Impacts of local and global stressors on coral biodiversity

by

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We acknowledge with respect the Lək̓ʷəŋən peoples on whose traditional territory the university stands and the Songhees, Esquimalt and W̱SÁNEĆ peoples whose historical relationships with the land continue to this day.

Supervisory Committee

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Abstract

Global biodiversity losses are being driven by human actions, and coral reef communities are not immune. Local anthropogenic stress and global climate change are rapidly changing coral reefs, through coral bleaching and mortality. How these stressors impact the biodiversity and community structure of corals on tropical reefs will not only affect the communities of fish and invertebrates that rely on coral reefs, but they could have lasting impacts on ecosystem functioning. The record-breaking marine heatwave caused by the 2015/2016 El Niño was superimposed on a strong local human disturbance gradient on Kiritimati, Kiribati, allowing for the investigation of how these combined disturbances affect coral communities. In Chapter 2, I investigated how soft coral cover varies with these disturbances and natural environmental factors, using benthic photoquadrats collected on Kiritimati's forereefs from 2007 to 2019. Additionally, I conducted a literature review to establish what is already known about soft coral and disturbances, to compare Kiritimati data to that found in the literature. I show that soft corals are grossly understudied, with only a fifth (19/94) of coral studies presenting any results of heat stress effects on soft corals, and even fewer (5%) presenting taxonomic-specific results. On Kiritimati, prior to the 2015/2016 El Niño, soft corals were more common at sheltered sites with lower net primary productivity, but no effect of local disturbance was found. Soft corals were, however, highly vulnerable to heat stress, with a documented complete loss after the heatwave. I also show that soft coral skeletons persisted for years after the heatwave and provided substrate for hard coral recruitment. In Chapter 3, I examined how local and global stressors affected coral diversity, using community composition photoquadrat data collected from 2013 to 2017, and developed a conceptual framework for understanding effects of multiple stressors, when there are both discrete and continuous stressors. Coral alpha diversity (assessed as Hill diversity) exhibited a non-linear relationship with local anthropogenic stress, peaking at intermediate levels, and was negatively impacted by the marine heatwave, such that sites tended to decrease in both coral richness and evenness. Coral beta diversity (assessed as community composition turnover) was significantly impacted by both stressors, but sites exposed to higher levels of anthropogenic stress tended to experience less turnover during the heatwave. Explicitly considering the relationships between the two stressors, I found that it varied depending on the intensity of anthropogenic stress and the diversity metric (*i.e.*, richness vs. composition) examined. For Hill-Richness, I found a tipping point at moderate levels of local anthropogenic stress, below which there was an additive response and above which the response tended towards synergy. In contrast, for Hill-Shannon and Hill-Simpson the responses were additive and there was an antagonistic effect between stressors for community composition. By using the frameworks outlined in this thesis for reporting changes to soft coral due to disturbances, and examining relationships between discrete and continuous stressors, we may better predict how reefs will look in the future and what actions will conserve and assist in the recovery of coral reef ecosystems.

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Acknowledgments

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Dedication

To all the women in science -

We belong.

Chapter 1 - Introduction

Human actions are driving biodiversity losses on a global scale (Barnosky et al. 2011; Ceballos et al. 2015; Lewis and Maslin 2015), but these losses are not always reflected at local scales (Vellend et al. 2013; Dornelas et al. 2014; McGill et al. 2015; Chase et al. 2019). The biodiversity within an ecosystem plays a crucial role in that ecosystem's functions or processes, including the cycling and storage of nutrients, materials and energy within an environment, which are necessary to support life (Tilman et al. 2014; Trivedi et al. 2018; Brandl et al. 2019). Increases in biodiversity support productivity and ecosystem functioning, making biodiversity conservation a high priority (Isbell et al. 2011, 2015, 2017; Tilman et al. 2014). Recent analyses suggest that marine ecosystems are experiencing greater rates of biodiversity change than terrestrial systems (Blowes et al. 2019), putting important ecosystems such as coral reefs at risk (Hughes et al. 2018; Williams et al. 2019).

Coral reef ecosystems have some of the highest biodiversity on Earth and are the most biologically diverse marine ecosystems (Plaisance et al. 2011; Putnam et al. 2017). Between a quarter to a third of all marine species rely on coral reefs during their life cycles (Plaisance et al. 2011) and more than 500 million people also rely on coral reefs for food, protection or income (Wilkinson 2008; Speers et al. 2016). Conservation of coral reefs may help to promote increased biodiversity in reef fish communities, thereby increasing reef functioning (Bellwood et al. 2003; Topor et al. 2019), and corals themselves contribute to the ecosystem functioning of their environment through nutrient cycling and calcium carbonate production (Brandl et al. 2019).

Corals are both ecosystem engineers, organisms that are able to physically modify or create an environment (Wright et al. 2002), and foundational species (*i.e.*, an abundant species that is important for structuring a community and controlling ecosystem processes; Dayton 1972; Byrnes et al. 2011; Ellison 2019). Most fundamentally, reef-building corals (order Scleractinia), which are hard corals that form colonies and produce the structure of coral reefs, through the production of their hard calcium carbonate skeletons (Jackson 1991; Cordes et al. 2008). Corals alter ecosystems through their mutualistic associations with dinoflagellate endosymbionts, which provide the necessary nutrients for many species (De Goeij et al. 2013; Putnam et al. 2017). Even in oligotrophic waters, nutrients like nitrogen and carbon are delivered by the coral hosts to their endosymbiotic dinoflagellate symbionts (Tansik et al. 2015), which supports the photosynthetic production of organic carbon by the dinoflagellate symbionts (Muscatine and Porter 1977). Dinoflagellate photosynthate is then translocated back to the host coral to support coral growth and biomineralization, but much of the organic carbon is released from the coral holobiont to the water column and the organisms and communities that rely on corals (Moberg and Folke 1999; Wild et al. 2004; De Goeij et al. 2013; Putnam et al. 2017). Up to half of the organic carbon produced by endosymbionts within the tissues of corals, is secreted in the form of mucus, and provides nutrients to the benthic reef community (Wild et al. 2004). Without the presence of corals and their endosymbionts, the diversity of life seen on coral reefs would not be sustained (De Goeij et al. 2013; Putnam et al. 2017). Corals are also able to affect other aspects of their environment, including sedimentation rates and water currents, due to the structure they add to their environment, thus creating drastically altered physical conditions on coral reefs compared with the surrounding ocean (Moberg and Folke 1999; Poulos et al. 2013; Valisano et al. 2016; Paoli et al. 2017; Sánchez 2017). Corals therefore provide organisms living on and around coral reefs with nutrients and with microhabitats generated from the structure of the corals themselves.

Coral reefs are comprised of two forms of corals, hard and soft corals, which differ in their skeletal structure. Hard corals (order Scleractinia) produce the foundation of tropical coral reef ecosystems, not only providing nutrients and altering environmental conditions, but also providing crucial structural complexity to their environment through the production of their hard calcium carbonate skeletons (Jackson 1991; Cordes et al. 2008; Figure 1.1). Soft corals (order Alcyonacea) do not produce the same skeleton as scleractinian corals, but instead have a skeleton formed of small calcium carbonate sclerites that provides skeletal support while the soft corals are alive, but the sclerites are thought to dissociate and disperse after the coral dies (Rahman and Oomori 2008). Soft corals are not considered reef building corals as they do not produce a lasting calcium carbonate structure contributing to the reef structure like that produced by scleractinian corals (Rahman and Oomori 2008; Figure 1.1). Soft corals and scleractinian corals both provide complex habitats to reefs and this structural complexity is exploited by a variety of different organisms (Alvarez-Filip et al. 2009; Figure 1.1). A structurally complex environment is able to support a greater degree of biodiversity than a more structurally homogeneous one due to taxa specific associations (Epstein and Kingsford 2019) and can increase ecosystem functioning (Alvarez-Filip et al. 2009; Isbell et al. 2011; Tilman et al. 2014).

Reef-forming hard corals are now commonly grouped into four functional groups based on life history strategies: competitive, weedy, stress tolerant, and generalist (Grime 1977; Darling et al. 2012; Figure 1.2). These functional groups were adapted from Grime's (1977) original descriptions of plant life history strategies by Darling et al. (2012) to fit corals. Competitive corals (*e.g.*, *Dendrogyra cylindricus* and some species from *Acropora*, *Pocillopora, Montipora and Turbinaria*) are able to dominate reefs when conditions are good due to their efficient use of resources (Grime 1977; McClanahan et al. 2011; Darling et al. 2012). However, weedy corals (*e.g.*, *Pocillopora damicornis*, *Stylophora pistillata*, *Seriatopora hystrix* and some species within the genera *Madracis, Agaricia, Cyphastrea*, *Goniastrea* and *Leptastrea*) reproduce faster and are able to colonize disturbed habitats before other coral types, which may be in part due to high trait variation in weedy coral species, fostering rapid accommodation to new conditions (Grime 1977; Darling et al. 2012; Figure 1.2). Stress tolerant corals (*e.g.*, *Montastraea annularis, M. cavernosa, Colpophyllia natans* and some species from *Diploria, Favia, Favites*, *Platygyra* and *Goniastrea*) are often dome shaped, slow growing corals, with long generation times contributing to lower energetic costs, which allows for survival in low light and even high sedimentation conditions (Grime 1977; Darling et al. 2012; Figure 1.2). Finally, generalist corals (*e.g.*, *Montastraea faveolata*, *M. franksi* and species from

Echinopora, Hydnophora, Montipora, Turbinaria and *Pachyseris*) are a grouping of corals that do not fit clearly into the other three categories, tend to have moderate growth rates, produce large colonies, and may do well in conditions of low stress and low competition (Grime 1977; Darling et al. 2012; Figure 1.2).

Overall there are estimated to be approximately 1600 species of hard corals (35 families) and 3400 species of soft corals (41 families; WoRMS Editorial Board 2021), with the highest diversity of corals in what is known as the Coral Triangle, a roughly triangular region of the western equatorial Pacific that lies between Southeast Asia, Papua New Guinea and the Philippines (Dinesen 1983; Barber 2009; Veron et al. 2009). Approximately 600 hard coral species can be found in the Coral Triangle, an area that encompasses the 16 ecoregions with over 500 coral species each (Veron et al. 2009). There are many different hypotheses as to why the coral diversity is so high in the Coral Triangle, including the overlapping of species ranges, constantly changing geography due to plate tectonics allowing for evolutionary changes, converging water currents that carry dispersing coral larvae, and complex genetic mixing (Barber 2009; Veron et al. 2009). However, the high coral diversity seems to be a result of a large number of overlapping ranges of widespread species, and not high levels of endemism, as is often seen in terrestrial biodiversity hotspots (Hughes et al. 2002). The central equatorial Pacific, where my thesis research is based, is not as diverse as sites in the Coral Triangle, and is a part of the Line Islands - North ecoregion, which has less than 100 coral species recorded (Veron et al. 2009).

1.1 Coral reef stressors

Coral reefs are crucial to both marine organisms and coastal human populations; however, they are also greatly threatened by climate change and more localized disturbances (Blowes et al. 2019). Climate change has largescale impacts on coral reefs through increases in sea surface temperatures and ocean acidification, which are often overlaid on gradients of local fishing pressures, nutrient pollution and physical destruction of reefs (Walsh 2011). Gradual global temperature increases in addition to short-term temperature pulses (now known as marine heatwaves) as the result of higher intensity El Niño cycles are expected to continue to increase in intensity and duration due to climate change (Cai et al. 2014; Grothe et al. 2020).

Corals are particularly vulnerable to marine heatwaves, and sea surface temperatures above the bleaching threshold can begin to break down the relationship between corals and their photosynthetic dinoflagellate endosymbionts (family Symbiodiniaceae; Glynn 1983; Putnam et al. 2017). The bleaching threshold is the sea surface temperature above which coral begin to bleach, which is usually around 30ºC for low-latitude reefs and calculated as 1ºC above the maximum mean monthly sea surface temperature (Glynn and Croz 1990; Hoegh-Guldberg 1999; Wooldridge 2009). Without their dinoflagellate partners, corals' white skeleton becomes visible through their translucent tissue, leading to a phenomenon called coral bleaching (Glynn 1983). If temperatures remain high and corals cannot regain their dinoflagellate endosymbionts, this bleaching typically leads to starvation and ultimately death (Glynn 1983; Putnam et al. 2017). The Symbiodiniaceae family is made up of a number of different genera, of which some can associate with corals (LaJeunesse et al. 2018) and can have variable tolerances to heat stress (Coffroth and Santos 2005; Abrego et al. 2008; Littman et al. 2010). Thus, some corals undergoing heat stress may use bleaching as an adaptive strategy to increase heat tolerance (Buddemeier and Fautin 1993) by exhibiting either symbiont 'switching' (acquisition of novel symbiont genera) or symbiont 'shuffling' (shifts in relative abundances of existing symbionts already in the coral; Berkelmans and Van Oppen 2006; Hume et al. 2016). Some symbionts may increase a coral's ability to survive a heat stress event, while others can leave corals susceptible (*e.g.*, to bacteria and pathogens), so altering symbiont community composition during a bleaching even may be beneficial to a coral's survival (Rowan 2004; Abrego et al. 2008; Littman et al. 2010). Other corals seem to have a high fidelity to a few specific endosymbionts, and do not undergo changes even under heat stress (Goulet 2006).

Other disturbances such as changes in pH, sedimentation rates and physical damage can also lead to coral bleaching (Knowlton and Jackson 2008; Smale et al. 2019). However, increases in sea surface temperature are causing frequent and severe coral bleaching events which are predicted to continue to increase, and therefore may lead to changes in biodiversity and ecosystem functioning (Knowlton and Jackson 2008; Cai et al. 2014; Heron et al. 2016; Claar and Baum 2019; Smale et al. 2019). Reefs may be able to recover from large scale bleaching events though some effects can be permanent and a decreased recovery period between bleaching events may not allow for reefs to recover before they are disturbed again (Claar et al. 2018).

Marine heatwaves, such as those caused by El Niño events, cause loss of coral cover due to the bleaching and subsequent death of corals, and are recorded as especially reducing the coral cover associated with tabular and branching shaped corals, as well as competitive corals (Grime 1977; Brown and Suharsono 1990; Aronson and Precht 1995; Arthur 2000). Marine heatwaves can cause many secondary responses other than just coral cover loss, such as decreases in the 3D structure of reefs (*e.g.*, rugosity) and increases in bioerosion (Glynn and Colgan 1992; Sheppard et al. 2002). This can lead to increases in the abundance of herbivorous and detritivorous fishes and decreases in abundances of fishes that rely on corals directly, whether for nutrients or habitat (Glynn and Colgan 1992; Sheppard et al. 2002).

Losses in coral cover on reefs which can be due to marine heatwaves, can trigger a phase shift, where a coral dominated reef will become dominated by another organism, such as macroalgae (Norström et al. 2009). Phase shifts away from corals can greatly reduce the complexity of the reef structure making reefs unable to support the diversity of species they were capable of supporting prior to the disturbance and causing largescale losses in diversity (Hughes 1994; Norström et al. 2009). Returning to a coral dominated reef from a reef dominated by another organism can be difficult as the alternative state may be supported by positive feedbacks which reinforce the alternative state (Norström et al. 2009).

The negative effects of marine heatwaves may be compounded by other stressors on coral reefs, with the result that there are virtually no ‘pristine’ reefs remaining (Knowlton and Jackson 2008). Every modern-day reef has been degraded by some form of anthropogenic disturbance, including nutrient runoff, overfishing, or even physical damage of the reefs through dredging, mining or blast fishing (Moberg and Folke 1999; Knowlton and Jackson 2008). Instead of periods of destruction and recovery as can occur with acute disturbance from heatwaves, disturbance of reefs due to coastal human populations are often chronic and may not provide disturbance free periods allowing coral reef recovery (Connell et al. 1997). Chronic disturbance can lead to a degraded reef, which in turn may lower resilience to other disturbances, or cause altered community composition and ecosystem functioning (Alvarado et al. 2017; Vargas-Ángel et al. 2019). Local human populations are altering the biophysical features of reefs through direct and indirect means, the scale of which is increasing due to growing populations and changing lifestyles (Hughes et al. 2003). In 2008, it was determined that the second largest threat to coral reefs after global climate change was detrimental local human activities (Wilkinson 2008) and in 2004, it was estimated that 24% of coral reefs were under threat of destruction due to human populations (Wilkinson 2004). The impacts of human populations on coral reefs will continue to increase in future years unless actions are taken to reduce human impacts on reefs.

1.2 Effects of multiple stressors

Studies investigating the effects of a single stressor such as marine heatwaves or local human disturbance on coral reef communities may not properly quantify the combined effects of multiple stressors (often termed ‘cumulative effects’), as these stressors will very rarely occur on their own (Folt et al. 1999; Crain et al. 2008; Darling et al. 2013; Jackson et al. 2016; Kroeker et al. 2017). Often there are multiple disturbances acting on an environment at the same time, leading to interactions between disturbances and unpredictable outcomes (Folt et al. 1999; Crain et al. 2008; Darling et al. 2013;

Jackson et al. 2016; Kroeker et al. 2017). Investigating every possible combination of stressors would be difficult, if not impossible, but the study of generalities and patterns that occur when multiple stressors are acting in an ecosystem may allow researchers to produce more accurate models and predictions of how various environments will react to multiple stressors (Folt et al. 1999; Crain et al. 2008; Darling et al. 2013; Jackson et al. 2016; Kroeker et al. 2017). In the past two decades, there has been an increase in studies recording how disturbances interact in environments, to determine if stressor interactions can be predicted and accounted for in conservation and management (Folt et al. 1999; Crain et al. 2008; Darling et al. 2013; Jackson et al. 2016; Kroeker et al. 2017).

Multiple stressors may cause different outcomes, some interactive (*i.e.*, antagonistic or synergistic) and others non-interactive (*i.e.*, additive, multiplicative or dominant; Brook et al. 2008, Kroeker et al. 2017; Figure 1.3). Most simply, additive stressors cause effects that are equivalent to the sum of the effect of each individual stressor (Folt et al. 1999; Brook et al. 2008; Piggott et al. 2015; Côté et al. 2016; Figure 1.3). Alternatively, one stressor could dominate over the other, resulting in the same effect when both stressors are present, as there would be if only the dominant stressor is present (Folt et al. 1999; Brook et al. 2008; Piggott et al. 2015; Côté et al. 2016; Figure 1.3). Stressors can also interact and produce smaller than additive effects, which is known as an antagonistic (or multiplicative) effect, or produce a larger effect than additive effect, known as a synergistic effect (Folt et al. 1999; Brook et al. 2008; Piggott et al. 2015; Figure 1.3). Often synergistic interactions are hypothesized to occur in natural environments as stressors interact to create greater destruction of communities, however a meta-analysis of multiple stressor impacts on freshwater, marine and terrestrial communities showed that synergies only occurred in roughly one third of studies, and that antagonistic effects were just as, if not more, common (20/57 studies showed synergistic effects and 24/57 showed antagonistic; Darling and Côté 2008).

Interactions between stressors can have large effects on biodiversity due to losses in species, which can lead to losses in ecosystem functioning and less productive environments (Vinebrooke et al.

2004; Butchart et al. 2010; Barnosky et al. 2011; Lewis and Maslin 2015). Synergistic and antagonistic interactions may be as a result of co-tolerance between stressors (Vinebrooke et al. 2004; McClanahan et al. 2014). Some life history characteristics that allow taxa to tolerate a stressor may also make them able to tolerate additional stressors, which show an antagonistic relationship between stressors, known as stress-induced community tolerance (Vinebrooke et al. 2004; McClanahan et al. 2014). With an antagonistic relationship, the addition of a second stressor will have a lesser effect when in the presence of the first stressor than it would have in the absence of the first stressor due to positive co-tolerance of species (Vinebrooke et al. 2004; McClanahan et al. 2014). Alternatively, taxa that can tolerate a first stressor may be unable to tolerate other stressors due to a trade off in life history characteristics. Specifically, a tolerance strategy triggered by a first stressor may increase vulnerability to a second stressor, a phenomenon described as negative co-tolerance (Vinebrooke et al. 2004; McClanahan et al. 2014). This would show a synergistic relationship between stressors and is known also as stress-induced community sensitivity (Vinebrooke et al. 2004; McClanahan et al. 2014).

Coral communities are vulnerable to both global climate change and local human disturbance, with likely interactions between these stressors. However, most studies conducted on the most recent 2014-2017 global bleaching event, only focused on the effects of the heat stress event and did not quantify the interactive effects of local human disturbance (Baum unpublished data). A global analysis of local stressors and marine heatwaves suggests that local conditions may interact with heat stress affecting coral loss, though proxies rather than direct measures were used to quantify the local anthropogenic effects (Donovan et al. 2021). Without adequate monitoring programs and studies looking into the effects of these disturbances on coral community, it can be difficult to determine how reefs will look in the future and what kinds of conservation and management practices will be the most beneficial for maintaining diverse coral communities.

Studies that have examined the effects of these two disturbances on coral communities suggest that stress-tolerant and weedy corals will be the best at surviving these disturbances (Darling et al.

2012, 2013). However, one study by Darling et al. (2013; McClanahan et al. 2014) found there are no clear trends of disturbance co-tolerance in corals, while a study by Carilli et al. (2009) saw some trends suggesting negative co-tolerance. Largely, how corals respond to multiple stressors, and co-tolerance trends within corals are unknown (Darling et al. 2013; McClanahan et al. 2014; Côté et al. 2016), but there is the potential for large, reef scale changes in diversity due to these stressor interactions (Vinebrooke et al. 2004).

1.3 Diversity changes on coral reefs

Marine systems are particularly at risk for biodiversity change as they experience higher rates of change compared with freshwater or terrestrial systems, and tropical oceans contain many biodiversity hotspots (Hughes et al. 2002, 2003; Deutsch et al. 2008). There are also higher amounts of variation in responses of marine systems, which may be due to marine organisms often living at temperatures that are near to their thermal maxima (Deutsch et al. 2008; Pinsky et al. 2019) and high endemism in marine systems (Hughes et al. 2002; Roberts et al. 2002). As coral reefs are home to some of the highest levels of biodiversity on Earth (Putnam et al. 2017), and corals in particular are important foundational species on these reefs (Cordes et al. 2008), coral reefs are at a high risk for changes in biodiversity.

Biodiversity can be difficult to quantify in a natural system, such as coral reefs, because there are many metrics of an ecosystem that play into its biodiversity, and there is no one metric that is able to quantify all aspects together (Magurran and McGill 2011). Richness, evenness, abundance, occurrence, range size, vulnerability, functional traits and phylogeny are all aspects of biodiversity that when examined together in the same ecosystem, can produce a more complete illustration of an ecosystem's biodiversity (Magurran and McGill 2011). Regardless of the specific diversity metric used, diversity is generally considered from either a taxonomic (*e.g.*, species) or a functional diversity perspective (Magurran and McGill 2011; Gagic et al. 2015). Taxonomic diversity can include examinations of species richness, abundance and evenness, and is often considered to be a classic measure of species diversity (Magurran and McGill 2011; Jarzyna and Jetz 2018; Roswell et al. 2021). In contrast, functional diversity is based on trait differences within an ecosystem (Magurran and McGill 2011). Measures such as functional richness, abundance and evenness can be measured and are often associated with various ecosystem functions or ecosystem services, such as nitrogen fixation or pollination (Petchey and Gaston 2006; Magurran and McGill 2011; Gagic et al. 2015). Often, taxonomic and functional diversity are closely associated, likely due to taxonomic clades sharing similar ecological and functional traits as a result of a shared evolutionary history (Magurran and McGill 2011).

Alpha diversity is local scale species diversity, which describes the extent to which resources within a community are distributed (Sepkoski 1988; Socolar et al. 2016). Global trends in alpha diversity are currently being contested in the literature (Chase et al. 2019). Some studies have found that there has been no net change in alpha diversity after an ecosystem has experienced a disturbance because biotic homogenization (increased similarity of taxa between communities) and community turnover occurring instead (Vellend et al. 2013; Dornelas et al. 2014). However, these alpha diversity claims are from studies that underrepresent impacted sites, and therefore are only examining changes in alpha diversity at less impacted sites (Elahi et al. 2015; Gonzalez et al. 2016). Also, there is little examination of a baseline from which to later detect changes in diversity or the presence of biotic homogenization and there is a large amount of extrapolation occurring for these studies which span short time lines (Gonzalez et al. 2016; Cardinale et al. 2018). However, analyzing alpha diversity may still provide insight into changes in ecosystems due to the effects of disturbances, especially when paired with other measures of diversity.

Beta diversity is the diversity that occurs on a more regional scale, driven by species variation among sites within the regional diversity pool (Socolar et al. 2016; Chase et al. 2019). Understanding trends that occur in beta diversity, may allow for larger scale predictions to occur from trends being seen in alpha diversity and can be useful in understanding alpha diversity trends (Anderson et al. 2011; Kraft et al. 2011; Dornelas et al. 2014; Socolar et al. 2016). Beta diversity can measure turnover (species at one site being replaced by species at another site) within an environment, or the nestedness (lower species richness sites are subsets of the communities of sites with a larger species richness) of species among sites (Socolar et al. 2016).

Biotic homogenization is often associated with high turnover in an environment and it leads to increasing similarity of taxa among sites (Rahel 2007; Socolar et al. 2016). Homogenization can be the result of human actions that have made it easier for invasive species to move into new areas and bypass previous biogeographic barriers that inhibited dispersal (Olden and Rooney 2006; Rahel 2007; Socolar et al. 2016), or disturbances could increase the turnover and biotic homogenization that is seen in the environment due to differences in survival of species. In contrast, disturbances may lead to the reduction of widespread species if they cannot persist through disturbances, leaving rare species to persist, which could increase the beta diversity among sites, even with an overall decrease in abundance due to the disturbance (Socolar et al. 2016). Therefore, it is crucial to understand how beta diversity is affected by disturbances in order to be able to implement conservation strategies (Iacarella et al. 2018).

1.4 Kiritimati Island

The 2015/2016 El Niño event was one of the strongest on record, and is often considered one of three recorded extreme El Niño events, along with the 1982/1983 and 1997/1998 events (Philander 1983; McPhaden 1999; L'Heureux et al. 2017; Paek et al. 2017). While the 2015/2016 event is not the strongest El Niño event on record, as it had weaker sea surface temperature (SST) anomalies in the Niño1+2 and Niño3 regions than the 1982/1983 and 1997/1998 events, it caused record breaking cumulative heat stress on corals and extreme temperature highs in the central Pacific Ocean, with record breaking Niño3.4 region SST anomalies (L'Heureux et al. 2017; Santoso et al. 2017; Claar et al. 2018). This unprecedented heat stress was devastating to corals causing increased bleaching as average sea surface temperature increased (Claar et al. 2018).

Two central equatorial Pacific islands, Kiritimati and Jarvis, were at the epicentre of the 2015/2016 El Niño event, experiencing the most intense heat stress recorded (Claar et al. 2018, 2019; Eakin et al. 2016; Vargas-Ángel et al. 2019). Kiritimati reefs experienced an unprecedented ten months of heat stress, with approximately 25°C heating weeks (degree heating weeks; DHW) when calculated using NOAA Coral Reef Watch remotely-sensed data, or around 31.6°C heating weeks when calculated with *in situ* temperature loggers (Claar et al. 2019, 2020b). Degree heating weeks are the sum of the magnitude of daily temperatures that are 1ºC above an area's mean monthly maximum temperature over a 12-week rolling window, all divided by two to measure ºC weeks (Claar et al. 2019). Jarvis also experienced immense heat stress, approximately 31.6°C heating weeks using NOAA Coral Reef Watch remotely-sensed data, though it is a much smaller atoll and less well studied (Vargas-Ángel et al. 2019). The 2015/2016 El Niño led to reefs surrounding Kiritimati experiencing major coral cover loss of approximately 90% and large scale changes in reef structure (Claar et al. 2020b; Baum in prep). Before this heatwave, benthic photoquadrats had been collected on Kiritimati since 2007, providing a baseline prior to the El Niño event, and until 2019, allowing me to examine how this heatwave affected coral diversity.

Kiritimati is inhabited by approximately 6500 people (Kiribati National Statistics Office 2016), which rely heavily on fishing for subsistence (Watson et al. 2016) and cause nutrient pollution on reefs near villages (McDevitt-Irwin et al. 2019). Additionally, there is dredging due to a port and an oil company at the north side of the lagoon, contributing to major anthropogenic stress/disturbance (Claar et al. 2020a; Baum in prep). Local anthropogenic stress occurs across the atoll in a gradient as the majority of the human population is concentrated in villages located on the atoll's northwest side with few people living in the southeast (Watson et al. 2016; Magel et al. 2020). This produces a spatial gradient across the atoll that can be utilized to examine the effect that local anthropogenic stress has on coral reef diversity changes and how local anthropogenic stress interacts with a marine heatwave.

1.5 Thesis Research

This thesis aims to examine how local and global stressors affect various aspects of coral reef community composition. I tackled this specifically through the examination of local anthropogenic stress and a marine heatwave on 1) soft coral communities and 2) the diversity of hard and soft coral communities, while disentangling how multiple stressors interact. Here, I took advantage of the natural experiment that has occurred at Kiritimati, and the Baum Lab's long-term monitoring program there. The 2015/2016 El Niño event and gradient of local anthropogenic stress provided a unique opportunity to examine how these stressors interacted and influenced the coral community composition. I hypothesised that the local and global stressors affecting Kiritimati Island would lead to changes in the diversity of coral communities, with particularly negative impacts on the soft coral community. Specifically, I predicted that local and global stressors would both lead to a decrease in diversity, regardless of the metric of diversity used, resulting in a decrease in richness, evenness and reef complexity. Additionally, I predicted that these stressors would interact with each other, producing antagonistic (positive co-tolerance) responses.

In Chapter 2, I quantify the impact of the 2015/2016 El Niño event on the soft coral community of Kiritimati using coral cover from photoquadrat data. I examined the extent to which existing literature documents how heat disturbances affect soft coral communities and then I examined how factors such as human-induced disturbance and the 2015/2016 El Niño heat stress event affected the soft coral communities on Kiritimati. Through a literature review of studies reporting the effects of the 2014-2017 marine heatwave on corals, I also show that soft corals are often ignored when quantifying the effects of large-scale heatwaves. I found that abiotic factors, including wind exposure and net primary productivity had a greater influence on soft coral cover than local human disturbance, and I show that marine heatwaves can be devastating to soft coral communities, leading to complete loss of soft coral cover in my study site after the 2015/2016 El Niño event. I also document the persistence of soft coral skeletons, years after the soft coral has died, with this structure providing a location for hard corals to recruit. These findings demonstrate the extent to which heat stress can affect soft coral communities, and the vulnerability of soft corals are to different disturbances and changing environments. Additionally, these findings provide an example that other researchers can use to help describe changes in soft coral communities at their study locations.

Chapter 3 examines diversity changes in hard and soft coral communities on Kiritimati due to local anthropogenic stress and a heatwave event. Multiple stressors can interact producing unexpected results (Côté et al. 2016) which may have devastating impacts to coral reef environments, so this chapter aims to examine local and global stressors on Kiritimati to better understand the relationships between these stressors and their impact on coral diversity. Through this I created a general conceptual framework, which can be used by other researchers examining multiple stressors, to quantify the types of interactive effects between a discrete stressor and a continuous stressor. As many stressors can occur along a continuous gradient, this modification to the previously understood additive models involving only discrete stressors (Côté et al. 2016), allowed for better understanding of complex relationships such as tipping points. I showed through the use of Hill diversity metrics (alpha diversity) and examination of community composition (beta diversity), that corals are susceptible to both local anthropogenic stress and heatwave events. However, our framework showed that interactions between these stressors provided different relationships depending on which metric of diversity was examined. I showed that there is a tipping point in the relationship of Hill-Richness and the interaction between stressors, such that there is an additive response at low levels of local anthropogenic stress until a tipping point where the stressors interact causing an interaction with richness that trends towards synergy. This chapter broadens the understanding of how multiple stressors interact and provides a framework for other researchers to examine continuous stressors, such that we can better understand how the magnitude of stress and the metrics used to quantify the ecological effect will influence how communities and environments are altered.

Collectively, this thesis provides new insights into how multiple stressors interact to affect coral diversity on different scales, and the influence of soft corals on coral reef communities. This type of information is critical for the understanding of how future stressors will affect coral reef composition and function as climate change continues to affect reef ecosystems. By understanding how multiple stressors affect different elements of coral reef ecosystems, we can better predict how reefs will look in the future and what actions will best be able to conserve and assist in recovery of coral reef ecosystems.

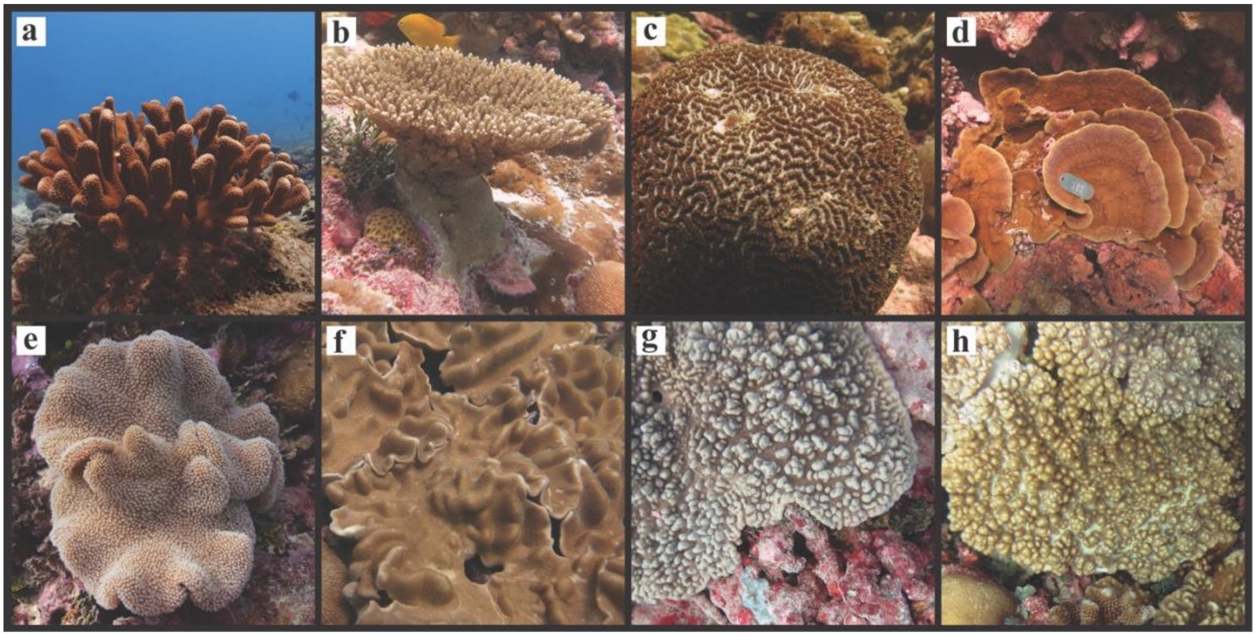

Figure 1.1. Examples of hard and soft corals on Kiritimati. *(top)* Hard coral. *(bottom)* Soft coral. *(a)* Pocillopora, photo © Kristina Tietjen. *(b)* Tabulate *Acropora*, photo © Kristina Tietjen. *(c) Platygyra*, photo © the Baum Lab. *(d)* Foliose *Montipora*, photo © the Baum Lab. *(e) Sarcophyton*, photo © Hannah Epstein. *(f) Lobophytum*, photo © Kristina Tietjen. *(g) Sinularia*, photo © the Baum Lab. *(h) Cladiella*, photo © the Baum Lab.

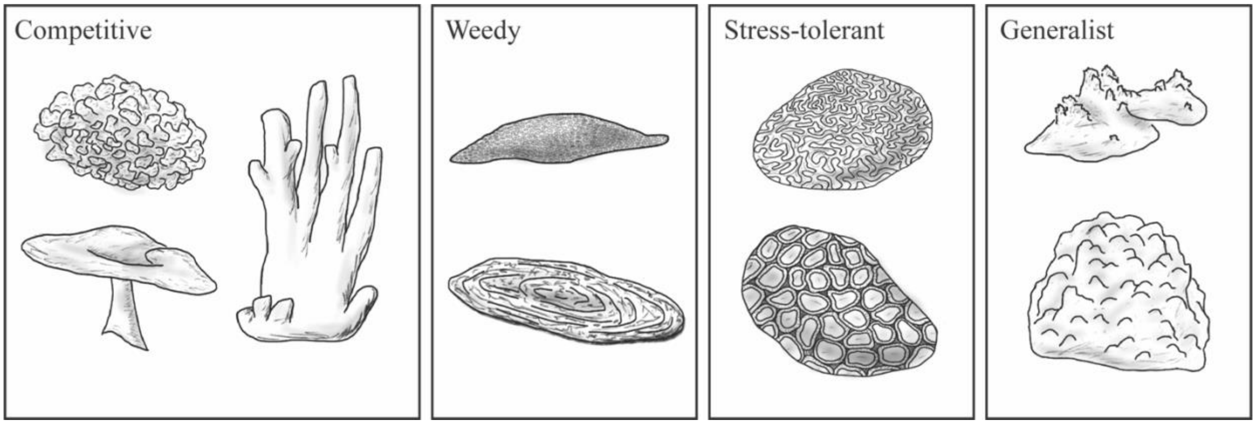

Figure 1.2. Illustration of the morphologies of reef-forming hard corals in four coral functional groups. **Competitive corals:** *Pocillopora meandrina* (top left), tabulate *Acropora* (bottom left) and *Dendrogyra cylindricus* (right). **Weedy corals:** *Leptastrea purpurea* (top) and *Agaricia fragilis* (bottom). **Stress-tolerant corals:** *Platygyra* (top) and *Favia* (bottom). **Generalist corals:** *Hydnophora exesa* (top) and *Montastraea faveolata* (bottom).

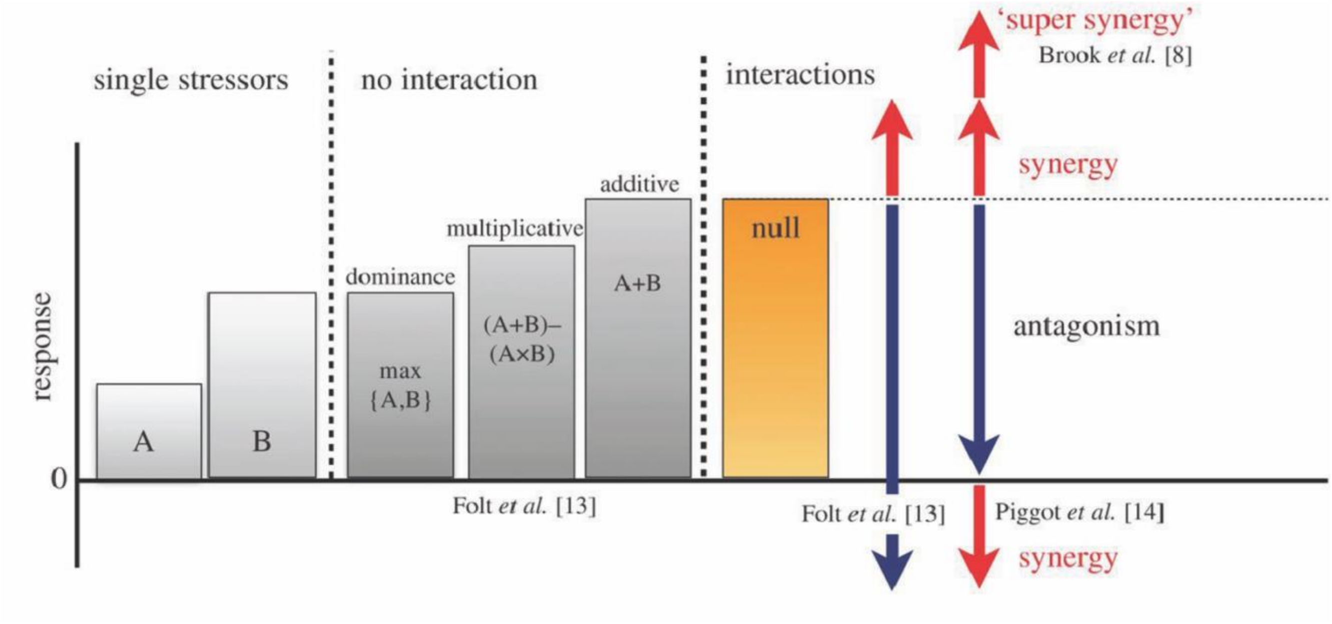

Figure 1.3. Diagram of the possible effects of multiple stressors and categorization of effects when stressors A and B have the same direction result on a response variable. As described by Folt et al. (1999) this can result in a dominance of the stressor that had a larger individual effect, multiplicative or additive effects. However, if there is an interaction between stressors, there can be smaller than additive (or could also be multiplicative) effect, known as antagonism, or larger than expected from additive results, known as synergy or super synergy, though classifications differ (Folt et al. 1999; Brook et al. 2008; Piggott et al. 2015). Reproduced from Côté et al. (2016).

Chapter 2 - Impacts of heat stress on soft corals, an overlooked and highly vulnerable component of coral reef ecosystems, at a central equatorial Pacific atoll

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2.1 Abstract

Climate change threatens coral reefs, with recent heatwaves causing widespread coral bleaching and mortality. Soft corals (order Alcyonacea) provide reef structure and habitat, but most research has instead focused on reef-building hard corals (order Scleractinia). Reviewing the primary literature documenting the effects of recent (2014-2020) marine heatwaves on corals, a period including the third global coral bleaching event, we found that only 20% (19/94) of studies presented any results of heat stress effects on soft corals, and even fewer (5%) presented taxonomic-specific results, highlighting the need for further study. Using images (n=6265) collected on 16 expeditions to the world's largest atoll (Kiritimati; central equatorial Pacific) between 2007 and 2019, we quantified soft coral cover around the atoll's shallow (10-12m depth) forereefs before and after a prolonged heatwave (the 2015/2016 El Niño). Prior to the heatwave, soft coral accounted for 3.0% of the benthic community, with greater cover at sheltered sites with lower net primary productivity; *Lobophytum* and *Sinularia* were the most common genera. We documented a complete loss of soft coral after the heatwave within our study sites. No new soft corals were detected until 2019, three years after the heatwave. Individual colonies tracked over time revealed that soft coral structures can persist for several years post-mortality, and that hard corals can recruit onto these structures. Our study exposes the extreme vulnerability of soft corals to heat stress, which has received scant previous documentation. Future studies examining the effects of heatwaves on coral bleaching and mortality should include soft corals.

2.2 Introduction

Coral reefs, which are the most biologically diverse marine ecosystems and provide essential ecosystem services to hundreds of millions of people (Hoegh-Guldberg 2011), are seriously threatened by climate change (Hughes et al. 2017; Hoegh-Guldberg et al. 2019). Increases in the frequency and duration of marine heatwaves threaten the survival of corals due to coral bleaching (Cai et al. 2014; Claar et al. 2018; Hughes et al. 2018; Oliver et al. 2018). When corals become stressed by factors such as temperature anomalies, their symbiotic relationship with the photosynthetic algae (family Symbiodiniaceae) living within their cells break down, leading to the ejection of the symbionts and coral bleaching. In the absence of temperature reductions, this generally leads to coral mortality (Glynn 1983; Brown 1997; Putnam et al. 2017). Between 2015 and 2016 an extreme El Niño (L'Heureux et al. 2017) led to widespread coral bleaching and mortality on many reefs around the world, with higher accumulated heat stress on corals than any previously documented El Niño event (Eakin et al. 2016; Claar et al. 2018; Hughes et al. 2018). A major focus of the coral literature since has been to understand how this El Niño, and the broader 2014-2017 global coral bleaching event (Eakin et al. 2016; Heron et al. 2017), affected reef-building corals and the conditions that lead to coral bleaching and mortality (Eakin et al. 2016). This is important, not only because of the diversity of corals that are threatened, but also because widespread coral losses could have major negative consequences for marine biodiversity more broadly (Burke et al. 2011), as well as for people, through the loss of food, livelihoods and coastal protection (Moberg and Folke 1999).

Reef building scleractinian corals (order Scleractinia) are important ecosystem engineers and the foundation of tropical coral reef ecosystems (Moberg and Folke 1999; Putnam et al. 2017). These organisms not only provide important nutrients to their community (Wild et al. 2004) in their oligotrophic environments, but also create critical habitat structure, and provide many other ecosystem services (Moberg and Folke 1999; Putnam et al. 2017). Soft corals (order Alcyonacea) have skeletons formed of small calcium carbonate sclerites, which allow a degree of rigidity, but they do not form the large calcium carbonate structures of scleractinian corals, which form reefs (Rahman and Oomori 2008). However, soft corals can still be considered ecosystem engineers, as they provide structure and habitat complexity to their communities, and are also able to regulate sedimentation and affect water currents (Poulos et al. 2013; Valisano et al. 2016; Paoli et al. 2017; Sánchez 2017). Some predatory fish species are closely associated with soft coral species (Sánchez 2017). Although soft corals are important components of coral reef communities, most studies focus on reef-building corals, while information and investment into monitoring soft corals is generally lacking (Dinesen 1983; Richardson et al. 2017a). Consequently, less is known about how soft coral communities will react to increasing heat stress events in the future, let alone under multiple disturbances associated with global climate change (Côté et al. 2016).

Our objectives here were twofold: *1)* to evaluate the extent to which the impacts of recent heat stress events on soft corals have been studied and *2)* to assess the vulnerability of soft corals to prolonged heat stress. To meet these objectives, we first conducted a systematic literature review to quantify the extent to which soft corals are represented in studies examining the effects of marine heatwaves on corals, focusing specifically on the past seven years, which includes the most recent global coral bleaching event (2014-2017). We then conducted our own empirical analysis, examining the effects of the 2015/2016 El Niño event on soft coral relative abundance on the world's largest atoll, Kiritimati, which experienced ten months of anomalously high temperatures during this period (Claar et al. 2019, 2020b). Four genera of soft coral have been identified on Kiritimati: *Lobophytum*, *Sinularia*, *Sarcophyton*, and *Cladiella* (see Figure A1 for live and bleaching photos). Using community composition data from small benthic photoquadrats, we quantified changes in soft coral cover over a thirteen-year period (2007 to 2019) that included this heatwave. We hypothesized that the relative abundance of soft coral (overall and individual genera) would vary spatially around the atoll's forereefs due to differences in chronic local disturbance and environmental conditions across sites, and that the atoll’s El Niño-induced prolonged heatwave would cause significant declines in soft coral cover at all sites.

2.3 Methods

We first conducted a systematic literature review to quantify the extent to which field studies assessing the impacts of recent marine heatwaves (*i.e.*, 2014 to 2020) on corals included soft corals. This date range was selected to examine heatwaves that included the same time span as the El Niño event that we examined on Kiritimati Island, and to encompass the third global coral bleaching event. On August 25, 2020, we conducted two searches for papers published between 2015 and 2020 using all databases on the Web of Science: one using the search terms: ((coral*) AND (mortal* OR bleach* OR cover* OR health*) AND (“El Niño” OR “El Nino” OR ENSO OR “heat stress” OR “heatwave” OR “thermal stress” OR “temperature anomaly”)); a second using the search terms: ((“soft coral” OR octoc* OR alycon*) AND (mortal* OR bleach* OR cover* OR health*) AND (“El Niño” OR “El Nino” OR ENSO OR “heat stress” OR “heatwave” OR “thermal stress” OR “temperature anomaly”)). On September 2, 2020, we also conducted a search using the previously mentioned search terms on Google Scholar, specifically searching for papers from the Atoll Research Bulletin because this journal is not included in Web of Science.

We evaluated each paper that was returned from these searches, reviewing the titles, abstracts and method sections, to determine if they examined corals during a heatwave between 2014 and present day (Figure 2.1). We excluded papers describing lab-based studies or heatwaves prior to 2014 (Figure 2.1). The remaining papers that met our criteria, were classified based upon: i) if the study mentioned soft corals (using the terms ‘soft coral’ or ‘octocoral’), ii) if data was collected about soft corals, iii) if results were presented about soft corals, iv) if soft corals were included in figures, v) if soft corals were identified as being from specific genera, or species, vi) if quantitative results were presented, and vii) if there were quantitative results reported, were they regarding bleaching, mortality, growth, cover or disease (Figure 2.1).

2.3.1 Study Site and Design

Kiritimati (01°52’N, 157°24’W), Republic of Kiribati, located in the central equatorial Pacific Ocean, is the world’s largest atoll by land mass (388 km^2 with 150 km perimeter), and has a population of approximately 6500 people (Kiribati National Statistics Office 2016). The atoll’s villages are concentrated on the northwest coast, with few people living in the southeast, creating a spatial gradient of the local population and associated disturbances across the atoll (Watson et al., 2016; Magel et al., 2020; Figure 2.2). Chronic local human disturbance for each of 40 shallow forereef monitoring sites has previously been quantified by combining data on the size of the human population within a two-kilometer radius of each site and the location of fishing activities, calculated from a kernel density of fishing activity (Watson et al. 2016; Claar et al. 2019). For visualization purposes, sites were also grouped into five categorical local human disturbance categories (Very Low, Low, Medium, High and Very High), based on clear breakpoints in the continuous local disturbance measure, as in Magel et al. (2020) and Claar et al. (2020b). Reef sites also varied due to oceanographic factors, including primary productivity and wind exposure. We defined site-level exposure (*i.e.*, windward versus sheltered) based on the dominant wind direction (southeasterly; Bosserell et al., 2015), with sheltered sites grouping leeward sites with other sites that are protected from the dominant wind direction. Additionally, we extracted site-level maximum net primary productivity (mg C m^{-2} day^{-1}) data from the Marine Socio-Environmental Covariates (MSEC), an open source data product that uses satellite-derived measures of photosynthetically available radiation, SST, and chlorophyll-*a* concentrations (Yeager et al. 2017). The MSEC data product is based on NOAA CoastWatch and calculated maximum net primary productivity over a 2.5 acrmin grid (Yeager et al. 2017).

Around the atoll, the forereef monitoring sites were surveyed in 16 expeditions between 2007 and 2019, although all sites were not surveyed in every expedition (mean = 16.7 sites/expedition) due to weather and timing constraints (Table A1). Of these, 37 sites are the same as Walsh (2011), which were established in 2007, along with three additional sites (L2, VL12 and H1) established in 2009. At each site, transects were laid along the 10-12m isobath, and photos of the benthic substrate were taken at each of 20 to 35 randomly selected points along the transect. Quadrats of 0.54 m^2 (0.9 m by 0.6 m) were used from 2007 to 2011, and $1m^2$ quadrats were used from 2013 to 2019.

Coral reefs on Kiritimati sustained heat stress for 10 months during the 2015/2016 El Niño event, reaching ~25°C-weeks (degree heating weeks; DHW) according to NOAA Coral Reef Watch remotely-sensed data (Claar et al. 2019, 2020b) and 31.6°C heating weeks according to *in situ* temperature loggers (Claar et al. 2019, 2020b). Jarvis, a nearby island to Kiritimati, is the only other location to experience heat stress of this intensity (Vargas-Ángel et al. 2019). These two islands were at the epicenter of this El Niño event, one of the most extreme El Niño events on record (Claar et al. 2018, 2019; Eakin et al. 2016). Benthic surveys were conducted on Kiritimati before, during and after the heat stress event.

To examine how quickly soft corals degrade following mortality, we also examined images of permanent 4m x 4m photoquadrats, in which the same individual corals were photographed at multiple time points between 2015 and 2019. These photoquadrats were established at nine of the Kiritimati monitoring sites (three per site), along the 10-12m isobath in early 2015 as part of a separate study (Magel et al. 2019; Bruce 2021). These have been photographed before (May 2015), during (March 2016) and after the El Niño event (November 2017, July 2017 and July 2019). We visually examined the soft corals in the photoquadrats from two sites (VL3 and M1) as they had large soft coral colonies that could be relocated in subsequent years to allow for the documentation of the bleaching and death of soft corals during the heat stress event and the persistence of structure after the heat stress event.

2.3.2 Data Processing

We identified benthic substrate (*n* = 6381 quadrats) using randomly placed points overlaid on each image using CoralNet, an opensource program created for analysing coral benthic communities (Beijbom et al. 2015). We placed 54 and 100 random points on the 0.54m^2 and 1m^2 sized quadrats, respectively, in order to maintain an average density of one point per cm^2 of quadrat. Additionally, for coral cover analysis, we cropped the 1m^2 quadrats after all benthic substrate annotations were completed, so that the quadrat area would be 0.54m^2 and match the smaller sized quadrats. These cropped quadrats contained an average of 54 randomly annotated points, with variation due to the randomly placed annotation points, and any quadrats that had fewer than 35 or more than 65 were removed from analysis (31 quadrats, 0.49%). The identity of the substrate under each randomly placed point was determined, and soft corals were identified to genus based on visual characteristics. We were unable to identify soft corals to species as this would have required examination of sclerites or genetic analysis, neither of which was able to be performed as the necessary data were not collected. We determined percent cover for each coral genus by dividing the number of points for members of that genus by the total number of useable points in each quadrat. Unusable points included shadows, transect and quadrat hardware or unclear points where accurate identification was not possible. Quadrats where more than 10% of the annotated points were unidentifiable were removed from analysis (85 quadrats; 1.3%). In total, 6265 quadrats (98.1%) were used in analysis.

2.3.3 Statistical Analysis

All statistical analyses were conducted in RStudio (R version 4.0.1). To examine variability in soft coral cover prior to the heat stress event, we fitted a series of generalized linear mixed models, each with a zero inflated beta probability distribution and a logit link function because soft coral cover (*i.e.*, the response variable) was calculated as a proportion of benthic cover. Models were fit using the ‘glmmTMB’ package (Magnusson et al. 2020). As these data spanned eight expeditions before the heat stress event (July 2007 - May 2015), we averaged soft coral cover across years for each site after testing for and confirming that there was no trend over time in soft coral cover within this timespan.

We designed 11 models based on a set of *a priori* hypotheses about the relationship between soft coral cover, site exposure (windward vs sheltered), local human disturbance, and net primary productivity (mg C m^{-2} day^{-1}; all fixed effects). Local human disturbance and net primary productivity were continuous variables and were centered and scaled for analysis. Additionally, we included a fixed effect for 'region' to acknowledge that areas of this large atoll may differ for other non-quantified reasons, ran a global model (Table 2.1 and A2). For categorical variables, Helmert contrasts (which compare each factor level with the mean of the preceding factor levels) were used because there were no control variables; the site exposure variable was ordered windward then sheltered, and region was ordered Bay of Wrecks, North Shore, North Lagoon, Mid Lagoon, South Lagoon, Vaskess Bay and then Korean Wrecks. Akaike Information Criterion (AIC) was used for model selection and all models within 6 AIC units from the best model were considered to be part of our final model set. We also ran separate models for each individual soft coral genera to examine if relationships between the overall soft coral community and abiotic factors held at this finer taxonomic scale.

Finally, to examine the effect of the heat stress event on soft coral cover, we qualitatively examined the amount of soft coral cover present on the reefs during the three years after the heat stress event. Percent soft coral cover loss was determined for each region around the atoll, except for Korean Wrecks as it was not sampled after the El Niño event (Table A1).

All data, as well as the code for figures and data analyses will be made publicly available through GitHub (https://github.com/baumlab) and archived through Zenodo upon manuscript acceptance.

2.4 Results

2.4.1 Literature Review

Our literature search returned 256 papers, of which 94 met the scope of our study, being papers that examined the impacts of a recent marine heatwave (2014 – 2020) on coral reefs (Figure 2.1). Of these 94 papers, only one (1.1%) was soft coral focused (Quintanilla et al. 2019), but a further 27 (28.7%) collected data on soft corals along with hard corals. Over two thirds of papers (69.1%), however, either did not mention soft corals at all (64.9%) or mentioned them in passing but did not collect or analyze soft coral data (4.3%; Figure 2.1). The single paper focused on soft corals considered one species, *Pacifigorgia cairnsi* (Breedy & Guzman, 2003), and examined how El Niño events affected environmental conditions, which in turn affected the soft coral's growth (Quintanilla et al. 2019). Only 18 of the 27 other papers that collected data on soft corals presented any results on soft corals, and of these, five (5.3%) only presented qualitative trends (Figure 2.1). Of the thirteen general coral papers that did present quantitative results on the impacts of heat stress on soft corals, the majority (n = 9) did not classify soft corals into specific species or even genera, and two papers grouped soft coral results with that of hard corals. When quantitative soft coral results were presented, some papers only included soft coral on plots, and others included a sentence or two summarizing the changes observed in soft corals. For papers other than the one focused on soft corals, results related to soft corals were not investigated further and the focus was on understanding the patterns in hard coral cover. Most papers that were not focused on soft corals found small changes in soft coral cover and low amounts of soft coral mortality, though one paper, which focused on documenting soft coral species diversity more thoroughly than other papers found that there was a 93% decline in soft coral cover resulting in soft coral cover being less than 1% of the reef (Cerutti et al. 2020).

2.4.2 Pre-heat stress soft coral cover

Within our focal study location, Kiritimati, soft coral accounted for 3.0% (± 0.18 SEM) of the benthic community cover, on average across sites around the atoll, prior to the 2015/2016 El Niño (Figure 2.3b). Overall, *Lobophytum* was the most common soft coral genus (1.3% ± 0.12 SEM), *Sinularia* (0.87% ± 0.087 SEM) the second most common, *Sarcophyton* (0.67% ± 0.093 SEM) the second least common, and *Cladiella* (0.19 ± 0.042 SEM) the rarest genus (Figure 2.3c). The abundances of the different genera did show some spatial variability across the atoll, with *Lobophytum* the most common soft coral in most regions other than the south sheltered area (Korean Wrecks), where *Sarcophyton*, despite not being abundant elsewhere on the island, was most common (Figure 2.3c).

Mean soft coral cover varied significantly amongst sites, with region, wind exposure and net primary productivity all being significant predictors in at least one model in the final model set (Table 2.1, A1, Figure 2.3b). The top model, which only included region, revealed two regions close to one another on the more sheltered side of the island (Vaskess Bay ($z = 6.1$, $p < 0.001$) and Korean Wrecks ($z = 2.7$, $p < 0.01$)) that both had significantly higher mean soft coral cover than elsewhere (Figure 2.3a,b). At the other extreme, the Bay of Wrecks on the windward side of the island had negligible coral cover (Figure 2.3b). Two of the top five models did not include region. Instead, both models indicated that mean soft coral cover was significantly higher at more sheltered sites, and one indicated that it was also significantly negatively related to net primary productivity (Table 2.1, Figure A3). Four out of the five top models included local human disturbance, but the relationship was never statistically significant (Table 2.1, Figure A3). These patterns – significant relationships between soft coral cover and wind exposure and net primary productivity, but not for human disturbance – held for the two most abundant soft coral genera (*Lobophytum* and *Sinularia*; Table 2.2, Figure A4); there were no significant relationships for the two least abundant soft coral species (*Sarcophyton* and *Cladiella*; Table 2.2).

2.4.3 Heat stress event

In the two years following the prolonged heatwave (sampled during three expeditions: November 2016, July 2017, June 2018), we did not observe any live soft corals in any photoquadrats (n = 1439 quadrats), suggesting 100% loss of soft coral cover due to the heat stress event, at least on shallow forereefs around the atoll. Examination of individual soft coral colonies in permanent photoquadrats showed that although *Lobophytum* and *Sinularia* colonies bleached and died during the prolonged heat stress event, the colony structures persisted for at least three years providing a structure which hard corals recruited to (Figure 2.4). In contrast, *Sarcophyton* colonies in the permanent photoquadrats all died and completely degraded between the 2015 and first 2016 sampling seasons (Figure 2.4). Three years after the end of the 2015/2016 El Niño event, during our July 2019 expedition, we observed five sites with one colony each of healthy, young soft corals (Figure 2.5).

2.5 Discussion

Our literature review reveals how little is known about how heat stress events impact soft coral communities and demonstrates the literature’s focus on hard corals. We also found that on a large coral atoll (Kiritimati), soft coral cover varied spatially across the atoll’s shallow forereefs. Our subsequent models suggested that this spatial variation might be attributed to differences in wind exposure and net primary productivity amongst sites; local human disturbance was not found to significantly affect soft coral cover, which was unexpected. However, as expected, a prolonged El Niño event had devastating consequences on the soft coral community, with a documented 100% loss of soft coral in our study area. Finally, we found evidence of soft corals leaving behind structures on the reef after they die, adding to reef structural complexity, as well as initial signs of soft coral recovery three years after the heatwave.

Our literature review indicates that few studies have examined how heat stress events affect soft coral communities, even when overall benthic community cover data have been collected. Soft coral assemblages provide habitat, structure and can alter environmental conditions for organisms living on or around the corals (Poulos et al. 2013; Valisano et al. 2016; Paoli et al. 2017; Sánchez 2017), however the minimal understanding of how soft corals are affected by heat stress means that we do not know how these environments have been altered, or how they will recover. While not all coral reefs have soft coral assemblages present, this literature review shows that most reef studies do not acknowledge soft corals, which suggests that they may be overlooked on many reefs, not just absent from them. Some research groups collected data on soft coral benthic cover but did not analyze these data in detail or at all. This is problematic because it means the scientific literature is not reflective of the amount and types of data being collected. There needs to be a greater effort put into not only collecting soft coral data, but collecting these data at higher taxonomic resolutions (*i.e.*, species or genera), in order to understand dynamics between different soft coral assemblages and the fish and invertebrate assemblages associated with them (Sánchez 2017). Data being collected by current researchers regarding soft coral in different areas and being exposed to different environmental stressors also needs to be reported in the literature to help inform conservation and restoration initiatives, and to help us understand how reefs will continue to change into the future. As recommended by Claar et al.’s (2018) meta-analysis, when heat stress events are being reported in the literature, along with information on hard coral, researchers should also record and report soft coral taxonomic composition, species- or genera-specific responses to heat stress, and the overall community response of all soft corals.

In our empirical analysis of Kiritimati’s forereefs, we found that prior to heat stress, soft coral cover varied spatially, with areas on the southern side of the island (Vaskess Bay and Korean Wrecks) having high soft coral cover. These sites are sheltered from the predominant wind direction and have little exposure to anthropogenic disturbance, with no infrastructure or pollution and virtually no fishing in them. We found that wind exposure and net primary productivity affected mean soft coral cover, but that the local human disturbance had no effect. The effects of local anthropogenic disturbance have been understudied in soft corals, but we hypothesized that higher nutrient concentrations and pollution near human populations would lead to a decrease in soft coral cover (Cornish and DiDonato 2004; Januar et al. 2015). Our study suggests that other abiotic factors, which may be related to local human disturbance such as net primary productivity have a negative relationship with mean soft coral cover. However, net primary productivity variation is not only due to human activity (Walsh 2011), but also upwelling (Claar et al. 2019), which therefore may play a crucial role in soft coral growth. More sheltered sites, such as those in the high mean coral cover regions (Vaskess Bay and Korean Wrecks), but also those on the leeward side of the island are sheltered from trade winds and likely experienced lower wave exposure, though this needs to be confirmed with the use of *in situ* current meters. Soft corals tend to grow in more sheltered sites with lower wave energy as wave energy is known to be damaging to soft corals and to inhibit their growth (Dinesen 1983; Fabricius 1997).

We also found spatial variation in the dominant soft coral genera amongst sites, suggesting variability in environmental preferences amongst different soft coral taxa. Our analyses of the relationships between individual soft coral genera and environmental variables did not, however, shed light on the factors underlying these differences because the two most common soft coral genera (*Lobophytum* and *Sinularia*) showed similar relationships, with both negatively influenced by wind exposure and primary productivity. This similarity may have arisen because of these species' phylogenetic relatedness, as both genera are from the Alcyoniidae family (McFadden et al. 2006), or similar life history characteristics. As these were the most abundant soft coral genera, these genera likely influenced the total soft coral cover. The other two genera (*Sarcophyton* and *Cladiella*) were rare, which likely led to a lack of power to detect relationships, as there were no significant main effects in these models. In general, little is understood about how soft coral species differ in their responses to environmental conditions and stressors, but there have been documented differences in survival among species due to stressors (Loya et al. 2001; Slattery et al. 2019). Further studies with soft coral from these and other families will help researchers to better understand if there are clear genera specific differences within the response of soft coral communities to abiotic factors and heat stress events which would allow for similar conservation actions being able to assist many genera, instead of general or species-specific actions needed to maintain soft coral communities.

Our study also revealed that prolonged heat stress can be devastating for soft corals, with a complete loss of soft coral cover at our study sites over the course of the 2015/2016 El Niño event. The mortality of soft corals (100%) exceeded that of hard corals on Kiritimati Island (Baum unpublished data), suggesting soft corals are especially sensitive to extreme sea temperatures. Soft coral skeletons are made of calcified sclerites, which are not as solid as hard coral skeletons, but permanent photoquadrats on Kiritimati Island documented the persistence of soft coral skeletons after coral death. *Sinularia* and *Lobophytum* soft corals in our study left behind a structure that contributed to the overall complexity of the reef and provided structure for new hard coral recruits to settle on for three years post-mortality (Figure 2.4). Some soft corals from the genus *Sinularia* are known to lithify individual calcitic sclerites at the base of the colony, with a cement known as spiculite, which consists of aragonite crystals (Konishi 1982; Jeng et al. 2011; Shoham et al. 2019). We propose this may be occurring in some corals from the genus *Lobophytum* as well. These corals, after they die, left structures behind which became areas colonized by turf algae and crustose coralline algae growth, eventually allowing for the settlement and recruitment of at least five hard coral species (including *Pocillopora* and *Porites*), which to our knowledge is the first documentation of hard coral recruitment on soft coral skeletons (shown in Figure 2.4). The mechanism of this settlement warrants further investigation to determine if soft coral skeletons have higher rates of hard coral recruitment than the surrounding benthos.

The structure that soft corals provide while they are alive is not well understood, with only a few papers examining soft coral community habitat complexity (Wilson et al. 2007; Richardson et al.

2017b, 2017a). Recent studies suggest that soft corals contributed important habitat to reef and fish communities (Epstein and Kingsford 2019) and that under current ocean acidification projections, we may see a shift from hard coral communities to those dominated by soft corals (Inoue et al. 2013; Gómez et al. 2015). Even less is known about the structure provided by dead soft corals, but if soft corals are contributing the formation of reefs, they could still influence reef composition. Hard coral skeletons are formed of aragonite crystals while soft coral sclerites consist of calcite crystals, some of which have been recorded as being high magnesium calcite and others low magnesium calcite (Konishi 1982; Rahman et al. 2011; Januar et al. 2017; Shoham et al. 2019). The composition of soft coral sclerites would influence the solubility of reefs as high magnesium calcite is more soluble than aragonite, making reefs that are formed from high magnesium calcite soft corals more susceptible to ocean acidification (Andersson et al. 2005; Rahman et al. 2011; Eyre et al. 2014). Soft coral reef formation needs to be studied further in order to understand how reef structures will react to changing oceanic conditions and the role of soft corals in community structure, reef recovery and coral recruitment needs to be better understood, in order to understand how to conserve coral reefs and their biodiversity.

Despite apparent local extinction of soft corals during the El Niño event, we found initial signs of recovery three years after the event, with the detection of a small number of young colonies. Although it is possible that some soft corals persisted in shallow areas outside of our monitoring sites, we suspect that the source of these new corals was colonies in deeper waters than those we surveyed (10 to 12 m) that had survived the event. Soft corals may not be as restricted by depth as hard corals, which may have provided conditions that allowed for soft coral survival in deeper waters (Pupier et al. 2019). Soft corals are known to quickly colonize the benthos after a mass mortality of hard corals (Richardson et al. 2017b). However, with such an extreme loss of soft coral cover, there may not be enough adult soft coral colonies to be able to recolonize and dominate the benthos of Kiritimati. Further sampling to determine how the soft coral populations recover from the bleaching event will allow for better-informed conclusions about how surviving soft corals will affect patterns of soft coral recovery.

In conclusion, there is a lack of understanding in the current scientific literature of how global heat stress events impact soft coral cover. We provide some new insights in this regard, by examining changes in a soft coral community during a prolonged marine heatwave on the world’s largest atoll. First, by examining shallow forereefs on the atoll prior to the heatwave, we found evidence that spatial variability in soft coral cover may have arisen due to differences in wind exposure and net primary productivity, both of which negatively influenced soft coral cover. We then documented a 100% loss of soft coral in our study area during the 2015-2016 El Niño-induced heatwave, indicating that soft coral species are very susceptible to prolonged thermal stress. We also showed that soft coral skeletons can persist for several years after the colony dies, and that the remaining structures can provide substrate for hard corals to settle on, leading to increases in reef complexity even after the death of the soft corals. Finally, we recorded initial signs of soft coral community recovery, however, it is too soon to tell how the soft coral community will recolonize, so further studies are needed to understand rates of soft coral recover after extreme mortality events.

2.6 Tables and Figures

Table 2.1. Parameter estimates for fixed effects from generalized linear mixed effects models describing the factors influencing mean soft coral cover prior to the heat stress event. Years analyzed were July 2007 to May 2015.

Rank	HD	WE	Region	NPP	HD * WE	*df*	AICc	ΔAICc	w_i
1			**+***			9	-96.5	0	0.531
2	-1.48		**+***			10	-94.8	1.74	0.223
3	-1.21	**0.800***		**-1.90***		6	-93.8	2.73	0.136
4	-1.37		**+***	-1.14		11	-91.5	5.03	0.0429
5	1.28	**0.744***			-3.23	6	-90.9	5.61	0.0321

Note: HD = local human disturbance; WE = wind exposure; NPP = max net primary productivity; *df* = degrees of freedom; AIC_c = AIC corrected for small sample sizes; ΔAIC_c = difference from the lowest AIC_c value, models with $\Delta AIC_c < 6$ are shown, all models available in Table A2; w_i = model weight for each model. Boldface and asterisk indicate statistical significance ($\alpha = 0.05$; $*p < 0.05$). Plus (+) sign represents parameters included with multiple factor levels.

Table 2.2. Parameter estimates for fixed effects from generalized linear mixed effects models describing the abiotic factors influencing each soft coral genera's mean cover prior to the heat stress event. Years analyzed were July 2007 to May 2015.

Model	HD	WE	NPP
Lobophytum	-1.08	**0.807***	**-2.20***
Sinularia	-0.861	**0.565***	**-2.05***
Sarcophyton	-1.48	0.351	0.351
Cladiella	-0.237	0.123	-3.54

Note: HD = local human disturbance; WE = wind exposure; NPP = max net primary productivity. Boldface and asterisk indicate statistical significance ($\alpha = 0.05$; $*p < 0.05$).

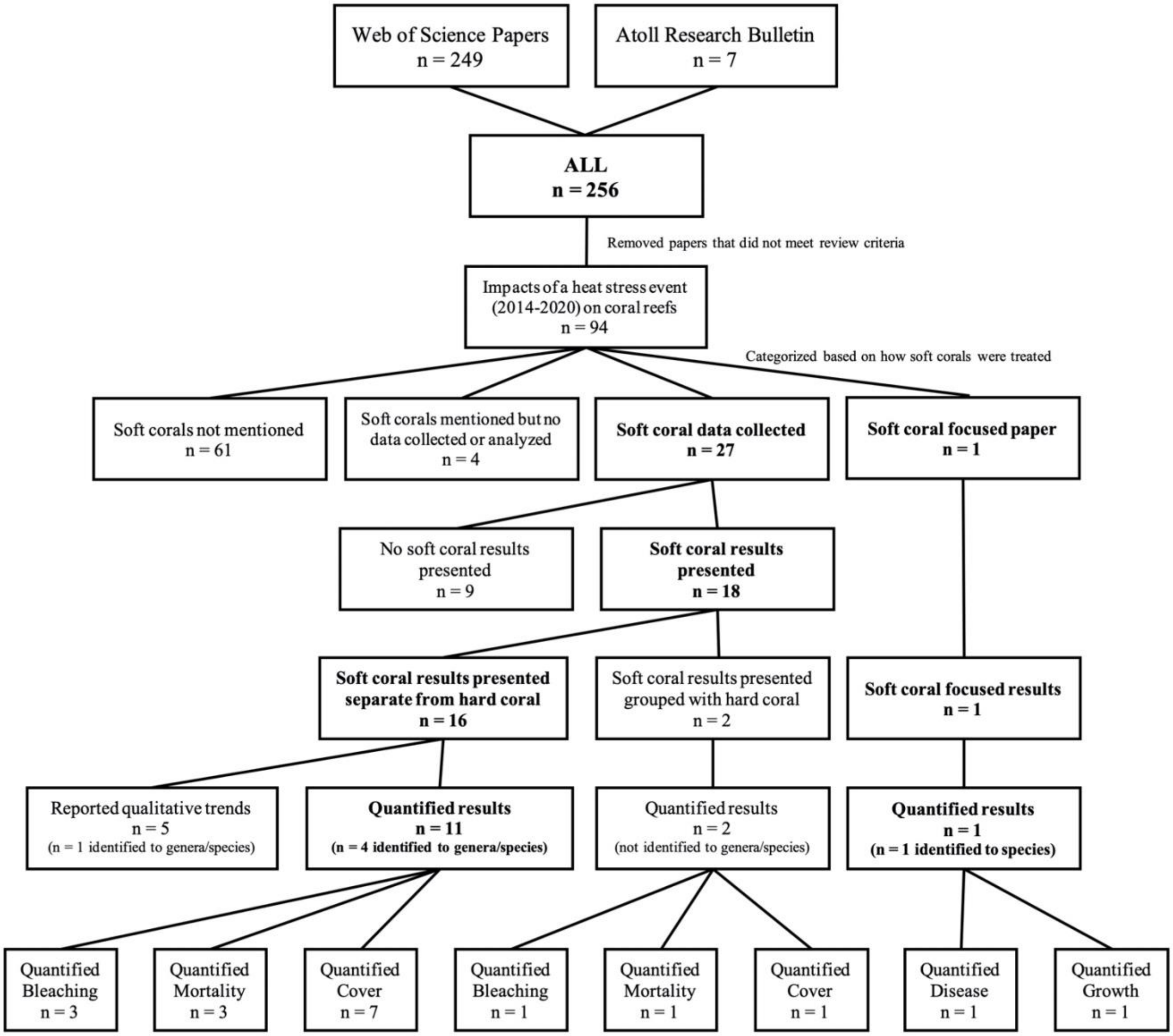

Figure 2.1. PRISMA diagram showing results of literature review of the documentation of recent heat stress events (2014-2020) on soft corals.

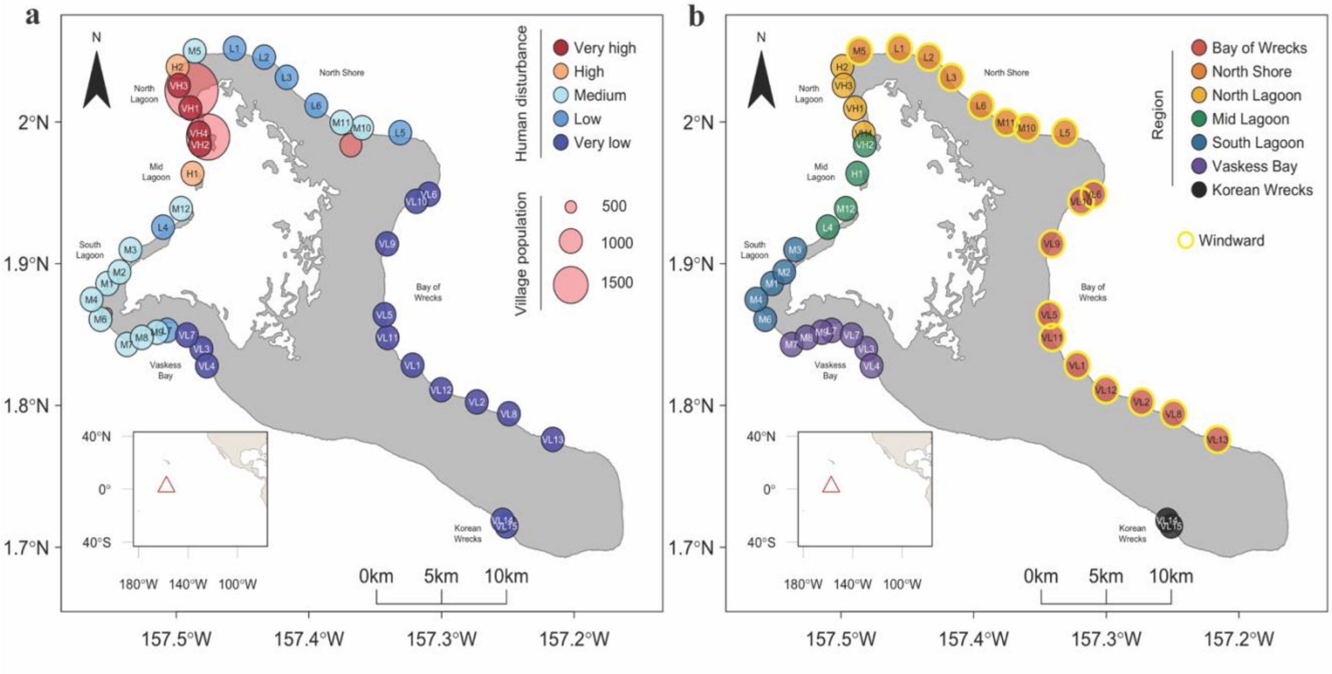

Figure 2.2. Monitoring sites on Kiritimati (Christmas Island) classified by: *(a)* level of chronic local human disturbance, with village locations also shown; *(b)* regions and wind exposure (*i.e.*, classified as ‘windward’ if on the side of the atoll exposed to the predominant wind direction; Bosserell et al., 2015). Inset shows the location of Kiritimati in the central equatorial Pacific Ocean.

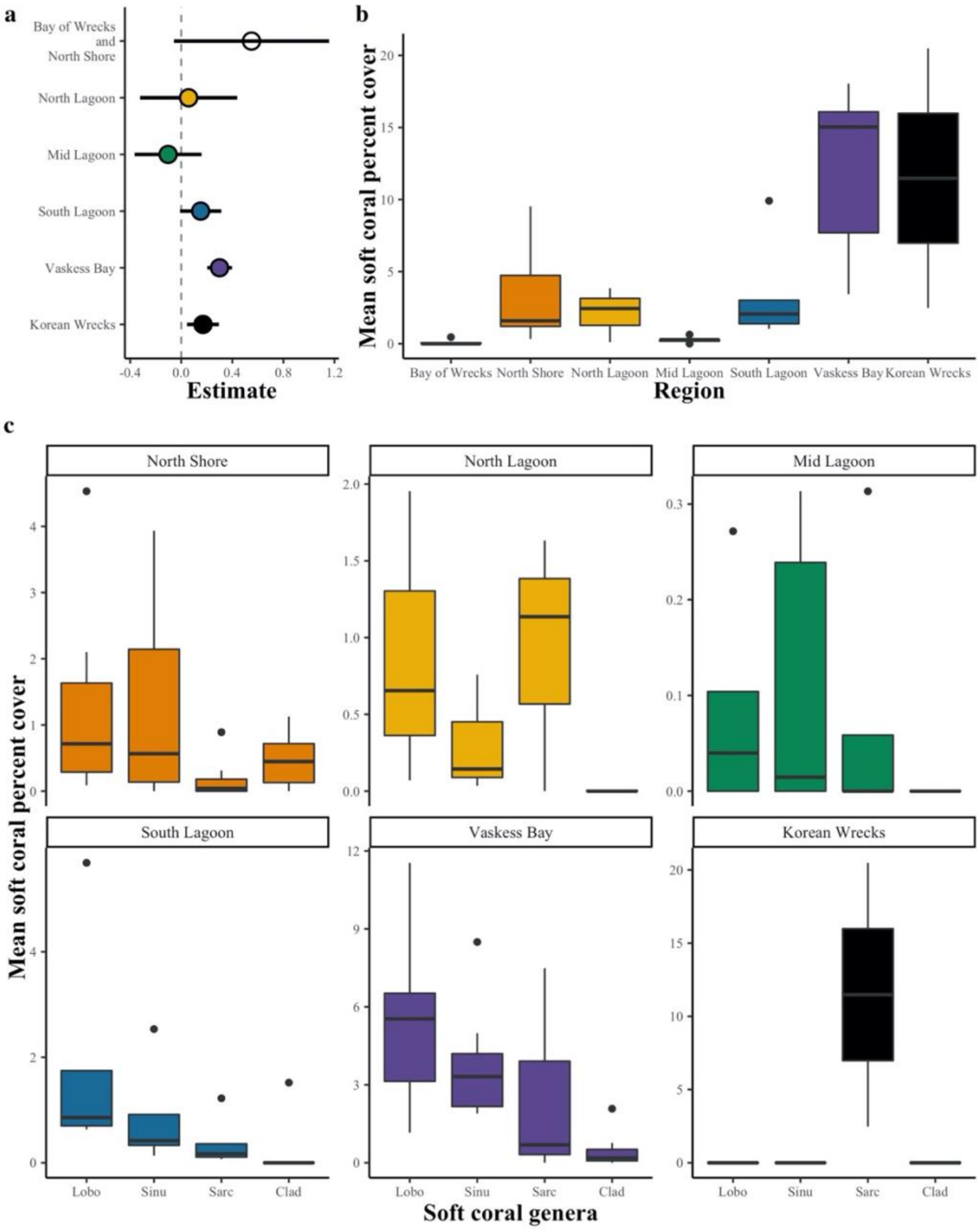

Figure 2.3. Soft coral cover prior to the El Niño event. Colors match region colors in Figure 2.2. *(a)* model parameters and 95% confidence intervals for island region. Helmert contrasts were used so each region was compared to the mean of the regions listed above them on the y-axis. *(b)* Mean soft coral cover on Kiritimati. *(c)* Mean soft coral percent cover in each region. Lobo = *Lobophytum*, Sinu = *Sinularia*, Sarc = *Sarcophyton* and Clad = *Cladiella*. Note: y-axes differ in scale amongst panels and Bay of Wrecks was not displayed as soft coral cover was negligible (see Figure A2 for Bay of Wrecks data).

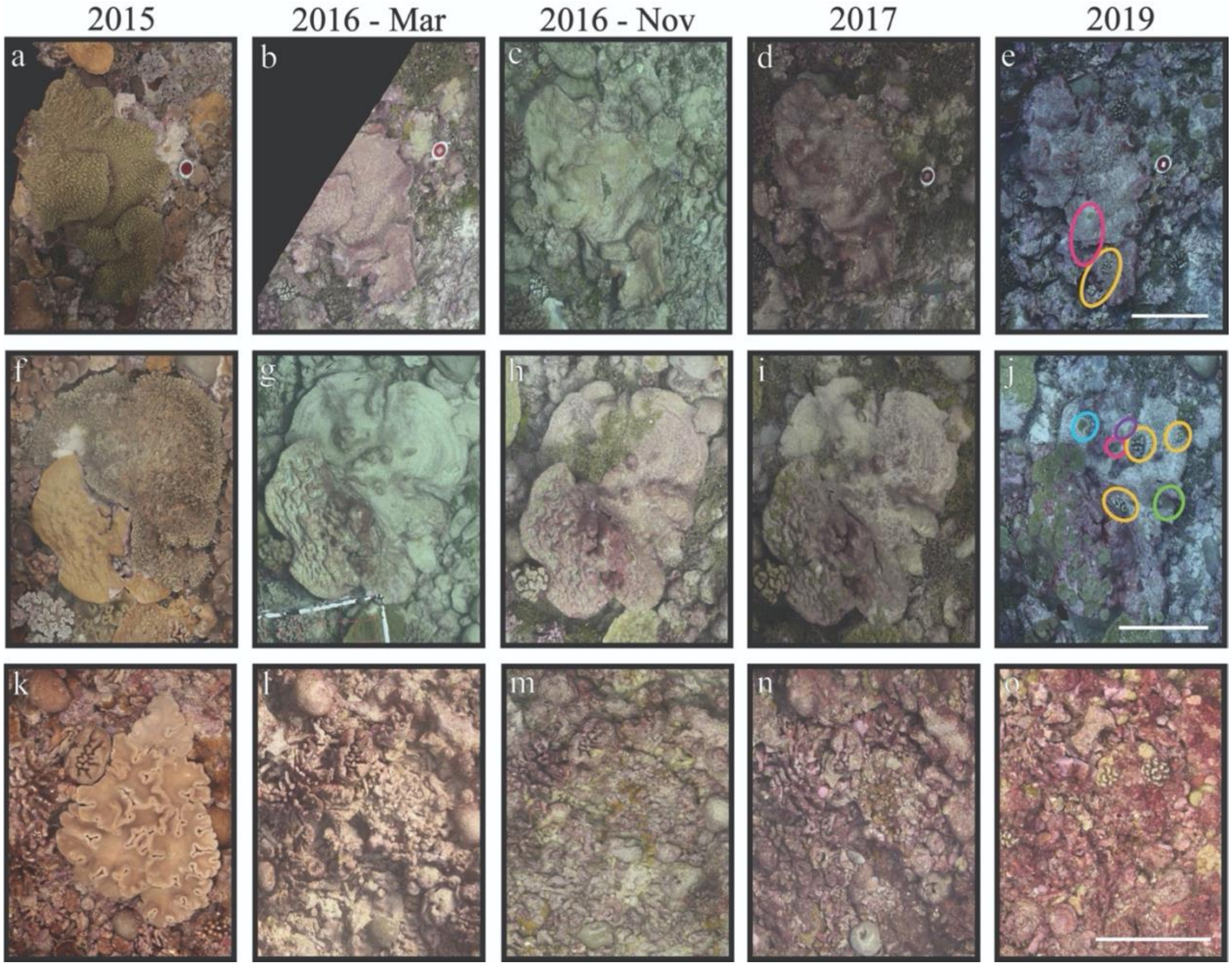

Figure 2.4. Photos of three individual soft coral colonies (top - *Lobophytum* sp., middle - *Sinularia* sp., bottom - *Sarcophyton* sp.) taken in permanent photoquadrats at two forereef sites VL3 *(top, middle rows)* and M1 *(bottom row)* on Kiritimati over a four-year period, showing the progression from live coral, to mortality and decay. 2015 sampling period was before the El Niño event, March of 2016 was during the El Niño event, and November 2016, 2017, and 2019 sampling periods were after the El Niño event. Circles in panels *(e)* and *(j)* show location of hard coral recruits on dead soft coral structures with colors representing different genera; orange for *Pocillopora*, blue for *Porites* and purple, pink and green for separate morphotypes. Note: some hard coral recruit identities are only to morphotype as genera cannot be accurately determined at this size. White bar in panels *(e)*, *(j)* and *(o)* show scale bars representing 50 cm for each row.

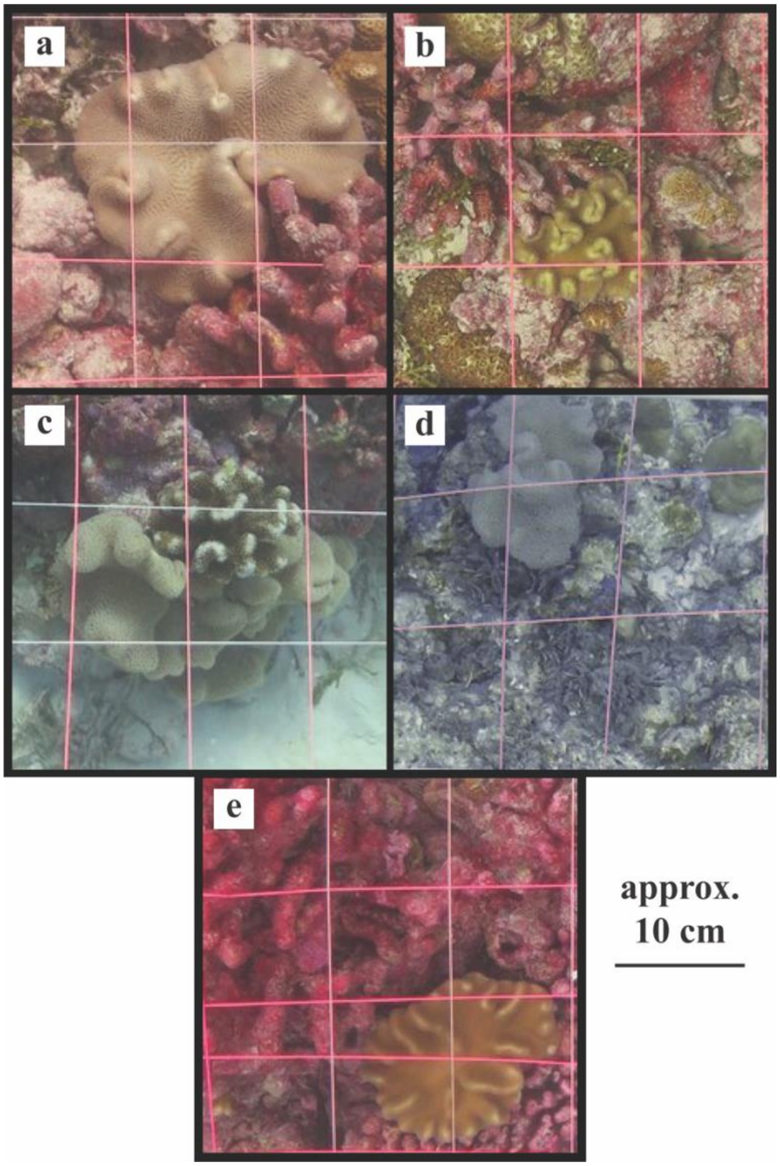

Figure 2.5. Photos of the recorded soft corals from small photoquadrats present on Kiritimati after the 2015/2016 El Niño event. All are from 2019 and provide the first evidence of recovery following the El Niño event. *(a-d) Sarcophyton* from sites VL4, M6, M1 and M2 respectively *(e) Lobophytum* from site M12.

Chapter 3 - Disentangling the relationships between multiple stressors on coral reef diversity: tipping points and interactive effects

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3.1 Abstract

Coral reefs are being rapidly transformed by global-scale climate change and local-scale anthropogenic stress. Yet, questions remain about how such stressors interact, and what their combined impacts will be on the composition and diversity of coral reef ecosystems. Here, we investigate how interacting global and local stressors alter coral alpha and beta diversity and develop a general conceptual framework for understanding interaction outcomes of multiple continuous and discrete stressors. Examining coral community composition data spanning a globally unprecedented marine heatwave superimposed upon a gradient of chronic local anthropogenic stress (on Kiritimati, Kiribati), we found a non-linear relationship between alpha diversity and local anthropogenic stress with the maximum alpha diversity at an intermediate stress, as well as a negative relationship between alpha diversity and the heatwave, with lower diversity after the heatwave. Coral beta diversity (assessed as community composition turnover) was significantly affected by both stressors, but sites exposed to higher levels of local anthropogenic stress tended to experience less turnover during the heatwave. Additionally, we found that the nature of the interaction between stressors depended on the underlying strength of the local anthropogenic stress, and that it also varied depending on the diversity metric examined. When examining community composition, we found that the stressors interacted antagonistically, suggesting positive co-tolerance by corals to both stressors. For coral species richness, examined here using Hill-Richness, we found that although increasing local anthropogenic stress initially led to an additive effect, suggesting no interaction between stressors, there was a tipping-point at moderate levels of stress, above which the effect of the two stressors approached synergy, such that they had a larger effect on Hill-Richness. Our conceptual framework for analysis of multiple stressors reveals how complex interaction outcomes can arise when more realistic stressors occurring along a continuum are considered, which is critical for predicting future composition and function of coral reef ecosystems.

3.2 Introduction

In modern natural ecosystems, natural and anthropogenic stressors rarely occur in isolation, but instead occur temporally and spatially together, making ecological predictions a challenge (Folt et al. 1999; Crain et al. 2008; Jackson et al. 2016; Kroeker et al. 2017). When the effect of a stressor, defined here as a factor that causes a quantifiable change in an ecosystem (Côté et al. 2016), is examined on its own, usually under laboratory conditions, it is often possible to predict the outcomes of that stressor, but interactions between stressors can create unpredictable outcomes associated with aspects of ecosystems such as overall ecosystem biodiversity, productivity, or species abundance, identity, growth, or reproduction (Folt et al. 1999; Crain et al. 2008; Darling and Côté 2008; Holmstrup et al. 2010; Côté et al. 2016). Diversity is necessary for the maintenance of ecosystem functioning within an environment (Isbell et al. 2011; Tilman et al. 2014), but interactions between stressors could have large and unforeseeable consequences on the diversity and functioning of future ecosystems (Harley et al. 2012). Interactions between stressors may arise when taxa that are capable of tolerating one type of stressor are also better able to tolerate additional stressors (positive co-tolerance), or, conversely, when taxa that are tolerant of one stressor are intolerant of another (negative co-tolerance; Vinebrooke et al. 2004; McClanahan et al. 2014; Côté et al. 2016). In marine systems, roughly 40% of the ocean is strongly influenced by multiple co-occurring anthropogenic stressors (Halpern et al. 2008), so it is crucial to understand the relationships between multiple stressors and how these relationships affect populations, communities and ecosystems to conserve marine ecosystems for future generations.

Coral reef environments are crucial for many marine species, but are threatened by anthropogenic stressors (Moberg and Folke 1999; Hughes et al. 2003, 2017). These stressors can occur on local scales because of the actions of human populations (*e.g.*, fishing, trawling or nutrient and waste run-off), or they can occur on global scales due to larger consequences of climate change (*e.g.*, increasing water temperature, ocean acidification and changes in storm frequency and intensity; Lewis and Maslin

2015). Corals are foundation species that form the structure of coral reefs from their hard calcium carbonate skeleton, which provides habitat for a wide diversity of organisms (Knowlton 2001; Knowlton and Jackson 2008). Additionally, corals provide nutrients to their community in an otherwise nutrient poor environment, through mutualistic relationships with dinoflagellate symbionts in the family Symbiodiniaceae (Moberg and Folke 1999; Putnam et al. 2017). Without the corals providing structure and nutrients, many ecological services would not be provided to humans and ecological processes may be affected, including ecological goods (*e.g.*, fish and components of pharmaceuticals), ecological services (*e.g.*, nursery, hunting ground or breeding ground for fish and other marine invertebrates), social and cultural services (*e.g.*, tourism) and protection of coastlines from storms (Moberg and Folke 1999). Factors such as depth (Harborne et al. 2006; McDevitt-Irwin et al. 2021), geomorphology (Arias-González et al. 2008), proximity to human populations (Smith et al. 2010; Crane et al. 2017), temperature (Gomez et al. 2018), storms (Connell et al. 2004), wave exposure (Harborne et al. 2006; McDevitt-Irwin et al. 2021) and the presence of other biotic taxa (Smith et al. 2010; McDevitt-Irwin et al. 2021) have all been shown to influence coral diversity, but interactions between these factors remain poorly understood.

Trends in diversity can be complex to interpret because relationships can vary scale-dependently and often depend on the metrics used (McGill et al. 2015; Gomez et al. 2018; Chase et al. 2019). Commonly, alpha diversity (the examination of the diversity at a very small, local scale) is used to examine how coral diversity differs between sites or environments (Connell et al. 1997; Fabricius et al. 2011; Darling et al. 2013; Graham et al. 2015; Socolar et al. 2016; Vargas-Ángel et al. 2019; McDevitt-Irwin et al. 2021), by quantifying the number of species at a site (richness) and their relative abundances (evenness; Magurran and McGill 2011; Roswell et al. 2021). Hill diversity is now the preferred method of measuring alpha diversity, as it does so without separating the number of species from their relative abundances, acknowledging that relative abundances cannot be fully eliminated and are not fully independent of species occurrences (Roswell et al. 2021). This approach provides a single equation, with the same scale and units (varying only in its exponent), to examine species richness and evenness (Shannon and Simpson variations) metrics (Roswell et al. 2021). Beta diversity (variation in community composition across sites) can be used to measure the relationship between stressors and community composition and whether sampling areas are becoming more or less similar with ongoing anthropogenic change (Connell et al. 1997; Fabricius et al. 2011; Burman et al. 2012; Darling et al. 2013; Graham et al. 2015; Socolar et al. 2016; McDevitt-Irwin et al. 2019, 2021; Vargas-Ángel et al. 2019). Measuring beta diversity is complex; researchers must consider whether relative abundances or just species occurrence should be used, how to treat joint absences, and which component of beta diversity (turnover or variation) to assess (Anderson et al. 2011). Examining patterns of beta diversity will be crucial for understanding how stressors change coral reef community function (Darling et al. 2013; Socolar et al. 2016), because the maintenance of ecosystem services depends on maintaining variation in community composition across the landscape (Isbell et al. 2011; Tilman et al. 2014).

Despite the pervasive nature of multiple stressors in our oceans (Halpern et al. 2008), relatively few studies have explored the relationship between multiple stressors and the diversity of coral ecosystems (Darling et al. 2013). Moreover, what few studies exist tend to treat these stressors as binary (*e.g.*, fished vs. marine protected area; Crain et al. 2008; Darling et al. 2013; McClanahan et al. 2014; Côté et al. 2016; Galic et al. 2018; Donovan et al. 2020; Montefalcone et al. 2020). Perhaps this explains why past studies have been inconsistent in their findings regarding the relationships between multiple stressors. Some coral reef multiple stressor studies report synergistic responses, though others report antagonist responses (Darling et al. 2010; Ban et al. 2014). We hypothesize that this may reflect a tipping point at which the relationship between stressors changes. Specifically, coral communities experiencing low levels of local anthropogenic stress may exhibit positive co-tolerance with a heatwave, because the corals remaining in a community exposed to low levels of local anthropogenic stress may be those that are tolerant of local anthropogenic stress, and these ‘stress-tolerant’ species may be tolerant of other stressors too (McClanahan et al. 2014). However, at high levels of local anthropogenic stress, a heatwave may overwhelm the corals with stress and lead to larger declines in diversity. Examining stressors as binary can inform of the presence of an interaction between stressors but may generalize the complexity of interactive relationships between stressors if there are tipping points at different magnitudes of a stressor. In reality, most stressors are continuous and ecological communities exist on gradients of stress, therefore we hypothesize that the relationship between stressors may be dependent on the strength of the individual stressors when they act together.

Here, we examined how local anthropogenic stress mediates the relationship between marine heatwaves and coral community composition by examining: *(i)* coral community composition and diversity across the local anthropogenic stress gradient before and after a marine heatwave through alpha and beta diversity metrics. *(ii)* how interactions between local anthropogenic stress and extreme marine heatwaves affect coral community composition and diversity, and *(iii)* whether these interactions differ depending on the strength of the underlying stressors. We hypothesised that together the heatwave and the underlying local anthropogenic stress would lead to reductions in alpha diversity, due to losses in coral cover associated with the heatwave, and poor growth conditions for corals caused by local anthropogenic stress and coastal development. Additionally, we hypothesized that there would be differences in community composition between sites, specifically with stressors leading to a homogenization of reef communities. Finally, we hypothesised that these stressors would interact leading to differences in responses to the marine heat wave depending on the degree of local anthropogenic stress, and that there would be antagonistic interactions between stressors due to co-tolerance of corals to both stressors.

3.3 Methods

3.3.1 Study Site and Design

We conducted this study on the world's largest atoll (388 km^2 with 150 km perimeter), Kiritimati (01°52'N, 157°24'W), located in the central equatorial Pacific Ocean, in the Republic of Kiribati (Figure B1). Kiritimati has a local population of approximately 6500 people (Kiribati National Statistics Office 2016), concentrated in villages primarily on the northwest side of the atoll. Along the perimeter of the atoll, 17 forereef sites, spanning a gradient of local human and fishing impacts, were sampled during 6 expeditions between 2013 to 2017. However, not all sites were surveyed in every expedition (mean = 10.2 sites/expedition) due to weather and timing constraints (Table B1, Figure B1). Sites were subset from a larger sampling of sites, to only include those that were sampled both before and after the 2015/2016 marine heatwave. At each site, transects were laid following the 10 to 12 m isobath and benthic photo quadrats of 1m^2 were taken at 20 to 35 random locations along the transects.

Local anthropogenic stress on Kiritimati was previously calculated by quantifying the human population within a two-kilometre radius of each site and the local fishing stress due to fishing, sewage runoff and dredging, calculated from a kernel density of fishing activity (Watson et al. 2016; Claar et al. 2019; Magel et al. 2020). We used a square root transformation for all examinations of the local anthropogenic stress, to account for the right skew in the data. Additionally, this continuous measure of local anthropogenic stress was grouped, based on clear breakpoints, into five categorical anthropogenic stress categories (Very Low, Low, Medium, High and Very High) as in Magel et al. (2020) and Claar et al. (2020b) when analyses would not allow for a continuous metric to be used. Additionally, we extracted site-level maximum net primary productivity (mg C m^{-2} day^{-1}) data from the Marine Socio-Environmental Covariates (MSEC), an open source data product that uses satellite-derived measures of photosynthetically available radiation, SST, and chlorophyll-*a* concentrations from NOAA CoastWatch to calculate maximum net primary productivity over a 2.5 acrmin grid (Yeager et al. 2017).

To date, the 2015/2016 El Niño event was the longest and most intense of any El Niño event on record, leading to the highest cumulative heat stress inflicted on any coral reef to present (Eakin et al. 2016; Claar et al. 2018, 2019). Kiritimati experienced approximately 25°C-weeks (degree heating weeks; DHW) according to NOAA Coral Reef Watch remotely-sensed data (Claar et al. 2019, 2020b) and 31.6°C heating weeks according to *in situ* temperature loggers (Claar et al. 2019, 2020b). This largescale heatwave provided a design from which to examine coral communities before, during and after the heatwave as there was approximately a 90% loss in coral cover due to the effects of the heatwave (Claar et al. 2020; Baum unpublished data).

3.3.2 Data Processing

We analyzed benthic community composition (1731 quadrats) using CoralNet, an opensource software used to characterize benthic community composition (Beijbom et al. 2015). There were 100 points randomly overlaid onto each image and we identified the substrate below each point to the lowest possible taxonomic classification. We determined percent cover for each coral taxonomic group by dividing the number of points for that taxonomic group by the total number of useable points in each quadrat. Unusable points included shadows, transect and quadrat hardware or unclear points where accurate identification was not possible and all quadrats where more than 10% of the annotated points were unusable were removed from analysis (7 quadrats: 0.4%). In total, 24 individual taxonomic groups were analyzed for this study (Table B2). Of this, soft corals (order Alcyonacea) were identified into four genera, all free-living hard corals were grouped at the family level (order Scleractinia, family Fungiidae) and the remaining 19 taxonomic groups were reef building hard corals (order Scleractinia) identified to genus or species (Table B2).

Sites were classified as before the heatwave if they were sampled between July 2013 and May 2015, and after if they were sampled in November 2016 or July 2017. To ensure a proper coral cover baseline was represented in our analysis, all sampling before the heatwave was examined to ensure there was no show large fluctuations in total coral cover between years. For subsequent analyses, if a site was sampled multiple times before or after the heatwave, one sampling year was randomly selected so that each site was only sampled once before and once after the heatwave (Figure B1, Table B1).

3.3.3 Alpha Diversity Analysis

To assess alpha diversity, we used Hill diversity metrics, which provide a method of quantifying richness and evenness at sites by using various types of means of the community species' rarity (*i.e.*, arithmetic, geometric and harmonic means) that scale rarity differently (Hill 1973; Jost 2006; Botta-Dukát 2018; Roswell et al. 2021). The Hill diversity equation uses a parameter 'ℓ' to scale rarity (Equation 1), where D is the diversity of S number of species, with p_i being the proportion of individuals in species i, and r_i being the rarity of species i:

$$D = \left(\sum_{i=1}^{S} p_i (r_i)^{\ell}\right)^{\frac{1}{\ell}} \tag{1}$$

This allows the effect of rarity to be examined while providing a more intuitive calculation of alpha diversity (Hill 1973; Jost 2006; Botta-Dukát 2018; Roswell et al. 2021). Hill-Richness metrics (arithmetic means) emphasize rare species, while Hill-Simpson metrics (harmonic means) emphasize common species, and Hill-Shannon metrics (geometric means) are an intermediate between Hill-Richness and Hill-Simpson metrics (Jost 2006; Roswell et al. 2021).

We used all 17 sites for alpha diversity calculations. To ensure equal sampling effort across sites, we used coverage based methods from the 'iNEXT' package (Hsieh et al. 2016) to equalize samples (Roswell et al. 2021). Our use of coverage based equalization ensures that the diversity of each sampling unit is not biased by sampling effort or sampling size, by accounting for the amount of sampling that was conducted and the communities' species abundance distributions (Roswell et al.

2021). We equalized samples at 90% coverage because this coverage allowed us to maximize the use of quadrats while requiring extrapolation of very few data points (Figure B2, B3). We then determined Hill diversity for each site, at each time point (before or after the heatwave), when q is equal to 0, 1 and 2 which relate to Hill-Richness, Hill-Shannon and Hill-Simpson, respectively (Roswell et al. 2021).

We performed three polynomial regressions with each Hill diversity measure as a response variable, as initial examination revealed nonlinear relationships among variables. These regressions were implemented using a Gaussian distribution in the 'glmmTMB' package (Magnusson et al. 2020). Each model included net primary productivity (NPP), marine heatwave period (before or after the heatwave), local anthropogenic stress (linear and quadratic relationships) and an interaction between time and local anthropogenic stress as fixed effects, with site as a random effect.

3.3.4 Beta Diversity Analysis

We considered beta diversity in two different contexts. Firstly, we considered the relationship between the heatwave and the community composition of individual sites through time. This allowed us to ask whether community composition was more or less affected by the heatwave when exposed to varying degrees of local anthropogenic stress. Secondly, we tested the relationship between beta dispersion (*i.e.*, dissimilarity across sites) and the combined effects of local anthropogenic stress and the heatwave. Specifically, this allowed us to determine whether either stressor (in isolation or through interacting effects) led to either biotic homogenization or heterogenization (Socolar et al. 2016). In both cases, we used Bray-Curtis dissimilarity to quantify beta diversity (Bray and Curtis 1957; Clarke et al. 2006; Anderson et al. 2011) as this allowed us to take into account relative abundances and exclude joint absences (Bray and Curtis 1957; Clarke et al. 2006; Anderson et al. 2011). There is currently no framework that can be used to apply coverage-based sampling to beta diversity analyses, so we standardized by quadrat number. Due to unequal quadrat sample sizes across sampling years (Table B1), 25 quadrats were randomly selected for each site, and we removed sites with fewer than 25 quadrats from analyses (*n* = 3, Figure B1, Table B1). As our interest was in community composition at the site level, we averaged the cover of each coral taxon across all 25 quadrats.

We visualized community composition across sites and timepoints using a distance-based Redundancy Analysis (dbRDA; ‘vegan’ package) with Bray-Curtis dissimilarity (Oksanen et al. 2019). We then used a PERMANOVA (1000 iterations) to compare the centroids of each time point (before and after the heatwave) and local anthropogenic stress level, including interactions. This allowed us to examine whether community composition changed due to the heatwave and local anthropogenic stress and whether these stressors interacted. We analyzed dispersion using the betadisper function to quantify the amount of variation due to the heatwave and local anthropogenic stress levels in site-level community composition (‘vegan’ package; Oksanen et al. 2019). Local anthropogenic stress categories were used but the High and Very High category were grouped as the High category contained a single sample. A two-way ANOVA was used to analyze differences in dispersion between anthropogenic stress categories and time block, and a Tukey’s HSD test was used to determine differences in the dispersion among local anthropogenic stress categories.

We performed multiple regressions on distance matrices (MRMs) to analyze how differences in stressor levels and spatial distances affects community composition differences due to the nature of the data being matrixes of distances and dissimilarities (Lichstein 2007), specifically a Bray Curtis dissimilarity matrix, a spatial distance matrix, and matrix of differences in level of local anthropogenic stress. We performed two MRMs, one on communities before the heatwave and one on communities after with Bray Curtis dissimilarity matrices of each respective community as the dependent matrix using the ‘ecodist’ package (Goslee and Urban 2007). Spatial distances were calculated using a least cost analysis in QGIS (version 3.16) to measure the distances among sites by water rather than as straight distances over land. Finally, a distance matrix was calculated from the absolute difference between the numeric local anthropogenic stress for each pairwise site. Then to compare across time (before and after the heatwave), we performed two Mantel tests, one on the Bray Curtis dissimilarity matrix before the heatwave and one after, with only the significant variable from the MRM analysis (difference in anthropogenic stressor level) as an independent variable. Then we used the coefficient values and 95% confidence limits to compare time blocks based on overlap.

3.3.5 Multiple Stressor Conceptual Model

We propose a conceptual model to describe the potential responses to multiple stressors, when stressors are a combination of discrete and continuous (Figure 3.1). This model can be used to formally examine whether the relationship between multiple stressors is non-interactive (*i.e.*, additive or dominance effects) or interactive (*i.e.*, synergistic or antagonistic effects), and whether the type of relationship varies by the degree of the continuous stressor. This is through the calculation of a standardized effect size, referred to here as the adjusted response (as the observed response has been adjusted to remove the additive response of the stressors), for each stressor in isolation and together. To calculate the adjusted response, we make comparisons of each sample (denoted by i) to each pristine 'unstressed' sample (denoted by k).

We defined the response actually experienced by each sample adjusted to the baseline response of unstressed samples as the 'observed response'. The observed response is the change in diversity metric that was actually experienced by each sample, which we normalized to metric values at samples that did not experience either stressor. We then calculated a null response, termed here the 'additive response' to determine whether this observed response differed from simple additive effects of both stressors. We calculated this by taking the sum of the independent responses to each stressor, quantifying how large the response would be if the stressors did not interact with each other. Finally, we calculated the independent response for each stressor by taking the difference of the diversity metric before and after each stressor.

The adjusted response for each sample i (*i.e.*, the deviation from additive expectation; AR_i), is the difference between the observed response for sample i ($\chi_{o,i}$) and the additive response if the effect of each stressor for sample i ($\chi_{a,i}$; Equation 2). The additive response for sample i ($\chi_{a,i}$) was therefore determined by taking the sum of the isolated response of the continuous stressor for sample i ($\chi_{c,i}$) and the isolated response of the discrete stressor (χ_d), a constant across samples (Equation 3).

$$AR_i = \chi_{o,i} - \chi_{a,i} \tag{2}$$

$$= \chi_{o,i} - \left(\chi_{c,i} + \chi_d\right) \tag{3}$$

To calculate the overserved response of both stressors for sample *i* ($\chi_{o,i}$) samples that experienced both stressors ($Y_{o,i}$) were compared individually to each pristine, ‘unstressed’ sample *k* ($Y_{u,k}$), and then averaged (Equation 4). For some scenarios, this calculation is equal to comparing each sample that experienced both stressors ($Y_{o,i}$) to the mean of the pristine ‘unstressed’ sites ($\overline{Y}_u$), however, to keep this methodology applicable for inclusion of pairwise similarity or dissimilarity indices, we have outlined the calculation of this metrics in this pairwise manner.

$$\chi_{o,i} = \frac{\sum_{k=1}^{n} \frac{Y_{u,k} - Y_{o,i}}{Y_{u,k}}}{n} \tag{4}$$

The isolated response of the continuous stressor for sample *i* ($\chi_{c,i}$) was calculated by comparing the samples that experienced only the continuous stressor ($Y_{c,i}$) to each pristine ‘unstressed’ sample *k* ($Y_{u,k}$), which was then averaged (Equation 5).

$$\chi_{c,i} = \frac{\sum_{k=1}^{n} \frac{Y_{u,k} - Y_{c,i}}{Y_{u,k}}}{n} \tag{5}$$

To calculate the isolated response of the discrete stressor (χ_d), which was a constant across sample *i*'s, the samples that experienced only the discrete stressor ($Y_{d,k}$) were compared to each pristine ‘unstressed’ sample *k* ($Y_{u,k}$), and then averaged (Equation 6).

$$\chi_d = \frac{\sum_{k=1}^{n} \frac{Y_{u,k} - Y_{d,k}}{Y_{u,k}}}{n} \tag{6}$$

3.3.6 Application of Conceptual Model

We used Kiritimati as a case study to investigate biological responses to multiple stressors, as the atoll provided a ‘natural experiment’ that allowed us to assess the relationship between two stressors, one of which was discrete (*i.e.*, the marine heatwave) and one of which was continuous (*i.e.*, local anthropogenic stress). Our biological responses of interest were alpha and beta diversity. For our study, during the calculations, we treated each sample as a single site during one sampling season. We followed the methods outlined above to calculate the adjusted response of each sample (denoted by i) to each pristine ‘unstressed’ sample ($n = 4$; denoted by k). We determined this adjusted response between the heatwave and the local anthropogenic stress for Hill-Richness, Hill-Shannon, Hill-Simpson and community composition data, to our discrete and continuous stressors.

Calculations were modified for the community composition data as the Bray-Curtis dissimilarity metric used measured how dissimilar communities are to each other. The above notation will not yield accurate results with a dissimilarity metric, as a smaller additive response than observed response, which would suggest synergy, will result in a negative adjusted response and be interpreted as antagonism. This is due to our metric being a dissimilarity index, and to account for this, all adjusted responses for dissimilarity indices are multiplied by a negative.

Finally, to assess if there are statistically significant tipping points or inflection points along the range of the continuous stressor, a breakpoint analysis was performed on each relationship examined, using the ‘strucchange’ package (Zeileis et al. 2019). A linear model was run on each relationship, or segment of relationship (if there is at least one significant breakpoint along the range of the continuous stressor), to determine the kind of relationship (additive, synergistic, antagonistic, or a combination with a tipping point) between stressors.

3.4 Results

3.4.1 Impacts of local and global stressors on alpha diversity

We found that all three Hill diversity measures (Hill-Richness, Hill-Shannon and Hill-Simpson) were significantly influenced by both local anthropogenic stress and the heatwave (Table 3.1). Prior to the heatwave there was a non-linear relationship between all three Hill diversity measures and the local anthropogenic stress gradient (Figure 3.2). As local anthropogenic stress increased, diversity also increased until a maximum was reached towards intermediate levels of stress, after which diversity declined (Table 3.1, Figure 3.2). This pattern was consistent across all three metrics of Hill diversity.

Regardless of the metric, there was a negative relationship between the marine heatwave negatively and alpha diversity across the atoll, such that sites tended to decrease in both richness and evenness (Table 3.1, Figure 3.2). The impact of the heatwave appeared to be greater for Hill-Shannon (average loss of 4.30 ± 0.462 SEM) and Hill-Simpson (average loss of 4.46 ± 0.478 SEM) metrics than Hill-Richness (average loss of 3.37 ± 0.664 SEM), though the difference was not very large (Hill-Shannon 1.28x larger and Hill-Simpson 1.32x larger than Hill-Richness; Table 3.1). While the impact of the heatwave on Hill-Shannon and Hill-Simpson was generally uniform across the local anthropogenic stress gradient, we found that the effect on richness depended on the strength of local anthropogenic stress. Specifically, Hill-Richness was the only diversity metric for which we identified a significant interaction between local anthropogenic stress and the heatwave (Table 3.1). Sites that experienced intermediate levels of local anthropogenic stress tended to retain greater richness through the heatwave (Table 3.2, Figure 3.2). In contrast, evenness decreased consistently across the local anthropogenic stress gradient such that local anthropogenic stress and the heatwave did not interact to influence Hill-Shannon and Hill-Simpson (Table 3.2, Figure 3.2).

3.4.2 Impacts of local and global stressors on beta diversity and community composition

The heatwave and the local anthropogenic stress gradient interacted significantly to impact coral community composition (PERMANOVA, $F = 4.41$, $p < 0.01$). Coral community composition was significantly impacted by both the marine heatwave (PERMANOVA, $F = 13.0$, $p < 0.001$) and local anthropogenic stress (PERMANOVA, $F = 3.42$, $p < 0.01$; Figure 3.3a), but sites that experienced higher levels of local anthropogenic stress tended to experience less change in composition during the heatwave (Figure 3.3a). *Acropora, Montipora* and *Pocillopora* were among the most abundant genera before the heatwave but became nearly absent from reefs after the heatwave. In particular, *Acropora* was more abundant at lower local anthropogenic stress sites while *Montipora* and *Pocillopora* were abundant at all sites before the heatwave. In contrast genera and species like *Porites, Platygyra* and *Goniastrea stelligera*, while experiencing a reduction in alpha diversity due to the heatwave, became more dominant in the community after the heatwave. *Porites* and *Platygyra* increased in dominance across the local anthropogenic stress gradient while *Goniastrea stelligera* increased in dominance at lower local anthropogenic stress sites. Together these changes in community composition contributed to the interaction between the local anthropogenic stress and the heatwave.

Although we found a significant effect of local anthropogenic stress on community dissimilarity before the heatwave (MRM, $b = 0.029$, $p < 0.05$) and after (MRM, $b = 0.037$, $p < 0.01$; Figure 3.3d), there was no effect of spatial distance between sites on community dissimilarity prior to (MRM, $b = 0.0009$, $p = 0.92$) or following (MRM, $b = – 0.020$, $p = 0.15$; Figure 3.3c) the heatwave. Sites that experience very different levels of local anthropogenic stress were more ecologically dissimilar (Figure 3d) and there is no difference in the amount of community composition dissimilarity between sites before (Mantel Test, 0.56, + 0.70, – 0.36; mean ± 95%CI) and after (Mantel Test, 0.54, + 0.69, – 0.38; mean ± 95%CI) the heatwave. This indicates that although our highly stressed sites are spatially clustered on the atoll, space alone cannot explain the observed patterns.

We found no significant difference in the amount of dispersion in community composition before and after the heatwave (ANOVA, $F = 0.106$, $p = 0.75$) and no significant interaction between both stressors (ANOVA, $F = 0.588$, $p = 0.630$), but that there was a significant difference in the amount of variation in community composition among the local anthropogenic stress categories (ANOVA, $F = 3.69$, $p < 0.05$; Figure 3.3a,b). The combined High and Very High anthropogenic stress categories have significantly higher community dispersion than the Medium category (Tukey's HSD, $p < 0.05$), but there were no other significant differences in the amount of community composition dispersion between other anthropogenic stress categories (Tukey's HSD, $p > 0.05$; Figure 3.3a,b).

3.4.3 Stressor relationships and tipping points

The type of relationship between multiple stressors depended on the underlying strength of anthropogenic stress. For Hill-Richness, we found a tipping point at moderate levels of local anthropogenic stress (lm, $p < 0.05$; Figure 3.1, 3.4a) below which there was an additive response, but as it increased above the tipping point, it tended towards synergy. At low levels of local anthropogenic stress, the relationship between the impact of both stressors on Hill-Richness (the adjusted response of Hill-Richness) and local anthropogenic stress had both a non-significant intercept and slope (lm, $p > 0.05$), consistent with an additive, rather than an interactive response. Beyond the tipping point, we found that the relationship between adjusted response and local stress had both a significant intercept (lm, $t = – 2.73$, $p < 0.05$) and slope (lm, $t = 2.62$, $p < 0.05$). When we examined the relationship with the 95% confidence intervals, this suggests that the adjusted response increases with the local stress has not reached high enough local stress to become significantly synergistic but is significantly increasing towards synergy, as the confidence intervals still overlap the x-axis (Figure 3.4a). This shows that sites at low levels of local anthropogenic stress responded to both stressors at the magnitude expected by our additive model, the summation of the adjusted response of both stressors in isolation. However, high local anthropogenic stress sites showed larger adjusted responses to both stressors than predicted under the additive model due to both stressors interacting with each other.

We examined the relationships between stressors for Hill-Shannon and Hill-Simpson diversity metrics to ensure our conceptual model would support our earlier finding that there was no significant interaction between these diversity metrics and the stressors. We identified that this relationship was additive (Figure 3.4b,c), as adjusted responses had non-significant intercepts and slopes as well as no significant inflection point (lm, $p > 0.05$). We found a significant negative relationship between the adjusted response of coral community composition along the range of the local anthropogenic stress (lm, $t = -4.41$, $p < 0.001$; Figure 3.4d), showing that there was a significant effect of the local anthropogenic stress on the adjusted response of coral community composition. There was no significant tipping point along the range of the local anthropogenic stress, nor a significant intercept (lm, $p > 0.05$) and when we examined the 95% confidence intervals, we found that the relationship between the adjusted response of coral community composition for both stressors become more antagonistic as the local anthropogenic stress increased (Figure 3.4d).

3.5 Discussion

In this study, we demonstrated that the relationships between multiple stressors can depend strongly on stressor strength as well as the metric of diversity compared. We found the effect of global and local stressors on Hill-Richness transitioned from additive towards synergistic at intermediate levels of anthropogenic stress. In contrast, we found that the relationship between stressors was antagonistic when considering the relationships between these stressors and coral community composition. Individually, both local and global stressors affected diversity measures, though not all relationships were linear. There was also an increase in the dispersion of coral communities at Very High / High anthropogenic stress compared with Medium, showing an increase in beta diversity at higher local anthropogenic stress sites. The development of a framework to examine multiple stressors when there is a continuous stressor allowed for complex relationships to be examined within our study system. This framework may reconcile conflicting results from past multiple stressor work, and give further insights into community responses to stressors

3.5.1 Stressor relationships depend on the strength of stressors

Other studies describing and investigating the effects of multiple stressors used discrete stressors, for which effect sizes are straightforward to calculate and relationships between stressors can be easily analyzed (Crain et al. 2008; Darling et al. 2013; McClanahan et al. 2014; Côté et al. 2016; Galic et al. 2018). The local anthropogenic stress gradient on Kiritimati enabled us to examine multiple stressors, one of which was a continuous stressor. If one stressor occurs on a continuous gradient such as the degree of local anthropogenic stress, a single effect size cannot be calculated for that stressor (Dunne 2010), as there may be differences in the effect size along the continuous gradient. Through analysis of the local anthropogenic stress gradient, we created a framework (Figure 3.1) from which experiments examining one discrete and one continuous stressor can be examined to determine if the relationship between stressors shows an antagonistic, synergistic or additive (null) result. Having a framework through which we could compare the relationships between on coral diversity, we were able to detect tipping points and discover that relationships for some diversity metrics were dependent on the level of local anthropogenic stress.

Our findings may explain why some studies report antagonist responses and others with the same system and stressors report additive or synergistic responses (Crain et al. 2008; Carilli et al. 2009; Darling et al. 2013; McClanahan et al. 2014; Jackson et al. 2016). However, if studies that report conflicting results were to quantify the degree of stress being experienced by a study system and relate the effect size (adjusted response) to a continuous stressor, we may begin to see important tipping points within systems. The presence of tipping points would indicate that relationships are dependent on the level of stress, which may be why studies report conflicting results. This would not only help resolve conflicting conclusions within the literature but help to unify our understanding of multiple stressors relationships in environments and if there are critical levels of stress than conservationists should be concerned with as they result in large changes to our environments.

3.5.2 Co-tolerance in coral richness depends on local anthropogenic stress

The relationship between both stressors for richness measures was additive at low levels of local anthropogenic stress, then after its tipping point at a low level of local anthropogenic stress, the response increased significantly with local anthropogenic stress. This increasing interactive response may not be significantly synergistic in our data, but it is significantly increasing towards synergy. The presence of this tipping point for richness clearly demonstrates that the type of relationship can vary with the strength of the continuous stressor.

The heatwave disproportionately impacted richness at very low and very high levels of local anthropogenic stress, relative to intermediate levels. We hypothesized that there would be a greater loss in richness at sites with minimal local anthropogenic stress due to the loss of non-tolerant rare species or genera. These sites may be less tolerant to the heatwave, because absence of local anthropogenic stress would not have previously eliminated non-tolerant taxa (Tomascik and Sander 1985; Fabricius 2005). Species not exposed previously to local anthropogenic stress may be intolerant of both stressors, while species that had tolerated local anthropogenic stress may also better tolerate the heatwave (Tomascik and Sander 1985; Fabricius 2005). A small amount of local anthropogenic stress may ensure that the corals present can tolerate stress, resulting in a positive co-tolerance with the heatwave and a greater survival of species or genera (Tomascik and Sander 1985; Fabricius 2005). Specifically this may have included rare taxa as was seen by the highest richness prior to the heatwave and the smallest reduction in richness due to the heatwave tending to occur at low local anthropogenic stress levels (Tomascik and Sander 1985; Fabricius 2005). The addition of nutrients from villages and human actions may facilitate coral growth (Tomascik and Sander 1985; Fabricius 2005) supporting the growth of a wider range of coral species or genera. However, at very high levels of local anthropogenic stress, increases in nutrients may become detrimental, due to algal growth, high sedimentation rates, and intense fishing pressure reducing growth and survival of corals, leading to large reductions in already rare species or genera (Fabricius 2005; Fabricius et al. 2005; Erftemeijer et al. 2012). This could have led to our sites that experienced very high local anthropogenic stress tending to show a reduction in richness prior to the heatwave and larger losses in richness due to the heatwave when compared to low local anthropogenic stress sites (Fabricius 2005; Fabricius et al. 2005; Erftemeijer et al. 2012).

Past studies on Kenyan reefs that examined coral life histories reported no co-tolerance between a heat stress event and local anthropogenic stress (Darling et al. 2013; McClanahan et al. 2014). However, when corals are examined at a higher taxonomic resolution (genera or species) and over a gradient of local anthropogenic stress as we show in our study, co-tolerance may be possible under lower levels of anthropogenic stress. Additionally, we found that the relationship between alpha diversity and the local anthropogenic stress gradient is not linear but stressor-dependent, suggesting that coral communities are susceptible to the degree of anthropogenic stress. Our Hill diversity results show in the absence of any local anthropogenic stress, alpha diversity is low, but under low levels of local anthropogenic stress, alpha diversity increases.

3.5.3 Antagonistic interactions in coral community composition

As alpha diversity does not consider the identity of coral taxa that are lost, beta diversity was examined to determine how community structure differed or remained the same due to the heatwave and the local anthropogenic stress. The interaction we saw in richness on Kiritimati was accompanied by an interaction in community composition as well, but community composition had an antagonistic response to the presence of both stressors. This interactive response in community composition may be due to the greater losses in coral richness at sites experiencing higher anthropogenic stress levels as well as changes in coral identity. Before the heatwave, higher anthropogenic stress sites had lower abundance of corals, which may have led to smaller changes in community composition after the heatwave, compared to lower anthropogenic stress sites that experienced large losses in coral cover (Baum unpublished data) as well as changes in coral identity, resulting in an antagonistic interaction.

Among sites, communities experiencing very low local anthropogenic stress differed more in abundance and identity of species, than those at higher local anthropogenic stress. Variation in low local anthropogenic stress communities may be mediated by different abiotic conditions between sites, as these sites experienced different levels of wind exposure and net primary production. Greater losses in richness for Very Low and Very High local anthropogenic stress combined with losses in coral abundance and differences in species and genera identity between sites, may have resulting in the interaction between the heatwave and the local anthropogenic stress on coral community composition.

We ensured that differences in coral community composition were not due to the spatial patterns of our study site, where dispersal could be restricted between sites that are on opposite sides of the atoll from each other and sites experience differing abiotic conditions such as wind exposure and net primary production. However, we found no relationship between the dissimilarity between sites and how close the sites were from each other by water. This is consistent with other studies which found that corals on the same reef and across reefs, are able to disperse well, such that beta diversity it not primarily determined by spatial separation (Cornell et al. 2007), but may suggest that there is minimal interactions between species influencing their cooccurrence (McDevitt-Irwin et al. 2021). This is an interesting result, as spatial patterns are expected to influence community structure due to shared environmental conditions (Borcard et al. 1992). The differences in community structure appear to be influenced by the difference in stress between sites despite there being no effect of spatial separation, suggesting that a significant factor affecting changes community composition is the local anthropogenic stress gradient.

Differences in community composition were accompanied by differences in the amount of beta dispersion within each anthropogenic stress category. However, there was no significant effect of the heatwave on the amount of beta diversity on Kiritimati. We found that beta diversity was greater at sites that experience Very High / High anthropogenic stress, and we propose that highly stressed communities became dissimilar to each other through the process of subtractive heterogenization (Socolar et al. 2016). A loss in coral cover and diversity, as seen through our alpha diversity results may occur through subtractive heterogenization if the loss of diversity does not result in the survival of a few stress-tolerant taxa that are common between sites but causes the death of the common and widespread taxa, leaving behind a few rare taxa which differ in identity among sites, leading to higher overall beta dispersion. Our increase in beta diversity after a stressor is similar to the Anna Karenina principle described in beta diversity of coral microbes, where community composition is altered under the response of stressors so that communities become more different from each other, while unstressed communities look very similar to each other (Zaneveld et al. 2017; Ahmed et al. 2019). This differs from the common narrative that stress leads to homogenization in reef communities and therefore decreases in ecosystem functioning (Aronson et al. 2004; Isbell et al. 2011; Burman et al. 2012; Riegl et al. 2012, 2013; Darling et al. 2013; McClanahan et al. 2014; Tilman et al. 2014). However, heterogenization of reefs does not mean that there is sufficient ecological diversity, or substrate complexity to support reef recovery after stressors. As Kiritimati did not experience homogenization of coral diversity due to the heatwave and the local anthropogenic stress, there may be great potential for recovery due to genetic diversity still present on the island. However, the implications of heterogenization on ecosystem functioning and community recovery needs to be examined further.

3.6 Conclusion

Relationships between multiple stressors may depend on the strength of underlying stressors as well as the metric of diversity compared. We introduce a framework for examining how the combined effects of discrete and continuous stressors affect ecosystems, including a novel examination of tipping points within multiple stressor interactions. Co-tolerance for new stressors such as heatwaves, can be dependent on the degree of local anthropogenic stress, meaning local management practices may influence how species respond to heatwaves. Our results provide context and a critical new framework for predicting the future composition and function of coral reef ecosystems experiencing multiple stressors. This study is important for increasing our understanding of relationships between multiple stressors and coral diversity, which can be used to understand diversity in other environments as well.

3.7 Tables and Figures

Table 3.1. Parameter estimates for fixed effects from polynomial regression models describing the factors influencing Hill-Richness, Hill-Shannon and Hill-Simpson diversity.

Model	LAS - 1º poly	LAS - 2º poly	MHW	LAS - 1º poly : MHW	LAS - 2º poly : MHW	NPP
Hill-Richness	2.80	**– 7.76****	**– 3.37*****	– 3.80	**– 8.98****	– 0.014
Hill-Shannon	1.55	**– 7.76*****	**– 4.30*****	– 1.31	– 2.03	– 0.011
Hill-Simpson	0.48	**– 7.39*****	**– 4.46*****	– 0.073	0.79	– 0.0075

Note: LAS = local anthropogenic stress; MHW = before or after the heatwave; 1º poly = first order polynomial, the linear term; 2º poly = second order polynomial, the quadratic term; NPP = max net primary productivity. Boldface indicates statistical significance ($\alpha = 0.05$; **p* < 0.05, ***p* < 0.01, ****p* < 0.001).

Table 3.2. Mean (± SEM) loss in diversity for each local anthropogenic stress (LAS) category after the heatwave. High and Very High category were grouped due to single sample in the High category.

LAS Category	Hill-Richness	Hill-Shannon	Hill-Simpson
Very Low (*n* = 4)	4.47 ± 0.724	4.30 ± 1.03	4.10 ± 0.980
Low (*n* = 3)	1.99 ± 1.94	4.63 ± 1.39	5.33 ±1.32
Medium (*n* = 6)	1.65 ± 1.00	3.68 ± 0.945	4.30 ± 0.997
Very High & High (*n* = 4)	5.86 ± 0.812	5.00 ± 0.451	4.39 ± 0.782

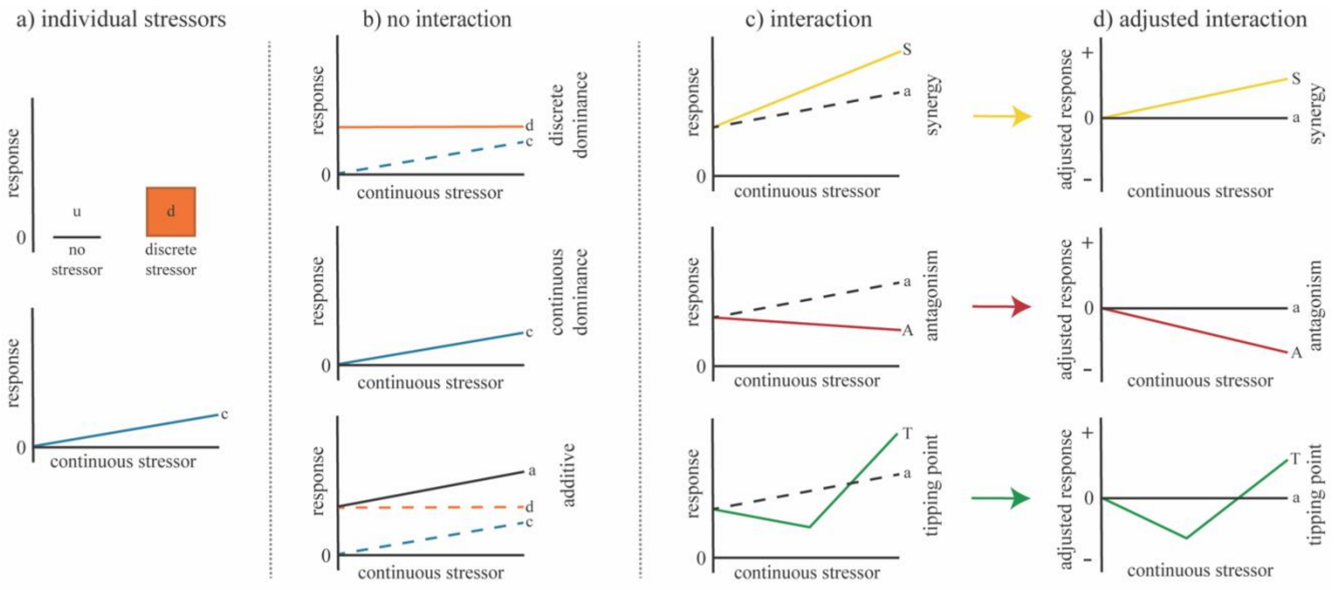

Figure 3.1. Models of potential responses to multiple ecosystem stressors, when the individual stressors are a combination of discrete and continuous. *(a)* Two individual stressors, one a **discrete stressor** (**d**; orange bar) and one a **continuous stressor** (**c**; blue line), acting separately in a biological system elicit individual responses (a change due to the stressor that can be quantified), here in the same direction. *(b)* When there is no interaction between the stressors, their combined effect on the biological response could be equal to the effect of one of the two stressors (*i.e.*, dominance effect), or to the sum of the two stressors (*i.e.*, additive effect). Dominance of the discrete stressor (orange line) will elicit a constant response across the continuous stressor (**c**; dashed blue line), whereas when the continuous stressor is dominant (**c**; blue line) the response will increase with it. An **additive effect** (**a**) will show the same trends over the continuous gradient as those seen for the individual continuous stressor, but the response will be shifted upwards by the magnitude of the discrete stressor (**a** = **c** + **d**; black line = blue line + orange line). *(c)* Interactions between the two stressors can produce a **synergistic response** (**S**; yellow line) when the response seen across the continuous stressor is larger than the additive effects (**a**; black line) of both stressors; an **antagonistic response** (**A**; red line) when the response seen across the continuous stressor is smaller than the additive effects (**a**; black line) of

both stressors; or a **tipping point response** (**T**; green line), when there is a point along the continuous stressor, where there is a shift from one type of response to another. The tipping point response shown here is a shift from antagonism to synergy around the center of continuous stressor. *(d)* When the response is adjusted so that the additive response is seen as the baseline (**a**; black line), synergistic responses produce a positive response (**S**; yellow line), antagonistic responses produce a negative response (**A**; red line) and tipping point responses (**T**; green line) can show both negative and positive responses, depending on the value of the continuous stressor.

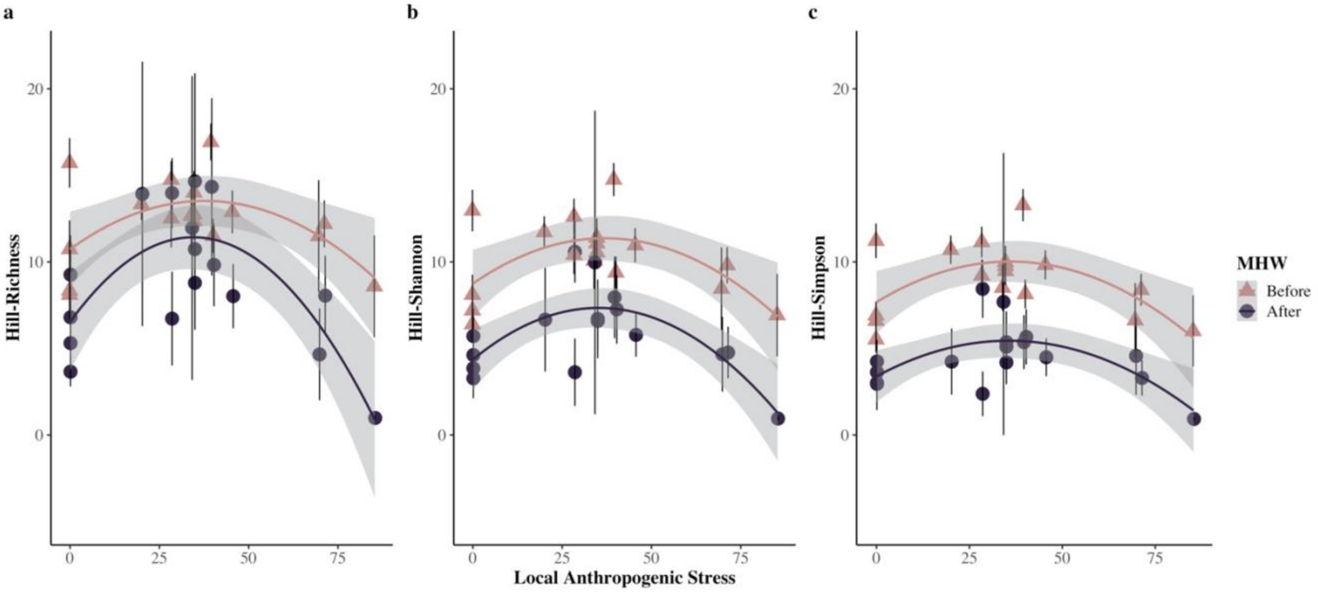

Figure 3.2. Relationships between coral diversity (assessed via *(a)* Hill-Richness, *(b)* Hill-Shannon, and *(c)* Hill-Simpson) and chronic local anthropogenic stress (quantified as a relative index), before and after a prolonged marine heatwave (MHW). Vertical bars represent 95% confidence limits for each site, and grey shading is the standard error for the polynomial lines.

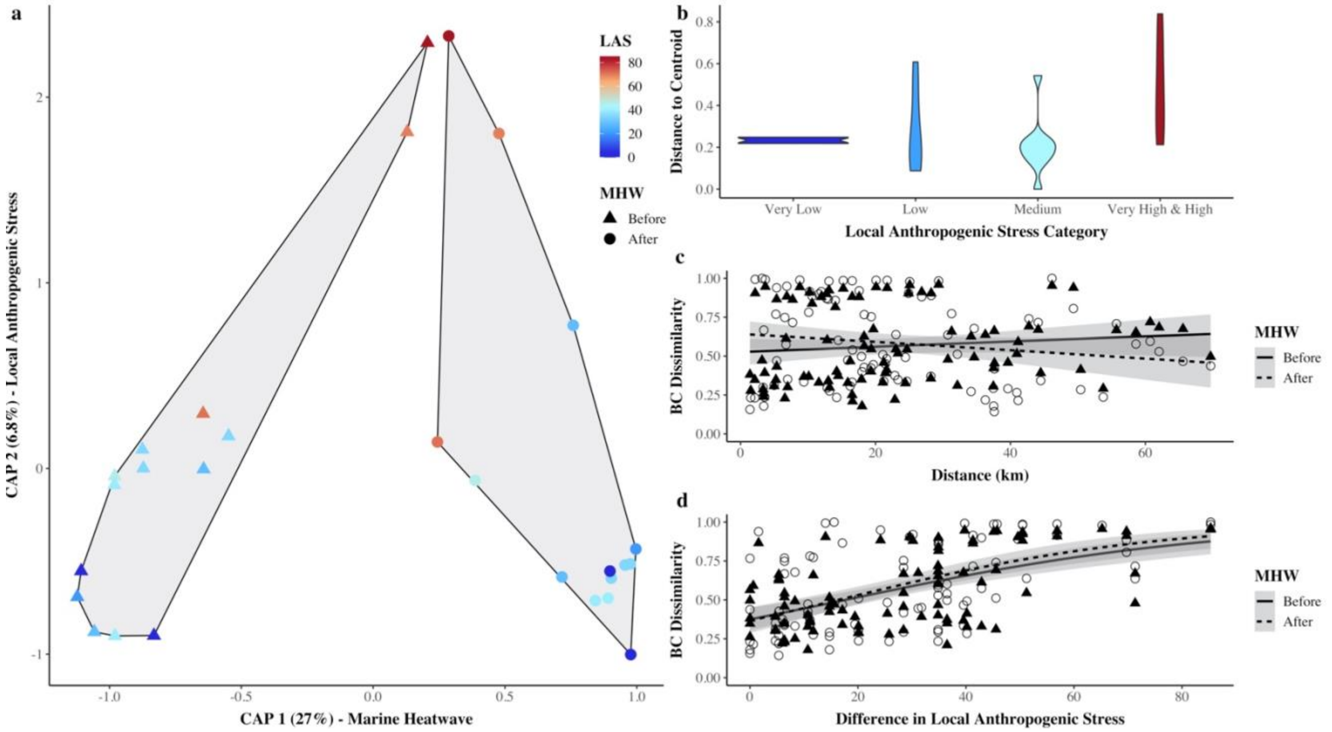

Figure 3.3. Influence of global (marine heatwave (MHW) and local (coastal development, fishing, pollution) stressors on coral community composition, assessed via different beta diversity analyses. *(a)* Site-level coral community composition (db-RDA), before (▲) and after (●) a prolonged marine heatwave, with sites coloured by intensity of underlying chronic local anthropogenic stress (LAS). Grey hulls group time blocks together. *(b)* the distance to centroid for four categories of local anthropogenic stress, showing increased variability in coral community composition between sites as a larger distance to centroid. The width of the violin shape representing relative locations of samples. *(c)* the Bray-Curtis (BC) dissimilarity with the respective distance between sites for all pairwise site combinations, separated by marine heatwave period. *(d)* the Bray-Curtis (BC) dissimilarity with the difference in the local anthropogenic stress between sites for all pairwise site combinations, separated by marine heatwave period.

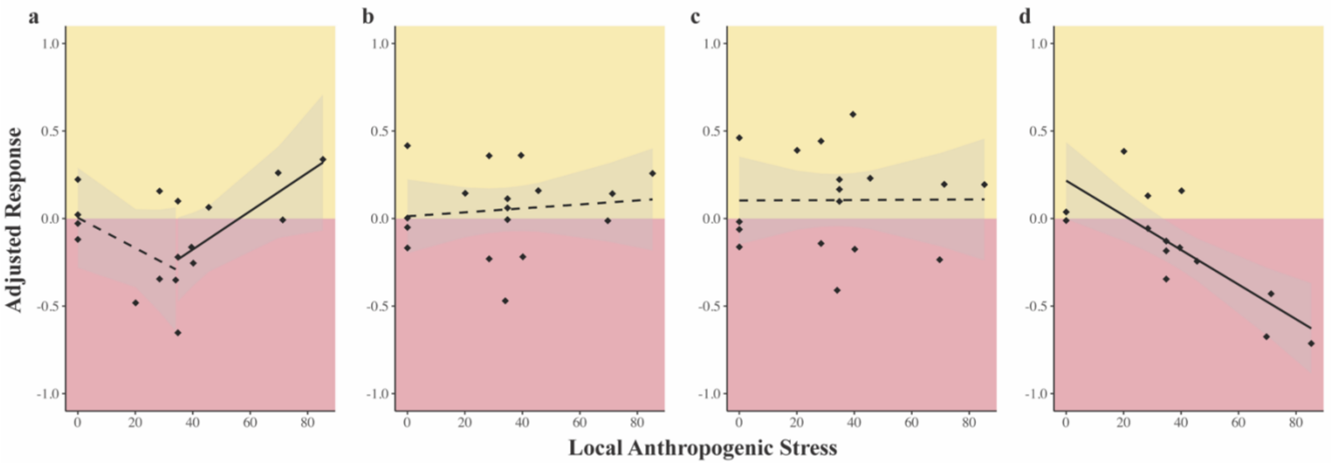

Figure 3.4. Application of conceptual models describing potential responses to multiple stressors, when stressors are a combination of discrete and continuous, to coral diversity analyses. Adjusted responses are quantifiable changes due the stressors that were adjusted so that the additive response is seen as a baseline (Figure 3.1). *(a)* Adjusted response for changes in Hill-Richness, after the heatwave, over the local anthropogenic stress gradient. Shows tipping point interaction. Polygon shows standard error. *(b)* Adjusted response for changes in Hill-Shannon, after the heatwave, over the local anthropogenic stress gradient. Shows no interaction, indicated by a dashed line ± standard error. *(c)* Adjusted response for changes in Hill-Simpson, after the heatwave, over the local anthropogenic stress gradient. Shows no interaction, indicated by a dashed line ± standard error. *(d)* Adjusted response for changes in Bray-Curtis community composition, after the heatwave, over the local anthropogenic stress gradient. Shows antagonistic interaction. Grey shows standard error. Non-significant slopes are dashed, and significant slopes are solid.

Chapter 4 - Conclusion

Coral reefs are the marine ecosystem considered most at risk from climate change (IPCC 2019) and as coral reef ecosystems have some of the highest biodiversity on Earth (Plaisance et al. 2011; Putnam et al. 2017), losses of coral reef environments could have devastating consequences to our planet (Hoegh-Guldberg et al. 2007; Hughes et al. 2017; IPCC 2019). There are no reefs today which have escaped degradation entirely (Knowlton and Jackson 2008), though some have experienced the effects of local and global stressors to a lesser degree than others (Wilkinson 2008; Walsh 2011; Blowes et al. 2019). As corals are a foundational species and ecosystem engineer in tropical reef ecosystems, large scale losses in coral cover and diversity due to local and global stressors/disturbances could have devastating impacts on the biodiversity and functioning of coral reef ecosystems and the oceans in general (Isbell et al. 2011, 2017; Putnam et al. 2017). Additionally, lesser studied soft corals may provide complex habitats and support different organisms than hard corals, also making them an important component to coral reef environments (Alvarez-Filip et al. 2011; Poulos et al. 2013; Valisano et al. 2016; Paoli et al. 2017; Sánchez 2017).

Marine heatwaves and local human disturbance are two stressors that are estimated to present the highest threats to coral reef survival (Wilkinson 2008; Oliver et al. 2018; IPCC 2019; Smale et al. 2019). While there is research examining how each of these stressors affect hard coral diversity (Aronson and Precht 1995; Crain et al. 2008; Butchart et al. 2010; Gomez et al. 2018; Hughes et al. 2018), less is known about how these stressors interact (Darling et al. 2013; Donovan et al. 2020; Montefalcone et al. 2020), especially if considering local anthropogenic stress on a continuous scale. Even fewer papers examine how soft corals are affected by disturbances (Dinesen 1983). By examining the gradient of local human disturbance on Kiritimati and the effect of the 2015/2016 El Niño event, this thesis examines how local and global disturbances influence soft coral communities and how the interaction of these stressors affects hard and soft coral diversity.

In the second chapter of this thesis, my literature review demonstrated that soft corals are understudied, which has led to very little being recorded/known about how disturbances such as marine heatwaves affect soft coral survival (Figure 2.1). In my analysis of soft coral on Kiritimati, I demonstrated that they are extremely vulnerable to heatwaves, as all soft corals in my study site died after exposure to the 2015/2016 El Niño event. Further my analysis suggests that they are less impacted by local human populations than they are by abiotic conditions such as wave exposure and net primary productivity (Table 2.1). However, there were no soft corals at very high disturbance sites prior to the heatwave, making it difficult to disentangle whether the cause of this was due to local human disturbance or abiotic factors, so more investigations into this are needed to tease this apart. With extreme climate events only predicted to continue to increase in intensity and frequency (Knutson et al. 2010; Dettinger 2011; Cai et al. 2014, 2015; Bacmeister et al. 2018), soft corals and potentially the species that rely on soft corals for habitat, recruitment or protection are vulnerable to losses during heatwaves. Very little is known about soft corals and their environmental interactions, so the loss of soft corals could have substantial impacts on coral reef environments that are not currently being accounted for. A species does not need to be in high abundance to be important, as is the case for keystone species (Bond 1994), and as hard corals are important ecosystem engineers and foundational species (Moberg and Folke 1999; Putnam et al. 2017), soft corals may also play such crucial roles in coral reef ecosystems.

Within my second chapter, I also documented the persistence of soft coral skeletons three years after the coral mortality and the recruitment of hard corals onto those skeletons (Figure 2.4). This may have larger impacts on reef structure and integrity under ocean acidification due to the different forms of calcium carbonate among soft and hard corals (Konishi 1982; Andersson et al. 2005; Rahman et al. 2011; Eyre et al. 2014; Januar et al. 2017; Shoham et al. 2019). With predictions of soft coral dominated communities becoming more common with increasing ocean acidification (Inoue et al. 2013; Gómez et al. 2015), this could mean large scale changes to reef structure and ecosystems, especially if soft corals are more susceptible to marine heatwaves. In order to understand how changes in environmental conditions and marine heatwaves will alter soft coral communities, more research is needed to document changes in soft coral cover in long-term monitoring projects, and researchers need to report findings regarding soft corals in the literature. This will allow for reviews synthesizing the trends in soft coral cover changes to provide an understanding of the conditions that need to be present for soft coral survival, recovery or persistence in environments, which can then be used to inform conservation decisions.

In chapter three, I examined how multiple stressors interact to affect coral diversity, at various scales using data from Kiritimati collected between 2013 and 2017. These analyses showed that at different scales, such as alpha or beta diversity, there are differences in how local and global stressors interact, affecting corals (Figure 3.4). For beta diversity (*i.e.*, coral community composition across sites), I found an antagonistic response between the heatwave and local anthropogenic stress for community composition, such that as the degree of local anthropogenic stress increased, there was an increasingly smaller than additive interactive response by community composition due to both stressors (Figure 3.3, 3.4). In contrast, for coral richness, I found at low levels of local anthropogenic stress that there was an additive response due to the effects of both stressors. At an intermediate anthropogenic stress level, there was a significant tipping point that changes the interactive response for coral richness due to both stressors from an additive response to an increasingly synergistic response (Figure 3.2, 3.4). Not only do these results show the importance of quantifying the degree of stress that is being experienced by the corals in order to understand the effect both stressors will have on coral diversity, but it led to the description of a framework for discrete and continuous stressor relationships (Figure 3.1).

Current literature examining multiple stressors examines discrete stressors even when many of the stressors could be quantified on a continuous scale (Done 1982; Crain et al. 2008; Fabricius et al. 2008; Darling et al. 2013; McClanahan et al. 2014; Côté et al. 2016; Galic et al. 2018; Donovan et al.

2020; Montefalcone et al. 2020), leading to generalizations regarding stressor interactive relationships. Using the framework outlined in this thesis (Figure 3.1), our understanding of how multiple stressors interact can be expanded to include ranges of stressors, and new complex dynamics, such as tipping points where the types of relationships are dependent on the strength of the stressor. This is important to apply understandings of multiple stressors to larger scales, or new areas, especially for conservation initiatives.

Coral reefs are at risk of continuing to decline in health and cover (IPCC 2019), especially from heatwaves and local anthropogenic stress (Wilkinson 2004, 2008), and as such, many countries and organizations are trying to find innovative and unique solutions to battle the harmful effects of these stressors (Coelho et al. 2017; Damjanovic et al. 2017; Rodgers et al. 2017; Biscéré et al. 2018). However, local mitigation strategies may not be as effective, or effective at all, for protecting and restoring coral populations if the relationships between corals and their environments are not understood. Increased research into other aspects of coral reef communities, such as soft corals, and how coral responses change with various degrees of stressors, can inform policy makers and conservationists so that the strategies used to help coral comminutes to survive into the future, will be effective and preserve as much biodiversity as possible. Failing to consider tipping points may lead conservationists to apply an incorrect strategy to communities, where it could have a beneficial impact for some but be devastating for others. This could be due to the presence of tipping points changing how stressors interact at different magnitudes, or due to the presence or absence of less well studied organism, such as soft corals.

Kiritimati provided a great site at which to test how a local anthropogenic stress gradient and marine heatwave interact to affect coral diversity, and how soft corals vary within an ecosystem, but this study encompasses one atoll. The long-term monitoring done on Kiritimati by the Baum Lab provided strong baseline data from which I was able to assess how marine heatwaves impact coral reef communities. These results are a great start and provide framework that can be used by future researchers, but more is needed. To understand coral reef communities and how coral reefs will be impacted as our oceans continue to change, there needs to be more studies, from many countries and marine environments to be able to determine if there are consistencies among coral reef communities that or if each community will require completely unique mitigation strategies. It is my goal with this thesis to begin conversations and investigations into how soft corals and the inclusion of continuous stressors in multiple stressor investigations can increase our understanding of these impacts on coral reefs and ensure the survival of these crucial and beautiful environments in the future.

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Appendices

Appendix A: Supplemental information for Chapter 2

Table A1. Number of quadrats in each year for each site on Kiritimati. Heat wave years are show in shaded grey

Region	**Site Name**	**2007 - Jul**	**2009 - Aug**	**2010 - May**	**2011 - Jul**	**2013 - Jul**	**2014 - Aug/Sep**	**2015 - Jan**	**2015 - May**	**2015 - Jul**	**2016 - Mar**	**2016 - Nov**	**2017 - Jul**	**2018 - Jun**	**2019 - Jul**
Bay of Wrecks	**VL13**	28	20	0	17	0	0	0	0	0	0	0	0	0	0
	VL8	28	28	0	24	0	0	0	0	0	0	0	20	0	0
	VL2	30	28	26	21	20	0	0	0	27	0	0	26	0	0
	VL12	0	22	0	0	0	0	0	0	0	0	0	0	0	0
	VL1	30	23	26	25	23	0	26	14	29	27	30	30	30	0
	VL11	28	26	0	0	0	0	0	0	0	0	0	0	0	0
	VL5	28	0	0	0	30	0	0	0	0	0	0	17	0	0
	VL9	26	0	0	0	0	0	0	0	0	0	0	0	0	0
	VL10	30	0	0	0	0	0	0	0	0	0	0	0	0	0
	VL6	17	21	32	0	0	0	0	0	29	0	0	22	0	0
North Shore	**L5**	30	28	0	0	25	0	0	0	0	0	0	29	0	0
	M10	22	30	0	0	28	0	0	0	0	0	0	29	0	0
	M9	30	20	0	0	18	0	0	0	0	0	0	0	0	0
	L6	25	28	0	0	0	0	0	0	0	0	0	0	0	0
	L3	29	35	0	21	31	0	0	0	0	0	0	0	0	0
	L2	0	25	0	20	0	31	0	0	29	29	0	0	28	28
	L1	28	20	30	25	27	32	0	0	29	0	0	29	28	23
	M5	30	22	21	24	25	25	0	0	30	0	0	15	26	0

North Lagoon	**H2**	30	27	22	25	30	0	0	0	0	0	0	29	0	0
	VH3	30	28	23	0	28	25	30	30	30	30	30	30	16	28
	VH1	30	26	18	24	26	30	30	30	29	29	30	29	29	30
	VH4	20	27	20	26	0	0	0	0	0	0	0	20	0	29
Mid Lagoon	**VH2**	10	18	18	24	30	0	0	30	30	30	30	30	30	28
	H1	0	21	0	0	0	0	0	0	0	23	30	31	0	25
	M12	21	27	0	27	0	0	0	0	0	30	0	31	0	0
	L4	35	28	13	27	24	0	0	0	0	30	0	30	0	0
South Lagoon	**M3**	22	27	23	19	28	31	0	30	29	30	30	29	27	30
	M2	21	20	44	25	26	31	30	30	29	26	30	27	30	28
	M1	30	0	0	0	28	27	30	30	30	30	30	29	30	29
	M4	29	22	22	25	13	21	0	0	29	16	0	30	0	0
	M6	29	19	0	27	27	0	0	0	0	0	28	30	0	29
Vaskess Bay	**M7**	30	20	0	0	0	0	0	0	0	0	0	25	0	0
	M8	30	0	0	0	0	0	0	0	0	0	0	22	0	0
	M11	28	25	0	0	0	0	0	0	0	22	30	31	0	27
	L7	30	0	0	0	0	0	0	0	0	0	0	0	0	0
	VL7	21	22	0	0	0	0	0	0	0	0	0	25	0	0
	VL3	29	0	0	0	0	0	0	29	30	30	29	26	29	29
	VL4	22	27	0	0	0	0	0	0	0	29	30	29	29	27
Korean Wrecks	**VL15**	21	0	0	0	0	0	0	0	0	0	0	0	0	0
	VL14	21	0	0	0	0	0	0	0	0	0	0	0	0	0

Table A2. Models describing the factors influencing mean soft coral cover prior to the heat stress event. Plus signs (+) indicate which variables were included in each model. Years analyzed were July 2007 to May 2015.

Rank	HD	WE	Region	NPP	HD * WE	HD * Region	*df*	AICc	ΔAICc	w_i
1			+				9	-96.5	0	0.531
2	+		+				10	-94.8	1.74	0.223
3	+	+		+			6	-93.8	2.73	0.136
4	+		+	+			11	-91.5	5.03	0.0429
5	+	+			+		6	-90.9	5.61	0.0321
6	+	+					5	-90.2	6.29	0.0229
7		+					4	-87.1	9.38	0.00486
8	+						4	-87.1	9.43	0.00475
9				+			4	-85.8	10.7	0.00257
10	+			+			5	-84.5	12.1	0.00128
11	+		+			+	16	#N/A	#N/A	#N/A
12	+	+	+	+			12	#N/A	#N/A	#N/A

Note: HD = local human disturbance; WE = wind exposure; NPP = max net primary productivity; *df* = degrees of freedom; AIC_c = AIC corrected for small sample sizes; ΔAIC_c = difference from the lowest AIC_c value, all models are shown; w_i = model weight for each model.

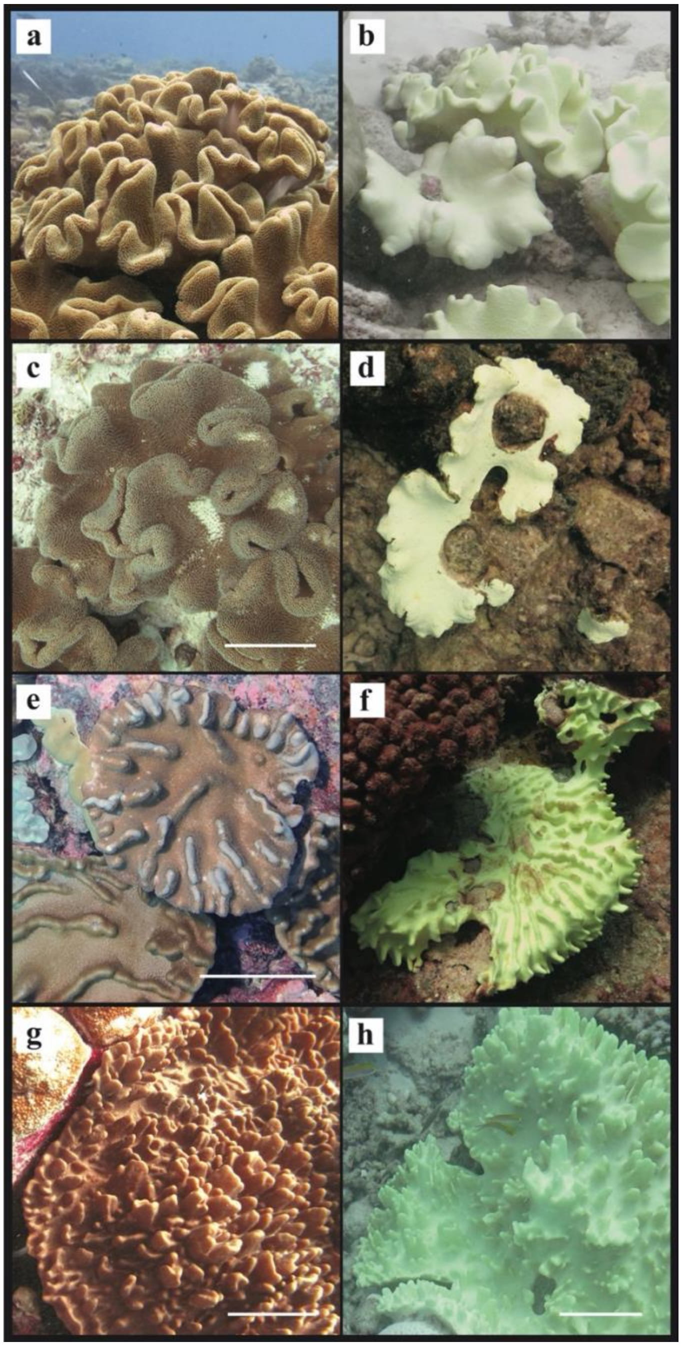

Figure A1. Examples of healthy soft corals compared to bleaching soft corals of the same species. Scale bars showing approximately 10 cm when scale could be determined *(c, e, g and h)*. Note: comparisons are not of the same coral colony. *(a-d) Sarcophyton (e-f) Lobophytum (g-h) Sinularia*.

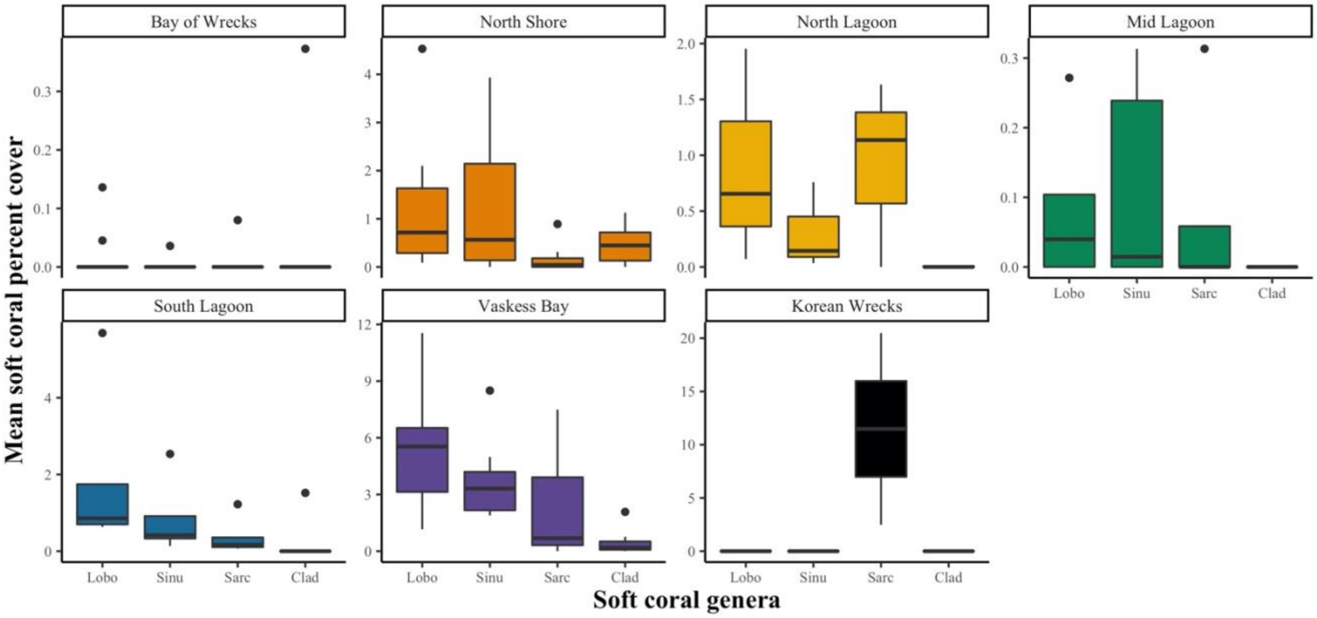

Figure A2. Mean soft coral percent cover in each region before the El Niño event. Colors represent regions of the atoll, as displayed in Figure 2.2. Note: y-axis differ in scale.

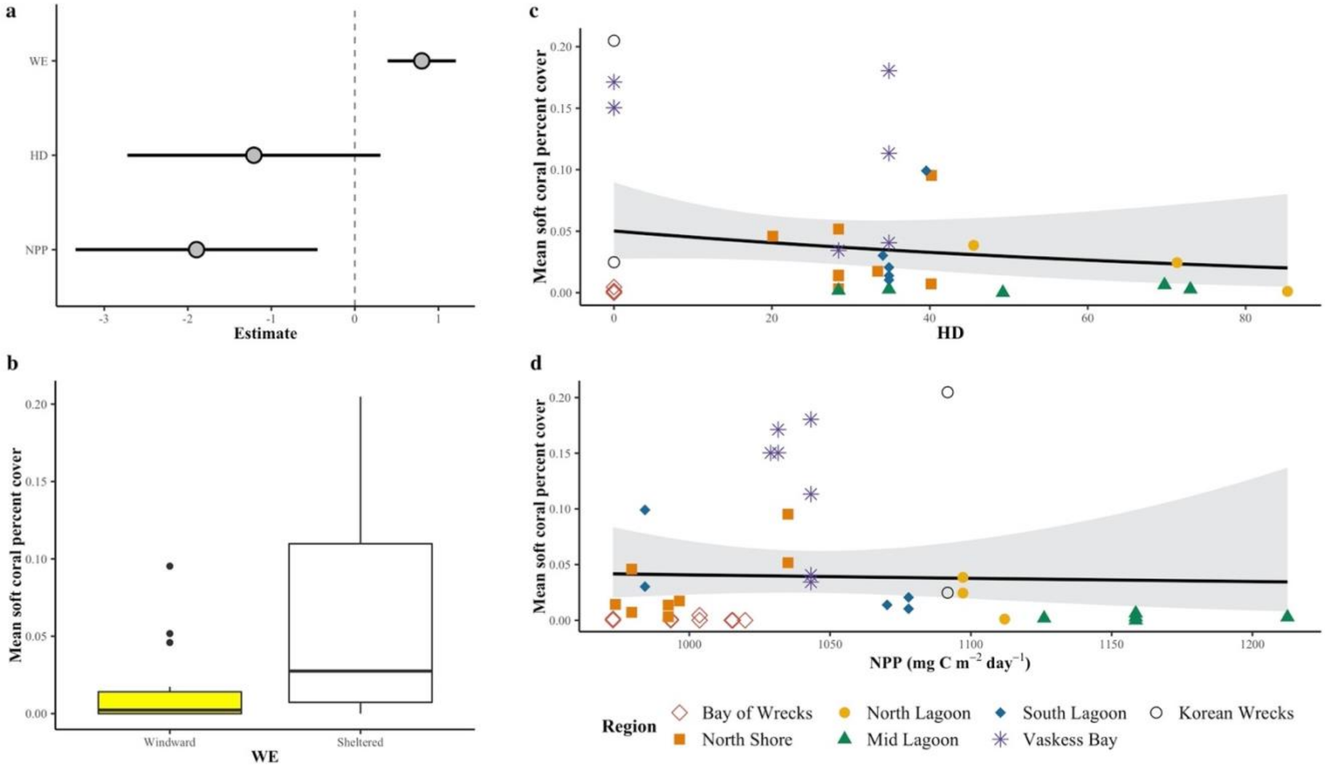

Figure A3. Soft coral cover prior to the El Niño event for different abiotic factors. Colors match region and wind exposure colors in Figure 2.2. *(a)* model parameter estimates and 95% confidence intervals for model containing all abiotic factors. *(b)* Mean soft coral cover on for different wind exposures (WE). *(c)* Mean soft coral percent cover over the local human disturbance (HD) with colors and shapes showing each region. *(d)* Mean soft coral percent cover over maximum net primary productivity (mg C m^{-2} day^{-1}; NPP) with colors and shapes showing each region.

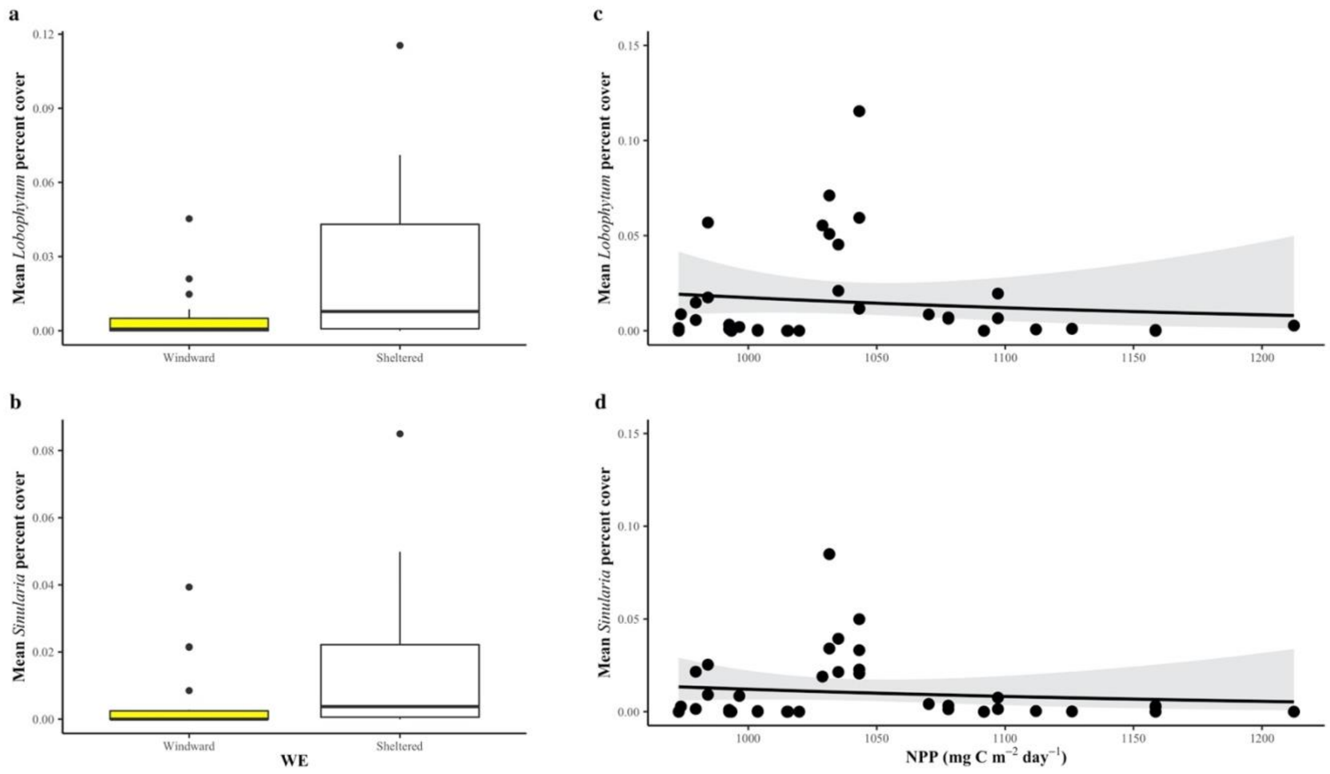

Figure A4. Soft coral genera cover prior to the El Niño event for different abiotic factors. *(a)* Mean soft coral cover for *Lobophytum* over maximum net primary productivity (mg C m^{-2} day^{-1}; NPP). *(b)* Mean soft coral cover for *Sinularia* over maximum net primary productivity (mg C m^{-2} day^{-1}; NPP). *(c)* Mean soft coral cover for *Lobophytum* at different wind exposures (WE). *(d)* Mean soft coral cover for *Sinularia* at different wind exposures (WE).

Appendix B: Supplemental information for Chapter 3

Table B1. Number of quadrats in each year for each site on Kiritimati. Shaded grey cells were sampled after the El Niño event. Bolded sites were randomly selected to be included in analyses and sites marked with asterisks (*) were not included in beta diversity analyses.

Region	Site Name	2013 - Jul	2014 - Aug/Sep	2015 - Jan	2015 - May	2016 - Nov	2017 - Jul
Bay of Wrecks	**VL2***	**20**	0	0	0	0	**26**
	VL1	23	0	**28**	15	30	**30**
	VL5*	**30**	0	0	0	0	**19**
North Shore	**L5**	**25**	0	0	0	0	**29**
	M10	**28**	0	0	0	0	**29**
	L1	28	**32**	0	0	0	**29**
North Lagoon	**H2**	**30**	0	0	0	0	**30**
	VH3	**29**	25	30	30	30	**30**
	VH1	28	30	**30**	30	**30**	29
Mid Lagoon	**VH2**	30	0	0	**30**	30	**30**
South Lagoon	**L4**	**25**	0	0	0	0	**30**
	M3	28	31	0	**30**	**30**	29
	M2	**26**	31	30	30	**30**	29
	M1	29	27	30	**30**	**30**	29
	M4*	0	**21**	0	0	0	**30**
	M6	**28**	0	0	0	30	**30**
Vaskess Bay	**VL3**	0	0	0	**29**	**30**	27

Table B2. Classification system used in this study. Shows how each taxonomic name was grouped and what possible species are included. Possible species were determined as either being strongly predicted or confirmed to occur within the Kiribati, north-east Line Islands (Veron et al. 2016).

Taxonomic Name	**Coral Type**	**Grouped by**	**Possible species include**
Acropora spp	Reef-building hard coral	Genus	All branching and tabulate forms of *Acropora* seen on Kiritimati
Astrea spp	Reef-building hard coral	Genus	*Astrea annuligera, A. curta*
Astreopora spp	Reef-building hard coral	Genus	*Astreopora cucullata, A. listeri, A. myriophthalma, A. scabra, A. suggesta, A. expansa, A. gracilis, A. ocellata*
Cladiella spp	Soft coral	Genus	Possible species are not known
Dipsastraea spp	Reef-building hard coral	Genus	*Dipsastraea favus, D. laxa, D. matthaii, D. pallida, D. rotumana, D. speciosa*
Favites spp	Reef-building hard coral	Genus	*Favites chinensis, F. abdita, F. complanata, F. flexuosa, F. halicora, F. pentagona*
Fungiidae	Free-living hard coral	Family	*Sandalolitha dentata, S. robusta, Herpolitha limax, H. weberi, Ctenactis echinata, Cycloseris cyclolites, Danafungia scruposa, D. horrida, Fungia fungites, Lithophyllon repanda, L. concinna, Lobactis scutaria, Pleuractis granulosa, P. paumotensis*
Gardineroseris planulata	Reef-building hard coral	Species	*Gardineroseris planulata*
Goniastrea stelligera	Reef-building hard coral	Species	*Goniastrea stelligera*
Hydnophora exesa	Reef-building hard coral	Species	*Hydnophora exesa*
Hydnophora microconos	Reef-building hard coral	Species	*Hydnophora microconos*

Leptastrea spp	Reef-building hard coral	Genus	*Leptastrea bewickensis, L. purpurea, L. transversa*
Leptoseris myceteroides	Reef-building hard coral	Species	*Leptoseris myceteroides*
Lobophyllia spp	Reef-building hard coral	Genus	*Lobophyllia corymbosa, L. hataii, L. hemprichii, L. robusta*
Lobophytum spp	Soft coral	Genus	Possible species are not known
Montipora spp	Reef-building hard coral	Genus	All foliose and encrusting forms of *Montipora* seen on Kiritimati Island
Pavona duerdeni	Reef-building hard coral	Species	*Pavona duerdeni*
Pavona varians	Reef-building hard coral	Species	*Pavona varians*, but also may include *P. chiriquiensis* and *P. venosa*
Platygyra spp	Reef-building hard coral	Genus	*Platygyra contorta, P. daedalea, P. lamellina, P. pini, P. ryukyuensis, P. sinensis*
Pocillopora spp	Reef-building hard coral	Genus	All branching forms of *Pocillopora* seen on Kiritimati Island
Porites spp	Reef-building hard coral	Genus	*Porites australiensis, P. lichen, P. lobata, P. lutea, P. lukoensis, P. solida, P. superfusa, P. vaughani*
Psammocora profundacella	Reef-building hard coral	Species	*Psammocora profundacella*
Sarcophyton spp	Soft coral	Genus	Possible species are not known
Sinularia spp	Soft coral	Genus	Possible species are not known

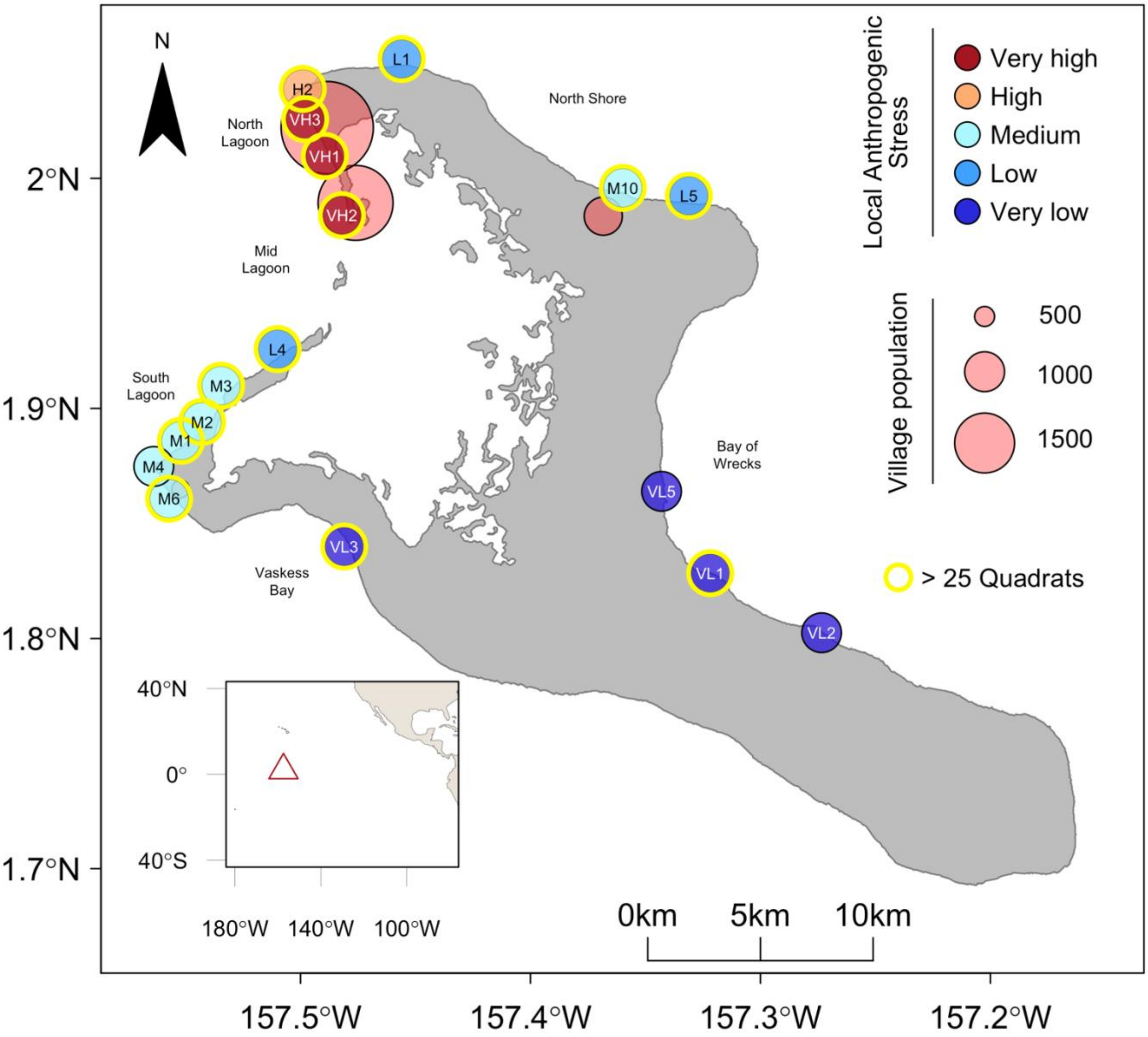

Figure B1. Map of Kiritimati. Inset shows larger geographic location in the equatorial central Pacific Ocean. Sites are marked around the atoll with colored circles representing the local anthropogenic stress classification. The human population is illustrated with the relative size of semi-transparent red circles. Yellow circles around site names identifies sites used in beta diversity analyses as they had more than 25 quadrats at two sampling periods, one before and one after the heatwave.

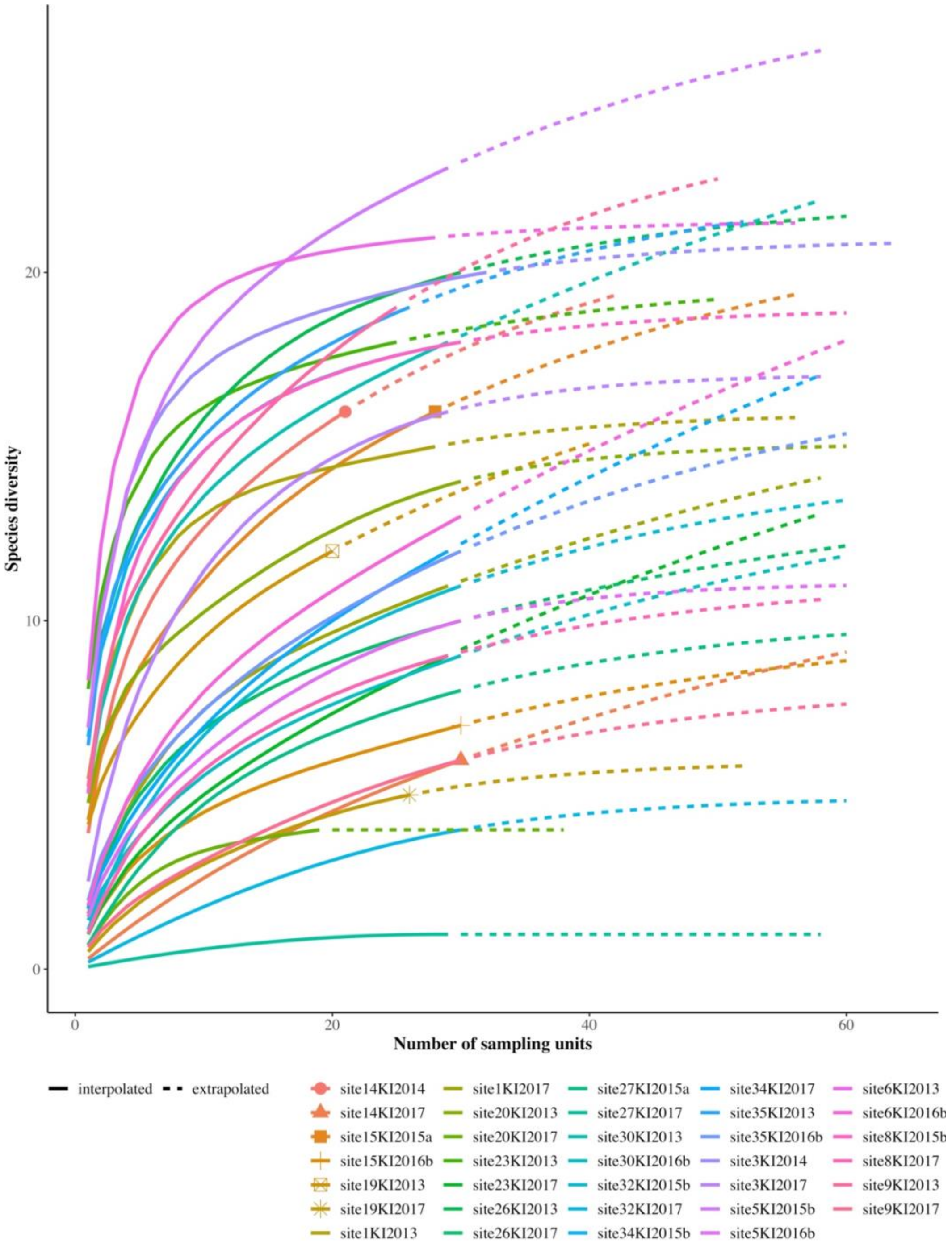

Figure B2. Species diversity for each site in each time (before and after the El Niño event) over number of quadrats included in the diversity calculation. Solid line shows interpolated results while the dashed lines show extrapolated results.

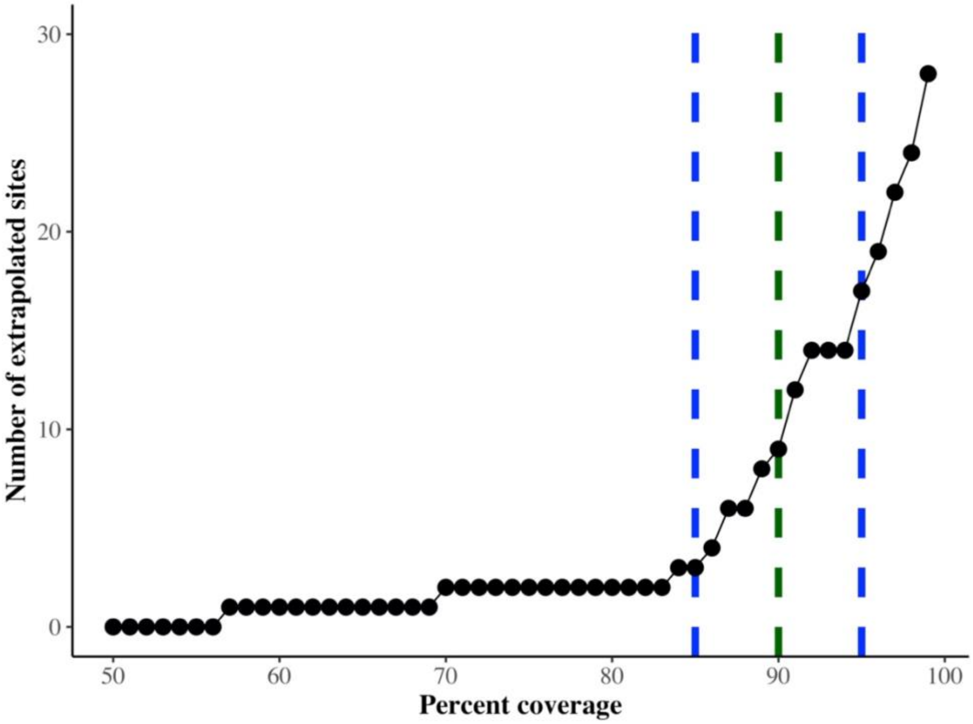

Figure B3. The number of extrapolated points as the data's equalized percent coverage changes. Dashed green line shows 90% coverage, the equalization used in the manuscript while the blue lines show 85% and 95% which results are presented below in the supplemental materials to display how differences in coverage affect results and interpretations.

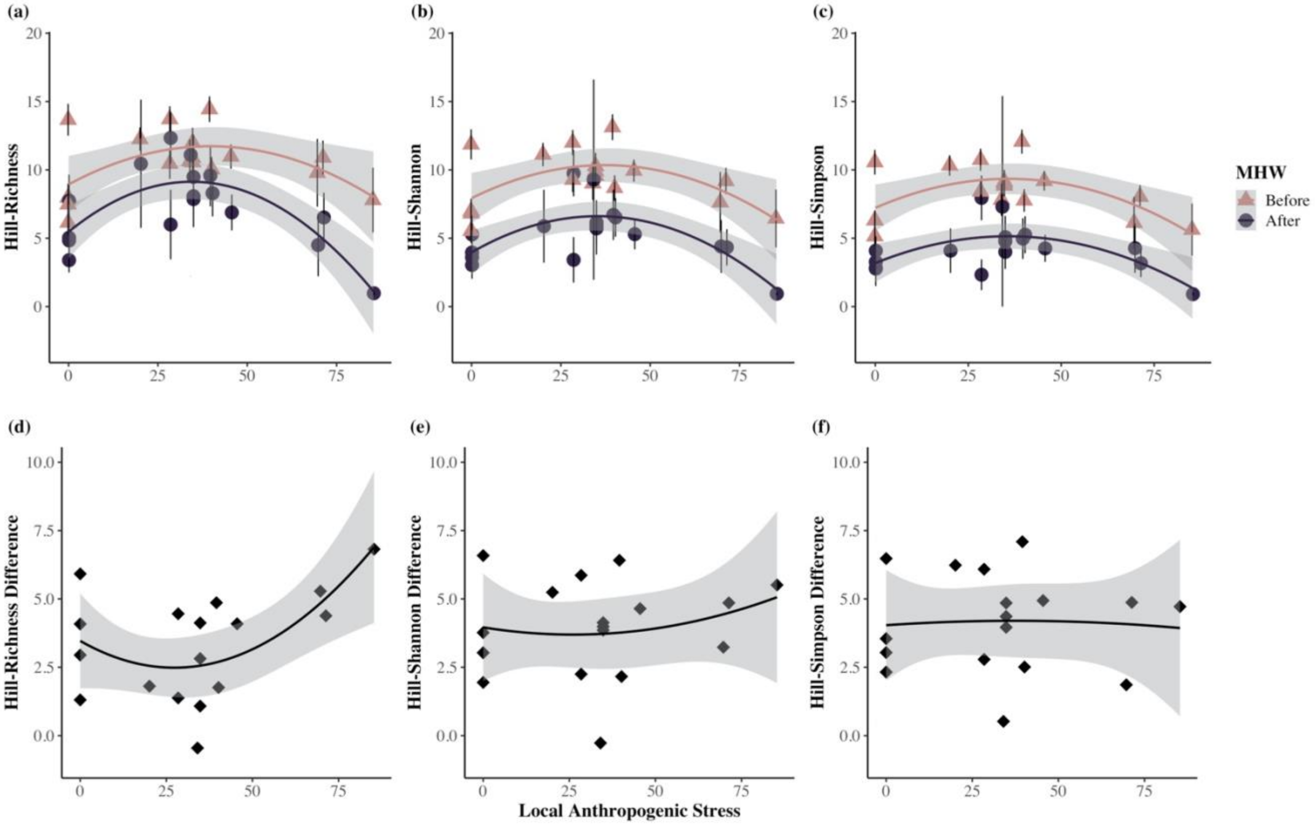

Figure B4. Hill diversity for each site along the local anthropogenic stress gradient. This data was equalized to 85% cover. Panels *(a), (b)* and *(c)* display Hill-Richness, Hill-Shannon and Hill-Simpson measured respectively. Data is shown split into before and after the El Niño event, vertical bars represent 95% confidence limits for each site, and grey represents standard error for the polynomial lines. Panels *(d), (e)* and *(f)* display the difference in Hill diversity between each site before and after the El Niño event, for Hill-Richness, Hill-Shannon and Hill-Simpson respectively.

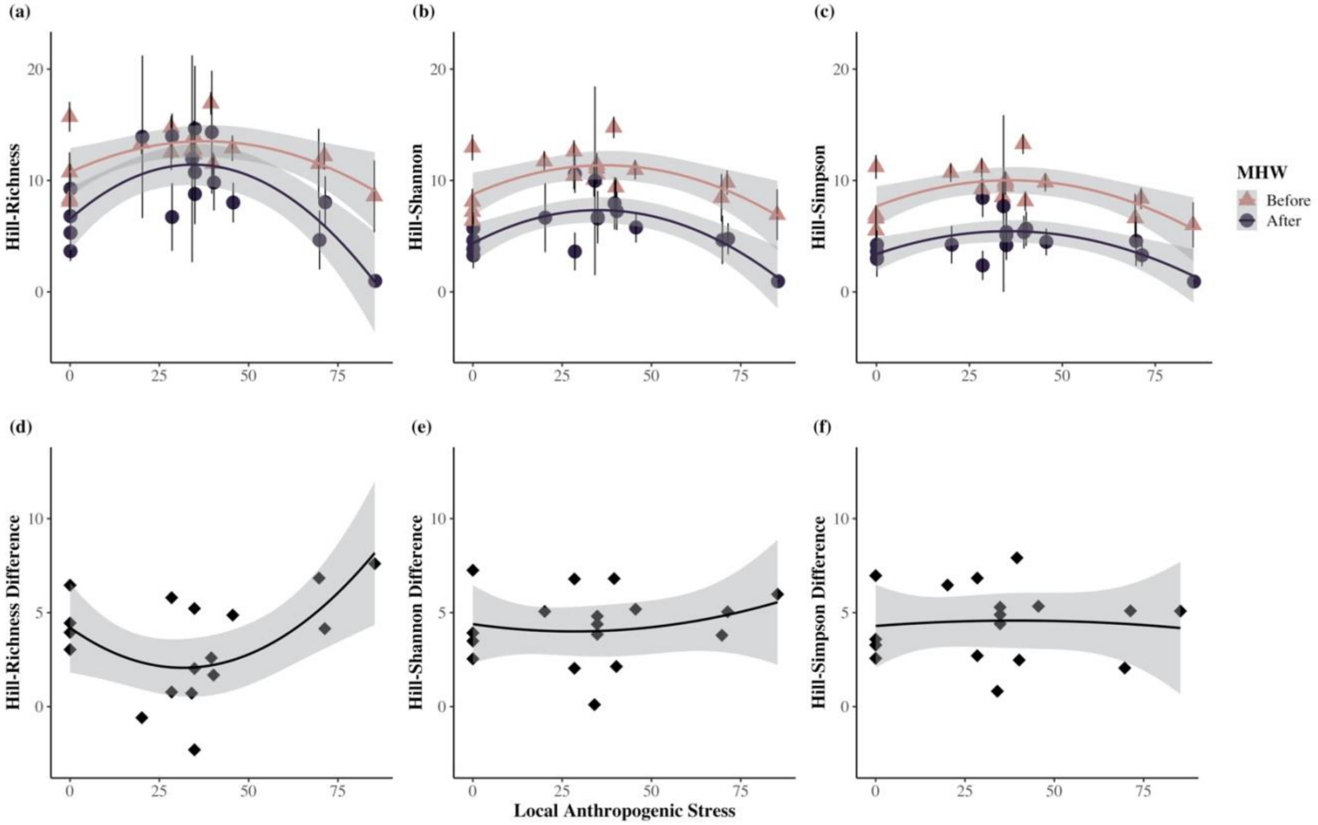

Figure B5. Hill diversity for each site along the local human anthropogenic stress gradient. This data was equalized to 90% cover. Panels *(a)*, *(b)* and *(c)* display Hill-Richness, Hill-Shannon and Hill-Simpson measured respectively. Data is shown split into before and after the El Niño event, vertical bars represent 95% confidence limits for each site, and grey represents standard error for the polynomial lines. Panels *(d)*, *(e)* and *(f)* display the difference in Hill diversity between each site before and after the El Niño event, for Hill-Richness, Hill-Shannon and Hill-Simpson respectively.

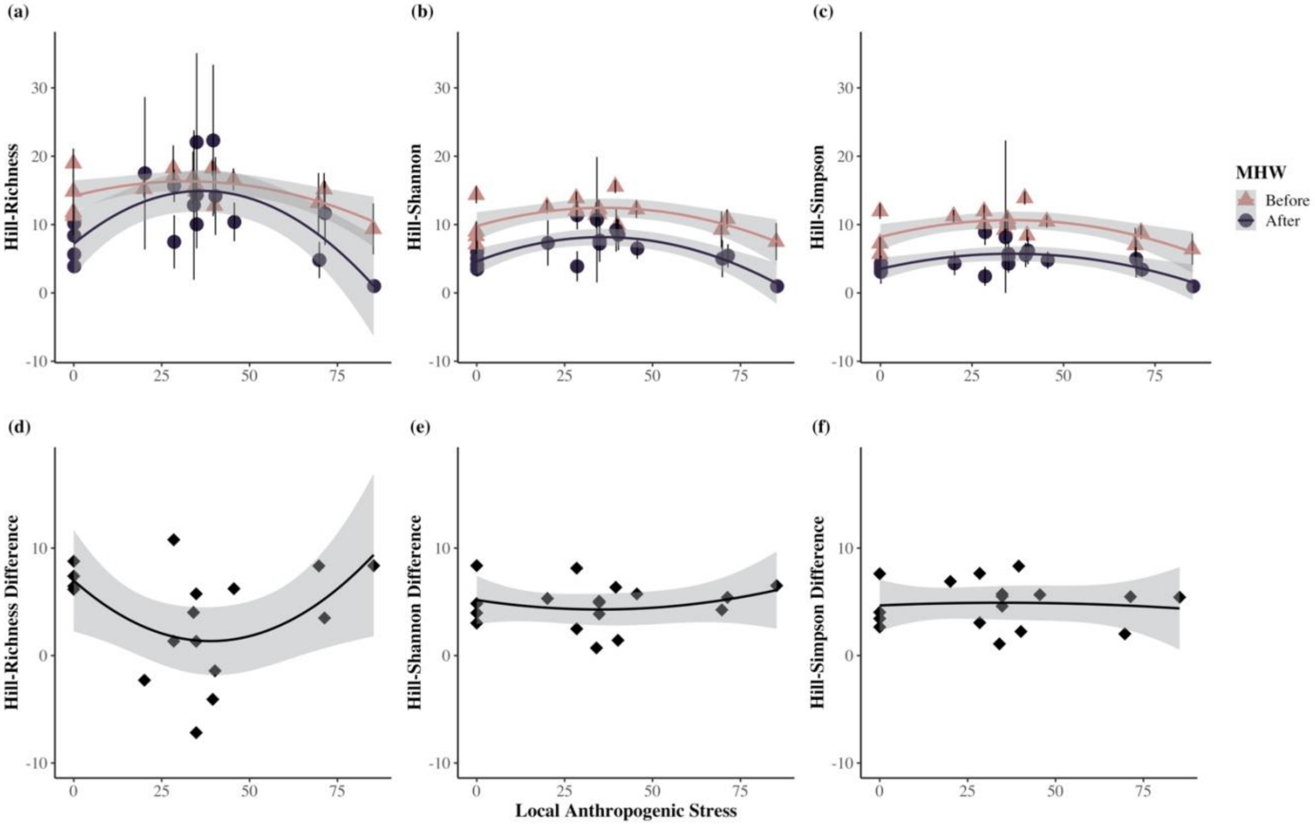

Figure B6. Hill diversity for each site along the local anthropogenic stress gradient. This data was equalized to 95% cover. Panels *(a)*, *(b)* and *(c)* display Hill-Richness, Hill-Shannon and Hill-Simpson measured respectively. Data is shown split into before and after the El Niño event, vertical bars represent 95% confidence limits for each site, and grey represents standard error for the polynomial lines. Panels *(d)*, *(e)* and *(f)* display the difference in Hill diversity between each site before and after the El Niño event, for Hill-Richness, Hill-Shannon and Hill-Simpson respectively.

Table B3. Parameter estimates for fixed effects from polynomial regression models describing the factors influencing Hill-Richness, Hill-Shannon and Hill-Simpson diversity. Each Hill diversity model was conducted on data that had been equalized to 85, 90 and 95% coverage. Cells filled grey represent the models that were used in the manuscript and others are to show how differences in coverage affected model outcomes.

Model	LAS - 1º poly	LAS - 2º poly	MHW	LAS - 1º poly : MHW	LAS - 2º poly : MHW	NPP
Hill-Richness						
85% Coverage	3.098374	**-7.115000****	**-3.333235*****	-3.996851	**-5.545241****	-0.010909
90% Coverage	2.80018	**-7.76270****	**-3.36594*****	-3.80986	**-8.97593****	-0.01449
95% Coverage	0.01762	-8.18759	**-3.73394*****	1.04902	**-15.73564****	-0.01732
Hill-Shannon						
85% Coverage	1.590186	**-6.996675*****	**-3.953707*****	-1.327062	-1.647390	-0.009310
90% Coverage	1.549540	**-7.755289*****	**-4.303176*****	-1.310906	-2.030854	-0.010518
95% Coverage	1.092166	**-8.269011*****	**-4.730051*****	-0.575387	-3.026929	-0.010678
Hill-Simpson						
85% Coverage	0.461803	**-6.727069*****	**-4.128235*****	0.015729	0.488883	-0.007191
90% Coverage	0.484751	**-7.387219*****	**-4.455059*****	-0.073007	0.790979	-0.007462
95% Coverage	0.261876	**-7.884811*****	**-4.790117*****	0.181635	0.878027	-0.007039

Note: LAS = local anthropogenic stress; MHW = before or after the marine heatwave event; 1º poly = first order polynomial, the linear term; 2º poly = second order polynomial, the quadratic term; NPP = max net primary productivity. Boldface indicates statistical significance (α = 0.05; *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$).

Figure B7. Mean scaled proportion cover for each site included in the beta diversity analysis. Each site's cover is shown before and after the El Niño event. Unscaled data is shown in Figure B8.

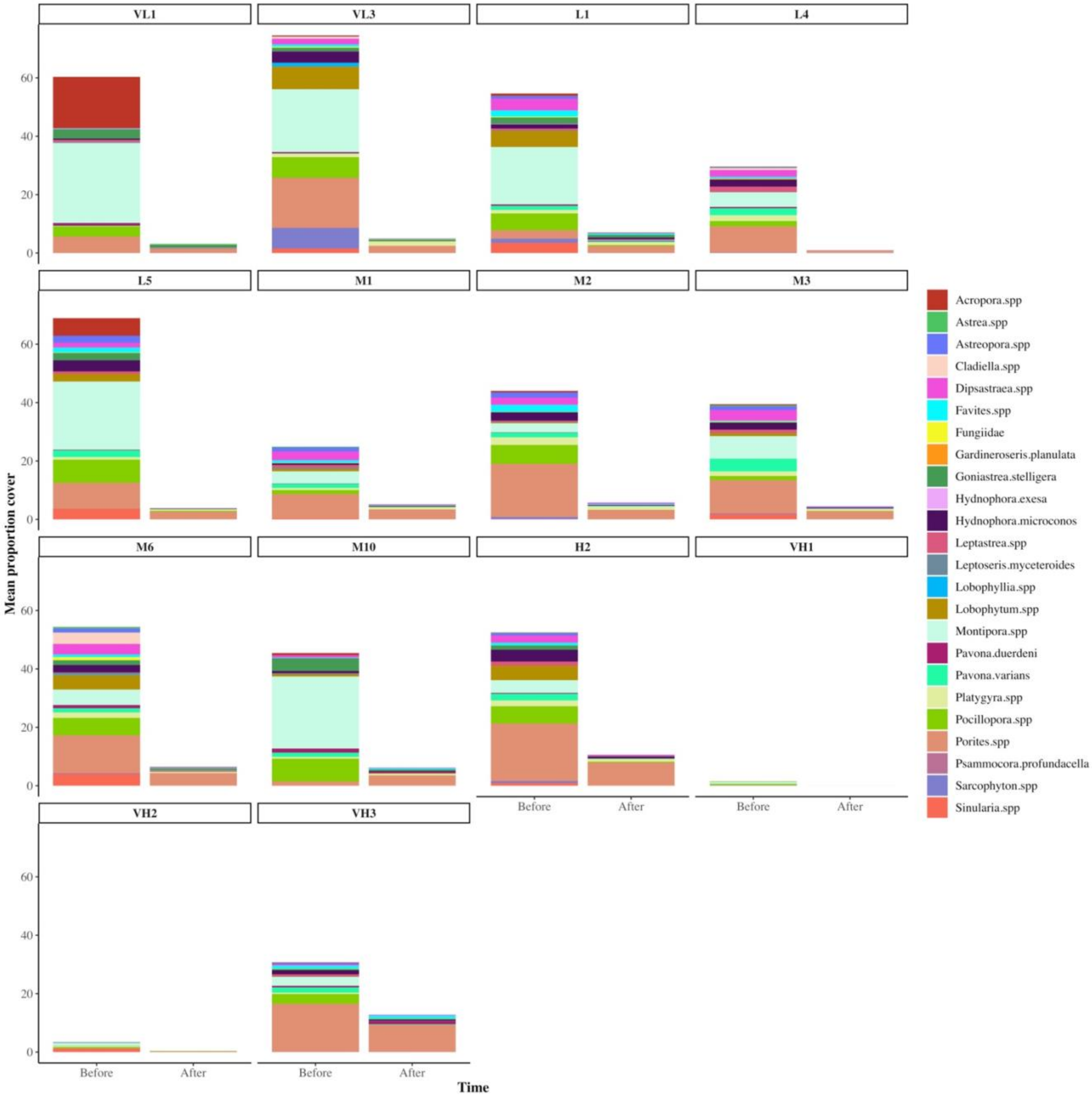

Figure B8. Mean unscaled proportion cover for each site included in the beta diversity analysis. Each site’s cover is shown before and after the El Niño event. Scaled data is shown in Figure B7.