciae	X						X	
Orbicella faveolata			X				X	
Phyllangia americana					X		X	

Porites astreoides	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**
Porites divaricata	**X**	**X**		X	X		**X**	**X**
Porites furcata	**X**	**X**		X		X	**X**	**X**
Porites porites		X						X
Pseudodiploria clivosa	X						X	
Pseudodiploria strigosa	X						X	
Scolymia cubensis	X						X	
Stephanocoenia intersepta					X		X	
Siderastrea radians	X				X		X	
Siderastrea siderea	**X**	**X**	X		**X**	**X**	**X**	**X**
Total number of species:	**17**	**11**	**11**	**6**	**12**	**8**	**24**	**12**

Table B2 Light, temperature, and depth of the four experimental treatments coral were transplanted into to determine effects of habitat (e.g., mangrove vs reef) and light on coral bleaching and survival.

	Photosynthetically Active Radiation (µmol s^{-1} m^{-2})			Temperature (°C)			Depth (cm)		
Treatment	Mean ± SE	Minimum	Maximum	Mean ± SE	Minimum	Maximum	Mean ± SE	Minimum	Maximum
Mangrove High Light	571 ± 43	333.4	952.2	29.6 ± 0.0	28.2	33.0	46 ± 3	26	57
Mangrove Control	193 ± 16	101.3	322.7	29.6 ± 0.0	28.1	31.7	39 ± 2	29	52
Reef Control	1341 ± 67	869.1	1833	29.9 ± 0.0	28.4	31.8	99 ± 7	53	140
Reef Low Light	276 ± 15	109.9	468.5	29.8 ± 0.0	28.4	31.5	99 ± 8	61	144

Table B3 lsmeans pairwise comparison of mortality between coral species. Results were averaged over the levels of habitat, source, and light with 95% confidence. Contrast estimates were derived using the Sidak method and the Tukey method was used to compare estimates for p value adjustments.

	Estimate	SE	p value
CNAT - DLAB	5.440	0.591	0.000
CNAT - MCAV	1.557	0.379	0.001
CNAT - OFAV	1.515	0.356	0.000
CNAT - PAST	1.662	0.590	0.055
CNAT - PCLI	0.033	0.415	1.000
DLAB - MCAV	-3.883	0.600	0.000
DLAB - OFAV	-3.925	0.537	0.000
DLAB - PAST	-3.778	0.659	0.000
DLAB - PCLI	-5.407	0.640	0.000
MCAV - OFAV	-0.042	0.362	1.000
MCAV - PAST	0.105	0.612	1.000
MCAV - PCLI	-1.524	0.461	0.012
OFAV - PAST	0.147	0.561	1.000
OFAV - PCLI	-1.482	0.433	0.008

B.2 Supplementary figures

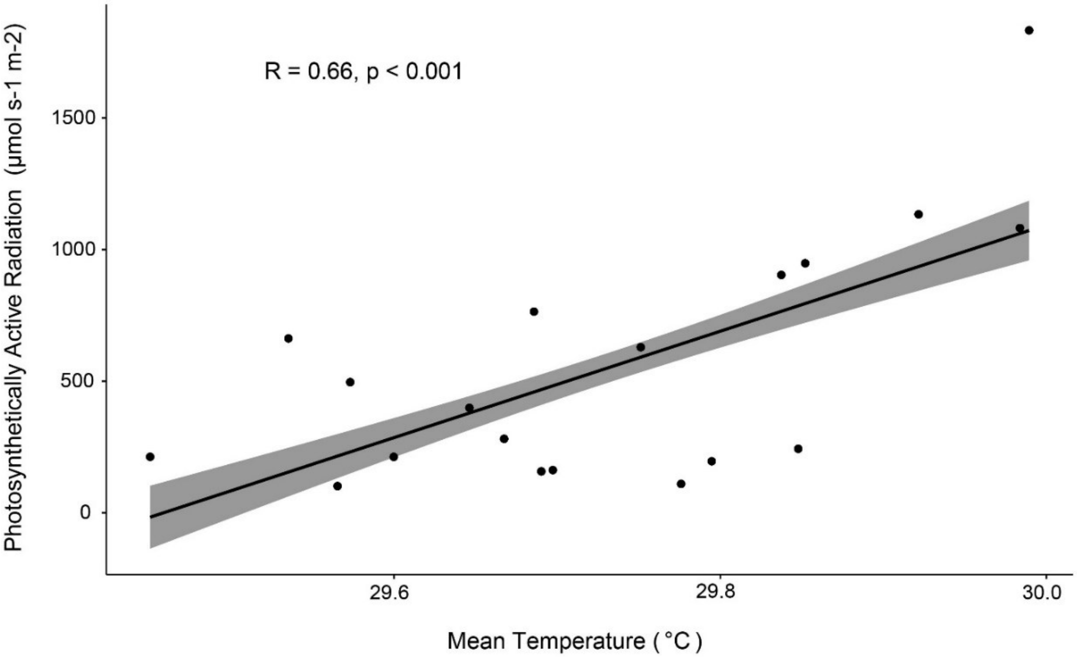

Figure B1 Linear regression between mean temperature and photosynthetically active radiation. Positive correlation ($p < 0.001$) between mean water temperature and photosynthetically active radiation (PAR) values with 95% confidence interval (shaded region).

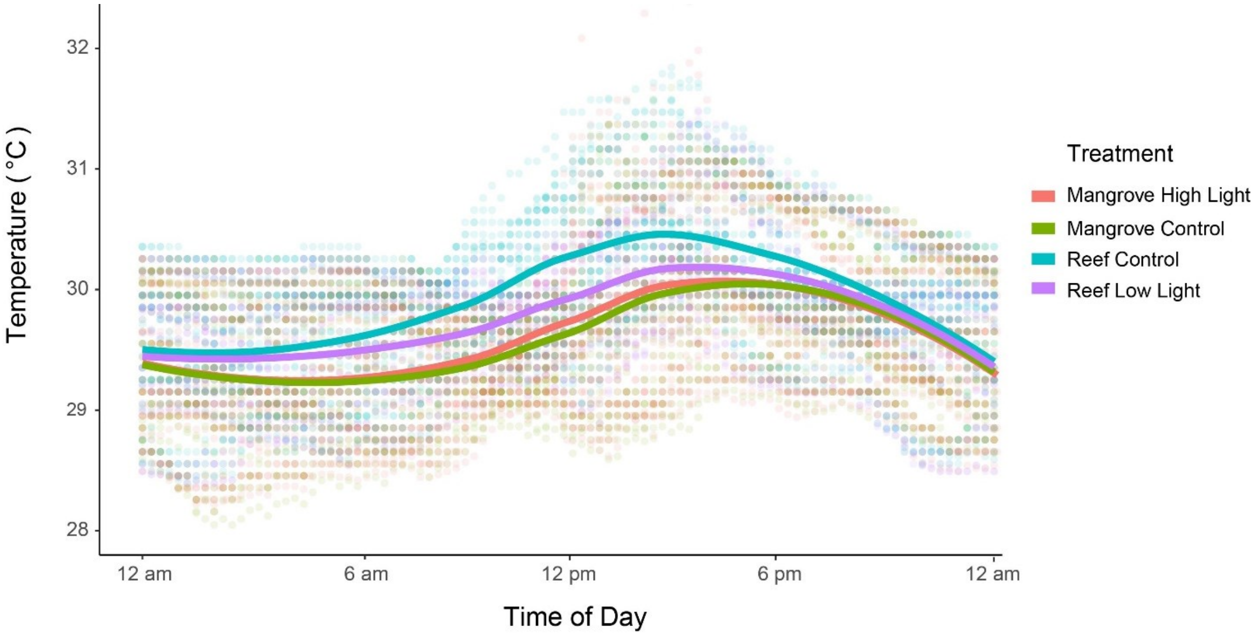

Figure B2 Daily and mean temperature fluctuations among mangrove and reef habitats. Daily temperature fluctuations (dots) and averages (splines) over one week for the four experimental treatments recorded on HOBO Pendant® 64K Data Logger with an accuracy of ± 0.53 °C.

Appendix C: Supplementary materials for Chapter 3

C.1 Supplementary tables

Table C1 Multiple comparisons of means of change in root length due to deterioration and growth among treatments. Estimate gives the difference between each treatment in the comparisons. Significant p-values are in bold.

Treatment Comparison	Estimate	Standard Error	z value	P value
PVC – Natural	10.700	6.643	1.611	0.491
Wood – Natural	-10.025	6.643	-1.509	0.557
Cut – Natural	-45.050	6.643	-6.781	**<0.001**
Scraped – Natural	-18.200	6.643	-2.740	**0.048**
Wood – PVC	-20.725	6.643	-3.120	**0.016**
Cut – PVC	-55.750	6.643	-8.392	**<0.001**
Scraped – PVC	-28.900	6.643	-4.350	**<0.001**
Cut – Wood	-35.025	6.643	-5.272	**<0.001**
Scraped – Wood	-8.175	6.643	-1.231	0.734
Scraped – Cut	26.850	6.643	4.042	**<0.001**

Table C2 Most common sessile taxa among root treatments. Most common sessile taxa (lowest taxonomic group identified), defined as presence most frequently detected, by root treatment. Numbers indicate the percentage of roots in each treatment that had that taxon present.

Phylum	Taxa	Natural	Scraped	Cut	Wood	PVC
Chordata	*Eudistoma olivaceum*	100	85	100	63	79
	Pyuridae	38	15	0	16	63
	Styela sp.	81	38	0	37	79
	Pyura sp.	69	23	0	21	26
Arthropoda	*Amphibalanus spp.*	75	77	33	79	100
Mollusca	*Brachidontes exustus complex*	44	23	17	37	58
	Isognomon alatus	69	54	83	26	53
	Crassostrea rhizophorae	88	85	67	79	84
	Pinctada imbricata	81	69	33	58	89
	Ostrea stentina	88	92	67	84	100
	Dendostrea frons	63	62	0	32	58
Rhodophyta	Turf algae	50	31	50	47	74
Porifera	*Tedania ignis*	69	23	83	47	68
	Haliclona piscaderaensis	56	38	17	53	58
	Haliclona manglaris	81	62	50	42	84
	Mycale microsigmatosa	50	69	33	63	89

Table C3 Most common mobile morphospecies among root treatments. Most frequently detected mobile morphospecies (lowest taxa group able to be identified) by root treatment. Numbers indicate the percentage of roots in each treatment that had that morphospecies present.

Phylum	Morphospecies	Natural	Scraped	Cut	Wood	PVC
Annelida	Nereididae	94	85	50	63	100
	Terrebelidae	75	23	0	26	47
Arthropoda	Amphipoda	100	69	33	84	100
	Cuapetes americanus	100	85	50	58	89
	Cirolana spp.	75	38	17	53	74
	Paracerceis spp.	88	85	67	53	89
	Majoidea	75	46	0	32	47
	Synalpheus apioceros	81	31	33	37	63
	Xanthoidea	44	23	17	47	53
Echinodermata	Ophiuroidea	75	69	33	58	84
Mollusca	*Littoraria angulifera*	63	31	50	47	47

Table C4 Bivalve and sponge biomass and richness models. Analysis of deviance results of generalized linear models examining bivalve and sponge biomass and richness response to the main effects of root treatment and site, with initial root length as a covariate. Significant p-values are in bold.

Response variable	Explanatory variables	Chi-square	Df	P value
Sponge biomass	Treatment	15.182	4	**0.004**
	Site	2.499	1	0.114
	Initial root length	0.182	1	0.670
Sponge richness	Treatment	21.251	4	**<0.001**
	Site	0.928	1	0.336
	Initial root length	0.059	1	0.809
Bivalve biomass	Treatment	26.878	4	**<0.001**
	Site	6.547	1	**0.011**
	Initial root length	0.000	1	0.997
Bivalve richness	Treatment	25.839	4	**<0.001**
	Site	0.004	1	0.953
	Initial root length	0.034	1	0.855

C.2 Supplementary figures

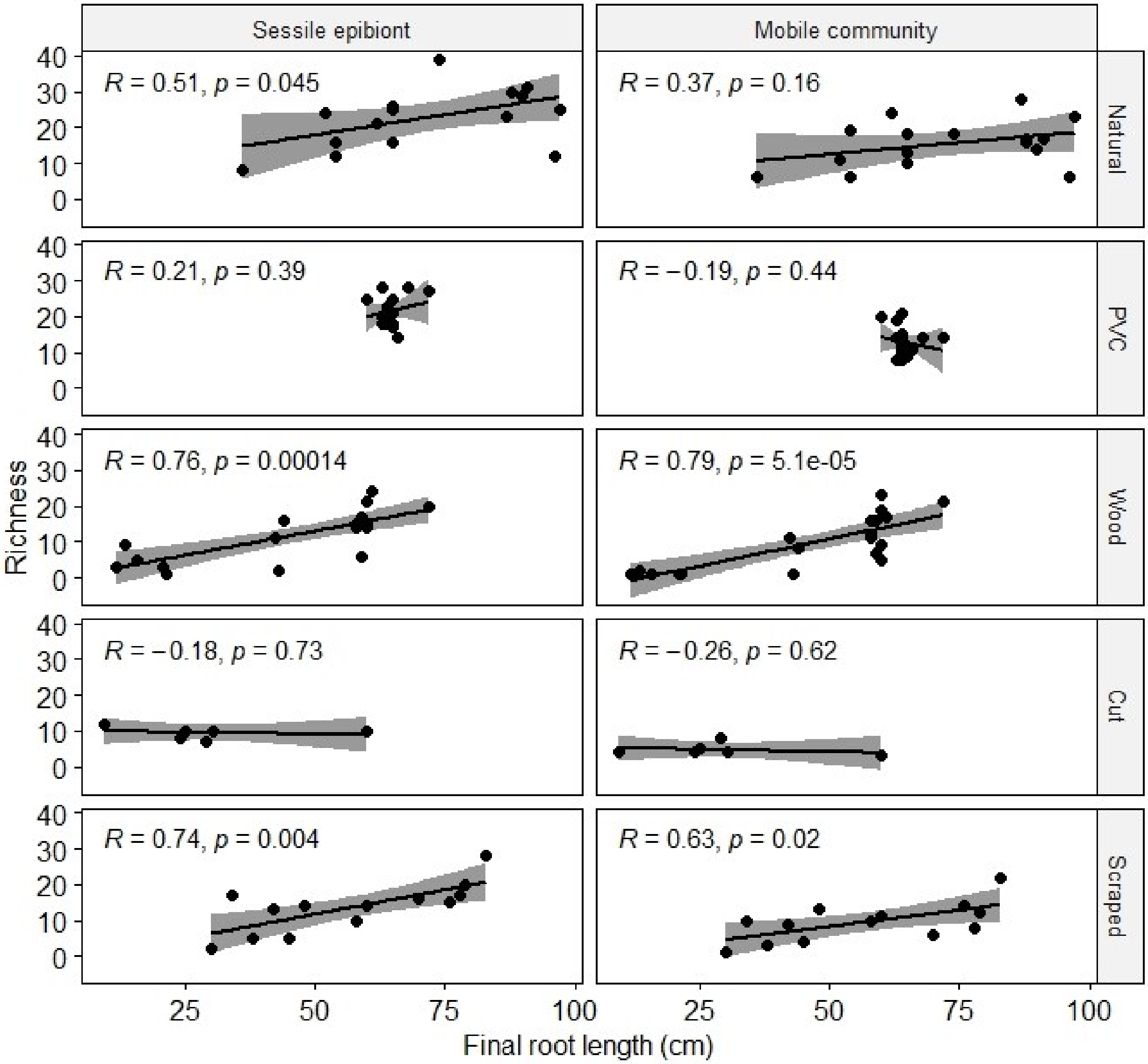

Figure C1 Linear regression between richness and final root length among root treatments. Linear regression plots with 95% confidence interval for sessile epibiont and mobile community species richness within each root treatment and correlation with final root length. r = Pearson's correlation coefficient.

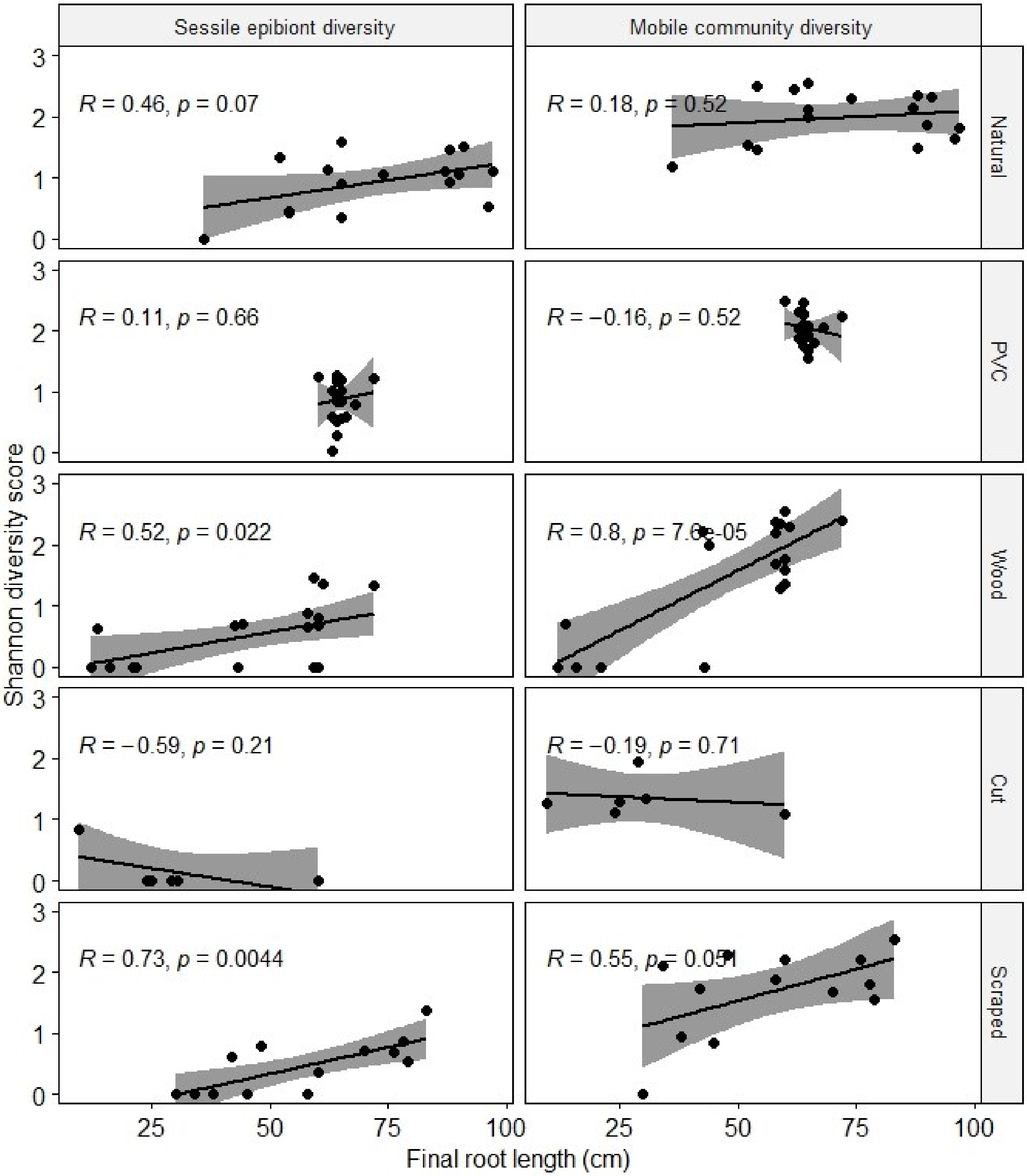

Figure C2 Linear regression between diversity and final root length among root treatments. Linear regression plots with 95% confidence interval for sessile epibiont and mobile diversity (Shannon-Wiener index) within each root treatment and correlation with final root length. r = Pearson's correlation coefficient.

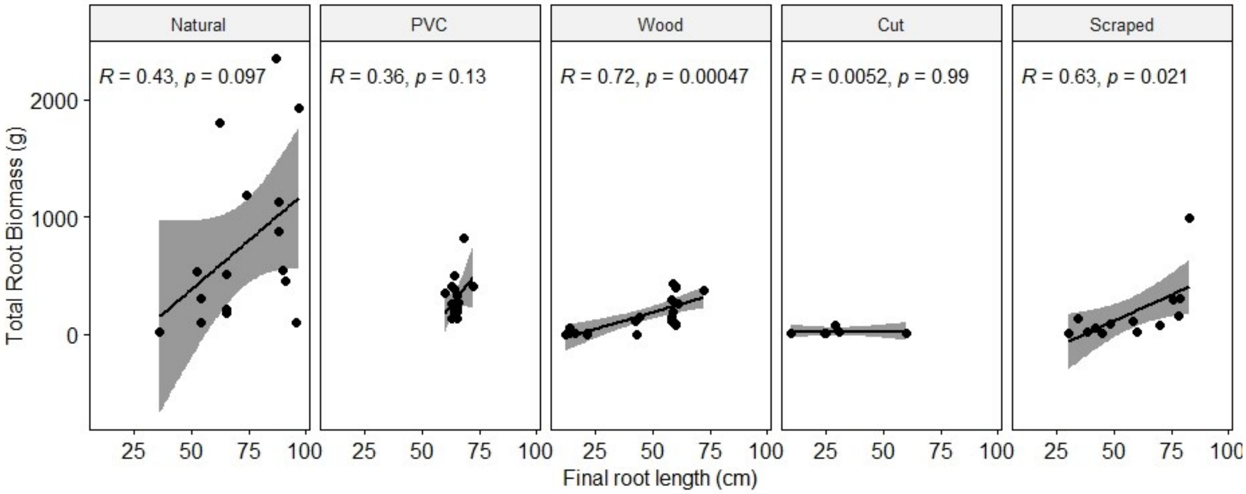

Figure C3 Linear regression of total root biomass and final root length among root treatments. Linear regression plots with 95% confidence interval for total epibiont biomass within each root treatment and correlation with final root length. r = Pearson's correlation coefficient.

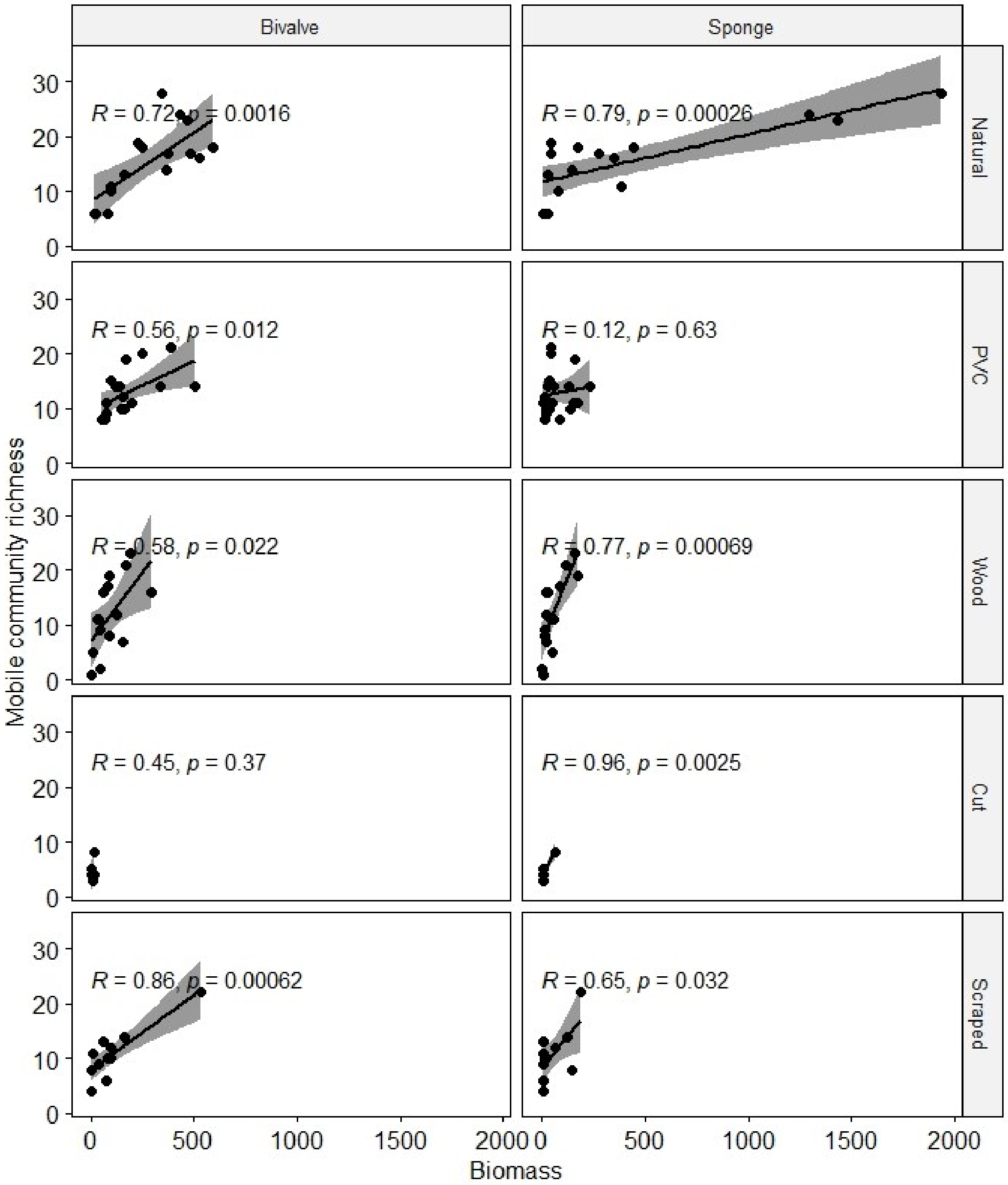

Figure C4 Linear regression between mobile richness and biomass of bivalves and sponges among root treatments. Linear regression plots with 95% confidence interval for mobile community richness within each root treatment and correlation with sponge and bivalve biomass. r = Pearson's correlation coefficient.

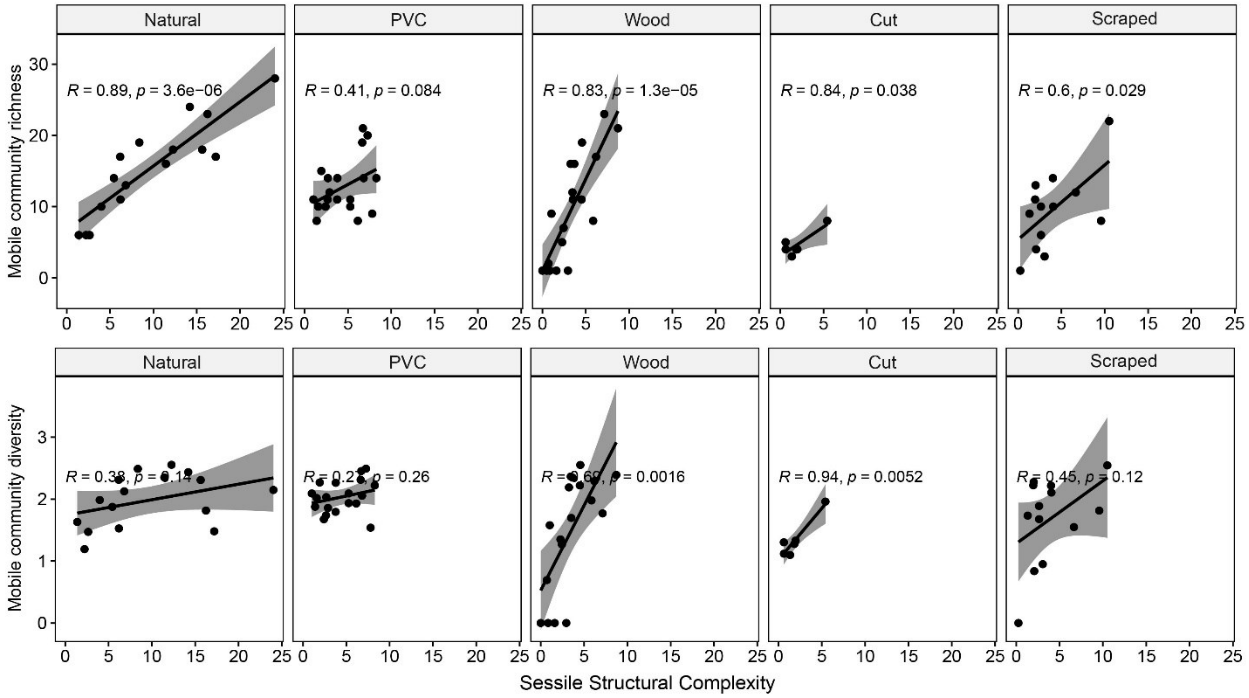

Figure C5 Linear regression between mobile diversity and richness and sessile structural complexity among root treatments. Linear regression plots with 95% confidence interval for mobile community richness and diversity within each root treatment and correlation with sessile structural complexity. r = Pearson's correlation coefficient.

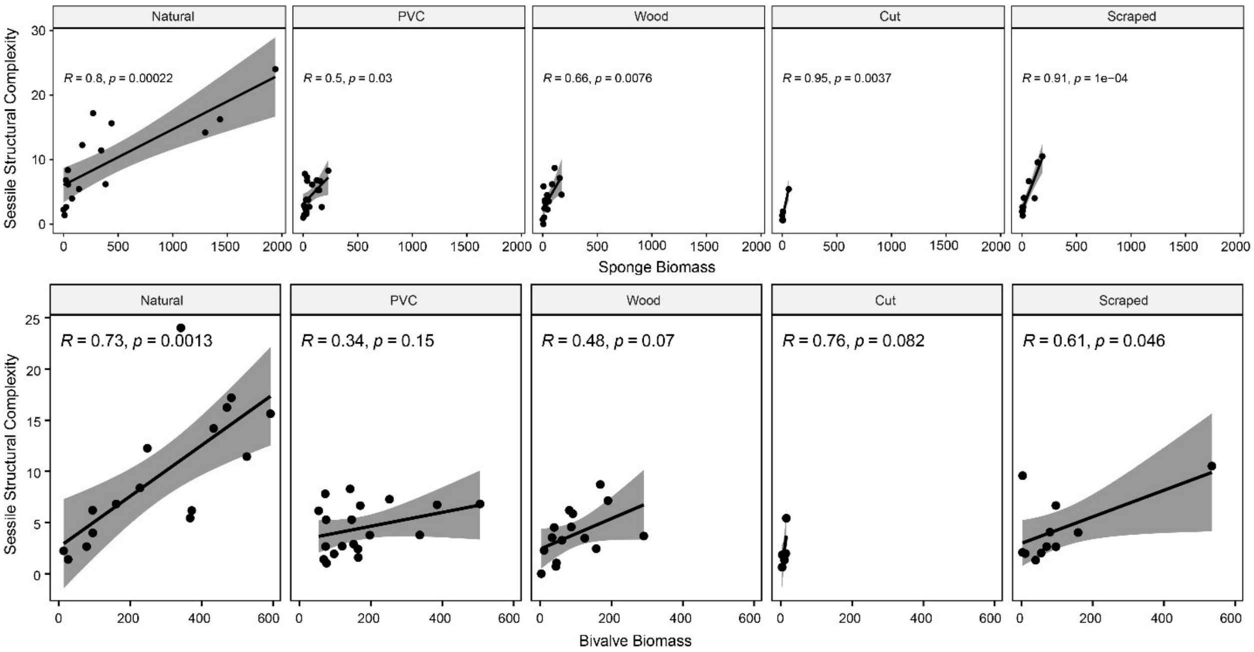

Figure C6 Linear regression between sessile structural complexity and biomass of bivalves and sponges among root treatments. Linear regression plots with 95% confidence interval for sessile community structural complexity within each root treatment and correlation with sponge (top) and bivalve (bottom) biomass. r = Pearson's correlation coefficient.

Appendix D: Supplementary materials for Chapter 4

D.1 Supplementary tables

Table D1 Table of permutational multivariate analysis of variance (PERMANOVA) models. The adonis function from the *vegan* package was used to characterize patterns of epibiont community structure of mangrove roots and root mimics under conditions of low and high wave exposure with the main effects of root treatment (i.e., natural mangrove control, scraped mangrove root, and root mimic), wave exposure, and the interaction of root treatment and wave exposure, and with island replicate as a random effect. The first model (top) used windward and leeward sides to represent wave exposure, while the second model used dissolution rate to account for overlap of water flow between sides among islands. Island replicate was treated as a random effect**.**

	Df	Sum of Squares	Mean Squares	F Model	R^2
Side	1	7.959	7.959	66.687	0.122
Treatment	2	1.564	0.782	6.554	0.024
Side:Treatment	2	0.312	0.156	1.308	0.005
Residuals	464	55.377	0.119		0.849
Total	469	65.212			1.000
Dissolution	1	7.504	7.504	62.283	0.115
Treatment	2	1.510	0.755	6.266	0.023
Dissolution:Treatment	2	0.295	0.147	1.222	0.005
Residuals	464	55.904	0.121		0.857
Total	469	65.212			1.000