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The functional diversity and redundancy of corals

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Abstract

Corals are major contributors to a range of key ecosystem functions on tropical reefs, including calcification, photosynthesis, nutrient cycling and the provision of habitat structure. The abundance of corals is declining at local and regional scales, and the species composition of assemblages is responding to escalating human pressures, including anthropogenic global warming. An urgent challenge is to understand the functional consequences of these shifts in abundance and composition in different biogeographical contexts. To address this problem, I develop and analyse a series of coral traits to quantify the trait-based dissimilarity (functional diversity) and similarity (functional redundancy) of corals using multidimensional trait space. This thesis is focussed on (i) biogeographical patterns in the functional diversity and redundancy of corals, (ii) how these patterns are changing in response to anthropogenic pressures, and (iii) the implications of these changes for the biodiversity and functioning of coral assemblages.

Biogeographical patterns of coral species richness are well known. However, the biogeography of coral functions in provinces and domains with high and low redundancy is poorly understood. My first objective was therefore to quantify the functional traits of all currently-recognized zooxanthellate coral species ($n = 821$) in both the Indo-Pacific and Atlantic domains, to examine the relationships between species richness and the diversity and redundancy of functional trait space. I found that trait diversity was conserved ($> 75\%$ of the global total) along latitudinal and longitudinal gradients in species richness, falling away only in species-poor provinces (richness < 200), such as the Persian Gulf (52% of the global total), Hawaii (37%), the Caribbean (26%) and the East-Pacific (20%), where redundancy is also diminished. In the more species-poor provinces, large and ecologically important areas of trait space are empty, or occupied by just a few, highly distinctive species. These striking biogeographical differences in redundancy could affect the resilience of critical reef functions, and highlight the vulnerability of relatively depauperate, peripheral locations which are often a low priority for targeted conservation efforts.

I next analyse temporal trends in the regional-scale trait diversity of corals before and after a severe episode of mass coral bleaching within the Great Barrier Reef (GBR). I show that in the aftermath of the record-breaking marine heatwave on the GBR in 2016, an exposure of

6°C-weeks or more drove an unprecedented, regional-scale shift in the trait composition of coral assemblages, reflecting markedly divergent responses to heat stress by different taxa. Fast-growing staghorn and tabular corals suffered a catastrophic die-off, transforming the three-dimensionality and ecological functioning of 29% of the 3,863 reefs comprising the world's largest coral reef system. The increasing prevalence of post-bleaching mass mortality of corals represents a radical shift in the disturbance regimes of tropical reefs, and poses a severe threat to the functional diversity of all regions. Nonetheless, long-term analysis is required to understand how trait composition is likely to be permanently affected by these recurrent disturbances.

A key challenge is to understand whether assemblages exposed to recurrent disturbances will lack important functional attributes, or whether a range of species with diverse ecological roles can respond differently to environmental change, and replace those in decline (response diversity). To explore these patterns, I next analysed case studies of long-term trends in coral composition from three biogeographical provinces (the Great Barrier Reef, French Polynesia, and Jamaica) to quantify shifts in multidimensional trait space throughout cycles of disturbance and recovery. The analysis shows that decades after disturbances, assemblages with diverse functional attributes have failed to recover at sites in all regions. Abundance-weighted trait diversity in recovering assemblages was diminished by 29% on the Great Barrier Reef, 18% in Polynesia, and 48% in Jamaica. Disturbance and recovery has favoured a subset of species with limited functional attributes, including smaller, shorter and morphologically simpler taxa with submassive, tabular or bushy morphologies. The degree to which depleted areas of trait space ('losers') were restored by taxa which have increased in abundance ('winners') reveals limited response diversity across locations.

To understand the ecological implications of these shifts in functional diversity through time, we must test the relationship between diversity and ecosystem function. To analyse this relationship at a local scale, experimental coral communities were assembled to quantify the performance of coral colonies with and without neighbours, and in the presence of conspecifics versus heterospecifics. I found a positive effect of coral species richness on primary productivity (gross and net photosynthesis), indicated by a 53% increase in productivity in multispecies assemblages (2 or 4 species) relative to monocultures. Productivity in monocultures was predicted by traits associated with different species

morphologies. In contrast, multispecies assemblages maintained high levels of productivity even in the absence of the most productive species, reflecting non-additive effects of species richness on community functioning. Assemblage performances were regulated by positive and negative interactions between colonies, with many colonies performing better among functionally diverse heterospecific neighbours than in isolation (facilitation). Facilitation occurred primarily among flow-sensitive taxa with simple morphological traits, and did not occur under low flow, suggesting that modifications to flow microclimates by corals generated beneficial, interspecific interactions.

Overall, the results of this thesis suggest that future trajectories in the functioning of reefs will depend on how different biogeographical pools of distinctive and redundant species will reassemble in the wake of global warming. The thesis demonstrates that the diversity and identity of corals within colony aggregations can influence coral community productivity, and highlights the importance of traits or trait diversity in regulating ecosystem function. Nevertheless, the functional trait diversity of corals is changing rapidly at local and regional scales, driven by recurrent disturbances, including mass bleaching. The thesis also reveals a considerable amount of similarity, or redundancy, among corals, and the role of this redundancy in maintaining functional diversity through time. Nevertheless, redundancy varies in the major coral reef provinces of the world, revealing locations that are potentially more vulnerable to the collapse of ecological functions.

Table of contents

Acknowledgements	I
Statement of the contribution of others	II
Abstract	IV
List of tables	IX
List of figures.....	X
Chapter 1: General Introduction	1
<i>Thesis aim and outline</i>	<i>6</i>
Chapter 2: Biogeographical disparity in the functional diversity and redundancy of corals	8
<i>Introduction.....</i>	<i>8</i>
<i>Materials and methods.....</i>	<i>10</i>
<i>Results.....</i>	<i>16</i>
<i>Discussion</i>	<i>25</i>
Chapter 3: Global warming transforms coral assemblage functions	28
<i>Introduction.....</i>	<i>28</i>
<i>Materials and methods.....</i>	<i>29</i>
<i>Results and Discussion.....</i>	<i>36</i>
<i>Conclusions</i>	<i>48</i>
Chapter 4: Disturbance, recovery, and the depletion of functional diversity on coral reefs.....	50
<i>Introduction.....</i>	<i>50</i>

<i>Materials and methods</i>	52
<i>Results</i>	57
<i>Discussion</i>	62
Chapter 5: Neighbour diversity regulates the productivity of coral assemblages	65
<i>Introduction</i>	65
<i>Materials and methods</i>	66
<i>Results and Discussion</i>	71
Chapter 6: General discussion	85
References	89
<i>Appendix A</i>	115
<i>Appendix B</i>	116
<i>Appendix C (Chapter 3)</i>	117
<i>Appendix D (Chapter 4)</i>	118
<i>Appendix E (Chapter 5)</i>	121

List of tables

Table 2.1: Seven traits used in the analysis and their functional relevance	12
Table 2.2: Formulae and values used in models to calculate colony surface area and volume.	15
Table 3.1: Eight traits used in the analysis and their functional relevance.	34
Table 3.2: Trait scores for each of 12 groups of corals.	35
Table 5.1: Results of linear mixed effects model examining the factors influencing neighbour interactions in coral assemblages.	82

List of figures

Figure 1.1 The functional diversity of corals on the Great Barrier Reef revealed from a wide variety of morphologies.	5
Figure 2.1: The predictive accuracy of the trait infilling procedure for four traits.	13
Figure 2.2: Principal Components Analysis of the trait space of corals across biogeographically distinct provinces.	17
Figure 2.3: The relationship between species richness and the occupancy of trait space across major biogeographical provinces.	20
Figure 2.4: The diversity and redundancy of trait space on the Great Barrier Reef and Caribbean.	24
Figure 3.1: Large-scale spatial patterns in change in coral cover and in heat exposure on the Great Barrier Reef, Australia.	37
Figure 3.2: The initial and longer-term response of coral assemblages to heat exposure.	39
Figure 3.3: Mortality rates differ among taxa and increase over time.	41
Figure 3.4: Differential sensitivity of coral taxa to temperature stress.	42
Figure 3.5: Changes in assemblage structure and functional traits of corals following mass bleaching.	45
Figure 3.6: Change in coral assemblages in response to heat exposure.	47

Figure 4.1: Positions of 44 taxonomic groups in trait space constructed using a PCA of seven functional traits.	54
Figure 4.2: Disturbance-recovery cycles and loss of coral trait diversity.	56
Figure 4.3: Shifts in abundance in coral trait space across three locations.	59
Figure 4.4: Response diversity following disturbance and recovery in three locations.	60
Figure 5.1: Difference in productivity between reef habitats measured in situ and comparison with the average flume productivity in this study.	69
Figure 5.2: Experimental flumes quantifying the effects of species richness and morphological complexity on coral community productivity.	73
Figure 5.3: Box plots showing influence of species diversity on respiration and gross productivity.	74
Figure 5.4: Interactions between neighbour colonies, quantified from the difference between assemblage productivity and the sum of their individuals measured in isolation.	77
Figure 5.5: Effects of water flow and colony flow-sensitivity on neighbour interactions in coral assemblages.	81

Chapter 1: General Introduction

In a time of escalating human influences on the global environment, attention is turning towards the roles of species in maintaining ecological functions, such as primary productivity, trophic interactions, nutrient cycling, and habitat construction (Lawton 1994, Chapin et al. 1997, Naeem et al. 2012). Initiatives such as the Millennium Ecosystem Assessment (2005), have brought ecosystem function to the forefront of global change research, calling attention to the rapid loss of biodiversity and ecosystem function, and the adverse consequences for ecosystem services and human well-being. In the wake of global biodiversity loss (Pimm et al. 2014, McGill et al. 2015), a surge of interest in how biodiversity affects ecosystem function has led to a paradigm shift, in which functional traits are increasingly recognised as the underlying link between species and ecosystem processes. Consequently, following a long history in ecology and evolutionary biology, the analysis of species traits is increasingly used as way of understanding and predicting patterns in the functioning of ecosystems (Hooper and Vitousek 1997, Tilman et al. 1997, Loreau et al. 2001, Reiss et al. 2009).

The term ‘trait’ refers to a morphological, physiological or behavioural attribute of an organism (Violle et al. 2007). The term ‘functional’ implies that this trait has implications for higher-level processes at the population (Adler et al. 2014), community (McGill et al. 2006, Mouillot et al. 2013b), or ecosystem level (Hillebrand and Matthiessen 2009). Early plant classification schemes used traits to describe adaptive strategies associated with species distributions (Grime 1974, Westoby 1998), and similar classification schemes were devised to predict broader-scale ecosystem processes such as such as productivity, nutrient cycling and evapotranspiration (Lavorel et al. 1997, Walker et al. 1999, Díaz and Cabido 2001, Walker and Langridge 2002). At higher trophic levels, consumers such as herbivores have often been classified based on their feeding structures or behaviours (Bellwood et al. 2004, Glynn and Enochs 2011, Pringle et al. 2014). Nevertheless, assigning species into groups often involves the division of continuous trait dimensions into categories, potentially obscuring important variation (Petchey and Gaston 2006). Continuous measures of trait-based dissimilarity (functional diversity) are therefore receiving greater attention. Many of these measures quantify how species are arranged in “functional space” (Walker et al. 1999,

Villéger et al. 2008, Mouillot et al. 2013b), whereby similar species fall into clusters that are tantamount to functional groups, and unique species can be identified as outliers (Mouillot et al. 2013a, Violle et al. 2017). Such analyses have now been performed on plants (Diaz et al. 2004, Laughlin et al. 2010), lizards (Winemiller et al. 2015), birds (Ricklefs and Travis 1980, Ricklefs 2012) and fish (Bellwood et al. 2002).

A growing body of evidence suggests that differences in trait diversity can generate community-driven variations in ecosystem function (Hooper and Vitousek 1997, Tilman et al. 1997, Cardinale et al. 2012, Duffy et al. 2017). Species with diverse traits lead to complementary use of space or resources (Griffin et al. 2009, Burkepile and Hay 2010, Jucker et al. 2015), generate a greater representation of high-value traits (Cardinale et al. 2006), or allow distinctive species to facilitate the performance of others through beneficial habitat modifications (Stachowicz 2001, Cardinale et al. 2002, Wright et al. 2017). Although many of these studies focus on productivity or biomass accumulation, recent work highlights the importance of functional diversity for multiple ecosystem processes that act simultaneously (Mouillot et al. 2011, Clark et al. 2012, Pasari et al. 2013). Indeed, any trait that affects the rate at which organisms acquire and allocate resources, or the way in which it interacts with its environment, is likely to affect ecosystem functions relating to the fluxes of energy and matter, or the structuring of habitats and food webs (Chapin et al. 1997). Nevertheless, the influence of trait diversity on ecosystem function is often strongly regulated by the abundance and size structure of organisms (Enquist et al. 2015), species interactions (Wright et al. 2017), and environmental parameters, such as nutrient availability or climate (Mulder et al. 2001, Hodapp et al. 2016, Ratcliffe et al. 2017). Consequently, caution must be taken when drawing information on ecosystem function from traits or trait spaces alone, particularly when simple or ‘easy-to-measure’ traits are used without empirical testing of their importance (Bellwood et al. 2018).

The inverse of functional diversity is functional redundancy, which describes the similarity of species traits in an assemblage. As postulated by Walker (1992), functional redundancy suggests that distinct species in diverse assemblages may exert similar control over ecosystem processes. The concept was originally met with confusion, because of the misinterpretation that species are superfluous or unnecessary (e.g. Blake 1993). In a subsequent essay, Walker (1995) draws attention to the value of redundancy, arguing that

under fluctuating environmental conditions, redundant species can provide resilience through compensatory dynamics. This phenomenon (often described as the insurance or portfolio effect) depends on the capacity for functionally similar species to respond differently to environmental changes (response diversity), and to substitute for their equivalents that have declined (Yachi and Loreau 1999, Elmqvist et al. 2003). The maintenance of ecosystem functions under changing conditions may therefore be enhanced by species with overlapping traits (Oliver et al. 2015). Nevertheless, many diverse ecosystems are characterised by low functional redundancy, in which ecosystem functions are regulated by species with unique sets of traits (Bellwood et al. 2003), or by complementary effects among species (Pringle et al. 2014).

Recent increases in the availability of trait data has facilitated the analysis of functional diversity and redundancy at the broadest scale of ecology, namely, the scale of biogeographical provinces (Violle et al. 2014). For example, plants from distinct biomes such as the tropics and tundra converge along similar axes of trait variation relating to leaf structure and metabolism (Reich et al. 1997), and this convergence may apply to plants globally (Wright et al. 2004, Díaz et al. 2016). Consequently, the analysis of the spatial patterns (Lamanna et al. 2014), environmental drivers (Van Bodegom et al. 2014), and the ecological consequences (Reichstein et al. 2014) of plant functional diversity are now occurring at a global scale. The functional biogeography of animals is also being developed. For instance, the trait diversity of marine fishes and bivalves is concentrated in the tropics. However, many of these tropical functional groups are rare, contributing to a greater unevenness in species abundances, and resulting in complex global patterns of marine trait diversity (Stuart-Smith et al. 2013, Edie et al. 2018). Functional redundancy is also prevalent in the tropics. However, a wide range of species with unique traits (suggesting limited redundancy) account for a large proportion of fish faunas in both marine (Mouillot et al. 2014) and freshwater (Toussaint et al. 2016) environments. These patterns are critical for identifying locations of high conservation value, or high functional vulnerability, to inform management actions (Stuart-Smith et al. 2015).

Coral reefs are distinguished for having the greatest diversity per unit area of any marine ecosystem, and they supply vast numbers of people with food, recreation, economic benefit, and coastal protection (Moberg and Folke 1999). Nevertheless, reefs are responding rapidly

to human activities, particularly climate change, overfishing, and pollution (Bellwood et al. 2004). Coral communities worldwide have suffered unprecedented shifts in composition as vulnerable species decline faster in response to natural and anthropogenic pressures, including mass bleaching (Van Woesik et al. 2011, Hughes et al. 2017b), predator outbreaks (Pratchett et al. 2011), disease (Aronson et al. 2004), storms (Hughes and Connell 1999), and land-based pollution (Cleary et al. 2008). In some cases, reefs have undergone regime shifts into alternate ecological states, demonstrated by a catastrophic loss of corals, and the rise of a different assemblage of benthic organisms such as macroalgae (Knowlton 1992, Hughes 1994). Reef scientists and managers are therefore embracing the idea that reefs are continuing on trajectories towards new configurations of species, and turning their attention to the preservation of ecosystem functions (Graham et al. 2014, Hughes et al. 2017a).

The functional diversity of coral reef organisms is likely to have considerable implications for ecosystem stability and functioning. A notable example is the numerous guilds of herbivorous fish, which have varying roles in top-down trophic control and bioeroding processes (Bellwood et al. 2004). Ecosystem function on coral reefs is also strongly influenced by corals, which build the physical reef structure, and therefore act as ecosystem ‘engineers’ (Lawton 1994). The functional diversity of corals (**Figure 1.1**) has typically been measured using morphological groups, reflecting their role in reef processes such as carbonate accumulation and the creation of three-dimensional habitat (Bellwood et al. 2004). Corals have clonal life cycles, size-dependent growth and fecundity, and a mix of sexual and asexual reproductive modes (Hughes et al. 1992). Assemblages of corals constitute species with striking differences in their patterns of colonisation, persistence and growth (Jackson and Hughes 1985), a variety of morphologies (Jackson 1979, Coates and Jackson 1985) and a range of physiologies (Anthony and Hoegh Guldberg 2003, Hoogenboom et al. 2015). Coral functional diversity is therefore complex and multifaceted, and must consider a wide range of traits (**Figure 1.1**).



Figure 1.1 The functional diversity of corals on the Great Barrier Reef revealed from a wide variety of morphologies. From left to right moving down: stunted column-like structures of *Coscinarea* (Lizard Island); Fast-growing branching *Acropora* (Pelorus Island); Large corallites of *Lobophyllia* (Lizard Island); Encrusting *Montipora* with upright projections (Lizard Island); Fast-growing tabular *Acropora* (Heron Island); Column-forming colonies of *Isopora* (Lizard Island); Meandering corallites of *Platygyra* (Rib reef); Bushy thickets of *Pocillopora* (Orpheus Island); Giant colonies of *Porites* (Lizard Island).

At the community or ecosystem level, differences in coral traits are likely to affect how assemblages fix and store carbon (Anthony and Hoegh Guldberg 2003), capture and use resources (Jackson 1991, Ferrier-Pagès et al. 2011), and modify the environment through their physical structure (Done et al. 1996). Corals differ in their trophic relationships, with some specialising in primary production, others in filter feeding (Porter 1976), and some provide important food sources for corallivores (Pratchett 2005, Cole et al. 2012). Perhaps most importantly, coral taxa differ in their influence on reef framework accretion. For instance, processes such as calcification are likely to be strongly influenced by species that are larger, denser, faster-growing, and more abundant than others. Consequently, shifts in species abundance and composition can have widespread effects on reef geomorphology (Perry et al. 2013), three-dimensionality (Alvarez-Filip et al. 2009) and the provision of habitat to associated species, such as fish (Graham and Nash 2013) and invertebrates (Shirayama and Horikoshi 1982, Vytopil and Willis 2001). Considering the trait-based identity of corals with respect to a wide range of processes may therefore reveal important trends in the functioning of reef communities.

Thesis aim and outline

Considerable gaps remain in our understanding of coral functional diversity. Specifically, the analysis of the functional diversity of corals with respect to a wide range of morphological, physiological and life history traits, is yet to occur. Moreover, studies exploring the relationships between coral functional diversity and reef biogeography, resilience, and functioning, are conspicuously lacking (Madin et al. 2016b). The primary aim of this thesis, therefore, is to investigate spatial and temporal patterns in the functional diversity and redundancy of corals, and to explore the implications of these patterns for the stability and functioning of coral communities. To do so, I employ the use of multidimensional trait spaces in combination with a wide range of different techniques, including geographical analysis, reef monitoring, 3D reconstructions, and experimental manipulations, drawing upon data from the recently developed Coral Traits Database (<https://coraltraits.org>). Furthermore, this thesis employs the use of satellite-derived sea surface temperatures anomalies measured in ‘Degree Heating Weeks’ (quantifying both the amount and duration of heat exposure), to test how the trait composition of coral assemblages is affected by global climate change.

In **Chapter 2**, I examine global biogeographical patterns in the functional diversity and redundancy in corals, measuring the occupancy of trait space across biodiversity gradients in both the Indo-Pacific and Atlantic domains. In **Chapter 3**, I examine how this functional diversity has changed during mass coral bleaching on the Great Barrier Reef, analysing the shift in the trait composition on reefs at a regional scale following a severe marine heatwave. In **Chapter 4**, I conduct a long-term temporal analysis of shifts in functional diversity throughout cycles of disturbance and recovery, with the aim of quantifying response diversity and resilience across reefs, and the events that lead to functional collapse. Finally, in **Chapter 5**, I test how species and trait composition can influence reef productivity using a controlled mesocosm experiment, providing the first provisional exploration of the relationship between biodiversity and ecosystem function among corals.

Chapter 2: Biogeographical disparity in the functional diversity and redundancy of corals

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Introduction

The species composition and biodiversity of ecosystems are increasingly responding to human activity (McGill et al. 2015), highlighting the urgent need to manage and preserve ecosystem functions (Cardinale et al. 2012, Hughes et al. 2017a). A key challenge is to understand the components of biodiversity that contribute to essential functions, and that support their resilience to chronic and acute stressors (Oliver et al. 2015). The influence of biodiversity on ecosystem function is underpinned, not by species richness per se, but by the diversity of functional roles among species, as measured by their characteristics or traits (Walker et al. 1999, Reiss et al. 2009, Cardinale et al. 2012). A diverse range of functional roles (functional diversity) is critical for maintaining multiple functions (Reiss et al. 2009, Cardinale et al. 2012) and for the sustainable provision of ecosystem services to people (Díaz et al. 2007).

Loss of functional diversity can cause major shifts in ecosystem function (Symstad et al. 1998, Bellwood et al. 2003, Díaz et al. 2007). This loss of function can be avoided, however, if each functional role is supported by multiple species, each with different responses to anthropogenic or natural change (Walker 1995). Groups of species with overlapping functional roles generate functional redundancy and provide a chance for declining species to be replaced by other similar species, thereby maintaining certain functions (Walker 1995, Bellwood et al. 2004). The stabilising effect of functional redundancy is often described as ecosystem reliability (Naeem 1998), the insurance effect (Yachi and Loreau 1999), or the portfolio effect (Tilman et al. 2006), and has been documented in a wide range of ecosystems (Hughes 1994, Walker et al. 1999, Steneck et al. 2002). On coral reefs, for example, herbivory is shared among a diverse range of species, including some that are susceptible to over-fishing (e.g. parrotfish), and others that are not heavily targeted (e.g. sea urchins). In the Caribbean, the decline of herbivory due to overfishing was ameliorated because a redundant

species, the sea urchin *Diadema antillarum*, maintained this key processes (Hughes 1994), thereby providing a “reservoir of resilience” (Walker et al. 1999). For this source of resilience to take effect, redundant species must show different tolerances to environmental stressors, or different regeneration rates after perturbation, a phenomenon often referred to as response diversity (Elmqvist et al. 2003). However, over-reliance on a smaller group of tolerant species can reduce resilience, a scenario that occurred on many Caribbean reefs when *Diadema* populations were drastically reduced by disease (Hughes 1994).

Coral reef assemblages differ in species richness at global and provincial scales (Stehli and Wells 1971, Veron 1995, Bellwood and Hughes 2001). Their biogeography is characterized by a global biodiversity hotspot in the central Indo-Pacific (the Coral Triangle), by decreasing diversity with increasing latitudinal and longitudinal distance from this hotspot, and by a secondary, less diverse hotspot in the Caribbean (Stehli and Wells 1971, Veron 1995, Bellwood and Hughes 2001). Such gradients in species richness can alter biogeographical pools of functional trait diversity and redundancy, and therefore potentially influence the resilience of different provinces (Bellwood et al. 2004). Quantifying the diversity of functional traits along gradients of increasing species richness can reveal the extent to which additional species provide new functions, or increase the number of redundant species supporting the same functions (Ricklefs 2012, Lamanna et al. 2014, Swenson et al. 2016). Furthermore, although functional redundancy is likely to be common in tropical ecosystems, a critical question is whether redundancy is restricted to a subset of functions, leaving other functions supported by just one, or a few, unique species (Bellwood et al. 2003, Mouillot et al. 2014).

Reef-building corals (in the order *Scleractinia*) are often dominant contributors to a range of ecological (Buss and Jackson 1979, Jackson 1991), biogeochemical (Done et al. 1996), structural (Lawton 1994) and geological (Stoddart 1969) reef functions. This complex interplay of functions influences some of the defining features of coral reefs, such as reef growth and development, productivity and nutrient recycling, and the provision of habitat to other reef-associated species. As coral assemblages respond to escalating human stressors (Bellwood et al. 2004, Hughes et al. 2017a), critical reef functions are being impaired, including calcification (Perry et al. 2013), and the provision of three-dimensional reef structure (Alvarez-Filip et al. 2011). Understanding the potential functional roles of corals is

an essential task, which must consider a large number of species and a large number of functionally relevant traits. In addition, since many traits, including morphological dimensions and physiological rates, fall along a continuum, quantifying the diversity and importance of species functional roles must move beyond categorical groups, and instead use quantitative estimates of trait-based dissimilarity (Petchey and Gaston 2006).

In this study, I provide a comprehensive analysis of the functional traits of all extant reef-building coral species. My aim is to quantify how the functional diversity and redundancy of corals changes with species richness across twelve biogeographical provinces in both the Indo-Pacific and Atlantic domains. Using seven quantitative traits that capture the essence of coral functional roles, I generate a seven-dimensional trait space in which species are positioned according to their functional dissimilarity (Petchey and Gaston 2006). In this trait space, I examine the global pattern of functional diversity (the range of unique trait combinations) and functional redundancy (the number of species sharing similar sets of traits), testing the relationship of each with species richness. My analysis focusses on functional redundancy at multiple levels of trait-based dissimilarity, allowing me to identify locations and functions where redundancy is critically lacking. Finally, I conduct an analysis of specific traits that influence dispersal and regeneration, and of additional traits that influence reef productivity and growth, providing insights into the potential for the occurrence of response diversity among functionally similar species.

Materials and methods

Coral trait space: Seven traits were selected for their functional importance: Growth Rate, Skeletal Density, Corallite Width, Maximum Colony Size, Colony Height, Interstitial Space Size and Surface Area to Volume ratio (**Table 2.1**). Mean trait scores for every zooxanthellae coral species (n=876) were obtained from the Coral Traits Database (Madin et al. 2016a), and subsequently placed into numerical (1-5) categories (**Table 2.1**). Three ordinal morphological traits (Colony height, Interstitial Space Size, and Surface Area to Volume ratio) were assigned to species based on their morphological types and a simplified model of coral geometry (**Table 2.2**) (Madin et al. 2016b). The Coral Traits Database includes most of the empirical data from the literature. However, deficiencies in the data remain for certain traits. To ensure that nearly every known reef-building coral species was included in the analysis, a

regression approach (Madin et al. 2016b) was used to fill in missing data for four traits: growth rates (131 empirical values), colony sizes (348 empirical values), skeletal densities (54 empirical values) and corallite width (842 empirical values). Using log-transformed trait values, a linear model was run for each trait against predefined predictor variables using the *lm* function in R (R development Core Team 2017). Since each of these trait are known to be phylogenetically (Madin et al. 2016b) and morphologically (Hughes 1987, Pratchett et al. 2015) conserved, the predictor variables chosen were molecular family and growth form (for growth rates and skeletal densities), and molecular family and growth rates (for corallite widths and maximum colony sizes). The predictive functions were then used to return model estimates for each species. The strength of the predictive functions is demonstrated by their ability to accurately predict known empirical values from the trait database (**Figure 2.1**). Combinations which were not predicted by the function were based on the taxonomy and growth form of a species. Unknown reproductive modes (brooding or broadcast spawning) were also predicted, as reproductive modes in corals are generally conserved among congeners, except for well-known exceptions such as *Porites* and *Pocillopora*. Taxa that are not associated with reef habitats were subsequently removed from the dataset, leaving 821 species.

Table 2.1: Seven traits used in the analysis and their functional relevance

<i>Trait</i>	<i>Categories used</i>	<i>Reef function</i>
<i>Growth rate</i>	<i>In mm/year: 0-5 (1), 5-10 (2), 10-25 (3), 25-50 (4), 50-200 (5).</i>	<i>Carbonate framework accretion; reef regeneration</i>
<i>Skeletal density</i>	<i>In g/cm³: 0-1.2 (1), 1.2-1.5 (2), 1.5-1.8 (3), 1.8-2.1 (4), 2.1-3 (5)</i>	<i>Carbonate framework accretion</i>
<i>Corallite width</i>	<i>In mm: 0-1.5 (1), 1.5-6 (2), 6-12 (3), 12-25 (4); 25-100 (5)</i>	<i>Filter feeding; nutrient capture</i>
<i>Interstitial space size</i>	<i>(1-5) Based on morphological categories.</i>	<i>Habitat provision</i>
<i>Colony height</i>	<i>(1-5) Based on morphological categories.</i>	<i>Carbonate framework accretion; habitat provision</i>
<i>Surface area to volume ratio</i>	<i>(1-5) Based on morphological categories</i>	<i>Primary productivity; nutrient cycling</i>
<i>Maximum colony size (diameter)</i>	<i>In cm: 0-50 (1), 50-100 (2), 100-200 (3), 200-400 (4), 400-2000 (5).</i>	<i>Carbonate framework accretion; habitat provision</i>

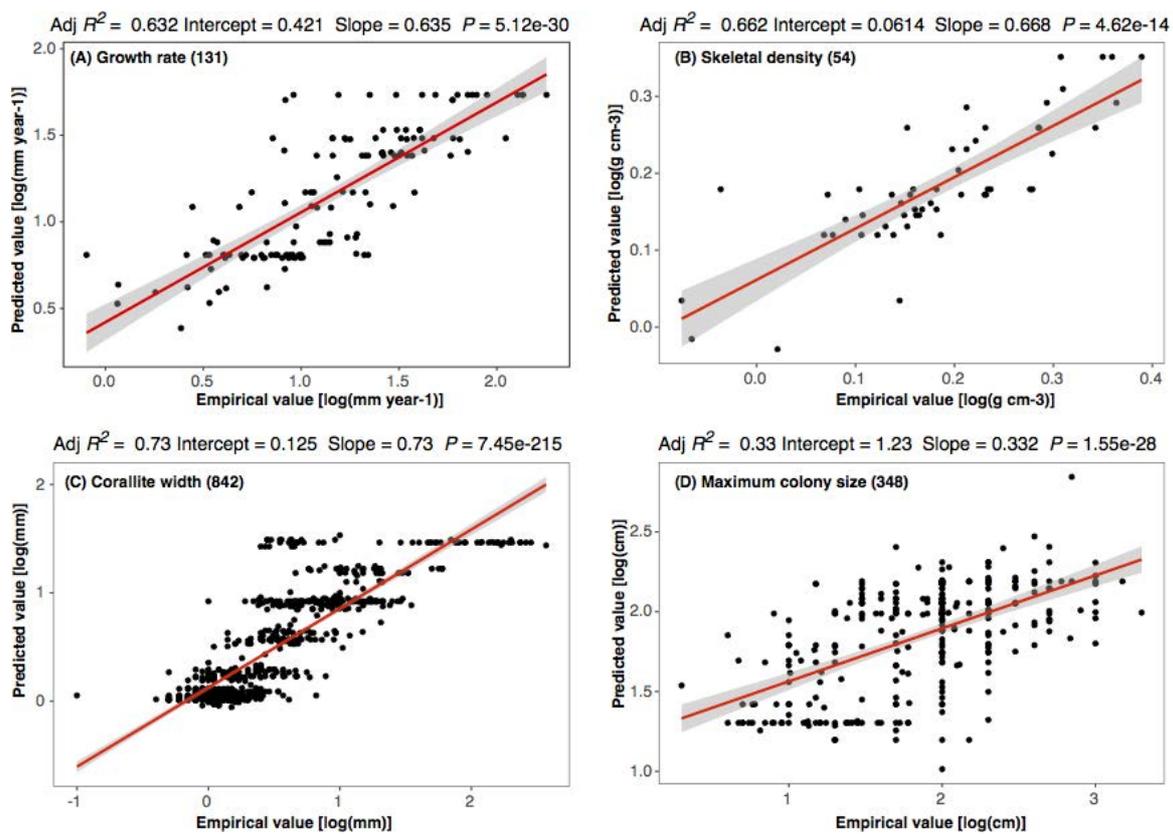


Figure 2.1: The predictive accuracy of the trait infilling procedure for four traits. (A) growth rate, (B) skeletal density, (C) corallite width, and (D) maximum colony diameter. Each panel shows log-transformed empirical trait values from the coral trait database on the x-axis, against the same log-transformed trait values estimated using an lm-predictive function (see methods) on the y-axis. The linear relationship between empirical and predicted trait values is shown in red, with 95% confidence intervals in grey. The adjusted R^2 , slope and p-value for the relationships are presented at the top of each panel. The numbers in the brackets after each species trait indicate the number of species with empirical data.

Occurrence data: Species pools for distinct Indo-Pacific provinces separated by faunal boundaries were based on the system used by Keith et al. (Keith et al. 2013). Atlantic provinces were based on the system used by Veron (1995).

Tissue biomass and Skeletal Accretion: Absolute values for these two key traits at the colony level were estimated using a simple model of colony geometry (**Table 2.2**) standardised by empirical values of maximum size, growth and skeletal density for Caribbean and Great Barrier Reef species. Tissue biomass (in g) was measured by multiplying estimates of tissue biomass per cm² by total colony area (**Table 2.2**). Skeletal accretion rates (in g yr⁻¹) were estimated by finding the difference in maximum colony diameter values after one year of uninterrupted linear growth (based on empirical values of species growth rates), finding the subsequent difference in total colony volume (**Table 2.2**), and multiplying by skeletal density.

Functional trait diversity and redundancy: Trait diversity was measured as the four-dimensional convex hull volume of trait space, signifying the outer boundary of trait space, or the most extreme trait values (Cornwell et al. 2006). Four dimensions were used to maximise the amount of variation explained by functional diversity metrics (88%). Provincial values were divided by the global convex hull to get a percentage occupancy of trait space. Neighbour similarity is based on the sum of nearest neighbour distances for the nearest 5 species, calculated using the R package “FNN” (R development Core Team 2017). This metric was then averaged over all species, and presented for each province. Assigning different numbers of neighbours did not change the results. Fine-scale clustering of species in trait space was calculated by binning species co-ordinates in the global trait space, with a consistent bin width of 0.6 (resulting in 80 global clusters). The proportion of clusters with only 1 species was then quantified (Mouillot et al. 2014). Broader aggregations of species in trait space were derived from a clustering analysis, in which the optimal number of clusters (k=8) was determined from the Bayesian Information Criterion for a k-means clustering algorithm. For each analysis, a null model was created to compare observed provincial values with a random sample from the global species pool. Samples were taken without replacement, with species richness fixed at a specific level (each increment of 5 species from 0 to 600). Analyses were repeated on each sample 100 times before presenting the mean and 95% confidence interval for the replicate samples.

Table 2.2: Formulae and values used in models to calculate colony surface area and volume. Calibrated formulae were used in estimates of tissue area and skeletal accretion. The models link colony radius (r_c) to colony surface area (SA) and volume (V). The values used to calibrate the formulae shown are: h_c = plate thickness (cm), N_b = branches per unit area, r_b = branch radius (cm), and h_b = branch height (cm). Each of these traits were measured for a total of 60 Great Barrier Reef and Caribbean species. Values shown are the average for each morphological type. NA = not applicable. Diagrams below indicate the structure of the models for eight different morphologies.

Morphology	Colony height	Surface Area to Volume ratio	Interstitial space sizes	Surface area formula	Volume formula	Formula values	Tissue Biomass (mg.cm ⁻²)
Hemisphere	4	1	1	$2\pi r_c^2$	$\frac{2}{3}\pi r_c^3$	NA	55
Frondiforous	3	5	2	$\pi r_c^2 (N_b(2\pi r_b^2))$	$h_c(SA)$	$r_b = 2$ $N_b = 0.5$ $h_c = 0.2$	12
Laminar	2	4	2	$2\pi r_c \sqrt{r_c + h_b}$	$h_c \left(\frac{1}{2} SA\right)$	$h_b = 20$ $h_c = 0.8$	20
Simple branching	5	4	5	$\pi r_c^2 (N_b(2\pi r_b h_b + \pi r_b^2))$	$\pi r_c^2 (N_b(\pi r_b^2 h_b))$	$r_b = 1$ $h_b = 15$ $N_b = 0.01$	7
Complex branching	4	3	4	See simple branching	See simple branching	$r_b = 1$ $h_b = 5$ $N_b = 0.5$	15
Digitate	3	4	3	See simple branching	See simple branching	$r_b = 2$ $h_b = 5$ $N_b = 0.2$	10
Columnar	5	1	5	See simple branching	See simple branching	$r_b = 3$ $h_b = 25$ $N_b = 0.05$	30
Corymbose	3	5	3	See simple branching	See simple branching	$r_b = 1$ $h_b = 5$ $N_b = 0.5$	30
Tabular	2	5	2	See simple branching	See simple branching	$r_b = 0.5$ $h_b = 1$ $N_b = 2.5$	37
Encrusting	1	2	1	πr_c^2	$\pi r_c^2 h_c$	$h_c = 1.5$	43
Encrusting (uprights)	2	3	2	Encrusting + [simple branching]	Encrusting + [simple branching]	$r_b = 0.5$ $h_b = 5$ $N_b = 0.2$ $h_c = 1$	17



Results

A Principal Component Analysis (PCA) of the global trait space for 821 species of corals, based on seven functional traits (*Table 2.1*), reveals four significant axes of correlated trait variation, representing major dimensions of coral functional diversity. Along PCA axis 1 (48.6% of variation explained), coral species are positioned from small, slow-growing taxa with large corallites and dome-shaped morphologies, to large fast-growing taxa with small corallites and complex morphologies. Along PCA axis 2 (18.3% of variation explained), coral species are positioned from short taxa with large surface areas and high skeletal densities, to tall taxa with small surface areas and low skeletal densities (see vector plot axes 1 and 2 in *Figure 2.2*). Skeletal densities and maximum colony sizes also load heavily onto PCA axes 3 and 4 respectively (see vector plot axes 3 and 4 in *Figure 2.2*). The periphery of the four dimensions is occupied by taxa with the extreme trait values, and individual species (points in *Figure 2.2*) are dispersed widely between these outer points, leaving few areas of the trait space unoccupied. Thus, this analysis shows a wide variety of unique trait combinations in corals that can be condensed into just a few dimensions, and that 67% of the trait variation in this analysis can be expressed two axes, and 88% in four axes.

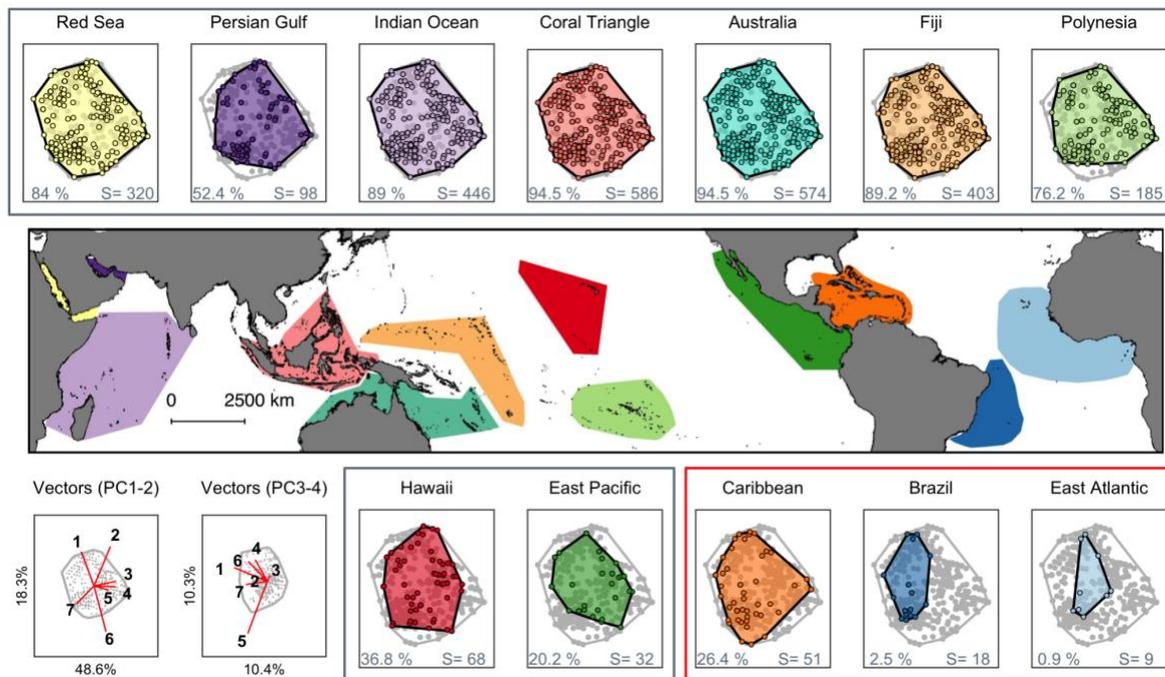


Figure 2.2: Principal Components Analysis of the trait space of corals across biogeographically distinct provinces. In each panel, the global multi-dimensional trait space for all corals is presented in grey, with each provincial trait space overlaid in colour. Coloured points represent the positions of species along PCA axes 1 and 2. Values in each panel indicate the percentage occupancy of the four-dimensional global trait space and species richness (S) for each province. The seven traits used to construct the principal components analysis, and the four axes making up the trait space, are shown in the two bottom left panels along with their percentage of explained variance. The trait vectors are (1) skeletal density, (2) surface area to volume ratio, (3) growth rate, (4) interstitial space size, (5) maximum colony size, (6) colony height, and (7) corallite width.

The percentage occupancy of the global coral trait space by the species pool in the Atlantic is small, even in the Caribbean hotspot, where only 25% of the trait space is occupied. The Brazilian and West African provinces occupy only 3% and 1%, respectively. In the Indo-Pacific, trait diversity is greatest in the Coral Triangle, where 95% of the global range of traits occurs. Trait diversity is largely maintained across five other provinces stretching from the Red Sea and western Indian Ocean, and eastwards to Polynesia in the central Pacific (**Figure 2.2**). These five provinces each contain >75% of the global functional diversity, despite a decrease from 586 coral species in the Coral Triangle to 320 westwards across the Indian Ocean, and a drop to 185 species eastwards across the West-Pacific Ocean (**Figure 2.2 and 2.3A**). In contrast, as species richness declines further in more peripheral Indo-Pacific provinces, functional diversity diminishes sharply, indicating that smaller regional species pools support a relatively depauperate mix of functional traits (**Figure 2.2 and 2.3A**). Consequently, the analysis reveals an asymptotic relationship between species richness and trait diversity (**Figure 2.3A**), consistent with a null model in which provincial species pools are randomly assembled from the global species pool (see grey bootstrapped confidence limits in **Figure 2.3A**).

The average distance between neighbouring species in multidimensional trait space is markedly lower in provinces with higher species richness, signifying a closer degree of similarity, or more redundancy, between species (**Figure 2.3B**). These differences in average species similarity are heavily influenced by clustering in trait space. For the global species pool, I identified 80 fine-scale clusters of highly similar species, or “functional entities”. The number of clusters occurring in each province increases asymptotically with species richness (solid red line, **Figure 2.3A**). In addition, the proportion of clusters in each province represented by just one species decreases with species richness (solid red line, **Figure 2.3B**). In the Caribbean, for example, only 25% (20 of the 80) of the clusters are represented. Furthermore, 65% of the clusters in the Caribbean are represented by just one unique species (i.e. the remaining 35% have redundancy), while in the Coral Triangle only 18% of the clusters are represented by a single species (82% exhibit redundancy) (**Figure 2.3B**). Thus, redundant species in species-rich provinces are spread widely throughout multidimensional trait space; whereas, in depauperate regions, limited levels of redundancy are necessarily more restricted to smaller portions of the total trait space (**Figure 2.3B**). Notably, the number of occupied clusters and the proportion of single-species clusters in each province differ from

a null model in which species are randomly assigned to clusters (dotted red lines, **Figure 2.3A-B**). This disparity between these observed results and null expectations is highest in the Indo-Pacific, where species are confined to smaller areas of trait space (**Figure 2.3A**), and packed into fewer clusters in trait space (i.e. there are more single-species clusters, **Figure 2.3B**), than expected by chance.

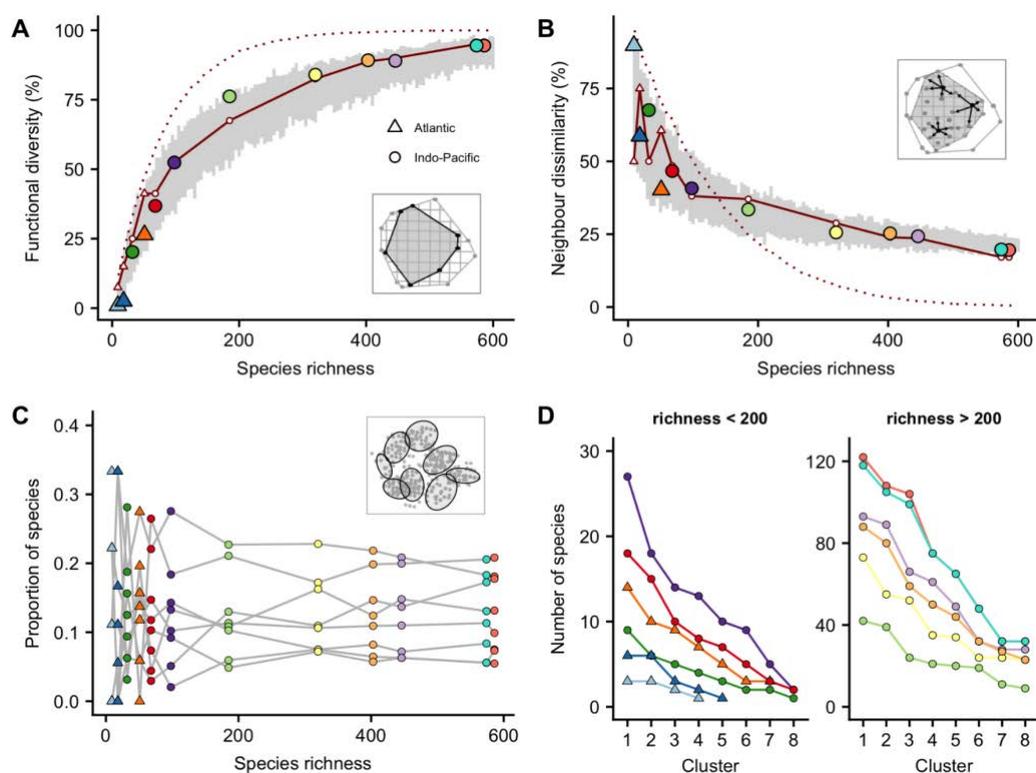


Figure 2.3: The relationship between species richness and the occupancy of trait space across major biogeographical provinces. (A) functional diversity, (B) species dissimilarity, (C) imbalances in trait space and (D) redundancy. In A and B, coloured points represent twelve provinces with the corresponding colour code from Fig. 2.2. Functional diversity is measured as the percent occupancy of the global trait space hypervolume in each province. Species dissimilarity is measured as the average distance between species and their closest neighbours in trait space (see grey boxes for visual representation of each metric). Grey bars show a null model of random species allocation for each species richness value, indicating the mean and 95% confidence intervals of 100 iterations. Solid red lines indicate an alternative analysis of 80 fine-scale clusters of species (or functional entities), indicating (A) the proportion of clusters occupied by species and (B) the proportion of occupied clusters that contain only one species. Dotted red lines indicate the same metrics under a null model of random assignment of species to clusters. In C and D, coloured points represent eight coarse-scale clusters of species in trait space, coloured by province (see grey box for the positioning of clusters in trait space). Imbalances in trait space are indicated by the proportional representation of each major cluster in the species pool of each province, with grey lines linking the same clusters across provinces. Redundancy in trait space is indicated by the

number of species occupying major clusters in each provincial trait space (coloured lines), plotted in rank descending order along the x-axis from high to low redundancy.

A broader cluster analysis of trait space reveals eight distinct clusters and shows that major disparities exist in the density of species across large areas of trait space (**Figure 2.3C-D and 2.4**). These imbalances are most prominent in species-poor provinces ($n < 200$), where large clusters in trait space are heavily under-represented (**Figure 2.3C**) and supported by just one or a few species (**Figure 2.3D**). In contrast, in species-rich provinces ($n > 200$), imbalances across trait space are less extreme due to higher levels of redundancy in all clusters. These larger areas of trait space represent key morphological types, including mound-like corals of various sizes, two-dimensional corals including solitary and non-attached species, plate-like or foliose corals, branching corals, tall, complex mounds or columnar corals, and digitate or tabular corals (Fig. 3). The proportional representation in provincial species pools of each of the major clusters is constrained within a narrow range of values across the Indo-Pacific (varying between 0.05 and 0.25, depending on the cluster) (**Figure 2.3C**), where each major cluster is supported by tens or even hundreds of species (**Figure 2.3D**). Furthermore, the proportion of the species pool represented in each cluster is remarkably constant across a very broad gradient in species richness (**Figure 2.3C**).

The occupancy of trait space is strikingly different between the two major domains, exemplified by the disparity between the Caribbean and the Great Barrier Reef (**Figure 2.4**). The two domains have no native species in common (Veron 1995), yet they share a range of functional roles, because Caribbean species occupy similar areas of trait space to those on the Great Barrier Reef, despite an 11-fold difference in species richness (**Figure 2.1 and 2.4A**). Contours of high redundancy in trait space (based on kernel density estimation) for the Great Barrier Reef indicate that the highest redundancy occurs in three major clusters of species that are predominantly mound-shaped, tabular, or digitate and branching (**Figure 2.4A-B**). These clusters represent a broad range of traits for > 200 species with a wide range of taxonomic affiliations. In contrast, the Caribbean trait space is heavily depleted, with only one high-redundancy cluster of massive and submassive corals, no fast-growing digitate (bushy) or tabular corals, and only three species of branching corals (*Acropora palmata*, *A. cervicornis*, and a hybrid between them) (**Figure 2.4A-B**). The clustering of species in the Caribbean trait space (**Figure 2.3B-D**), therefore, leaves large portions of trait space unoccupied, or populated by just one or a few functionally distinctive species.

The distinct biogeographical patterns of diversity and redundancy in coral trait space can have major consequences for the dynamics of coral assemblage functions in different provinces. In particular, critical attributes underlying reef resilience and function are poorly represented in the Caribbean trait space (**Figure 2.4C-D**). For example, two fundamental traits, maximum tissue biomass and skeletal growth rates of whole colonies, reach their highest overall value among species with complex morphologies (such as many species of *Acropora*) and with large mound-like skeletons, (e.g. *Diploastrea*, *Orbicella*, *Pavona*, and *Porites*) (**Figure 2.4C**). In the Caribbean, species with these attributes are poorly represented (**Figure 2.4A-C**). In contrast, on the Great Barrier Reef, these species are widely distributed across trait space, comprising a diverse mix of taxa (**Figure 2.4A-C**). Furthermore, a key trait, the mode of larval development (i.e. brooders, spawners), is distributed differently in trait space among the two domains (**Figure 2.4D**). Although there are proportionally more brooding species in the Caribbean, they are limited to a subset of functional types and devoid of large, three-dimensional species. In contrast, both brooding and spawning strategies are widely distributed across the Great Barrier Reef trait space, indicating that a diversity of dispersal and recruitment patterns occurs across a broad range of functional types of corals in this region (**Figure 2.4**).

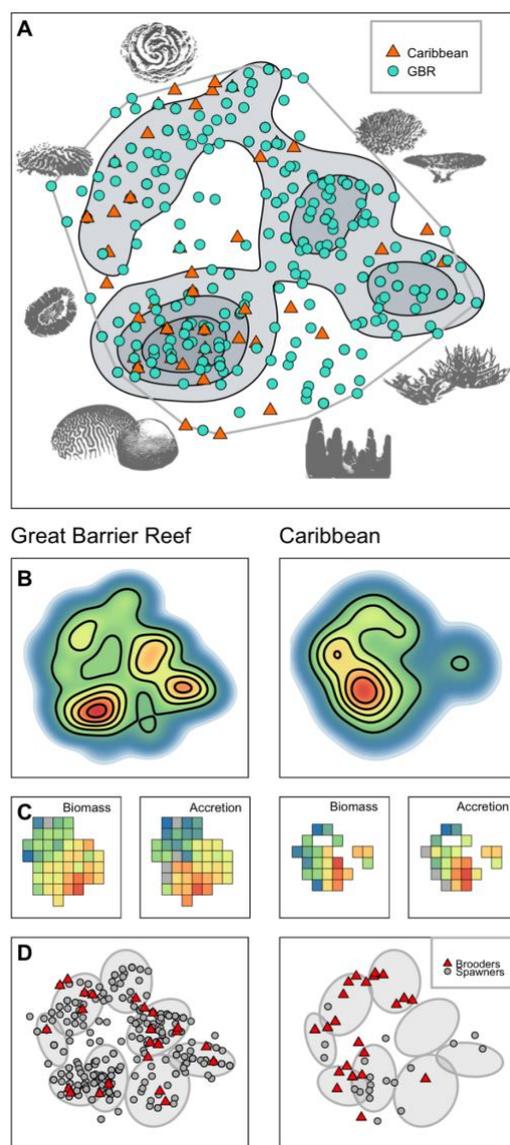


Figure 2.4: The diversity and redundancy of trait space on the Great Barrier Reef and Caribbean. (A) Coral trait space, with species (points) coloured blue for the Great Barrier Reef and orange for the Caribbean, showing the overlap in trait space between the two domains, and contours of high species density in grey. (B) A heatmap of species density in the global trait space, for each domain, with contours indicating peaks of richness and similarity. (C) A heatmap for each domain of two functional traits, the total tissue biomass and skeletal accretion rates of colonies. The squares represent the portion of 80 fine-scale species clusters or functional entities that are occupied in each province (grey = data deficient). (D) The distribution of reproductive modes in trait space in both domains. The ellipses illustrate eight coarse-scale species clusters.

Discussion

This study reveals that a diverse variety of coral functional trait-combinations can be represented along the same few axes of correlated trait variation. The boundaries of these axes differ among the two Indo-Pacific and Atlantic domains, and along regional-scale gradients in reef biodiversity. Provinces with higher species richness exhibit a greater range of traits and trait-combinations, in addition to a greater similarity, or redundancy, among species. Moreover, the proportion of coral species in different hotspots of trait space is remarkably consistent across the major provinces of the Indo-Pacific, consistent with their high species richness, and their uniform taxonomic composition at the family level (Bellwood and Hughes 2001). Like reef fish (Mouillot et al. 2014), all Indo-Pacific provinces contain a mix of high-redundancy clusters of species with similar traits, alongside an unexpectedly high number of distinctive species that are relatively isolated in trait space. For corals, however, peripheral provinces with comparatively low species richness are particularly low in redundancy, because major functional roles are supported by just a few, unique species, occupying large areas of trait space. This lack of functional redundancy is critical, because it can reduce the collective potential of groups of similar species to resist or recover from a variety of stressors (Walker et al. 1999, Bellwood et al. 2004).

The broader functional roles of corals, as measured here by numerous morphological and life history traits, correspond with previously used groupings based on colony shape (**Figure 2.4A**) (Bellwood et al. 2004, Denis et al. 2017), highlighting the functional relevance of colony morphology, and the intrinsic association of numerous morphological and physiological traits (Hughes 1987, Madin and Connolly 2006, Hoogenboom et al. 2015, Pratchett et al. 2015, Madin et al. 2016b). By analyzing a more comprehensive range of traits, however, I reveal a greater dissimilarity between species, creating a more accurate and quantitative depiction of the potential functional roles of species. Trait diversity is high in most Indo-Pacific provinces, making them even greater hotspots of functional diversity than previously assumed (Bellwood et al. 2004). Some Indo-Pacific species break the rules of conventional trait associations, and therefore occupy remote corners of trait space where there are fewer species than expected by chance. For example, they are species with unusually low skeletal densities, large corallites on branches, or enormous colony sizes. In depauperate provinces, the most unique species are often the sole representatives of large

areas of trait space, thereby upholding critical functions such as reef productivity, carbonate accretion and habitat complexity. For example, *Acropora palmata*, a species that was once abundant but now considered to be in danger, is the tallest 3-dimensional coral in the Caribbean. Its decline has dramatically reduced rates of reef accretion, and the provision of habitat on shallow reefs (Alvarez-Filip et al. 2011, Perry et al. 2013). Declines in such unique and essential species can severely compromise reef function with little hope of compensation by other, dissimilar species.

How biogeographical differences in trait diversity and redundancy translate into differences in ecosystem function depends on how regional pools of species assemble at local scales, accounting for the abundance and trait variability of individual species, and for non-coral taxa with similar functional roles (e.g. calcifying algae). Clearly, coral reefs can develop and flourish even in depauperate provinces with substantially lower functional diversity. For example, Clipperton Atoll, in the remote East Pacific, has only seven species of corals, and assemblages there are dominated by mound-shaped *Porites* (Glynn et al. 1996), highlighting the ability of just a few species to maintain a broad array of functions sufficient to sustain a coral reef. In addition, reef growth and development in the Atlantic has persisted independently of a tenfold variation in coral species richness over the past 28 million years (Johnson et al. 2008). Nevertheless, many studies highlight the importance of high coral functional diversity, for example, to maintain complex variations in microhabitat (Vytöpil and Willis 2001), and for the provision of habitats and resources used by different fish and invertebrate species (Shirayama and Horikoshi 1982). Measuring redundancy, therefore, requires a careful consideration of the functions of interest, and of the resolution of a trait-based analysis necessary to distinguish functionally important and redundant species. The analysis used measures the similarity between species at two scales; fine scale clustering of 80 aggregates, and coarser scale similarities within eight hotspots of trait similarity. At both scales, redundancy is substantially lower in depauperate regions, highlighting their vulnerability to both major shifts in function, in addition to more intricate shifts that may otherwise go unrecognised.

For redundancy to enhance the resilience of high-richness regions compared to depauperate ones, redundant species must exhibit response diversity, i.e. have different tolerances to environmental change, or have different regeneration capacities after a perturbation (Elmqvist

et al. 2003). Numerous species traits influence resistance to stress, reproductive capacity, dispersal ability, or growth rate. However, low redundancy in key groups can reduce the diversity of these traits and limit the extent of response diversity among species (Suding et al. 2008, Oliver et al. 2015). Indeed, the poor representation of key reproductive modes in large areas of Caribbean trait space may be a liability, since it may reduce the potential for response diversity when only one reproductive mode (brooding or broadcast spawning) is dominant. Low morphological diversity in large areas of Caribbean trait space may also limit the diversity of tolerances to mechanical disturbances such as storms (Madin and Connolly 2006). Response diversity is common in highly redundant marine and terrestrial ecosystems (Hughes 1994, Walker et al. 1999, Steneck et al. 2002), and has been observed in Indo-Pacific coral assemblages (Denis et al. 2017). Nevertheless, the stabilizing influence of response diversity becomes weaker as the severity of multiple stressors increases. For example, response diversity within similar guilds of terrestrial plants (Laliberté et al. 2010) and tropical birds (Karp et al. 2011) diminishes under land-use intensification. Thus, a key challenge for coral research is to understand the role of response diversity among functionally similar species, especially in the context of multiple chronic and acute stressors, and to identify the traits that enhance the resistance or recovery of assemblages.

Coral reefs face an uncertain future, and already in many cases, the goal of returning degraded reefs to their original state is no longer an option. Instead, the global challenge in the face of climate change is to maintain reefs in a way that preserves their ecological functions, recognizing that the species composition is already changing rapidly (Hughes et al. 2017a). Across the world's reefs provinces, there is an increasing prevalence of heavily impacted coral assemblages, where more tolerant or regenerative species are favoured (Darling et al. 2013). In many regions, the extent of shifts in ecosystem functions, or the prospects of returning to a normal functioning state, are unknown. Ultimately, the degree of functional transition by reefs depends on shifts in the abundance of corals, and on the level of similarity between persistent and declining species. The critical task of understanding and preserving reef function rests on our comprehension of these phenomena, including the wide range of functional traits among species, and the vulnerability of reef functions within and across biogeographical regions.

Chapter 3: Global warming transforms coral assemblage functions

Manuscript published in *Nature* as ‘Global warming transforms coral reef assemblages’

Introduction

Extreme weather events due to anthropogenic global warming are rapidly emerging as a major contemporary threat to virtually all ecosystems (IPCC 2014). On coral reefs, severe heatwaves trigger episodes of mass bleaching (Heron et al. 2016, Donner et al. 2017, Hughes et al. 2018a), when the relationship between corals and their photosynthetic symbionts (zooxanthellae, *Symbiodinium* spp.) breaks down, turning the coral pale. Bleached corals are physiologically damaged and nutritionally compromised, and they can die if bleaching is severe and recovery of their symbionts is prolonged (Baird and Marshall 2002, Baker et al. 2008). However, the relationship between heat exposure, bleaching and the subsequent mortality of different taxa is not well understood or quantified. While the concept of winners versus losers has been widely applied to describe inter-specific differences in the degree of bleaching (Loya et al. 2001, Hughes et al. 2003, 2017b, Swain et al. 2016), predicting the definitive losers, namely the corals that fail to regain their colour and ultimately die following heat stress, is key to understanding how climate change affects biodiversity, species composition and ecosystem function.

To date, no study has examined the quantitative relationship between a broad range of heat exposures and the response of coral assemblages. Establishing the shape of this response curve is essential for identifying the critical levels of heat exposure that trigger bleaching and mass mortality, and for predicting the amount of heat exposure that could drive a transformation in species composition and the widespread collapse of ecological functions. Here, the geographic patterns of heat exposure and the resultant mortality of coral assemblages are examined along the 2,300 km length of the Great Barrier Reef, following the record-breaking marine heatwave of 2016 (Australian Bureau of Meteorology 2016). The die-off of corals drove a radical shift in the composition and functional traits of coral

assemblages on hundreds of individual reefs, transforming large swaths of the Great Barrier Reef from mature and diverse assemblages to a highly altered, degraded system.

Materials and methods

Initial mortality and heat stress: Aerial surveys were conducted in March/April 2016, to measure the geographic extent and severity of bleaching on the Great Barrier Reef, and the bleaching scores were subsequently converted into mortality estimates using a calibration curve based on underwater measurements of coral losses (Extended Data Figure 1 in Hughes et al. 2018b). The aerial surveys were conducted throughout the Great Barrier Reef Marine Park and the Torres Strait between Australia and Papua New Guinea, from the coast of Queensland to the outermost reefs, and along the entire Reef from latitudes 9.5-23.5°S. Each of 1,156 individual reefs was scored into one of five bleaching categories: (0) less than 1% of corals bleached, (1) 1-10%, (2) 10-30%, (3) 30-60%, and (4) more than 60% of corals bleached. The accuracy of the aerial scores was ground-truthed by measuring the extent of bleaching underwater, also during March/April 2016 (Hughes et al. 2017b, 2018c).

Underwater, the initial mortality of different taxa due to heat stress was assessed at the same time as the aerial surveys, on 83 reefs that spanned the full spectrum of heat exposures and bleaching. On each reef, the extent of bleaching and mortality on individual coral colonies was measured at two sites using five 10 x 1 m belt transects placed on the reef crest at a depth of 2 m. Colonies were identified (at the species or genus level) and recorded a categorical bleaching score for each one (n = 58,414 colonies): (1) no bleaching, (2) pale, (3) 1-50% bleached, (4) 51-99% bleached, (5) 100% bleached, and (6) recently dead. The dead colonies had suffered whole-colony mortality, were white with fully intact fine-scale skeletal features, typically still had patches of rotting coral tissue, and they were experiencing the initial week or two of colonization by filamentous algae, features which distinguished them from corals that died earlier. The timing of the initial underwater censuses, at the peak of the bleaching in March/April 2016, was critical for identifying corals that were dying directly from heat stress, and for measuring the baseline composition of the assemblages.

Heat stress on the Great Barrier Reef in 2016 was quantified at 5 km resolution, using the NOAA Coral Reef Watch version 3 Degree Heating Week (DHW) metric (Liu et al. 2014).

DHW values are presented in the results as a heat-map (Stretch type: Histogram Equalize) using inverse distance weighting (IDW; Power: 2, Cell Size: 1000, Search Radius: variable, 100 points) in ArcMap 10.2.1.

Longer term mortality: To measure longer-term coral loss (decrease in coral cover after eight months) and its relationship to the level of bleaching and heat exposure, detailed before-after assessments of taxon-specific abundances were conducted by re-visiting 63 of the 83 reefs. Abundances in March/April and eight months later were measured at the same locations in October/November, and changes in coral cover for 15 ecologically and taxonomically distinct components of benthic assemblages were compared on reefs exposed to a broad spectrum of heat stress. These measurements were conducted at the same two geo-referenced sites per reef, on reef crests at a depth of 2 m, using five 10 m long line-intercept transects per site. There were no cyclones or flood events on the GBR during the March-November period (Austral Winter) in 2016. Unbleached reefs typically showed small increases in cover due to growth, which were included in the regression analyses. Analysis of change in coral cover was undertaken using the log₁₀-transformed ratio of final to initial cover.

The initial and final composition of corals was compared using non-metric multi-dimensional scaling (nMDS) based on a Bray-Curtis similarity matrix of square-root transformed data, and quantified the shift over time using the Euclidean distance between before-after assemblages at each location. The relationship between the shift in composition at each reef versus the level of heat exposure experienced was then estimated. To include all species, the majority of which are too rare to analyse individually, each was pooled into 15 ecologically cohesive groups depending on their morphology, life history, and taxonomy. Three of the 15 are ubiquitous species or species complexes: *Pocillopora damicornis*, *Seriatopora hystrix*, and *Stylophora pistillata*. In each of the multi-species groups, the dominant species or genera on reef crests were: Other *Acropora* (*A. gemmifera*, *A. humilis*, *A. loripes*, *A. nasuta*, *A. secale*, *A. tenuis*, *A. valida*); Favids (i.e. species and genera from the formerly recognized Family Faviidae - *Cyphastrea*, *Favia*, *Favites*, *Goniastrea*, *Leptastrea*, *Montastrea*, *Platygyra*); Mussidae (*Lobophyllia*, *Symphyllia*); *Isopora* (*I. palifera*, *I. cuneata*); Other *Pocillopora* (*P. meandrina*, *P. verrucosa*); Other sessile animals (sponges, tunicates, molluscs); *Porites* (*P. annae*, *P. lobata*); *Montipora* (*M. foliosa*, *M. grisea*, *M. hispida*, *M. montasteriata*, *M. tuberculosa*); Staghorn *Acropora* (*A. florida*, *A. intermedia*, *A.*

microphthalma, *A. muricata*, *A. robusta*); Soft Corals (alcyonaceans, zooanthids); and Tabular *Acropora* (*A. cytherea*, *A. hyacinthus*, *A. anthocercis*).

Longer-term mortality for all species combined at the scale of the entire Great Barrier Reef was calculated in three ways, all of which yielded consistent results. The first approach, which provided the best spatial resolution, was based on a comparison of the observed loss of total coral cover on 63 reefs that extend along the entire Great Barrier Reef measured underwater between March and November, with aerial bleaching scores of the same locations in March/April (Extended Data Figure 1 in Hughes et al. 2018b). This calibration allowed for the conversion of the aerial scores of bleaching that were recorded for 1,156 reefs into mortality estimates for each of the five aerial score categories, and to map the geographic footprint of losses of corals throughout the Great Barrier Reef. The spatial patterns of coral decline are presented as a heat-map of the calibrated scores (Stretch type: Histogram Equalize) using inverse distance weighting (IDW; Power: 2, Cell Size: 1000, Search Radius: variable, 100 points) in ArcMap 10.2.1.

The second methodology for estimating large-scale mortality is independent of aerial surveys of bleaching, and based on the loss of total coral cover on 110 reefs (**Appendix C**), including the 63 reefs that were re-censused for change in composition. The median cover on these reefs declined between March and November from 34% to 20% (Extended Data Figure 3 in Hughes et al. 2018b). For method two, the observed loss of coral cover was averaged for replicate reefs surveyed within each of eight sectors of the Great Barrier Reef Marine Park and the Torres Strait), corrected for differences in reef area for each sector based on GIS data provided by the Great Barrier Reef Marine Park Authority, and then summed to calculate the total loss. For method three, the fitted relationship between satellite-derived Degree Heating Weeks and observed change in cover was used to score the losses or gains on all 3,863 individual reefs comprising the Great Barrier Reef, and average the total. These two alternative approaches for estimating large-scale loss of cover, both based on before-after underwater surveys yielded consistent results with the first methodology – a 29.0 and 27.7% decline, respectively, after eight months.

Differential mortality among coral taxa: To estimate how exposure to heat (measured as Degree Heating Weeks, DHW) affects loss of cover differentially among taxa, a linear mixed

effects model was used. The fixed effect was DHW, and a random effect of taxonomic grouping on both the intercept and slope of the relationship between coral cover change and DHW was allowed. Excluded from the analysis were observations with zero initial coral cover of a particular taxonomic group. Change in coral cover was transformed prior to analysis by calculating $\log\left(\frac{C_{final}+\epsilon}{C_{initial}+\epsilon}\right)$, where C_f and C_i were final and initial coral cover, respectively, and ϵ was the minimum observed value of coral cover. The estimated random effect on intercepts was approximately zero, so they were eliminated from the final model. Thus, in the final model, there was a common intercept, but differences between taxa in sensitivity to DHW (i.e., there was a random effect of taxonomic group on the slope). To illustrate these differences, the estimated slope of the coral cover response variable was plotted for each taxon versus DHW as the overall mean effect of DHW plus the taxon-specific random effect.

Shifts in functional traits: To calculate how differential mortality affected the mix of traits in the coral assemblages, I scored eight traits for 12 of the 15 functional groupings (excluding Soft Corals, Other Scleractinia, and Other Sessile Fauna, **Table 3.1 and 3.2**). Traits were chosen that are likely to influence ecosystem functions. For example, corals with fast growth rates and high skeletal density strongly influence calcification, colony shape affects photosynthesis and the provision of three-dimensional habitat, and the size of corallites is a measure of heterotrophy. The traits were scored using the Coral Trait Database (Madin et al. 2016a), with the exception of colony size which were measured directly for each group on reef crests using the geometric mean of intercept lengths for each taxon from the initial transects. For multi-species groups, the traits were generally identical for all species. Otherwise, for *Montipora* and *Porites*, I used the mean score across the reef crest species encountered. To measure the depletion of traits based on changes in absolute abundances between March and November, I used a community weighted mean (CWM) analysis of each trait:

$$CWM = \sum_{i=1}^n a_i \text{ trait}_i$$

where a_i is the abundance of coral taxa i and $trait_i$ is the trait value of coral taxa i . This metric provides a trait value for each reef weighted by the total abundance of each taxa. To visualise the overall shift in functional composition, I used a non-metric multi-dimensional scaling analysis (nMDS) based on a Bray-Curtis dissimilarity matrix of square-root transformed data for each trait community weighted mean, creating a multi-dimensional trait space in which reefs are positioned according to the value and abundance of critical traits.

Table 3.1: Eight traits used in the analysis and their functional relevance.

Trait	Trait scores	Reef function
Growth rate	In mm/year: 0-10 (1), 10-20 (2), 20-40 (3), 40-60 (4), >60 (5).	Carbonate framework accretion; reef regeneration
Skeletal density	In g/cm ³ : <1 (1), 1-1.4 (2), 1.4-1.7 (3), 1.7-2 (4), >2 (5)	Carbonate framework accretion
Corallite width	In mm: <1 (1), 1-2 (2), 2-5 (3), 5-15 (4) ; <15 (5)	Filter feeding; nutrient capture
Interstitial space size	(1-5) Based on morphological categories.	Habitat provision
Colony height	(1-5) Based on morphological categories.	Carbonate framework accretion; habitat provision
Surface area to volume ratio	(1-5) Based on morphological categories	Primary productivity; nutrient cycling
Colony size	Rank (1-12) measured from reef crest transects	Carbonate framework accretion; habitat provision
Reproductive mode	Brooders (1), Mixed (2), Spawners (3)	Reef connectivity and regeneration

Table 3.2: Trait scores for each of 12 groups of corals.

Taxon	Corallite size	Growth rate	Colony size	Skeletal density	Colony height	Tissue area	Interstitial space size	Reproductive mode
Bushy <i>Acropora</i>	2	3	7	3	3	5	3	Spawner
Favids	4	1	4	3	2	1	1	Spawner
<i>Isopora</i>	2	2	10	3	2	2	1	Brooder
<i>Montipora</i>	2	3	9	5	1	1	1	Spawner
Mussidae	5	1	3	2	2	1	1	Spawner
Other <i>Pocillopora</i>	1	3	8	3	3	4	3	Spawner
<i>Pocillopora damicornis</i>	1	3	2	4	2	4	3	Brooder
Poritidae	2	2	6	2	4	1	1	Mix
<i>Seriatopora hystrix</i>	1	3	1	5	2	3	3	Brooder
Staghorn <i>Acropora</i>	2	5	11	4	5	3	5	Spawner
<i>Stylophora pistillata</i>	2	3	5	4	2	3	3	Brooder
Tabular <i>Acropora</i>	2	4	12	4	3	5	5	Spawner

Results and Discussion

The 2016 bleaching event triggered an unprecedented loss of corals on the northern third of the Great Barrier Reef, and to a lesser extent, the central third, with virtually no heat-stress mortality occurring further south (*Figure 3.1a*). The geographic footprint and intensity of the coral die-off closely matched the observed north-south pattern in accumulated heat (*Figure 3.1b*), measured as satellite-derived Degree Heating Weeks (DHW, °C-weeks), a widely-used measure that incorporates both the duration and intensity of heat stress¹⁶. The 5 km-resolution DHW values (*Figure 3.1b*) were significantly correlated with the independently-estimated losses of corals on 1,156 reefs (*Figure 3.1a*; $r^2 = 0.50$, $p < 0.001$). In the northern, 700 km-long section of the Great Barrier Reef (from 9.5-14.5°S), where the heat exposure was the most extreme, 50.3% of the coral cover on reef crests was lost within eight months (*Figure 3.1b*). More broadly, throughout the entire Great Barrier Reef, including the southern third where heat exposure was minimal (*Figure 3.1b*), the cover of corals declined by 30.0% between March and November 2016. In comparison, the massive loss of corals from the 2016 marine heatwave was an order of magnitude greater and more widespread than the patchier, localized damage that typically occurs on reefs sites within the track of a severe tropical cyclone (Beeden et al. 2015).

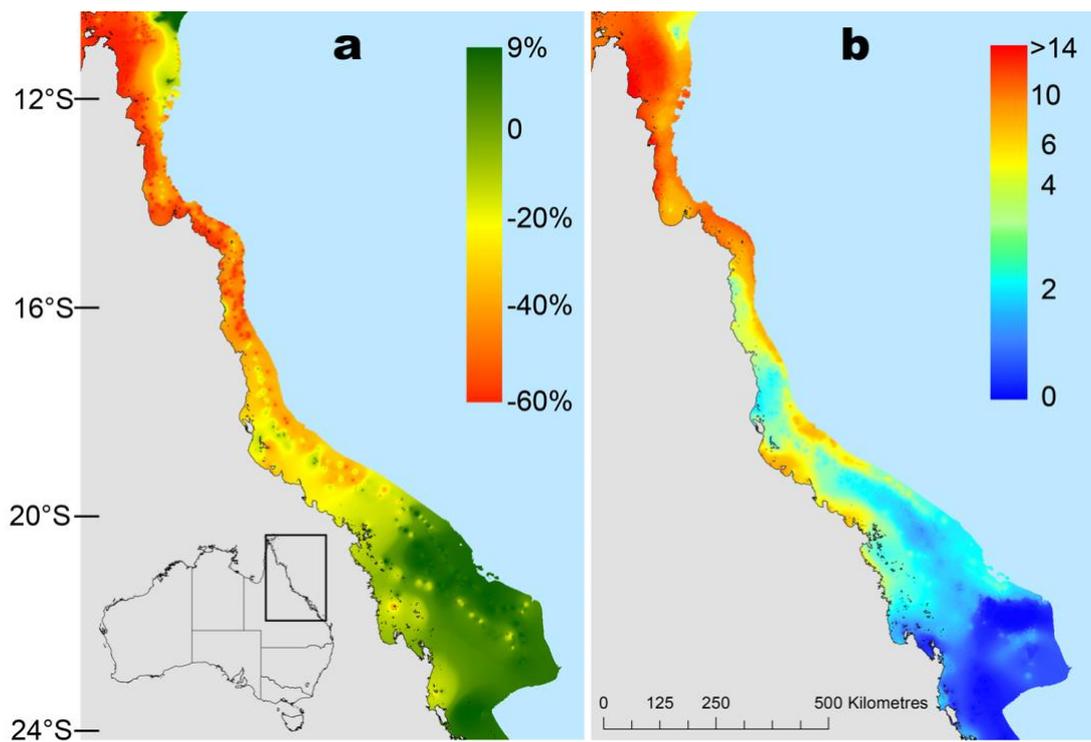


Figure 3.1: Large-scale spatial patterns in change in coral cover and in heat exposure on the Great Barrier Reef, Australia. (a) Change in coral cover between March and November 2016. (b) Heat exposure, measured as Degree Heating Weeks (DHW, °C-weeks) in the summer of 2016.

At the scale of individual reefs, the severity of coral mortality was also highly correlated with the amount of bleaching, and with the level of heat exposure (**Figure 3.2**). Initially, at the peak of temperature extremes in March 2016, many millions of corals died quickly in the northern third of the Great Barrier Reef over a period of just 2-3 weeks (**Figure 3.2a**). These widespread losses were not due to the attrition of corals that slowly starved because they failed to regain their symbionts (Baker et al. 2008). Rather, thermally-sensitive species of corals began to die almost immediately where they were exposed to heat stress of $>3-4^{\circ}\text{C}$ -weeks (**Figure 3.1b and 3.2a**). The amount of initial mortality increased steadily with increasing heat exposure ($r^2 = 0.50$, $p < 0.001$); where the exposure was $<4^{\circ}\text{C}$ -weeks, fewer than 5% of the corals died, whereas there was an initial median loss of 15.6% of corals on reefs with 4-8 $^{\circ}\text{C}$ -weeks exposure, and a median loss of 27.0% of corals at locations that experienced $\geq 8^{\circ}\text{C}$ -weeks (**Figure 3.2a**). Across the entire Great Barrier Reef, 34.8% of individual reefs experienced $\geq 4^{\circ}\text{C}$ -weeks, and 20.7% of reefs were exposed to $\geq 8^{\circ}\text{C}$ -weeks of accumulated heat stress in 2016 (**Figure 3.1a**). The amount of initial mortality at the peak of summer varied strikingly among different groups of corals, and was highest for *Pocillopora damicornis*, two species of *Isopora*, *Stylophora pistillata*, and staghorn *Acropora* (**Figure 3.3a**).

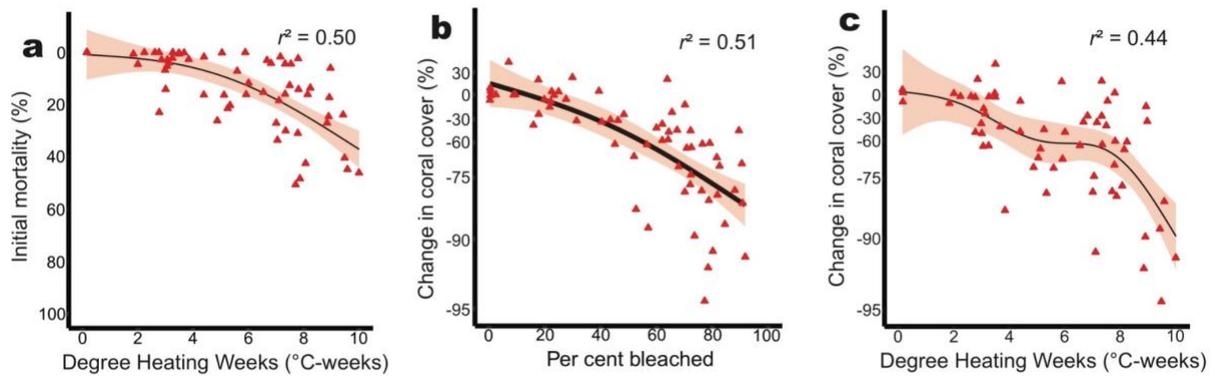


Figure 3.2: The initial and longer-term response of coral assemblages to heat exposure. Regression curves are fitted using Generalised Additive Models (GAMs), with 95% confidence limits (ribbons). Data points represent individual reefs. (a) Initial coral mortality measured at the peak of bleaching, versus the heat exposure each reef experienced (satellite-based Degree Heating Weeks, DHW, °C-Weeks). (b) Longer-term change in coral cover (log10) between March and November 2016 on individual reefs, versus the initial amount of bleaching recorded underwater. (c) Longer-term change in coral cover (log10) between March and November 2016, versus heat exposure (DHW) on individual reefs.

During the ensuing Austral winter, the bleached corals in the northern and central Great Barrier Reef either slowly regained their colour and survived, or they continued to die at unprecedented levels. Fewer than 1% of surviving colonies remained bleached after eight months. The severity of the longer-term loss of corals, measured *in situ* as the decline in coral cover between March and November, was accurately predicted by the percent of corals that were initially bleached (**Figure 3.2b**; $r^2 = 0.51$, $p < 0.001$). Specifically, reefs that experienced less than 25% bleaching in March typically had almost no loss of cover after eight months (**Figure 3.2b**). In contrast, above this threshold, the loss of coral cover increased progressively, indicating that fewer of the bleached corals survived. Furthermore, the longer-term loss of coral cover intensified with increasing levels of heat exposure of each reef (DHW, $r^2 = 0.44$, $P < 0.001$; **Figure 3.2c**). Consequently, there was almost no loss of coral cover for reefs exposed to 0-3 °C-weeks, compared with a 40% decline at 4° C-weeks, 66% for 8 °C-weeks, and extreme declines of >80% for exposures of ≥ 9 °C-weeks. The non-linear responses to heat exposure varied significantly among coral taxa (**Figure 3.4**), illustrating a spectrum of survivorship among winners versus losers, driving a radical shift in species composition.

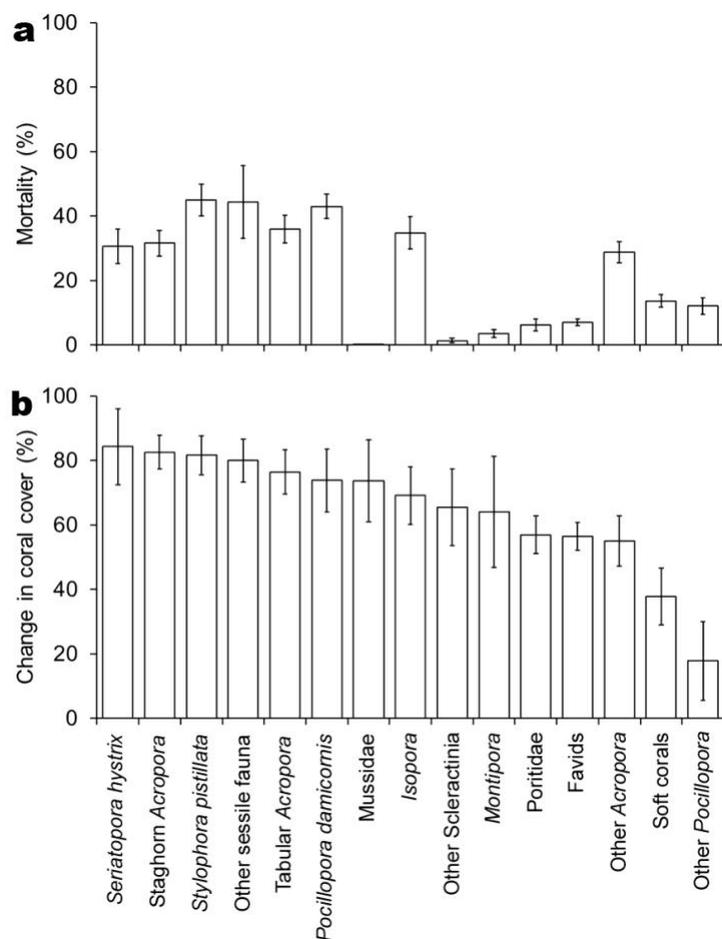


Figure 3.3: Mortality rates differ among taxa and increase over time. (a) The initial mortality of corals recorded on belt transects on 83 reefs with >60% bleaching (b) Longer-term average loss of cover for taxonomic categories recorded between March and November on 63 re-censused reefs with >60% bleaching. Taxa are plotted in rank order along the x-axis from high to low decreases in cover, with a spectrum of relative winners on the right and losers to the left. Error bars are one standard error.

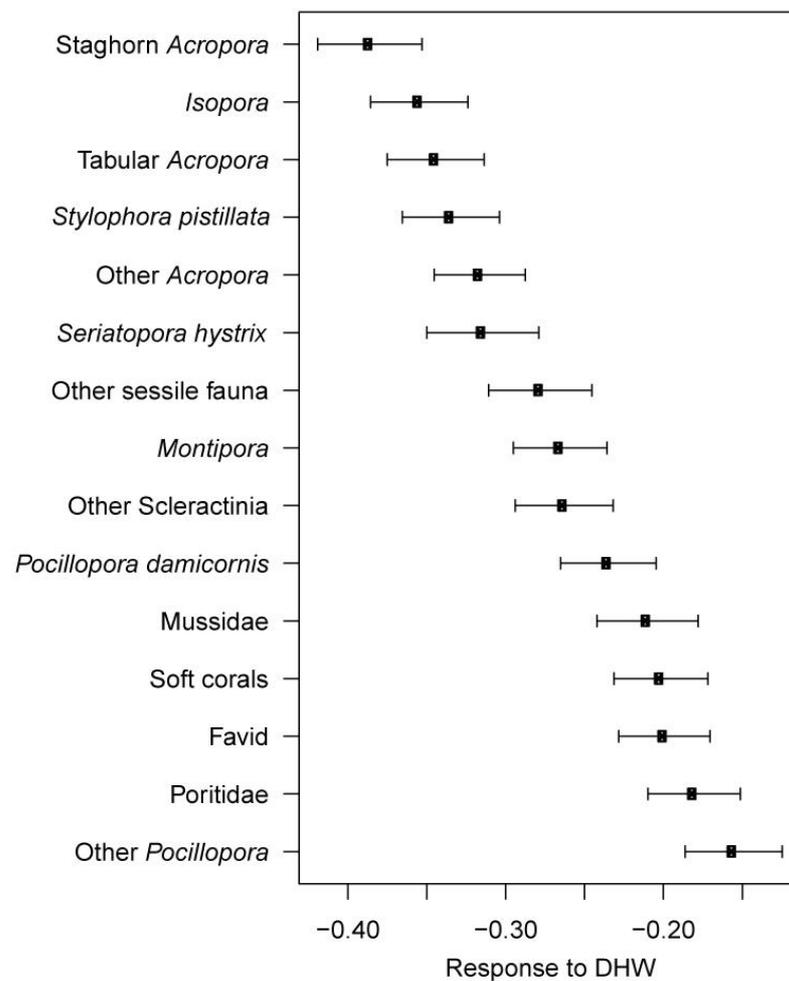


Figure 3.4: Differential sensitivity of coral taxa to temperature stress. Differential sensitivity is illustrated by the estimated loss of cover for different groups of corals between March and November as a function of heat exposure (DHW). The horizontal axis is the slope of the relationship between the log-ratio of final and initial coral cover (response variable) and degree-heating weeks (explanatory variable). Values plotted for each taxonomic grouping (ordered from most sensitive to least sensitive) are random effects estimates, with conditional standard errors.

Post-bleaching mortality has disproportionately transformed the assemblage structure and functional diversity of corals on reefs that experienced high levels of bleaching (affecting >60% of colonies), as illustrated by a non-metric multi-dimensional scaling (nMDS) analysis (**Figure 3.5**). The abundances of all categories of corals decreased to varying degrees on these heavily bleached reefs, shown by the orientation of the nMDS vectors (**Figure 3.5a**) and the directional shift in the before-after assemblages (**Figure 3.5b**). Tabular and staghorn *Acropora*, *Seriatopora hystrix* and *Stylophora pistillata* - fast-growing, three-dimensional species that dominate many shallow Indo-Pacific reefs – all declined by >75% (**Figure 3.3**). In contrast to the radical shifts on heavily bleached reefs, assemblages changed very little between March and November on reefs that experienced moderate (30-60%) or minor (0-30%) bleaching. On these reefs, the nMDS analysis of before and after assemblages shows that shifts in composition were small and multi-directional (**Figure 3.5c**).

The response curve of coral assemblages exposed to a range of heat stress, from 0-10 °C-weeks, (measured as the Euclidean distance between before and after compositions on each reef, **Figure 3.5b-c**), is strikingly non-linear (**Figure 3.6**). The changes in assemblage structure after eight months were small on reefs that were exposed to <6 °C-weeks, whereas reefs subjected to >6 °C-weeks lost >50% of their corals (**Figure 3.2c**) and shifted dramatically in composition (**Figure 3.6**). Satellite-derived DHW data indicate that 28.6% of the 3,863 reefs comprising the Great Barrier Reef experienced thermal exposures of >6° C-weeks during the 2016 bleaching event, and 20.7% (800 reefs) were exposed to >8 °C-weeks (**Figure 3.1**). Individual reefs with this severity of heat exposure have undergone an unprecedented ecological collapse, extending southwards from Papua New Guinea for up to 1,000 km (**Figure 3.1**). Reefs that were exposed to <6 °C-weeks were located predominantly in the southern half of the Great Barrier Reef, and in a narrow northern patch at the outer edge of the continental shelf where temperature anomalies in 2016 above the local long-term summer maximum were small (**Figure 3.1b**).

The abrupt, regional-scale shift in coral assemblages has radically reduced the abundance and diversity of species traits that facilitate key ecological functions (**Figure 3.5d-f**, **Table 3.1 and 3.2**). A before-after analysis of the multi-dimensional trait space of coral assemblages, weighted by the absolute abundance of taxa contributing to each trait, reveals

a transformation in the functional-trait composition of assemblages on heavily bleached reefs (affecting >60% of colonies) in the eight month period after March 2016 (*Figure 3.5e*). In most cases, reefs shifted away from the dominance of fast-growing, branching and tabular species that are important providers of three-dimensional habitat, to a depauperate assemblage dominated by taxa with simpler morphological characteristics and slower growth rates. In contrast, on less-bleached reefs the weighted abundances of functionally important traits typically showed small gains (*Figure 3.5f*).

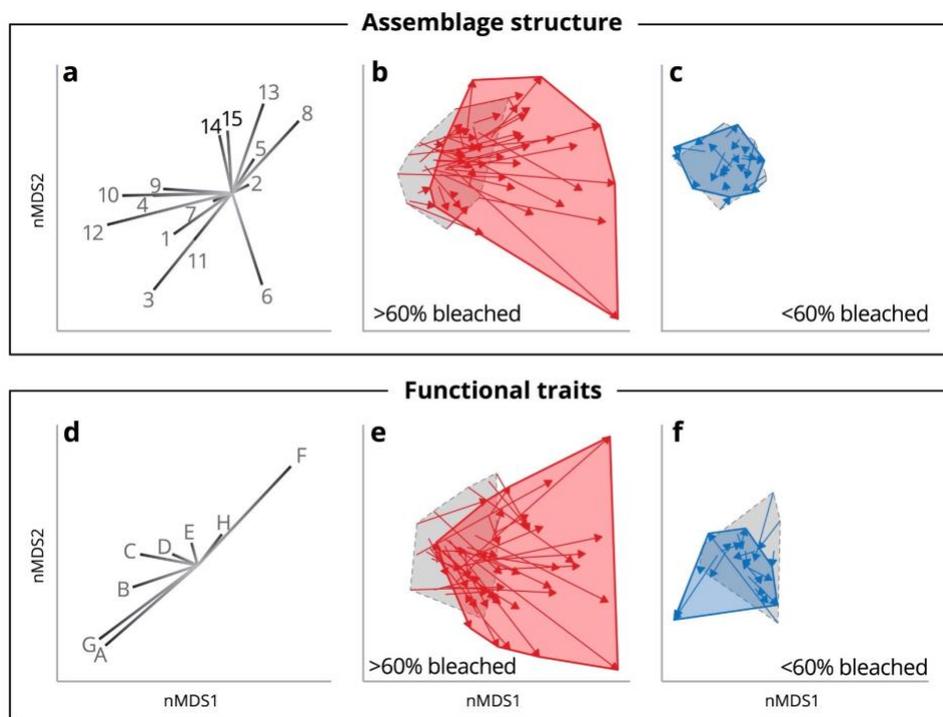


Figure 3.5: Changes in assemblage structure and functional traits of corals following mass bleaching (a-c) A non-metric multi-dimensional scaling (nMDS) analysis of shifts in coral assemblages between March and November 2016. (a) Fifteen nMDS vectors indicate the responses of individual taxa: (1) Other *Acropora*, (2) Favids, (3) *Isopora*, (4) *Montipora*, (5) Mussidae, (6) Other *Pocillopora*, (7) *Pocillopora damicornis*, (8) Poritidae, (9) *Seriatopora hystrix*, (10) Staghorn *Acropora*, (11) *Stylophora pistillata*, (12) Tabular *Acropora*, (13) Soft corals, (14) Other Scleractinia, and (15) Other sessile fauna. (b) Bounding polygons indicate the ordination space occupied by coral assemblages on each reef in March (dotted line) and again eight months later (solid line). Red arrows connect the before-after pairs of data points for each location to show changes in composition on severely bleached reefs (>60% of colonies bleached) after eight months. (c) Blue arrows connect the before-after pairs of data points for each location on reefs that were lightly or moderately (<60%) bleached. (d-f) An nMDS analysis of shifts in assemblage trait composition between March and November at the same locations. (d) The eight vectors indicate the absolute contribution of traits to coral assemblages: (A) Surface area to volume ratio, (B) Growth rate, (C) Colony size, (D) Skeletal density, (E) Colony height, (F) Corallite width, (G) Interstitial space size, (H) Reproductive mode. (e) The shift in abundance-weighted trait space co-ordinates for coral assemblages

over eight months for reefs with >60% bleaching. (f) The shift in abundance-weighted trait space co-ordinates for coral assemblages on reefs with <60% bleaching.

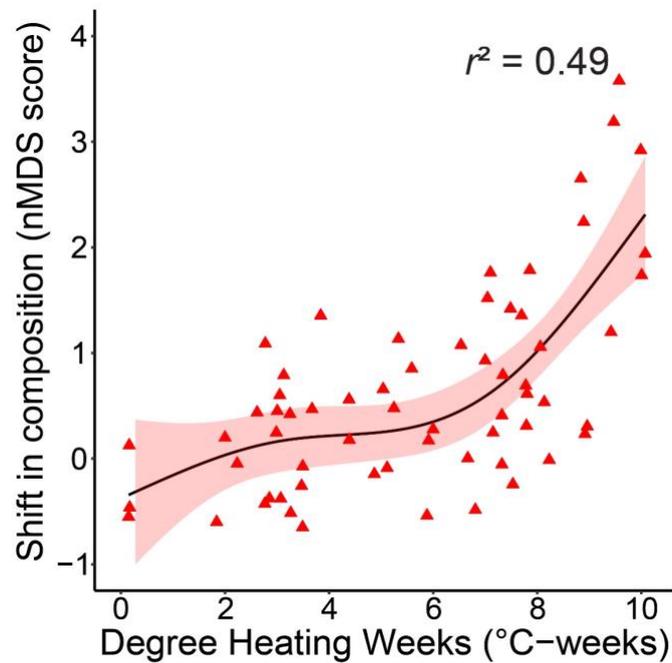


Figure 3.6: Change in coral assemblages in response to heat exposure. Regression curve is fitted using a Generalised Additive Model (GAM), with 95% confidence limits. Each data point represents the shift in composition, based on the Euclidean distance in a non-metric multi-dimensional scaling analysis of assemblages on individual reefs sampled at the peak of bleaching and eight months later. Heat exposure for each reef was measured as satellite-derived Degree Heating Weeks (DHW, °C-weeks).

Conclusions

In conclusion, this study shows that acute heat stress from global warming is a potent driver of a 1000 km-scale collapse of coral assemblages, affecting even the most remote and well-protected reefs within an iconic World Heritage Area. Forecasts of coral bleaching made continuously by the US National Oceanic and Atmospheric Administration (NOAA) are accompanied with guidance that a DHW exposure of 4° C-weeks is expected to cause significant bleaching, and 8 °C-weeks may also result in mortality of corals (Eakin et al. 2010, Liu et al. 2014, Kayanne 2017). Similarly, a model for predicting the locations of resilient reefs on the Great Barrier Reef assumed that coral mortality starts to occur only once thermal exposure exceeds 6 °C-weeks (Hock et al. 2017). However, this study shows that substantial mortality occurred on the Great Barrier Reef in 2016 well below 6 °C-weeks, beginning instead at 3-4 °C-weeks, and with typical losses exceeding 50% at 4-5 °C-weeks (**Figure 3.2c**). Furthermore, the threshold identified for the breakdown of assemblage structure, approximately 6 °C-weeks (**Figure 3.6**), was transgressed in 2016 throughout most of the northern, as well as much of the central, region of the Great Barrier Reef (**Figure 3.1**). The prospects for a full recovery to the pre-bleaching coral assemblages are poor, for several reasons. First, many of the surviving coral colonies continue to die slowly even after recovery of their algal symbionts, because they have lost extensive patches of tissue, are injured and fragmented, and because corals weakened by bleaching are susceptible to subsequent outbreaks of disease (Muller et al. 2008, Miller et al. 2009). Secondly, the replacement of dead corals by larval recruitment and subsequent colony growth will take at least a decade even for fast-growing, highly fecund corals, such as species of *Acropora*, *Pocillopora*, *Seriatopora* and *Stylophora* (Kayanne et al. 2002, Gilmour et al. 2013a). The success of future recruitment will depend upon an adequate supply of larvae from lightly bleached locations, the rapid break down of many millions of dead coral skeletons to provide a more enduring and stable substrate for settling larvae, and the availability of suitable settlement cues and conditions for survival of juvenile corals (Webster et al. 2011). Thirdly, for longer-lived, slow-growing species, the trajectory of replacement of dead corals on heavily damaged reefs will be far more protracted, almost certainly decades longer than the return-times of future bleaching events. The recurrence of mass bleaching during the recovery period will be

critical, in view of the global rise in the frequency of bleaching events (Heron et al. 2016, Donner et al. 2017, Hughes et al. 2018a).

The 2015-2016 global bleaching event is a watershed for the Great Barrier Reef, and for many other severely affected reefs elsewhere in the Indo-Pacific (Hughes et al. 2018a). Furthermore, the Great Barrier Reef experienced severe bleaching again in early 2017, causing additional extensive damage (GBRMPA 2017, Hughes and Kerry 2017). The most likely scenario, therefore, is that coral reefs throughout the tropics will continue to degrade over the current century until climate change stabilises (IPCC 2014), allowing remnant populations to reorganize into novel, heat-tolerant reef assemblages. The 2016 marine heatwave has triggered the initial phase of that transition on the northern, most-pristine region of the Great Barrier Reef (*Figure 3.6*), changing it forever as the intensity of global warming continues to escalate. The large-scale loss of functionally-diverse corals is a harbinger of further radical shifts in the condition and dynamics of all ecosystems, reinforcing the need for risk assessment of ecosystem collapse (Bland et al. 2018), especially if global action on climate change fails to limit warming to +1.5°C above the pre-industrial base-line.

Chapter 4: Disturbance, recovery, and the depletion of functional diversity on coral reefs

Manuscript in preparation

Introduction

Ecosystems are defined as resilient if they can withstand change or bounce back from perturbation (Holling 1973). Coral reefs are naturally exposed to frequent disturbances such as storms, yet the rate and severity of pulse disturbances is increasing rapidly because of human influences (Nyström et al. 2000), especially anthropogenic climate change. For instance, in recent decades coral communities have been subjected to recurrent episodes of mass bleaching and mortality because of global warming (Hughes et al. 2017b), and the time interval between these events is diminishing (Hughes et al. 2018a). Increasingly, the maintenance of ecosystem functions under recurrent disturbances is determined by how the functions of resistant or rapidly recovering species compares to the original set of functions prior to degradation (Oliver et al. 2015). If the frequency and intensity of disturbances is raised, and the survival and/or recovery of species is compromised, transitions into new configurations of species can occur (Dornelas et al. 2014, Graham et al. 2014). Moreover, disturbances in combination with chronic stressors (e.g. overfishing, pollution, and recruitment failure) can lead to catastrophic regime shifts into alternate ecological states, such as from coral reefs to macroalgae (Hughes 1994, Scheffer et al. 2001).

Resilience can be bolstered if declining species are replaced by functionally similar, but less vulnerable species that have a greater tolerance to environmental change, or faster regeneration rates after perturbation. Differences in response to environmental change among functionally similar species is known as response diversity (Walker et al. 1999, Elmqvist et al. 2003, Mori et al. 2013). Response diversity occurs in many complex systems (e.g. genomes, brains, machines) where seemingly redundant elements can continue to support critical functions when other components fail (Meyer and Van de Peer 2003, Drachman 2005). In ecological systems, response diversity has been shown to stabilise functions in a range of species assemblages, including plants, sea urchins, insects, fish, birds, and microbes

(Walker et al. 1999, Steneck et al. 2002, Allison and Martiny 2008, Karp et al. 2011, Cariveau et al. 2013, Nash et al. 2015, Stavert et al. 2017). Species may be replaced by other taxa contributing to the same ecosystem functions on acute timescales, such as the time between intermittent disturbances (Lavorel and Garnier 2002), and on large timescales, such as the time taken for vulnerable species to be lost to more gradual stressors (Karp et al. 2011). Nevertheless, response diversity is far from ubiquitous, and many diverse ecosystems have been confronted with the loss of unique species with no redundancy, or the loss of groups of species with similar responses, ultimately leading to collapsed ecological functions (Bellwood et al. 2003, Laliberté et al. 2010).

On coral reefs, a range of processes rely on the ability of reef-building corals to fix carbon, build skeletons, and produce a complex and dynamic reef framework. The abundance of corals (usually measured as coral cover of all species combined) is frequently used to quantify reef condition. However, a focus on coral cover alone masks important changes to reef composition and biodiversity. These shifts can have major consequences for the functional trait composition of assemblages (Hughes et al. 2018b, McWilliam et al. 2018b), potentially affecting ecosystem functions such as carbonate accretion (Kennedy et al. 2013, Perry et al. 2013) or the provision of habitat structure (Alvarez-Filip et al. 2009). Shifts in the composition of species can also diminish response diversity, reducing the capacity of ecosystems to maintain functions under successive disturbances (Vinebrooke et al. 2004). A key example of diminishing response diversity comes from Caribbean coral reefs, where heavily exploited herbivorous fish were initially replaced by grazing sea urchins, which maintained reef herbivory. However, elevated populations of grazing sea urchins succumbed to disease, overpowering the response diversity inherent to coral reefs, causing loss of herbivory (Hughes 1994). Analysis of species-level abundances and functional traits over years and decades can therefore reveal changes to ecosystem functions during cycles of disturbance and recovery, and the capacity for response diversity to maintain functions as vulnerable species decline.

Here, I analyse changes in the total cover, taxonomic composition and traits of coral assemblages over multiple decades, to quantify changes in functional diversity during cycles of disturbance and recovery. I focus on case studies of reefs located in three biogeographical provinces; the Great Barrier Reef (GBR), French Polynesia, and Jamaica. This broad

biogeographical scope allows for the comparison of reefs which differ markedly in their inherent species richness and functional composition (McWilliam et al. 2018b). For each region, I focus on case studies of coral assemblages that declined following disturbance, and subsequently made a complete or partial recovery towards coral dominance. I generate a functional trait space of corals to estimate changes to reef functions through time, and quantify the resilience and response diversity of coral assemblages by comparing the trait diversity of “winners” (species that increased in abundance after recovery) with that of “losers” (species that decreased).

Materials and methods

Time series data: Time series data were assembled for reefs from three biogeographical provinces; the GBR (North Reef, Lizard Island, 12°S, 145°E), French Polynesia (Tiahura Reef, Moorea, 17°S, 149°W), and the Jamaica (Rio Bueno, 18°N, 77°W). For each case study, coral assemblage composition was surveyed over a timespan of a decade or longer on reef slope habitats (7-15m depth). On the GBR, I collected data on community composition at six dates between 1995 and 2017. In Polynesia, I use data on community composition at five censuses between 1979 and 2009, with additional data on coral cover at 12 periods (1990-2002) taken from Traçon et al (2011). In Jamaica, I collated data on community composition at 16 periods between 1977 and 2013. At each census, the mean abundance of coral taxa was quantified along 5 replicate 10m transects (GBR and Polynesia) or 5 replicate 1m quadrats (Jamaica). Datasets were selected to include at least one cycle of disturbance and recovery, and to maximise the biogeographical scope of the study. In doing so, I increase the range in biodiversity encountered in the analysis, spanning a gradient in species richness from approximately 60 coral species in Jamaica, 180 species in Polynesia, to >400 on the GBR (Veron 1995). These patterns provide a useful backdrop on which to analyse response diversity.

To measure taxonomic and functional trait composition consistently across these three studies, it was necessary to pool taxa that were measured on the surveys into 44 taxonomic categories. Of these 44 taxonomic categories, 28 are genera, 5 are families, and 11 are morphological subgroups for diverse genera, such as *Acropora* (e.g. staghorn *Acropora*, digitate *Acropora*, tabular *Acropora*), *Pocillopora* (e.g. *P. damicornis*, Other *Pocillopora*)

and *Porites* (e.g. branching *Porites*, massive *Porites*). Of these 44 categories, 30 occurred at sites on the GBR, 20 in Polynesia, and 16 in Jamaica, reflecting the overall biodiversity at these 3 locations. See **Appendix D** for the structure of taxonomic categories in relation to the original datasets.

Coral trait diversity: In order to measure shifts in the functional trait diversity of coral assemblages through time, seven traits were used to measure trait-based dissimilarities between taxa: growth rate, skeletal density, colony size, corallite width, interstitial branch spacing, colony height and colony surface area. Raw species-level data on coral growth rates, skeletal densities, colony diameter, corallite widths and growth forms was gathered from the coral traits database (Madin et al. 2016a). Species were pooled by their taxonomic category (Table S1), and average trait values were found for each category. To account for uncertainty in trait data and variability within groups, trait values were placed into numerical groups between 1 and 5 (**Table 2.1**). Interstitial branch spacing, colony height, and surface area to volume ratio were derived from species growth form (“growth form typical” in the coral trait database) following the protocols outlined by McWilliam et al (2018b). A multidimensional coral trait space was generated using a principal component analysis (PCA) of 44 taxonomic groups. The PCA explained 65% of the variance in the trait data, and positions of the 44 groups in the PCA are shown in **Figure 4.1**.

Functional trait diversity was quantified across locations and time intervals using an abundance-weighted metric of species dispersion in trait space; Functional Dispersion (FDis) (Laliberte and Legendre 2010), and an alternate metric; Rao’s Quadratic Entropy (Botta-Dukát 2005). These parameters measure the distances of each taxon from the mean coordinates of the assemblage, weighted by abundance (community-weighted mean, Lavorel et al. 2008), thereby providing an estimation of the diversity of traits, and the degree to which abundance is distributed evenly among different sets of traits. Large values indicate that the predominant species occupy broad areas of trait space, representing a functionally diverse community. Low values indicate that the most abundant taxa are concentrated into a single area of trait space, suggesting a community dominated by functionally similar species (Mouillot et al. 2013b). Functional diversity calculations were conducted for each location using the ‘FD’ package in R and trait-based differences were based on the Euclidean distance matrix of PCA coordinates in the combined trait space (Laliberte and Legendre 2010).

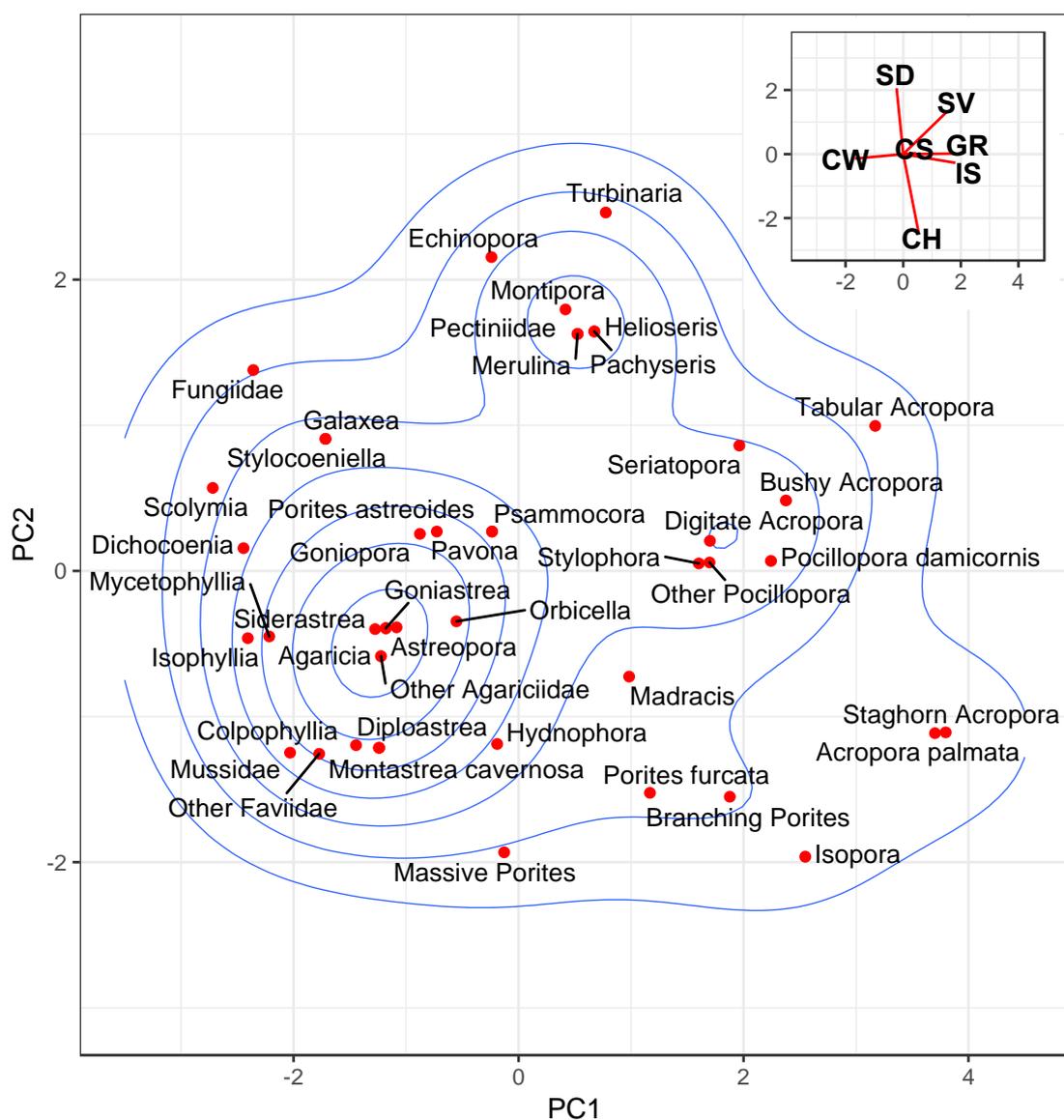


Figure 4.1: Positions of 44 taxonomic groups in trait space constructed using a PCA of seven functional traits. Blue contour lines indicate the presence of distinct clusters of taxa. PCA axis 1 explains 44% of the trait variation, while PCA axis 2 explains an additional 18% of the trait variation. The subplot indicates the seven trait vectors used to generate the trait space; (CW) corallite width, (SV) surface-area to volume ratio, (GR) growth rates, (IS) interstitial branch area, (CH) colony height, (CS) colony size, and (SD) skeletal density.

Resilience and response diversity: My analysis focuses on assemblages in three different states: (1) pre-disturbance, (2) disturbed, and (3) recovering. Pre-disturbance assemblages are not considered to be reflective of pristine or climax assemblages, but are simply the assemblages on the earliest surveys (i.e. in 1995, 1979 and 1977). Recovering assemblages are defined as assemblages where coral cover has returned, or where coral cover is closest to its original level prior to disturbance. Resilience (the capacity of assemblages to resist or recovery from perturbation) was quantified using trajectories in coral cover, taxonomic composition, and functional trait composition at each time interval. Shifts in taxonomic composition through time were analysed using a non-metric multi-dimensional scaling (nMDS) based on a Bray-Curtis similarity matrix of square-root transformed data. Functional trait composition was measured using coral trait space (see above).

Response diversity can lead to the maintenance of ecosystem functions despite shifts in taxonomic composition and diversity. It is defined as differences in response to environmental change among taxa that contribute to the same ecosystem functions (Elmqvist et al. 2003). Unlike previous metrics of response diversity which measure different responses within functional groups, I quantified response diversity continuously by plotting shifts in abundance in trait space, and measuring the degree to which the trait space of losers (taxa that decreased in abundance after recovery) was replaced by the trait space of winners (taxa that increased in abundance after recovery). High response diversity occurs when winners and losers each occupy broad areas of trait space, allowing winners to maintain the same range of traits and ecosystem functions of losers. Low response diversity occurs when losers occupy a larger range of trait space than winners, or when the traits of winners and losers are distinct. Moreover, my analysis of response diversity identifies differences in the trajectories of winners and losers through time, allowing me to determine whether the replacement of taxa is driven primarily by differential survival, regeneration, or both.

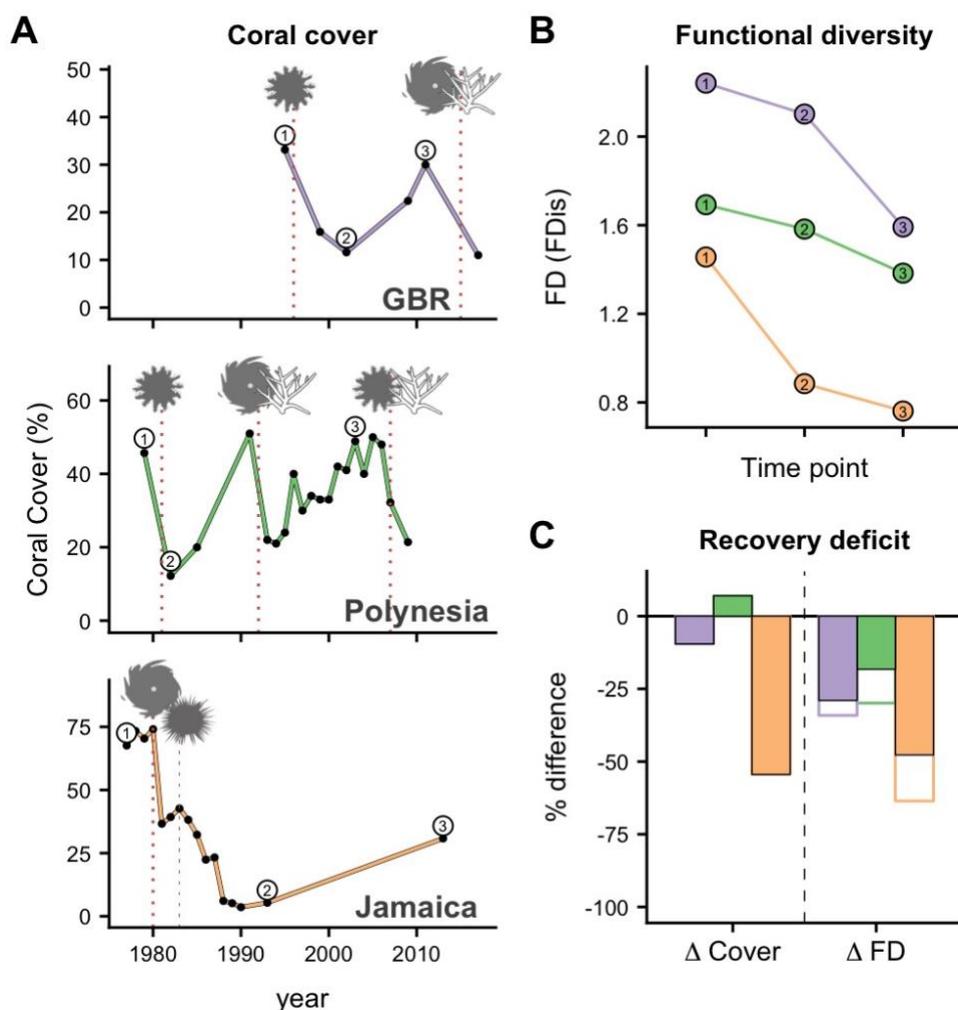


Figure 4.2: Disturbance-recovery cycles and loss of coral trait diversity. (A) Changes in coral cover on repeatedly surveyed reefs. Timing of original surveys varies between regions; Jamaica: 1977; Polynesia: 1980; GBR: 1995. Numbers indicate pre-disturbance (1), disturbed (2) and recovering (3) assemblages. Vertical red lines indicate the timing of major disturbance events. (B) Shifts in abundance-weighted functional diversity between pre-disturbance (1), disturbed (2), and recovering (3) assemblages. (C) The percentage difference in coral cover and functional diversity (filled bars = Δ FDIs, unfilled bars = Δ RaoQ) between pre-disturbance (1) and recovering (3) reefs in each region. Negative values indicating a deficit, and positive values indicating a gain.

Results:

In the decades following major disturbances, the taxonomic and functional composition of coral assemblages has failed to fully recover at all reefs in the analysis, even in locations where coral cover has returned to pre-disturbance (original) levels (**Figure 4.2**). Disturbances such as storms, macroalgae blooms, outbreaks of predatory starfish, and mass bleaching, drove rapid declines in coral cover in each location (Time points 1 and 2, **Figure 4.2A**). These disturbances were followed by periods of recovery which have varied in duration across different locations (Time points 2 and 3, **Figure 4.2A**). Following disturbances at sites on the GBR and in Polynesia, coral cover bounced back to over 90% of its original level within periods of approximately 10 years. In contrast, recovery was lacking following a hurricane in 1980 at sites in Jamaica, where coral cover declined to approximately 5% of its original level for at least 8 years, followed by a partial recovery of coral cover over approximately 20 years (**Figure 4.2A**). Despite return trajectories of coral cover in each location, functional diversity (measured using abundance-weighted Rao's Q) declined following disturbance (Time points 1 to 2, **Figure 4.2B**), and continued to decline in all locations following recovery (Time points 2 to 3, **Figure 4.2B**), driven by shifts in absolute abundance and taxonomic structure.

Comparisons with the original assemblages surveyed decades ago reveal substantial deficits in the functional trait composition of recovering assemblages (**Figure 4.2C**). On the GBR, coral cover in 2011 reached 90% of its original level measured in 1995 (10% loss), yet the original trait diversity was diminished by 29% (or 34% Rao's Q, **Figure 4.2C**). Similarly, following two cycles of disturbance and recovery in French Polynesia, coral cover in 2007 exceeded its original level measured in 1979 (7% absolute gain), yet the original trait diversity was diminished by 18% (or 30% Rao's Q). These patterns reflect limited capacities for maintaining the functional diversity of assemblages due to shifts in taxonomic structure. Meanwhile, after a prolonged regime shift in Jamaica, coral cover in 2013 returned to 46% of its original level measured in 1977, and the original trait diversity of assemblages was diminished by 49% (or 64% Rao's Q). Reef assemblages in Jamaica have therefore shown a limited capacity to maintain both coral cover and trait diversity through time. Although trait diversity remains highest on the GBR (and pre-disturbance levels of trait diversity were also highest in this location), assemblages in Polynesia had the greatest capacity to maintain their

original trait diversity during cycles of disturbance and recovery (**Figure 4.2C**). As a result, the disparity in functional trait diversity between Polynesia and the GBR has diminished through time as proportional losses were greater on the GBR (**Figure 4.2B**).

Shifts in abundance across trait space in all locations between original and recovering assemblages has favoured a subset of taxonomic groups with limited trait diversity. Consequently, recovering assemblages (Time point 3 in **Figure 4.2**), have shifted towards different areas of trait space (**Figure 4.3**). In coral trait space, taxa are positioned continuously according to seven key traits, falling into clusters which correspond to broad morphological types (**Figure 4.1 and 4.3A**). Assemblages were originally composed of abundant species with diverse functional attributes (including, massive, staghorn, and tabular corals on the GBR, bushy, digitate and non-attached corals in Polynesia, and staghorn, digitate and submassive corals in Jamaica). However, following disturbance and return trajectories of coral cover, the abundance-weighted means have shifted towards a subset of species (**Figure 4.3B**), which are good colonists, characterised by high rates of recruitment and growth (e.g. Tabular *Acropora* on the GBR, *Pocillopora* in Polynesia, *Agaricia* in Jamaica). Crucially, these early successional taxa represent different areas of trait space in each of these three locations, causing the three recovering assemblages to be dominated by distinct sets of traits (**Figure 4.3B**).

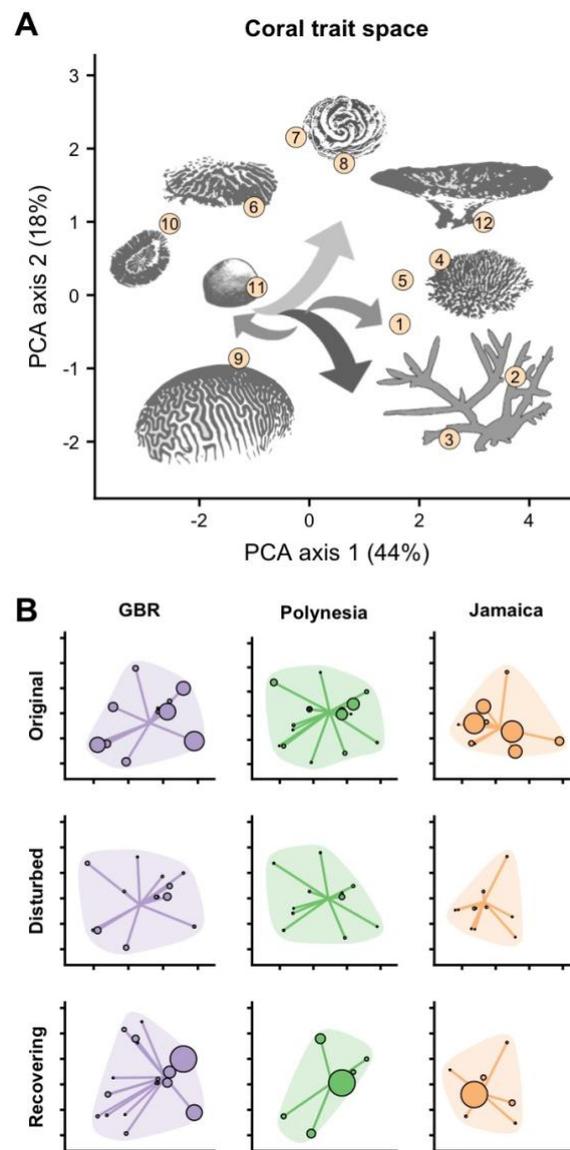


Figure 4.3: Shifts in abundance in coral trait space across three locations. (A) Coral trait space for 44 taxonomic groups pooled across the three locations. The centroids of eight morphological types are indicated by numbers; (1) complex-branching, (2) staghorn, (3) columnar, (4) corymbose, (5) digitate, (6) encrusting, (7) upright-encrusting, (8) laminar, (9) massive, (10) solitary, (11) submassive, (12) tabular. (B-D) Abundances of taxa in trait space between original, disturbed and recovering assemblages in three locations. Sizes of points indicate the abundance of each taxon at each time interval. Lines connect each taxon to the abundance-weighted means of trait space.

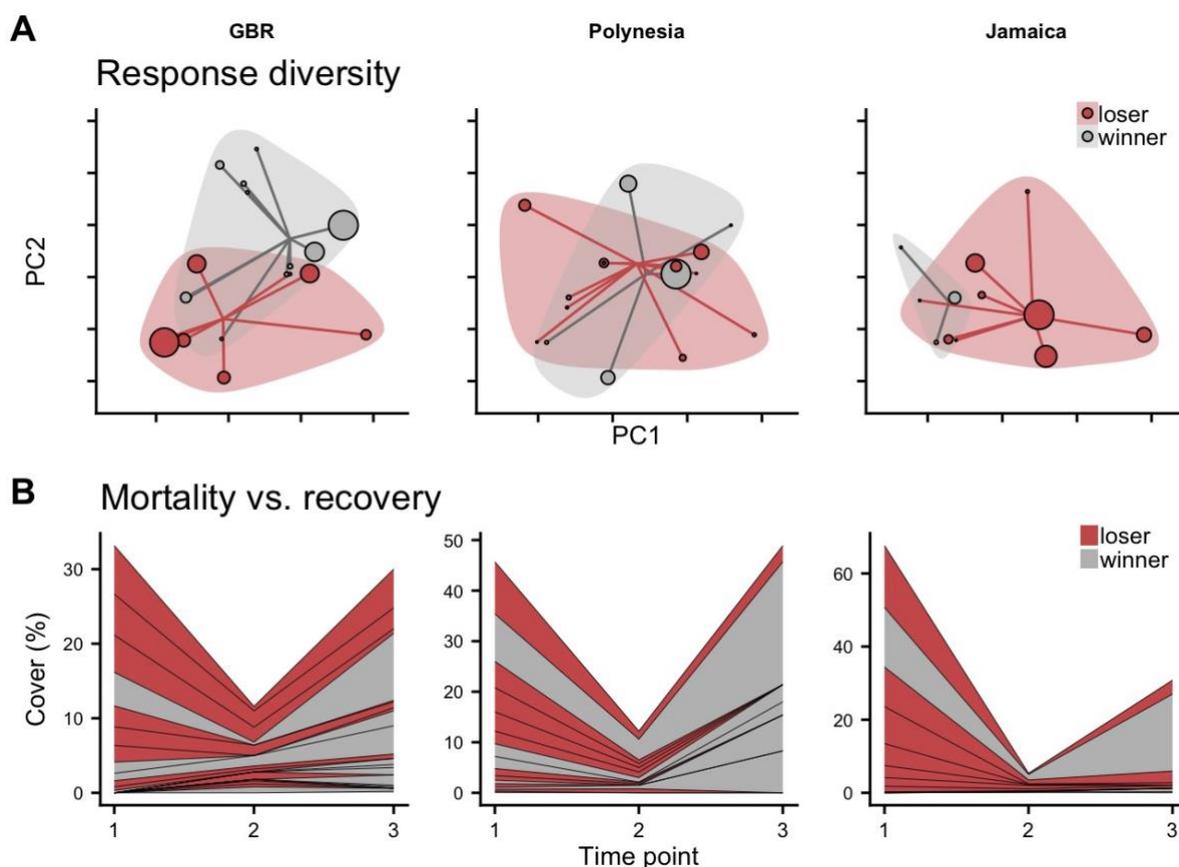


Figure 4.4: Response diversity following disturbance and recovery in three locations. (A) The positions of winner and loser taxa in coral trait space. Size of points indicates the amount in which taxa increased (for winners: grey) or decreased (for losers: red) in absolute abundance following disturbance and recovery (Time points 1 and 3). Lines connect each taxon to the mean coordinates of winners and losers, weighted by the increase or decrease in abundance respectively. (B) Shifts in the abundance of winners versus losers through time (1=pre-disturbance, 2=disturbed, 3=recovering). Stacked wedges indicate the abundances of each taxon. Differences on the downward trajectory (1 to 2) reveal differential mortality. Differences on the upward trajectory (2 to 3) reveal differential recovery.

Changes in absolute abundances between original and recovering assemblages reveal taxa which are “winners” and “losers” (**Figure 4.4**). The overlap in the distribution of winners and losers across trait space reveals limitations to response diversity across all locations, because many areas of trait space have declined with no alternate responses by functionally similar species (isolated red points in **Figure 4.4A**). On the GBR and in Polynesia, loss of abundances in loser taxa was largely matched by increases in winner taxa. Nevertheless, in both locations, winners did not replace the functional attributes of losers. On the GBR, the abundance-weighted centroids of winners and losers were distinct (red and grey lines in **Figure 4.4A**), reflecting different functional attributes of taxa with large losses and gains in abundance. In contrast, in Polynesia, abundance-weighted centroids of winners and losers were similar. However, winners occupied a small area of trait space relative to losers (shaded areas in **Figure 4.4A**), indicating that distinct traits have been lost without replacement. In Jamaica, a critical lack of taxonomic replacement was demonstrated by the disparity between loss and gain of taxa. Consequently, winners are concentrated into localised areas of trait space, and the abundance-weighted traits of winners are distinct from losers (**Figure 4.4A**).

Increases in abundance in ‘winner’ taxa can occur by two mechanisms. The first is by greater survival, allowing taxa to maintain high abundances throughout recurrent disturbances. The second is through faster recovery. On the GBR and in Polynesia, most ‘winner’ taxa underwent severe declines during disturbance which was followed by rapid recoveries, indicating that many winners are good regenerators (grey bars in **Figure 4.4B**). Nevertheless, some exceptions are evident. For example, one highly abundant taxon in Polynesia (*Pocillopora spp.*) maintained relatively high cover during the initial disturbance, leading up to its subsequent replacement of other taxa, indicating that winners may also be good survivors. In addition, some winners on the GBR and in French Polynesia have increased despite being initially rare, suggesting that disturbance and recovery can generate new patterns of dominance and rarity. In Jamaica, survival was very low among all taxa during the decline trajectory, and the prominence of ‘winner’ taxa has been almost entirely reliant on rapid recruitment (**Figure 4.4B**). The high reliance on recovery for maintaining coral populations in Jamaica, and to a lesser extent on the GBR and in Polynesia, has led to the depletion of many areas of trait space where other taxa have not recovered, but continued to decline (**Figure 4.4**).

Discussion

Recovering coral assemblages in this analysis have shown varying degrees of resilience to disturbance over recent decades, demonstrated by long-term (decadal) shifts in the total abundance and functional trait composition of coral assemblages. A hallmark of resilience is the capacity of ecosystems to resist, or rapidly recover from pulse disturbances, and maintain their original, equilibrium state (Holling 1973). Nevertheless, a distinction can be made between assemblages that maintain their original composition despite recurrent disturbances, versus those that maintain ecosystem functions despite shifts in taxonomic composition (Oliver et al. 2015). Despite apparent resilience, recently recovering assemblages at both Indo-Pacific and Caribbean reef sites regained a limited subset of the original functional trait composition observed decades ago, indicating an inability to return to a functionally diverse state across all cases in the analysis.

Reefs in all regions of the world are changing decade by decade, as coral communities reassemble into new configurations following chronic and acute disturbances or recruitment failure (Hughes 1994, Connell 1997, Graham et al. 2014). Consequently, the loss of functional attributes is increasingly determined by response diversity; the degree to which persistent taxa replace the functions of vulnerable taxa in decline. Response diversity can occur if taxa are similar in many respects, but differ in a fundamental attribute, such as susceptibility (e.g. stress tolerance, physical robustness) or rebound potential (e.g. fecundity, dispersal, recruitment, growth). For example, differences in mobility and site-fidelity in reef fishes permit certain taxa to be more resistant to disturbances (e.g. storms and bleaching), potentially stabilising fish assemblage functions (Nash et al. 2015, Brandl et al. 2016). In corals, response diversity can arise from differences in recruitment rate (Edmunds 2018), biomechanical stability (Madin et al. 2012) and bleaching tolerance (Van Woesik et al. 2011). Indeed, as climate change progresses, differences in thermal tolerance among photosynthetic symbionts (*Symbiodinium*) will no doubt be a valuable source of response diversity, allowing some species and/or populations of corals to survive severe bouts of heat stress while others decline (Nyström 2006, Suggett et al. 2017). Critically, response diversity is a continuum based on the capacity of winner taxa to maintain the functions of losers. The occurrence of response diversity in this analysis is revealed by the presence of winner and loser corals after recovery. Nevertheless, limitations to response diversity are demonstrated

by the distinctiveness of winners and losers in multidimensional trait space, reflecting differences in the contributions of taxa to a range of potential functions (*Table 2.1*).

Severe disturbance events in which even tolerant taxa succumb to mortality can drastically limit response diversity. In such cases, the onus of maintaining functions is placed on rapidly recovering taxa which often occupy limited portions of trait space. These regenerative taxa are important for coral reefs, because reefs are naturally subjected to disturbances that leave them reliant on larval dispersal, colonisation and regrowth. Nevertheless, critical ecosystem functions are provided by larger and more long-lived taxa that can take many decades or centuries to rebuild populations once they are depleted. Loss of these long-lived taxa can lead to collapsed reefs that are functionally compromised for decades or more because of their limited capacity to recruit and recover following mass mortality. Low levels of survival among corals in the analysis has led to limited response diversity, and favoured taxa with smaller, shorter and simpler morphologies, with moderate-to-fast growth rates, and ‘weedy’ life histories, such as high size-specific fecundity (Hall and Hughes 1996), and high rates of mortality and recruitment (Hughes and Jackson 1985). Such taxa often exhibit transient dynamics, because they are most susceptible to storms (Hughes and Connell 1999), mass bleaching (Marshall and Baird 2000, Loya et al. 2001) and predator outbreaks (Pratchett 2010), potentially leaving reefs more susceptible to future disturbances. Consequently, this study emphasizes the need for both resistance and recovery among corals in order to maintain a wide range of functions, requiring response diversity among corals on both downward and return trajectories in coral cover (Baskett et al. 2014).

The escalation of anthropogenic impacts has revealed biogeographical differences in coral reef resilience. In the Caribbean, regime shifts (Hughes 1994) and functionally depleted assemblages (Perry et al. 2015), are increasingly widespread, while recovery is limited (Jackson 1992, Connell 1997). Regime shifts and changes to community structure have also been observed in the Indo-Pacific (Berumen and Pratchett 2006, Johns et al. 2014, Graham et al. 2015, Adjerdoud et al. 2018, Torda et al. 2018). A critical question is; to what extent do biogeographically distinctive pools of species equip reefs with a greater insurance against anthropogenic stress? Answering this question is problematic, because differences in the history of exploitation, coastal development and cultural activity across regions makes it difficult to distinguish intrinsic reef resilience from socioeconomic or environmental drivers.

The trajectories in functional composition observed in this analysis are likely to have been influenced by the intrinsic functional diversity of the regions where reefs are located. For example, the high abundance of tabular and bushy corals in the Indo-Pacific has favoured shifts towards different areas of trait space to that of the Caribbean, where these groups are lacking. Moreover, despite ongoing losses, functional diversity remains highest on the GBR, possibly providing greater insurance to ongoing degradation and biodiversity loss.

The disturbance dynamics of coral reefs are changing and in particular, long-term trajectories in community composition are increasingly affected by mass bleaching (Van Woesik et al. 2011, Gilmour et al. 2013b, Hughes et al. 2018b), land-based pollution (Cleary et al. 2008), disease (Aronson and Precht 2001), and predator outbreaks (Pratchett et al. 2011). Mass bleaching events in particular present a fundamental challenge to the maintenance of reef functions. The increasing severity of bleaching can limit survival amongst even the most tolerant taxa (Hughes et al. 2017b, 2018b), and the increasing frequency of bleaching can limit their potential for recovery (Hughes et al. 2018a). This study shows that reefs in different regions are already relying on their high biodiversity to maintain coral assemblage dominance and functional attributes, mostly favouring rapid colonisers with more transient or unstable dynamics. The potential for response diversity in these depleted assemblages will dictate the traits and functions that persist as new disturbance regimes progress.

Chapter 5: Neighbour diversity regulates the productivity of coral assemblages

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Introduction

The importance of species richness and composition for ecosystem function is widely acknowledged across a range of ecosystems, matching and often exceeding the importance of environmental variables such as nutrient availability or climate (Duffy et al. 2017). However, the mechanisms linking taxonomic diversity to ecosystem function can vary depending on the system and on the functional traits of the species in question (Cadotte 2017). Ecosystem functions, such as productivity, nutrient cycling, and trophic interactions, can be strongly affected by species with particular trait values, such as large body sizes (Solan et al. 2004), fast growth rates (Vile et al. 2006), unique feeding strategies (Bellwood et al. 2006), or high biomass or nutrient contents (Fortunel et al. 2009), which can enhance the functioning of diverse assemblages (Loreau and Hector 2001). Alternatively, biodiversity can enhance ecosystem functions by increasing the range or diversity of traits within assemblages (Cadotte 2017), leading to a more complete utilisation of resources (Tilman et al. 1997, Griffin et al. 2009), or by generating beneficial interactions between species (Wright et al. 2017). Emerging evidence indicates that such synergies are common in ecosystems, often occurring when functionally distinctive taxa modify the biotic or abiotic environment and subsequently increase the performance of others (facilitation) (Cardinale et al. 2002, Heemsbergen et al. 2004).

Tropical coral reefs are renowned for their high productivity per unit area (Odum and Odum 1955, Hatcher 1988), and coral assemblages typically maintain high community metabolic rates (Kinsey 1979, Atkinson and Grigg 1984), providing energetic input for critical reef functions such as calcification and habitat construction. Productivity is known to vary considerably among reef habitats (Pichon 1997, Nakamura and Nakamori 2009); however, the influence of coral diversity and composition on productivity is poorly understood. In this study, my aim was to quantify the interactions between coral individuals, species, and

functional groups and to identify a mechanistic link between coral diversity and assemblage productivity in the context of environment conditions. Communities were assembled in experimental flumes with comparable metabolic activity to natural reef communities and were composed of eight distinctive yet common coral taxa from shallow reef environments, representing a diverse mix of functional traits. Differences in photosynthetic productivity were quantified among eight monocultures and sixty multispecies (mixed) assemblages with distinct taxonomic and functional compositions. I focussed on water flow velocity (7.0 cm s^{-1} and 3.5 cm s^{-1}) as a key environmental parameter regulating how species composition affects productivity because of the known interactions between water flow, morphological complexity, and metabolism (Hoogenboom and Connolly 2009, Comeau et al. 2014).

Materials and methods

Experimental assemblages: Eight coral taxa were selected to represent a wide range of morphologies and functional groups. These were *Acropora millepora* (digitate/corymbose), *Acropora muricata* (staghorn), *Echinopora lamellosa* (plate-like/foliose), *Goniastrea retiformis* (massive/submassive), *Pavona cactus* (plate-like), *Pocillopora damicornis* (bushy), *Porites cylindrica* (digitate) and *Symphyllia recta* (massive-meandroid). For each species, four colonies 12 - 15cm in diameter were collected from 3 – 6 m depth at sites around Orpheus Island (Great Barrier Reef, Australia) in April 2017 and allowed to acclimate to aquaria conditions for one week. Experimental coral assemblages were set up in respirometry flumes (100cm x 10cm x 16cm), with recirculating flow and an open-top. Eight monocultures were each composed of four colonies of the same species. Mixed assemblages were composed of four colonies of either four ($n = 49$) or two ($n=11$) species. The exact composition of mixed assemblages was determined by randomly selecting the species in the assemblage from the species pool of eight, and then randomly selecting the colony to represent each species from four possible colonies that were collected. The result was 8 monocultures and 60 mixed assemblages with distinct taxonomic and functional compositions, each derived from the same 32 colonies. Using the same set of colonies was critical for the experiment, because it allowed the performance of each colony to be compared with and without neighbours, and among conspecifics or heterospecifics (see below).

Experimental conditions: Coral colonies were stored in a large outdoor flume for approximately two months and were temporarily transferred to indoor temperature-controlled flume chambers for measurement throughout the study. In the indoor flume chambers, seawater was filtered using a 5 μ m mesh, and temperature was fixed at 25°C (mean ambient seawater temperature for April-June at the study sites). Light was kept constant at approximately 700 mol photons m⁻² s⁻¹ (Maxspect R420R LED lights set to 70% intensity). Measurement of light using a LiCor Quantum Sensor (LI-193) at different underwater positions within flume chambers gave an estimate (mean \pm s.e.) of 699.0 \pm 17.0 mol photons m⁻²s⁻¹. Light levels were selected to be saturating with respect to photosynthesis but low enough to avoid photoinhibition (e.g. (Anthony and Hoegh Guldberg 2003, Hoogenboom and Connolly 2009)). Unidirectional water flow inside the flume chambers was controlled using a large 240V-24W pump (AQUAPRO AP1050) for higher flow rates and a small 240V-5.5W pump (AQUACLEAR 30) for lower flow rates. I quantified distinct fast and slow flow rates of approximately 7.0 and 3.5 cms⁻¹ respectively through the visual tracking of coloured dye across a fixed distance of 30 cm within flume chambers. Repeated analysis of the rate of flow of dyes in four chambers on two occasions gave estimates (mean \pm s.e.) of 6.95 \pm 0.41 cms⁻¹ for higher flow rates and 3.43 \pm 0.11 cms⁻¹ for lower flow rates. These flow rates correspond to dimensionless Reynolds numbers (UD/ν where U = flow speed, D = the hydraulic diameter of flumes, ν = the viscosity of seawater (Comeau et al. 2014)) of 10,640 and 5,320 for higher and lower flow respectively, and 9,450 and 4,725 for individual colonies (where D = the average diameter of colonies). When colonies were assembled in flumes, regular distances of 5 - 10 cm were kept between each colony, and the positioning of colonies was determined using a randomly assigned values of one to four (upstream to downstream). The influence of colony ordering within flumes on assemblage productivity was not found to be significant (data not shown).

Colony surface area and morphology: The total surface area of colonies was calculated using 3D reconstruction (Figueira et al. 2015), whereby 120 photos for each colony were used to generate points in 3D space using the alignment software VisualSFM (Changchang Wu, 2011), and a calibrated 3D surface was generated from points (including a scale bar) using the processing software MeshLab (Visual Computing Lab, ISTI-CNR). While these techniques are widely used for coral colony reconstruction, the precision of models decreases

with more finely branching morphologies, possibly leading to slight underestimations of surface area in these groups (see (Figueira et al. 2015) for discussion). Other morphological dimensions, such as planar surface areas and branching dimensions (e.g. height, width, density, and spacing), were quantified using image analysis in Image J (version 1.51h, US National Institute for Health) or measured directly from colonies. Tissue biomass values (Ash-Free Dry Weight, AFDW) were taken from subsamples of each colony at the end of the experiment by removing and homogenising the tissue, placing 8ml of slurry into a freeze dryer for 48 hours (Christ, Alpa 1-1 LO plus), incinerating in a muffle furnace at 550°C, and then dividing the weight of the ash by the surface area of the subsample.

Community metabolism: Net primary productivity of assemblages in the flume chambers was measured using oxygen respirometry under recirculating flow, in which photosynthetic O₂ production was logged using optical dissolved O₂ probes (Hach company, Colorado USA, model LDO101) placed downstream of coral colonies, and connected to portable data loggers (Hach company, Colorado USA, model HQ30D). Probes were calibrated twice per week using air-bubbled seawater as 100% saturation values. The linear increase in O₂ concentration over a 1-hour period (i.e., the rate of oxygen production due to photosynthesis in mg m⁻³ hr⁻¹) was then determined from the data. For productivity measurements, each assemblage was measured twice, and the average photosynthesis rate was calculated from these replicate measurements. Respiration rates were measured using one-hour incubations of assemblages in darkness (after daylight hours), allowing gross primary productivity to be calculated by the sum of light-O₂ production and dark O₂-depletion. A literature search was conducted to compare the productivity of the flume chambers with natural reef habitats observed *in situ* (see Supplementary Information). To ensure that the observed metabolic rates in flume chambers were comparable with other studies, hourly changes in the concentration of oxygen in the flume chambers (in mg m⁻³ hr⁻¹) were normalised to per unit area rates (in mg m⁻² hr⁻¹) by multiplying rates of change by the volume of seawater (0.038m³), and dividing by the planar area of the chambers (0.1 m²) occupied by the coral colonies. Metabolic rates measured in the flumes were comparable to data from natural coral-dominated environments recorded *in situ* over timescales of hours to days (**Figure 5.1**), suggesting that the productivity patterns observed in experimental assemblages are consistent with natural reef communities.

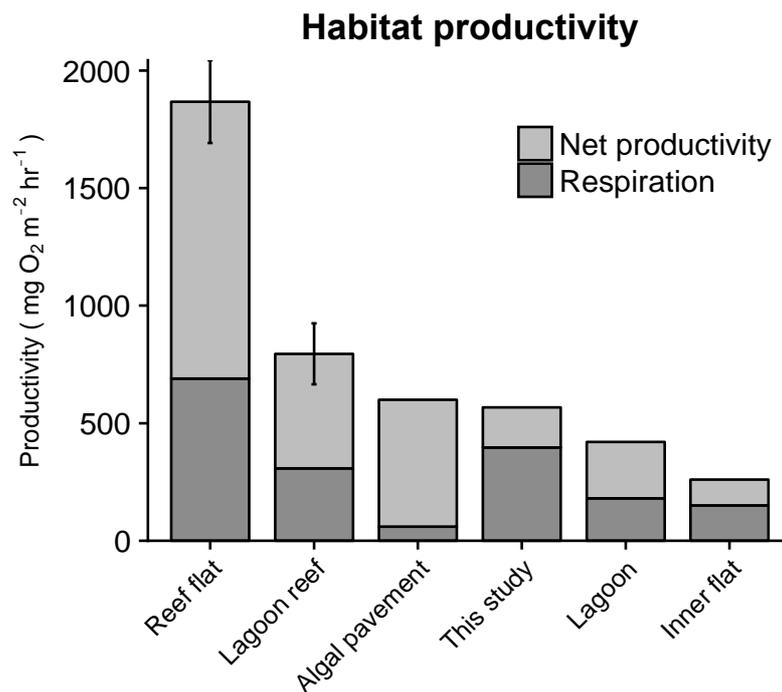


Figure 5.1: Difference in productivity between reef habitats measured in situ and comparison with the average flume productivity in this study. A literature search (*Appendix E*) was conducted to identify studies that used hourly oxygen flux to measure community-level photosynthesis and respiration of communities with coral cover > 10%. Studies were primarily based in the Pacific or Caribbean, and publishing dates ranged from 1957-2013. The studies included numerous methodologies to measure in situ changes in water chemistry, including flow-tracking dye or buoys, transparent tents, chambers or channels to isolate communities of interest, and more recently, sustained autonomous measurements.

Diversity effects: The effect of species richness on net-productivity was calculated as the difference between the observed productivity of mixtures and the expected productivity of mixtures when projected from monocultures. Thus, the diversity-effect on productivity D_p can be expressed by:

$$D_p = P_O - \sum_{i=1}^i a_i M_i$$

where P_O is the observed productivity of a mixture, a_i is the proportion of species i in the mixture, and M_i is the productivity of monoculture i . Proportions (a_i) were calculated from the fraction of the total planar area occupied by species i within the mixture. The second term on the right-hand side of the above equation therefore indicates a null expectation of productivity under additive contributions of species, based on their performance in monocultures. Diversity-effects (D_p) are presented as a percentage of this expected productivity.

Neighbour interactions: To identify positive and negative interactions occurring between neighbouring colonies, I tested the productivity of individual colonies alone in the flume chambers, and compared them with the performance of colonies in groups. Individual colonies were placed in the centre of the flume and productivity was measured by following the same protocols as described above. The impact of neighbouring colonies was then quantified as the difference between the productivity of combined assemblages and the expected productivity given by the sum of individuals incubated separately. Thus, neighbour interactions N_p can be expressed by:

$$N_p = P_O - \sum_{j=1}^j P_j$$

where P_O is the observed productivity of a mixture or monoculture, and P_j is the productivity of individual j measured separately. Neighbour interactions are presented as a percentage of the expected productivity (i.e. the second term in the right-hand side of the above equation). Differences between assemblage productivity and the sum of their individual colonies were

either driven by neighbour interactions or by random variability between the two assemblages. To distinguish true neighbour interactions from random variability, I calculated a threshold of 8% given by the average absolute difference in productivity between pairs of identical replicate assemblages (see *community metabolism*). I define facilitation as any assemblage in which positive neighbour interactions greater than 8% occurred and competition as any assemblage in which negative neighbour interactions less than -8% occurred.

Two analyses were used to link neighbour interactions to the composition of assemblages. First, I plotted interactions in coral trait space to identify species or traits that influenced, or were influenced by others. To generate the coral trait space, I quantified the functional traits of each colony, and created a trait space based on a principal component analysis (PCA). I focussed on traits which could potentially influence productivity or water flow. These were (1) colony planar area, (2) colony height, (3) colony rugosity (surface area to planar area ratio), (4) interstitial space size, (5) branch density, (6) branch length, (7) branch width, and (8) tissue biomass. The first two axes of the PCA explained 39.2% (PC1) and 20.4% (PC2) of variation in colony traits. For each pair of species, I identified all assemblages in which both species occur (6 – 8 assemblages per species pair), and found the mean neighbour interaction, allowing me to plot the pairwise interactions between species in trait space. Second, I used linear mixed effects models (LMEs) to test the statistical relationship between key traits and neighbour interactions. The predictors used were maximum surface area and the average flow-sensitivity of colonies (calculated as the change in colony productivity when flow is reduced from 7.0 to 3.5 cm s⁻¹). The model selected (based on AIC values) had no interactions between the two fixed effects, and included one random effect (flume chamber). All analyses were done using the statistical program R (R Development Core Team, 2006). LME models were produced using the function `lmer` in package `lme4`. I tested the strength of the model using r^2 values generated using the package `MuMIn`. Outputs for the model are presented in **Table 5.1**.

Results and Discussion

Manipulations of species composition in experimental coral assemblages (**Figure 5.2A**) revealed a significant positive effect of species richness on primary productivity when water

flow velocity was fixed at 7.0 cm s^{-1} (representative of moderate flow speeds on reefs (Patterson et al. 1991, Yates and Halley 2003, Long et al. 2013)). Net photosynthetic productivity (photosynthesis minus respiration) in mixed communities of two or four species was, on average, 53% greater than in monocultures (**Figure 5.2B**), and gross productivity (photosynthesis including respiration) was, on average, 18% greater (**Figure 5.3**). The average net productivity of mixed assemblages exceeded the productivity of all monocultures, except for monocultures of densely branching *Acropora*, which was the most productive single-species assemblage due to the high tissue surface area of colonies (**Figure 5.2B-C**). I found no effect of species richness on community-level respiration, suggesting that higher productivity in mixed assemblages was primarily a result of increased rates of photosynthesis (**Figure 5.3**). The observed value of net productivity for mixed assemblages was significantly greater than the productivity expected under a null model of additive species contributions projected from the productivity of monocultures ($D_p=44\%$, paired $t=11.21$, d.f.=60, $P<0.001$). This non-additive effect of species richness on productivity (often described as “over-yielding”) is widely observed in other marine systems where greater numbers of species can enhance short-term photosynthetic activity (Arenas et al. 2009) or long-term biomass accumulation (Bruno et al. 2005, Stachowicz et al. 2008), often through resource partitioning or facilitation.

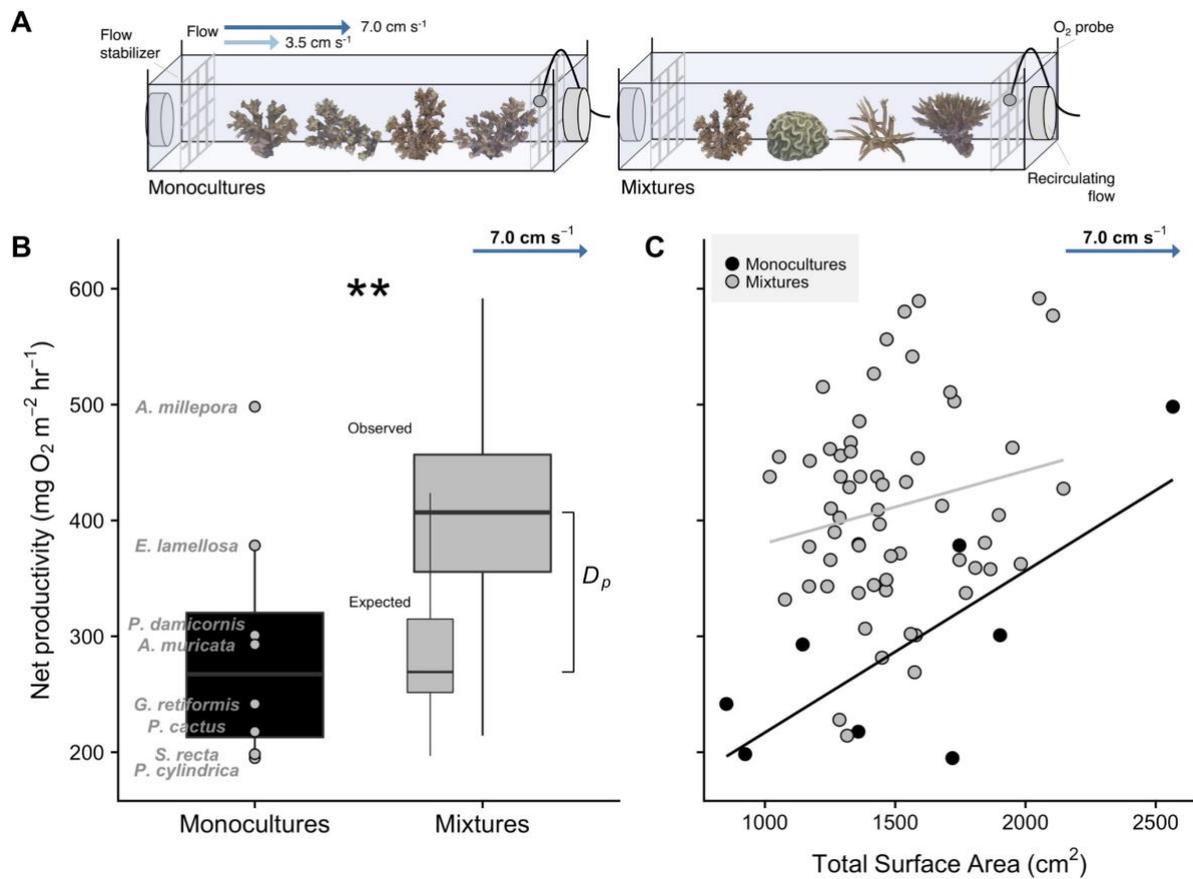


Figure 5.2: Experimental flumes quantifying the effects of species richness and morphological complexity on coral community productivity. (A) Experimental set-up showing flumes in which monocultures (1 spp.) and mixtures (2 or 4 spp.) were assembled. Productivity was then tested at two flow rates. (B) Boxplots indicating the productivity of monocultures versus mixtures at higher flow. Monoculture values are displayed with the taxonomic identity of each assemblage. Observed mixture values are presented alongside their expected values when projected from the performance of monocultures. The diversity effect (D_p) indicates the difference between observed productivity and additive expectations. (C) Linear regressions of total surface area against net productivity for each assemblage at higher flow (individual points), shown separately for monocultures (black, $R^2 = 0.58$) and mixtures (grey, $R^2 = 0.03$).

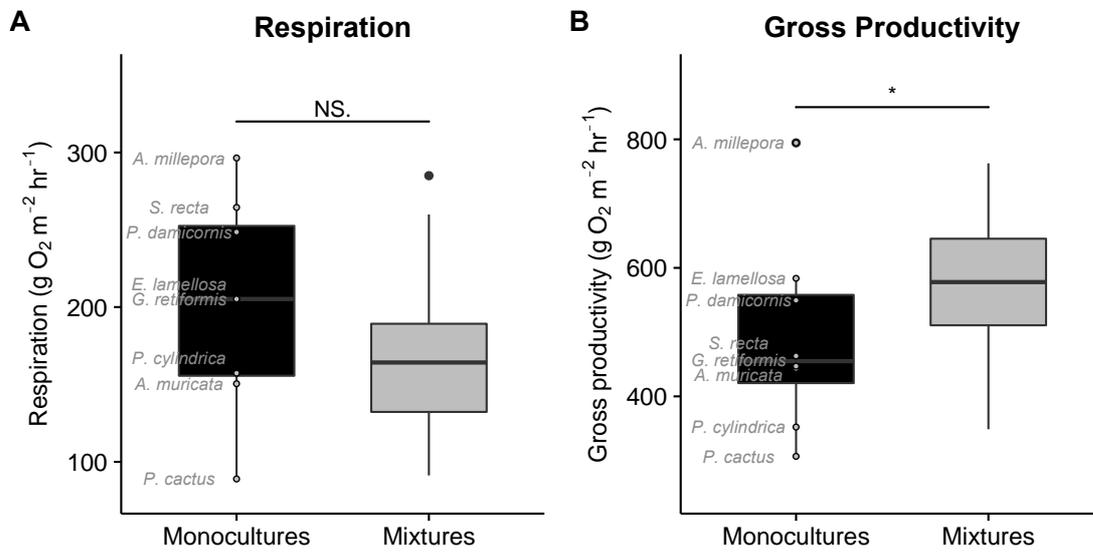


Figure 5.3: Box plots showing influence of species diversity on respiration and gross productivity. Monoculture values are displayed with the taxonomic identity of each assemblage.

The productivity of assemblages was positively associated with the total surface area of living tissue present in flumes (calculated using 3D reconstructions and influenced by colony size and morphology). However, the relationship between community-aggregated tissue surface area and productivity was considerably stronger for monocultures than for mixtures (Linear regression: $R^2=0.58$, $P<0.05$ and $R^2=0.03$, $P>0.05$ respectively, **Figure 5.2C**) and was also strong among colonies measured individually (Polynomial regression: $R^2=0.72$, $P<0.001$, **Figure 5.4A**). At the assemblage level, studies have speculated on the relationship between three-dimensional tissue area and productivity based on isolated observations *in situ* (Smith 1981, Nakamura and Nakamori 2009) and simulations (Hoogenboom et al. 2015); however the relationship has never been experimentally quantified. Across the spectrum of coral morphologies in this analysis, the greater than two-fold increase in aggregated surface area generated a proportional increase in the net productivity of monocultures (**Figure 5.2C**) and an exponential increase in the productivity of individual colonies (**Figure 5.4A**). In mixed assemblages, however, productivity was greater than expected based solely on tissue areas, and was more variable, suggesting that additional processes affect productivity in mixtures (**Figure 5.2C**). The accuracy of predictions of individual-colony and monoculture productivity based on coral tissue surface area is comparable to that of plant leaf traits (e.g. specific leaf area), which are used as single-trait indicators of ecosystem function in terrestrial communities (Garnier et al. 2004). Consistent with these results, studies of plant communities show that single-trait metrics often generate less reliable predictions in diverse communities where species interactions can distort the relationship between individual traits and function (Cadotte 2017).

Competition versus facilitation: Under higher flow, the productivity of groups of coral colonies was often lower than expected based on the sum of the productivity of each colony measured individually (negative values in **Figure 5.4B**), indicative of competition between colonies. In monocultures, combining colonies into groups of four instead of measuring them in isolation (described here as “neighbour interactions”) had a consistent, negative effect on community productivity (35% decrease on average), with relatively small differences in the strength of negative interactions between monocultures of different species (ranging from -48% to -19%). In contrast, in mixed species assemblages, the negative effect of neighbouring colonies was significantly weaker (-5% on average) and was considerably more varied (ranging from -54% to +43%). Indeed, in some mixed assemblages, neighbouring colonies had a positive effect on productivity (positive values in **Figure 5.4B**). Thus, competition between colonies was lower, on average, among heterospecifics than among conspecifics, and in some cases, the presence of heterospecifics allowed colonies to perform better than they would in isolation. To the best of my knowledge, these results provide the first evidence for interspecific facilitation of photosynthetic productivity among corals. In addition, the results support previous observations that intraspecific competition can be greater than interspecific competition among corals (Dizon and Yap 2005, Horwitz et al. 2017).

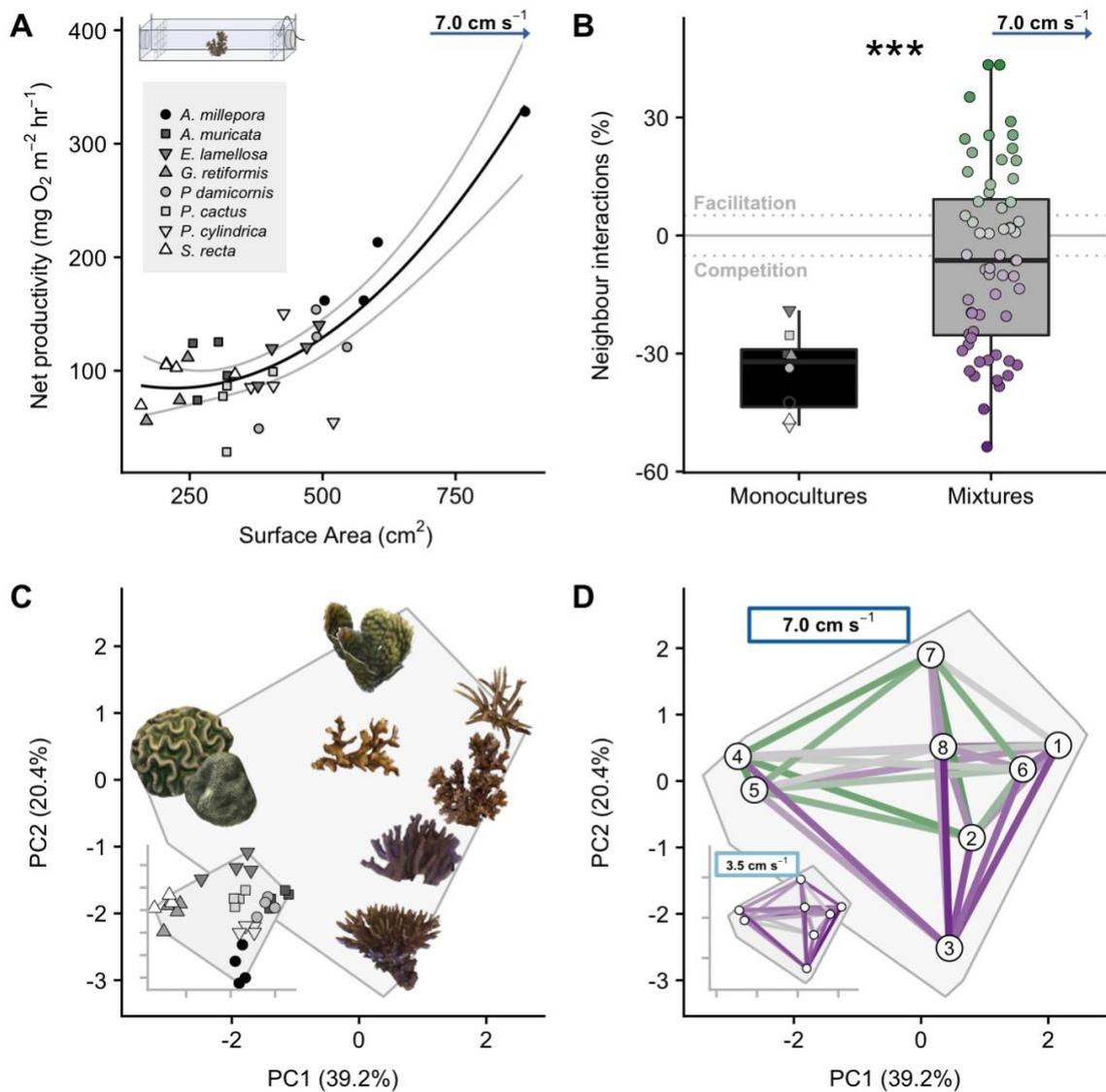


Figure 5.4: Interactions between neighbour colonies, quantified from the difference between assemblage productivity and the sum of their individuals measured in isolation. (A) Polynomial regression of tissue surface area against individual productivity for individual coral colonies at higher flow ($R^2 = 0.72$). The flume indicates the positioning of colonies. (B) Boxplots indicating the effect of neighbour colonies on community-level productivity at higher flow in monocultures versus mixtures. Mixed assemblage points are coloured by their position along the y-axis. Positive neighbour interactions above a significance threshold (dotted lines) are considered facilitation. (C) PCA of coral trait space showing the positions of eight species (indicated by 3D models) separated by traits (planar area, height, rugosity, interstitial space size, branch density, branch length, branch width, and tissue biomass). The

subplot indicates the positions of each individual colony, with species distinguished by colour and shape following Figure 5.4A. (D) Neighbour interactions for each species pair at higher flow, indicated by lines that are coloured by the type and strength of interactions following Figure 5.4B. Taxa are (1) *A. muricata*, (2) *P. cylindrica*, (3) *A. millepora*, (4) *S. recta*, (5) *G. retiformis*, (6) *P. damicornis*, (7) *E. lamellosa*, and (8) *P. cactus*. The subplot indicates the same analysis under reduced flow.

Each of the taxa included in this analysis had a unique combination of morphological and physiological traits (summarised by a principal components analysis explaining 60% of trait variation, **Figure 5.4C**) and, therefore, had the potential to influence their surrounding biotic and abiotic environment in distinct ways. For instance, branching colonies (e.g. *A. millepora*) had high tissue surface area and high productivity, whereas mound-shaped colonies (e.g. *Symphyllia* and *Goniastrea*) had low surface area and low productivity (**Figure 5.4A**). In addition, each coral taxon had unique colony dimensions (height, width) and different branching structures (height, width, density and spacing, **Figure 5.4C**) with the potential to influence downstream water flow, turbulence, and nutrient delivery to other colonies (Chamberlain and Graus 1975). Analysis of the pairwise interactions between taxa indicated that, under higher flow treatments, the strongest negative interactions occurred in assemblages containing highly productive, densely branching *Acropora* (species 3 in **Figure 5.4D**). In contrast, positive interactions occurred more frequently in assemblages that contained pairs of taxa with relatively low productivity such as those with massive, staghorn or foliose morphologies (**Figure 5.4D**). Facilitation therefore occurred primarily in the absence of the most productive species, allowing mixed assemblages with comparably low tissue surface areas to maintain high levels of productivity (**Figure 5.2 and 5.4C-D**).

Evidence for facilitation and its role in ecosystem function is rapidly emerging in a range of systems and is often found to occur when key taxa alter the immediate local environment in a way that benefits other taxa (Cardinale et al. 2002, Heemsbergen et al. 2004, Wright et al. 2017). I suggest that facilitation is the primary mechanism regulating differences in productivity between monocultures and mixtures in this experiment for three reasons. First, the diversity-effect (Dp) reveals that neither aggregated tissue surface area, nor the additive productivity of colonies in monocultures, accurately predicted the productivity of those same colonies when combined in mixed-species assemblages (**Figure 5.2**). This indicates that it is not merely the inclusion of highly productive species (i.e. the “sampling effect”) that enhances productivity in mixed assemblages because, if that were the case, there would be little or no deviation from the productivity of their component species in monocultures. Second, productivity was often higher when colonies were placed in multispecies groups rather than in isolation (**Figure 5.4B**). Moreover, these positive interactions were common, occurring in 45% of multispecies assemblages. Finally, these results are consistent with other facilitative systems in which taxa with low-performance monocultures benefit the most from

the presence of other species (**Figure 5.4C-D**). Congruent results have been observed in marine and terrestrial plant communities, where slow-growing taxa typically show the greatest increase in growth when put into mixtures, because they are otherwise limited by unfavourable conditions or a lack of resources (Mulder et al. 2001, Bruno et al. 2005).

Environmental regulation of neighbour interactions: Water flow velocities on reefs are highly variable in space and time. Although maximum recorded flow rates on shallow reefs can be very high for short time periods (e.g. 144 cm s^{-1} tidal flow on Enewetak atoll (Odum and Odum 1955)), average recorded flow rates generally fall between 1 and 15 cm s^{-1} (Patterson et al. 1991, Yates and Halley 2003, Long et al. 2013). To assess the effect of variation in water flow regimes on neighbour interactions, I re-measured the productivity of the same assemblages under reduced flow (3.5 cm s^{-1}). At the lower flow rate, the difference in productivity between monocultures and mixtures was reduced from 53% to 23%. The non-additive effect of species richness (i.e., the difference between measured productivity and null expected productivity based on monocultures) remained positive and statistically significant ($D_p=18\%$, paired $t=7.78$, d.f.=60, $P<0.001$) but was diminished under lower flow conditions (**Figure 5.5A**). The facilitation that occurred in mixed assemblages under high flow was also diminished (**Figure 5.4D**), with the average effect of neighbouring colonies in facilitative assemblages (above the positive threshold in **Figure 5.4B**) dropping from positive (15%) under high flow, to negative (-5%) under low flow (**Figure 5.5B**). In contrast, the strength of interactions in assemblages with competition under high flow (below the negative threshold in **Figure 5.4B**) remained unchanged when flow was reduced (**Figure 5.5C**). Water flow, therefore, can alter the relationship between species richness and community productivity on coral reefs by influencing neighbour interactions. Specifically, water flow promotes facilitation in a subset of diverse reef assemblages, while others exhibit negative interactions are unaffected by flow (**Figure 5.5B-C**).

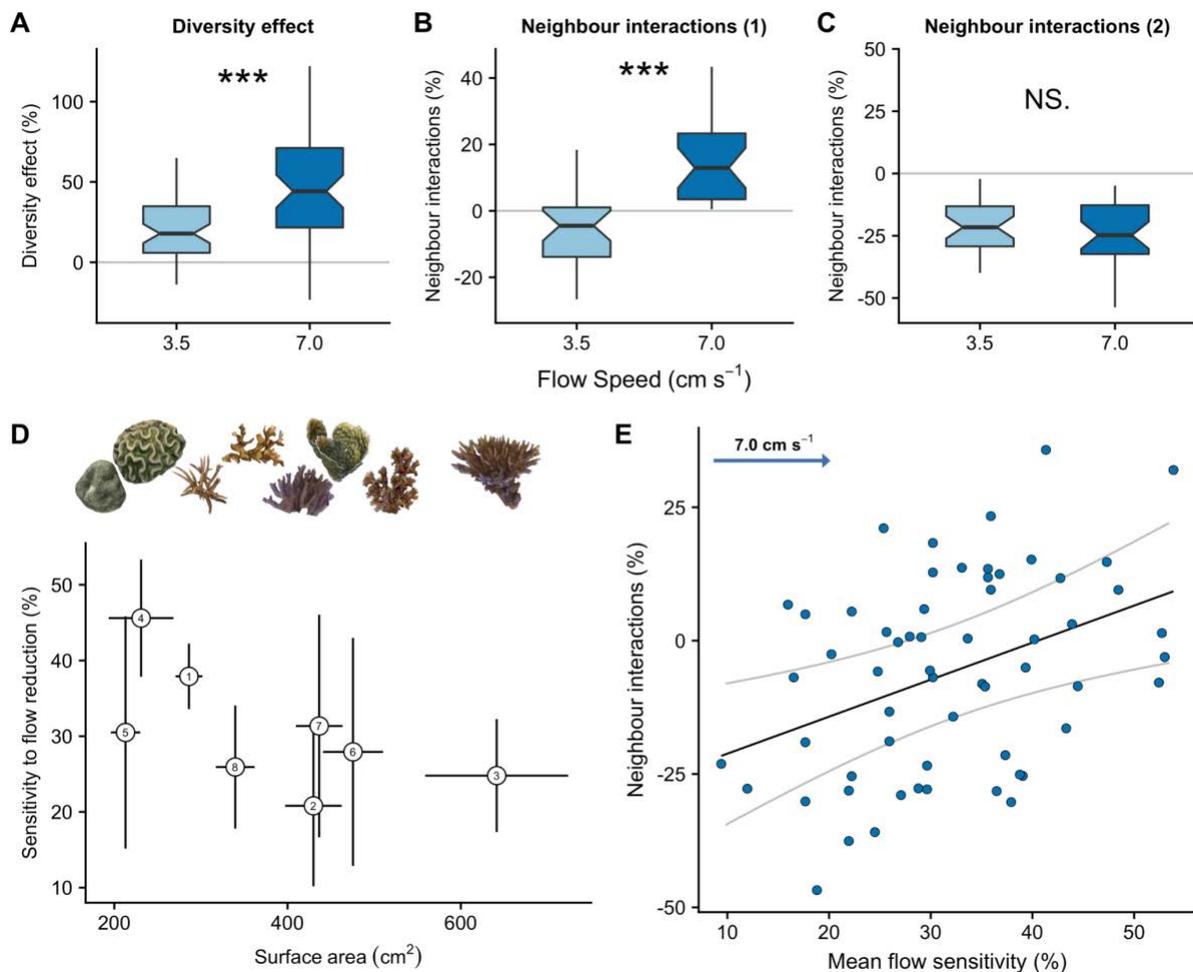


Figure 5.5: Effects of water flow and colony flow-sensitivity on neighbour interactions in coral assemblages. Boxplots show the influence of two flow rates on (A) the diversity effect (or the difference between null and observed mixture productivity), (B) neighbour interactions that are positive at higher flow (or assemblages above the facilitation threshold, Figure 5.4B), (C) neighbour interactions that are negative at higher flow (assemblages below the competition threshold, Figure 5.4B). Asterisks indicate significant differences (NS. Indicates $P > 0.05$, *** indicates $P < 0.001$). (D) Relationship between colony surface area and the flow sensitivity of colonies. Colonies are numbered by taxon (see Figure 5.4 caption). (E) Partial effects plot showing the how the average flow-sensitivity among colonies in each assemblage affected neighbour interactions under higher flow (Linear Mixed Effects Model, $R^2 = 0.41$). In figures D and E, flow sensitivity is measured as the change in colony productivity when flow is reduced from 7.0 to 3.5 cm s^{-1} .

	Estimate	s.e.	df	t	p	r²_m	r²_c
Intercept	-28.13	8.41	32	-3.34	0.002**	0.30	0.41
Av. flow-sensitivity	0.69	0.22	59	3.07	0.003**		
Max. surface area	-9.64	2.27	56	-4.25	<0.0001***		

Table 5.1: Results of linear mixed effects model examining the factors influencing neighbour interactions in coral assemblages. Average flow-sensitivity is calculated as the change in individual colony productivity when flow is reduced from 7.0 to 3.5 cm s^{-1} . The model (selected using AIC values) included flume chamber as a random effect. The r^2 values shown are the marginal r^2 (r^2_{m}), indicating the variance explained by fixed factors, and conditional r^2 (r^2_{c}), indicating the variance explained by fixed and random factors.

Colony productivity was increased under lower flow, and this increase was largest (approximately 40%) among low surface-area colonies with massive or staghorn morphologies (**Figure 5.5D**). This is contrary to expectations based on physiological first principles because decreased flow should decrease diffusion of photosynthetic gases between coral tissue and seawater and, thereby, reduce productivity (Patterson et al. 1991, Hoogenboom and Connolly 2009). The cause of the increase in colony productivity under reduced flow is unknown, although other experimental studies report similar results when O₂ concentrations are high (Finelli et al. 2006), and similar results have been observed *in situ* when irradiances are high (Long et al. 2013). The colonies which benefited from reduced flow were more likely to experience positive interactions when placed in mixed assemblages. This was shown by a significant positive relationship (**Table 5.1**, LME flow effect, $P < 0.01$, model $R^2 = 0.41$) between the occurrence of facilitation between neighbours and the “flow-sensitivity” of colonies; i.e., the degree to which colony productivity changed under reduced flow (**Figure 5.5E**). Thus, facilitation between neighbours occurred only when flow was high and primarily among morphologically simple taxa that benefited from reduced flow, suggesting that beneficial modifications to flow by corals were primarily responsible for facilitation in this experiment. In contrast, taxa with high tissue surface areas such as digitate or bushy colonies were less affected by flow and were associated more with negative interactions that remained unchanged at different flow speeds (**Figure 5.5C-E**). The cause of these negative interactions may involve the creation of “stagnant-zones” of no flow between colonies or, possibly, chemical interference (allelopathy) (Dizon and Yap 2005).

Biodiversity-ecosystem function relationships in the wild are regulated by resource availability, resource heterogeneity, climate conditions, and physical stress, each of which can alter the performance of particular species, and modify species interactions (Mulder et al. 2001, Hodapp et al. 2016, Ratcliffe et al. 2017). In this experiment, increased species richness of corals was most beneficial for productivity under high water flow, because taxa that had increased photosynthesis under lower flow rates benefited from the presence of other species. This phenomenon is equivalent to microclimatic facilitation in terrestrial plant communities, in which local humidity, salinity or temperature is modulated by key species for the benefit of their immediate neighbours (Wright et al. 2017). For example, under arid conditions, drought-sensitive plants are most likely to show an increase in biomass when placed in mixed communities, because other taxa regulate the local humidity (Mulder et al.

2001). These results indicate that facilitation could occur in natural conditions on coral reefs where functionally diverse assemblages create complex flow microhabitats that enhance the productivity of flow-sensitive taxa. Indeed, the intrinsic complexity of reef communities is known to promote nutrient uptake by dissipating current or wave-generated energy at reef-wide scales (Hearn et al. 2001). I therefore suggest that the regulation of diversity-productivity relationships by flow is likely to be widespread in coral assemblages where different morphologies react to, or influence flow in different ways (Chamberlain and Graus 1975, Hoogenboom and Connolly 2009).

Conclusions

Reefs of the future will almost certainly contain a different mix of species to those of today. In the coming decades, climate change and other human activities are likely to alter the abundance, growth and fitness of corals (Pandolfi et al. 2011). Indeed, vulnerable species are already declining rapidly and over large scales, leaving behind a restricted set of functional forms, which are often lacking in important attributes such as fast growth rates or three-dimensional morphologies (Hughes et al. 2018b). Such findings suggest that loss of biodiversity may be an important driver of shifts in productivity and functioning of reefs (Kayanne et al. 2005), ultimately affecting critical functions such as calcification (Comeau et al. 2014), geological reef growth (Kleypas et al. 2001), and the net accumulation of biomass (Pauly and Christensen 1995). These results show that changes in diversity and composition of corals may be an important driver of shifts in the performance and functioning of reef assemblages, which are often highly reliant on photosynthesis for energetic input (Hatcher 1988). Morphological traits such as tissue surface area may accurately predict productivity in large, monospecific stands. However, productivity in multispecies assemblages may be influenced by the species richness and functional identity of neighbour corals, which can regulate the type of interactions between colonies in relation to the surrounding flow environment. In mixed assemblages under moderate flow, the hierarchy of functional contributions among species broke down, and seemingly “redundant” species with lower productivity benefited, or were benefited by, other taxa. Quantifying species interactions in variable environments is therefore essential to understand the consequences of ongoing shifts in marine biodiversity, and the drivers of ecosystem function in current and future assemblages of species.

Chapter 6: General discussion

Coral reef scientists and managers are increasingly focussing their attention towards understanding and preserving ecological functions as a necessary step to address facing the challenges of the next century (Hughes et al. 2017a). A functional approach provides the basis for managing resilience in an uncertain future by focussing on the species and traits that support essential ecosystem processes (Bellwood et al. 2004). Species traits have gained a central role in ecology, allowing scientists to explore in more detail the relationships between biodiversity and ecosystem function (Chapin et al. 1997, Díaz and Cabido 2001) and elucidate mechanisms of community assembly (McGill et al. 2006). Nevertheless, critical knowledge gaps remain in our understanding of how species, traits and reef functions are changing through time under the broadening impacts of global warming.

This thesis explores the functional trait diversity in coral assemblages through space and time. Rather than delineating functional groups, I use continuous measures of trait diversity to quantify the relative contributions of species to a range of potential functions. I first quantified the functional diversity of all zooxanthellate coral species (Chapter 2; McWilliam et al. 2018b), and identified vulnerable biogeographical provinces in which critical traits are lacking. From this global-scale analysis, I next moved into a regional analysis of the Great Barrier Reef (Chapter 3; Hughes et al. 2018b), documenting a catastrophic, heat-induced shift in the abundance and functional traits of corals following mass coral bleaching and mortality. Expanding on this temporal analysis, I then conducted a long-term study of coral functional trait dynamics (Chapter 4), showing a loss of trait diversity following recovery from severe disturbances in three biogeographical provinces. Finally, I quantified the influence of critical traits in diverse and monospecific assemblages of corals (Chapter 5; McWilliam et al. 2018a), revealing a positive influence of species and trait diversity among closely situated neighbours. By quantifying the diversity and redundancy of corals, this thesis has improved understanding of the capacity for different reefs to maintain ecosystems functions through time. The data and information provided in this thesis may therefore be used by coral reef scientists and managers to analyse the consequences of continued anthropogenic impacts.

The functional importance of corals for calcium carbonate deposition and reef formation has been recognised for centuries (e.g. Darwin 1842 Chapter IV, pp 71-79). Analysis of reef

geology in the mid-1900s revealed differences in the framework building roles of corals and other calcifying organisms. Examples of these roles include builders, fillers and cementers, each of which contribute to the growth and formation of reefs on geological timescales (Goreau 1963, Stoddart 1969). On ecological timescales, the distribution of corals in space and time has been attributed to differences in functional form, particularly morphology (Jackson 1979). Such analyses mirrored plant-based studies in the terrestrial realm, which identified collections of traits that predicted the dynamics and distribution of species (Grime 1974). By the end of the past century, coral reef researchers had begun to focus their attention on widespread and conspicuous patterns of degradation to reefs, and roles of species in maintaining reefs in a stable (coral-dominated) state (Hughes 1994, Bellwood et al. 2004). These developments in coral reef research over time have underscored a need to understand the functional roles of corals for a range of important processes, occurring on vastly different scales.

In many cases, the analysis of coral functional diversity should be focussed around colony morphology, because of the relevance of morphology to a wide range of reef processes. Morphology is associated with important traits such as growth (Pratchett et al. 2015), skeletal density (Hughes 1987), fecundity (Álvarez-Noriega et al. 2016), life history (Jackson and Hughes 1985) and susceptibility to disturbance (Marshall and Baird 2000, Madin and Connolly 2006). Morphology can determine a species fundamental niche (Hoogenboom et al. 2008, Hoogenboom and Connolly 2009) and is important for ecosystem processes, such as habitat provision (Graham and Nash 2013), productivity (Chapter 5) and carbonate accretion (Kennedy et al. 2013). It is not surprising, therefore, that previous measures of functional diversity in corals have focussed on morphological groups (Bellwood et al. 2004, Hughes et al. 2012, Denis et al. 2017). Nevertheless, colony morphology represents a range of continuous dimensions, such as size, width, height, surface area, volume, branch spacing (Jackson 1979), and its correlation with important traits may be complicated or messy, associating more closely with phylogeny or biogeography than with morphology (e.g. Szmant 1986). This thesis introduces a more in-depth technique of quantifying functional diversity in corals using trait spaces based on morphological dimensions (e.g. size, height, surface area) and morphology-associated traits (e.g. growth rate, skeletal density, corallite width). Thus, while the trait spaces produced in this thesis are morphology-focussed, they provide a more precise estimation of functional variation among species. These developments allow for a

more refined analysis of coral functional diversity and its relation to reef biogeography (Chapter 2), mass bleaching (Chapter 3), response diversity (Chapter 4), and community functioning (Chapter 5).

Several of the results presented in this thesis provide important avenues for future research. For example, measures of functional diversity and redundancy must be linked with the abundance and trait variability of individual species to gain a more accurate estimate of species contributions to ecosystem function. For example, the loss of dominant taxa with distinctive traits is likely to have a greater impact than the loss of taxa that are distinctive but scarce (Sala et al. 1996, Grime 1998). This topic is introduced in Chapter 4, which weighs the capacity of a species to replace the functions of those in decline via increases in its absolute abundance. In addition, incorporating abundance into the biogeographical trends observed in Chapter 2 may reveal unforeseen levels of vulnerability and distinctiveness across regions. For instance, Violle et al. (2017) distinguish 12 different forms of functional rarity which account for the geographic range, local abundance, and trait-distinctiveness of species, each influencing the potential vulnerability of functions. Along the same lines, measures of functional diversity must also consider intraspecific variability in traits, often described as the functional “niche” (Rosenfeld 2002). Individual species can occupy large areas of trait space, and they can overlap with others completely or partially, influencing the capacity of species to maintain different functions (Hérault et al. 2008, Brandl and Bellwood 2014). Coral species exhibit high plasticity in traits (e.g. along gradients in depth, Anthony et al. 2005, Hoogenboom et al. 2008), possibly generating greater redundancy and resilience if species can modify their phenotype to replace the functions of those in species decline. Nevertheless, intraspecific trait diversity can reveal further vulnerability if important components of trait variation are lost. For example, shifts in the size structure of corals towards smaller individuals can deplete a range of ecosystem functions (e.g. Chapter 4), and loss of large, long-lived individuals may become more prevalent as species fail to fully recover between consecutive bleaching events (Hughes et al. 2018a).

More broadly, the results of this thesis can be used to build towards a better understanding of coral reef functioning, and how it is changing through time. Plant-based research has emphasized the need to link species functional contributions with their responses to environmental change in order to facilitate better predictions of how ecosystem functions are

changing (Lavorel and Garnier 2002, Suding et al. 2008). This thesis addresses the degree to which corals differ or overlap in the expression of critical traits, and quantifies their response to change in different locations (Chapters 2-4). Nevertheless, in order to utilise coral traits to project reef functions into the future, a number of key challenges lie ahead. Perhaps most importantly, the influence of traits on a range of processes occurring at the population, community and ecosystem level must be tested empirically, and placed in the backdrop of species interactions and environmental heterogeneity (e.g. Chapter 5). For example, traits have great potential to inform scientists and managers on the potential demographic responses of corals to local and global stress, on time intervals from weeks to decades, and on evolutionary timescales (Madin and Connolly 2006, Álvarez-Noriega et al. 2016).

Addressing the link between traits and demography can therefore help to build towards a more accurate and well-informed understanding of coral functional diversity, and a more predictive trait-based ecology (Salguero-Gómez et al. 2018). Finally, while this thesis focusses on coral traits alone, projecting the response of species and functions to future change relies on our understanding of traits across the entire coral ‘holobiont’ (i.e. host and symbiont community), including the wide variety of thermal tolerances observed among photosynthetic symbionts (Suggett et al. 2017).

In summary, the most dramatic trend on coral reefs in the last half century has been changes to their composition and function (Bellwood et al. 2004). This thesis presents evidence for a wide variety of trait-based functional roles among corals, and shows that this diversity is threatened by mass bleaching under anthropogenic global warming, and the limited capacity of assemblages to maintain a full range of functional roles following recovery from severe disturbances. Collectively, the evidence presented here suggests that future trajectories in the functioning of reefs will depend on how different biogeographical pools of distinctive and redundant species will reassemble in the wake of global warming. Although continued degradation to reefs is inevitable, this thesis supports the view is that it is feasible for reefs of the future to avoid total collapse, and persevere as highly altered systems. Such an outcome will depend critically on the mitigation of global climate change (Hoegh-Guldberg et al. 2007, Hughes et al. 2017a), and successful management scenarios that are focussed on protecting the species and traits that support essential ecosystem functions.

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Appendix A

Publications arising from this thesis:

1. McWilliam, M., M. O. Hoogenboom, A. H. Baird, C. Kuo, J. S. Madin, and T. P. Hughes. 2018. Biogeographical disparity in the functional diversity and redundancy of corals. *Proceedings of the National Academy of Sciences*:1–6.
2. Hughes, T. P., J. T. Kerry, A. H. Baird, S. R. Connolly, A. Dietzel, C. M. Eakin, S. F. Heron, A. S. Hoey, M. O. Hoogenboom, G. Liu, M. J. McWilliam, R. J. Pears, M. S. Pratchett, W. J. Skirving, J. S. Stella, and G. Torda. 2018b. Global warming transforms coral reef assemblages. *Nature* 556:492–496.
3. McWilliam, M., M. Pratchett, M. O. Hoogenboom, T.P. Hughes. Disturbance, recovery, and the depletion of functional diversity on coral reefs. *In preparation*.
4. McWilliam, M., T. J. Chase, and M. O. Hoogenboom. 2018. Neighbor Diversity Regulates the Productivity of Coral Assemblages. *Current Biology* 28:3634–3639.

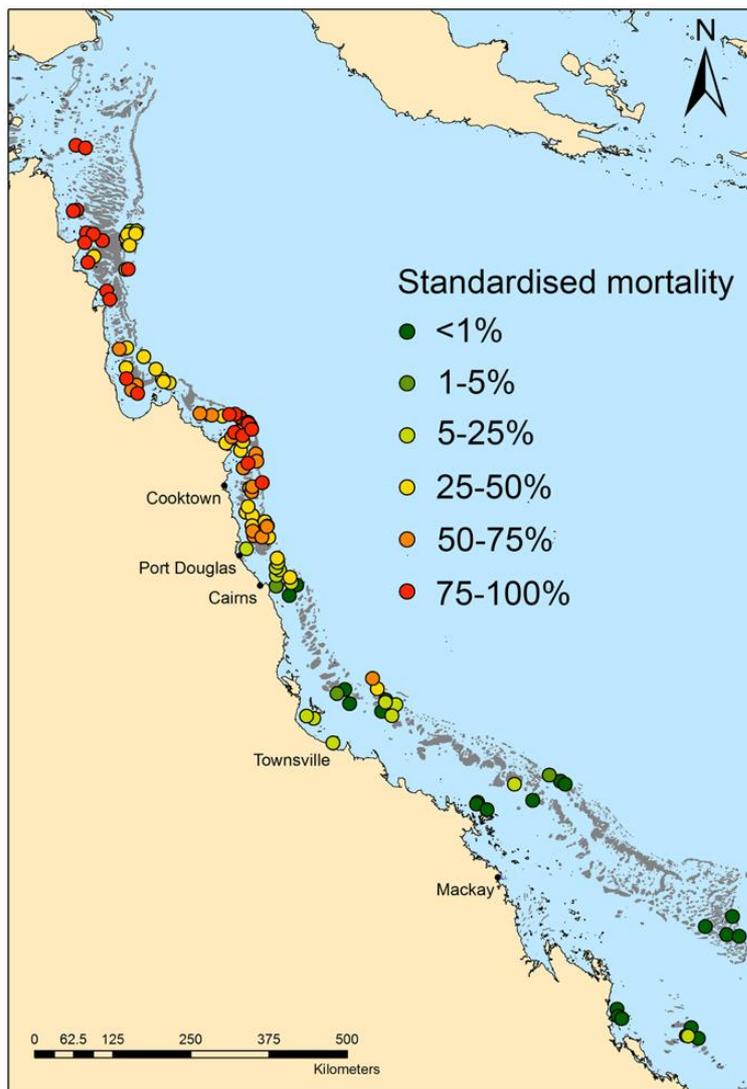
Appendix B

Publications *not* arising from this thesis:

- 1) Hughes, T. P., J. Kerry, M. Álvarez-Noriega, J. Álvarez-Romero, K. Anderson, A. Baird, R. Babcock, M. Beger, D. Bellwood, R. Berkelmans, T. Bridge, I. Butler, M. Byrne, N. Cantin, S. Comeau, S. Connolly, G. Cumming, S. Dalton, G. Diaz-Pulido, C. M. Eakin, W. Figueira, J. Gilmour, H. Harrison, S. Heron, A. S. Hoey, J.-P. Hobbs, M. Hoogenboom, E. Kennedy, C.-Y. Kuo, J. Lough, R. Lowe, G. Liu, H. M. Malcolm McCulloch, M. McWilliam, J. Pandolfi, R. Pears, M. Pratchett, V. Schoepf, T. Simpson, W. Skirving, B. Sommer, G. Torda, D. Wachenfeld, B. Willis, and S. Wilson. 2017b. Global warming and recurrent mass bleaching of corals. *Nature*. 543:373

Appendix C (Chapter 3)

Loss of coral cover along the Great Barrier Reef in 2016. Losses, measured on 110 reefs between March and November 2016, range from 0 (dark green) to 100% (1–5% (green), 5–25% (light green), 25–50% (yellow), 50–75% (orange) and 75–100% (red). Map template is provided by Geoscience Australia (Commonwealth of Australia (Geoscience Australia) 2018).



Appendix D (Chapter 4)

The structure of 44 taxonomic groups used in the analysis in relation to the data that was originally collected. For French Polynesia, two species lists are provided, one for the data collected from the literature (Bouchon) and one for our data. Grey indicates no taxa.

Category	Jamaica	French Polynesia	GBR
Morphological groups			
1. Staghorn <i>Acropora</i>	<i>A cervicornis</i>	Bouchon: <i>A abrotanoides</i> ; <i>A intermedia</i> ; <i>A nobilis</i> ; <i>A robusta</i> ; <i>A palmarae</i> Our data: <i>A abrotanoides</i> ; <i>A austera</i> ; <i>A formosa</i> ; <i>A robusta</i> ; <i>A lutkeni</i>	<i>A aspera</i> group; <i>A florida</i> group; <i>A formosa</i> group; <i>A robusta</i> group; <i>A lovelli</i> group; <i>A horrida</i> group
2. Elkhorn <i>Acropora</i>	<i>A palmata</i>		
3. Tabular <i>Acropora</i>		Bouchon: <i>A cytheriea</i> ; <i>A hyacinthus</i> Our data: <i>A clathrata</i> ; <i>A hyacinthus</i>	<i>A hyacinthus</i> group; <i>A divaricata</i> group
4. Bushy <i>Acropora</i>		Bouchon: <i>A cerealis</i> ; <i>A tenuis</i> ; <i>A valida</i> ; <i>A variabilis</i> Our data: <i>A cerealis</i> ; <i>A nasuta</i> ; <i>A secale</i> ; <i>A tenuis</i> ; <i>A valida</i> ; <i>A verweyi</i> ; <i>A striata</i> .	<i>A echinata</i> group; <i>A lallistella</i> group, <i>A loripes</i> group, <i>A nasuta</i> group; <i>A selago</i> group
5. Digitate <i>Acropora</i>		Bouchon: <i>A. humilis</i> Our data: <i>A. globiceps</i> <i>A retusa</i>	<i>A humilis</i> group
6. Branching <i>Porites</i> – Indo-Pacific		Bouchon: <i>P irregularis</i> ; <i>P rus</i> Our data: Same	Branching <i>Porites</i>
7. Branching <i>Porites</i> - Caribbean	<i>P. furcata</i>		
8. Massive <i>Porites</i> – Indo-Pacific		Bouchon: <i>P lobata</i> ; <i>P lutea</i> ; <i>P australiensis</i> ; <i>P lichen</i> Our data: <i>P lobata</i> ; <i>P lutea</i>	Massive <i>Porites</i>
9. Massive <i>Porites</i> – Caribbean	<i>P. astreoides</i>		
10. <i>Pocillopora damicornis</i>		<i>P damicornis</i>	<i>P damicornis</i>

11. Other <i>Pocillopora</i>		Bouchon: <i>Pocillopora verrucosa</i> <i>Pocillopora eydouxi</i> Our data: Same	Other <i>Pocillopora</i>
Families			
12. Mussidae – Indo-Pacific		Bouchon: <i>L hemprichii</i> ; <i>A echinata</i> Our data: <i>Acanthastrea</i> ; <i>Lobophyllia</i>	<i>Acanthastrea</i> ; <i>Symphyllia</i> ; <i>Homophyllia</i> ; <i>Lobophyllia</i>
13. Other Faviidae	<i>Diploria</i> ; <i>Favia</i> ; <i>Solenastrea</i>	Bouchon: <i>M curta</i> ; <i>C microphthalmia</i> ; <i>C serailia</i> ; <i>F abdita</i> ; <i>L purpurea</i> ; <i>L transversa</i> Our data: <i>M curta</i> ; <i>Cyphastrea</i> ; <i>F abdita</i> ; <i>Leptastrea</i> ; <i>Platygyra</i> ;	<i>Caulastrea</i> ; <i>Dispastrea</i> ; <i>Pleisiastrea</i> ; <i>Montastrea</i> ; <i>Leptastrea</i> ; <i>Leptoria</i> ; <i>Favia</i> ; <i>Favites</i> ; <i>Platygyra</i> ; <i>Cyphastrea</i>
14. Other Agariciidae – Indo-Pacific		Bouchon: <i>L incrustans</i> ; <i>L mycetoseroides</i> ; <i>G planulata</i> ; Our data: <i>Coleoseris</i> ; <i>Leptoseris</i> ; <i>Gardinoseris</i>	<i>Coeloseris</i> ; <i>Coscinaraea</i> ; <i>Leptoseris</i>
15. Pectiniidae			<i>Echinophyllia</i> ; <i>Mycedium</i> ; <i>Pectinia</i> ; <i>Oxypora</i>
16. Fungiidae		Bouchon: <i>Fungia sp</i> ; <i>Herpolitha sp</i> . <i>Sandolitha sp</i> Our data: <i>Fungia</i>	Fungiidae
Genera			
17. <i>Agaricia</i>	<i>A lamarcki</i> ; <i>A agaricites</i>		
18. <i>Madracis</i>	<i>M. mirabilis</i> ; <i>M pharensis</i>		
19. <i>Montipora</i>		Bouchon: <i>M verrucosa</i> ; <i>M erythraea</i> ; <i>M informis</i> ; <i>M circumvallata</i> Our data: <i>M efflorescens</i> ; <i>M verrucosa</i> ; Encrusting <i>Montipora</i>	<i>Montipora</i>
20. <i>Astreopora</i>		Our data: <i>A myriophthalma</i>	<i>Astreopora</i>
21. <i>Goniopora</i>			<i>Goniopora</i>
22. <i>Psammocora</i>		Bouchon: <i>P contigua</i> ; <i>P haimeana</i> ; <i>P profundacella</i> ; <i>P nierstraszi</i> . Our data: <i>Psammocora</i>	<i>Psammocora</i>
23. <i>Pavona</i>		Bouchon: <i>P cactus</i> ; <i>P minuta</i> ; <i>P maldiviensis</i> ; <i>P varians</i> . Our data: <i>P cactus</i> ; Encrusting <i>Pavona</i>	<i>Pavona</i>
24. <i>Stylocoeniella</i>		Bouchon: <i>S armata</i> ; <i>S guentheri</i> Our data: None	
25. <i>Pachyseris</i>		Bouchon: <i>P speciosa</i>	<i>Pachyseris</i>

References

		Our data: <i>Pachyseris</i>	
26. <i>Goniastrea</i>		Bouchon: <i>F stelligera</i> Our data: <i>F stelligera</i>	<i>Goniastrea</i>
27. <i>Colpophyllia</i>	<i>Colpophyllia</i>		
28. <i>Dichocoenia</i>	<i>Dichocoenia</i>		
29. <i>Helioseris</i>	<i>Helioseris</i>		
30. <i>Isophyllia</i>	<i>Isophyllia</i>		
31. <i>M. cavernosa</i>	<i>M. cavernosa</i>		
32. <i>Mycetophyllia</i>	<i>Mycetophyllia</i>		
33. <i>Orbicella</i>	<i>Orbicella</i>		
34. <i>Siderastrea</i>	<i>Siderastrea</i>		
35. <i>Scolymia</i>	<i>Scolymia</i>		<i>Scolymia</i>
36. <i>Seriatopora</i>			<i>Seriatopora</i>
37. <i>Stylophora</i>			<i>Stylophora</i>
38. <i>Isopora</i>			<i>Isopora</i>
39. <i>Galaxea</i>			<i>Galaxea</i>
40. <i>Hydnophora</i>			<i>Hydnophora</i>
41. <i>Merulina</i>			<i>Merulina</i>
42. <i>Diploastrea</i>			<i>Diploastrea</i>
43. <i>Echinopora</i>		Our data: <i>E horrida</i> Bouchon: None	<i>Echinopora</i>
44. <i>Turbinaria</i>			<i>Turbinaria</i>
TOTAL	16	20	30

Appendix E (Chapter 5)

Literature used to quantify oxygen flux across coral reef habitats. See **Figure 5.1**.

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