# USING SPECIES TRAITS TO UNDERSTAND REEF CORAL DISTRIBUTIONS AND RESPONSES TO STRESS



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For Raena and Dad, Two amazing examples of Perseverance and determination

> And their reminders to Live long and prosper

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# STATEMENT OF CANDIDATE

I certify that the work in this thesis entitled "Using species traits to understand reef coral distributions and responses to stress" has not previously been submitted for a degree nor has it been submitted as part or requirements for a degree to any other university or institution other than Macquarie University.

I also certify that the thesis is an original piece of research and it has been written by me. Any help and assistance that I have received in my research work and the preparation of the thesis itself have been appropriately acknowledged. In addition, I certify that all information sources and literature used are indicated in the thesis.

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## SUMMARY

Coral reef ecosystems provide important ecological goods and services, but are threatened by climate change and other anthropogenic impacts. The numerous scleractinian coral species that build coral reefs vary in tolerance to environmental conditions and stressors. Therefore, in response to environmental change, coral reefs are likely to change significantly rather than disappear completely. Explicitly quantifying relationships between corals and their environment will provide a better understanding of the mechanisms influencing species distributions and local persistence. However, the lack of overlap in the composition of coral assemblages across different geographic regions has limited the development of a broad-scale understanding of global coral-environment relationships. In this thesis, I therefore focused on species traits to describe biogeographical patterns over large spatial scales, which enabled an integrated, systematic approach for explicitly linking environmental conditions with species distributions. This thesis specifically aimed to: 1) quantify multi-decadal change in coral assemblages within a climate change hotspot, 2) characterize species traits that dominate marginal environments globally, 3) model multiple species distributions in relation to species traits along environmental gradients, and 4) quantify how species traits mediate the responses of corals to a key environmental stressor (increased sea surface temperature, SST). I used a variety of techniques including conducting field surveys, collating published coral distribution data, analyzing bleaching surveys, and applying statistical modeling techniques to investigate coral distributions and responses to stressors. My research resulted in several key findings. First, I unexpectedly found little evidence of change in assembly structure of high latitude reef corals in southeast Australia over the last 20 years where SST has increased. Second, reef corals found at high latitudes - beyond reef growth - were generally found to share traits associated with environmental tolerance, as opposed to dispersal potential. Third, I incorporated coral traits into a multispecies distribution model to quantify how three traits modulate responses to three environmental gradients across northeast Australia. The strongest xiii

link was a positive response between species depth range and SST variability. Finally, I demonstrated that growth form and family explain more variation in global coral bleaching responses than other morphological or physiological traits; hence including these traits in bleaching surveys will increase predictive power of surveys. My thesis has generated a richer understanding of coral trait-environment relationships, which ultimately allows for more accurate predictions of the ways in which future environmental changes will impact different coral species.

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### INTRODUCTION

The physical environment has enormous and complex influence on species abundance and distributions. Relationships of species with their environment have been widely observed for centuries; however, these observations usually lead to qualitative conclusions, leaving underlying processes poorly understood. Nonetheless, these early observations have been critically important for understanding the key contributors to patterns of biodiversity, ecosystem function, ecological goods and services and the effects of environmental change (Hooper *et al.*, 2005).

Climate change and other anthropogenic effects have impacted ecosystems globally in both terrestrial and marine environments (Walther *et al.*, 2002; Parmesan & Yohe, 2003; Poloczanska *et al.*, 2013). To persist through changing environmental conditions, species must adapt through genetic changes, acclimate or shift distributions (Feeley *et al.*, 2012). As ocean temperatures have increased, the redistributions of species have been commonly observed to track temperature regimes (Sunday *et al.*, 2012). Historic records of reef coral distributions through geologic history document poleward and equatorward shifts during periods of warming and cooling signifying a strong connection with abiotic conditions, especially temperature (Precht & Aronson, 2004; Kiessling *et al.*, 2012).

Corals reefs are some of the most diverse and productive ecosystems that provide ecological goods and services (Moberg & Folke, 1999). Some regions at the center of coral diversity (*i.e.* the Coral Triangle) contain up to 600 scleractinian coral species (Veron *et al.*, 2015). These corals are distributed across and between reef environments that vary by temperature, hydrodynamic energy, light availability, biological controls, sedimentation, and other water quality measures (Veron, 2000). As climate change and other anthropogenic impacts alter any of these conditions in complex ways, many coral species persistence has become threatened (Carpenter *et al.*, 2008). Dramatic declines in coral cover are being documented (Gardner *et al.*, 2003; Bruno & Selig, 2007; Wilkinson, 2008; De'ath *et al.*, 2012). In addition to a decline in total coral cover, species assembly structure has changed and is expected to continue to change because of variable tolerances to stressors (Loya *et al.*, 2001; Hughes *et al.*, 2003; Alvarez-Filip *et al.*, 2013). Coral assemblages are therefore key to evaluate the relationships between coral occurrences and environmental conditions to understand how species might respond to environmental change.

High coral diversity restricts the use of species-specific approaches to explain coral biogeography. Frequently, coral assemblages have been described at the reef scale by grouping the species commonly found together which are associated with particular habitats and identified by the dominant species (Goreau, 1959; Done, 1982; Dustan, 1985). Since species distributions often do not overlap between regions, determining consistency in biogeographical and zonational patterns has been nearly impossible.

In lieu of species-specific approaches, trait-based approaches offer the opportunity for a mechanistic understanding of functional responses to the environment (Westoby & Wright, 2006; Violle *et al.*, 2007). These relationships influence associations with the environment and ultimately impact species distributions (McGill *et al.*, 2006; Shipley *et al.*, 2006). For example, plant seed size was found to vary along a latitudinal gradient with an abrupt change at the edge of the tropics, corresponding to plant growth form and vegetation type (Moles et al. 2007). Similarly, stream fish assembly decribed by swimming, habitat preferences and food resource use traits were related to environmental variables at the local and landscape scales (Pease et al. 2012). In addition to describing how species traits are distributed across landscapes, species traits rather than species alone can help inform predictions of how species and assemblages are likely to be impacted by changing environmental conditions. Quantitative trait-based approaches have been used to compare vulnerability to climate change within and between taxa underscoring the use of such approaches for large-scale yet

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comprehensive assessments (Foden et al. 2013; Jeppeson & Forslund 2013). Morphology, growth rate and reproductive mode are primary coral traits that were found to categorize lifehistory strategies suggesting how coral species may respond to environmental disturbances (Darling et al. 2012). Trait-based approaches to understand organismal and population biology, community assembly and response to disturbance that can advance coral reef science have so far been limited by a lack of available trait data (Madin et al. 2016a).

Throughout this thesis, I helped develop and used the Coral Trait Database (Madin *et al.*, 2016b) to access trait information for hundreds of reef coral species. This database contains morphological, physiological, ecological, phylogenetic and biogeographic information compiled from published literature and field surveys. I used coral trait information available to quantify species' responses to environmental conditions and to stressors. This approach allowed an understanding of functional responses elucidating global, trait-based patterns rather than local, species-based patterns.

I started by quantifying multi-decadal coral assembly change in the southeast Australia global warming hotspot (Chapter 1). Since a subset of corals has shifted poleward in other regions of warming, I measured whether change in composition or species abundance in southeast Australia was similar to other regions. Change in species cover was related to biogeographic distributions to suggest whether there was a poleward shift of corals based on their center of distribution.

In Chapter 2, I quantified the extent of coral species diversity loss at the boundary between reefal and non-reefal habitats in the Indo-Pacific. I then tested whether or not the traits associated with beyond reef species were a non-random subset of species on coral reefs, and subsequently if these trait patterns were consistent for the approximately 400 species in three latitudinal gradients. Based on the traits that tended to be associated with beyond reef species, I considered whether dispersal traits (*e.g.* those related to larval access to and time in

ocean currents) or establishment traits (*e.g.* those related to environmental tolerance) best explain the capacity to live beyond reef.

In Chapter 3, I incorporated species traits into a multispecies distribution modeling framework to measure how coral characteristics modulate responses to the environment and influence species distributions across northeast Australia. Relationships between all possible interactions of three coral traits and three environmental factors, each hypothesized to shape coral assemblages, were quantified to measure relative differences in the strength of trait-environment responses. These results help clarify relationships to better predict how a change in one or many environmental factors could impact coral assembly.

Of the environmental factors I studied, temperature is expected to change the most in coming decades. Therefore, in Chapter 4, I evaluated the use of species traits in capturing variability in responses to a primary stressor, increased sea surface temperature. I compiled species-specific coral bleaching surveys and quantified how well coral traits captured bleaching responses to various warming events globally. The trait-based approach highlights not only the mechanisms of stress response but also how surveys to inform management can best capture responses within assemblages.

Finally, I conclude with a synthesis of my overall results and identify applications of coral traits in patterns of species distributions and responses to stressors. Coral traits provide great detail in measuring functional responses to the environment. I focus here only on abiotic influence of species distributions but discuss how biotic features can also affect biogeographic patterns. The use of trait-based approaches to coral science described here will not only advance research efforts but will also enhance conservation measures to protect coral diversity and ecosystem function (Madin *et al.*, 2016a).

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## STATEMENT OF THE CONTRIBUTIONS TO THESIS CHAPTERS

I was involved in the conception and design of all studies presented in this thesis. I performed all data management, analysis and interpretation. I was also the lead author of all the chapters of this thesis. My estimated proportion of contribution to each of the chapters of this thesis is outlined below.

| Thesis<br>chapters | Ex                          | xtent of intelle    | ctual input by the cand             | idate (%)              |                   |
|--------------------|-----------------------------|---------------------|-------------------------------------|------------------------|-------------------|
|                    | Study concept<br>and design | Acquisition of data | Analysis and interpretation of data | Drafting of manuscript | Critical revision |
| Chapter 1          | 75%                         | 70%                 | 80%                                 | 95%                    | 90%               |
| Chapter 2          | 75%                         | 90%                 | 80%                                 | 100%                   | 80%               |
| Chapter 3          | 100%                        | 90%                 | 90%                                 | 100%                   | 90%               |
| Chapter 4          | 80%                         | 90%                 | 80%                                 | 100%                   | 90%               |

### OTHER RELEVANT PUBLICATIONS DURING CANDIDATURE

Madin JS, M Hoogenboom, SR Connolly, E Darling, D Falster, D Huang, S Keith, **TL Mizerek**, JM Pandolfi, H Putnam, AH Baird (2016). A trait-based approach to advance coral reef science. *Trends in Ecology and Evolution*.

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# MULTI-DECADAL CORAL ASSEMBLY CHANGE IN A

# CLIMATE CHANGE HOTSPOT

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Multi-decadal coral assembly change

## ABSTRACT

Our aim was to determine whether the assemblage structure of high latitude reef corals in Solitary Islands region, New South Wales, Australia has changed in response to ocean warming since pioneering work in the 1970s. We used point and line intercept transect to quantify coral assemblage structure at six locations within the region. We compared our data to studies using a similar approach in the 1970s and 1990s. There was evidence suggesting a general decline in coral cover since the 1970s although little evidence for a change in assemblage structure. However, the lowest latitude island in the region had a number of subtropical taxa that have increased in abundance since the 1990s. In contrast to a dramatic tropicalization of high latitude coral assemblage in the northern hemisphere, there has been little change in the assemblage structure of locations at similar latitudes in Australia, despite SST warming. These results suggest that factors other than temperature control the spread of species into the sub-tropics of eastern Australia.

## 1.1 INTRODUCTION

Climate warming has resulted in the redistribution of species and reassembly of communities globally (Parmesan & Yohe, 2003; Hickling *et al.*, 2006; Sorte *et al.*, 2010; Cheung *et al.*, 2013). Many higher latitude marine environments that were once unsuitable for some warm water species have become habitable (Ling *et al.*, 2009; Figueira & Booth, 2010). Warming at higher latitudes is up to three times faster than the mean surface global rate where western boundary currents move tropical waters poleward (Wu *et al.*, 2012). There is an expectation that continued ocean warming will result in poleward expansion or shift of marine species distributions, particularly in regions where temperature limits species' range boundaries (Parmesan, 1996; Perry *et al.*, 2005; Sagarin *et al.*, 2006; Doney *et al.*, 2012).

Increased sea surface temperature (SST) has resulted in significant changes in distributions for a variety of taxa. For example, near 33°N in Japan, both tropical and temperate seaweeds across a 700 km coastline have shifted poleward (Tanaka *et al.*, 2012). In the same temperate system, the fish fauna have become dominated by tropical species that moved north (Nakamura *et al.*, 2013). In addition, four of nine coral species surveyed over 80 years from similar latitudes in Japan have been shown to expand their ranges poleward where winter SSTs increased by up to 1.6°C (Yamano *et al.*, 2011). Given these changes in Japan, similar patterns in Australia could be expected where western boundary currents bring warm, equatorial water to higher latitudes. As expected, subtropical systems in Western Australia have been reconfigured as kelp forests transitioned to dominant seaweed turfs with frequent SST anomalies up to 3°C above monthly averages (Wernberg et al. 2016). There has been a similar climate mediated loss of kelp populations along Australia's east coast as tropical herbivores shifted poleward as the average SST increased by 0.6°C from 2001-2008 (Vergés et al. 2016). However, long-term records of coral assemblages in subtropical and temperate

#### Multi-decadal coral assembly change

environments have limited precise conclusions about comparable changes for corals.

Southeast Australia is recognized as a globally important climate change hotspot where the East Australian Current has extended poleward and the continued intensification of warm water flow is projected for decades (Hobday & Lough, 2011). This flow of tropical water is projected to facilitate shifts of coastal marine species (Poloczanska et al., 2007). The Solitary Islands (SI) region lies within this climate change hotspot at approximately 30°S and represents an important coral biogeographic transition zone because of the dominance of subtropical species and presence of tropical species near their southern range edge (Sommer et al., 2014). SST in Southeast Australia has increased by approximately 0.4°C per decade (Lima & Wethey 2012); however within SI the overall minima, average and maxima vary by as much as 1.4°C between islands (Malcolm et al. 2011). A pioneering study in the early 1970s (exact dates unknown) documented 34 coral species belonging to 18 genera around SI, with abundance and occurrence quantified around one island (Veron et al., 1974). Approximately 20 years later, a 1992 survey in the same area documented a total of 90 species and cover was quantified at multiple locations regionally (Harriott *et al.*, 1994). These coral surveys provide a unique opportunity to investigate how species have responded to increased SST, and whether any changes are similar to what has been observed in other regions, such as sub-tropical Japan.

Poleward range shifts attributed to climate warming have been documented by changes in abundance of species with different biogeographic distributions. For example, tropical species shifted poleward in Japan, subtropical species remained stable, and responses of cosmopolitan species were inconsistent so that some shifted poleward while others remained stable (Yamano *et al.*, 2011). Similarly, Barry *et al.* (1995) quantified an increase in abundance of warm-water species and a decrease in abundance of cold-water species using a long-term dataset of a rocky intertidal temperate community in central California. Rocky

intertidal species near their northern range limit in Britain and Ireland extended their ranges poleward but also increased in abundance (Mieszkowska *et al.*, 2006). Changes in species abundance near range edges provide stronger evidence of range shifts or expansion and responses of marine species assemblages due to increased SST than records of occurrence can do alone. Therefore, to better understand distribution patterns and the processes that drive them, it is necessary to consider changes in distribution and relative abundances over time.

The concentration of hard corals in warm, tropical waters and the prominent latitudinal attenuation suggests that SST is a primary factor limiting coral distributions into higher latitudes (Dana, 1843; Veron 1995). Additionally, historical shifts of corals toward the poles during warming periods, or retreating toward the equator during cooling periods further support geographic ranges that track SST changes (Precht & Aronson, 2004; Kiessling *et al.*, 2012). Recently documented coral occurrences poleward of their previously known distributions suggests that some species ranges are currently changing (Yamano *et al.*, 2011; Baird *et al.*, 2012). However, evidence of the effect of increased SST on coral range edges is limited because of the lack of long-term data for comparison and incomplete understanding of population dynamics near these edges. Clearly more research is needed to provide firm evidence of changes to species range limits.

Given historic and current increases in poleward SSTs, a restructuring of coral assemblages, particularly in subtropical systems is to be expected. Coral species that are abundant in both the tropics and subtropics can be expected to not only appear in the subtropical SI but also increase in abundance, as conditions become more favorable and approximate thermal regimes in tropical systems. To determine multi-decadal change in coral assemblage in this subtropical environment, we documented and updated the coral species list as well as measured coral cover across multiple locations in the SI region. We extracted the finest level of detail possible from surveys two and four decades earlier to quantify change in

#### Multi-decadal coral assembly change

cover. Additionally, we evaluated whether changes in species abundance over two decades were related to species biogeographical distributions, i.e. corals with cosmopolitan or subtropical distributions. These results offer insight into how coral assemblages in subtropical systems may shift under a changing climate and specifically whether Australian cosmopolitan corals may be expanding their ranges poleward as SSTs become more optimal.

## 1.2 MATERIALS AND METHODS

#### 1.2.1 40-year comparison at South West Solitary Island

Percentage coral cover was visually estimated during historic surveys for the most abundant genera every 10m along four 200 m transects (Veron et al., 1974). We extracted coral cover of the four most abundant genera (Acropora, Pocillopora, Paragoniastrea, Turbinaria) at South West Solitary Island (SWSI) from the early 1970s based on diagrammatic representations of percentage area cover in Figures 8-11 in Veron et al. (1974) using ImageJ software (Rasband & ImageJ, 1997) to extract quantitative estimates of coral cover. We quantitatively resurveyed coral cover on SCUBA in December 2014. We placed four transects along the substratum from the shoreline to 200 m offshore in approximately the same location and direction as previous surveys (Figure 7 from Veron et al., 1974) (Fig. 1). Corals were identified to species following Veron (2000) and accepted taxon names following Hoeksma (2014) were adopted. Along each transect, we measured depth, identified corals to genus and determined coral cover using the line intercept transect method (LIT; Hill & Wilkinson, 2004). Using this method, the length of each colony under the transect tape was noted. Percentage cover per genus and depth were calculated in alternate 10 m sections along the transect tape from 0 to 200 m. Depth was determined by depth gauge every 10 m and averaged for the section surveyed.

To create comparable quantitative estimates of cover, we merged all transect data for the historic study and estimated cover by depth for each genus. We similarly merged transect data for current surveys to calculate cover by depth. Total average coral cover as well as average cover of each genus by depth was measured to estimate change over four decades. Multi-decadal coral assembly change



Figure 1.1. Locations of survey sites and transects at six islands around the Solitary Islands region.

### 1.2.2 20-year regional comparison

Historic data for the 20 year regional comparison were accessed from Harriott *et al.* (1994) who sampled seven locations across the SI region. The authors did not provide details on the precise location of their samples; however, they did state that areas of high coral cover were targeted. Therefore, rather than trying to match sites as for the 40 year comparison, we targeted between one and three sites at each island where coral cover was highest. We resurveyed a total of nine sites across the six locations [North Solitary Island (NSI), North West Solitary Island (NWSI), South Solitary Island (SSI), South West Solitary Island (SWSI), Split Solitary Island (SPSI) and Muttonbird Island (MUI), (Fig. 1)]. Sites were surveyed using the point intercept transect method with four replicate 50m transects placed along the depth contour at between 8-10m depth (PIT; Hill & Wilkinson, 2004).

Total hard coral cover was calculated for each transect and averaged per location to compare with historic totals. The number of coral species found along each transect was summed. We determined average species richness per location by averaging across all transects. Presence and abundance of *Acropora* species were highlighted in historic studies due to their higher than expected diversity given the relatively low SST at SI (Veron *et al.*, 1974) and the significant contribution to site-specific differences throughout the region (Harriott *et al.*, 1994). To compare change in *Acropora* cover over 20 years, we calculated cover of only *Acropora* spp. on each transect and averaged across all transects per location.

Harriott *et al.* (1994) reported coral cover for only 13 species that had a minimum of 1% cover in at least one location. Therefore, quantitative comparisons of change could only be evaluated for these species. At locations where these 13 species were recorded in historic surveys as present but not quantified due to less than 1% cover, we assumed cover to be 0.25%, which approximated average cover of species with less than 1% in current surveys (Baird unpub. data). We corrected values for the historic cover of *Acropora solitaryensis* as

follows. Cover of *A. solitaryensis* at NWSI (7.7%, Table 3 from Harriott *et al.*, 1994) is greater than the total cover of all *Acropora* species at the same island (5%, Table 4 from Harriott *et al.*, 1994). We therefore reduced cover of this species at NWSI from 7.7% to 3.7% as the most conservative adjustment so that total *Acropora* cover would have been less than 5% (Table 4 from Harriott *et al.*, 1994). Additionally, *A. glauca* was described as being a locally abundant subtropical species but it was omitted from quantitative results (Harriott *et al.*, 1994). We assumed historic cover to be 1% at locations where the species was present, which is the minimum cover possible for Harriott *et al.* (1994) to have considered it "dominant".

Change in cover after 20 years was quantified regionally for those species with a minimum of 1% cover in at least one location historically or currently. Average species cover was measured at all six locations during each time. We evaluated change in cover by calculating  $log_{10}(average cover+1)$  for both historic and current surveys. A ratio of change, which was calculated by  $log_{10}((average current cover +1)/(average historic cover+1))$ , was quantified to determine relative change in cover between species. Both historic studies of coral cover at NSI describe the assemblage as distinct from the other locations in the SI region (Veron *et al.*, 1974; Harriott *et al.*, 1994). Therefore, we also determined the change in cover of the same species at NSI as  $log_{10}((NSI \text{ species cover } +1))$  for both historic and current surveys. Change in cover was described according to distributions of biogeographic regions where species are most abundant. In other words, species with subtropical distributions are abundant in both the tropics and subtropics.
## 1.2.3 Species turnover

To test for species turnover in the SI coral assemblage, we compared the list of species from each of the three studies, Veron *et al.*, (1974), Harriott *et al.*, (1994) and a species list based on our collections, field photographs and corals identified on the transects (Table 1). Species names from Harriott *et al.*, (1994) were changed where appropriate to the currently accepted species names as listed in the World Register of Marine Species (WoRMS, 2016).

To determine change in species composition over time, we calculated dissimilarity between the three surveys (1970s, 1990s, 2010s) using the beta.temp function in the betapart package (Baselga & Orme, 2012) with R statistical software (R Development Core Team, 2015). Temporal dissimilarity (Sorensen dissimilarity,  $\beta_{sor}$ ) was measured on species presence-absence between each of the consecutive surveys.

 Table 1.1. Species occurrence records around the SI region updated through time, "X" indicates

 species presence per study.

| Species                    | Veron <i>et al.</i> (1974) | Harriott <i>et al.</i> (1994) | Current study |
|----------------------------|----------------------------|-------------------------------|---------------|
| Acanthastrea echinata      | Х                          | Х                             | Х             |
| Acropora abrotanoides      |                            | Х                             | Х             |
| Acropora anthocercis       |                            | Х                             | Х             |
| Acropora cerealis          |                            | Х                             | Х             |
| Acropora chesterfieldensis |                            | Х                             |               |
| Acropora clathrata         |                            | Х                             | Х             |
| Acropora cytherea          | Х                          | Х                             | Х             |
| Acropora dendrum           |                            | Х                             | Х             |
| Acropora digitifera        | Х                          | Х                             | Х             |
| Acropora florida           |                            | Х                             |               |
| Acropora gemmifera         |                            |                               | Х             |
| Acropora glauca            | Х                          | Х                             | Х             |
| Acropora granulosa         |                            | Х                             |               |
| Acropora humilis           | Х                          | Х                             | Х             |
| Acropora hyacinthus        | Х                          | Х                             | Х             |
| Acropora intermedia        |                            |                               | Х             |
| Acropora listeria          |                            | Х                             | Х             |
| Acropora longicyathus      |                            |                               | Х             |
| Acropora loripes           |                            | Х                             |               |
| Acropora lutkeni           |                            | Х                             | Х             |
| Acropora microclados       |                            |                               | Х             |
| Acropora millepora         |                            | Х                             |               |
| Acropora monticulosa       |                            |                               | Х             |
| Acropora muricata          |                            | Х                             |               |
| Acropora nasuta            |                            | Х                             | Х             |
| Acropora palmerae          |                            | Х                             | Х             |
| Acropora polystoma         |                            | Х                             | Х             |
| Acropora pulchra           |                            | Х                             |               |
| Acropora robusta           | Х                          | Х                             | Х             |
| Acropora sarmentosa        |                            | Х                             | Х             |
| Acropora secale            |                            |                               | Х             |
| Acropora selago            |                            |                               | Х             |
| Acropora solitaryensis     | Х                          | Х                             | Х             |
| Acropora subulata          |                            |                               | Х             |
| Acropora valida            | Х                          | Х                             | Х             |
| Acropora verweyi           |                            |                               | Х             |
| Acropora willisae          |                            |                               | Х             |
| Astrea curta               | Х                          | Х                             | Х             |
| Coscinaraea columna        | Х                          |                               | Х             |
| Coscinaraea mcneilli       |                            | Х                             | X             |

| Table 1.1 continued | 1 continued |
|---------------------|-------------|
|---------------------|-------------|

| Cyphastea salae            | Х |   | Х |
|----------------------------|---|---|---|
| Cyphastea serailia         |   | Х |   |
| Cyphastera microphthalma   |   |   | Х |
| Cyphastrea chalcidicum     |   | Х |   |
| Duncanopsammia peltata     | Х | Х | Х |
| Echinophyllia aspera       |   | Х |   |
| Favites abdita             |   | Х |   |
| Favites fle1uosa           |   | Х |   |
| Favites magnistellata      |   | Х |   |
| Favites valenciennesi      |   | Х |   |
| Gardinoseris planulata     |   |   | Х |
| Goniastrea favulus         |   | Х |   |
| Goniopora djiboutiensis    |   | Х | Х |
| Goniopora lobata           |   | Х |   |
| Goniopora norfolkensis     |   | Х |   |
| Goniopora stokesi          | Х | Х | Х |
| Homophyllia bowerbanki     | Х | Х | Х |
| Hydnophora elesa           |   | Х | Х |
| Hydnophora microconos      |   | Х | Х |
| Hydnophora pilosa          |   | Х |   |
| Leptastre purpurae         |   |   | Х |
| Leptastrea transversa      |   | Х |   |
| Leptoseris hawaiiensis     |   | Х | Х |
| Micromussa lordhowensis    | Х | Х | Х |
| Montipora aequituberculata |   |   | Х |
| Montipora angulata         |   | Х |   |
| Montipora caliculata       |   |   | Х |
| Montipora efflorescens     |   |   | Х |
| Montipora foveolata        | Х |   | Х |
| Montipora grisea           |   |   | Х |
| Montipora mollis           | Х |   | Х |
| Montipora spongodes        | Х | Х | Х |
| Montipora turtlensis       |   | Х |   |
| Montipora venosa           | Х | Х | Х |
| Mycedium elephatotus       |   | Х |   |
| Paragoniastrea             | V | V | V |
| australiensis              | Х | Х | Х |
| Pavona deurdeni            |   |   | Х |
| Pavona explanulata         |   | Х | Х |
| Pavona minuta              |   | Х |   |
| Pavona varians             |   | Х | Х |
| Table 1.1 continued        |   |   |   |

| Pavona venosa            |    | Х  |    |
|--------------------------|----|----|----|
| Platygyra lamellina      | Х  |    |    |
| Plesiastrea versipora    | Х  | Х  | Х  |
| Pocillopora aliciae      | Х  |    | Х  |
| Pocillopora damicornis   | Х  | Х  | Х  |
| Porites cf heronensis    | Х  | Х  | Х  |
| Psammocora albopicta     |    |    | Х  |
| Psammocora profundacella | Х  | Х  |    |
| Stylophora pistillata    | Х  | Х  | Х  |
| Turbinaria frondens      | Х  | Х  | Х  |
| Turbinaria heronensis    |    |    | Х  |
| Turbinaria mesenterina   | Х  | Х  | Х  |
| Turbinaria patula        |    | Х  | Х  |
| Turbinaria radicalis     | Х  | Х  | Х  |
| Total number of species  | 31 | 68 | 68 |

## 1.3 RESULTS

## 1.3.1 40-year comparison at South West Solitary Island

Current coral cover by depth has decreased to approximately half the original cover since the 1970s for each of the four most abundant genera (Fig. 2a-d). Maximum cover of *Acropora* and *Paragoniastrea* was approximately 75% in some locations historically and cover of these genera is currently less than 20%. However, patterns in the relationship of cover by depth per genus over forty years were generally consistent. *Acropora* decreased with depth (Fig. 2a), *Paragoniastrea* increased with depth (Fig. 2b) and peak *Turbinaria* cover was greatest around 12-13 m depth (Fig. 2c). The exception to this pattern was found at shallow depths for *Pocillopora* where historic and current patterns of cover by depth were inconsistent where historic cover increased with depth but current cover descreases by depth (Fig. 2d).

Average cover of each of these four genera has decreased from the 1970s to the present (Fig. 3). The genus with the highest average coral cover at both times was *Turbinaria* and the genus with the largest decrease in cover was *Acropora* (Fig. 3). The total cover of these four genera in the 1970s was 45% compared to 15% at present.



**Figure 1.2.** Coral cover by depth in 1974 and 2014 for each of the dominant genera. a) Acropora, b) Paragoniastrea, c) Turbinaria, d) Pocillopora (note: different scale) at South West Solitary Island. All figures represent the combination of four 200 m transects around the north side of the island from 2.5 m to 18 m depth. Data are fit with loess smoothers for ease of interpretation.

Cover of Dominant Coral Genera at SWSI



**Figure 1.3.** Average coral cover (+SD) of each of the most abundant genera at South West Solitary Island (SWSI). Estimates are based on four transects at 3-18 m depth from the north side of the island where coral cover was highest. Estimated total coral cover in 1974 (45%) is indicated by solid line and in 2014 (15%) is indicated by dashed line.

## 1.3.2 20-year regional comparison

Total coral cover decreased at all islands; the largest decrease was at SWSI (11%) and the smallest at NSI (2%) (Fig. 4a). The average number of species per transect increased at all sites except for SSI (Fig. 4b). The largest increases in average number of species per transect was at SSI (50%, 3 species) and NSI (27%, 2.5 species) (Fig. 4b). Cover of *Acropora* spp. ranged between <1% (MUI) to 7% (NSI), where NSI experienced the greatest decrease in cover (11%) (Fig. 4c). The smallest change in *Acropora* cover was at NWSI (0.5%) (Fig. 4c).

Average change in regional cover for dominant species (i.e. those with a minimum of 1% cover) varied where some increased, others decreased and many stayed approximately the same (Fig. 5a). Two cosmopolitan and two subtropical species were dominant in at least one location during current surveys but not in historic surveys: *Acanthastrea echinata* (subtropical; up to 4.5%), *Astrea curta* (cosmopolitan,up to 2.25%), *Micromussa* 

*lordhowensis* (subtropical, up to 2.75%) and *Stylophora pistillata* (cosmopolitan, up to 1%) for a total of 18 species with a minimum of 1% cover per location at either time. The majority of cosmopolitan species (63%) decreased in average cover and 50% of subtropical species increased in average cover after 20 years (Fig. 5a). *Acropora glauca* had the largest increase in cover (ratio of change=2.86); however, we assumed minimum historic cover where present (1%) since quantitative estimates were not reported. Of species that had at least 1% cover during past surveys, *Turbinaria mesenterina*, a species with a cosmopolitan distribution, had the largest average increase in cover (ratio of change=1.45). *Acropora nasuta*, also cosmopolitan, had the largest average decrease (ratio of change=-2.93).

Directional change in cover for species at NSI could not be determined confidently. Three species that were not previously found at NSI (i.e. *Micromussa lordhowensis, Turbinaria mesenterina, Cyphastrea* spp.) became dominant. The majority of the cosmopolitan species that were dominant at both times (71%) decreased in cover; however, the majority of the subtropical species (86%) increased (Fig. 5b). The direction of change could not be confidently determined for the remaining four species. Three species (*Acropora hyacinthus, Turbinaria radicalis, Psammocora* spp.) had less than 1% cover during both historic and current surveys but past cover was not quantified and was assumed to be 0.25%. The current cover of *Acropora glauca* is 2.13%; however, due to a lack of quantitative data provided in Harriott *et al.* (1994), therefore we could not determine if this was an increase or decrease from past cover (Fig. 5b).

Multi-decadal coral assembly change



**Figure 1.4.** Percent coral cover and mean richness per location in 1992 and in 2013/14. a) Percent coral cover (+SE) of all hard corals per location in 1992 and 2013/4. b) Average species richness (+SE) per transect per location in 1992 and 2013/4. c) Percent cover (+SE) of *Acropora* spp. per location in 1992 an 2013/4. All surveys are based on best-developed coral communities per location at 5-9 m depth. Past cover and richness (Harriott *et al.* 1994) did not report standard errors but have been included for current surveys. One *Acropora* sp. was documented at Muttonbird Island though not quantified at either time, therefore presence is indicated and 0.25% cover is assumed.



**Figure 1.5.** Change in species cover between 1992 and 2013/2014 for species with >1% cover at either time. a) Regional change in average cover between 1992 and 2013/14. b) North Island change in cover between 1992 and 2013/14. Species that were present but not quantified in 1992 were assumed to have a cover of 0.25%. *Acropora glauca* 1992 cover is the minimum 1% because quantitative results were omitted even though it was described as locally abundant (as describe in the text). Uncertainty in direction of change in cover for four species is indicated by horizontal lines. The diagonal line on both figures represents no change, above the line and to the left represents an increase in cover; below the line and to the right represents a decrease in cover in time. Species identification for both figures is as follows, *1: Acanthastrea echinata, 2. Acropora cerealis, 3. A. glauca, 4. A. hyacinthus, 5. A. nasuta, 6. A. robusta, 7. A. solitaryensis, 8. Astrea curta, 9. Cyphastrea spp, <i>10. Micromussa lordhowensis, 11. Paragoniastrea australensis, 12. Pocillopora* spp, *13. Porites heronensis, 14. Psammocora* spp, *15. Stylophora pistillata, 16. Turbinaria frondens, 17. T. mesenterina, 18. T. radicalis.* Species are identified by whether they are most abundant in the subtropics (Subtropical) or abundant in both the tropics and sub-tropics (Cosmopolitan).

#### 1.3.3 Change in composition

A total of 94 nominal hermatypic scleractinian species were found across the three studies: comprising 31 in Veron *et al.* (1974); 68 in Harriott *et al.* (1994); and 68 in this study (Table 1). Of these species, only 24 were common to all three studies. One was unique to Veron *et al.* (1974), 25 were unique to Harriott *et al.* (1994) and 20 were unique to this study (Fig. 6). Temporal turnover of coral assemblages between surveys in the 1970s and 1990s 45

was approximately 19% ( $\beta$ sim=0.1935) and 37% between the 1992 survey to present ( $\beta$ sim=0.3676).



**Figure 1.6.** The number of scleractinian corals from the SI region visualized by number of species found during each of three surveys each separated by approximately 20 years. In total, 94 species were identified and the number of species unique to one survey, common to either two of the three surveys or all three surveys is indicated.

## 1.4 DISCUSSION

There is some evidence for a general and ongoing decline in coral cover for the most abundant taxa at SWSI since the 1970s. Despite warmer SSTs and inundation of tropical water in this subtropical location, there was no shift toward assemblages dominated by cosmopolitan corals. Rather, subtropical corals primarily increased at NSI. The number of species currently present in the Solitary Islands region is similar to the previous survey in 1992 and both are significantly greater than the pioneering survey in the early 1970s. However, as we argue below, the change in species composition is more likely the result of differences in taxonomic opinion rather than a response to climate change. Linking historical and current surveys that describe species assemblages are becoming increasingly important to document responses to changing environmental conditions. These links are critical in marine warming hotspots, which have been highlighted as areas where change in community structure is likely to occur earlier (Frusher *et al.*, 2014). Overall, the decline in coral cover since the 1970s and increase in the abundance of sub-tropical species since the 1990s in the Solitary Islands do not parallel changes observed in other regions (Yamano *et al.* 2011).

Multi-decadal patterns of change in SI coral assembly do not appear to be consistent with other records of coral biogeographic boundary shifts where SST has increased in other regions. In Japan where SST increased up to 1.5°C/century, four of nine coral species recorded expanded their ranges poleward (Yamano *et al.*, 2011). Two of the species whose ranges expanded had tropical distributions and were key to reef formation whereas no tropical species remained stable (Yamano et al., 2011). In the SI region at similar latitudes, most cosmopolitan species decreased in abundance rather than an increase, which would have been expected with warming SST. This trend was even more enhanced at the northern most island, which experiences the warmest average SST across the SI region (Malcolm et al., 2011). At NSI, most cosmopolitan species decreased in cover, most subtropical species increased in cover and Acropora cover decreased further when compared to other locations in the region. The coasts of Japan and Australia have warmed more than global averages; however the Western Boundary Currents that bring equatorial water poleward, have been more enhanced in the northern hemisphere than the southern (Wu et al., 2012), potentially contributing to these differences. Additionally, there is evidence for the tropicalization of marine systems in both regions although the signal is stronger in the north (Vergés et al., 2014).

Species distribution changes on Australia's east coast are likely not influenced solely by average temperature increases. The lack of increased tropical coral species abundance is similar to the lack of change in East Australian rocky intertidal communities over more than

50 years (Poloczanska *et al.*, 2011). Even as average SST increases at higher latitudes, minimum temperatures may restrict warm water species from increasing in abundance (Veron *et al.*, 1974). The increase in minimum temperatures along the SE Australian coast has allowed some tropical fish to overwinter; however, projected winter SST increases will not be sufficient for other tropical fishes for decades (Figueira & Booth, 2010). Additional environmental constraints in subtropical environments such as wave action or salinity (Endean *et al.*, 1956), biotic interactions (Schiel *et al.*, 2004) or turbidity and light (Veron *et al.*, 1974; Veron 1995) may limit tropical or cosmopolitan corals. Instead, subtropical species that can be considered habitat generalists because of their tolerance of broader environmental conditions (Sommer *et al.*, 2014) may be able to outcompete tropical recruits, even with SST warming. Increased average SST in subtropical environments may be more optimal for many coral species; however, distribution shifts may likely also track other aspects of climatic and environmental factors (Burrows *et al.*, 2014).

Documenting coral assemblage dynamics provides a necessary framework for capturing long-term change. In the subtropical region of the northern South China Sea, temporal change in species composition, shifts in the most abundant taxa and a decline in total coral cover were documented over 25 years (Chen *et al.*, 2009). Australian coral assemblages have not shifted in the same manner. West Australian coral reefs were found to be stable after 25 years; however, the spatial variability of change in cover and change in composition are noteworthy (Speed et al. 2013). In eastern Australia, Dalton & Roff (2013) found greater than 75% similarity in assemblage structure over 14 years in the SI region. However, this analysis found cover and diversity to be highly variable between sites within the region. Here, we quantified change in cover for the most abundant species regionally but also captured how change varied between islands as well as quantified change in cover over 40 years. The dominant genera at SWSI all declined in cover by depth after four decades

suggesting a consistent decline across taxa and no major restructuring. The majority of species that were most abundant regionally in 1992 remained regionally abundant after two decades, with only few exceptions of new occurrences or species no longer found. Additionally, species-specific responses varied. For example, some *Turbinaria* and *Acropora* species increased in abundance regionally while others decreased (Fig. 5a).

Historical data provide incredibly valuable information for comparison of change through time but come with inherent difficulties for accurate analyses (Tingley & Beissinger, 2009). The SI region spans a large area of approximately 72,200 hectares. Documenting species presence over forty years across this area was conducted opportunistically in welldeveloped coral communities. Our current survey effort replicated methods as closely as possible; however, some inconsistencies were unavoidable. Of the corals with the highest cover, many species occurrences both historically and currently were documented only outside of best-developed coral communities indicating the difficulty of detection. Undetected species are probable under these circumstances where small, cryptic and rare species would be less likely to be found (McCarthy et al., 2013). This could also be the cause of species detected in the 1970s and current surveys but not recorded in 1992 (e.g. Coscinaraea columna, Montipora foveolata; Table 1). We also could not confidently quantify change in cover at SWSI because of methodological inconsistencies. Visual estimates of historic cover from the pioneering survey exceeded 100% where colonies overlapped (Veron et al., 1974) but current surveys were quantified with more precise PIT survey methods where cover could not exceed 100%. However, quantitative estimates of species cover over two decades (i.e. between Harriott *et al.* (1994) and the current study) provided evidence that more accurately captured changes in community structure across a spatial gradient. Errors and omissions from previous results (e.g. while Acropora glauca was stated as being locally abundant, quantified cover was omitted by Harriott et al., 1994) increased the difficulty of complete and precise

comparisons. Merging multiple but distinct records of coral composition over four decades in the SI region has revealed important patterns of change and created a unified baseline for future evaluations.

Variable survey effort and taxonomic uncertainty also complicated temporal comparisons of long-term change. The number of unique species to each study suggests very high rates of change in the SI coral assemblage in the last 40 years. However, much of the change in species composition among these studies is likely to be due to sampling artifacts or differences in taxonomic opinion. In particular, it is highly unlikely that the number or species increased by more than 100% between 1970 and 1990, rather, it is far more likely that Veron *et al.*, (1974) were not as thorough as more recent surveys. In particular, *Acropora* were most likely under-sampled (8 spp vs more than 20 in each of the other studies, Table 1). Furthermore, the one unique species recorded in the original survey, *Platygyra lamellina* may have been confused with *Paragoniastrea australensis*, a dominant species on many eastern Australian high-latitude reefs (Fig 1a. in Sommer *et al.* 2014).

Of the 24 species unique to the 1992 survey, most are highly likely to be differences of taxonomic opinion or sampling artifacts. For example, unpublished molecular work has revealed that all the plocoid merulinid colonies in our collection are *Astrea curta*, some of which were probably identified as *Montastrea valenciennessi* and *M. magnistellata* by Harriott *et al.* (1994). Similarly, unpublished molecular work has all revealed that cerioid-meandroid merulinids in our collection are Paragoniastrea *australensis*, some of which were probably identified as *Goniastrea favulus*, *Favites flexuosa* and *F. abdita* by Harriott *et al.* (1994). In addition, molecular work suggests that all 12-septa *Cyphastrea* are a new undescribed species, *C. salae*, and therefore Harriott *et al.* (1994) records for *C. serailia* and *C. chalcidcium* are likely to be incorrect. *Leptastrea purpurea* is easily confused with *L. transversa; Montipora angulata* with *M. caliculata; Pavona minuta* with *P. duerdeni*; and *P.* 

*profundacella* can be difficult to distinguish from *P. albopicta* in the field. In addition, some of the richness in the 1992 surveys is likely to have been over estimated. For example, *Mycedium elephantotus* is often confused with *Echinophyllia aspera*, *Pavona venosa* with *P. varians*; *Hydnophora pilosa* with *H. exesa* and it is unlikely, based on our collection, that both species in these pairs can be found in the SI. It is also unlikely that there are four *Goniopora spp.* in the SI. Our collection suggests there are only two. Of the 20 species unique to this study, at least 10 records are likely due to differences of opinion as outlined above. The only well-defined additions are *A. monticulosa*, *A. longicyathus*, *A. microclados*, *A. subulata*, *A. verweyi*, *C. microphthalma*, *M. efflorescens*, *M. grisea*, *G. planulata*, *T. heronensis* the last eight of which were rare (only one colony of each seen) and therefore easily missed. So conservatively, we have 7 losses and 10 additions to the species pool in the 20 years since Harriott *et al.* (1994).

Historic studies of coral distributions at high latitudes are rare but provide key information for long-term comparisons in understanding dynamic communities. Total coral cover has decreased somewhat at SI but the species diversity, after consideration of taxonomic opinion has not changed significantly over four decades. SST along Australia's east coast (10.5°S to 29.5°S) increased by approximately 0.12°C/decade from 1950-2007 and resulted in climate shifts between these latitudes (Lough, 2008). However, warming associated with the inundation of tropical waters has not yet resulted in increased tropical coral species abundance in the SI region. These results provide a baseline for effective comparison into the future where SST is projected to increase by up to 2°C by 2050 compared to the 1990-2000 average (Hobday & Lough, 2011) and suggest how coral assemblages in high latitudes and those near their distribution limits will be impacted by warming. A comparison of coral distribution shifts between regions where SST is warming provides a more global understanding of species responses to a changing climate.

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# CHAPTER 2

# ENVIRONMENTAL TOLERANCE GOVERNS THE PRESENCE

# OF REEF CORALS AT LATITUDES BEYOND REEF GROWTH

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## ABSTRACT

## Aim

Understanding mechanisms that enhance survival outside a taxonomic group's usual range is key to understanding diversity gradients, how range boundaries operate, and how environmental change might influence geographic distributions. Our aims were to (1) identify species-level traits associated with reef-building coral species whose ranges extend into highlatitude, non-reefal habitats (i.e. "beyond reef"), (2) determine if these patterns were consistent in different global regions, and (3) determine if traits associated with living beyond reef were related to enhanced dispersal or tolerance to harsher environmental conditions in three regions of the Central Indo-Pacific with tropical-temperate gradients from 35°N to 36°S. Scleractinian coral richness was collated and analyzed as a function of latitude, region and whether or not reef accretion occurred. Species' traits that are hypothesized to contribute to living beyond the environmental limits of carbonate reef accretion were compiled, which included traits associated with dispersal potential and environmental tolerance. The contribution of species' traits to presence beyond reef was then quantified using a binomial generalized linear mixed effects model. In each region, coral species richness dropped up to 73% where reef accretion ceased. Compared to corals restricted to coral reefs, the subset of species extending beyond reef shared common traits related to environmental tolerance (larger depth ranges, more robust morphologies and tolerance of turbid water), but not to dispersal potential. Patterns were mostly consistent among regions. We show for the first time that coral species living successfully in beyond reef habitats share common characteristics that are consistent in three global regions. Environmental tolerance appears to play the dominant role in determining which species successfully establish beyond reef. Our traitbased approach sheds light on how species assemblages and ranges might be altered by environmental change or loss of reef habitats.

## 2.1 INTRODUCTION

A decline in species richness of tropical marine organisms from the low-latitude center of biodiversity in the Indo-Australian Archipelago (IAA) to higher latitudes is one of the most prominent patterns in biogeography (Stehli & Wells, 1971; Briggs, 1999). This latitudinal diversity gradient has been observed across varied taxa including reef fishes, snails, corals and lobsters (Roberts *et al.*, 2002). However, drivers of the gradient are not well understood (Hillebrand, 2004; Mittelbach *et al.*, 2007). Latitude is a surrogate for a number of important environmental variables that interact and are correlated with each other, making it difficult to tease apart the main drivers of decreased diversity with latitude (McArthur *et al.*, 2010).

For reef-building scleractinian corals, the IAA is the center of diversity, where 76% of all coral species are found (Veron *et al.*, 2009), and from where species richness also attenuates to the north and south (Veron, 1993; Hoeksema, 2015). Many abiotic factors have been suggested as potential drivers of the correlation between declining coral diversity and increasing latitude, particularly decreasing temperature (Dana, 1843; Veron & Minchin, 1992; Veron, 1995), light (Wells, 1957) and carbonate saturation (Gattuso *et al.*, 1998) that affect coral growth; as well as patterns of surface currents (Veron, 1995; Hughes *et al.*, 2002) and hydrodynamic forces (Done, 1982; Massel & Done, 1993; Ferrario *et al.*, 2014) that influence recruitment and mortality.

While coral richness attenuates with latitude, there is a dramatic decline in richness associated with the limits of coral reef accretion around the world (Veron & Minchin, 1992; Veron, 1995; Hoeksema, 2015). Beyond these boundaries globally, which occur at approximately 30°N and 30°S, corals fail to produce sufficient calcium carbonate to build the three-dimensional reef structure (Buddemeier & Smith, 1999). Nonetheless, a subset of the same corals that build tropical reef structure continues to exist in high-latitude non-reefal habitats - *i.e.* "beyond reef" (Harriott & Banks, 2002). While species assemblages on high-

latitude coral reefs have been relatively well documented (Harriott *et al.*, 1995; Yamano *et al.*, 2001; Celliers & Schleyer, 2008), much less is known about beyond reef assemblages (Harriott *et al.*, 1994; Nozawa *et al.*, 2008; Denis *et al.*, 2013). Therefore, we do not currently have a mechanistic understanding of why some species ranges successfully extend beyond reef while others do not.

The processes that structure beyond reef assemblages have been difficult to generalize, because research has focused on species composition that overlaps minimally in different regions around the world (Veron, 2000). For this reason, the current understanding of beyond reef assemblages is limited; for example, in the Indo-Pacific, coral reef and beyond reef assemblages have generally been differentiated based on coarse taxonomic groupings (*e.g.* dominance of Acroporidae, Poritidae, Faviidae) (Harriott & Banks, 2002; Nozawa *et al.*, 2008; Speed *et al.*, 2013). However, such patterns are not consistent globally and given the lack of species overlap across regions, a new approach is required. Combining species assemblage data with species trait data provides a structured framework for understanding relationships between organisms and their environment at multiple spatial scales (Poff, 1997). For example, are assemblages near range edges where diversity is lower dominated by species with certain traits? If so, what can these traits tell us about community assembly rules (*e.g.* the relative importance of dispersal versus establishment (Keith *et al.*, 2015)?

In this study, we first quantified the extent of coral species diversity loss at the boundary between reef and beyond reef habitats along three latitudinal gradients in the Indo-Pacific. We then tested whether or not the traits associated with beyond reef species were a non-random subset of species on coral reefs, and subsequently if these trait patterns were consistent for the three latitudinal gradients. Finally, based on the traits that tended to be associated with beyond reef species, we consider whether dispersal traits (*e.g.* those related to larval access to and time in ocean currents) or establishment traits (*e.g.* those related to

environmental tolerance) best explain the capacity to live beyond reef. Understanding the species traits associated with successfully living beyond reef is an important step for predicting how species ranges might shift with environmental change or loss of reef habitats.

## 2.2 MATERIALS AND METHODS

#### 2.2.1 Species occurrence data

We used all biogeographic data from Veron (1993) that included species occurrences at 43 sites along three latitudinal gradients spanning 35°N to 36°S through the Central Indo-Pacific Ocean. No additional surveys were included for consistency in survey effort within a temporally restricted period and to avoid differences in taxonomic opinion. In total, 535 species representing 74% of Indo-Pacific scleractinian corals were documented in at least one of the sites. Species' names were updated using the World Register of Marine Species (WoRMS, 2015) and, where necessary, occurrence records representing synonymous species were combined (*e.g. Cycloseris erosa* revised to *Cycloseris tenuis*. See also Supplementary Table 2.1 in Supporting Information). Any records not identified to species (9%) were retained for the species diversity analysis, but removed from species trait analysis.

Survey sites spanned from low latitude tropical coral reefs to high latitude, coral assemblages beyond reef accretion along three latitudinally contiguous but geographically distinct regions of the Indo-Pacific. The North region (N) included eleven sites from the Phillipines (12°N) to Tateyama, Japan (35°N); the Papua New Guinea and East Australia region (PNG-EA) included fifteen sites from Southern Papua New Guinea (8°S) to South Australia (36°S) and West Australia (WA) included seventeen sites from Ashmore Reef (12°S) to Recherche Archipelago (34°S) (Fig. 2.1). Each of these regions has different environmental and geological settings where separate pole-ward surface currents transport tropical water to higher latitudes.

Each site was classified as "coral reef" or "beyond reef" (*i.e.* coral communities that do not accrete the three-dimensional carbonate reef structure) following Veron (1995). Accordingly, a species could be restricted to "coral reef" or "beyond reef" habitats, or could occur in both. For this study we excluded high-latitude, beyond reef endemic species (~3% of species), because our goal was to evaluate differences in coral traits between species restricted to coral reefs and those also found beyond reef (Supplementary Table 2.1). As such, beyond reef corals were classified as species that occur both on coral reefs and beyond reef within any of the regions.

Figure 2.1. (opposite page) Survey locations throughout the Indo-Pacific (modified from Veron, 1993). Crosses (+) indicate coral reef and solid circles ( ) indicate high-latitude beyond reef sites.

Sites from Papua New Guinea to East Australia (PNG-EA): 12. Southern Papua New Guinea; 13. Torres Strait; 14. North GBR; 15. Coral Sea; 16. Central GBR; 17. Pompey and Swain Reefs; 18. Capricorn & Bunker Reefs 19. Flinders Reef; 20. Elizabeth & Middleton Reefs; 21. Lord Howe Island; 22. North NSW; 23. Solitary Islands; 24. South NSW; 25. Victoria; 26. South Australia.

<u>Sites in West Australia (WA):</u> 27. Ashmore Reef; 28. Scott Reef; 29. Kimberly Coast; 30. Rowley Shoals; 31. Dampier Archipelago; 32. Ningaloo Reef Tract; 33. Shark Bay; 34. Houtman; 35. Port Gregory; 36. Geraldton; 37. Jurian Bay; 38. Quinns Rock Region; 39. Marmion; 40. Rottnest Island; 41. Geographe Bay; 42. SW coast; 43. Recherche Archipelago.

<sup>&</sup>lt;u>Sites in the North (N):</u> 1. Tateyama; 2. Izu; 3. Kushimoto; 4. Shirahama; 5. Tosashimizu; 6. Amakusa; 7. Tanegashima; 8. Amami Is.; 9. Okinawa; 10. Yaeyama; 11. Phillipines.



## 2.2.2 Species richness patterns

Negative binomial regression was used to model species richness as a function of two and three way interactive effects of latitude (absolute), region (N, PNG-EA or WA) and reef accretion (coral reef or beyond reef). The regression was run with the *mod.nb* function from the "MASS" package (Ripley *et al.*, 2002) using R statistical software (R Development Core Team, 2014). Best subset modelling was applied to find the model with the lowest Akaike's information criterion (AIC) that best described the relationship between species richness and latitude, region, reef accretion and interactions of all factors.

## 2.2.3 Coral traits associated with species in beyond reef communities

Species-level trait data for corals were downloaded from the Coral Trait Database (CTDB) (Madin *et al.*, 2016;,Supplementary Table 2.2). We selected ten traits that (1) were considered *a priori* to be of potential importance for living in high-latitude non-coral reef habitats and (2) data were available for at least 80% of the study species to maximize number of species included. These traits capture reproductive and dispersal capacity, environmental tolerance of species, biomechanical vulnerability, and family to account for phylogenetic relatedness among traits (Table 2.1).

Coral reproductive traits that influence dispersal capacity to higher latitudes, including mode of larval development (*brooder* or *broadcast spawner*), sexual system (*hermaphrodite* or *gonochore*) and the presence of *Symbiodinium* species in propagules (*present* or *absent*), were hypothesised to contribute to successfully dispersing to and establishing at higher latitudes. Species' depth range, preference for water clarity and preference for wave exposure conditions were selected as traits that represent measures of tolerance to potentially stressful environmental conditions. Depth range measurements (m, log<sub>10</sub> transformed) were derived from differences in the lower and upper depth that each species has been observed to occupy. Water clarity and wave exposure preference or intolerance to environmental conditions. That is, original water clarity preference values (*clear, turbid, both*) were reduced so that species

found primarily in turbid water (*turbid*) or occasionally in turbid or clear (*both*) were considered tolerant to turbidity and those that are only found in clear water (*clear*) were considered intolerant. Similarly, original wave exposure values (*exposed*, *protected*, *broad*) were represented as tolerant (either *exposed* or *broad*) or intolerant (*protected*).

The Coral Traits Database describes the most common growth form of each coral species globally, with a total of fifteen growth forms represented among the species in this study. Growth forms with similar biomechanical vulnerabilities to dislodgement were combined into seven categories representing varying tolerances to hydrodynamic stress (Madin *et al.*, 2014) that may provide a survival advantage in higher wave energy environments (Table 2.1). Since lack of available substrata may limit coral colonization beyond reef growth (Veron, 1995), substrate attachment was included as a trait to categorize species whose colonies are attached to a substratum (*attached*) or can be found unattached (either *unattached* or *both*). Large corallite sizes can increase the potential for heterotrophic feeding especially in low light conditions where photosynthesis potential is limited (Crabbe & Smith, 2006). Maximum corallite size (cm, log<sub>10</sub> transformed) was included to evaluate the contribution of differences in energy gained through heterotrophic or autotrophic feeding to being found in assemblages beyond reef. Although some coral traits are more plastic than others, we used a single trait value for a species regardless of location, to generalize differences in patterns between hundreds of species.

Trait information was incomplete for 127 of the 535 species included in this study, including the 48 records not identified to species. These were excluded from the following analyses. To assess spatial variability in the distributions of traits, species presence was accounted for in each region (N, PNG-EA, WA), resulting in 1010 observations of the 408 remaining species. In total, 54% of species were found in all three regions while 28% were found in only one.

**Table 2.1.** Coral traits hypothesized to affect the probability of persistence in beyond reef assemblages including the possible values those traits can take after transforming or grouping. Original trait values are shown in parentheses.

| Trait Category               | Coral Trait  | Possible Trait Values  | Potential effect of<br>trait influence                   |
|------------------------------|--|--|--|
| Dispersal                    | Mode of larval development                                   | Brooder<br>Spawner   | Capacity for long distance dispersal                     |
|                              | <i>Symbiodinium</i><br>species in<br>propagules              | 1 (present)<br>0 (absent)  | Capacity for long distance dispersal                     |
|                              | Sexual system  | Gonochoric<br>Hermaphroditic   | Capacity for long distance dispersal                     |
| Environmental                | Depth range, log <sub>10</sub> transformed                   | 0.70 - 2.26<br>(4-150 m)   | Tolerance of low light, temperature                      |
|                              | Water clarity tolerance                                      | Tolerant (turbid, both)<br>Intolerant (clear)  | Tolerance of poor<br>water quality                       |
|                              | Wave exposure tolerance                                      | Tolerant (exposed, broad)<br>Intolerant (protected)  | Tolerance of wave exposure                               |
| Mechanical<br>vulnerability  | Growth form  | Massive<br>Tabular<br>Branching<br>Digitate<br>Encrusting<br>Foliaceous<br>Solitary  | Tolerance of stressful<br>conditions - energy            |
|                              | Substrate<br>attachment                                      | Attached<br>Unattached   | Whether or not<br>individuals attach to<br>substrates    |
| Structural/<br>Physiological | Maximum corallite<br>width, log <sub>10</sub><br>transformed | 0.146 -2.779<br>(0.4 – 600 cm)   | Potential for<br>heterotrophic vs<br>autotrophic feeding |
| Phylogenetic                 | Molecular family   | Acroporidae, Agariciidae,<br>Coscinaraeidae,<br>Dendrophylliidae,<br>Diploastraeidae, Euphylliidae,<br>Fungiidae, Lobophyllidae,<br>Merulinidae, Pachyseridae,<br>Plesiastreidae, Pocilloporidae,<br>Poritidae, Psammocoridae,<br>Siderastreidae | Phylogenetic<br>relatedness                              |

## 2.2.4 Model and model selection

Collinearity among species' traits was assessed visually and quantitatively with generalized variance inflation factors (GVIF). GVIF values were calculated using the "car" package and GVIF<sup>(1/(2\*Df))</sup> evaluated to account for factors with multiple degrees of freedom (Fox & Weisberg, 2011). Traits with large GVIF values relative to a cutoff of 2.5 were sequentially dropped from further analysis due to collinearity. Substrate attachment and corallite size had the largest GVIF values indicating collinearity and were consecutively removed from the model (Table 2.2A-C, Supplementary Figure 2.1). All remaining traits were included in a generalized linear mixed effects model (GLMM) with a binomial response variable (beyond reef = 1, restricted to coral reef = 0) and logit link function, to describe species' traits in assemblages beyond reef accretion.

**Table 2.2.** Calculated Generalized Variance Inflation Factors (GVIF) for each coral trait with degrees of freedom (d.f.) and GVIF<sup>(1/(2\*Df))</sup> provides relative GVIF for factors with more than one d.f. A) All traits evaluated for collinearity. B) Remaining traits evaluated for collinearity after *substrate attachment* was removed. C) Remaining traits evaluated for collinearity after *size* was removed.

| Α.                         |       |      |                     |
|----------------------------|-------|------|---------------------|
| Trait                      | GVIF  | d.f. | $GVIF^{(1/(2*Df))}$ |
| Mode of larval development | 1.250 | 1    | 1.119               |
| Symbiont transmission      | 1.897 | 1    | 1.377               |
| Sexual system              | 1.571 | 1    | 1.253               |
| Depth range                | 1.193 | 1    | 1.092               |
| Water clarity tolerance    | 1.072 | 1    | 1.035               |
| Wave exposure tolerance    | 1.186 | 1    | 1.089               |
| Growth form                | 9.180 | 6    | 1.203               |
| Substrate attachment       | 3.710 | 1    | 1.926               |
| Corallite Size             | 2.654 | 1    | 1.629               |

| В.                         |       |      |                     |
|----------------------------|-------|------|---------------------|
| Trait                      | GVIF  | d.f. | $GVIF^{(1/(2*Df))}$ |
| Mode of larval development | 1.251 | 1    | 1.119               |
| Symbiont transmission      | 1.895 | 1    | 1.377               |
| Sexual system              | 1.555 | 1    | 1.247               |
| Depth range                | 1.192 | 1    | 1.092               |
| Water clarity tolerance    | 1.071 | 1    | 1.035               |
| Wave exposure tolerance    | 1.183 | 1    | 1.088               |
| Growth form                | 3.874 | 6    | 1.119               |
| Corallite Size             | 2.661 | 1    | 1.631               |
|                            |       |      |                     |
| С.                         |       |      |                     |
| Trait                      | GVIF  | d.f. | $GVIF^{(1/(2*Df))}$ |
| Mode of larval development | 1.231 | 1    | 1.109               |
| Symbiont transmission      | 1.310 | 1    | 1.145               |
| Sexual system              | 1.410 | 1    | 1.188               |
| Depth range                | 1.191 | 1    | 1.091               |
| Water clarity tolerance    | 1.074 | 1    | 1.036               |
| Wave exposure tolerance    | 1.150 | 1    | 1.073               |
| Growth form                | 1.994 | 6    | 1.059               |

Common traits shared among phylogenetically related species were accounted for by including species' molecular family as a random factor with a model intercept offset. All remaining traits and biologically meaningful trait interactions were included as fixed effects. Region of occurrence (N, PNG-EA, WA) and region and trait interactions were also included as fixed effects to quantify any underlying differences among regions. Analyses were performed using the *glmer* function from the "lme4" package (Bates *et al.*, 2014). Model selection was conducted with a best subset modelling approach by comparing AIC values of all possible candidate models. The final reduced model with the lowest AIC described coral traits that best characterize beyond reef species. Diagnostic plots of model fit were visually inspected for homogeneity, normality and independence. The independent contribution of each trait to the final model total variance explained was quantified with the "hier.part" function and package (Walsh & Mac Nally, 2013).

## 2.3 RESULTS

## 2.3.1 Species richness

Overall, coral species richness is greatest in the N region (459 total species) compared to PNG-EA (395 species) and WA (351 species). Species richness patterns varied by latitude, region and reef accretion (Fig. 2.2, Table 2.2). The latitudinal attenuation of corals was greater beyond reef compared to coral reef (Table 2.2, reef\*lat interaction) and richness beyond reef in PNG-EA and WA were significantly less than richness beyond reef in N (Table 2.2, reef\*region interaction) where richness declined between 35% and 73% in all regions beyond the coral reef boundary.



**Figure 2.2.** Coral species richness per site (coral reef or beyond reef) with fitted model predictions through the Indo-Pacific by latitude and region. Latitude is measured as the absolute value of the center latitude of the sites surveyed (Fig. 2.1) in the North (N), Papua New Guinea to East Australia (PNG-EA) and West Australia (WA).

**Table 2.3.** Results of the negative binomial regression capturing species richness gradients in three regions in relation to latitude (lat) and reef accretion (coral reef or beyond reef). Interaction terms are indicated by \*.

| Coefficients                                    | Estimate | SE    | z-value | <b>Pr</b> (>  <b>z</b>  ) |
|---|----------|-------|---------|---------------------------|
| Intercept                                       | 6.594    | 0.298 | 22.160  | < 0.001                   |
| <b>Reef</b><br>Coral reef                       |          |       |         |                           |
| Beyond reef                                     | 6.302    | 1.139 | 5.532   | < 0.001                   |
| Latitude  | -0.036   | 0.011 | -3.321  | 0.001                     |
| <b>Region</b><br>N                              |          |       |         |                           |
| PNG-EA  | -0.602   | 0.204 | -2.953  | 0.003                     |
| WA  | -0.673   | 0.207 | -3.256  | 0.001                     |
| <b>Reef*Latitude</b><br><i>Coral reef * lat</i> |          |       |         |                           |
| Beyond reef * lat                               | -0.220   | 0.035 | -6.353  | < 0.001                   |
| <b>Reef*Region</b><br>Beyond reef * PNG-EA      | -1.016   | 0.304 | -3.343  | 0.001                     |
| Beyond reef * WA                                | -1.422   | 0.289 | -4.916  | < 0.001                   |

### 2.3.2 Coral traits

Species traits associated with reef corals beyond reef include region, depth range, water clarity tolerance and growth form (Table 2.4). Total model variance explained by fixed factors (marginal  $R^2$ ) was 18.6% and by fixed and random factors (conditional  $R^2$ ) was 31.1%. Within each region, the proportion of species found on coral reefs with ranges that extend beyond reef varied. Along the N gradient, 43% of species were found beyond reef, 33% in PNG-EA and 15% in WA. Depth range was the only trait that had a significant interaction with region. Beyond reef species in N and PNG-EA had a larger depth range on average than coral species restricted to reefs. The opposite pattern was found in WA. Species

beyond reef also tended to be more tolerant of turbid water conditions. Encrusting, tabular and massive growth forms were more likely to occur beyond reef, while branching and solitary growth forms were least likely. Region had the greatest independent contribution to the explained model variation (49%) followed by growth form (40%), depth range (8%) and tolerance to water clarity (3%) (Table 2.4). Mode of larval development, *Symbiodinium* species in propagules and sexual system were not included in the final model as none were significantly associated with an increased probability of being found beyond reef.

**Table 2.4.** Results of the generalized linear mixed effects model for describing coral traits for corals in communities beyond reef compared to on coral reefs and the independent contribution of each factor to the model total variance explained. All coral traits and region of occurrence (North (N); Papua New Guinea-East Australia (PNG-EA); West Australia (WA)) were included as fixed effects and coral family (n=15) was included as a random factor. Interactions of terms are indicated by \*.

|   | AIC      | Log<br>likelihood | Deviance |                 |
|---|----------|-------------------|----------|-----------------|
|   | 1160.43  | -566.22           | 1132.43  |                 |
| Random Effect                           | Variance | SD                |          |                 |
| Family Intercept (n=15)                 | 0.596    | 0.772             |          |                 |
|   |          |                   |          | Contribution of |
| Fixed factors                           | Estimate | SE                | z-value  | variance        |
| Intercept                               | -2.925   | 0.781             | -3.748   |                 |
| Region<br>N                             |          |                   |          | 48.8%           |
| PNG-EA                                  | 0.986    | 0.9856            | 1.000    |                 |
| WA                                      | 1.9934   | 1.159             | 1.720    |                 |
| Growth Form<br>Massive                  |          |                   |          | 39.8%           |
| Tabular                                 | 0.157    | 0.427             | 0.367    |                 |
| Encrusting                              | 0.101    | 0.268             | 0.377    |                 |
| Digitate                                | -0.190   | 0.334             | -0.570   |                 |
| Foliaceous                              | -0.588   | 0.259             | -2.272   |                 |
| Solitary                                | -0.986   | 0.459             | -2.148   |                 |
| Branching                               | -1.394   | 0.295             | -4.728   |                 |
| Depth Range (logged)                    | 0.949    | 0.223             | 4.259    | 8.3%            |
| Water Clarity Tolerance<br>Intolerant   |          |                   |          | 3.1%            |
| Tolerant                                | 0.254    | 0.182             | 1.397    |                 |
| Region * depth range<br>N * depth range |          |                   |          |                 |
| PNG-EA * depth range                    | -0.466   | 0.300             | -1.551   |                 |
| WA * depth range                        | -1.122   | 0.355             | -3.158   |                 |
| 71                                      |          |                   |          |                 |

## 2.4 DISCUSSION

While reef-building corals displayed the well-known diversity declines over each of the three main Indo-Pacific latitudinal gradients, we quantified these declines and found between 35% (N) and 73% (WA) decrease in richness associated with the cessation of carbonate reef accretion in each region (Fig. 2.2). Despite regional differences in diversity loss at the reef boundary, the probability of being found beyond reef was strongly associated with traits related to environmental tolerance, i.e. growth form, water clarity tolerance and depth range traits that promote survival in stressful conditions (Table 2.4). In contrast, none of the traits related either to reproduction or dispersal potential were found to be important, suggesting that environmental filtering plays the dominant role in structuring beyond reef coral assemblages. Environmental change is expected to impact species current distributions. Traits provide a more thorough understanding of relationships between species distributions and their current environment. These relationships can thus be incorporated to increase the predictability to changes in species distributions into novel environments as conditions change (Santini et al. 2016). By using trait-based rather than species-based approaches, three species traits capture differences between over 400 species on coral reefs or those found beyond.

## 2.4.1 Traits shared in beyond reef species

Despite little overlap in beyond reef species in all regions (< 7%), these species share traits that are likely to enhance survival beyond reef, including more robust morphologies, higher tolerance to turbid water and the capacity to survive at a greater range of depths, reflecting similar trait patterns of high-latitude assemblages in East Australia (Sommer *et al.*, 2014). In areas where shallow-water reef structures do not dissipate wave energy, massive and encrusting growth forms are less likely to be damaged, dislodged or killed compared to 72
the more vulnerable branching or unattached, solitary species (Dao-ru *et al.*, 2013). Corals tolerant to turbid water may be better adapted to low light conditions or more effective at sediment rejection (Loya, 1976; Veron *et al.*, 2009). Depth range is generally considered a proxy for environmental tolerance because colonies of species with broad depth ranges can live in a greater range of temperature and light conditions. Exceptions to these large-scale patterns can result from the influence of variation in local conditions.

Traits shared by beyond reef species were generally consistent; however, there was a three-fold difference in the proportion of species diversity loss among regions (15%-43%). Differences among regions have likely been affected by bathymetry, sea level fluctuations, and the direction, strength and seasonality of pole-ward currents. For instance, the greatest diversity of corals was found in the N region, where 43% of coral reef species' were also found beyond reef (Supplementary Table 2.2). In this region, bathymetric continuity that enabled coral assemblages to shift with past sea level changes would have been less disruptive to population persistence compared to the other regions that were submerged and re-emerged (Veron, 1995). Additionally, the Kuroshio Current moves the greatest volume of water to the highest absolute latitude of the Western Boundary Currents (Tomczak & Godfrey, 2013) and is strongest during the summer when coral spawning occurs. This northern transport of warm water, stronger than other boundary currents in the IAA, likely contributes to the regional differences in coral diversity and may be responsible for the higher proportion of reef species observed beyond reef. Conversely, the weakest pole-ward flowing current is the shallow Leeuwin Current (LC) in WA, which sits atop a strong equator-ward undercurrent (Tomczak & Godfrey, 2013). In this region, only 15% of species were found beyond reef (Supplementary Table 2.2) and this subset had a smaller average depth range compared to species restricted to reef. A potential explanation for this pattern is that two of the four species with the largest depth ranges (Leptoseris hawaiiensis, Echinophyllia aspera; Supplementary

#### Coral traits in beyond reef assemblages

Table 2.2) were found beyond reef in the N and PNG-EA regions but not in WA. This may be due to differences in oceanographic conditions, environmental filters that have not been accounted for, an artifact of fewer total species present in WA therefore a lower probability of occurrence beyond reef, or species with larger depth ranges may have been present but were not observed by Veron (1993). Variable hydrodynamic forces, seasonal fluctuations and poleward extent of major currents likely dominate differences in overall diversity and proportion of species beyond reef in all regions, regardless of species' traits.

## 2.4.2 Limitations and exceptions

Successful establishment beyond reef could additionally be influenced by traits not included in these analyses. For example, evaluating the contribution of growth rate, generation time, or skeletal density to successful establishment beyond reef can suggest whether faster growth, faster reproduction or additional skeletal strength is advantageous in these environments. However, limited trait information available for a large number of species prohibited further investigation of these traits in this study. Another potential limitation of our analyses was that we included global estimates of species' traits, which are assumed to be true of all individuals for each species throughout the Central Indo-Pacific. Trait plasticity that varies from global estimates can provide an advantage to individuals in different environments (Todd, 2008). Colonies of many species develop more robust morphologies in subtropical environments to better cope with physical stress of wave energy (Veron *et al.*, 2009). For example, many species with a tabular morphology in the tropics, such as *Acropora hyacinthus*, form side attached plates in the sub-tropics (Veron, 1995) supporting the results that tabular corals are the most likely growth forms to be found beyond reef (Supplementary Table 2.2).

Biotic and abiotic processes acting at scales smaller than these regions can also result in exceptions to the patterns in traits observed. The environment varies greatly within these regions, influencing the local species' assemblage. For example, while traits associated with dispersal were not associated with beyond reef coral species they can be important biogeographically. For instance, coral assemblage structure on Lord Howe Island is dominated by brooding corals, possibly because the rapid development of larvae is the key to successful population establishment on this isolated coral reef (Keith et al., 2015). In contrast, the distances between reefs along the latitudinal gradient we examined are not sufficient to provide a barrier to dispersal in species, such as coral, that have long lived larvae (Graham et Additionally, biotic interactions such as varied predator distributions or al., 2008). competition for space, especially with macroalgae, shape communities not captured by the regional patterns we evaluated (Johannes et al., 1983). While these analyses capture coral traits for over 400 species, additional detail provided by species abundance rather than presence-absence data, in addition to spatial climate velocities (Burrows et al., 2014), more specific environment-trait relationships (Jamil et al., 2013), and biotic interactions (Wisz et al., 2013) would also increase our understanding of these patterns among traits and their relative influence.

As sea surface temperatures increase pole-ward, higher latitudes may become more favorable for corals and have been suggested as a refuge from increased temperatures in the tropics (Glynn, 1996). However, a simultaneous decrease in aragonite saturation is projected to result in less overall reef accretion (Kleypas *et al.*, 2001; Guinotte *et al.*, 2003). Given these anticipated changes, more coral assemblages are likely to become non-reefal. Whether corals expand their ranges into higher latitudes where reefs do not accrete or net accretion decreases in the tropics, those corals with traits that enhance environmental tolerance will be more likely to persist and dominate the assemblages. These results highlight that the subset of

#### Coral traits in beyond reef assemblages

corals found at high latitudes and beyond reef growth are a non-random subset of those on coral reefs that share characteristics promoting environmental tolerance. As complex environmental changes occur, evaluating species traits associated with corals beyond reef globally provides a deeper understanding of the processes shaping assemblages near range edges and how they may be affected with environmental change.

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# SUPPORTING INFORMATION



**Supplementary Figure 2.1.** Pairwise plot of all coral traits to visually inspect collinearity. DR: Depth range; RM: Reproductive mode; ST: Mode of algal symbiont transmission; SS: Sexual system; WC: water clarity tolerance; WE: wave exposure tolerance; GF: Growth form; SA: substrate attachment; CW: Corallite width. Additional descriptions about each trait are provided in the main text and Table 2.1.

#### Coral traits in beyond reef assemblages

**Supplementary Table 2.1.** Coral occurrence records from Veron, 1993. "Original.species" are the species names from Veron,1993. "Revised.species" are the updated "Original.species" names based on WoRMS. Empty "Original.species" cells have only a "Revised.species" name that results from the combination of the preceeding species where names were synonomized and occurrence records were combined per site. Presence of species in each site indicated by 1 and absence indicated by 0. Available in: https://drive.google.com/file/d/0BylGCGgyr79mcG5UTXhwaUdSRms/view?usp=sharing

**Supplementary Table 2.2.** Traits included in analysis matched with coral occurrence records. "Original.species" are the original species names from Veron 1993. "Region" is the region of occurrence for that species, North (N), Papua New Guinea-East Australia (PNG-EA), West Australia (WA). "Response": 1=present on coral reef and beyond reef, 0=present only on coral reef, NA indicates presence beyond reef but not on coral reefs. All responses are per region. All traits were downloaded from the Coral Trait Database and transformed as described in the main text. Available in: https://drive.google.com/file/d/0BylGCGgyr79mcG5UTXhwaUdSRms/view?usp=sharing

CHAPTER 3

# CORAL DISTRIBUTION PATTERNS ALONG

# ENVIRONMENTAL GRADIENTS REVEALED THROUGH

# SPECIES TRAITS

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# ABSTRACT

Observations of coral distributions have frequently recognized environmental controls (temperature, depth and turbidity) on coral growth, and tolerances of these factors have been established for individual species. Coral zonation patterns have described associations between species assemblages and particular habitats (such as lagoons and reef slopes dominated by different species assemblages). These approaches have provided valuable information but lack an integrated, systematic way to explicitly link environmental constraints with species distributions. Species traits provide information on functional responses to environmental conditions. Here we incorporated coral traits into a distribution model for multiple species in northeast Australia. We evaluated how three coral traits (growth form, corallite size, depth range) modulated responses to gradients of three environmental factors (light, wave energy, temperature variability) hypothesized to shape coral assemblages. The strength and direction of each of these relationships revealed how traits modulated responses to the environment. The strongest response between species depth range and temperature variability was positive and precise based on subsets of test species. The weak responses between branching growth form and light was negative and imprecise. Trait-environment responses quantify which are more influential in coral distributions. Species distribution models that incorporate the explicit influence of species traits provide a means to more accurately predict how distributions may shift with projected environmental change.

# 3.1 INTRODUCTION

There is a long history of observations of relationships between reef building coral distributions and the environment. Early studies suggested that broad-scale coral distributional limits were associated with temperature, light and depth (Darwin, 1842; Dana, 1843). Reef-scale zonation patterns recognized more complex environmental control on species, which corresponded to interacting gradients in light, sedimentation, depth and water motion (Wells, 1954; Goreau, 1959; Done, 1983; Huston, 1985). (Wells, 1954) suggested that, based on species-level differences in environmental tolerance, the physical environment is central to shaping distributions and thus assemblage structure reflected in zonation patterns. Studies of coral distributions have demonstrated the importance of environmental constraints, but have rarely quantified the relationships between multiple species and large-scale environmental gradients.

Species distribution models (SDMs) have become widely adopted as powerful tools for improving our understanding of the relationship between the distribution of species and their environment (Guisan & Thuiller, 2005; Elith & Leathwick, 2009). SDMs provide ecological and evolutionary insights, but are also used to predict distributions across landscapes for conservation planning and management (Franklin, 2010). Recent advances in techniques have increased the use and application of SDMs (Zimmermann *et al.*, 2010). For instance, rather than evaluating single species distributions individually, multi-species distribution models test for similarities in responses among species to environmental variables (Ovaskainen *et al.*, 2010). By extending multi-species approaches to include functional traits, the key mechanisms that lead to species distributions can be inferred, because traits provide information on functional variation between species (Pollock *et al.*, 2012). While SDMs in marine systems are rare compared to in terrestrial systems, there is tremendous opportunity to utilize these methods to improve our understanding of marine species distributions (Robinson *et al.*, 2011). For example, associations have been tested between species traits and coral distributions in environments affected by disturbances by mapping objects in joint ordination (Rachello-Dolmen & Cleary, 2007). However, multispecies distribution models with parameters that vary by species to explicitly describe the influence of traits on those parameters have not yet been evaluated for corals in their typical environment.

Quantitative assessments of coral distributions patterns are lacking, particularly where diversity is high. Nearly 500 species of scleractinian corals are distributed across northeastern Australia and the Great Barrier Reef (GBR) (Veron *et al.*, 2015). Zonation patterns or patterns across individual reefs have primarily been based on common species because of high diversity (Sheppard, 1982). Done (1982) qualitatively described cross shelf distributions of corals in the central GBR. In this study, community types were described by the dominant species and classified into zones across a general framework of coarse physical environments (*i.e.* water motion and light gradients, slopes and lagoons, substrate type). By classifying species with assumed similar functional responses, the specific processes shaping species' distributions were difficult to infer (Done, 1982). Rather, a species-level trait approach provides a quantitative mechanism to describe multispecies distribution patterns across environmental gradients.

Coral traits shared amongst species within habitats reflect a variety of characteristics that provide an advantage to specific environmental conditions (Van Woesik, 2002). In addition, how species traits change over environmental gradients reveal certain functional trade-offs (Cornwell & Ackerly, 2009; Ben-Hur *et al.*, 2012). For example, a transition from branching to massive colony growth forms has been observed with increasing hydrodynamics stress; however, the transition is nearly opposite (*i.e.* from massive to branching) along gradients of increasing light. (Chappell, 1980). Similarly, the corallite morphology surrounding the coral polyp has been linked to environments that vary in light exposure and

sedimentation, which influence distribution patterns. In high light conditions where photosynthesis is optimized, a larger corallite can increase the exposure of live polyp tissue to harmful UV radiation. However, in low light conditions, small, compact corallite sizes may be beneficial if photosynthesis potential is increased (Hughes 1987). Though, larger corallites may also optimize heterotrophic nutrition where light is limited (Crabbe and Smith 2006; Todd et al. 2004). Species that can occupy deeper habitats are subjected to reduced light availability and lower temperatures but are offered refuge from high hydrodynamic stress at the surface (Lesser et al. 2009). Therefore, corals with large depth ranges are assumed to be tolerant of variable environmental conditions, which can contribute to broader distributions (Keith et al., 2013; Keith et al., 2015). These three coral traits (i.e. colony growth form, corallite size and depth range) provide an advantage in a particular environmental condition. While many trait – environment relationships have been described in isolation (i.e. growth form and hydrodynamic stress), the simultaneous influence of multiple trait - environment relationships on species distributions has not been evaluated. Quantifying how multiple coral traits are distributed across multiple environmental gradients and how those relationships interact would result in a clearer understanding of the mechanisms that shape species distributions and which are more influential.

Our goal was to use existing observations of coral distributions over a large-scale environmental gradient (Great Barrier Reef to Northern New South Wales) to evaluate the influence of multiple coral traits in shaping distributions across multiple environmental gradients. In doing so, we simultaneously model multiple species distributions where parameters vary by species to quantify the influence of traits on responses to environmental factors. Specifically, we focused on three environmental variables (wave energy, sea surface temperature [SST] variability and light) and several species traits that have been hypothesized to respond to these variables and for which sufficient trait data were available (growth form, corallite size and observed depth range for each species). Finally, we make predictions about species probability of occurrence across environmental gradients based on the modelled traits. We discuss how this approach can be used to support predictions of changes in coral distribution with projected climate change; in particular, how non-uniform change in environmental conditions (e.g. increased SST but no change in light availablility at higher latitudes) may impacts species distributions.

## 3.2 MATERIALS AND METHODS

#### 3.2.1 Species occurrence

Scleractinian coral distribution data from the monograph series "Scleractinia of Eastern Australia" were downloaded from the Atlas of Living Australia (ALA; http://collections.ala.org.au). The coral occurrence records from this dataset were based on observations across northeastern Australia across the Great Barrier Reef and south to Northern New South Wales. Additional coral occurrence records exist for northeastern Australia; however, we minimize observer bias (*i.e.* consistency in species identification and survey effort) by restricting occurrence records to this dataset. A total of 329 species were recorded at 225 sites from 1975-1983. Observations at each site defined by latitude and longitude were assumed to be exhaustive, so that species not recorded were categorized as absent. Species identification from ALA records was revised to current names based on World Register of Marine Species (WoRMS, 2015).

A small number of species relative to the number of sites surveyed was essential to reduce the potential for correlation between species due to biotic interactions at sites (Wisz et al. 2013). Therefore, we selected a subset of 14 zooxanthellate corals from the 329 species recorded. The species were restricted to either branching or massive growth forms only to most effectively capture strong patterns in responses to environmental gradients. Due to the 89

limited number of species in the subset, we selectively included seven of 49 branching species and seven of 115 massive species that represent a range of corallite width and depth range trait values (Table 3.1).

**Table 3.1.** Frequency of occurrence and summary statistics of massive and branching species traits and species trait values plus summary statistics for the species subset included in the model. Growth forms are either branching (BRA) or massive (MAS). Corallite size is the maximum corallite width observed for a species. Depth range represents the difference between the maximum lower depth and minimum upper depth that each species has been observed. All trait values were accessed from the Coral Trait Database.

|                                 | No. of sites present | Growth form     | Corallite  | Depth     |
|---------------------------------|----------------------|-----------------|------------|-----------|
|                                 |                      |                 | width (cm) | range (m) |
| Range of all species            | 1-46                 | 115 MAS, 49 BRA | 0.5-370    | 4-90      |
| Average of all species          | 18                   |                 | 25         | 31        |
| Median of all species           |                      |                 | 5          | 29        |
| Acropora aspera (A.asp)         | 12                   | BRA             | 1.8        | 15        |
| Acropora austere (A. aus)       | 26                   | BRA             | 1.5        | 40        |
| Acropora lutkeni (A. lut)       | 26                   | BRA             | 1.2        | 26        |
| Alveopora catalai (A. cat)      | 10                   | BRA             | 4.1        | 30        |
| Coscinaraea columna (C.col)     | 18                   | MAS             | 6          | 30        |
| Goniastrea retiformis (G. ret)  | 11                   | MAS             | 6.5        | 20        |
| Goniastrea stelligera (G. ste)  | 20                   | MAS             | 5.1        | 40        |
| Montipora foveolata (M. fov)    | 20                   | MAS             | 2.9        | 25        |
| Pocillopora damicornis (P. dam) | 20                   | BRA             | 1          | 55        |
| Porites australiensis (P. aus)  | 30                   | MAS             | 1.4        | 50        |
| Porites lutea (P. lut)          | 26                   | MAS             | 1.3        | 70        |
| Porites nigrescens (P. nig)     | 12                   | BRA             | 1.6        | 20        |
| Sandalolitha robusta (S. rob)   | 19                   | MAS             | 4.6        | 21        |
| Stylophora pistillata (S. pis)  | 23                   | BRA             | 1.4        | 65        |
| Range of model species subset   | 12-30                | 7 MAS, 7 BRA    | 1.0-6.5    | 15-70     |
| Average of model species subset | 20                   |                 | 3          | 38        |

### 3.2.2 Coral traits

Coral traits were downloaded from the Coral Trait Database (Madin *et al.*, 2016). We included coral species typical colony growth form observed globally. Each growth form (*i.e.* massive or branching) was represented as a unique trait with a binary response to assess how the presence or absence of each growth form modulated responses to the environment. Corallite size was included as the species maximum corallite width observed. Depth range was calculated as the difference between species maximum lower depth and minimum upper depth observed globally and included per species. Each of the selected species was present at 12 to 30 sites and 133 of the 225 sites contained at least one of these 14 species (Table 3.1).

## 3.2.3 Environmental factors

Ocean temperature, light, wave energy, water quality and substrate are primary environmental factors that shape coral distributions globally (Veron, 2000). Gradients of temperature, light and wave energy that vary across large spatial scales were selected to determine how coral traits influence broad distributions across these factors.

## 3.2.3.1 PAR

We included estimates of photosynthetically active radiation (PAR) (Einstein/(m<sup>2</sup>/day)) at the ocean surface to describe the light available for photosynthesis across the latitudinal gradient. Data was accessed from the Ocean Productivity web site (http://www.science.oregonstate.edu/ocean.productivity /index.php) based on SeaWiFS R2010.0. Average monthly PAR measurements from 1998-2007 during the Austral winter (June and July) were used to capture minimum PAR available. Grid spacing is 1/12 of a degree where all latitude and longitude locations are designated for the center of a grid cell. PAR values were extracted for all latitude and longitude coordinates where a coral occurrence

was recorded. The average Austral winter PAR ranged from 24-38 Einstein/ $(m^2/day)$  in locations where corals occurred (Fig. 3.1a).

#### 3.2.3.2 SST variability

Sea surface temperature and PAR are highly correlated and therefore cannot both be used in this analysis to differentiate how coral traits modulate responses to these environmental factors. However, decreased diversity and abundance has been associated with environments that experience large temperature fluctuations (Hennige *et al.*, 2010). Thus, we included SST variability rather than SST in the analysis, measured as the coefficient of variation for mean monthly time series to investigate how coral traits modulate responses to temperature fluctuations.

Sea surface temperature variability was obtained from the Coral Reef Temperature Anomaly Database (CoRTAD), second version. SST measurements were available from weekly recordings at approximately a 4km resolution and are derived from the Advanced Very High Resolution Radiometer (AVHRR) sensor. The coefficient of variation for mean monthly time series (*i.e.* "SST variability") from 1982-2008 was calculated (Maina *et al.*, 2011). SST variability values were extracted for all latitude and longitude coordinates of coral records. Where corals were recorded in the study location, the unitless SST variability ranged from 1.56-2.72 (Fig. 3.1b).

#### 3.2.3.3 Wave energy

We included mean wave energy (E) (J m<sup>-2</sup>) at each site calculated as:

$$E = \frac{1}{16} \rho g H_s^2$$

Where  $\rho$  is water density (1025 kg m<sup>-3</sup> for sea water), g is acceleration due to gravity (9.81 m s<sup>-2</sup>), and  $H_s$  is significant wave height, which is the mean wave height of the highest 1/3 of waves and is a common wave for wave height to be measured and modelled. Mean  $H_s$  for each site was obtained from a combination of satellite altimeter data and wave buoys.  $H_s$ between 10 °S to 24 °S and from 143 °E to 156 °E (where 102 out of 133 sites were located) was obtained from satellite altimeter data spanning 1992 to 2008 (described by (Gallop et al., 2014). A wave energy map was generated by block-averaging  $H_s$  within 20 km by 20 km cells, where the number of observations per cell ranged between 0-2159. For coral records within a cell where satellite altimeter tracks did not pass, wave energy measurements were interpolated from the surrounding cell where distances to the closest cell ranged from 1-14 km. For seven coral sites poleward of 24 °S, wave buoys in Brisbane, Byron Bay and Coffs Harbour were used to estimate wave energy using Eq 1. Significant wave heights from these buoys were accessed from: https://www.qld.gov.au/environment/coasts-waterways/beach/ waves-sites/brisbane/ (Brisbane) and http://new.mhl.nsw.gov.au/data/realtime/wave/Latest (Byron Bay and Coffs Harbour). The distance between the wave buoy in Byron Bay and coral occurrences was 17 km. The distances between the Brisbane and Coffs Harbour wave buoys and six coral occurrence sites range from 22-64 km. These distances are farther than those used to calculate wave energy from altimeter tracks; however, we feel that these estimates are sufficient for these analyses and approximate the nearest wave energy values from altimeter tracks. Twenty-four sites were beyond where altimeter tracks passed or were greater than 500km from wave buoys and were therefore excluded because wave energy could not be determined confidently. It must be emphasized that we used mean wave energy only, and did not consider temporal variability, direction, and extreme events such as cyclones that impact coral distributions (Harmelin-Vivien, 1994). The total range of wave energy in the study area where corals were observed was 290-8190 J m<sup>-2</sup> (Fig. 3.1c).



**Figure 3.1.** Gradients of three primary environmental factors that influence coral distributions across the study area in northeast Australia. 1a) Winter PAR (Einstein/(m<sup>2</sup>/day); 1b) SST variability; 1c) Wave energy (J m<sup>-2</sup>). Coral occurrence locations are plotted on top of gradients of Winter PAR (a) and SST variability (b). Satellite altimeter tracks used to calculate average wave energy are indicated by dotted lines on top of wave energy gradient (c) and are solid where tracks overlap.

#### 3.2.4 Analyses

Continuous traits (corallite size and depth range) and all environmental variables were  $log_{10}$  transformed to improve normality of model residuals. These variables were also centered on zero and scaled to more easily interpret relative differences between model coefficients.

Species' responses to environmental gradients were modeled with a hierarchical modeling approach that combined a species distribution model with species traits using the multispecies model (*msm*) function from the msmod package (Morris, 2016) using R statistical software (R Development Core Team, 2015). The response variable was a binary factor of presence (1) or absence (0) of each species at each location where environmental data were available. There were a total of 1526 observations of 14 species at 109 sites. 94

Observed presence or absence of each species per site was modeled by each environmental factor and all possible interactions of each environmental factor and trait. The multispecies model included species as random effects where slope and intercept parameters were allowed to vary for each.

## 3.2.5 Model evaluation

The model to assess the role of three coral traits in species distributions was evaluated for overall model fit and discriminatory capacity to determine whether the model is acceptable for its intended use (Rykiel 1996). Model fit was measured by determining the proportion of variance explained by fixed factors alone as well as by fixed and random factors combined (Nakagawa & Schielzeth, 2013) using the *sem.model.fits* function in the piecewiseSEM package (Lefcheck, 2015). The discriminatory capacity of the model was determined by calculating the area under the receiver operating characteristic (ROC) (Robin *et al.*, 2011).

The influence of species traits on coral distributions was evaluated by partial trait contributions to species partial responses to each environmental variable. Responses indicated how corals on average are distributed along environmental gradients according to traits as well as how each species varied in response. The strength and direction of each traitenvironment relationship allowed relative comparisons of the relationships for all species included. Model predictions based on model output were also used to estimate the probability of occurrence per species, given their traits, at each site. The probability of occurrence across each environmental gradient was visualized for species to compare variability in responses.

## 3.2.6 Model testing

The way in which coral traits were found to modulate responses to environmental gradients was evaluated with five random subsets of test species. We randomly selected unique subsets of 14 coral species from the same ALA dataset to evaluate the same trait-environment relationships at the same 109 sites. Test species were similarly restricted to those with either massive or branching growth forms for equal comparison. Therefore, each random subset was composed of seven species from the 49 branching species and seven species from the 109 massive species. Environmental parameters for all test coral occurrence locations were extracted in the same way as for model species. All analyses were carried out for test species using the same methods described above. Consistency in coral trait-environment relationships was evaluated by comparing the strength and direction of the responses between the 14 model species and each of the five random subsets of 14 test species.

# 3.3 RESULTS

The overall variance explained by both fixed and random effects was 16% and explained variance by only the fixed effects was 6.5%. The area under the ROC curve was 0.6878. The average species with mean trait values would have approximately 16% probability of occurrence given average environmental conditions ( $\mu$ = -1.69 ± 0.13 (logit scale)).

#### 3.3.1 How coral traits modulate responses to the environment

There were nine trait and environment responses evaluated. Each of the coral traits modulated responses to the environment with variable strength. The average response of each species to each environmental variable was summarized visually (Fig. 3.2). Species

prevalence intercepts and environmental response intercepts indicated departure of species from their expected environmental responses given their traits.



**Figure 3.2.** Species prevalence intercepts and species response intercepts to each environmental factors: Wave energy, SST variability and PAR. Species response intercepts indicate deviation from the expected average environmental response given their traits. Refer to Table 3.1 for species identification.

The three strongest responses were between depth range and SST variability, corallite size and PAR and corallite size and wave energy (Fig. 3.3; largest absolute value of trait coefficients). The larger depth range that a species has been observed to occupy had a positive

response to SST variability as indicated by the largest, positive trait coefficient (Fig. 3.3). The larger a species maximum corallite size, the more negative the response that species has to both wave energy and PAR (as indicated by large negative trait coefficients; Fig. 3.3). The trait coefficient for the response of depth range to wave energy was the closest to zero suggesting weak to no response between this trait and environmental factor (Fig. 3.3). Overall, all trait-environment responses were highly variable as indicated by standard errors.

The analysis only included branching and massive growth forms, therefore the response of each growth form to each environmental factor was relative to the other growth form. Branching corals had a more positive response to SST variability than massive corals. The response of branching corals to wave energy and PAR was more negative than for massive corals (Fig. 3.3).



**Figure 3.3.** Trait contributions to partial responses to environmental factors averaged for all species. Trait coefficients describe relative differences of how each trait (Branching growth form (GF), 98

Corallite size and Depth Range) modulates responses to each environmental factor (Wave energy, SST variability and PAR). The strongest relationships are indicated by the coefficients with the largest absolute value. The direction of the relationship is indicated by positive or negative coefficient values. Bars represent standard errors around parameter estimates.

The effect size of average trait-environment relationships can be depicted in detail to visualize the extent of trait modulation along environmental gradients (Fig. 3.4). For example, species depth range had the strongest response to SST variability on average (Fig. 3.3). While this trait-environment relationship is positive on average indicating that the probability of occurrence increase with increasing depth range, variability exists in the relationship (Fig. 3.4a). For example, *Alveopora catalai* (*A. cat*) and *Coscinaraea columna* (*C. col*) both have the same depth range; however, *A. cat* had a more positive response to SST variability compared to *C. col* (Fig. 3.4a). Similarly, while the average coral response to wave energy is negative with increasing corallite size (Fig. 3.3), the response for *Montipora foveolata* (*M. fov*) is positive (Fig. 3.4b). Each species had variable responses to wave energy regardless of their depth range so that little to no relationship was detected (Fig. 3.4c). Categorical traits are measured relative to each other. Corals with branching growth forms had a more negative response to wave energy and thus have a lower probability of occurrence in high energy environments compared to corals with massive growth forms (Fig. 3.4d).

Explicit relationships between the probabilities of occurrence for example species were visualized along gradients of each of the environmental factors separately given the three traits evaluated for each species (Fig. 3.5). As wave energy increases, the probability of occurrence for *A. cat* decreases (Fig. 3.5a), the probability of occurrence for *M. fov* increases (Fig. 3.5b) and the probability of occurrence for *P. aus* does not change (Fig. 3.5c). As PAR increases, the probability of occurrence increases for all three of these species (Fig. 3.5d-f). As SST variability increases, the probability of occurrence for *A. cat* increases (Fig. 3.5g) and

the probability of occurrence for *M. fov* and *P. aus* decreases, though the relationship for *P. aus* is weak (Fig. 3.5h).



**Figure 3.4.** Partial responses of effects of traits by environmental variables. a) Partial response to SST variability explained by depth range. b) Partial responses of all species to wave energy by corallite size. c) Partial responses of all species to wave energy explained by depth range. d) Partial responses to wave energy whether a species growth form is massive or branching. Corallite size and depth range were scaled and centered on zero as described in the text for ease of comparison. Violin plots indicate variability of species responses. Grey ribbons are 95% confidence intervals representing the uncertainty of average responses for all species.



**Figure 3.5.** Examples of three species (*A. cat, M. fov, P. aus*) probabilities of occurrence based on model output along environmental gradients of wave energy (a-c), average winter PAR (d-f), and SST variability (g-i) given each species respective traits.

## 3.3.2 Model testing

Generally, partial responses of the trait contributions to partial responses to environmental variables for all subsets of test species were similar to patterns for model species and were within model species standard error. However, variability in these responses indicated some dissimilar results. The strongest overall response for original or test species subsets was a negative relationship between branching species and wave energy for one subset of test species (Fig. 3.6; blue test species). Additionally, all five subsets of test species had stronger, positive responses between corallite size and SST variability than for the original model species, which was close to zero (Fig. 3.6). Responses of test species were most precise between depth range and all environmental variables compared to model species. Only three of nine trait-environment responses were consistent in the direction (positive or negative) of responses between the original and all test subsets of species (*i.e.* corallite sizewave energy; corallite size-SST variability; depth range-SST variability). However, many model species responses were closer to zero (*i.e.* depth range-wave energy); therefore, both positive and negative responses of random subsets would be expected.



**Figure 3.6.** The contributions of traits to partial responses to environmental factors for original species subset and tests species subsets. The original model species subset is indicated with black circles and five different random test species subsets are indicated with unique colored triangles. Standard error bars are shown for only the original species evaluated.

# 3.4 DISCUSSION

For the first time, we systematically link coral traits to various environmental conditions for multiple species. Quantified responses of species traits to environmental gradients provide a relative comparison of the strength and direction of various traitenvironment responses. Depth range modulated responses to SST variability with the greatest strength followed by corallite size responses to both wave energy and PAR. Mechanisms governing coral distributions can be inferred from these quantified relationships of how multiple species traits simultaneously relate to multiple environmental conditions. We discuss

how model predictions can be used to recognize how coral distributions, based on species traits may be impacted where environmental conditions are projected to change.

Complex information about trait-environment responses facilitates a more thorough understanding of coral distributions across their environment. Species average responses to environmental gradients vary, regardless of their traits. For example, Montipora foveolata (M. fov) has a positive response to wave energy, a negative response to SST variability and a weak response to PAR (Fig. 3.2). In contrast, Alveopora catalai (A. cat) has a positive response to all three environmental factors that vary in strength (Fig. 3.2). However, the contributions of species traits to responses to these environmental factors, rather than solely species distributions themselves, reveal underlying functional responses. Overall, the strongest trait-environment response was between species depth range and SST variability (Fig. 3.3). Weak responses of depth range to wave energy and PAR were close to zero and indicate that depth range does not modulate responses to either of these environmental variables. In other words, species with large depth ranges do not have strong relationships with environments of either high or low wave energy nor high or low PAR but rather would be associated with environments that vary in any of these conditions. The strong, positive response of coral species depth range to SST variability and weak responses to wave energy and PAR all support the assertion that species with broad depth ranges have broad environmental tolerance and are distributed across variable environmental conditions (Stevens, 1996; Harley et al., 2003; Keith et al., 2015).

Corallite size modulated responses to both wave energy and PAR. These two responses were both negative and strong albeit not as strong as the positive relationship between depth range and SST variability. The corallite size and wave energy response indicates that species with large corallites have negative responses to wave energy. Therefore, species with small corallites may be provided a benefit in environments of high wave energy (Fig. 3.4b and 3.6). Energetic environments may be more tolerable for species with small corallites and thick walls between them, which provides additional structural support (Hughes, 1987). The relationship between corallite size and PAR was also strong and negative. However, Crabbe and Smith (2006) found a positive relationship where small but compact corallites were more likely in light limited areas and suggested this morphology optimized photosynthetic potential. Sommer *et al.* (2014) similarly found that corals at high latitudes, where winter PAR is reduced, were dominated by species with small corallites. Based on the variation of corallite size-PAR responses indicated by test species subsets (Fig. 3.6), this trait-environment response is variable based on subset of species evaluated. The variability in this trait-environment response may instead be due to capacity for heterotrophy because of greater heterotrophic plasticity. Species with large corallites may be better adapted to heterotrophic feeding in low light conditions (Anthony & Fabricius, 2000). Based on the precision in direction of responses between test species subsets (Fig. 3.6), corallite size modulates responses to wave energy and SST variability more so than PAR.

Coral traits help explain patterns of multiple species distributions over a large spatial extent covering approximately 20° latitude and up to 800km offshore. Across this area, there is a strong latitudinal attenuation in light represented by the coarse winter PAR measurements evalauted. The reduced available light at higher latitudes is suggested to limit species poleward range expansion if corals track increased SST associated with climate change (Muir *et al.*, 2015). Our results identify which species, based on their traits, have greater probabilities of occurrence (*i.e. P. aus* compared to *A. cat* or *M. fov*; Fig. 3.5d-f) in novel environments where light is low. However, smaller-scale processes also affect coral distributions across different segments of a reef environment hyperspace and may not have been captured by large scale trends captured here contributing to only a modest amount of variance explained by the model. For example, hydrodynamic energy on a back-reef is

generally lower than the fore-reef, and therefore leads to different coral assemblages (Done, 1983). However, we were not able to capture this level of detail for wave energy across the large spatial extent. Additionally, we used species-level traits, which represent characteristics of all colonies per species. Yet, trait plasticity may have contributed to variation in coral characteristics that proved to be more beneficial within a certain environment (Todd, 2008). For example, in more energetic environments of a reef, colony morphology tends to be less mechanically vulnerable (Madin & Connolly, 2006). Coral species' typical traits explain patterns of species distributions across large environmental gradients; however, reef scale patterns may suggest more specific responses that influence distributions on a local scale.

Multifaceted patterns emerge from responses between three coral traits and three environmental factors. Additional traits may provide useful information along these environmental gradients. The lack of agreement between model and test species subsets reveals that relationships between branching growth form and all environmental factors are quite variable (Fig. 3.6). In fact, the range of morphologies, rather than only massive or branching can benefit a colony in various environmental conditions (Chappell, 1980). Evaluating additional growth forms may better suggest how colony morphology modulates responses to the environment; however, the added complexity may increase the difficulty in interpretation of broad scale patterns. Skeletal density or growth could also indicate how species are distributed across environments by highlighting the environments where increased density or faster growth is beneficial (Risk & Sammarco, 1991; Smith *et al.*, 2007). Coral traits influence on distribution patterns can also be revealed by understanding biotic interactions. For example, corallivores are less likely in high wave energy environments. Therefore, colonies that can withstand strong energy, whether due to shape, size or density traits should be less likely to be preyed upon (Lenihan *et al.*, 2015). Within diverse coral assemblages, multispecies distribution models with parameters that vary by species reveal patterns based on few but important responses of traits to environmental gradients.

The physical environment shapes coral distributions and diversity (Veron, 1995). The trait-environment relationships evaluated provide insight into the role of coral traits that modulate responses to the environment by quantifying which trait-environment responses are stronger than others. In addition, these relationships shed light on the underlying mechanisms that shape species distributions. The strongest trait-environment response between depth range and SST variability, which was consistent across all test species, suggest that coral species with large depth ranges are more likely to be distributed in environments where temperatures are variable. Conversely, the weak relationship of branching growth form to PAR, and where test species responses were both strong positive and strong negative suggest that distributions of massive or branching growth forms are not as clearly associated with PAR. As species distributions are likely to be altered as projected climate change modifies the environment, this trait-based approach across a large extent provides the framework for assessing how environmental change may impact future distributions for multiple coral species due to functional responses. With sufficient environmental change projections, predictions of occurrence based on trait-environment relationships will more confidently predict the types of species, rather than species identification that will persist because of species traits.

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# CHAPTER 4

# VARIATION IN CORAL BLEACHING BY SPECIES TRAITS

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## ABSTRACT

Coral bleaching as a response to increased sea surface temperature is regularly surveyed, but our understanding of species-specific differences is limited. We compiled bleaching response data for multiple warming events in which corals were identified to species — which were surprisingly rare — and quantified the relationship between species' traits and their general bleaching response. Coral family explained more variation between species bleaching responses (11%) than any other trait. Other morphological and physiological traits explained between 6.7% and 10.5% of total model variation; however, the majority of variation was attributed to differences among studies rather than the coral trait. Some relationships between traits and bleaching response (*e.g.* symbiont genotype) vary greatly by study, suggesting that characteristics of the location and/or warming event determine those relationships. Conversely, other traits (*e.g.* family and growth form) describe enough variation in bleaching responses among species to be useful as global indicators. Training bleaching survey teams to identify corals to family, in conjunction with recording colony growth form, would significantly improve the predictive power of coral species responses to warming events.

## 4.1 INTRODUCTION

Coral bleaching is a stress response that results in a breakdown of the relationship between a coral host and its symbiotic algae (genus: *Symbiodinium*) (Hoegh-Guldberg & Smith, 1989; Glynn, 1993; Fitt & Warner, 1995; Brown, 1997). The breakdown is a consequence of a buildup of toxic oxygen radicals produced causing the coral host to expel the symbiotic algae and photosynthetic pigments (Dove & Hoegh-Guldberg, 2006; Van Oppen & Lough, 2008). *Symbiodinium* are essential to coral energy budgets, providing up to 95% of the corals' carbon requirements for growth, reproduction, and maintenance (Muscatine, 1990). As such, the breakdown of this symbiosis threatens coral survival.

Elevated sea surface temperatures (SST) for prolonged periods of time are the most common cause of coral bleaching (Brown, 1997). While thermal stress is the primary cause of bleaching, multiple environmental conditions such as UV exposure, warming duration, timing of SST anomaly, maximum temperature and exposure to previous warming events also contribute to variable bleaching patterns (Glynn, 1993; Glynn, 1996; Podestá & Glynn, 2001; McClanahan *et al.*, 2005). Regardless of all contributing factors, thermally induced coral bleaching events have resulted in high levels of mortality globally (Goreau *et al.*, 2000; Hoegh-Guldberg *et al.*, 2007; De'ath *et al.*, 2012). Under climate change projections, increased ocean temperatures are expected to result in even greater coral mortality in the future (Hoegh-Guldberg, 1999; Baker *et al.*, 2008). Since resource managers cannot control thermal stress directly, efforts to protect corals focus instead on limiting mortality by enhancing resilience (Marshall & Schuttenberg, 2006). However, efforts to enhance resilience rely on understanding variability in bleaching responses. Countless bleaching events have been documented globally, and yet the susceptibility of coral assemblages is still not well understood or predictable.

Varying thermal tolerances complicate our understanding of bleaching response

patterns (Loya et al., 2001; Hughes et al., 2003; West & Salm, 2003). A number of hypotheses have been proposed to explain susceptibility to warming. Both the algal symbiont and coral host influence thermal stress responses as well as molecular interactions between the two (Baird et al., 2009). For example, Symbiodinium genotypes hosted within corals tolerate different types and levels of environmental stressors (Baker, 2001; Oliver & Palumbi, 2011; Fabina et al., 2012). Therefore, the genetic identity and diversity of Symbiodinium can influence bleaching responses. Coral colony surface area also affects bleaching through mass transfer capacity (the exchange rates of gases and metabolites over a colony) (Nakamura & Van Woesik, 2001). Specifically, flat morphologies or small sizes increase the ability to remove toxic oxygen radical buildup and reduce bleaching responses (Loya et al., 2001; Shenkar et al., 2005; Brandt, 2009; Van Woesik et al., 2012). The morphology of the corallite skeleton surrounding the live polyp tissue also affects exposure to UV radiation. Wide corallite structures expose more live tissue to harmful radiation while smaller corallites can protect the tissue, particularly when the corallite structure is deeper (Todd et al., 2004; Crabbe & Smith, 2006). Intraspecific differences in coral colony susceptibilities observed also suggest that susceptibility is not solely species specific (Glynn, 1984; Hoeksema, 1991). Not only are increased SSTs expected to increase coral mortality but also varying tolerances are likely to result in an additional loss of diversity (Walther et al., 2002).

Coral bleaching surveys have provided the framework for understanding the extent of responses to numerous warming events. However, inconsistency in survey methods has complicated comparisons of effects. Some surveys have measured the total proportion of colonies bleached (Jiménez *et al.*, 2001; Stimson *et al.*, 2002; Oxenford *et al.*, 2008), while others have measured more detailed intra-colony levels of severity (Marshall & Baird, 2000; Bruno *et al.*, 2001). Species-specific surveys provide detailed information about responses; however, they are rare because they are time and cost intensive. Therefore, surveys have

described responses by growth form (Loya *et al.*, 2001; Gilmour *et al.*, 2013), colony size (Shenkar *et al.*, 2005; Brandt, 2009) or taxa, typically identified by family or genera but rarely by species (Gleason, 1993; Marshall & Baird, 2000; McClanahan *et al.*, 2004). Due to its ease in identification, growth form has been widely accepted by a number of organizations (*e.g.* GBRMPA, Reef Check Australia, Eyes of the Reef Network, Florida Keys Bleach Watch, Coral Watch) to categorise bleaching responses and describe response patterns by less trained observers. However, without the capability to compare surveys across multiple events, these provide little support to understand general bleaching responses globally (Van Oppen & Lough, 2008).

To our knowledge, there has not yet been a quantitative assessment comparing how well coral traits, including growth form, relate to bleaching responses. The goal of this paper was to test how well a range of morphological and physiological species traits explain variation in coral colony bleaching responses at the onset of bleaching. In doing so, we evaluated if growth form is a good predictor of bleaching intensity, and also if other easy-tomeasure traits can help improve predictive power. Ultimately, we aim to make recommendations to improve the value of survey data, and subsequently improve our understanding of the susceptibility of coral assemblages.

### 4.2 MATERIALS AND METHODS

#### 4.2.1 Bleaching survey data

We collated bleaching data from the literature and monitoring surveys that (1) recorded species-level responses, (2) were conducted within three months of temperatures reaching 1°C above the average summer maximum and (3) reported the number of colonies surveyed to enable comparisons of bleaching across surveys. The final dataset included nine studies that spanned fourteen years and eight locations across the Pacific, Indian, and Atlantic 116

Oceans (Table 4.1). Five of these studies documented responses to the 1997/1998 mass bleaching event in different locations. Each study surveyed between three and 38 sites per location and between four and 22 species. Species names were updated to their most current names using the World Register of Marine Species (WoRMS, 2014)

The bleaching responses of surveyed coral assemblages were measured in three different ways. The first group measured the proportion of colonies that bleached per species (Jiménez *et al.*, 2001; Stimson *et al.*, 2002; Oxenford *et al.*, 2008). The second measured the proportion of colonies per species that fell into predetermined categories of bleaching intensity (*i.e.* pale, partially bleached, moderate, severe) (Marshall & Baird, 2000; Bruno *et al.*, 2001; Neilson, unpub. data). The final group calculated the average proportion of an individual colony's surface area that was affected (*i.e.* pale, partially bleached, fully bleached) (Obura, 2001; Charpentier, 2014).

To standardize surveys, we calculated the bleaching intensity index (BI) outlined by Charpentier (2014):

$$BI = (0.5 * P) + (0.5 * PB) + (1.0 * BL)$$

Where P was the percentage of all colonies (or average proportion of colony surface area) of a given species at a survey site that was pale; PB was the percentage that was partially bleached; and BL was the percentage that was bleached. We grouped categories of bleaching (*i.e.* normal, pale, partially bleached, fully bleached) to match across surveys as similarly as possible (Supplementary Table 4.1). For studies that included only the total proportion of colonies bleached (Jiménez *et al.*, 2001; Stimson *et al.*, 2002; Oxenford *et al.*, 2008), BI was calculated without P and PB. In total, 101 bleaching responses were calculated

for 74 unique species. Some species occurred in more than one survey (Supplementary Table 4.2).

| Study ID      | Warming<br>year | Location                  | Number<br>of species<br>surveyed | Number<br>of sites<br>surveyed | Reference                 |
|---------------|-----------------|---------------------------|----------------------------------|--------------------------------|---------------------------|
| Jiménez       | 1997            | Costa Rica                | 12                               | 5                              | Jiménez et al., 2001      |
|               |                 | Western                   |                                  |                                |                           |
| Bruno         | 1998            | Caroline                  | 5                                | 5                              | Bruno et al., 2001        |
|               |                 | Islands, Palau            |                                  |                                |                           |
| Marshall &    | 1008            | Great Barrier             | 1                                | 4                              | Marshall & Baird,         |
| Baird         | 1990            | Reef, Australia           | 4                                | 4                              | 2000                      |
| Obura         | 1998            | East Africa               | 14                               | 38                             | Obura, 2001               |
| Stimson       | 1998            | Okinawa,<br>Japan         | 4                                | 3                              | Stimson et al., 2002      |
| Charpentier05 | 2005            | Discovery Bay,<br>Jamaica | 12                               | 3                              | Charpentier, 2014         |
| Oxenford      | 2005            | Bermuda                   | 22                               | 6                              | Oxenford et al., 2008     |
| Charpentier10 | 2010            | Discovery Bay,<br>Jamaica | 12                               | 3                              | Charpentier, 2014         |
| Catlin Survey | 2014            | Hawaii, USA               | 16                               | 10                             | Neilson, unpublished data |

Table 4.1. Summary of the coral bleaching surveys included in the analyses.

## 4.2.2 Coral traits

We downloaded coral species-level morphological and physiological traits from the Coral Trait Database that were hypothesized to affect a colony's bleaching response (Madin *et al.*, 2016). Morphological traits included growth form, species maximum colony diameter and species maximum corallite width. We included each species typical colony growth form and reduced the number of growth form categories to five by grouping similar morphologies Table 4.2). The massive grouping included submassive and columnar forms; the branching group included branching open, branching closed and encrusting long uprights morphologies; the digitate group included both digitate and corymbose growth forms; neither laminar nor encrusting were combined with any other growth forms. These categories most closely resemble existing bleaching survey protocol (Supplementary Table 4.3). Colony sizes were

A .....

not reported in most studies included in this analysis. Therefore, we included the species' maximum colony size ( $log_{10}$  transformed) and assume that the maximum size a species can reach has the same approximate ranking as the species' mean size in an assemblage (Table 4.2). The maximum corallite width of a species ( $log_{10}$  transformed) was also included to evaluate whether species with larger corallites tend to bleach more severely because of increased tissue exposure to UV radiation (Table 4.2).

 Table 4.2. Summary of coral traits used to describe patterns of species' bleaching intensity across multiple warming events. Descriptions of each trait and the range of possible values are described.

| Trait                        | Description   | Value range  |
|------------------------------|---|--|
| Growth form                  | Typical growth form of a species globally   | Massive, digitate, laminar,<br>encrusting, branching   |
| Species maximum colony size  | Observed maximum colony diameter of species (logged)  | 2 – 1000 cm<br>(0.6931- 6.9080)  |
| Corallite size               | Observed maximum corallite width of species (logged)  | 1.2 – 170 mm<br>(0.1823- 5.1360)   |
| <i>Symbiodinium</i><br>clade | The presence of Symbiodinium clades A, B, C, D  | 0: Absent<br>1: Present  |
| Symbiodinium<br>diversity    | The total number of <i>Symbiodinium</i> clades (A-D) each species has been observed to host | 1-4  |
| Family                       | Coral molecular family  | Acroporidae, Agariciidae,<br>Astrocoeniidae, Euphylliidae,<br>Fungiidae, Meandrinidae,<br>Merulinidae, Mussidae,<br>Pachyseridae, Plesiastreidae,<br>Pocilloporidae, Poritidae,<br>Psammocoridae, Siderastreidae |

respons

es to warming events have been associated with the genetic identity of *Symbiodinium* hosted within corals. For example, coral colonies in the eastern Pacific containing predominantly *Symbiodinium* clade C bleached more severely than those containing predominantly *Symbiodinium* clade D (Glynn *et al.*, 2001). As such, the presence or absence of each of the 119

four primary *Symbiodinium* clades A-D that have been observed hosted by a coral species were included to evaluate the relationship between each *Symbiodinium* clade and bleaching intensity (Table 4.2). Each *Symbiodinium* clade was treated as a separate trait with a binomial response representing whether each coral species has been documented to host each clade or not (presence = "1", absence = "0").

The Adaptive Bleaching Hypothesis suggested that corals bleach to establish relationships with more thermally tolerant *Symbiodinium* genotypes (Buddemeier & Fautin, 1993; Fautin & Buddemeier, 2004). Therefore, we hypothesized that corals observed to host diverse *Symbiodinium* clades, would be less likely to bleach due to the increased likelihood of a more tolerant symbiont genotype becoming dominant (Berkelmans & Van Oppen, 2006). We included symbiont diversity by summing the total number of *Symbiodinium* clades (A-D) that each species has been observed to host (Table 4.2).

Missing traits values for species were completed where possible based on searches of the literature, reports, surveys, and field guides (Supplementary Table 4.2). *Montastrea* species (*Montastrea annularis, M. faveolata* and *M. franksi*) were difficult to visually identify during surveys conducted by Oxenford (et al. 2008) and therefore were recorded as *Montastrea* complex. We included *Montastrea* complex as one species with average trait values representing the three *Montastrea* species (Supplementary Table 4.2). Additional coral traits that have been suggested to influence bleaching responses but could not be tested here due to lack of complete trait data include but are not limited to: live tissue thickness, growth rate, heterotrophic capacity and the presence of photoprotective pigments (Hoegh-Guldberg, 1999; Salih *et al.*, 2000; Marshall & Schuttenberg, 2006).

#### 4.2.3 Data analyses

Generalized linear mixed-effects models (GLMM) were used to evaluate the relationship between coral species' traits and bleaching intensity. Models were run using the *glmer* function (Hoegh-Guldberg, 1999; Bates *et al.*, 2014) for R (R Development Core Team, 2015). BI was modelled with a binomial link function weighted by the total number of colonies per response.

BI was initially modeled as a function of each coral trait or family separately to evaluate and compare how well bleaching responses vary solely by trait or family. Study was included as a random effect in all models to account for variation among studies (*i.e.* survey type, location, thermal event, etc.) as follows:

#### $BI \sim coral trait + (1|study)$

Akaike information criteria (AIC) was used to evaluate how each of the nine traits individually explained bleaching intensity and provided a relative comparison to other traits. Marginal and conditional  $R^2$  values were also calculated with the *r.squaredGLMM* function (Bartoń, 2013) to determine goodness-of-fit and the contribution of each trait to BI. Marginal  $R^2$  ( $R^2$ <sub>(M)</sub>) describes variance explained by fixed factors and conditional  $R^2$  ( $R^2$ <sub>(C)</sub>) describes variance explained by fixed and random factors (Nakagawa & Schielzeth, 2013). The relative contribution of the random factor (study) as well fixed factors (traits) to goodness-of-fit was also calculated as the percentage of each to total model explained variance ( $R^2$ <sub>(C)</sub>).

Not all coral traits can be easily identified in visual surveys. Therefore, we also compared how combinations of the subset of traits that are easy to measure in the field increase explanatory power as follows:

#### $BI \sim family + growth form + colony size + corallite size + (1|study)$

Traits were tested for collinearity with generalized variance inflation factors (GVIF) (Fox & Weisberg, 2011), which allow an evaluation of categorical variables. GVIF<sup>(1/(2\*df)</sup> values of

each trait were calculated to allow equal comparison between categorical traits with more than one degree of freedom due to the number of categories. Traits with  $\text{GVIF}^{(1/(2*df)}$  values of 2.5 or greater were visually inspected for collinearity and sequentially dropped from the analysis. We then modelled BI with more than one trait by sequentially adding traits to quantify how much more explanatory power was gained with additional information being surveyed. We determined which combination of two and three traits explained most of the variation between species bleaching responses. Relevant interactions of traits (*e.g.* colony size and growth form) could not be evaluated due to the lack of replicate interactions within each study.

## 4.3 **RESULTS**

Each of the nine coral traits individually explained between 6.7% and 11.0% of total model variation (Table 4.3a). The relationship between BI and family had the lowest AIC (1850) and highest  $R^{2}_{(M)}$  (9.6%) and  $R^{2}_{(C)}$  (11.0%; Table 4.3a). The majority of explained model variation (87%) was due to family (Table 4.3a). The model with the next highest  $R^{2}_{(C)}$  (10.5%) was one that evaluated the relationship between BI and *Symbiodinium* clade diversity. However, the majority of overall model fit (84%) was due to differences among studies identified by the random factor and only a very small percentage of model variation was due to the trait ( $R^{2}_{(M)}$ =1.8%). The model with the largest AIC quantified the relationship between BI and *Symbiodinium* clade A where nearly all variation in overall model fit was due to differences in studies (Table 4.3a).

There was evidence of collinearity found between coral family and corallite size (Supplementary Table 4.4a-c). Therefore, these two traits were not included together to evaluate how additional traits increase predictability of bleaching response. Collinearity was

not detected between family, growth form and colony size (Supplementary Table 4.4b) or growth form, colony size and corallite size (Supplementary Table 4.4c).

Of coral traits that can be used in visual surveys to assess bleaching responses, the two that best explain variation between species are family and growth form (Table 4.3b). A model with these two traits together has a lower AIC and greater explanatory power compared to models of either trait individually (Table 4.3a,b). The addition of a third coral trait described slightly more variation in BI relative to two traits (Table 4.3c). Coral family, growth form and colony size together explained the most variation in species BI with the lowest AIC (Table 4.3b).

**Table 4.3.** Model comparison of the contributions of coral traits to BI. Study was included as a random factor in all models and coral traits were included as fixed factors. Models are sorted according to (AIC). Conditional ( $R^2_{(C)}$ ) and the percent contribution of random effect (study) and fixed effect (trait) to ( $R^2_{(C)}$ ) are estimated for each model. A. Individual coral trait contributions to BI. B. Multiple trait contributions to BI. Only the best models to describe variation in BI using two or three traits that are easy to measure in the field are included. The percentage of  $R^2_{(C)}$  explained by random factor (study) is 100%- the percentage of  $R^2_{(C)}$  explained by fixed factor (trait).

| BI ~ Coral Trait                   | AIC  | R <sup>2</sup> (C) | Percentage of R <sup>2</sup> (C)<br>explained by fixed<br>factor (trait) |
|------------------------------------|------|--------------------|--|
| Family                             | 1850 | 0.110              | 87%  |
| Symbiodinium clade D               | 2285 | 0.076              | 17%  |
| Symbiodinium clade diversity       | 2416 | 0.105              | 16%  |
| Colony size                        | 2447 | 0.079              | 8%   |
| Growth form                        | 2537 | 0.088              | 26%  |
| Symbiodinium clade B               | 2690 | 0.067              | <1%  |
| Corallite size                     | 2709 | 0.084              | 8%   |
| Symbiodinium clade C               | 2709 | 0.071              | 3%   |
| Symbiodinium clade A               | 2711 | 0.070              | <1%  |
| Growth form + Family               | 1637 | 0.143              | 90%  |
| Family + Growth form + Colony size | 1554 | 0.149              | 87%  |

## 4.4 DISCUSSION

Bleaching surveys that identify colonies to species are costly and time intensive. Therefore, our goal was to quantify how well bleaching in response thermal events are related to species traits. Differences among locations and warming events captured by the surveys that we analysed were expected to account for the majority of variation in species-level responses. However, despite these local differences, several species traits greatly improved the predictability of bleaching responses across studies globally. Specifically, coral family accounted for the majority of variation explained. By also accounting for colony growth form with coral family, predictability increased. Standardizing bleaching surveys so that both family and growth form information are consistently captured would allow a more accurate comparison of bleaching responses globally regardless of the severity of each warming event. The additional detail could therefore provide necessary information to assist management efforts to enhance coral resilience.

Previous studies have identified relationships between coral bleaching and traits within an assemblage, but so far have mostly focused on one trait at a time. For instance, bleaching responses have often been surveyed by and shown to vary among growth forms (Spencer *et al.*, 2000; Loya *et al.*, 2001). Whereas, in other surveys, variation in bleaching responses were surveyed by, and shown to vary among colony sizes (Obura, 2001; Brandt, 2009). Using a dataset compiled from multiple studies, we have shown multiple traits have likely been used to identify bleaching patterns because no single trait explains more than 11% of the variation in bleaching responses across multiple bleaching events. We were able to simultaneously compare how each coral trait contributed to variation in bleaching responses ( $R^2_{(M)}$ ) across multiple warming events. In addition, we determined the contribution of study differences contributed to variation in bleaching responses given the traits included. Coral family explained variation in bleaching responses across warming events, similarly to

McClanahan *et al.* (2004), more than any other trait. Coral families may share multiple characteristics, some of which could not be accounted for in these analyses that promote resistance, such as metabolic rates, tissue thickness, particular *Symbiodinium*-host specificity, or heterotrophic feeding capacity (Marshall & Baird, 2000; Wooldridge, 2014).

Of all traits tested individually in these analyses, those that contributed the most to explained model variation (highest  $R^2_{(M)}$ ; *i.e.* family group, growth form) were traits that are easy to measure in the field and could be used in visual surveys. However, the large proportion of explained variation in bleaching responses due to studies rather than traits suggest how local effects may contribute to bleaching intensity. Each of the four Symbiodinium clades as well as clade diversity explained between 6.7% and 10.5% of the total model variation. Yet, the added contribution of these traits to overall variation was low and never greater than 17%. Specific symbioses with particular Symbiodinium genotypes can be more beneficial for particular local environmental stressors or conditions (Baker, 2001; Knowlton & Rohwer, 2003; Stat & Gates, 2010). Though, Symbiodinium distribution limitations and host-symbiont specificity may prohibit certain combinations from occurring naturally (Baker, 2003; Fabina et al., 2012). We were only able to evaluate the potential influence of coral symbiont specificity that has been observed historically rather than evaluating the colony specific symbioses. These hypothetical rather than realized relationships are a potential explanation for the majority of model variance explained by different studies. Due to the relatively low  $R^{2}_{(M)}$  compared to  $R^{2}_{(C)}$ , we suggest that Symbiodinium genotypes better describe bleaching responses locally; whereas, family and growth form, both with higher  $R^{2}_{(M)}$ , appear to be better predictors of bleaching responses globally across studies.

Bleaching surveys that include more than one trait increased the predictive power across warming events. By including growth form and family, 14.3% of total model variance

was explained, the majority of which was explained by the traits (90%) rather than differences in studies. Family and growth form together explain 3.3% and 5.5% more variation than either of these traits alone. Information about both of these traits has been suggested to help in describing variable bleaching resistance (Marshall & Schuttenberg, 2006) and occasionally documented (Marshall & Baird, 2000; Loya *et al.*, 2001; McClanahan *et al.*, 2004) but rarely have these been consistently reported in surveys. Three traits that could be included in visual bleaching surveys, family growth form and colony size explained the greatest amount of variation between species ( $R^2_{(C)}$ =14.9%). Increasing survey effort by including additional traits would enhance our understanding of coral bleaching responses; however increased time and cost associated with additional effort may not outweigh information gained.

Traits not considered in these analyses may capture physiological differences in bleaching responses with more accuracy; however, limited data prohibit an extensive comparison. For example, tissue retraction can protect the live polyp from thermal stress, particularly when tissue is thicker (Hoegh-Guldberg, 1999). However, species' tissue thickness or corallite depth information is rare and could not be evaluated across all species included in these models. The symbiotic make-up was also not determined for each colony evaluated in this study but knowledge of the relationships as well as environmental conditions may have suggested stronger patterns of responses to local stresses. We evaluated the most typical colony morphology of a species since each colony shape was not available; however, growth forms can be plastic for many species (Todd, 2008) and may have influenced susceptibility in these studies. The lack of colony specific detail also prohibited evaluating the effects of trait interactions even though some have been recognized in individual studies to explain BI (Charpentier, 2014). The coral traits included here capture variable responses across assemblages; however additional trait information is likely to provide further understanding of bleaching mechanisms and responses. Bleaching induced by increased SST is a primary threat to coral persistence globally (Hoegh-Guldberg, 1999; Carpenter *et al.*, 2008). More frequent thermal stress anticipated is likely to favour more tolerant colonies and may result in shifting assemblage structure (Done, 1999; Loya *et al.*, 2001; Van Woesik *et al.*, 2012). Coral traits provide insights into the mechanisms influencing bleaching both locally and globally and can therefore suggest how structure may change due to thermal stress. Colony growth form has been a standard way to survey coral bleaching responses. However, by quantifying how well traits contribute to variation among species and warming events, we identified that both growth form and coral family are key indicators of coral bleaching globally. Training surveyors to capture bleaching responses by coral family and standardized growth form classifications would result in more accurate response assessments while enhancing our understanding of impacts across coral assemblages.

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# SUPPORTING INFORMATION

**Supplementary Table 4.1.** Classification of bleaching intensity categories and descriptions of the category in each study and how they relate to our classifications of Pale, Partially bleached and Fully bleached. Dashed lines indicate that the study survey did not include that category. Any blank descriptions indicate that no definition of that category was provided in the study.

| Survey   |                 | Pale  | Partially Bleached  | Fully Bleached  |
|--|-----------------|---|---|---|
| Bruno <i>et al.</i> ,<br>2001                              | Category        | -   | Partially Bleached  | Bleached  |
|  | Description     |   |   | >90% of coral tissue was pale or white  |
| Catlin<br>Survey,<br>Nielson,<br>unpublished<br>data, 2014 | Category        | Pale  | Partial   | Severe  |
|  | Category        | Pale  | Partially Bleached  | Fully Bleached  |
| Charpentier,<br>2014                                       | Description     | Tissue that<br>appears pale<br>relative to what<br>is considered<br>"normal" for the<br>species, depth<br>and habitat or<br>colour of the<br>tissue having<br>retained its usual<br>hue but having<br>lost some of its<br>colour saturation | Areas that are fully<br>bleached or a<br>colony that is<br>mottled in<br>appearance | Tissue of the entire<br>colony is completely<br>white. Some fully<br>bleached corals may<br>appear pale purple, blue,<br>or pink, in addition to<br>being transparent |
|  | Category        | -   | -   | Bleached  |
| Jiménez <i>et</i><br><i>al.</i> , 2001                     | Description     |   |   | More than 5% of the colony surface area was white or pale   |
|  | Category        | Moderate  | -   | Severe  |
| Marshall &<br>Baird, 2000                                  | Description     | 1-50% of colony<br>bleached or<br>entire colony<br>pale   |   | >50% of colony bleached   |
| Supplementar   | y Table 4.1 coi | ntinued   |   |   |

| Obura, 2001 | Category | Pale | - | Bleached |
|-------------|----------|------|---|----------|
|             |          |      |   |          |

|             | Description | Generally pale<br>tissue color, but<br>not white |   | Brilliant white<br>tissue color,<br>sometimes with a<br>tinge of iridescent<br>color such as<br>green or blue |
|-------------|-------------|--|---|---|
| Oxenford et | Category    | -  | - | Bleached  |
| al., 2008   | Description |  |   | Percent bleached  |
| Stimson et  | Category    | -  | - | Bleached  |
| al., 2002   | Description |  |   | Percent bleached  |

**Supplementary Table 4.2.** Coral trait values for species included in the analysis. Trait values were accessed from CTDB and from the literature, field guides and reports where noted. Available in: https://drive.google.com/file/d/0BylGCGgyr79mWVRHNHVSS1YzWFk/view?usp=sharing

**Supplementary Table 4.3.** Examples of bleaching survey growth form categories from different monitoring programs.

| CDDMDA      | Doof Chook Australia              | Eyes of the reef | Florida keys     | Coral     |
|-------------|-----------------------------------|------------------|------------------|-----------|
| GDNNIFA     | Keel Check Australia              | network          | bleach watch     | Watch     |
| Branching   | Branching                         | Small/branching  | Branching        | Branching |
| Plate/table | Plate                             | Plate & pillar   | Leaf/plate/sheet | Plate     |
| Massive     | Massive                           | Mounding         | Mound/boulder    | Boulder   |
| Encrusting  | Encrusting                        | Finger           | Brain            | Soft      |
| Digitate    | Foliose                           | Rice             | Flowering/cups   |           |
| Bushy       | Others (digitate, columnar, etc.) |                  | Fleshy           |           |
| Soft        |                                   |                  |                  |           |

**Supplementary Table 4.4.** Generalized Variance Inflation Factors (GVIF) to assess collinearity between traits. Comparisons of GVIF<sup>(1/(2\*Df))</sup> were considered to account for categorical traits with more than one degree of freedom (DF). A. All traits that can be easily measured in the field were tested for collinearity. B. Collinearity was evaluated between coral family, growth form and colony size. C. Collinearity was evaluated between growth form, colony size and corallite size.

| А.             |    |                            |
|----------------|----|----------------------------|
| Trait          | DF | GVIF <sup>(1/(2*Df))</sup> |
| Family         | 14 | 1.172                      |
| Growth form    | 4  | 1.316                      |
| Colony size    | 1  | 1.438                      |
| Corallite size | 1  | 4.168                      |
| В.             |    |                            |
| Trait          | DF | $GVIF^{(1/(2*Df))}$        |
| Family         | 14 | 1.083                      |
| Growth form    | 4  | 1.277                      |
| Colony size    | 1  | 1.418                      |
| С.             |    |                            |
| Trait          | DF | $GVIF^{(1/(2*Df))}$        |
| Growth form    | 4  | 1.101                      |
| Colony size    | 1  | 1.132                      |
| Corallite size | 1  | 1.332                      |

# SYNTHESIS AND CONCLUSIONS

Species traits are becoming widely used in analyses seeking to understand the mechanisms that structure species assemblages and how these vary in space and time. Traitbased approaches focus on characteristics that are advantageous to some species in given environmental conditions (Violle *et al.* 2007). Furthermore, these approaches identify mechanisms that increase species' susceptibility to environmental stressors based on their traits (Verberk *et al.*, 2013). This information is necessary not only to deepen our ecological understanding of relationships between organisms and their environment, but also to provide a quantitative assessment for predictions of potential s on species (McGill *et al.*, 2006).

Trait-based approaches have the potential to accelerate our understanding of biological and ecological processes and provide an alternative strategy to species-based approaches. A focus on species restricts geographic transferability of results where species identity differs. Additionally, focus tends to be on common or abundant species that exclude the contribution of rare species to patterns and processes (Done 1982). Rather, trait-based approaches aim to link traits to ecological functional and define functional groups. Systems that are ideal for trait-based approaches are those that are relatively simple where traits identify and describe trade-offs between ecological functions (Litchman & Klausmeier 2008). For example, phytoplankton ecological niches are defined by the physical environment, resources and natural enemies and phytoplankton functional traits affect fitness along each of these ecological axes (Litchman & Klausmeier 2008). An understanding of biological relationships and community assembly resulting from trait-based analyses can then help link patterns that help shape diversity and ultimately predict changes in community structure. Until recently, trait-based coral ecology studies have been hampered by insufficient species trait information. However, with the recent compilation of coral trait data (Madin et al. 2016a), a variety of new coral ecology questions are now being addressed.

In this thesis, I used a large coral trait compilation to evaluate explicit relationships between corals and their environment. I combined species-specific occurrence, abundance, and stress response data with coral trait data for hundreds of species to address a variety of questions. I calculated how multi-decadal change in abundance in high-latitude coral assemblages was related to species' broader biogeographic distributions (i.e. cosmopolitan and subtropical distributions). I also identified which coral traits are more prevalent in species that occur beyond reef over three major latitudinal gradients. Additionally, I quantified detailed trait-environment responses between three primary traits and three primary environmental gradients that have been suggested to structure coral assemblages latitudinally. Finally, I used a trait-based approach to quantify the contribution of species traits to bleaching intensity across multiple warming events globally. Results from trait-based approaches I undertook have led to a deeper understanding of ecological relationships and can enhance predictive ability in efforts to protect resources and functional diversity.

The studies that make up this thesis identified the significance of environmental influence on both coral distributions and stress responses. Given the variety of environmental stressors that corals face, quantified relationships between individual traits and specific environmental conditions (i.e. high latitude non-reefal, low light, wave energy, sea surface temperature [SST] variability, increased SST) enrich the understanding of coral functional variation (Brandl & Bellwood, 2014). These relationships help facilitate predictions of species responses to complex changes in environmental conditions. Marine taxa globally are expanding or shifting their distributions poleward to track increased SSTs (Sunday *et al.*, 2012; Poloczanska *et al.*, 2013). However, more than SST alone affects coral distributions. Corals that may shift poleward into higher latitudes will face novel environments (i.e. decreased light availability, lower aragonite saturation state and potentially non-reefal habitats) (Kleypas *et al.*, 1999; Perry & Larcombe, 2003). Predictions of species responses to

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climate change require a fundamental understanding of functional responses to the environment before predictions of complex change can be addressed.

Across each of these studies, relationships identified between coral traits and environmental conditions were variable. Species traits have often been used to identify patterns; however, explained variance and predictive power are often low to moderate in traitbased approaches (Angert et al. 2011; Pocock 2011; Jeppsson & Forslund, 2014). The applicability of these approaches depends implicitly on sufficient explanatory power. Therefore, it is essential to understand determinants of explanatory power and how it can be improved. For example, a species distribution model that incorporated species traits for eucalyptus trees had much greater explanatory power (Pollock et al. 2012) than the model presented in this thesis. These differences may stem from issues related to the relative infancy of coral trait data use and suggest the need to further evaluate how the degree of variability in coral traits, lack of complete trait data, selection of species traits evaluated, or resolution of environmental detail contribute to explanatory power. The information gained using coral traits was also consistently tested of different questions. Corallite size was included in each of the studies included here. This trait had stronger relationships with wave energy and PAR (Chapter 2) compared to other trait-environment responses. Corallite size was also found to be important in analyses of bleaching responses though other trait relationships, suggesting the relative importance of the response of a trait to different envornmental variables though not explicitly tested.

Coral traits incorporated in each of these studies represented typical coral traits globally for more simplistic relationships to be drawn. In fact, phenotypic plasticity can significantly optimize persistence in environmental conditions (Hoogenboom *et al.*, 2008; Todd, 2008). Including measures of plasticity would likely increase explanatory and predictive power. In each test of coral traits included here, growth form was found to be

important to consider. However, this is one of the more plastic coral traits. While general patterns are associated with the most common form, more detailed information that addresses plasticity may provide additional detail about how growth form contributes to distributions patterns and responses to stress.

In addition to intraspecific variability in traits, interspecific trait variation at the appropriate spatial scale is essential (Messier *et al.*, 2010). Environmental processes that affect coral reef ecosystems act on a variety of scales (Connell *et al.*, 1997; Done, 1999; Karlson *et al.*, 2004). Ensuring that trait variation corresponds to the appropriate scale of environmental variation is necessary to capture accurate and informative relationships. While informative and useful relationships have been drawn from trait-based approaches in coral reef systems, the complexity of these ecosystems, similar to microbial communities, may require additional input for more accurate conclusions (Krause et al. 2014).

Trait-based approaches require comprehensive information. I was forced to exclude a subset of species from analyses due to incomplete information. Some entire traits (e.g. skeletal density, growth rate) could not be evaluated because information exists for only a limited number of species. Many coral traits included in these analyses did significantly contribute to distribution patterns and stress response. However, trait infilling will likely enhance trait-based approaches to coral ecology (Madin *et al.*, 2016b). Additional trait information as well as coral trait analyses are also likely to help identify a coral supertrait (i.e. a trait that captures a large amount of variation for a range of processes), similarly to the LMA (leaf mass per area) supertrait identified for plants (Madin et al. 2016b).

In conclusion, this thesis identifies how coral traits contribute to a richer understanding of coral ecology by evaluating species functional responses to the environment. Trait-based approaches provide useful tools to quantify variation of responses to the environment within assemblages, specifically how species redistributions and responses to stressors vary (Webb *et al.*, 2010; Pacifici *et al.*, 2015; Best *et al.*, 2015). Results from these studies provide a strong foundation in the use of coral traits to advance coral ecology and identify opportunities for future research. Changing environmental conditions will impact species; however, knowledge of environmental controls acting on species traits is a necessary foundation to understand and predict impacts on species' persistence and assemblage structure (Molinos *et al.*, 2015).

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Synthesis and Conclusions