Ecological Determinants of Depth Zonation In Reef-Building Corals

Thesis submitted by

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I come out of this thesis with more questions than answers, but an amazing future array of research possibilities to chase. I have sought to resurrect the basic ecological foundations of coral depth distributions, and set off down a path lately neglected, but with much to be revealed. I do not mean to leave this path unexplored. To quote Winston Churchill; "Now this is not the end. It is not even the beginning of the end. But it is, perhaps, the end of the beginning."

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- Thomas Edward Roberts: Study design, data collection, data analysis, writing and revision of the manuscript.
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Chapters 2,3, 4, and 5 are written in the format required for publication in the journals indicated on the chapter titles. As such, there is an inevitable amount of overlap in the methodology and background in some of the chapters.

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Abstract

Natural gradients in altitude, depth or latitude capture systematic variation in environmental variables that can be exploited to test hypotheses on the role of various processes in generating and maintaining patterns of biodiversity. The depth zonation of reef-building corals is one such pattern, where species rich assemblages vary across a small spatial scale that includes rapid and predictable changes in key environmental variables, such as light. These attributes allow a strong test of general hypotheses predicting biodiversity patterns, free from many of the confounding factors found in terrestrial habitats. Here, I first develop a novel method of data collection, referred to as the modified Point-Count Transect method, which is derived from avian survey methods. This approach avoids many of the pitfalls of previous sampling approaches, such as inconsistent sampling effort, poor detection of rare species, and limited sampling coverage of the gradient. I then utilise this methodology to assemble a dataset of 9,576 coral colonies representing over 300 corals species, on six reefs in three positions within Kimbe Bay, PNG to 1) test the validity of the Species Energy theory and the Mid-Domain Effect; two preeminent predictive theories of species richness gradients 2) identify the reef-scale community assembly processes which maintain the depth-diversity pattern and 3) quantify how individual species abundances vary over depth. I found that species richness is not consistent with the predictions of either theory, and instead shows a left-skewed hump consistent with results from terrestrial habitats. Examination of species turnover suggested that the hump-shaped pattern is maintained by large-scale processes acting on the regional species pool, rather than differential levels of reef-scale processes, such as competition and environmental filtering. These results demonstrate that the hump-shaped pattern is not an artefact of scale or sampling design. Finally, species-specific

abundance distributions across depth revealed species' depth use to be far more specialized than previously thought, demonstrating how commonly used metrics such as depth range, are very poor descriptions of how species use this domain. In conclusion, many of the preconceptions on the patterns and processes behind the depth zonation of corals on reefs are demonstrably flawed, and should be re-examined using suitable data and analysis. Although there remains no generally applicable explanation for how the hump-shaped pattern is created and maintained, this thesis provides new ways to overcome obstacles to continued research and move the field forwards.

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Chapter 1: General Introduction

"Nowhere else in the seas is there such a bewildering array of living things, and perhaps nowhere else is the pattern so uniform, characteristic, and widespread as in the coral reefs"

Wells, 1957

1.1: Natural Patterns Of Biodiversity In Space

Describing patterns of diversity in space and explaining how these patterns are generated and maintained is the core focus of modern ecology (Lomolino 2001). One of the more prominent observations is that more species are present in areas of low latitudes, low altitudes and shallow depths (Von Humboldt 1849; Wallace 1876; Stehli and Wells 1971; Gaston 2000; Lomolino 2001; Willig et al. 2003). These natural environmental gradients capture systematic variation in environmental variables, and therefore provide a window through which the causes of these patterns can be explored (Rosenzweig 1992).

While the historical focus has been on terrestrial gradients of latitude and altitude (Wright 1983; Colwell and Lees 2000; Hawkins et al. 2003; Willig et al. 2003; Whittaker et al. 2007), prominent diversity patterns are also present in the marine realm over longitude, latitude and depth (Stehli and Wells 1971; Connolly et al. 2003; Irigoien et al. 2004; Woolley et al. 2016). Intriguingly, these diversity gradients share many similarities, such as a decrease in species richness at high altitudes, latitudes and deeper depths (Huston 1985; Rahbek 1995; Lomolino 2001; Willig et al. 2003; Kraft et al. 2011). Consequently, the search to develop a predictive theory capable of explaining the distribution of biodiversity over different gradients remains a key challenge in ecology (Rosenzweig 1995).

Over two centuries of science have resulted in numerous ideas to explain diversity gradients in species richness. Carl Linneaus (Von Linnaeus 1743), originally hypothesized that gradients in species richness were caused by differences in the trajectory of each species' journey out from the biblical center of origin - the landing

site of Noah's ark. A more recent theory, Hubbell's (2001) neutrality theory, which seeks to explain patterns of biodiversity by stochastic events acting on species abundances, regardless of the ecological attributes of a specific species (Hubbell 2001; Volkov et al. 2007), has proved equally implausible (Dornelas et al. 2006; Connolly et al. 2017). Despite the high diversity of predictive theories, there remains little consensus on the underlying causes of biodiversity gradients. Additionally, many of these theories are clearly unsuitable for many habitats. For instance, the water-energy hypothesis (Hawkins et al. 2003) uses the balance of temperature and water availability to explain the distribution of biodiversity. However, this explanation is only applicable to terrestrial gradients (the focus of the study). As a result, it can offer no explanation for the 70% of the planet's surface occupied by marine taxa, where there is no variation in water availability, but diversity gradients persist. Marine habitats should not be ignored when considering the universality of a predictive theory of biodiversity, and are a vital test of any universal explanatory theories.

Fortunately, many predictive hypotheses are applicable to both marine and terrestrial habitats. For instance, the species energy theory (Wright 1983) seeks to link changes in species richness (the most fundamental measure of diversity) to the level of a 'limiting energetic resource', which can be represented by taxon specific factors (i.e., light, water, temperature). In this way, the common predictive element - energy - can change with the habitat in question (unlike in the water-energy hypothesis). Another approach is to avoid using environmental factors as predictive variables, instead examining the influence of attributes shared by all natural gradients, such as hard boundaries (e.g., sea level, polar limits of latitude). An example is the mid-domain

effect, which specifically seeks to capture the underlying diversity pattern over a gradient in the absence of any environmental factors (Colwell and Lees 2000). This is achieved by recoding the overlap in species ranges (and therefore species richness) when the possible locations of empirical species ranges within the bounded domain are randomized. Inevitably, the geometric constraints of the hard boundaries create a species richness pattern peaking at the mid-point of the domain (Colwell and Lees 2000; Colwell et al. 2004). While the species energy theory and the mid-domain effect both seek to explain universal species richness gradients, empirical tests of their predictions are often unclear (Colwell et al. 2005; Beck et al. 2016; Peters et al. 2016). The mid-domain effect predicts a unimodal pattern, peaking at the mid-point of the domain. However, the use of range extents to calculate species richness, and the assumptions of hard domain boundaries require a test case to feature a gradient where the full domain is sampled, without variation in the detectability of species, or sampling effort across the domain (Grytnes and Vetaas 2002; Colwell et al. 2004; Gotelli and Colwell 2011). Likewise, the species energy theory relies on a clear identification of the 'limiting energetic resource' (Wright 1983). In the majority of natural gradients, the identification of a single measurable factor that meets this requirement is not possible, leading to the use of multiple different factors, roughly categorized as thermal energy (e.g., temperature), radiation energy (e.g, light), and chemical energy (e.g, particulate organic carbon) (Fraser and Currie 1996; Hawkins et al. 2003; Evans et al. 2005; McGill 2010; Peters et al. 2016; Woolley et al. 2016; Laiolo et al. 2018). These factors often show a consistent monotonic change (where the trajectory of the function does not deviate over its range) across a gradient (such as the reduction in temperature with increasing altitude and latitude), and correspondingly predict a monotonic pattern of species richness. However, the

predictions of the theory are reliant solely on the correct identification and accurate measurement of the energetic resource over the gradient, an objective that is rarely, if ever, sufficiently met. Further adding to the confusion, simply quantifying the empirical pattern in species richness remains a difficult task, due to the way data used to measure diversity (in the form of species richness) is gathered.

1.2: Sampling Artifacts in Estimates of Diversity

Species richness is the most fundamental measure of diversity, but it is only confirmed by sampling a community to exhaustion (Magurran 2004; Chao et al. 2009; Gotelli and Colwell 2011). This is a practical impossibility when considering natural communities and especially so for highly diverse ecosystems, such as coral reefs (Lawton et al. 1998). Consequently, species richness is often calculated using species accumulation curves (Colwell et al. 2012). This process forms the basis for projections (e.g., rarefaction) and estimates of total species richness as if the community were sampled to exhaustion (Chao et al. 2004; Chao et al. 2006). Where suitable empirical data is not available, species richness measures are calculated using the overlap of species range extents, derived from historical data such as museum records. Crucially, both rarefaction and estimates of range overlap rely heavily on extensive, high quality data sets, and are highly vulnerable to statistical artifacts. For instance, species accumulation analysis requires each sample to be a true representation of the larger assemblage, without variation in sampling effort, sample size or bias (Gotelli and Colwell 2001). Meanwhile, compilation of range extent data is strongly reliant on sampling effort over the full domain to identify the range limits of a species, a requirement that is rarely achievable (e.g., pole to pole, sea level to mountain top). Both methods also assume no variation in sampling (such as changes in effort, or observer bias) throughout the sampling domain. Failure to meet these

assumptions produces values more informative of the sampling methodology than the desired species richness pattern, severely weakening subsequent tests of ecological theory (Gotelli and Colwell 2001; McCoy 2002; Rahbek 2004; Nogués-Bravo et al. 2008).

1.3: A Diversity of Diversities

Despite the identification of species richness as the fundamental measure of diversity (being a measure of the number of species within a specified region), the term 'diversity' has be used to describe many different things (Gotelli and Colwell 2001; Magurran 2004). A review of the existing literature detailing one specific diversity gradient, the diversity of reef-building corals over depth, returns measures of species density (Sheppard 1980), species richness (Goreau and Wells 1967; Kühlmann 1983), and species evenness (Loya 1972) all used as measures of 'diversity' (Fig. 1.1). This is an insidious issue which pervades all fields of research into biodiversity (Gotelli and Colwell 2001; Magurran 2004). Species density is often unknowingly misrepresented as a measure species richness (Sheppard 1980). This is highly misleading due to the fact that species density is calculated by dividing the number of species recorded by the sampling effort expended, assuming that species richness will increase linearly with increasing sampling effort. However, species do not occur in equal abundances and therefore accumulate in an asymptotic fashion, making species density a measure of sampling effort rather than species richness (Gotelli and Colwell 2001; Colwell et al. 2012). The extent to which species abundance distributions are uneven is the focus of species evenness. This measure, or a variation of it, is often reported using diversity indices, which weight species abundance distributions against species richness per sample, and the number of individuals per sample (Spellerberg

and Fedor 2003). While each of these measures is descriptive of a specific aspect of diversity, they are inherently different, and cannot be directly compared.

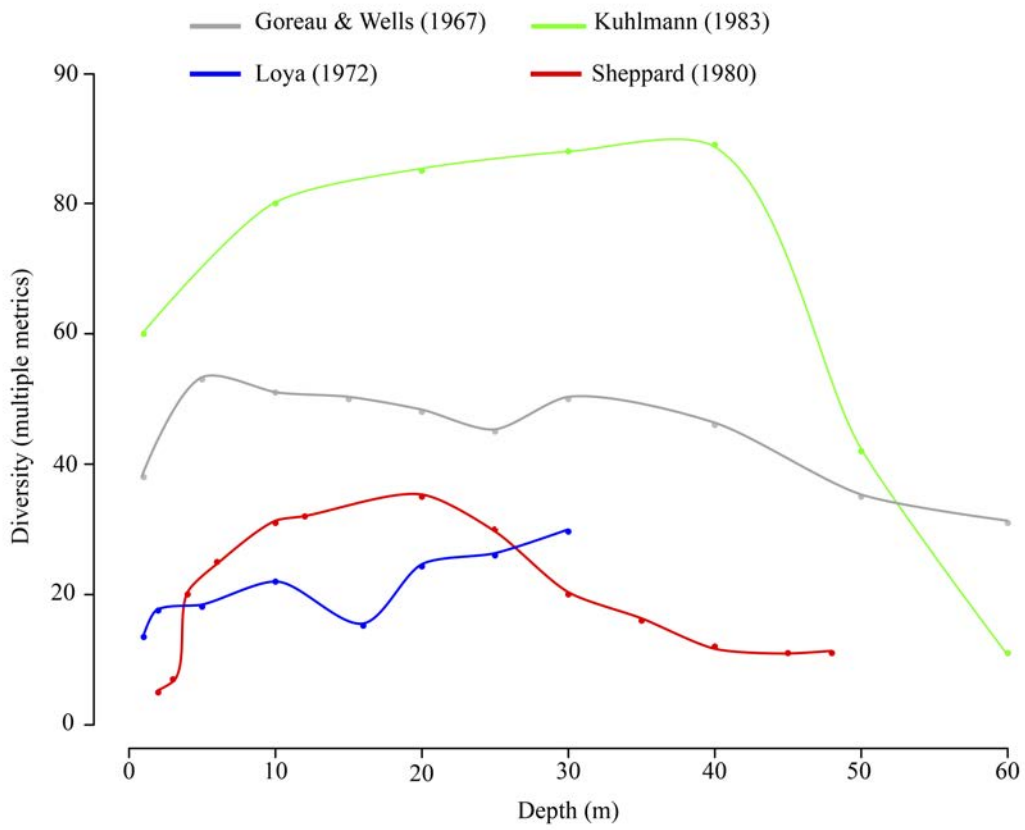


Figure 1.1: Coral diversity over depth.

For Khulmann (1983) and Goreau & Wells (1967) diversity is measured by species richness; Sheppard (1980), measured species density; Loya (1972) measured species evenness

1.4: A Question of Scale

Much of the confusion arising from tests of theories of diversity is the result of scale (Willig et al. 2003; Chase 2010; McGill 2010; Kraft et al. 2011; Laiolo et al. 2018). Predictive hypotheses such as the species energy theory and mid-domain effect seek to predict large-scale patterns, but the ecological and evolutionary processes which influence these patterns operate over multiple temporal and spatial scales (Caley and Schluter 1997; Lomolino 2001; Willig et al. 2003). To adequately explain the way biodiversity patterns are maintained over all scales, the influence of local scale ecological processes must be also considered (Caley and Schluter 1997; Chase and Leibold 2002). Biodiversity patterns often change as the spatial scale changes from large (global) to small (local) (Waide et al. 1999; Chase and Leibold 2002; Rahbek 2004). Most studies are done at small spatial scales and often show either a hump-shaped or monotonic pattern (Rosenzweig 1995). Large-scale patterns are harder to establish, but are most often reported to be monotonic (Gaston 2000). For example, a hump-shaped species richness pattern is often reported over a monotonic energetic gradient (e.g. elevation or depth), where the peak of the hump is skewed towards the high energy end of the gradient (Rahbek 1995; Gross et al. 2000; Lomolino 2001). The skewed-hump is thought to be a modification of the large-scale (monotonic) pattern by smaller-scale assembly processes such as competition and environmental filtering (Huston 1999; Chase 2007; Nogués-Bravo et al. 2008; Laiolo et al. 2018). Since effective biodiversity sampling is largely restricted to small geographic ranges, community assembly processes are expected to be more influential for the biodiversity pattern (Cornell and Karlson 1996; Chase 2007; Field et al. 2009; Kraft et al. 2011). For instance, high energetic availability might encourage rapid growth resulting in increased competition within an assemblage, reducing species richness

(Chase 2007). Alternately, some energetic resources (such as light) can be become challenging at high levels, filtering out species unable to cope physiologically (Baird et al. 2009b). Both processes (competition and environmental filtering) are most influential in the high-energy region of a gradient and are proposed to cause the corresponding drop in species richness (Huston 1985; Huston 1999; Colwell and Lees 2000). As the spatial scale increases, the influence of local-scale processes becomes inconsistent and the true regional pattern (often derived from predictions of the species energy theory) should then emerge (Chase and Leibold 2002; Chase 2010). However, little conclusive evidence exists to support the modification of large-scale patterns by local-scale processes outside of controlled experiments (Chase 2010; Kraft et al. 2011).

1.5: Species Abundance Response Curves

Individuals of a species are not evenly distributed throughout its range (Austin 1999; Dallas et al. 2017). The way in which a species occupies space over a gradient can be measured by an abundance response curve, which is hypothesized to reveal how the species responds to environmental factors and ecological processes that change over the gradient (Brown et al. 1995; Gravel et al. 2006; Dallas et al. 2017). For example, a species that occurs over a broad latitudinal range can presumably tolerate a greater range of temperatures than a species with a narrow range and therefore, range size is often used as a proxy for environmental tolerance. Likewise, the shape of the species abundance response curve within a given range can vary widely, reflecting the ecological preference of a species towards a specific subset of its range (Brown 1984; Brown et al. 1995; Oksanen and Minchin 2002; Austin 2007; Jansen and Oksanen 2013). The acuity of the curve, and location of the peak can be used to infer the

ecological specialization (more acute curves indicate a more specialist species) and preference (location of the optimum response) of a species over a gradient (Austin et al. 1994; Brown et al. 1995; Jansen and Oksanen 2013).

1.6: Testing Biodiversity Theory

In terrestrial habitats, issues of area (Rahbek 1997), dispersal boundaries (Willig et al. 2003; Fukami 2015), anthropogenic impacts (Nogués-Bravo et al. 2008) and unclear definition of energetic gradients (Rosenzweig 1995; Hawkins et al. 2003; Evans et al. 2005) all serve to confuse research conclusions. The specific attributes of each biological community and the natural gradient it occurs over can overcome many of these obstacles. For instance, geographically short gradients (particularly in the marine habitat) ameliorate the effects of dispersal boundaries and allow the full gradient to be sampled. Likewise, communities featuring a clearly identifiable limiting energetic factor allow a clear test of the species energy theory. By assembling species level data in an empirically sound and spatially hierarchical fashion, the predictions of competing theories can be explicitly tested without the influence of confounding factors. Coral reefs provide such a system.

1.7: Coral Diversity Over Depth

Photo-symbiotic reef-building corals are colonial cnidarians of the subclass Hexacorallia, within the class Anthozoa and form the foundation of tropical shallow water coral reefs; one of the most biodiverse ecosystems on Earth (Veron 2000). Hermatypic (reef-building) corals of the order Scleractinia build calcium carbonate skeletal structures, and form a symbiotic relationship with dinoflagellate species of the genus *Symbiodinium* (Wells 1957; Veron 2000). This relationship is central to the ability of the host coral to accrete its skeletal structure maintain a positive energy

budget (Yonge 1931; Chalker and Taylor 1975; Al-Horani et al. 2003). The symbiotic association between the coral host and the symbiont makes the availability of light a key environmental factor influencing coral physiology and a clearly identifiable limiting energetic resource (Verwey 1931; Anthony and Connolly 2004). As depth increases, light level declines exponentially, limiting the dominance of reef-building corals beyond ~60 m depth. Local environmental conditions dictate the maximum depth of light penetration, and in some cases allows corals to persist beyond 150 m (Brokovich et al. 2008; Kahng et al. 2010; Bridge et al. 2013). These characteristics are ideally suited to a clear test of the species energy theory, allowing sampling coverage of the physically short natural gradient of a clearly identified limiting energetic resource.

The pattern of coral species richness over depth is generally reported as either a monotonic decline with depth (Wells 1957; Goreau 1959; Porter 1976; Huston 1985), or a left-skewed hump peaking between 10 and 30 m depth (Sheppard 1980; Kühlmann 1983; Cornell and Karlson 2000). The monotonic pattern is considered a regional scale pattern resulting from the reduction in light availability as depth increases (Cornell and Karlson 2000), as predicted by the species energy theory (Wright 1983). Consequently, the left-skewed hump is thought to be a local scale pattern resulting from local processes modifying the regional scale (monotonic) pattern (Wright 1983; Huston 1985; Chase 2010). This conforms with existing results from other natural gradients, although there is no empirical confirmation of this assertion (Cornell and Karlson 2000). The local scale assembly processes identified to cause the drop in species richness at the shallowest depths are environmental filtering (e.g., through hydrodynamic disturbance) and competitive exclusion (driven by faster

growth rates in shallow, high light depths) (Goreau and Wells 1967; Sheppard 1980; Done 1982; Huston 1985; Huston 1999; Cornell and Karlson 2000). As is the case with light, the frequency and intensity of hydrodynamic disturbance events also decreases with depth, because wind driven wave energy declines as the inverse square of depth (Monismith 2007). This also allows the processes of environmental filtering and competitive exclusion to change in intensity over the gradient and produce the left-skewed hump pattern (Cornell and Karlson 1996; Cornell and Karlson 2000). Unsurprisingly, these two factors (light and hydrodynamic exposure) are often used to explain the strong patterns in coral zonation over depth (Done 1982,1983; Cornell and Karlson 2000; Roberts et al. 2015). However, evidence quantifying the influence of each of these factors on the assembly of coral communities over depth remains scarce.

The Depth Generalist Paradox

When basic range extent metrics are used to describe species depth distributions, an apparent paradox emerges, whereby the majority of species have wide ('generalist') depth ranges, yet empirical observations on reefs show strong patterns of zonation over depth, whereby particular species dominate at specific depths, often over very large geographical scale (Loya 1972; Done 1982; Kühlmann 1983; Bridge et al. 2013). The paradox arises because depth distributions of coral species have largely been classified as 'specialists' or 'generalists' based on their depth range (i.e. the maximum depth minus the minimum depth of occurrence), based on the assumption that species are distributed normally over their depth range (Goreau 1959; Goreau and Wells 1967; Loya 1972; Kühlmann 1983; Muir et al. 2015). The depth generalist paradox has been exacerbated by recent interest in mesophotic reefs, which are loosely defined as coral reef communities occurring between ~30-150 m depth (Hinderstein et al. 2010; Kahng et al. 2010). An increase in sampling effort at depth

has resulted in an extension of many species' lower depth limits, with a consequent increase in the number of depth generalists. However, because range extent metrics are often determined on the basis of single colony at the edge of the range, the ecological relevance of such measures is doubtful.

One way to reconcile the depth generalist paradox is to examine the abundance distribution response curve of corals species over depth, which can be used to describe a species ecological niche over depth (Brown et al. 1995; Gravel et al. 2006; Dallas et al. 2017). Abundance response curves are not bound by a pre-defined distribution (i.e., normal distribution assumed using depth range alone) and can potentially reveal how species with the same depth range can preferentially occupy distinct subsets of the depth domain. Occasionally, depth distributions are defined from estimates of abundance, such as numerical dominance in a particular reef zone (Sheppard 1980) or changes in density with depth (Baird et al. 2003, Pandolfi & Budd 2008). However, abundance response curves over depth have been produced for very few species. Effective statistical techniques to model abundance response curves have been developed (Oksanen and Minchin 2002; Jansen and Oksanen 2013), but these are dependent on extensive species level datasets, with limited sampling bias, balanced sampling effort and good coverage of the gradient in question. Without access to suitable abundance data, depth distributions continue to be assessed using range extent data and the depth generalist paradox remains (e.g., (Laverick et al. 2018)).

Life history traits and depth niches

Life history traits define the many different strategies employed by corals to survive in different habitats. Light levels and physical disturbance, two of the main influences

on coral survival, vary markedly over depth, therefore traits should also vary predictable with depth (Cooper et al. 2011; Darling et al. 2012; Madin et al. 2016b). For instance, the gross morphology of a coral colony represents a trade-off between light capture and physical resistance to disturbance (Chalker et al. 1983; Anthony and Connolly 2004; Madin et al. 2014). Species in shallow waters can exploit the abundance of light, but must also cope with frequent hydrodynamic disturbance. This can take the form of resisting damage by using a robust morphology, or selecting a morphology which can grow rapidly to re-colonise following a disturbance (Williams 1975). Meanwhile, a species that specializes at the deeper end of the gradient must prioritise light acquisition in its morphological shape, but does not experience disturbances of the same intensity or frequency (Done 1983; Roberts et al. 2015; Englebert et al. 2017). However, the variability in the morphological structure of a coral colony can vary widely between individuals of the same species, and even within a single colony, often responding to their local environmental conditions (Veron 2000; Todd 2008; Ow and Todd 2010). While this morphological plasticity might allow a species to occur across a wider depth range (Hoogenboom et al. 2008), it raises the prospect that intraspecific trait variability might also be more important than mean trait values for determining a species' ecological niche(Jung et al. 2010). Fortunately, recent advances in trait based ecology in terrestrial and marine ecosystems have led to rapid advances in the availability of coral species trait data, namely via the CoralTraits database (Madin et al. 2016a).

Methodological consistency

The myriad of sampling methodologies used to study coral depth diversity patterns acts to further complicate the situation. For example, methods used in studies reporting species richness over depth include line intercept transects (Loya 1972), un-

constrained species counts (Goreau 1959; Kühlmann 1983), and vertical belt transects (Porter 1976; Sheppard 1980) (Fig. 1.1). Each method has a distinct and often uncontrolled, and unquantifiable, level of bias towards certain taxa. In particular, the continued use of largely qualitative sampling methods to provide data to describe macro-ecological patterns of species richness is a very large problem (Muir and Wallace 2016; Muir et al. 2017). Unfortunately, rare and incidental taxa contribute the majority of the species in a coral assemblage (Dornelas and Connolly 2008) and are therefore likely to be underrepresented in most studies. This issue is accentuated by low replication, and small sample sizes, which is, unfortunately, highly characteristic of data from coral reef habitats, in particular at depth.

Restricted access

Despite the myriad of quality-associated data issues for studies of coral depth-diversity patterns, the greatest single limitation is the absence of data from deeper regions, due to the logistical difficulties associated with data collection at depth. Physiological stresses placed on the human body when using open circuit SCUBA equipment increase exponentially as depth increases, resulting in correspondingly reduced time limits for data collection. These limitations become prohibitive beyond ~45 m depth, and are restrictive for sampling effort beyond ~20 m, although modern closed circuit rebreather technology is now able to alleviate many of these restrictions. However, with the rise of increasingly risk-averse legal policies at research institutions, little primary data of a suitable nature has been gathered over a depth gradient since the mid 1990s (Goreau 1959; Loya 1972; Sheppard 1980; Done 1983; Kühlmann 1983; Huston 1985; Cornell and Karlson 2000). To overcome this restriction, most studies use depth-diversity information derived from historical records. The advantage of this approach is that it can access all available records to

fill data deficiencies. One of the most widely used and comprehensive datasets of this nature was compiled in 2008 (Carpenter et al. 2008). The data set consists of global estimates of species depth range limits using available records and expert opinion. This dataset has been central to multiple studies, where a species predicted ability to cross biogeographic boundaries (Keith et al. 2013), or risk of extinction with coming climate change (Carpenter et al. 2008) was strongly associated with its depth range. However, when reported depth ranges are compared to empirical records collected in the course of this PhD (Roberts 2018), it is abundantly clear that depth ranges of the majority of species are inaccurate (Fig. 1.2).

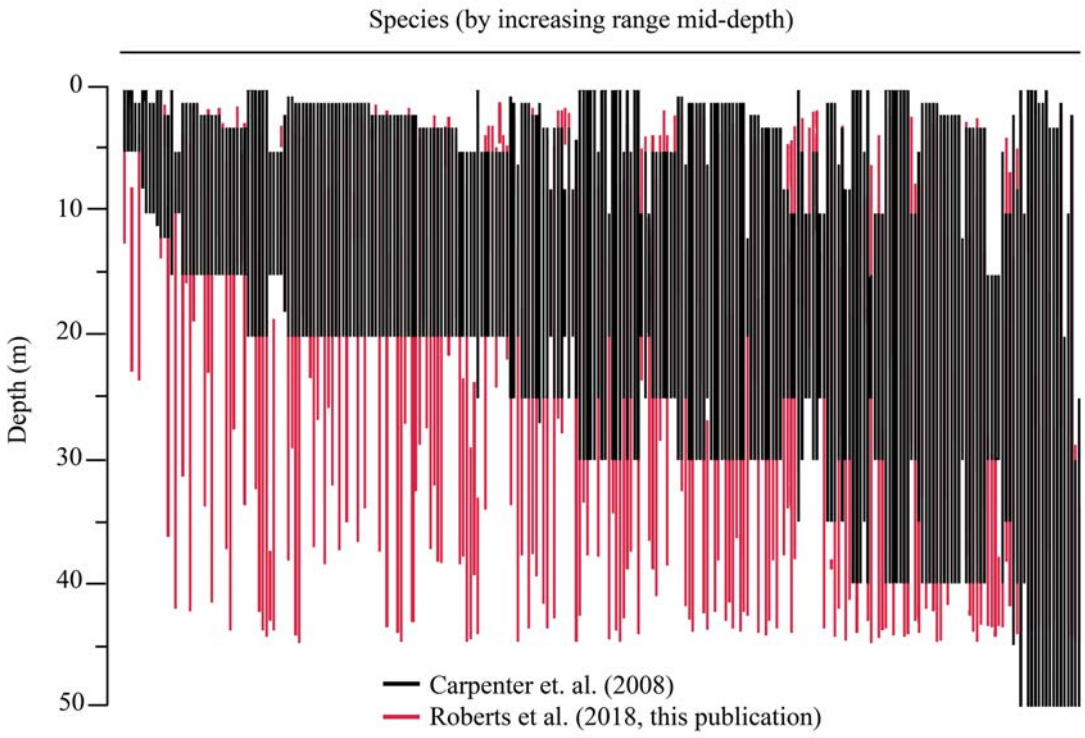


Figure 1.2: Depth ranges for 263 species from this publication (Roberts 2018).

Species are arranged by increasing range mid-depth according to Carpenter et al 2008 (Carpenter et al. 2008). Vertical black bars representing the depth range of each species from Carpenter et al 2008; red bars are from this publication (Roberts 2018).

Implications of taxonomic change

Finally, coral taxonomy has undergone significant changes over the last decade (Huang et al. 2014; Kitahara et al. 2016) making previous data (largely compiled prior to 1990) difficult to interpret (Knowlton and Jackson 1994). For instance, the previous tendency to lump closely-related species into a single 'species complex' is problematic. One example of this is the *Montastraea annularis* (Ellis and Solander, 1786) species complex, consisting of what is now recognised to be three distinct species in two different genera (Weil and Knowton 1994; Lopez and Knowlton 1997). While simple changes in a species accepted name could be accounted for, splitting of species complexes is not possible.

1.8: Thesis Outline

Natural gradients of diversity have formed a core focus of ecology for over 200 years and although predictive hypotheses have multiplied over that time, the effects of multiple confounding factors have conspired to confuse and obscure clear tests of the theory. In the natural diversity gradient of reef-building corals over depth an opportunity exists to overcome the chronic limitations of previous tests of the ecological theory, as the short physical gradient of light (the key limiting energetic resource) occurs in an ecosystem without biogeographic dispersal boundaries. By exploiting these characteristics, the processes that create and maintain diversity gradients over the regional, local, and species scales can be examined.

The most significant research gap is the lack of suitable data, particularly from habitats below 25 – 30 m depth. Where advancements in data collection and statistical methodology have brought new life to the study of diversity gradients in terrestrial ecosystems, marine habitats and coral reefs in particular, have lagged behind.

Furthermore, as the growing threat of anthropogenically induced changes casts an increasingly heavy shadow over the future health of coral ecosystems (Hughes et al. 2017), the quest to understand how corals utilise bathymetric space becomes ever more important. For instance, the theorised refuge provided by increasing depth (Bongaerts et al. 2010; Slattery et al. 2011) to a multitude of disturbances (Glynn 1993; Riegl and Piller 2003) relies on a firm understanding of how depth influences the ecological niche of a species, and the structure of coral populations (Bongaerts et al. 2015; Bongaerts et al. 2017).

Thesis aims

This aim of this thesis is to investigate the ecological determinants of diversity gradients, by examining the depth diversity gradient in corals. I will do this by applying current statistical techniques and ecological theory to interpreting novel data detailing the distribution of coral species over depth. Although coral reefs have been a productive research field for ecological theory (Darwin 1859; Connell 1978; Dornelas et al. 2006; Volkov et al. 2007; Connolly et al. 2017), significant knowledge gaps persist. Specifically, in this thesis I will (1) overcome the lack of useable data by establishing a new sampling methodology for examining natural patterns of diversity in habitats with logistical challenges; I will then use this methodology to gather an extensive data set to (2) test general hypotheses of biodiversity patterns (the mid-domain effect, and the species-energy theory) which operate on species richness at regional scales; (3) quantifying the influence of local-scale ecological processes (environmental filtering, competition) on the depth diversity gradient; and (4) model species-specific abundance response curves over depth to capture the depth occupancy of a species and the capacity of life history traits to describe the depth niche of a species.

Chapter 2

In Chapter 2, I develop and test a new field sampling methodology specifically designed for use in logistically challenging habitats (such as deep waters) and to address diversity related research questions. By adapting a methodology well established in avian ecology, a new methodology was developed (the Point-Count Transect method, or PCT). The PCT provides data with standardized sampling effort, strong detection of rare and incidental species, and reliable completion within 5 minutes. When tested against the established standard in the field for biodiversity data (the Line Intercept Transect, or LIT), the PCT and was not only far more time efficient, but revealed serious detectability issues in the LIT method. These results confirmed the PCT method to be capable of providing data suitable for biodiversity studies, as well as meeting the logistical time constraints of depths below 30 m.

Chapter 3

In Chapter 3, I tested the capacity of the two most commonly invoked general predictive hypotheses of species richness gradients (the Mid-Domain Effect, and the Species-Energy Theory) to capture the species richness pattern of corals over depth. Both models predict differing species richness patterns, but empirical support for both can be found in the literature. To provide a clear test of the theory predictions, I used a dataset of 9,576 coral colonies collected over a 45-m depth gradient, using the PCT method (Chapter 2). This approach freed the analysis from many confounding factors found in terrestrial studies, as well as previous coral reef studies, and revealed that neither model adequately captured the empirical pattern of a left-skewed hump. However, ongoing support for both models in the literature could be explained by the powerful influence of veil effects, which distort the model fit by hiding portions of the gradient.

Chapter 4

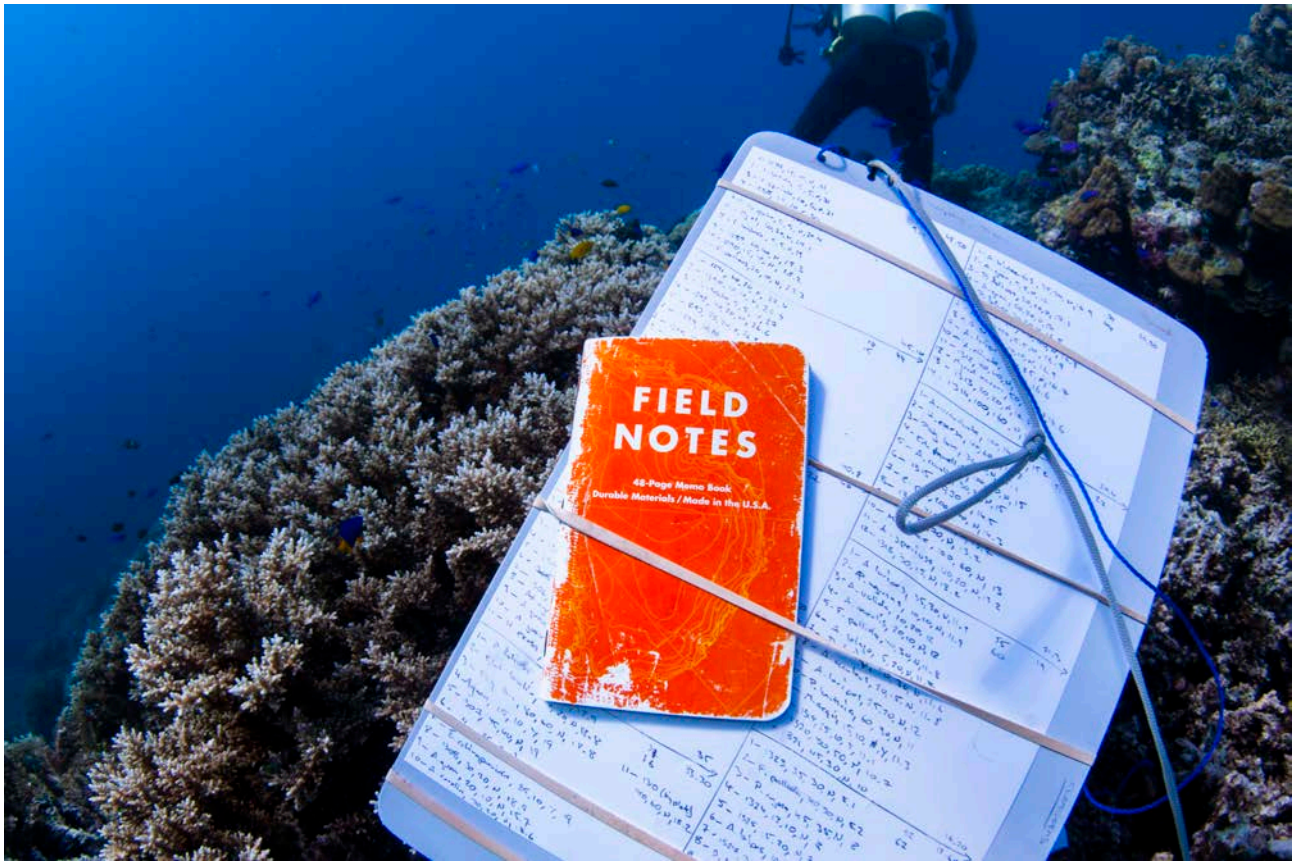
Chapter 4 drew on the same dataset gathered for Chapter 3, and addressed the question of how local-scale ecological processes influence the species richness gradient over depth. Specifically, I tested whether the skewed hump-shaped pattern found in Chapter 3 could be explained as a product of environmental filtering or competitive interactions. Empirical patterns in beta diversity were compared to null expectations at two spatial scales where environmental filtering (between reefs) and competitive interactions (sites within reefs) are most influential. While a strong influence of environmental filtering was evident, there was little evidence of competitive interactions significantly influencing community assembly. Crucially, there was no evidence that local scale processes created and maintained the hump-shaped species richness pattern. In fact, evidence of regional enrichment throughout the depth gradient suggested that regional-scale processes control the pattern, and rather than being a local scale artefact, the hump-shaped pattern is likely the true regional shape.

Chapter 5

Finally, Chapter 5 focused on the way individual species distributed over the depth gradient, and tested the capacity of four life history traits linked to depth distribution to predict the depth niche of a species. By using hierarchical logistical modelling methods on the PCT dataset collected for Chapter 3, I moved beyond simple metrics (such as range extent and range mid-point) to successfully describe species depth distributions for 170 species. This approach captures the myriad of ways that species utilise bathymetric space, and produced two model parameters capable of describing the depth preference (optimum depth), and depth specialization (niche breadth) of a species. When used in combination as replacements for the equivalent metrics derived

from range extent values (range mid-point, and total depth range), the model derived metrics resolved the depth generalist paradox. Finally, species with laminar and encrusting gross morphologies were more likely to have deeper optimum depths, while species with submassive morphologies had larger niche breadths than expected. The life history traits of larval development mode, morphological plasticity, and mean corallite size showed no correlation with the optimum depth, or niche breadth of a species. Limited availability of trait data, especially from deeper waters, intraspecific trait variability, and the use of mean trait values are likely to be at least partially responsible for this result. Nonetheless, there is no indication that corals inhabiting deeper (>30 m) habitats have a specific suite of life history traits that prevent them colonizing shallow waters following disturbance.

Chapter 2: The point count transect method for estimates of biodiversity on coral reefs: improving the sampling of rare species



"…as we know, there are known knowns; there are things we know we know. We also know there are known unknowns; that is to say we know there are some things we do not know. But there are also unknown unknowns – the ones we don't know we don't know."

Donald Rumsfeld, 2002

The point count transect method for estimates of biodiversity on coral reefs: Improving the sampling of rare species

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2.1: Abstract

Understanding patterns in species richness and diversity over environmental gradients (such as altitude and depth) is an enduring component of ecology. As most biological communities feature few common and many rare species, quantifying the presence and abundance of rare species is a crucial requirement for analysis of these patterns. Coral reefs present specific challenges for data collection, with limitations on time and site accessibility making efficiency crucial. Many commonly used methods, such as line intercept transects (LIT), are poorly suited to questions requiring the detection of rare events or species. Here, an alternative method for surveying reef-building corals is presented; the point count transect (PCT). The PCT consists of a count of coral colonies at a series of sample stations, located at regular intervals along a transect. In contrast the LIT records the proportion of each species occurring under a transect tape of a given length. The same site was surveyed using PCT and LIT to compare species richness estimates between the methods. The total number of species increased faster per individual sampled and unit of time invested using PCT. Furthermore, 41 of the 44 additional species recorded by the PCT occurred ≤ 3 times, demonstrating the increased capacity of PCT to detect rare species. PCT provides a more accurate estimate of local-scale species richness than the LIT, and is an efficient alternative method for surveying reef corals to address questions associated with alpha-diversity, and rare or incidental events.

2.2: Introduction

Coral reefs are one of the most diverse ecosystems on Earth (Wells 1957; Stehli and Wells 1971; Caley et al. 2014) containing both high species richness and heterogeneity of habitats at all spatial scales (Bellwood and Hughes 2001). For several decades, coral reefs have provided ecologists with important insights into processes that generate and maintain biodiversity, such as species richness gradients and species coexistence mechanisms (e.g. (Connell 1978; Dornelas et al. 2006)). A common feature of ecological assemblages is a species abundance distribution featuring a small number of common species, and many rare taxa (Fisher et al. 1943; Preston 1948; Magurran 2004). These rare taxa often form the bulk of biodiversity in an assemblage, but are the most time consuming to adequately record. A high number of rare species therefore requires a large sampling effort to effectively characterize a site. This presents a significant logistical issue in high-diversity ecosystems such as coral reefs and tropical rainforests, where the number of rare and incidental taxa is very high (Dornelas and Connolly 2008). Coral reefs in particular present additional challenges for data collection, as many reefs are remote and some habitats, such as at depth, are difficult to access.

Ecological studies of coral reefs were greatly enhanced by the advent of SCUBA diving in the 1950s, but the capacity to study reefs at depths >30 m is still limited (Bridge et al. 2013). Consequently, important questions surrounding the spatial extent, biodiversity and ecological significance of deeper reef habitats remain unresolved (Slattery et al. 2011). Overcoming this knowledge gap requires the development of new methods that enable more rapid collection of ecological data

from deeper habitats. Ideally, such methods would also be broadly applicable across a range of depths and sampling regions.

Standardized methods in empirical data collection for benthic communities in marine ecosystems were developed in the 1970s primarily in conjunction with the increased use of SCUBA (e.g. (Loya 1972)). The line intercept transect (LIT), adapted from terrestrial vegetation studies, has been widely used for coral reef studies (e.g. (Hill and Wilkinson 2004)). In this method, a transect line of a set length is placed along a reef, and the identification of each species under the line is recorded along with the distance it occupies. The LIT provides a precise estimate of abundance (i.e. coral cover and density), making it well suited to examination of temporal or spatial trends in the abundances of species. LITs, however, are not appropriate for all ecological questions or locations. For example, the length of time taken to complete a suitable number of replicate 10 m transects (typically ≥5) makes LITs impractical in depths >15 m, below which safe bottom times for divers become severely limiting factors for SCUBA based surveys. Furthermore, because of the time required to conduct 10 m LITs, the amount of replication achieved may result in under-sampling of rare and incidental species or events. Consequently, LITs are limited in their application according to habitat and ill equipped to address questions that require the detection of rare events or species.

A fundamental tenet of ecology is that the distribution of species is not random in time or space (Willig et al. 2003), and understanding how these non-random patterns are created and maintained is a major ecological goal (Lomolino 2001). The mechanisms generating patterns, such as species richness gradients, are now

investigated using increasingly complex statistical analyses (Colwell et al. 2012; Presley et al. 2012), which require extensive and precise data (Gotelli and Colwell 2001). Computationally demanding analyses, such as sample-based rarefaction, enable estimates of species richness at standardized levels of sampling effort; however, data for such analysis requires large sample sizes, consistent sampling methodology and data independence (Gotelli and Colwell 2001; Chao et al. 2009; Gotelli and Colwell 2011). The logistical restrictions imposed by LITs make them ineffective for addressing these questions in most situations. Consequently, little suitable data exists, or is being collected, to investigate fundamental ecological phenomena on coral reefs using these statistical techniques.

Here, we present a novel sampling technique more suitable than LITs for estimating species richness (Alpha diversity) and abundance on coral reefs: the point count transect (PCT). The method is derived from a well-established technique in avian ecology, the point count distance transect (Marsden 1999; Perry et al. 2012). Point sampling techniques are popular for monitoring songbirds, primarily for examining species richness and diversity (Buckland 2006). The detectability and mobility of different bird species is highly variable, resulting in continued refinement and calibration of this method (e.g. (Marsden 1999)). We adapted the point transect framework to the marine environment by conducting point counts of a constrained number of individuals at stations located along a transect. Rather than timed counts (as per the point count distance transect), we utilized point counts of a pre-determined number of colonies at each station. Although taxonomically complex, surveying corals presents fewer detectability problems (i.e. audible detection, mobility, cryptic behavior) than surveying birds, substantially reducing the main source of

methodological error (Lee and Marsden 2008). Moreover, standardizing the number of colonies sampled in each count controls for effort, ensuring a repeatable and efficient sampling unit. We compared the effectiveness and time efficiency of the PCT method to traditional LIT surveys for estimating species richness at the same reef site at Lizard Island, Australia. We compared 1) total species richness estimated from a standardized sample size, 2) species accumulation rate per unit effort (per additional individual, and per minute), and 3) species abundance distributions, to reveal detectability bias towards rare and incidental species.

2.3: Methods

Point Count Transect Survey Method

A linear transect of a specified length (in this case 50 m) is randomly deployed within the study site, with count stations located at regular intervals (in this case every 10 m) along the transect line (Fig. 2.1a). The transect length, and the spacing of count stations are highly flexible, depending on the research objective. For example, a study of species richness over depth could use a up-slope transect up a reef slope, with count stations at bathymetric, rather than distance intervals. In that case the transect length would be variable depending on the reef profile, as would the linear distance between count stations, but the survey principle remains the same. An initial coral colony situated on a consolidated section of reef substrate suitable for coral habitation is chosen and identified at each sampling station. The nearest neighboring colony to the initial colony is then chosen as the next in the survey (Fig. 2.1b). Successive colonies are identified such that the sampling area expands outwards in an approximately counterclockwise spiral shape from the initial colony (Fig. 2.1b). The directionality of the expanding spiral should remain consistent, but either counterclockwise or clockwise can be chosen. As this method details reef-building

coral occurrence patterns, areas known to be unsuitable for habitation, or which exclude the vast majority of species (eg. sand dunes, unconsolidated rubble banks) are not targeted. This is in contrast to existing area-based methods (eg. LIT) which often invest significant resources sampling areas of unsuitable habitat, which yields little relevant data. Additionally, the stipulation to survey suitable habitat, even when colonies are rare or absent, is an important measure of sampling effort, and represents a record of range limits, environmental filters, or other environmental factors influencing species range distributions. The requirement for types of habitat suitable for surveys can be expanded or restricted based on the research question. For a study focusing on species richness of *Acropora* spp. for example, areas of sand can be avoided, while a study focusing on *Fungia* spp. may only target sand areas. Colonies < 5 cm diameter were not recorded in this study due to difficulties consistently identifying juvenile corals to species level (Richards 2012). However, the minimum size of recorded colonies will be dictated by the taxonomic expertise of the surveyor. For instance, if fragments are collected for genetic analysis, or if the locally extant species are easily differentiated, this size limit may be significantly lower. After a pre-determined number of colonies is recorded at each station (in this case 12), the surveyor moves to the next sampling station (in this case located 10 m along the transect). Twelve colonies were selected at each sampling station for this study as experience suggested that this was the maximum number reliably recorded by the observer in ~5 minutes. This value should be determined prior to the start of the survey, and be suited to the question asked. The currency in this survey method is the individual colony, grouped into count stations, which allows for the number of individuals to be chosen to suit the research question and location of the study. For instance, the research question in this case focused on time efficiency at each site, in a

species rich region, so a short test revealed the maximum number of individuals reliable recorded in the chosen time limit (12 colonies in 5 minutes). In regions where coral density and/or richness is lower (such as the Caribbean, or East Pacific) a smaller number may be more suitable. Conversely, where time restrictions are not so severe, a larger number of colonies can be recorded at each sampling station. For this study, average colony densities allowed this number to be successfully recorded at each site, but to account for regions where colony densities are low, only colonies with at least part of the colony occurring within a two metre radius of the initial start colony are recorded. Colonies are countable as long as part of the colony occurs within the two metre radius. Where individual colonies extend beyond the sampling area, the size is recorded, but this is not deducted from the sampling area. If the pre-determined number of colonies cannot be found, the sampling will stop when the area is exhausted. For each colony, the species, water depth (to the nearest 0.1 m, corrected to lowest astronomical tide), maximum diameter and its perpendicular width (to the nearest 5 cm) are recorded. Species are identified *in situ* where possible, or with reference to a high-resolution image.

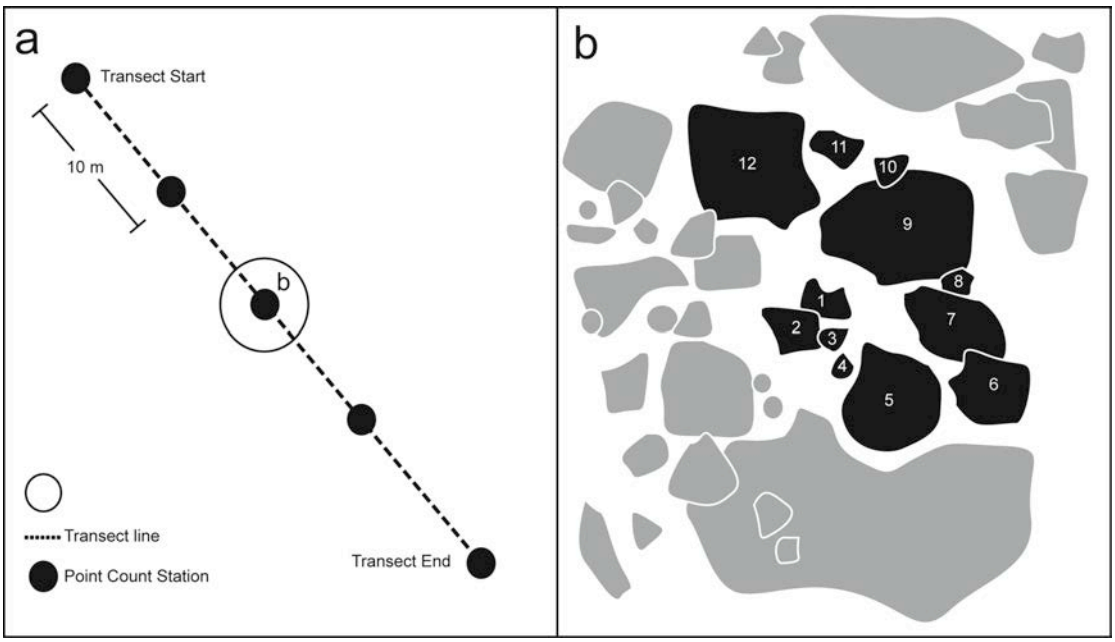

Figure 2.1: PCT Sampling Scheme.

A) overview of transect with count stations, b) one count sample (12 colonies). Shaded shapes represent recorded colonies, with numbers representing the progressive sampling order. Directionality of the count progression (in this case counterclockwise) is flexible, but should be decided prior to the study.

Comparing the Methods

Comparative surveys were conducted along the upper reef slope of 'Big Vickies' reef, Lizard Island, Australia (145.44^{o} E, 14.683^{o} S). No permit was required from the Great Barrier Reef Marine Park Authority (GBRMPA) due to the limited impact (non-extractive) nature of the research, conducted under the accreditation of James Cook University. Only visual surveys were conducted, and no endangered or protected species were collected or manipulated. Transects to be used for both methods were laid end to end along the reef slope where there was contiguous hard substrata between 2 and 4 m depth. Nineteen replicate 10 m LITs surveys were conducted, covering the same linear reef area as the PCT while representing a sampling intensity significantly greater than the three to five transect recorded in most studies. In addition to species identity, we recorded the time taken to complete each transect. We then conducted 4 PCTs of 50 m in length (containing 6 count stations per transect at 10 m intervals) as described above overlying the same reef area. The time taken to complete each survey was recorded.

The efficiency of the two methods was compared through the rate at which new species were observed against both time invested and the number of colonies surveyed. Species accumulation curves (Colwell et al. 2012) were used to compare estimates of alpha diversity from each method. Differences in sampling effort were accounted for using species accumulation curves extrapolated to a sample size of 50 samples (~600 individuals) through rarefaction using the program EstimateS (Colwell 2013). Curves were used to compare the rate of increase (indicating the rate of observing new species) and the number of species recorded at a common sample size (468 individuals). The average time taken to increase the sample size by one

individual was used to compare the time efficiency of each method. Species abundance distributions (SADs) were calculated to detect and display sampling bias towards or against rare species. Results are presented as mean ± 95% CI, unless otherwise stated.

2.4: Results and Discussion

Species Accumulation and Abundance

A total of 234 colonies were recorded on the LITs, compared to 288 colonies during the PCTs. A mean of 12.3 colonies were recorded for each 10 m LIT, compared to the 12 colonies sampled for each station of the PCT. PCTs recorded 85 species in 120 minutes, compared to the 41 in 171 minutes for the LIT. The rate of species detection was faster for the PCT and mean estimated species richness higher for any given sample size (Fig. 2.2). This difference was even greater when comparing species richness for any given sampling time (Fig. 2.3). Importantly, estimates of total site species richness did not converge with the PCT species accumulation curve when extrapolated using rarefaction (Fig. 2.2). At a comparable sample size (468 individuals), the estimated species number was substantially lower for the LIT (52.83, 95% CI: 41.13 – 64.53) than the PCT (100.99, 95% CI: 88.5 – 113.49). This disparity was even greater when time invested was accounted for (LIT: 42.85 95% CI: 35.44 – 50.27, PCT: 100.3 95% CI: 88.08 – 112.51 for 189 minutes) (Fig. 2.3). The number of species recorded by PCT after sampling 288 colonies (83 species) was also substantially higher than the estimated total species richness after sampling 600 colonies using LIT (56 species). Although both methods showed an asymptotic accumulation curve, the projected estimates of total species richness between the

methods were substantially different. Even with increased effort LITs are likely to underestimate the number of species present far more than comparable PCTs.

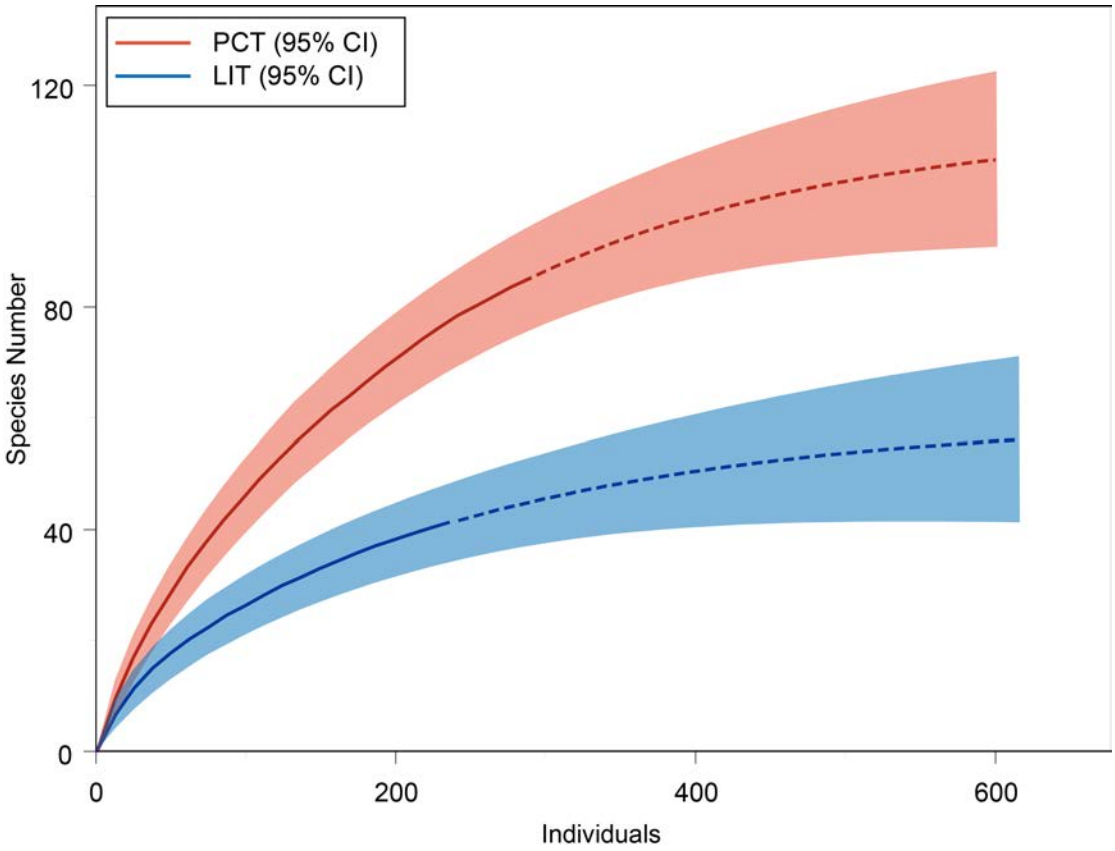

Figure 2.2: Species Accumulation Curves For PCT And LIT (by individuals added).

Species richness (y axis) by number of individual colonies sampled (x axis). Solid lines represent observed species richness, dashed lines show projected species richness rarefied to ~600 individuals, with corresponding 95% CI intervals (shaded area).

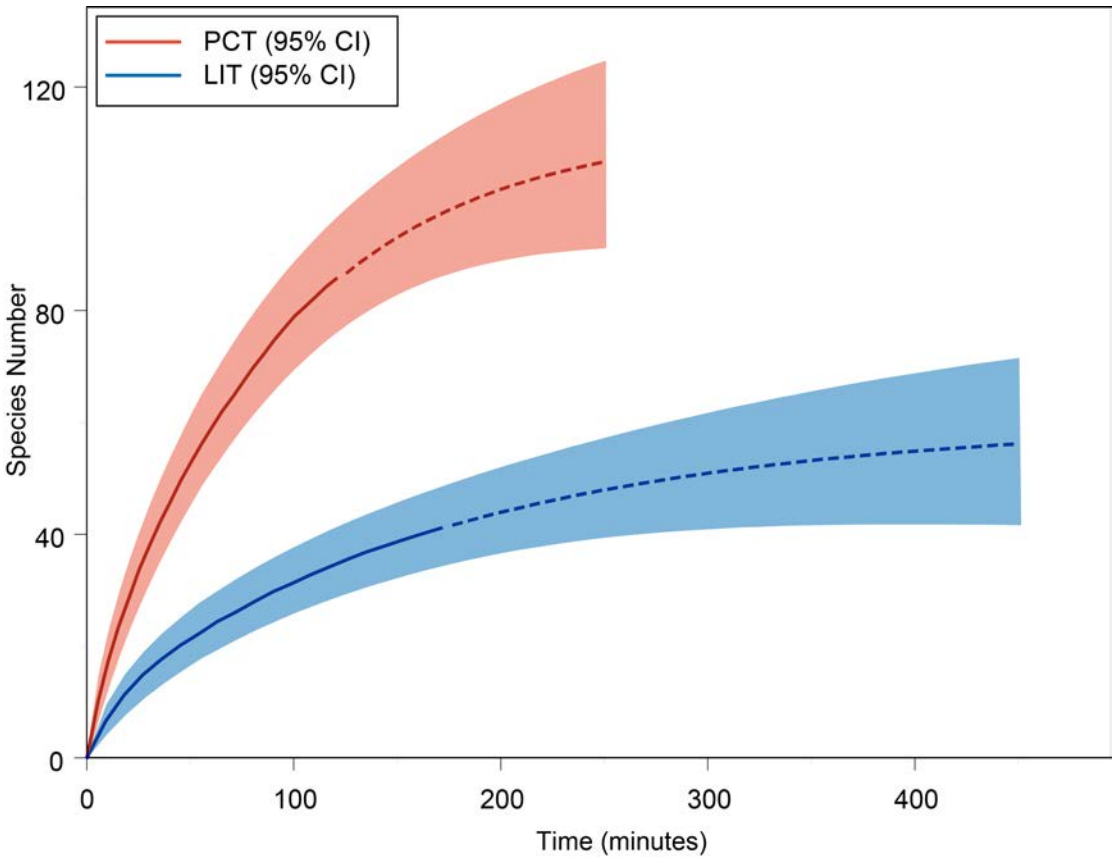

Figure 2.3: Species Accumulation Curves For PCT And LIT (by time invested). Species richness (y axis) by number of minutes invested in sampling (x axis). Solid lines represent observed species richness, dashed lines show projected species richness rarefied to ~600 individuals, with corresponding 95% CI intervals (shaded area).

The SADs revealed that 41 of the 44 species recorded in PCTs but not in LITs were rare (observed ≤ 3 times; Fig. 2.4). This indicates that the cause of the disparity between richness estimates was the failure of LITs to detect rare species (Fig. 2.4). Both methods indicated similar abundances among common species, but LITs consistently failed to detect rare species even though the number of replicate transects used at Big Vickies reef (n = 19) was considerably higher than the usual number of replicates used to characterize coral assemblages at any particular site (e.g. (Hughes et al. 1999,2012)). The cause of this chronic lack of detection of rare species by the LIT is likely due to the practical limitations of the method. Coral reef habitats are complex environments, with many microhabitats within a small region. The LIT method can only detect species that can be covered by a stationary line from above, and the application of the transect line is almost always unable to follow the reef contours precisely, missing most of the complex habitat. In theory, the LIT should not under-represent rare species, but the practical limitations of deploying the method in coral reefs causes errors. The real-world limitations of sampling methodologies are an important consideration, but are often overlooked in favour of theoretical justifications. Given the importance of detecting rare species for many ecological studies, we suggest that PCTs can be a more effective method of surveying coral assemblages than LITs.

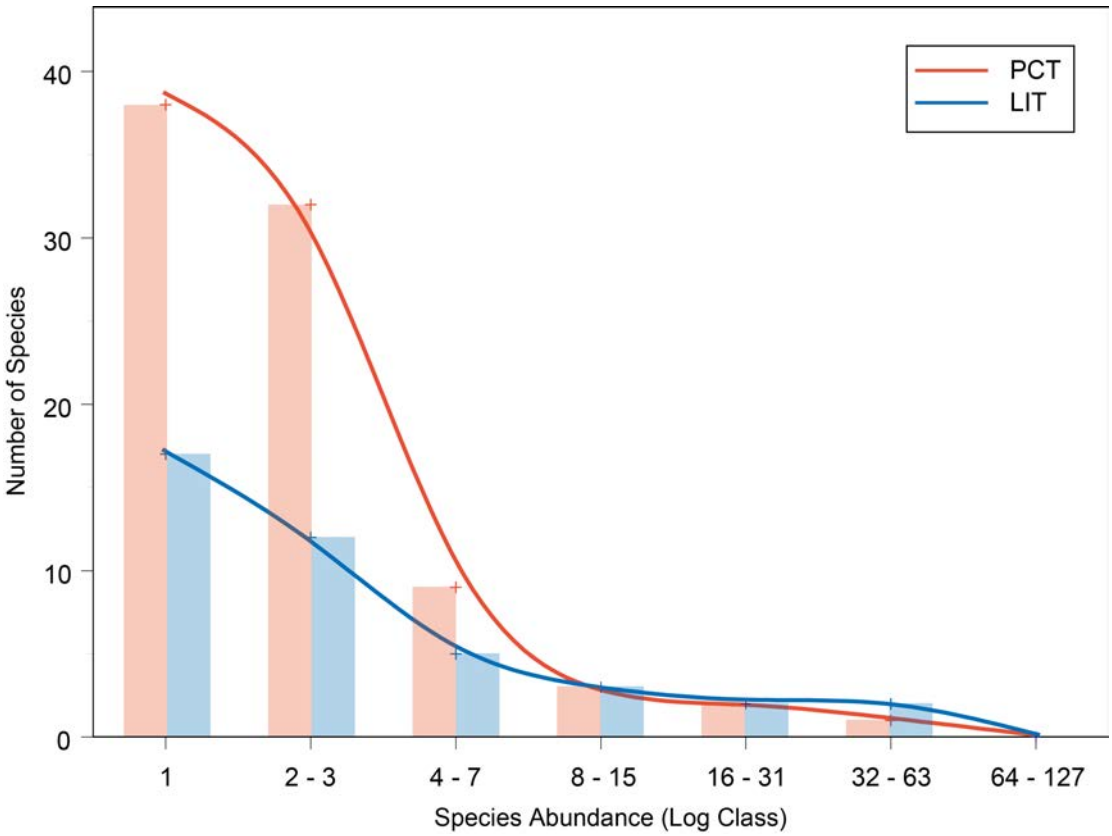

Figure 2.4: Species Abundance Distribution (SAD) Of PCT (red) and LIT (blue).

Frequency bins as per Gray et al. (Gray et al. 2006) (1, 2-3, 4-7, 8-15…).

The PCT was developed to assess patterns of species richness and meta-community structure along steep environmental gradients (e.g. depth) on coral reefs. These types of research questions do not require metrics of absolute abundance such as coral cover, which can be effectively obtained using LITs. As a result, the PCT represents a complementary data collection technique, rather than a replacement. The sensitivity of the PCT to rare and incidental species allows insight into the poor detection by the LIT, but emphasizes rapid capture of richness at the expense of absolute abundance measures. Using the PCT without considering its own strengths and weaknesses to a specific research question will likely result in an equally erroneous result as misuse of the LIT. Where detection of rare species is important, we propose the PCT as a robust and time-efficient method of collecting ecological data on coral reefs. This method will be particularly effective for examining questions such depth-diversity gradients, where the amount of survey time is greatly restricted. While this protocol was tested in a highly species rich habitat, with high coral abundance, it is applicable to any environment. The flexibility of the methodological framework allows for adjustment to specific systems, and questions.

Our results also highlight the importance of collecting field data using methods appropriate for the question being asked to avoid error in interpreting findings. For example, estimating species richness of a particular site using species accumulation curves requires samples to have no detectability bias towards or against any given species (Gotelli and Colwell 2001). Bias against rare species may confound results, and can be difficult to quantify unless the extent of the bias is known. The sensitivity of such analysis to sampling error and bias is well established (e.g. (Dornelas and

Connolly 2008)), yet basic errors continue to occur (Gotelli and Colwell 2001; Magurran 2004).

Coral reef ecologists should continue to develop new and improved methodologies to overcome logistical constraints, and improve the precision and scope of available data. Establishing the real-world strengths and weaknesses of various methodologies enables more researchers to make a more informed decision when collecting data. Methods such as the PCT can complement existing techniques, enabling researchers to better match data collection to suit the desired analysis.

Chapter 3: Energy limitation does not explain species richness gradients over depth in reef-building corals

Energy limitation does not explain species richness gradients over depth in reef-building corals

Short Title: Species richness and the left-skewed hump

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3.1: Abstract

Natural environmental gradients capture systematic variation in abiotic factors that influence the distributions of species, and can be exploited to test general hypotheses proposed to explain patterns of biodiversity. The *Species-Energy* hypothesis and the *Mid-Domain Effect* are the two theoretical models most commonly invoked to predict species richness gradients, featuring fundamentally different assumptions and predictions over an energetic gradient. Most tests of diversity hypotheses utilise terrestrial systems, and are often confounded by multiple factors. We overcome these obstacles by using observations of 9,576 colonies of photo-symbiotic corals over depth, (representing light; the key limiting energetic resource). Here, we show that neither model described the observed left-skewed hump, arguing against the assertion that the monotonic pattern is a "universal ecological law". Further, we demonstrate how veil effects, caused by truncated sampling of the gradient, materially distort these model fits, and can explain pervasive support for both models in the literature.

3.2: Introduction

Despite decades of research and over one hundred proposed explanations (Rahbek 1995; Gotelli et al. 2009), the underlying processes that generate and maintain species richness gradients remain poorly resolved (Rahbek 1995; Colwell and Lees 2000; Willig et al. 2003; Rahbek 2004). An important contributor to this lack of clarity is the limited availability of species abundance data with sufficient coverage and resolution to identify underlying patterns or distinguish between competing possible causes (Colwell and Lees 2000; Willig et al. 2003; Beck et al. 2016). In addition, the presence of ecosystem-specific differences in interspecific responses to environmental factors limits our ability to separate general ecological processes from local idiosyncratic effects (Field et al. 2009). Differences in dispersal boundaries (Karlson et al. 2004), area effects (Rahbek 1997,2004), sampling bias (Rahbek 1995; Gotelli and Colwell 2001), and the proportion of gradients sampled (Willig et al. 2003) have all contributed to a lack of consensus regarding the processes that generate and maintain species richness gradients.

The *Species Energy* hypothesis (*SE*) proposes that species richness gradients can be explained by energy availability, and predicts a monotonic decline of richness with declining energy (Wright 1983). However, despite many empirical field studies, there is still no consensus on the importance of *SE* in structuring ecological communities outside of controlled experiments (Chase 2010). A prominent alternative to the *SE* is the *Mid-Domain Effect* (*MDE*), which predicts a hump-shaped species richness distribution arising from geometric constraints of species ranges within a bounded domain in the absence of climatic or historical forces (Colwell and Lees 2000; Colwell et al. 2004). *MDE* models therefore predict peak species richness in the middle of a gradient within a bounded domain, irrespective of any underlying effect

of energy. These two models offer contrasting predictions, but both remain plausible and are much discussed explanations of the shape of species richness patterns along environmental gradients in natural ecosystems.

A strong test of the *SE* hypothesis can be achieved by examining a diverse biological community where all individuals occur along a geographically short but clearly defined energy gradient. In such a case, any effects of area and dispersal boundaries should be minimal, the limiting resource is clear, and the full gradient can be sampled. Coral reefs provide such a system because light provides photo-symbiotic reef-building corals with the vast majority of their energy requirements via photosynthesis (Anthony and Connolly 2004; Bongaerts et al. 2015), and the influence of energy availability on coral community composition is well understood (Connolly et al. 2005; Volkov et al. 2007). Although corals are mixotrophic, and can supplement their energetic budget with heterotrophic feeding (Williams et al. 2018), light availability is closely linked to the physiological process of calcification (Gattuso et al. 1999; Schneider et al. 2009), and heterotrophy supplements, rather than replaces, photosynthetic acquisition of energy. Importantly, photo-symbiotic reef corals occur over a relatively short energy gradient, as light energy declines exponentially and predictably from the surface to ~1% of surface irradiance at 60 m depth. Consequently, coral reefs allow sampling of virtually the entire gradient, thereby minimizing any potential effects of sampling a truncated energy distribution (Nogués-Bravo et al. 2008). Light irradiance, combined with competitive dynamics, has been invoked to explain the species richness gradient over depth (Connell 1978; Huston 1985; Cornell and Karlson 2000), although empirical support remains scarce primarily due to the logistical difficulty of obtaining data at depth.

Here, we quantified the abundance of photo-symbiotic reef-building corals over a depth range of 0 to 45 m, encompassing 98% of the light gradient, to assess whether species richness declined monotonically with decreasing energy availability or exhibited a hump-shaped distribution (Rahbek 2004). Specifically, we tested the competing predictions of a monotonic decline predicted by the SE, and a humped shaped distribution predicted by the MDE. We also test the potential influence of veil effects, by intentionally hiding portions of the gradient.

3.3: Results and Discussion

Model predictions for the *SE* and *MDE* models were monotonic and unimodal respectively, as expected (Fig. 3.1a). In contrast, the observed mean species richness showed a left-skewed hump, peaking at 12.5 metres depth (Fig. 3.1b). Over the full gradient, the *MDE* model offered greater explanatory power than the *SE* model (*MDE*: $r^2 = 0.31$, *SE*: $r^2 = 0.07$) due to its prediction of a unimodal hump-shaped distribution (Fig. 3.2). In contrast, there was little support for the monotonic decline predicted by the *SE* model. Importantly, both models are unable to predict species richness in the shallow high-energy section of the domain, with the *MDE* model predicting too few species and the *SE* model too many (Fig. 3.2b).

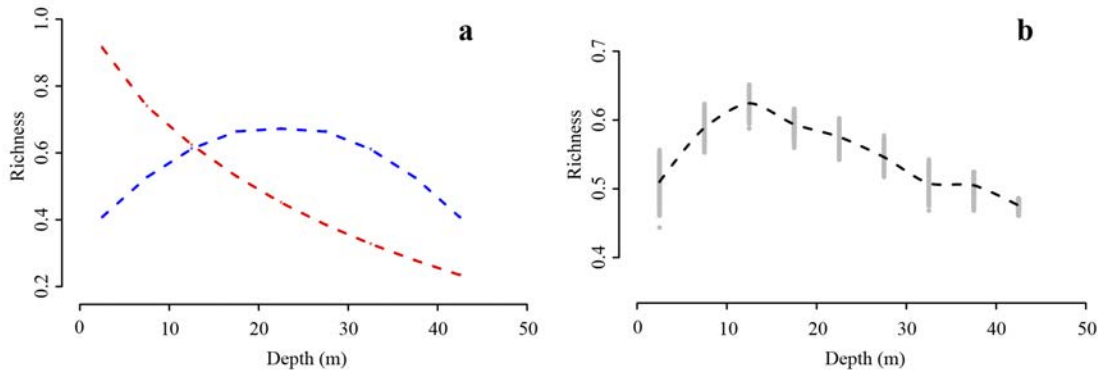

Figure 3.1: *Mid-Domain Effect model* and *Species Energy Model* predictions *vs* observed data.

a) Species Energy Model prediction using log light (red line) and Mid Domain Effect Model prediction (blue line). **b**) empirical species richness over depth, estimated using species accumulation. Grey dots are 999 values at each depth of species richness at a common sample size of 840 individuals. Black line represents mean values at each depth.

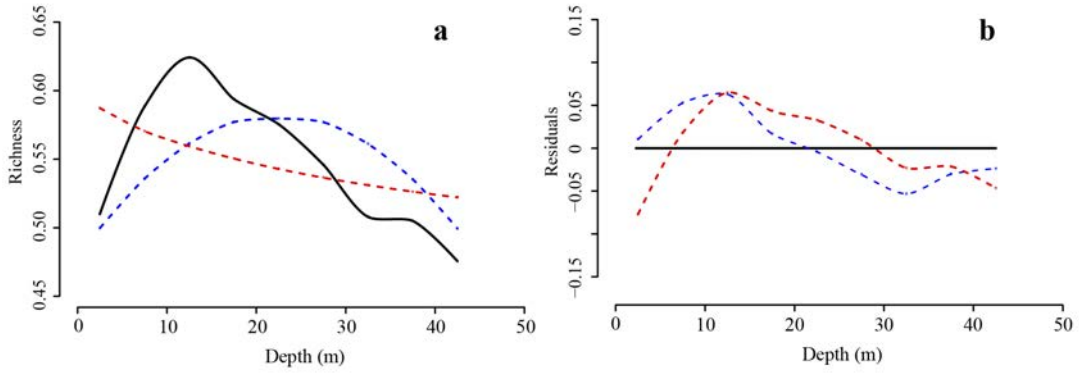

Figure 3.2: *Mid-Domain Effect model* and *Species Energy Model* model fits (a) and residuals (b).

Observed data (black dashed line) *Species Energy Model* prediction (red line, r^2 = 0.17), and *Mid Domain Effect Model* prediction (blue line, r^2 = 0.37).

While neither captures the observed pattern, only the null model *MDE* explicitly allows for further information from environmental factors, and captures the basic unimodal pattern (Colwell et al. 2016). The single factor *SE* can only conform to the empirical data by the addition of unspecified local factors, which must distort the proposed monotonic pattern by depressing species richness at the highest energy sites.

Similar declines in richness at the higher energy section of a domain has been observed in many terrestrial systems (Rosenzweig 1992; Rahbek 1995; Colwell et al. 2004; Beck et al. 2016; Bertuzzo et al. 2016), although the suggestion that the pattern is universal remains controversial (Rosenzweig 1995). The conflicting support for the *MDE* (Colwell et al. 2004) and *SE* (Evans et al. 2005) models as candidate explanations of species richness gradients can be explained to some extent by veil effects derived from truncated sampling of the energy gradient (McCoy 2002). Incomplete sampling is problematic in studies of species richness patterns along altitudinal gradients in terrestrial ecosystems (Nogués-Bravo et al. 2008). Here, the extent to which truncated sampling can influence the fit of either model is clearly demonstrated by veiling our data artificially (Fig. 3.3). Removing data from either the deepest (Fig. 3.3a) or the shallowest (Fig. 3b) thirds of the depth range produces an excellent fit for the *MDE* or the *SE* model respectively. These results confirm previous findings that incomplete sampling can obscure ecological patterns (McCoy 2002; Rahbek 2004; Nogués-Bravo et al. 2008), and emphasizes the need to collect data along the full gradient.

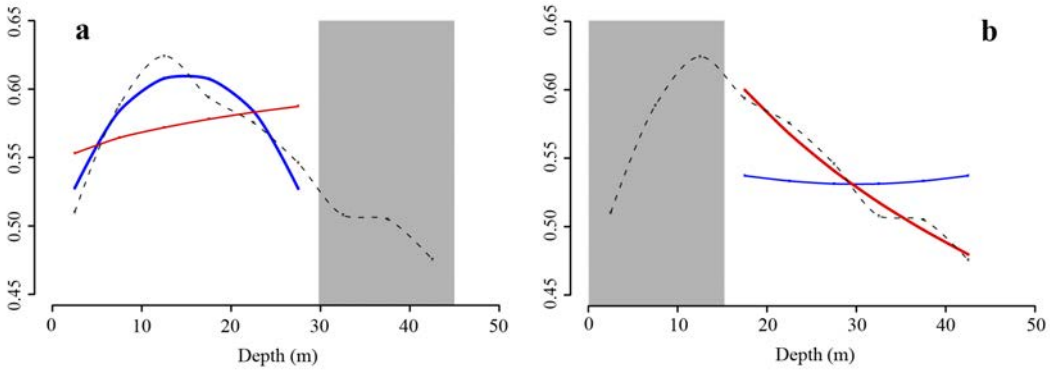

Figure 3.3: *Mid-Domain Effect model* and *Species Energy Model* model fits to truncated data.

Veiling of the low energy third (**a**) creates a very good fit for the *MDE* model (r^2 = 0.81), while veiling of the shallow third (**b**) provides a correspondingly excellent fit for the *SE* model (r^2 = 0.95).

The challenge of explaining the widespread pattern of species richness decline at the highest energy portions of a gradient (i.e., shallow depths, low altitudes) was first presented in the early 1990s (Rosenzweig 1992; Rosenzweig 1995). The pattern was thought to result from the effects of multiple energetic factors (Hawkins et al. 2003), scale effects (Chase and Leibold 2002), and local disturbance regimes (Connell 1978), but there remains no widely accepted explanation for the pervasiveness of this pattern. More recently, the challenge to explain the left-skewed hump has retreated into the background, often explained via post-hoc modification of model predictions based on local factors. Using observations free of commonly-occurring confounding factors such as area, definition of limiting energetic resource, sampling effort, and dispersal barriers, we show that the left-skewed hump remains. Monotonic patterns of increasing species richness with increasing energy are not a "universal ecological law" (Evans et al. 2005), rather they are more likely an artefact of idiosyncratic taxon-specific responses to environmental or ecological factors, or incomplete sampling of gradients of abiotic determinants. While there remains no satisfactory explanation for the degree of this left-skewed hump shaped pattern in species richness, identifying mechanisms and hypotheses that can better predict their occurrence and location would provide greater insight into the processes generating species richness gradients.

3.4: Methods

Field Surveys

Coral surveys were conducted within Kimbe Bay, Papua New Guinea. Kimbe Bay was chosen as it lies within the Indo-Australasian Archipelago (IAA) center of coral diversity, and hosts one of the largest regional coral species pools (Bellwood and Hughes 2001). Coral colonies were surveyed on six reefs, evenly distributed among

three locations (inner, mid, and outer bay), between April 2015 and November 2016. Inner bay reefs were defined as > 1.5 km from shore. Mid bay reefs were located between 8 km and 14 km from land, and outer bay reefs were located on the outer perimeter of Kimbe Bay, exposed to oceanic conditions. Corals were censused using up-slope point count transects to maximize species detection, especially rare species, and to standardize sampling effort (Roberts et al. 2016). At each reef, twelve replicate up-slope point count transect surveys were conducted, with a minimum of one count station completed in each depth bin. The nine separate depth bins were defined at five metre intervals from the surface (i.e. 0-5 m) to 45 metres (40-45 m). At least 144 colonies (mean = 177) were recorded and identified to species in each of 9 depth bins, at each of the six reefs (total n = 9,576 colonies, and > 864 colonies/depth bin). For each transect, the surveyor descended to the maximum depth bin, along a substrate of consolidated reef, with a maximum relief of at least 70^{o}. Once within the first depth bin, the surveyor selected the nearest live colony, on a consolidated substrate suitable for coral growth, and began the survey. Twelve colonies were recorded at each PCT site, ranging outwards from the central colony via the nearest neighbor. Only zooxanthellate reef-building scleractinia were recorded. For each individual, the genus, species, and depth (to 0.1m) were recorded. Where in-water species identification was uncertain, a high-resolution image of the colony was taken for later identification. Images were taken with a Nikon D300s DSLR and Tokina 10-17 lens in a Nauticam housing, with Inon strobes. Colonies were identified to species following current taxonomic guides (Veron 2000; Benzoni et al. 2007; Huang et al. 2014; Arrigoni et al. 2016), and species identified following Veron (2000) were updated to the currently accepted species names following Hoeksema and Cairns (accessed November 2016)(Hoeksema and Cairns 2018). Due to recent taxonomic

changes and uncertainties, colonies unable to be confidently attributed to an existing species were given working titles (e.g., *Acropora 1*) for the purpose of this study. To minimize variation in taxonomic identifications all observations were made by the same individual (TER). A voucher collection of 60 colonies representing uncertain species was collected and examined at the Museum of Tropical Queensland. Collected specimens were examined using morphological features in the skeletal microstructure, to verify field IDs.

Species Richness Analysis

Species Richness Values: To correct for any sampling effort discrepancies (Gotelli and Colwell 2001), species richness estimates for each depth bin were generated using species accumulation curves, and compared at a common sample size (840 individual colonies). Count data were pooled by depth bin, and species accumulation curves were generated, using the function 'specaccum' within the package 'Vegan' in R (Oksanen et al. 2007; R Core Team 2016). Curves for each depth bin were assembled by compiling counts randomly, and with replacement. Each curve was re-assembled 999 times to capture the variation in species richness, and was then subsampled at a sample size of 70 counts (representing 840 individual colonies). This sample size was chosen as it allowed species estimates to be compared at a size that did not require extrapolation of the accumulation curves beyond the reach of the empirical data at any depth. The resulting 8,991 data points were retained, and the mean of each depth taken to represent the empirical species richness.

Mid Domain Effect Null Model: A site-by-species matrix including all recorded species (n = 347), and all depth bins (n = 9) was used to generate MDE null model

predictions. Species ranges were retained, and the location on the empirical domain was randomized 999 times, using the function "rangemod1d" in the statistical R package "rangemodelR". Results were reported as mean expected species richness for each depth bin (Fig. 3.1a).

Species Energy Model: At each sample reef, a measure of light intensity was recorded at 5 metre intervals along the sampling gradient. Levels were recorded during November 2015, at a standardized time of day, using an Odyssey submersible photosynthetic irradiance recording system logger (Long et al. 2012). Each estimate was the mean of at least 3 estimates of irradiance recorded a minimum of 30 seconds apart. Light intensity values at each depth were calculated as a percentage of the light available at the surface. These values were used to estimate a standard light attenuation curve over depth for the study location. The *Species Energy* model prediction was then represented in analysis as the log of the percentage of surface irradiation available at each depth (Fig. 3.1a). The log was chosen, as the most suitable representative of the exponential decline in light, and best reflected the decline in energetic availability for the coral community.

SE and MDE Model Fit Analysis

General linear models: Model predictions were normalised to between 0 and 1. Empirical estimates were ranked by finding the proportion of the observed species pool captured by the species accumulation estimate at the highest sampling region (0 to 5 metres). This revealed that 81.77% of the observed species pool was captured at the sample size of 840 individuals, and the rest of the estimated values were taken to represent 81.78% of the total available species pool (347 species). The *MDE* range

overlap model was re-ranked as a proportion of the total observed species pool (347 sp). The *SE* model was represented by the log of the percentage of surface light available over depth. 1 was equal to 100% of surface light, 0.5 equal to 10% of surface light, and 0 represented 0% surface light. Both the *MDE* and *SE* were tested in single factor general linear models over the full gradient. Variance partitioning was calculated using the function *varpart* in the package *vegan* (Oksanen et al. 2007; R Core Team 2016).

Truncated Sampling

To simulate the effects of truncated sampling, *MDE* range re-sampling models were run using only the top two thirds of the empirical data (0 to 30 m) and the bottom two thirds (15 to 45 m). The relevant portion of the light gradient (representing the *SE* model) and observed richness were then retained, and general linear models performed as per the prior analysis.

Chapter 4: Depth Diversity Patterns On Coral Reefs Are Maintained by Regional Processes

Depth Diversity Patterns On Coral Reefs Are Maintained by Regional Processes

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4.1: Abstract

Processes that create and maintain patterns of diversity across environmental gradients operate at specific spatial scales. Therefore, identifying differences in species turnover at different scales can reveal the processes influencing community assembly. Hump-shaped diversity patterns at local scales (e.g., reef-building corals over depth) are often explained as a modification of a monotonic regional-scale pattern of decreasing diversity with depth by local-scale processes. Here, we test this hypothesis by comparing observations with null expectations to assess changes with depth in the species turnover among assemblages of reef-building corals at reef, and sites-within-reef scales. At the reef scale, coral assemblages were more heterogeneous than expected at all depths, consistent with an effect of environmental filtering. Conversely, site scale assemblages were only marginally more heterogeneous than expected at all depths, suggesting processes operating at this scale (i.e., competition) were not influential. Crucially, observations at neither scale provided evidence of processes influencing local species richness patterns. Instead, the regional species pool size was correlated with both reef- and site-scale richness within depths, indicating that regional factors were more important than local ecological processes in structuring depth diversity patterns in corals, and that the regional species richness pattern is not monotonic, but rather unimodal.

4.2: Introduction

Ecologists seek to understand the formation and maintenance of species richness patterns (Rosenzweig 1995; Lawton 1999). Well known species richness patterns include those observed over gradients of latitude, altitude, and depth (Rosenzweig 1992; Willig et al. 2003). Potential mechanisms maintaining these gradients are numerous, operating simultaneously at multiple spatial scales, making it difficult to discern their separate effects (Huston 1999; Rahbek 2004). However, the many processes that operate at specific spatial scales can be studied using multi-scale analyses, whereby the scale of operation of a process can be used to help estimate how it affects community assembly (Kraft et al. 2011; Myers et al. 2013; Lessard et al. 2016). For example, competition occurs among individuals within sites, whereas environmental factors such as exposure to wind and waves vary at larger scales. At regional scales, processes such as speciation, extinction and large-scale dispersal control the size and membership of the pool from which local assemblages are drawn (Ricklefs 1987; Caley 1997; Caley and Schluter 1997).

One way to reveal the processes structuring communities is to examine species turnover between sites (beta diversity) at multiple scales. Using a null model approach (Kraft et al. 2011),the expected level of beta diversity between sites based on the size of the regional species pool alone can be determined, and compared to empirical observations. Subsequently, deviations from the null expectation can be seen as informative of community assembly processes operating at the site scale (Myers et al. 2013; Segre et al. 2014). Since different ecological processes influencing community assembly operate at different scales, the relative scale of ‘regional’ and ‘site’ can be progressively stepped down, to examine processes operating at specific scales.

Applying this approach across a natural gradient can then be used to identify processes responsible for generating the observed patterns of species richness. This approach, however, requires assumptions to be made regarding the scale at which a specified process operates.

Reef-scale species richness gradients over depth in reef-building corals tend to be left-skewed and humped (Huston 1985; Cornell and Karlson 2000). The shape of this gradient at the regional scale, however, is unclear due to data deficiency, but is thought to decline monotonically as light, and therefore energy available to photosymbiotic corals, becomes increasingly limited with depth (Wells 1957; Cornell and Karlson 2000). The incongruence between local-scale empirical observations and the hypothesized regional-scale pattern is generally attributed to local-scale processes reducing coral species richness in shallow waters, thereby modifying the underlying monotonic species richness pattern across depth that may otherwise form (Fig. 4.1) (Huston 1985; Cornell and Karlson 2000). Environmental filtering, by virtue of increased disturbance frequency in shallower depths, and intensive competitive interactions in shallow, high-light habitats have both been suggested as possible modifying processes (Wells 1957; Connell 1978; Done 1982; Kühlmann 1983; Huston 1985; Cornell and Karlson 2000). However, there is little empirical evidence as to how these processes change over depth, nor their importance in creating and maintaining species richness patterns (Cornell and Karlson 2000).

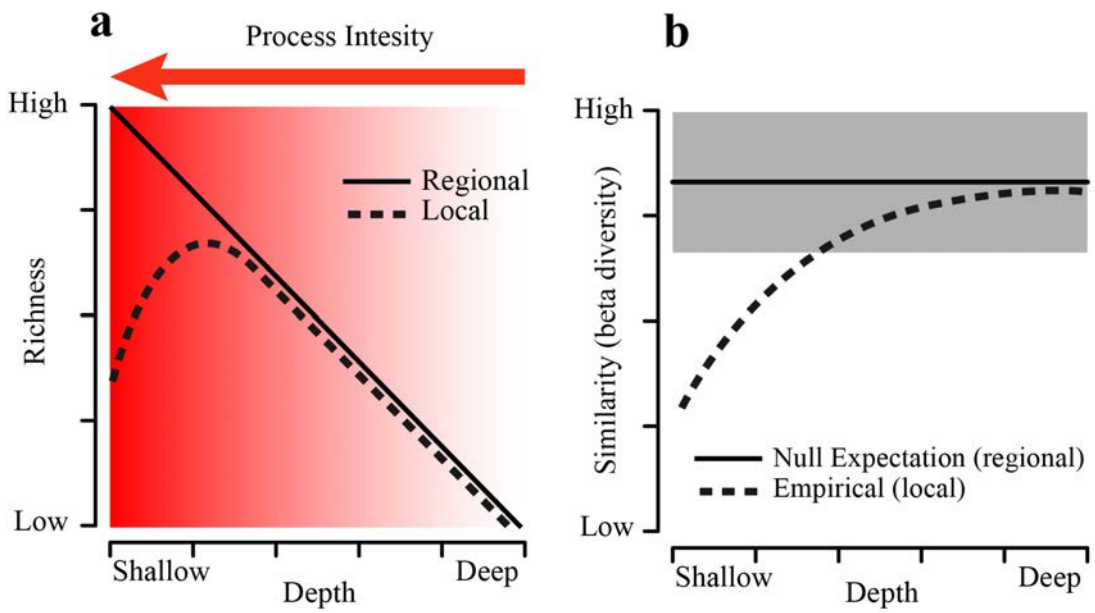


Figure 4.1: Theoretical modification of a species richness pattern by local processes.

a) The regional species richness pattern (solid line) can be distorted by local processes (red gradient), which change in intensity over the gradient (in this case depth) to produce a hump-shaped pattern (dashed line). b) This process will be reflected in levels of site similarity (beta diversity) over the gradient. Empirical levels of site similarity (dashed line) will show a corresponding deviation away from null expectations of beta diversity (black line, grey polygon), where local processes are more influential.

Coral communities are strongly influenced by numerous abiotic environmental factors, notably hydrodynamic exposure (Done 1982; Madin et al. 2014; Roberts et al. 2015), light (Anthony and Connolly 2004), and temperature (Baird et al. 2009b). These factors vary locally, and can potentially modify the hypothetical regional-scale pattern of monotonic decline in species richness with depth. Hydrodynamic energy, for example, dissipates rapidly with depth (Monismith 2007), producing a gradient of disturbance which might decrease local richness in shallow areas more frequently exposed to hydrodynamic disturbances (Connell 1978; Done 1982; Cornell and Karlson 2000; Madin et al. 2014). Similarly, high light levels in the shallows may facilitate rapid growth, leading to competitive exclusion of inferior competitors, and reduced species richness at local scales. Meanwhile, coral communities at greater depths generally feature a dwindling number of species, attributed to the smaller available regional species pool at depth (Cornell and Karlson 2000). However, there is little to no empirical evidence supporting the role of local-scale assembly processes in creating and maintaining the local-scale hump-shaped pattern of species richness over depth in corals. Here, we use empirical observations of beta diversity calculated using an extensive data set of 5,832 coral colonies incorporating three hierarchical spatial scales, and a null-model approach to examine the influence of local-scale community assembly processes on the species richness gradient of corals over depth. We test for trends in beta diversity over depth, and for deviations from the null expectation at scales relevant to environmental filtering (reef scale) and biological interactions (sites within a reef).

4.3: Methods

Field Surveys

Study sites were located in Kimbe Bay, in the West New Britain Province of Papua New Guinea. Surveys were conducted between April 2015 and November 2016. Six reefs were surveyed, with two reefs in each of three areas within Kimbe Bay (Inner, Mid, Outer)(Fig. 4.2). Inner bay reefs were defined as < 1.5 km from shore. Mid bay reefs were located between 8 km and 14 km from land, and outer bay reefs were located on the outer perimeter of Kimbe Bay > 14 km from land. At each of the six reef locations, nine up-slope point count transects (Roberts et al. 2016) were conducted, with sampling sites located within nine depth bins. The nine depth bins were defined at five metre intervals from the surface (i.e. 1-5 m) to a maximum depth of 45 m (40-45 m). A total of nine sampling sites were recorded at each depth bin (n = 9), at each reef (n = 6), with a total of 486 sites surveyed.

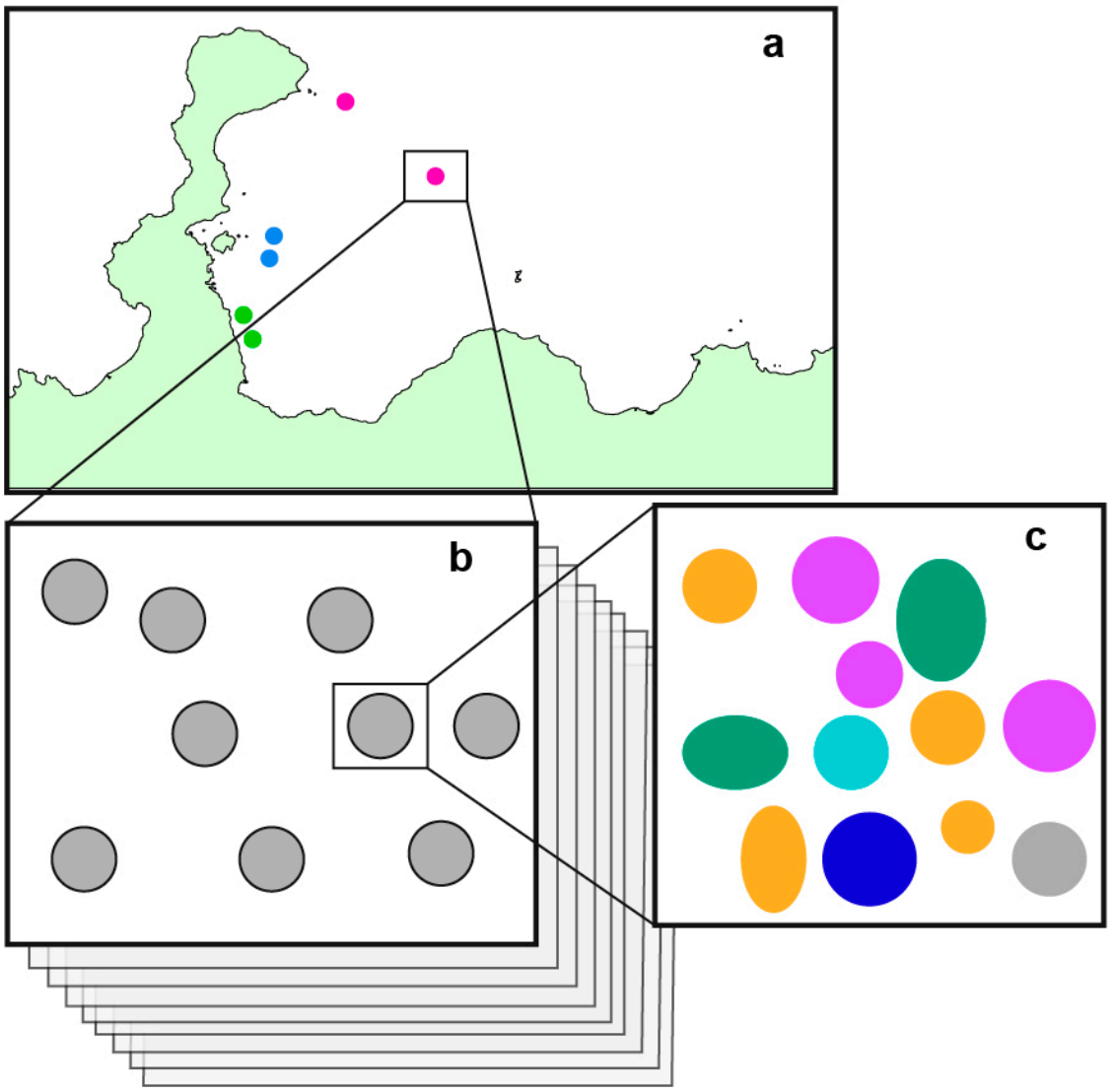


Figure 4.2: Hierarchical sampling design.

a) The regional scale included six reefs within Kimbe Bay, Papua New Guinea: Outer (red), mid (blue), and inner reefs (green). b) Reef scale sampling consisted of nine replicate sites, at each of the nine depth bins; and c) within reef sampling consisted on the twelve coral colonies within each site.

Sample sites were located on reef substrata with a maximum relief of at least 70º to minimize the potential effect of shading on coral occurrences. For each sample site, TER selected the nearest living zooxanthellate reef-building scleractinian colony of at least 5 cm diameter to begin the point-count survey. Each site sample consisted of the twelve nearest neighbor colonies radiating outwards from the initial colony. Species identity and depth of occurrence (to 0.1m) of each colony was recorded. Where in-water species identification was uncertain, a high-resolution image or small sample was taken for subsequent identification. Colonies were identified to species following current taxonomic guides (Veron 2000; Benzoni et al. 2007; Huang et al. 2014; Arrigoni et al. 2016), and species identified following Veron (2000) were updated to the currently accepted species names following Hoeksema and Cairns (accessed November 2016) (Hoeksema and Cairns 2018). Due to recent taxonomic changes and uncertainties, colonies unable to be confidently attributed to a valid species were given working titles (e.g., *Acropora 1*). To minimize misidentifications all observations were made by the same individual (TER). A voucher collection of 60 colonies representing uncertain species was collected and examined at the Museum of Tropical Queensland. Collected specimens were examined using morphological features in the skeletal microstructure, to verify field IDs. The sampling methodology was developed specifically to minimize detectability bias away from rare species, a common and insidious issue when comparing taxonomic communities (Beck et al. 2013).

Null Model Analysis

By using a null model to generate expected values of beta diversity for a given level of gamma diversity, differences in the magnitudes of observed beta diversity and/or the directions of these changes over an environmental gradient can be isolated and

understood within the context of community assembly. Expected values of beta diversity were generated following Kraft et al. (2011)(Kraft et al. 2011) across three spatial scales: bay, reef and site (Fig. 4.2): Bay included all data within the study region (Kimbe Bay). Reef included all data at each of the six survey reefs. Sites included the twelve colonies within each count survey, and represented the smallest spatial scale examined. For the purpose if this study, each depth bin (n = 9) is considered to be a distinct metacommunity. Beta diversity was calculated as pairwise comparisons of the relevant alpha (reef or site) using Sørensen's index (Sorensen 1948), using equation (1):

$$\frac{2A}{2A+B+C} \quad (1)$$

where *A* is the species common to both samples, *B* represents species restricted to the first sample, and *C* represents species found only in the second sample. Sørensen's index was chosen as the measure of beta diversity because it is sensitive to the turnover of rare taxa, and focuses on taxonomic differences between samples. While the index is compromised by unbalanced sample sizes and detectability of taxa (Chao et al. 2004), our data were fully balanced, and the sampling methodology specifically addressed detection bias between rare and common taxa.

Reef Scale (Environmental Processes)

For each of the nine depth bins, a species pool was assembled consisting of all species recorded within a bin, and the relative abundance of each species. Null assemblages were generated at each depth by selecting 108 individuals from the available species pool, with the species abundance distribution mimicking the empirical data. A sample of 108 individuals was used as this was the largest sample size available in the empirical data at every reef/depth combination. At each depth, six assemblages were

assembled using random draws from the sampling universe with replacement to represent the six reefs sampled. Pairwise analysis of taxonomic similarity between the six assemblages was then conducted using Sørensen's index, and the mean similarity value was recorded. This process was repeated 1000 times for each of the nine depths, and the values used to generate a grand mean expectation with 95% confidence intervals. At each depth, the full empirical species pool was available each time a new set of assemblages was drawn from the sampling universe. A corresponding empirical value was generated for each expected similarity measure generated by the null model. At each of the six reefs, the empirical reef assemblages of 108 individuals were compared using pairwise analysis of Sørensen's index, and the mean value recorded. This was repeated at each of the nine depths, which are considered to be distinct metacommunities. To examine the relationship between null expectations and empirical values, the empirical values were subtracted from the null grand mean, and the deviance plotted over depth (e.g., Fig. 4.1b). A linear model was fitted to the deviance of the empirical values from the null expectation to test for directional change over depth.

Sites Within Reefs Scale (Biotic Processes)

At the site scale, null communities were generated for each depth as per the methodology outlined above. In this case, species pools for null assemblies were constructed using the species sampled at each depth, within each reef. Nine assemblages of twelve individuals were then drawn from the sampling universe, replicating the empirical sampling. In this analysis, the processes mediating a species presence, and relative abundance at a reef and depth are accounted for, isolating the processes influencing the assembly of individuals into a site assemblage. As for the reef scale analysis, the nine assemblages at each depth were compared using pairwise

analysis of Sørensen's index, and the mean value recorded. This was repeated 1000 times, and the grand mean with 95% confidence intervals generated. The process was repeated for each of the six reefs, and corresponding empirical values were generated for each reef and depth. To assess the deviance of the empirical values from the null estimates, the empirical value of mean site similarity for each depth/reef combination was subtracted from the corresponding mean null estimate. As with the reef scale analysis, a linear regression was fitted to the empirical deviations from the null expectation to test for directional change over the depth gradient.

Regional Enrichment Analysis

All available data were compiled to generate a value for species richness at each of the nine depths, and tested for correlation with species richness values at both the reef and site within reef scales over depth. Reef scale values were empirical values of species richness at each reef/depth combination, and site scale values were represented by mean richness per site at each depth bin. Linear regressions were performed for both combinations to identify significant correlations indicative of regional enrichment across depth.

4.4: Results

At the reef scale, coral assemblages were less similar than expected at all sampling depths (Fig. 4.3a) with no detectable change in beta diversity over depth (Fig. 4.3b). In contrast at the site scale assemblages were only slightly less similar than expected at all depths (Fig. 4.4a). However, we did detect an increase in beta diversity (lower similarity) with depth, attributable to dissimilarity among assemblage at sites below 35 m (Fig. 4.4b). Neither the reef nor the within-reef scales showed evidence of processes changing in influence over depth in a way that could depress species richness in the shallows to produce the hump-shaped species richness pattern (Fig.

4.1b, Fig. 4.3b, Fig. 4.4b). However, richness at the regional scale (whole study area of Kimbe Bay) at each depth was positively associated with richness at both smaller scales (Fig. 4.5). It should be noted that the species pools at each spatial scale are not independently determined, requiring a degree of caution in interpreting the results.

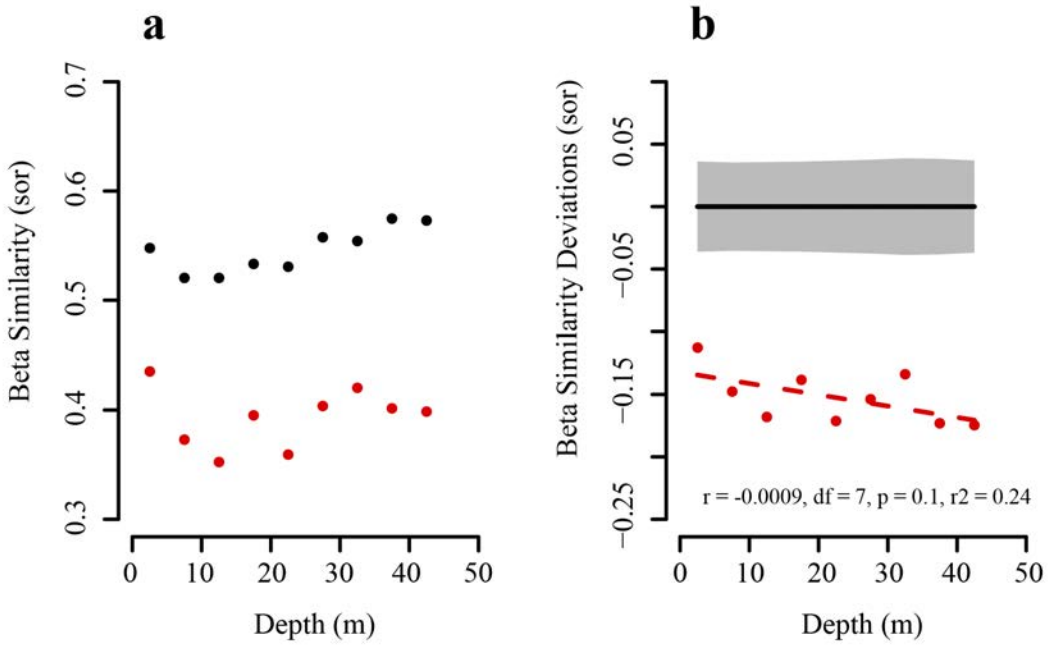


Figure 4.3: Reef scale relationships between Sørensen's beta diversity and depth. a) expected values in black and empirical in red. b) deviations of empirical beta values from expected values (black line, grey polygon represents 95% CI of the mean), showing linear model fit of response over depth (red line).

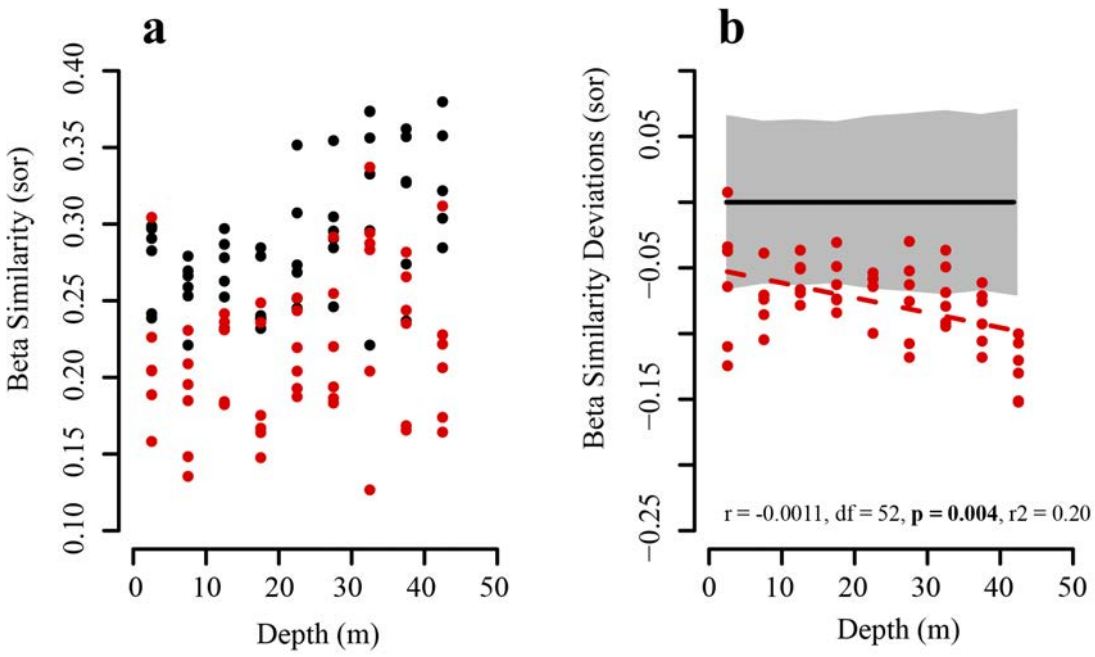


Figure 4.4: Site scale relationship between Sørensen's beta diversity and depth. a) expected values (black) and empirical (red), b) deviations of empirical beta values from expected values (black line, grey polygon represents 95% CI of the mean), showing linear model fit of response over depth (red line).

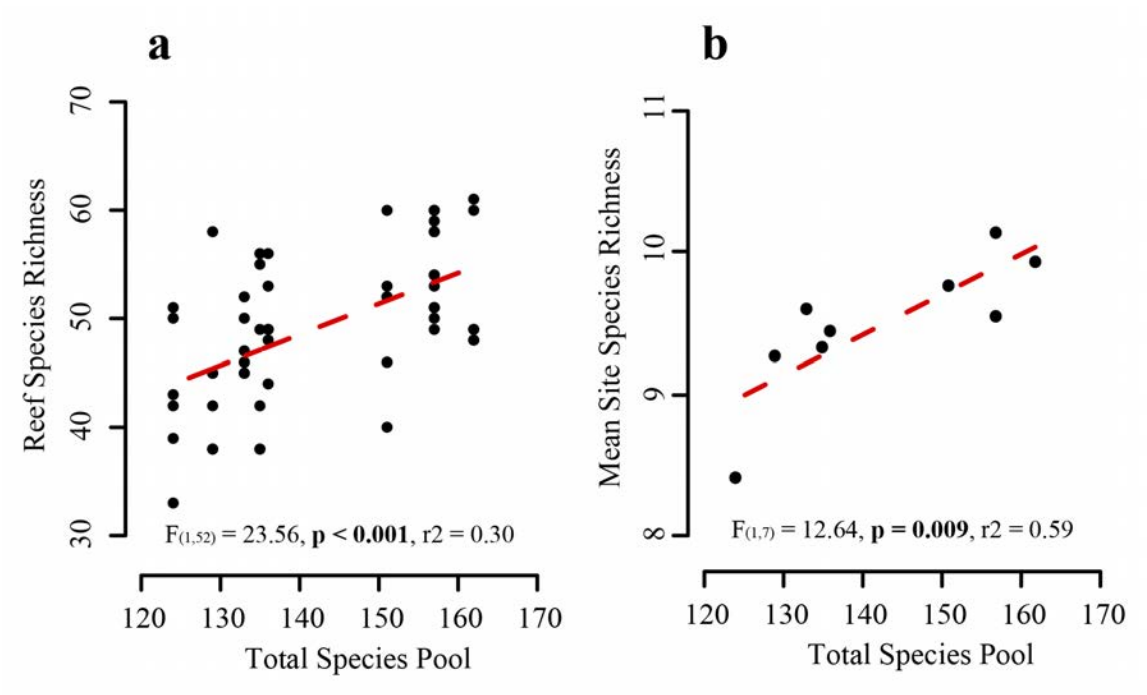


Figure 4.5: Relationship between regional and local species richness.

a) Species richness at each reef (black points), is positively associated with the size of the regional species pool (red line). b) Mean species richness at the site within reef scale also shows a positive association with the regional species pool.

4.5: Discussion

Coral assemblages were consistently less similar among reefs than expected by chance at all depths, indicating that environmental filtering strongly influences community assembly throughout the depth gradient. Conversely, assemblages at site scales (sites-within-reefs) were largely indistinguishable from null expectations (with the exception of sites below 35 m), suggesting that competition plays a negligible role in structuring coral communities. Neither scale showed evidence of decreasing similarity at shallow depths, which would be expected if local-scale processes were responsible for modifying a regional monotonic species richness pattern into a unimodal skewed hump (Fig. 4.1b). Finally, coral assemblages exhibited regional enrichment at both local scales throughout the depth range (Fig. 4.5), further suggesting that processes operating at larger spatial scales are predominantly responsible for the local-scale species richness patterns on coral reefs. Although the inevitable non-independence of the species pools at each spatial scale requires caution in interpreting these results, the findings suggest that it is possible that the unimodal skewed-hump pattern, rather than the hypothesized monotonic decline, is the regional-scale pattern of species richness over depth.

The reefs of Kimbe Bay are affected by a heterogeneous mix of environmental factors commonly observed to influence coral community assembly, including hydrodynamic exposure, turbidity, nutrient regimes and disturbance histories (Wells 1957; Done 1982; Madin et al. 2014; Roberts et al. 2015). These factors provide the opportunity for environmental filtering, where species composition is determined by prevailing local environmental conditions. Differences in the effects of dominant environmental factors between reefs (notably hydrodynamic disturbance) diminish quickly with

increasing depth (Monismith 2007) making environmental conditions increasingly homogeneous. This diminution potentially allows the increased effect of environmental filtering in the shallows to disproportionately depress local species richness at shallow depths (Huston 1985; Cornell and Karlson 2000). While higher than expected beta diversity between reefs suggests a strong role for environmental filtering, there was no evidence of a decrease in significance at greater depths. As such, our results indicate that reef scale processes are unlikely to be solely responsible for the decline in species richness at the shallowest depths.

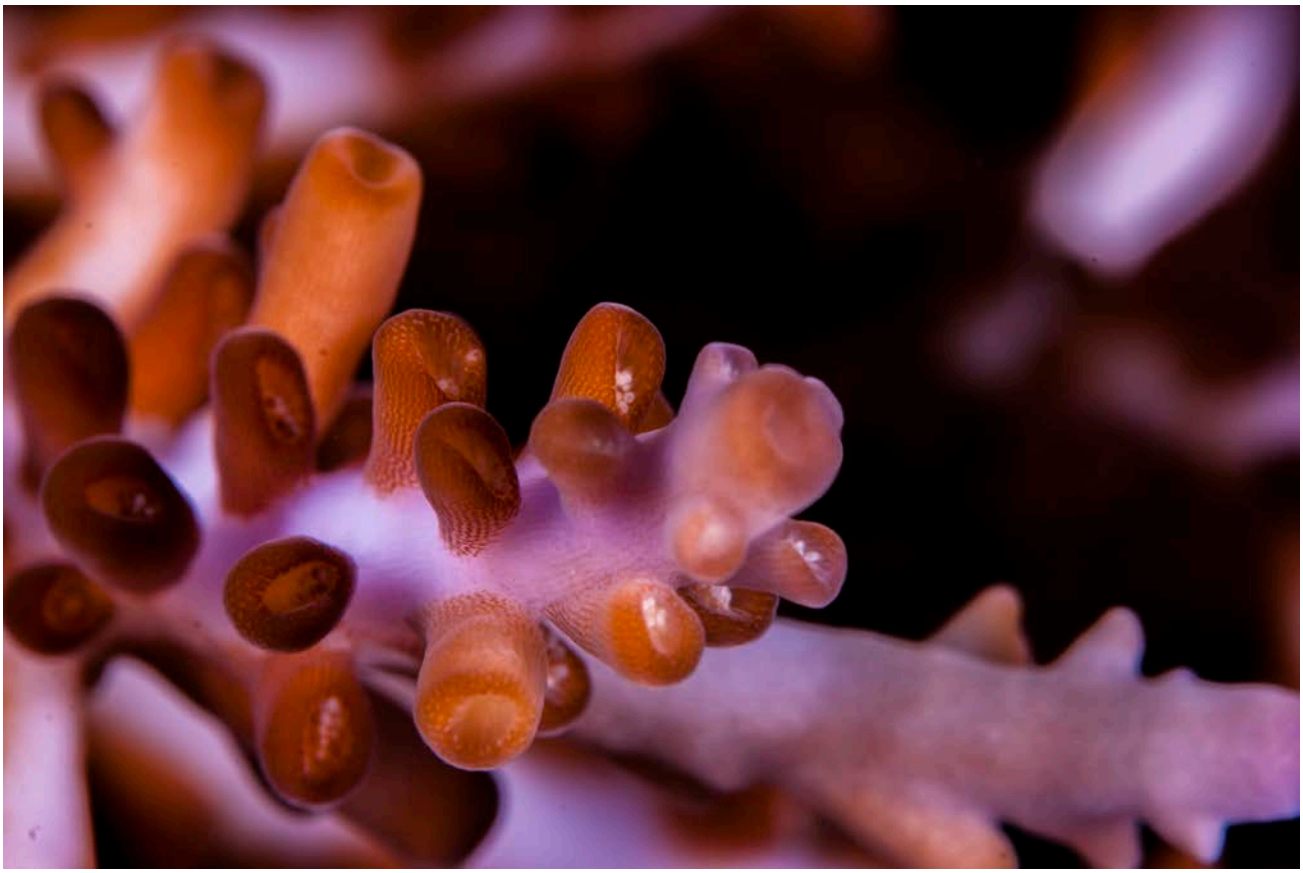
In contrast, patterns of similarity between sites within reefs were largely indistinguishable from the null (Fig. 4.4a), but were increasingly dissimilar at depths below 35 m (Fig. 4.4b). At this scale, the environmental conditions between sites (within a given reef) become more consistent, making competitive interactions the likely cause of the changing beta diversity patterns observed. Our results show that no significant competitive effects were evident in the upper 35m, suggesting these processes are ecologically unimportant for community assembly at this scale. This finding is consistent with previous results questioning the influence of competitive interactions on both coral community assembly (Cornell and Karlson 1996; Cornell and Karlson 2000), and physiological processes such as growth (Álvarez‐Noriega et al. 2018). One potential explanation for the decrease in similarity below 35m is that priority effects are maintained competitively over small scales, with the identity of the dominant colonizer inconsistent between sites (Fukami 2015). This would result in a greater than expected clustering of conspecifics in count samples, but low consistency in the identity of the dominant species in each count. Lower rates of recruitment (Turner et al. 2018) and extinction (Huston 1985) at greater depths would promote

priority effects, and this might contribute to consistently high rates of beta diversity at the reef scale at greater depths. Some degree of self-recruitment might also reinforce this pattern at a reef-scale, causing higher reef-scale beta diversity (Gleason and Hofmann 2011). However, the smaller sample size, and inherent non-independence of the reef scale and within-reef scale species pools requires a degree of caution when interpreting these results. It is also important to note that the attribution of community assembly processes to specific spatial scales requires a number of assumptions to be made, which allow for uncertainty in the results.

Results from our multi-scale dataset confirm a strong influence of reef-scale environmental factors in shaping coral assemblages across depths. In addition, we show that processes operating at smaller scales, such as competition, may have little influence on community assembly. Crucially, we found no clear evidence that local processes at either scale show changes in intensity consistent with modifying a theorized monotonic regional-scale species richness pattern over depth into the empirically demonstrated left-skewed hump local pattern. Instead, even at the smallest spatial scale, it appears that regional enrichment contributes substantially more to the species richness-depth gradients than local-scale processes. The importance of regional-scale processes in determining species richness gradients reported here is consistent with prior studies examining species richness across the Indo-Pacific (Cornell and Karlson 1996; Karlson et al. 2004; Cornell et al. 2007). This result indicates that rather than differential local scale processes, the hump-shaped species richness pattern over depth in corals is possibly formed by regional scale processes (e.g.; speciation, extinction, large-scale dispersal, endemism), which control the species pool from which local scale communities are assembled (Caley

and Schluter 1997; Cornell et al. 2007). Consequently, it is possible that the regional species richness pattern over depth is not monotonic, as assumed, but unimodal. Although hump-shaped species richness patterns are consistently reported along altitudinal gradients in terrestrial systems at regional scales, there remains little consensus regarding the processes that create and maintain them (Rosenzweig 1992; Rahbek 1995; Lomolino 2001; Nogués-Bravo et al. 2008). By showing that the hump-shaped pattern in species richness over depth is likely to be an empirical reality, we hope to precipitate the development of predictive hypotheses to understand how it is created and maintained.

Chapter 5: Modeling Depth Niches of Reef-Building Corals



Modeling Depth Niches of Reef-Building Corals

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5.1: Abstract

Understanding the distribution of species in space and time is a fundamental component of ecological research. While species abundance response curves (abundance over a bounded range) can vary widely, bounded abundance distributions are often represented by simple, highly correlated metrics, such as the mid- point, or the total extent of a species' geographic, altitudinal, or bathymetric range. Patterns of depth zonation are prominent in coral reef assemblages, yet most species have a broad depth range; a paradox that is unresolvable if distributions are represented by these simple metrics. Here, we use a unique dataset of 9,567 coral colonies representing 170 species over a 45 m depth range to model species depth abundance distributions, and generate two descriptive parameters: the optimum depth (i.e. the depth at which the species is most abundant) and the depth niche breadth (i.e. the depth range where species abundance are over 60% of the maximum value). We then compare the model parameters to equivalent metrics derived from range extent data, and test the capacity of four life history traits (gross morphology, morphological plasticity, mean corallite size, and larval development mode) to predict the optimum depth and niche breadth. Species with encrusting and laminar growth forms were more likely to have an optimum depth at the deeper end of the domain, while species with submassive growth forms were associated with a wider niche breadth. Niche breadth was unrelated to total range size, and the majority (67%) of species preferentially occupy less than half of their depth range. Optimum depth values were distributed throughout species' ranges, irrespective of mid-depth, and over half of all species had their optimum depth at the range limit (0 or 45 m). Together, these results reconcile the depth generalist paradox by invalidating the assumption that species abundance is

normally distributed over a species range, and demonstrating how coral species preferentially occupy a subset of their depth range.

5.2: Introduction

Variation in the abundances of species across space is a ubiquitous feature of the natural world (MacArthur 1972; Gaston 2000), and explaining this variation is a primary goal of ecology (Guisan and Zimmermann 2000). Measures of species abundance distributions in space (e.g., range size or area) are fundamental to many community ecology theories, notably niche theory (Hutchinson 1957; MacArthur and Levins 1967; McGill et al. 2006). Species abundance distributions are also widely used in fields such as conservation planning (Corsi et al. 1999; Carpenter et al. 2008; Rodríguez‐Soto et al. 2011), and for predicting the effects of environmental change (Araújo et al. 2005; Austin and Van Niel 2011).

Changes in the abundance of a species in space, for example along an environmental gradient, are often characterized using an abundance response curve. Where sufficient empirical abundance data is unavailable, the abundance response curve of a species is often extrapolated from its range limits, which can be obtained from sources such as museum records and historical references (Raxworthy et al. 2003; Elith and Leathwick 2007). For any given species, the shape of this curve is often assumed to follow a normal distribution, with abundance in the center of the range (Hutchinson 1957; Brown 1984; Gaston 2003). The range center is assumed to constitute a species optimal habitat, and consequently supports the greatest abundance. As distance from the center grows, the habitat suitability decreases, producing a decline in abundance until the physiological limits of a species are reached at the range boundary. In reality, however, the abundances of most species are poorly characterized by the normal distribution (Austin 2002; Ehrlén and Morris 2015; Dallas et al. 2017). Indeed, response curves can have an infinite variety of different shapes (Austin et al. 1994;

Austin 1999). Thus, range limits are not sufficient to accurately predict the abundance distribution of a species (Brown 1984; Austin et al. 1994; Brown et al. 1995; Austin 1999). Issues arise with more complex approaches as well. For instance, unconstrained generalized additive models (GAM) can produce excellent fits to empirical data but are difficult to interpret ecologically (McCune et al. 2002).

Another way to describe species abundance curves is to constrain the possible curves to a pre-defined set of shapes. The hierarchical set of logistic regression models proposed by (Huisman et al. 1993), and refined by (Jansen and Oksanen 2013), provide such an approach. While allowing for the infinite amount of variation possible in the way a species utilizes space within the domain, the Huismann-Olff-Fresco (HOF) models restrain the curve to one of seven basic shapes (Fig. 5.1) each of which can be readily interpreted ecologically. For example, model IV can be linked to the normal distribution of a species, where the gradient examined captures a consistent change in the dominant factors influencing a species' distribution. In cases where the key factor does not change consistently over the gradient (for instance, substrate type over depth) multimodal models, such as models VI and VII, may best capture the abundance distribution. This approach strikes a balance between the need to use multiple parameters to capture the potentially complex shape of a species abundance curve, and the inherent limitations of empirical data. In addition, this approach can yield informative model parameters, such as the optimum (point of highest response), and the breadth of the inner and outer niches (region of the curve featuring at least 0.6 of the maximum value, and 0.135 of the maximum value respectively, Fig. 5.2) (Huisman et al. 1993; Heegaard 2002; Jansen and Oksanen 2013).

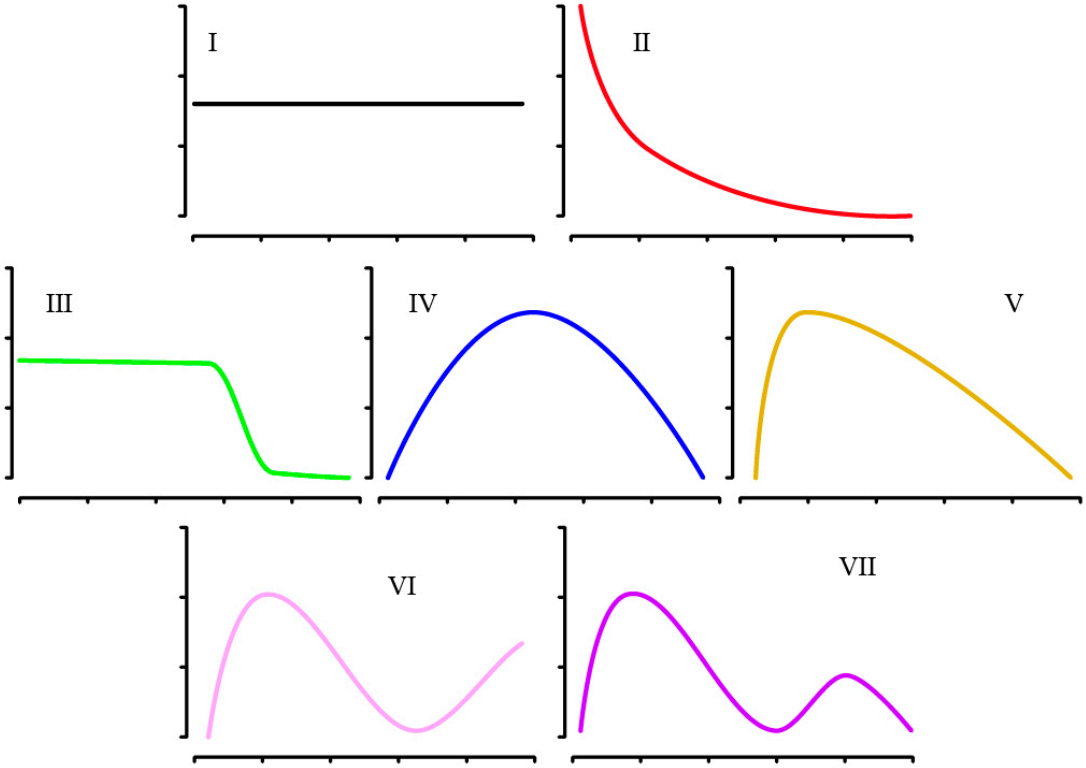

Figure 5.1: Seven types of models described by Huismann-Olff-Fresco analysis. Possible response shapes include monotonic (models I to III), unimodal (models IV and V) and bimodal (models VI and VII) patterns.

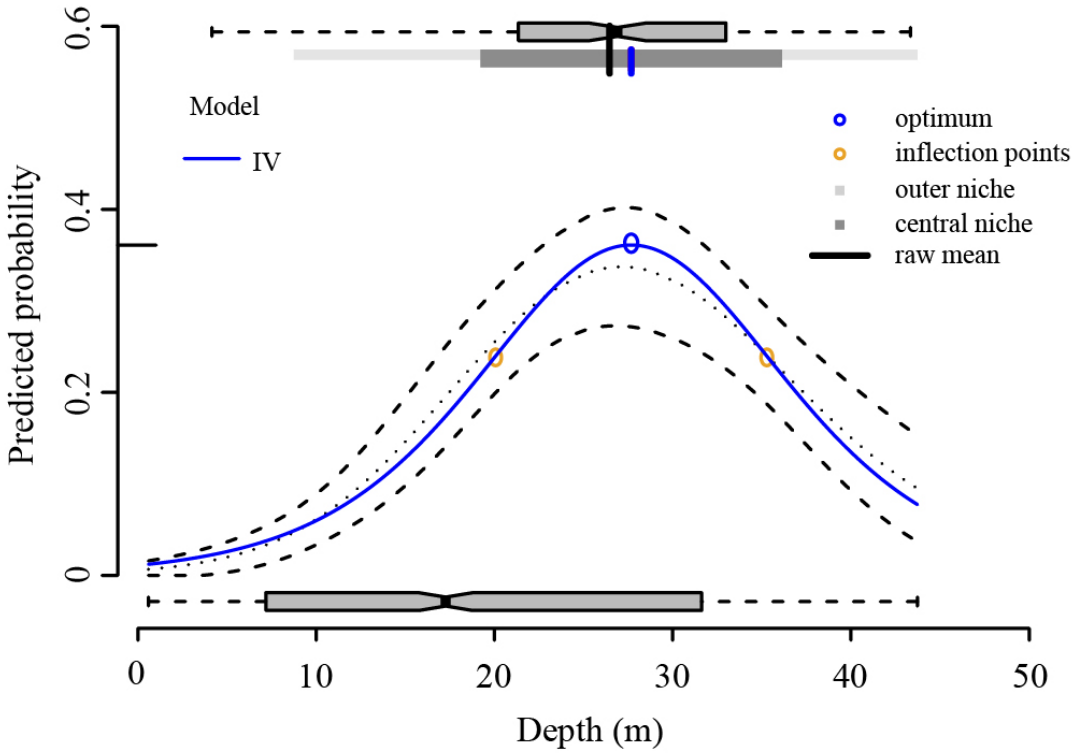

Figure 5.2: Species abundance response model over depth for *Acropora granulosa.*

Model response (blue lines) shows the predicted probability of the species (y axis) over the depth gradient (x axis), using the chosen model type (IV). Black dotted lines represent the unconstrained GAM model with 95% confidence intervals, to ascertain goodness of fit. Box plots show the presence (top) and absence (bottom) of the species in each of the 798 count stations. Grey bars represent the outer (light grey) and inner (dark grey) niche boundaries.

Reef-building corals inhabit the world's tropical oceans to a depth of 60 m or more (Veron 2000; Kahng et al. 2010). Strong and consistent patterns of zonation occur over the depth gradient, reflecting the influence of environmental factors, which change over depth (such as light, temperature, and hydrodynamic stress) on species depth distributions (Sheppard 1980; Done 1982; Kühlmann 1983). The width of a species depth range, and location on the domain are often used to characterize a species specialization and depth preference respectively, with wider depth ranges reflecting a more depth generalist species (e.g., Muir et al. 2015). However, the majority of species exhibit wide depth ranges (Loya 1972; Kühlmann 1983; Bridge et al. 2013) leading to a paradoxical situation, whereby a majority of depth generalist species produce strong patterns of depth zonation. Additionally, there has been a recent research focus on 'mesophotic' coral ecosystems (coral communities existing at the lower end of the photic zone) (Kahng et al. 2010; Bridge et al. 2013). Correspondingly, the maximum depth records for many species are being extended as data acquisition improves (e.g., (Englebert et al. 2017)), further exacerbating the depth generalist paradox. Moving beyond the one-dimensional metric of range extent by using species abundance response curves to describe how species occupy space within their range may resolve this situation.

Here, we test the capacity of HOF models to capture the depth response curves of 170 reef-building coral species over a depth gradient of 0-45 m, and compare the use of the two model parameters, optimum depth and niche breadth, to equivalent range derived metrics (depth range, and range mid-point) used to describe depth distribution in these species. Finally, we test the capacity of four life history traits linked to the depth distribution of a species, to predict the optimum depth and niche breadth.

5.3: Methods

Coral Surveys

We surveyed 9,576 reef-building corals over a 45 m depth gradient between April 2015 and November 2016 on six reefs in Kimbe Bay, West New Britain Province, Papua New Guinea. We chose Kimbe Bay because of the high species richness of the coral fauna (Veron 1995; Keith et al. 2013). Corals were surveyed using the 'point count transect' method (Roberts et al. 2016). At each of the six reefs, a minimum of 10 point count stations were recorded, at each of nine depth bins, progressing from 45 m depth to the surface in five metre intervals (i.e., 0-5m, 5-10m, 10-15m…). In each case, reefs were sampled along a consolidated reef slope extending beyond 45 m depth, and habitats likely to support a small specific subset of coral species (i.e., caves, sand) were avoided.

Count stations consisted of twelve reef-building coral colonies of >5 cm diameter. After the random selection of an initial colony, the nearest neighbor colonies were progressively chosen until a total of twelve colonies were recorded (see Roberts et al. (2016) for further details on sampling design). The depth (to the nearest 0.1 m) and species identity of each colony were recorded. Where in-water identification was uncertain, a high-resolution image or small sample was taken for later identification. Images were taken with a Nikon D300s DSLR and Tokina 10-17mm lens in a Nauticam housing, with two Inon Z240 strobes. Colonies were identified following (Veron 2000; Benzoni et al. 2007; Schmidt-Roach et al. 2013; Huang et al. 2014; Arrigoni et al. 2016). Species identified following Veron (2000) were updated to the currently accepted species names following Hoeksema and Cairns (accessed November 2016) (Hoeksema and Cairns 2018). Colonies unable to be identified as existing species were given working titles (e.g., *Acropora 1*). All observations were

made by TER. A voucher collection of 60 colonies representing uncertain species was collected and examined at the Museum of Tropical Queensland. Collected specimens were examined using morphological features in the skeletal microstructure, to verify field IDs.

Model Application

HOF models were applied following the methods of (Jansen and Oksanen 2013). To provide a more stable representation of species depth use, data were analyzed using presence/absence only. Each station was taken as a sampling unit, and the presence or absence of a species within the station was recorded. This was feasible due to the high number of replicate count stations in the dataset (n = 798). To minimize the influence of low sample frequency on the model fits, only species present in a minimum of 10 stations were included in the analysis (170 of the 347 species recorded) The depth of each count station was considered as the mean depth of all the corals recorded in that station. Models were run using the package *eHOF* (Jansen et al. 2017) in R (R Core Team 2016). The model type (I to VII, Fig. 5.1) which best reflected the abundance distribution of a species was chosen using Akaike Information Criteria (AIC). The analysis was re-run 100 times, and the most commonly chosen model type was regarded as the best-fit model. Model parameters for the model fit for each species were then exported from the analysis (Table. S5.1). General additive model fits were also generated for each species, as an unconstrained measure of model fit, as per Jansen and Oksanen (2013).

Model Parameters

Two parameters derived from the eHOF model outputs; optimum depth (representing depth preference), and niche breadth (representing depth specialization), were extracted for each species. To ensure an acceptable level of model fit, only species

occurring in a minimum of 20 stations (n = 110) were used for this analysis (Table. S5.2). Optimum depth was defined as the location on the domain (depth) where the response of the model was highest (Fig. 5.2). Niche-breadth was defined as the inner niche width, representing the range of the domain where the model response measures at least 60% of the highest response value recorded (Fig. 5.2) (Heegaard 2002). As such, a wider inner niche width reflects a more gradual curve shape (and more generalist response), while a narrower width is indicative of an acute response shape (and a more specialized response). For species fitted to model III, the mean of the depth range covered by the optimum was calculated and used in further analysis. Similarly, for species returning models VI and VII, the optimum, and corresponding inner niche for each of the two modes was recorded as *SpX.a*, and *SpX.b*. All analysis was conducted in R (R Core Team 2016).

Trait Analysis

Life history traits for all species occurring in at least 20 of the 798 count stations (n = 110) were extracted from the online database coraltraits.org (Madin et al. 2016a) (Table. S5.2). Gross morphological trait data was attributed to one of ten categories; *massive, submassive, encrusting, encrusting with uprights*, *laminar, tabular and plates, corymbose, digitate*, *hispidose*, *branching open.* Morphological plasticity was coded as the number of differing morphologies recorded for each species (1 to 5). Mean corallite size was kept as a raw measure in millimeters of the mean corallite diameter (0 to 285). Larval development mode was coded as: 1 = *spawner*, 2 = *brooder*. Missing data was in-filled using museum records from the Museum of Tropical Queensland, and personal observations from the collected data. For each trait, two linear models were run, using the trait values as predictor variable against

the two parameters derived from the eHOF model outputs (optimum depth and niche breadth.

Results

Model Fits

The depth response curves of the 170 species included examples of all of the seven possible shapes (Fig. S5.1, Table. S5.1). Forty six (46) species response curves were best described by model II, and 37 by model III, therefore the optimum depth of half of all species occurred at the limits of the domain. Of these species, 36 (21% out of all) had the optimum depth located at the lower limit of the domain (i.e. at 45 m) As the depth limit was not imposed by a hard boundary (such as the water surface), it is likely that these species have optimum depths below 45 m. The depth response curve was unimodal in 59 species (model IV = 39, model V = 20), and bi-modal in 9 (model VI = 5, model VII = 4). Seven species were fitted to model I, but all seven occurred in 16 sites or less, and were not included in subsequent analysis due to the uncertainty of model fits in species occurring in less than 20 sites.

Model Derived vs Range Derived Metrics

There was no correlation between the extracted model parameters of optimum depth and niche-breadth $F_{(1,120)} = 2.36$, $P = 0.127$) (Fig. 5.3a), in strong contrast to species depth range and depth mid-point ($F_{(1,120)} = 17.94$, $P < 0.001$) (Fig. 5.3b). Species with niche breadth values covering less than half of the total domain (more specialized species) represented 81% of all species (Fig. 5.4a), but only 15% of species met the same criteria when replacing niche breadth with depth range (Fig. 5.4b). Similarly, 61% of species showed optimum depth in the shallow half of the domain (<22.5 m) (Fig. 5.4a), while the same proportion (61%) had mid-depth values in the deeper half (>22.5 m) (Fig. 5.4b). Species niche breadth was not consistent with range size (Fig.

5.5a), and species optimum depth was not consistent with depth range mid-point (Fig. 5.5b).

Traits Analysis

Species possessing laminar and encrusting morphologies were more likely to have an optimum depth in deeper waters, while colonies with submassive morphologies were more likely to have wider niche breadths (Fig. 5.6). No other morphologies were associated with optimum depth or niche breadth (Table. 5.1, Fig. S5.2). Similarly, neither larval development mode, morphological plasticity nor corallite size were correlated with optimum depth or niche breadth (Table 5.1, Fig. S5.2).

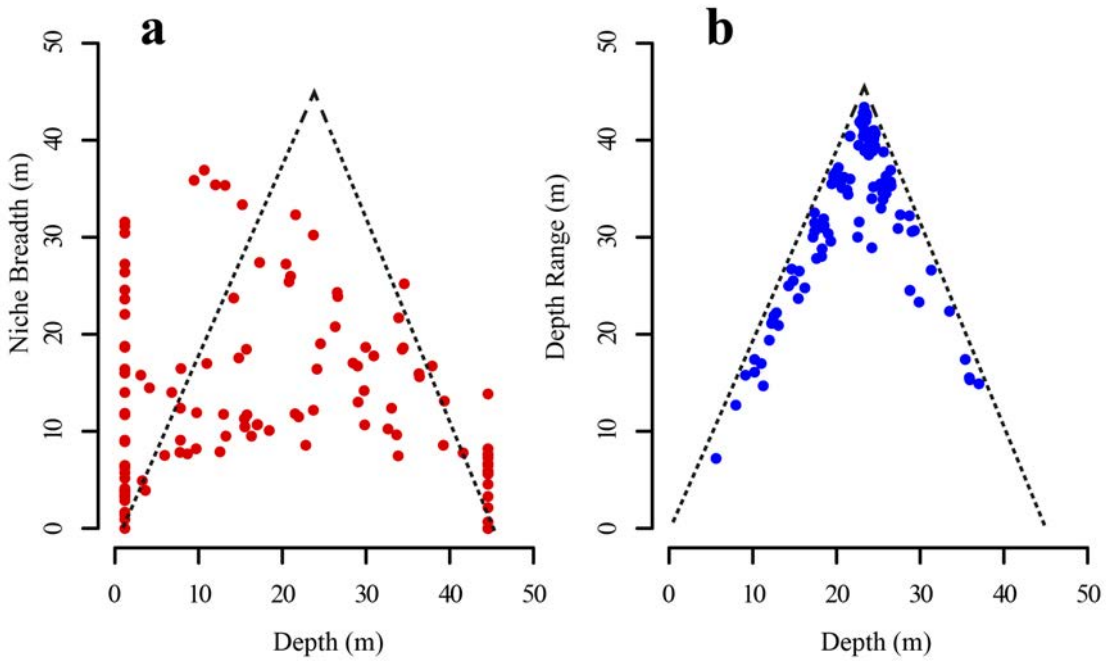

Figure 5.3: Relationship between measures of species depth preference and depth specialization.

a) the relationship between species optimum depth (depth preference, x axis) and niche-breadth (specialization, y axis) for each of the 110 species modeled. b) the relationship of between species depth mid- point (depth preference, x axis) to total depth range (specialization, y axis). Dotted lines display the boundaries of possible values derived from simple depth range information.

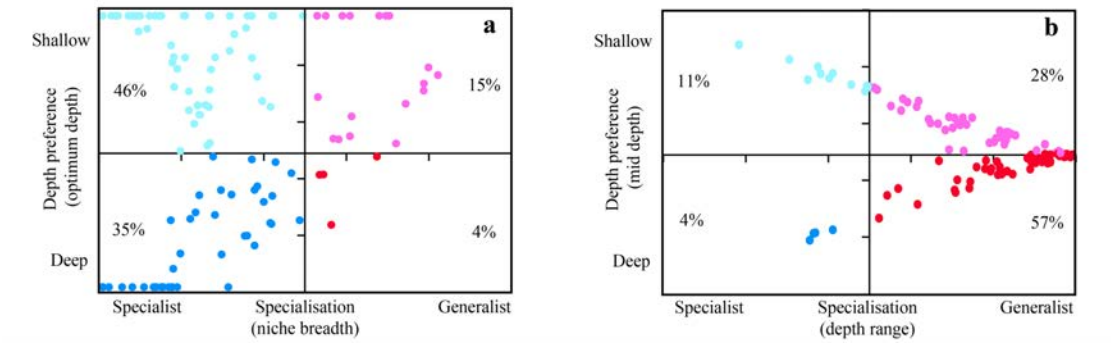

Figure 5.4: Classification of coral species as deep or shallow specialists or generalists.

a) using species modeled inner niche width as a measure of specialization, and depth of optimum model response as a measure of depth preference. b) using species range extents as specialization, and species' mid points of their depth range as depth preference. Intersection of the grid lines marks mid depth, or a species with a specialization measure covering 50% of the gradient, and a preference score occurring at 50% of the gradient. Percentage values represent the proportion of the species assessed occurring within each quadrant.

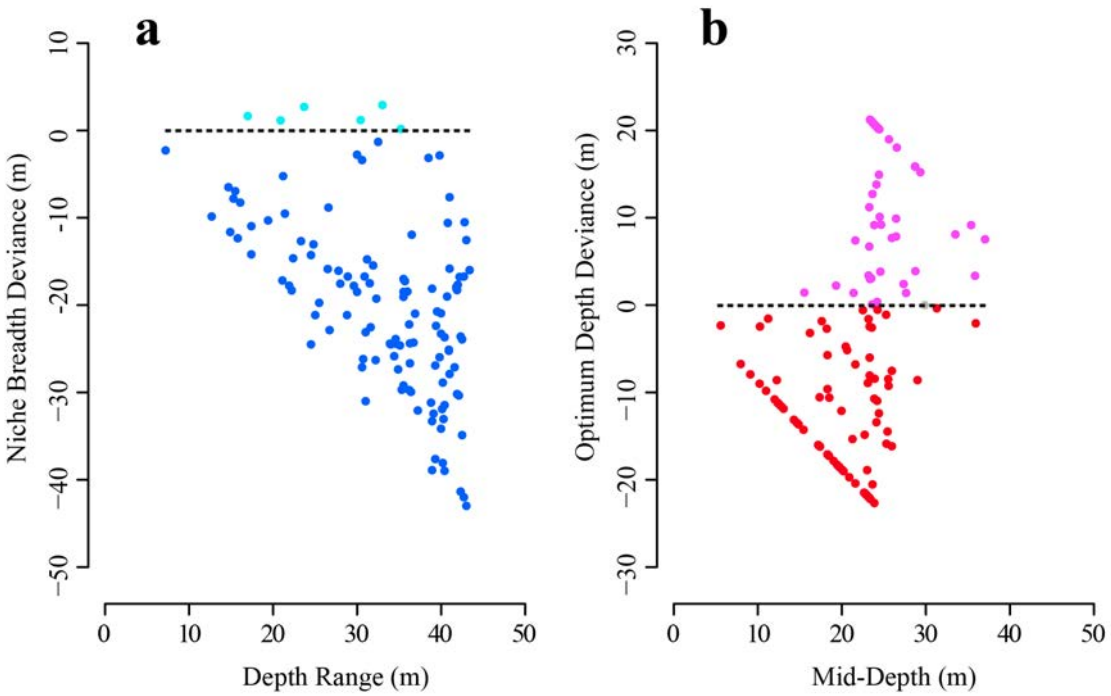

Figure 5.5: Comparative performance of range derived and model derived metrics.

a) deviation of niche breadth (inner niche width, y axis) from the total depth range (x axis) for each of the 110 species modeled. b) deviation of depth optimum (y axis) from range mid-depth (x axis) for the same species. Negative values represent smaller than expected values of a) niche breadth for the range size of a species, or b) depth optimum for the mid-depth of a species.

	Depth Preference *(depth optimum)*		Depth Specialisation *(inner niche width)*	
Traits	**F**	**P**	**F**	**P**
Morphological Plasticity	*0.269*	*0.605*	*0.366*	*0.546*
Gross Morphology	*3.125*	**0.001**	*2.035*	**0.036**
Laminar	-	**< 0.001**	-	-
Encrusting	-	**0.001**	-	-
Submassive	-	**-**	-	**0.002**
Mean Corallite Size	*1.951*	*0.165*	*0.085*	*0.771*
Larval Development Mode	*1.928*	*0.168*	*0.335*	*0.564*

Table 5.1: Linear model results for four coral life history traits predicting a species depth preference or specialization.

Significant results are shown in bold. Gross morphological characters with significant results are listed individually underneath the overall result.

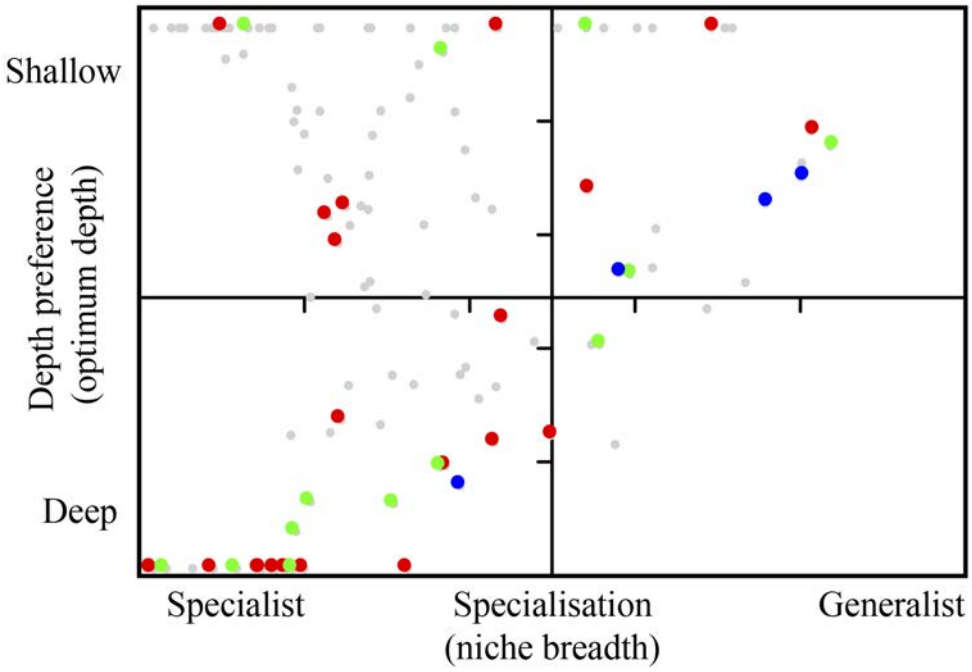

Figure 5.6: Distribution of coral morphologies significantly associated with niche breadth and depth optimum.

Blue dots represent species with submassive morphologies, associated with niche breadth. Red and green dots represent species with laminar, and encrusting morphologies respectively, associated with depth optimum. Grey dots represent all other species.

5.4: Discussion

Coral species display a wide array of abundance response shapes over their depth range, which are unrelated to the basic depth range measure. Instead of species abundance distributions being normally distributed over their depth range, we show the majority of species to occupy a smaller subset of their possible range, which is rarely located in the mid-depth. By moving beyond assumed abundance distributions, the predominance of generalist species identified using range metrics (Fig. 5.4b, 85% 'generalist') was reversed (Fig. 5.4a, 81% 'specialist'), reconciling the depth generalist paradox. Coral species with laminar and encrusting morphologies were more likely to prefer deeper waters, likely indicative of the limited light availability at depth, while species with submassive morphologies were more likely to have broader niche breadths. No other life history traits were associated with niche breath or optimum depth. As is the case with describing abundance distributions, the availability of suitable data, quantifying stable and informative traits, remains a key limitation.

The 170 coral species modeled using the eHOF approach demonstrated that different corals species utilize the depth gradient in different ways, irrespective of their depth ranges. All seven model fits were represented, and only species occurring in less than 20 count stations (2.5% of all stations) showed unacceptable model fits (Fig. S5.1). Slightly over half of all species analyzed (86) returned abundance response curves where the optimum depth occurred at the range limit, a phenomenon that clearly invalidates the normal distribution assumption. Applications of HOF models are not limited to depth ranges, and can capture response over any domain (Oksanen and Minchin 2002; Jansen and Oksanen 2013). For instance, the environmental factors

that enforce physiological distribution limits, such as light or temperature (Anthony and Connolly 2004; Hoogenboom and Connolly 2009), can replace the grouping variable of depth. This approach can quantify the response of a species to specific target factors, either environmental (such as temperature) or biological (such as the abundance of a competitor species) (McGill et al. 2006).

The depth generalist paradox arises from the assumption that a species is normally distributed over its habitable range. This assumption then infers that species with wider ranges are more generalized, and species will be most abundant at the center of their range, making the range metrics of range extent and mid-depth strongly co-correlated (Fig. 5.3b). HOF model analysis removes any assumption of abundance response shape, and as a result the metrics of niche breadth and optimum depth show no such correlation (Fig. 5.3a). Although many species possess wide depth ranges, variations in abundance throughout their range results in most species showing strong preferences for narrower depths (Fig. 5.3a, Fig. 5.4a, Fig. 5.5a). In fact, 67% of species had niche breadths occupying less that half of the species total range. Similarly, the optimum depths of species were not associated with the mid-depth (Fig. 5.3a, Fig. 5.4b, Fig. 5.5b). Instead, a quarter of all species had their optimum depth at the range edge, and the mid-depth was over 5 metres distant from the optimum depth in three quarters (76%) of species. By removing the normal distribution assumption, the prevalence of depth generalist species (i.e., species with depth ranges or niche breadths covering at least half of the domain) identified using range extent metrics (85% of all species, Fig. 5.3b) is reversed when using HOF model derived metrics (19% of all species, Fig. 5.3a), eliminating the perceived paradox.

Despite the demonstrable issues associated with simple range extent metrics, depth range remains one of the most commonly incorporated predictor variables in coral reef ecology, and is often a highly influential factor. For example, depth range was determined to be one of two key factors defining the extinction risk of reef corals (Carpenter et al. 2008). Depth range is also correlated with geographical range size in corals, in particular, the capacity of a species to cross biogeographic boundaries (Keith et al. 2013). However, our results indicate that depth range alone is of limited ecological relevance when quantifying a species' depth use, and should not be used to infer abundance distributions. Ultimately, the continued use of depth range as a descriptor of depth use is due to the lack of viable alternatives, largely due to the extensive species level abundance data required for methods such as HOF models. For example, tests of the feasibility of larval re-supply of damaged shallow reef habitats by mesophotic coral communities (>30 m depth) largely center around whether species are represented in both shallow and mesophotic assemblages, often using only depth ranges (Bongaerts et al. 2010; Kahng et al. 2010). While some studies acknowledge the limitations of depth range descriptions (e.g., (Bongaerts et al. 2017), many do not (e.g., (Muir et al. 2015; Laverick et al. 2018). Consequently, the significance or relevance of ecological interpretations based on range extent alone is limited.

Life history traits are often associated with how coral species utilise depth (Done 1982; Darling et al. 2012; Madin et al. 2016b). Key amongst these traits is the gross morphology of a species, which dictates its vulnerability to hydrodynamic stress (Madin et al. 2014), as well as its capacity to capture light (Stambler and Dubinsky 2004). Consequently, flattened growth forms (such as laminar or plating) are often

characteristic of communities occurring at 30 m and deeper, due to the rapid attenuation of light over depth (Done 1982; Kühlmann 1983; Roberts et al. 2015). This is supported in our results, where species with laminar growth forms are associated with deeper optimum depths (Fig. 5.6, Table. 5.1). However, species featuring the laminar growth form were not precluded from having an optimum depth in the shallow regions, suggesting that although this growth form is well suited to deeper waters, it is not excluded from the shallows. Likewise, the encrusting growth form was also associated with deeper optimum depth, but possesses no clear advantage for light acquisition over other forms, such as massives. As with laminar forms, encrusting species were not excluded from having shallow optimum depths, suggesting that they possess an advantage in deep habitats.

Species with submassive growth forms showed predominantly large niche breadths (Fig. 5.6), but this growth form was represented by only four species (*Galaxea astreata*, *Goniastrea pectinata*, *Hydnophora exesa*, and *Psammocora profundacella*). There is no clear explanation as to why this would be the case, but it is likely due, at least in part, to the way gross morphology is characterized. A single morphological category is given to a species, which represents the most common morphological state. However, intraspecific and even within-colony morphology is notoriously plastic, with many species displaying the capacity to radically alter their morphology based on the specific conditions in which they occur (Veron 2000; Todd 2008; Ow and Todd 2010). This makes the single character of morphology for a species unrepresentative of the way a species uses its morphological forms, and unlikely to produce meaningful results. One way to address this issue is to examine a species' capacity to utilise different morphologies, represented by morphological plasticity.

Theoretically, the range of morphological shapes available to a species would dictating the extent of a species niche breadth, as species with a wider array of ability differing forms gain an advantage at the extremes of their range (Hoogenboom et al. 2008), but this was not supported in the results. Regardless, this trait characteristic is likely to be more informative than simple gross morphology, and deserves further investigation.

The issue of intraspecific variability is also relevant to the two other traits tested. Larval development mode has strong implications for the dispersal capacity of a species, as planulae produced by brooders are both rapidly competent and neutrally buoyant. Conversely, larvae from spawners develop at the surface for days to weeks before recruiting (Baird et al. 2009a). Symbiont transmission from parent colonies to planulae is strongly influenced by larval development mode, and is proposed to affect the symbiont zonation, and consequent depth zonation of coral species (Bongaerts et al. 2015). While the results of this study do not support these conclusions, intraspecific trait variability is likely to influence or obscure clear results. Larval development mode is noted to vary within a species over its geographic range, while some species (i.e., *Pocillopora damicornis*) are recorded to both spawn and brood (Baird et al. 2009a).

Finally, the mean corallite size of a species is regarded as a measure of heterotrophic capacity, with larger corallites allowing a species greater capacity to supplement its energetic needs through heterotrophy regardless of the light conditions (Porter 1976). In this case, the level of intraspecific variability may be of less concern than the within colony variation. Corallites are not consistent in size throughout a colony, and the trait values for a species may be strongly influenced by subjective bias on the part

of the observer who records the trait values. Ultimately, trait analysis, as with depth abundance distributions, is reliant on the availability of accurate data from stable and representative traits (see (Jung et al. 2010; Madin et al. 2016b)). Significant progress to improve the availability and quality of coral trait data is currently being made, through resources such as the coral traits database (Madin et al. 2016a). Meanwhile, the data collection methods and HOF model analysis demonstrated in this study provides a clear path for progress to be made in describing the depth use of coral species.

Chapter 6: General Discussion

6.1: Key Findings

In this thesis, I have brought together new methods of data collection and analysis to examine the ecological determinants of depth zonation in reef-building corals. The thesis findings support the use of a new method for the collection of biodiversity data (Chapter 2), question the significance of two popular theories of biodiversity gradients (Chapters 3 and 4), and reconcile the depth generalist paradox (Chapter 5).

In Chapter 2, I outlined a novel sampling methodology, the modified point count transect (PCT), to be used for questions relating to biodiversity. The PCT was developed from a widely used method in terrestrial ecology (Perry et al. 2012), and specifically designed for time constrained habitats (such as deeper waters). Field testing of the PCT demonstrated its practicality at gathering species level data while keeping within a short time frame (5 minutes). When tested against the established standard in the field i.e. 10 m line intercept transects (LIT), the PCT captured species at a faster rate, both per individual counted, and per minute invested. Importantly, the PCT captured far more rare species than the LIT (Roberts et al. 2016). The development of this method represented an essential foundation for the research component of this thesis, allowing for clear tests of ecological theory, free from the pervasive obstacle of data quality. PCT was then used to assemble a species level dataset of reef-building corals along a 45 m depth gradient in Kimbe Bay, Papua New Guinea, which formed the basis for Chapters 3, 4, and 5. This dataset is unprecedented in its taxonomic resolution (347 species), depth range (0 – 45 m), and size (9,576 colonies).

In Chapter 3, I tested the two most commonly invoked predictive hypotheses to explain species richness patterns over natural gradients: the species energy theory (SE) and the mid-domain effect (MDE). In the absence of numerous factors that confounded previous research, species richness of corals over depth follows a left-skewed hump, in keeping with previous results from terrestrial communities over altitudinal gradients (Rahbek 1995; Lomolino 2001; Nogués-Bravo et al. 2008; Beck et al. 2016). However, neither the SE nor the MDE adequately predict this pattern. Rather, both rely on idiosyncratic additional factors to explain the hump (Evans et al. 2005; Beck et al. 2016; Colwell et al. 2016). I then show that by veiling either the lower or the upper third of the sampled depth domain (i.e., the top or bottom 15 m), strong support can be found for the mid-domain effect and species energy theory respectively. This result demonstrates the key importance of capturing a sufficient extent of the depth domain and explains continued support for both theories in the literature. While there remains no predictive hypothesis capable of explaining the left-skewed hump, null model approaches such as the mid-domain effect are a more promising research avenue than single factor hypotheses such as the species energy theory (Colwell et al. 2004,2005).

In Chapter 4, the same dataset was used to test whether or not local scale assembly processes, such as competition, are responsible for the left-skewed hump of species richness with depth. Instead of supporting the hypothesis, the analysis suggested that the left-skewed hump is maintained by regional scale processes (e.g.; speciation, extinction, large-scale dispersal, endemism) that control the species pool from which local scale communities are assembled (Caley and Schluter 1997; Cornell et al. 2007). While a strong influence of processes acting at the reef scale (e.g., environmental

filtering through hydrodynamic disturbance) was found over the full depth gradient, there was no clear evidence that these processes influenced patterns of species richness over depth. The same was true for processes acting at the smaller within-reef scale (i.e., competitive interactions). However, an increase in the effect of within-reef scale processes was detected below 35 m, consistent with small-scale priority effects. Instead of supporting the hypothesis of local assembly processes creating the species richness pattern, there was evidence of regional enrichment over the full depth gradient, at even the smallest scale. However, the strength of conclusions that can be reached from this study must be tempered by the inherent interdependence of species pools at different spatial scales, and the assumptions made surrounding the scale at which assembly processes operate. Even so, these results suggests that it is entirely possible that the true regional pattern is the left-skewed hump pattern revealed in Chapter 3.

Finally, in Chapter 5, I examined how each species occupied the depth domain, and resolved the depth generalist paradox (where the majority of species are depth generalists, yet produce strong patterns of depth zonation) by showing it to be an artefact of range extent based analysis. Hierarchical logistic model analysis (HOF) was used to move beyond the simple range extent descriptions of depth use, and was applied to the abundance of 170 coral species over depth. A wide variety of depth response curves were revealed, invalidating the assumption that species abundances are normally distributed over their range. Two model parameters, representing the depth preference (optimum depth) and depth specialization (niche breadth) of each species, were compared to the corresponding range derived metrics of depth range mid-point and total depth range. Using these model parameters, the proportion of

species described as ‘depth generalist’ was completely reversed; in fact 81% of species are depth specialists. Four key life history traits proposed as predictive of species depth niche (gross morphology, morphological plasticity, larval development mode, mean corallite size) were tested against the model parameters, but only gross morphology returned a significant result. Species with laminar and encrusting morphologies were likely to have optimum depths in deeper waters (>25 m), likely due to the light gathering capacities of those structures and fragility to hydrodynamic disturbance that are greater in shallow water. Meanwhile, species with sub-massive morphologies had larger niche breadths than expected, but there is no clear explanation for this pattern. Incomplete trait data, the use of trait averages (such as mean corallite size) and the influence of intraspecific trait variation (as seen in gross morphology and larval development mode) make any trait analysis difficult. However, this analysis does not support the hypothesis that corals occupying deeper waters have a specific suite of life history traits that prevent them colonizing shallow waters following a disturbance event.

6.2: Future Directions

The presence of a left-skewed hump shaped species richness pattern within many spatial domains remains a key question in ecology. In 1992, Mike Rosenzweig wrote of the hump “The regional pattern is unimodal. As productivity rises within a region, first diversity rises and then it falls. This pattern exists in mammals, birds, marine vertebrates and invertebrates, and some flora. We do not understand it.” (Rosenzweig 1992). Over a quarter of a century later we still do not properly understand it, and the results of Chapter 3 and Chapter 4 only serve to disprove several possible explanations. While Chapter 4 suggests that the hump-shaped pattern is present at regional scales, empirical proof that the left-skewed hump persists at larger spatial

scales is still unavailable. To test this assertion, additional data from different geographic locations should be assembled. By virtue of the PCT data structure, the species richness pattern can then be compared at a stable sample size over a range of spatial scales, from the scale of a reef, to a biogeographic region, and ultimately to a global scale. This will allow a conclusive test of whether the pattern changes with scale, which is relevant to all ecological systems (Cornell and Karlson 2000; Chase 2010; Kraft et al. 2011). Once the nature of the pattern over scale is confirmed, progress can be made to develop and test explanatory theories. One possible avenue of research is to investigate a combination of the SE and MDE theories. Using the MDE as the foundation, the energetic resource of light could be used to inform the skew of the species richness pattern towards the shallows, using the suggestions of Colwell and collaborators (Colwell et al. 2016). Conversely, light might have both negative and positive influences on richness. In the shallows, high light levels, in particular high levels of UV radiation, are detrimental to corals (Salih et al. 2000; Baird et al. 2009b), and might consequently reduce species richness. This could be thought of along the lines of the paradox of enrichment, where high levels of an energetic resource has a negative, instead of positive effect (Rosenzweig 1971).

One of the more intriguing results of this thesis is the indication that small-scale priority effects become increasingly prevalent below 35 m depth (Chapter 4). Coupled with hypothesized low rates of recruitment and extinction at deeper depths (Turner et al. 2018), it follows that deeper coral assemblages might follow similar ecological rules to assemblages on islands (MacArthur and Wilson 1967; Pinheiro et al. 2017). If this is the case, common ecological principles can be established, and the understanding of ecological processes operating on deeper coral reef ecosystems

could be greatly improved through the application of island biogeography theory. The consistency of community assembly processes over latitudinal scales also remains highly contentious (Chase 2010; Kraft et al. 2011; Bracewell et al. 2017), and expanding the current research approach to encompass a full depth gradient (60+ m) as well as geographic gradients (latitude and longitude) will add significantly to the current understanding of patterns of species richness in all three cases.

The use of HOF models to capture species abundance response curves is a promising research avenue. While species are examined over depth in this thesis, the use of depth as a grouping variable to represent key environmental factors (e.g., light, temperature, hydrodynamic stress) obscures clear insight into any one of the factors in isolation. To evaluate how each species responds to a specific factor, values can be recorded at the sampling sites, and values of the factors in question used as the gradient over which species abundance response is measured (Oksanen and Minchin 2002). This approach is a powerful way to examine the niche of a species, and the gradient in question can consist of not just environmental values, but also ecological variables such as the presence of competitors or conspecifics.

The key to continued research in this field is the availability of suitable data, covering the full extent of the depth gradient. The PCT method provides a way to gather data in time-restricted habitats and has been successfully deployed at depths of up to 140 m in collaboration with colleagues at the University of Hawaii. Together with the advent of closed circuit rebreather technology (CCR), the logistical limitations responsible for the data drought can now be overcome. It is my intention to continue this research, and apply the PCT over a depth gradient of at least 60 m. The need to adequately

cover the full depth gradient is clear throughout this thesis, most notably from the veil effects noted in Chapter 3. As all data collected with the PCT are comparable, this resource will continue to expand, and form a foundation from which research into depth zonation of corals can continue to grow.

6.3: Thesis Conclusions

The paucity of suitable data relating to corals over depth is the basis of the confusion surrounding the species richness gradient over depth (Chapter 3, Chapter 4). More insidiously, the quality of existing data is becoming increasingly questionable as chronic sampling artefacts are revealed (Chapter 1, Chapter 2, Chapter 5), while little new data is being generated due to the inherent logistical challenges (Chapter 2). The implications of misusing incomplete or inappropriate data to answer ecological questions are severe (Chapter 2, Chapter 5). The contribution of this thesis is to clarify the assumptions and misconceptions that surround the depth zonation of corals, and demonstrate the methodological and analytical techniques, which will move the field forwards. The use of the PCT sampling method to gather primary data, the species accumulation models to calculate species richness, HOF models to capture species abundance response curves, and null models of beta diversity to evaluate the influence of community assembly processes form a new approach to address some of the oldest questions in ecology, such as the ecological processes responsible for species richness gradients. Ultimately, this thesis does not stand alone. Instead it marks a step forwards in understanding the ecology of reef building corals and clears a path for continued research. This path should not go neglected, nor the questions raised go unanswered.

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Appendix 1: Electronic Supplementary Material

Chapter 2:

Table S2.1: 10 m LIT data.

Raw data detailing the number of times (column *Frequency*) each species (column *Species*) was recorded in each transect conducted (column *Transect #*). Data is located on the page "*10m_LIT* " in the datafile "*PCT_Data.xlsx".*

Table S2.2: PCT data.

Raw data detailing the number of times (column *Frequency*) each species (column *Species*) was recorded in each of the point count stations conducted (column *Count #*). Data is located on the page "*PCT*" in the datafile "*PCT_Data.xlsx".*

Table S2.3: LIT diversity analysis results.

Statistical output from the program *EstimateS* (Colwell 2013), for the 10 m LIT dataset. Data is located on the page "*LIT_Results*" in the datafile "*PCT_Data.xlsx".*

Table S2.4: PCT diversity analysis results.

Statistical output from the program *EstimaeS* (Colwell 2013), for the PCT dataset. Data is located on the page "*PCT_Results*" in the datafile "*PCT_Data.xlsx".*

Chapter 3:

Table S3.1: Source data for species richness analysis.

Raw data detailing the species identity (column *ID*) and depth of occurrence (column *Depth*) of each of the 12 coral colonies (column *Coral #*) within each of the PCT count stations recorded (column *Count #*). Data is located on the page "*Species_Richness_Data* " in the datafile "*Coral_Data.xlsx".*

Chapter 4:

Table S4.1: Source data for beta diversity analysis.

Site by species matrix detailing the number of times each species was recorded in each of the 486 PCT count stations used in this study. Columns *Depth, Site,* and *Count* record the mean depth of colonies within each count, the reef site which each count occurred at, and the count number respectively. Data is located in the datafile ""*Beta_Diversity_Data.xlsx".*

Chapter 5:

Table S5.1: eHOF model fits for all species analysed.

Model type fitted (column *Model*) to each of the 170 species analysed (column *Species*). Column *Frequency* records the number of count stations each species was present in. Data is located on the page "*Supp_Table_1* " in the datafile ""*eHOF_Model_Analysis.xlsx".*

Table S5.2: Species depth range descriptive parameters

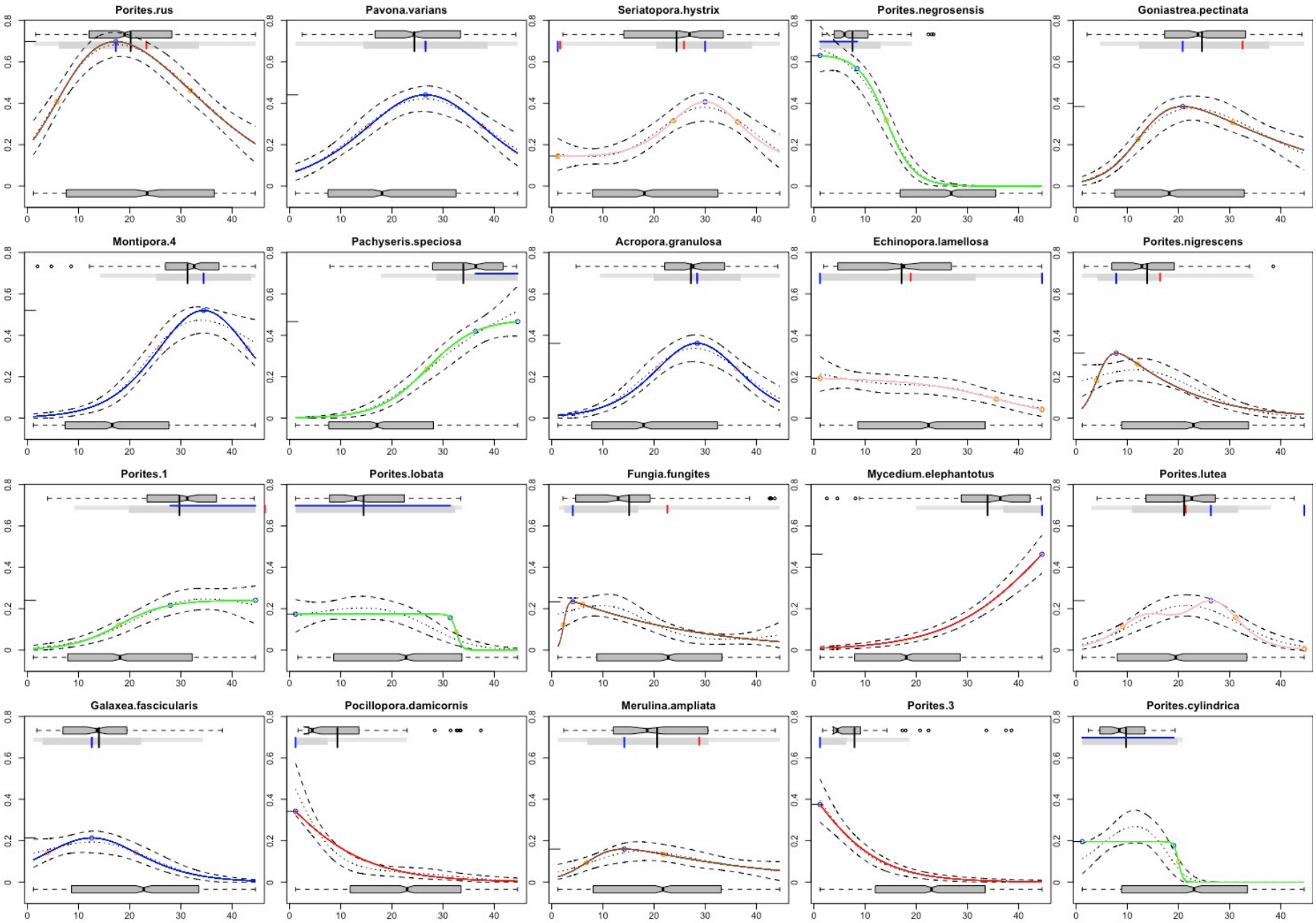
Range derived, and eHOF model derived parameters for all 110 species deemed to have acceptable model fit. Life history trait values used in the analysis are listed for each species. Data is located on the page "*Supp_Table_2* " in the datafile ""*eHOF_Model_Analysis.xlsx"*.

Appendix 2: Supplementary Figures

Chapter 5:

Figure S5.1: eHOF model fits.

Species ranked by frequency of occurrence, with the most frequently encountered species appearing first.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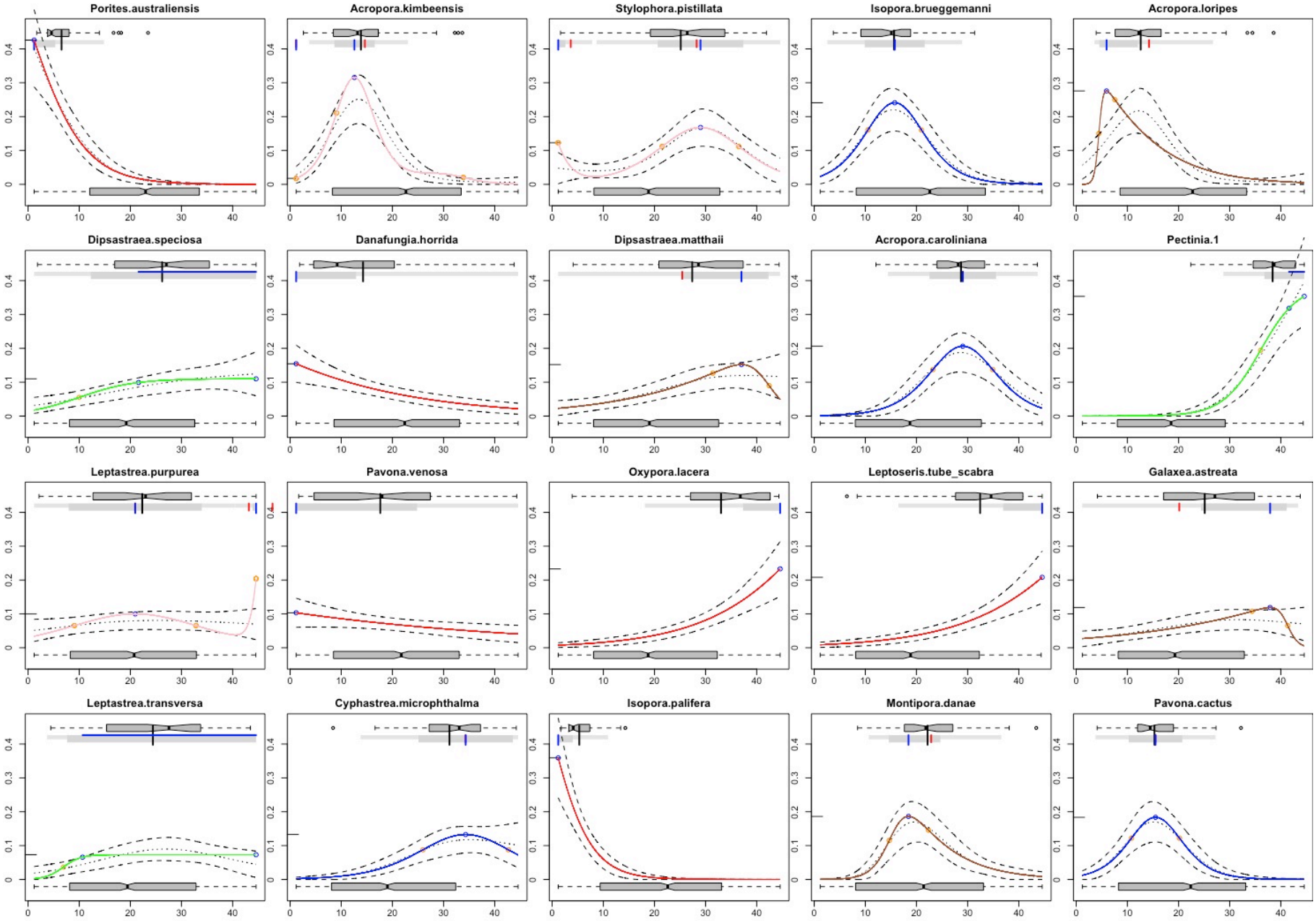
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Acropora.caroliniana
Pectinia.1
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Pavona.venosa
Oxypora.lacera
Leptoseris.tube_scabra
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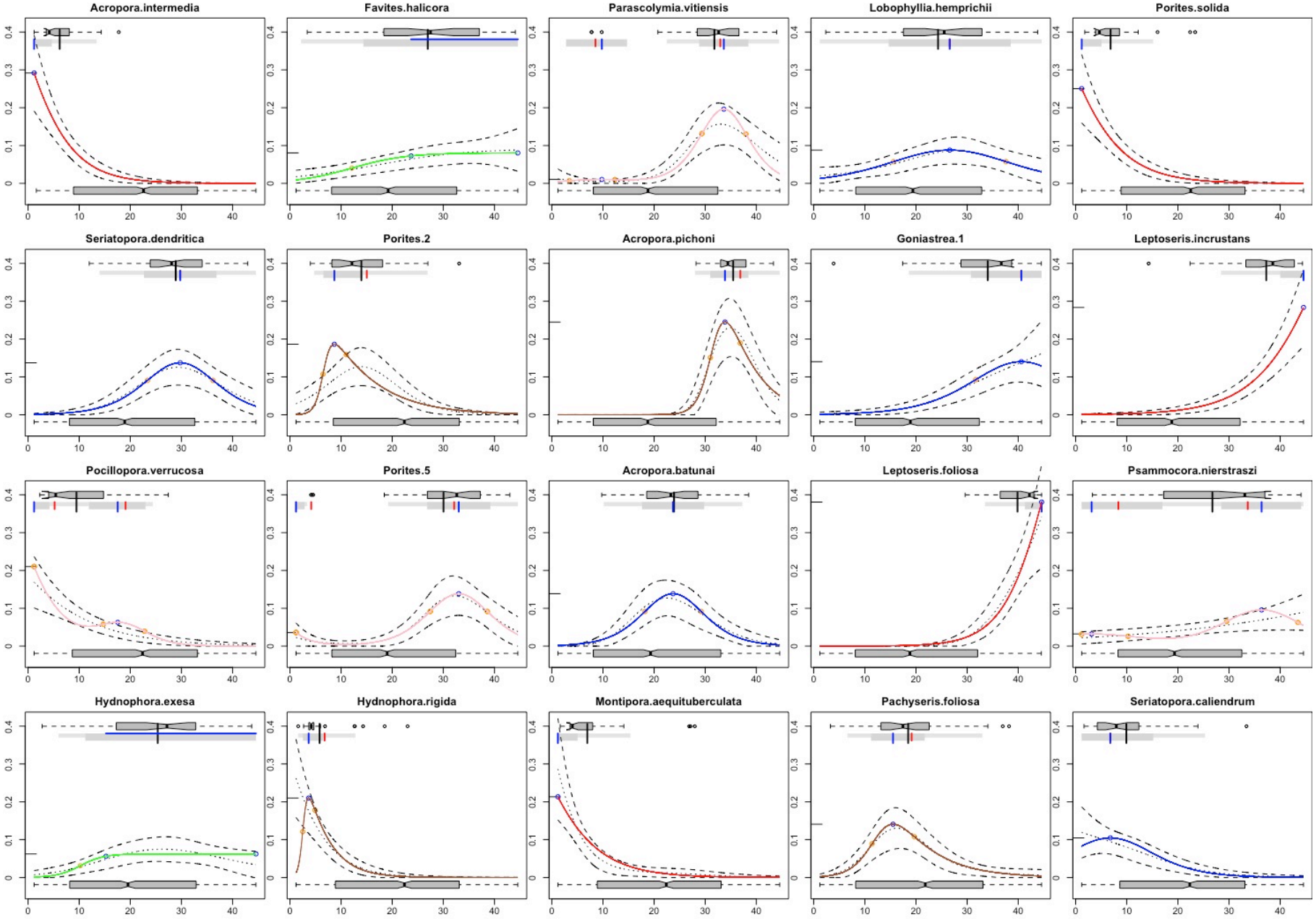
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Goniastrea.1
Leptoseris.incrustans
Pocillopora.verrucosa
Porites.5
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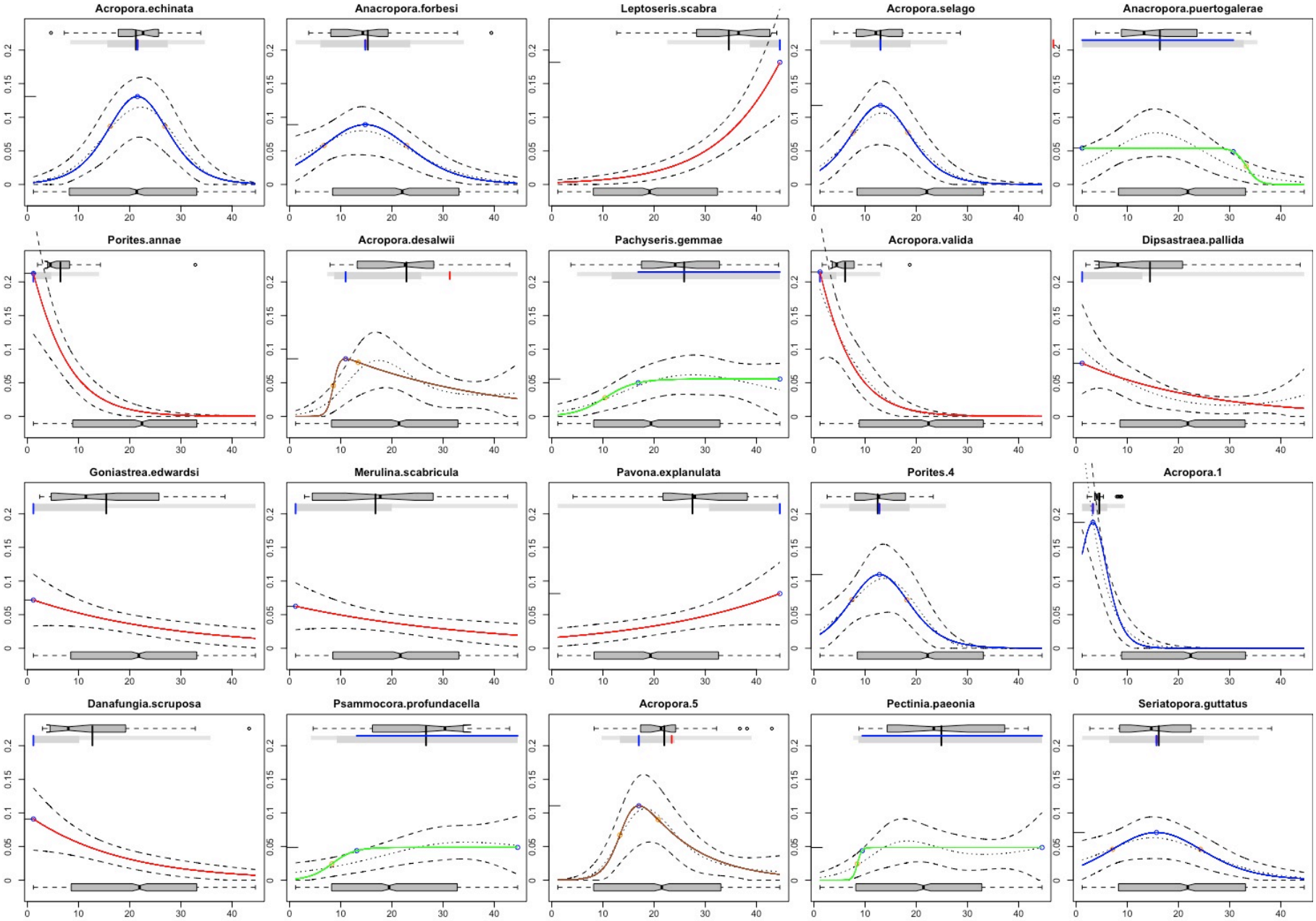
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Pavona.explanulata
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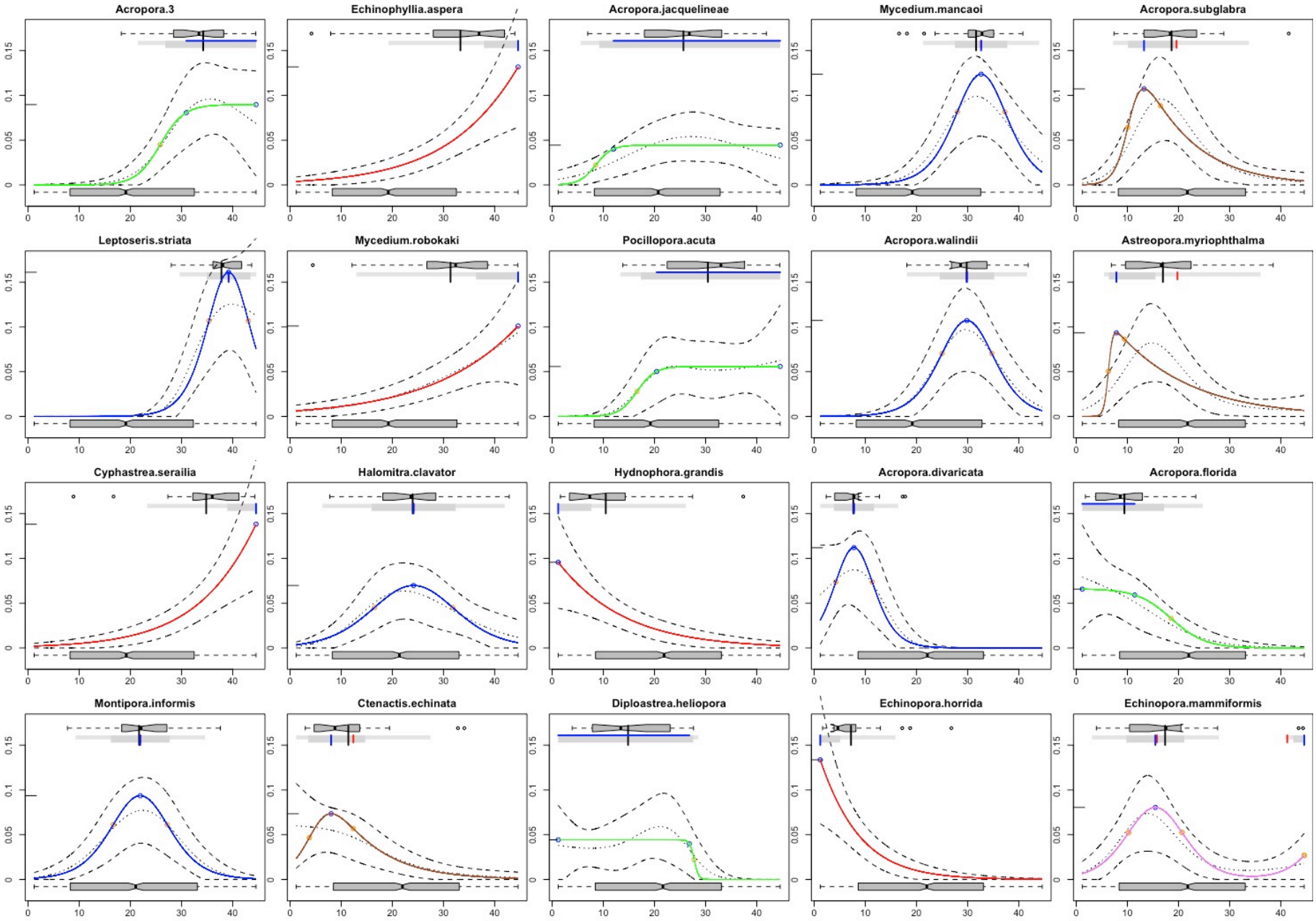
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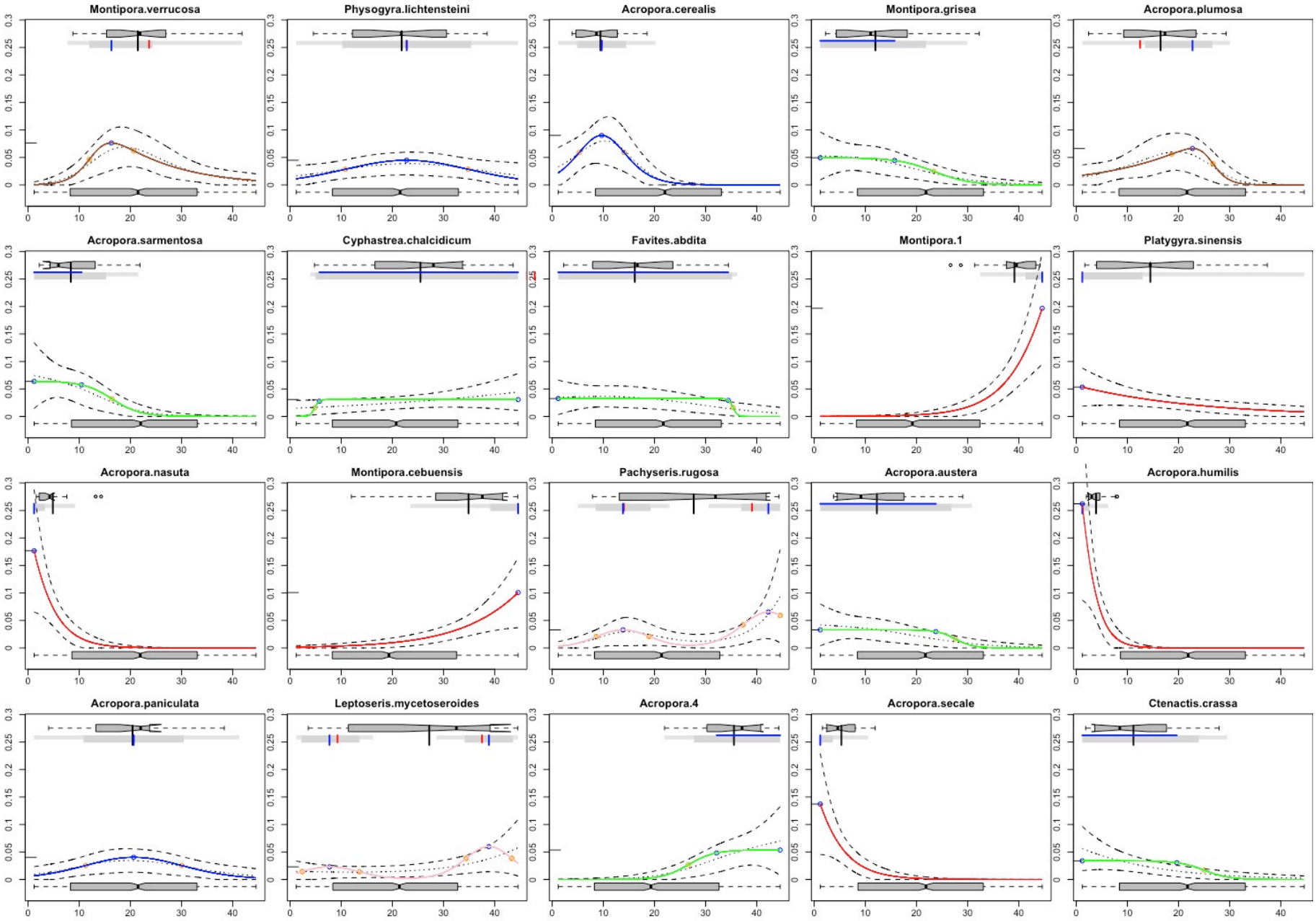
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Montipora.cebuensis
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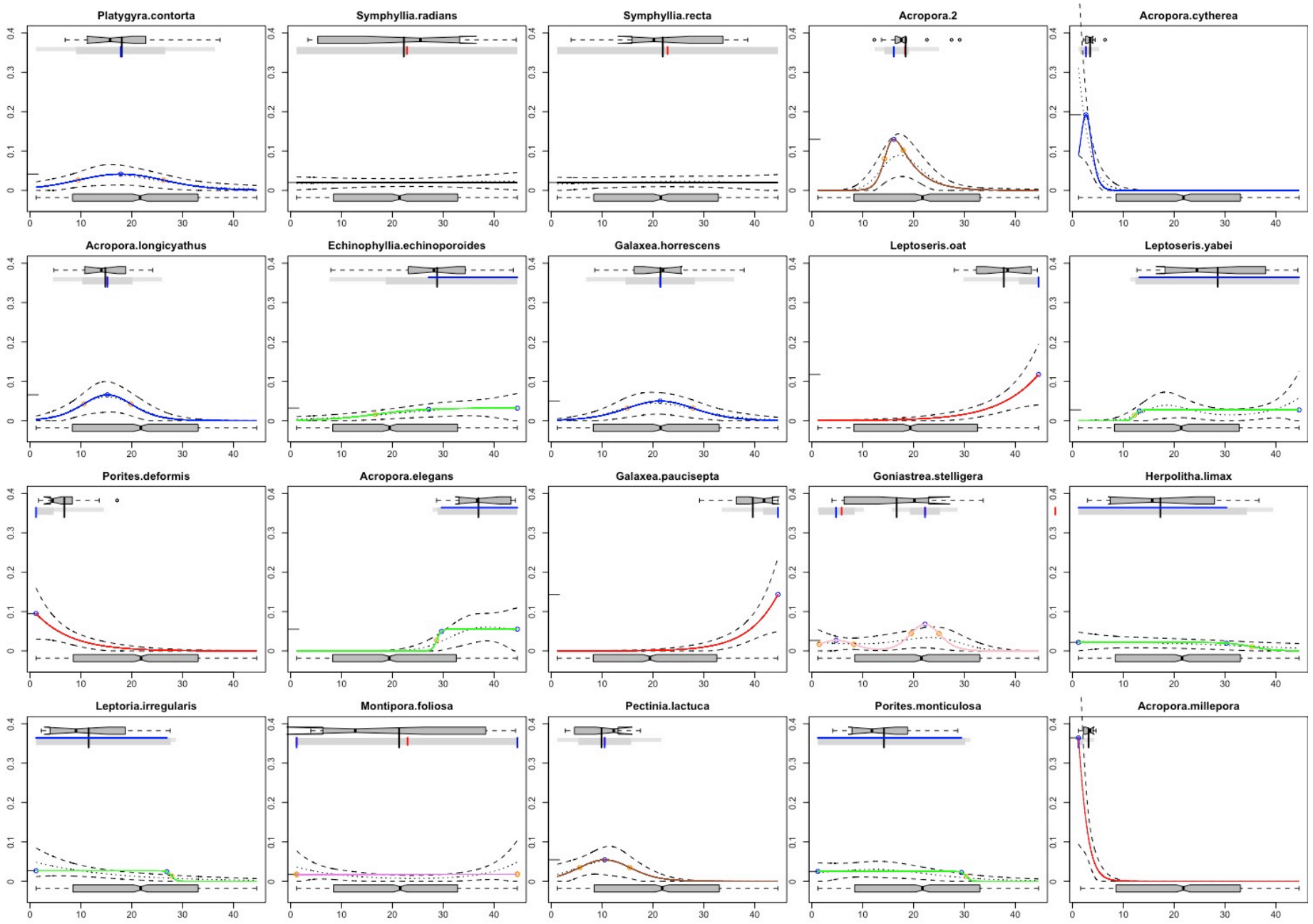
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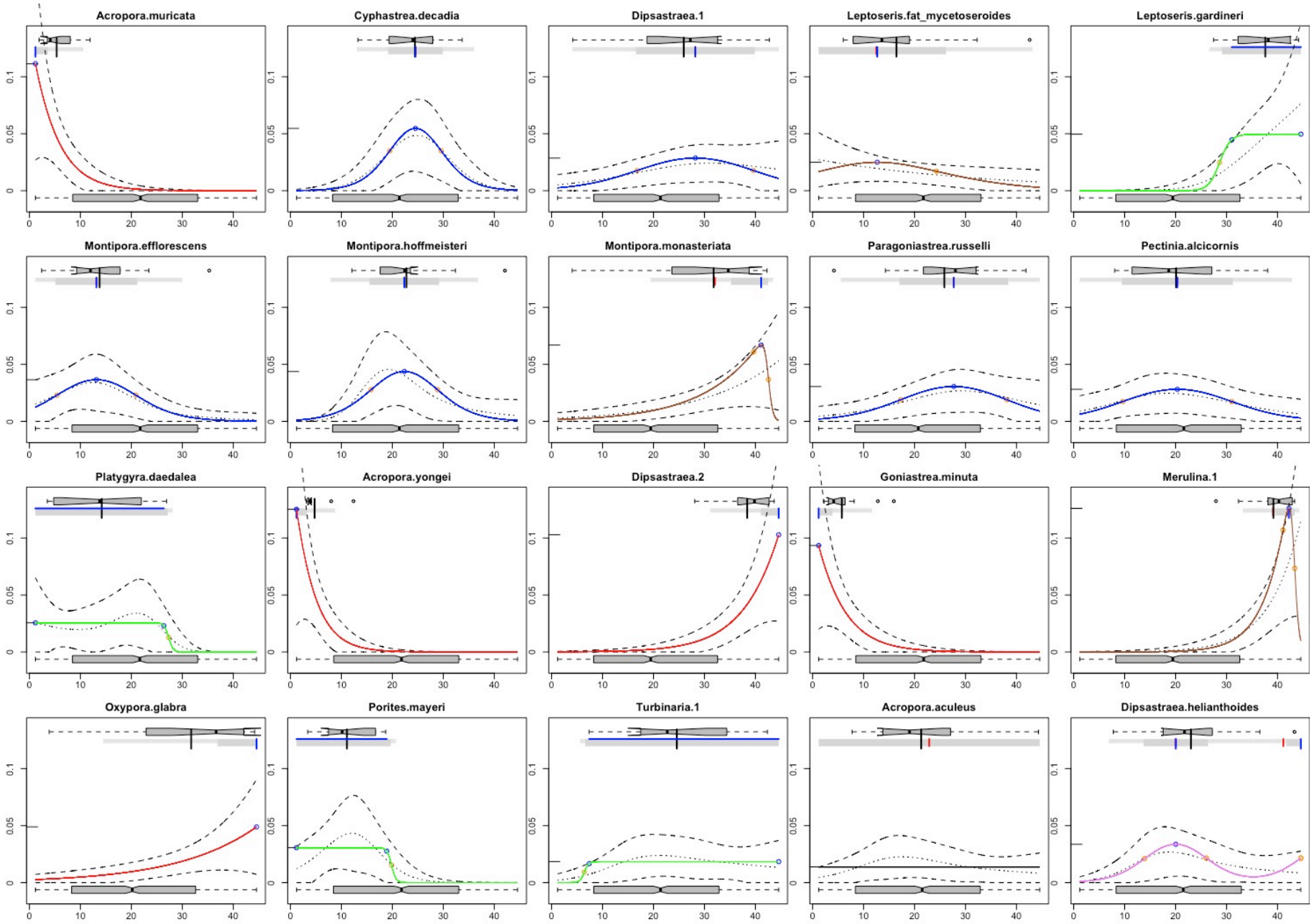
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Acropora.yongei
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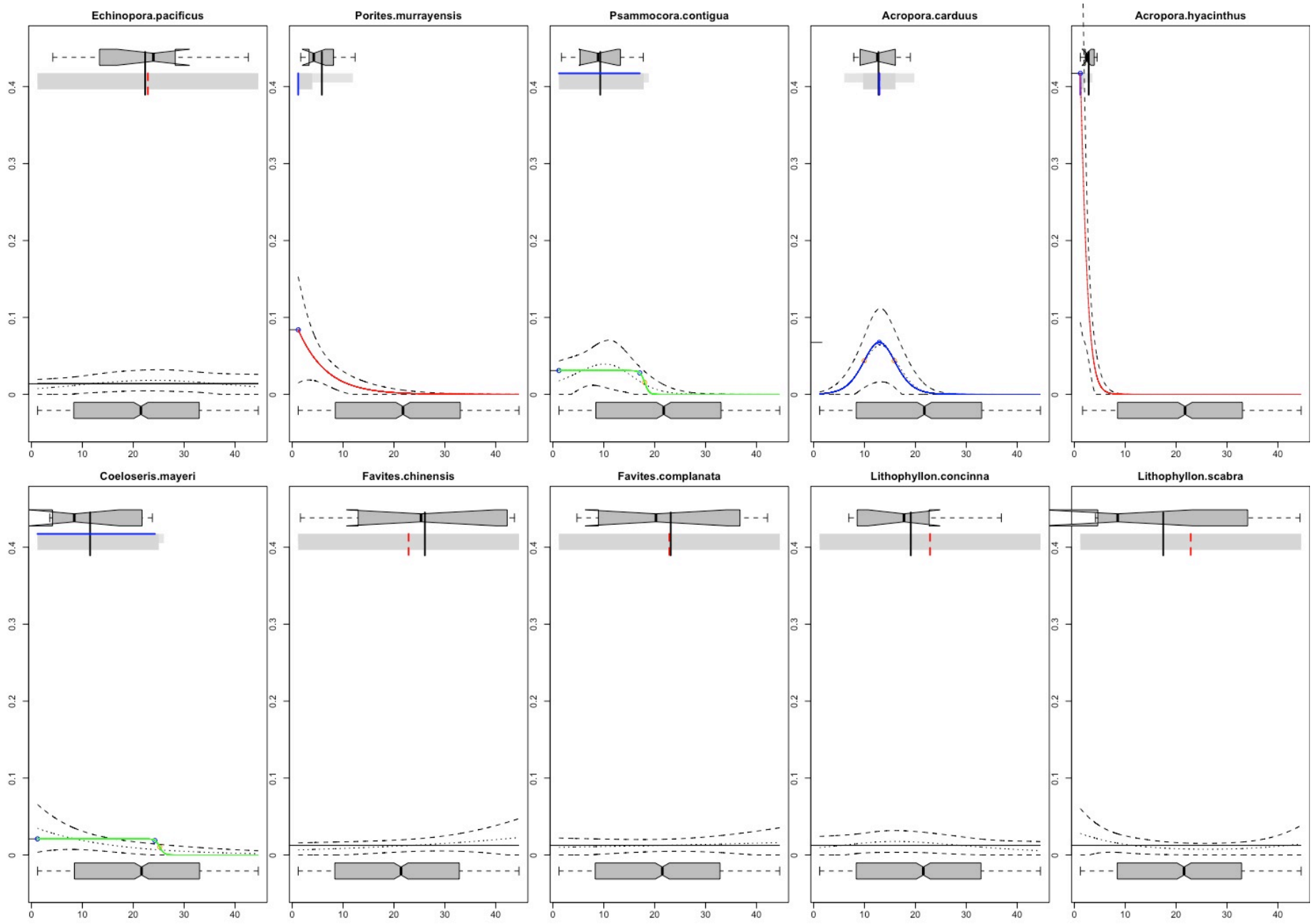
Acropora.aculeus
Dipsastraea.helianthoides


Echinopora.pacificus
Porites.murrayensis
Psammocora.contigua
Acropora.carduus
Acropora.hyacinthus
Coeloseris.mayeri
Favites.chinensis
Favites.complanata
Lithophyllon.concinna
Lithophyllon.scabra

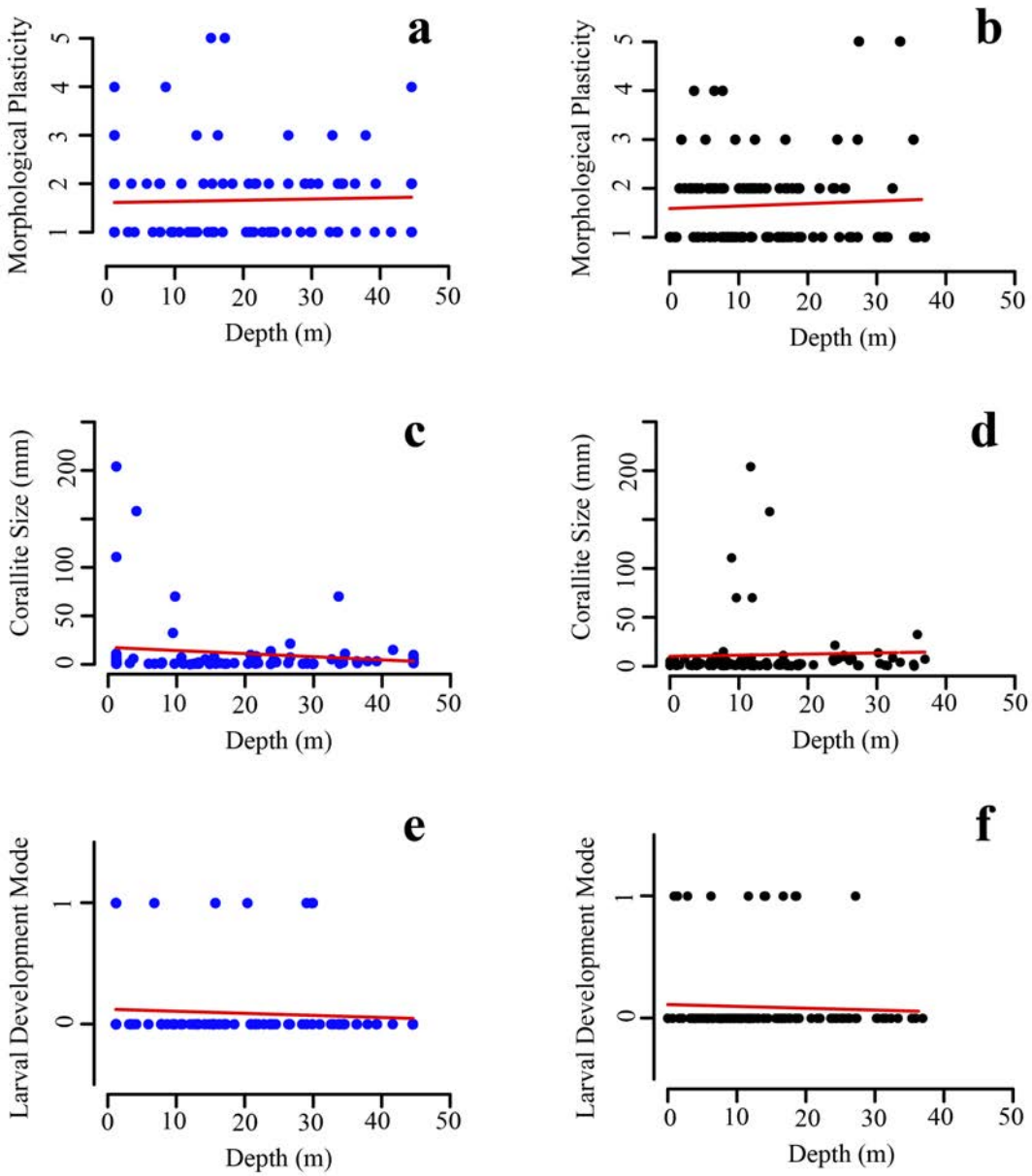


Figure S5.2: Capacity of life history traits to predict species depth preference (blue points) or depth specialization (black points).

Blue dots represent models featuring depth preference as the response variable, and black dots represent models with depth specialization as the response variable. Red lines show linear model fits.

Appendix 3: Publications

PLOS ONE

RESEARCH ARTICLE

The Point Count Transect Method for Estimates of Biodiversity on Coral Reefs: Improving the Sampling of Rare Species

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Abstract

Understanding patterns in species richness and diversity over environmental gradients (such as altitude and depth) is an enduring component of ecology. As most biological communities feature few common and many rare species, quantifying the presence and abundance of rare species is a crucial requirement for analysis of these patterns. Coral reefs present specific challenges for data collection, with limitations on time and site accessibility making efficiency crucial. Many commonly used methods, such as line intercept transects (LIT), are poorly suited to questions requiring the detection of rare events or species. Here, an alternative method for surveying reef-building corals is presented; the point count transect (PCT). The PCT consists of a count of coral colonies at a series of sample stations, located at regular intervals along a transect. In contrast the LIT records the proportion of each species occurring under a transect tape of a given length. The same site was surveyed using PCT and LIT to compare species richness estimates between the methods. The total number of species increased faster per individual sampled and unit of time invested using PCT. Furthermore, 41 of the 44 additional species recorded by the PCT occurred ≤ 3 times, demonstrating the increased capacity of PCT to detect rare species. PCT provides a more accurate estimate of local-scale species richness than the LIT, and is an efficient alternative method for surveying reef corals to address questions associated with alpha-diversity, and rare or incidental events.

Introduction

Coral reefs are one of the most diverse ecosystems on Earth [1] containing both high species richness and heterogeneity of habitats at all spatial scales [2]. For several decades, coral reefs have provided ecologists with important insights into processes that generate and maintain biodiversity, such as species richness gradients and species coexistence mechanisms (e.g. [3, 4]). A common feature of ecological assemblages is a species abundance distribution featuring a small number of common species, and many rare taxa [5–7]. These rare taxa often form the

bulk of biodiversity in an assemblage, but are the most time consuming to adequately record. A high number of rare species therefore requires a large sampling effort to effectively characterize a site. This presents a significant logistical issue in high-diversity ecosystems such as coral reefs and tropical rainforests, where the number of rare and incidental taxa is very high [8]. Coral reefs in particular present additional challenges for data collection, as many reefs are remote and some habitats, such as at depth, are difficult to access.

Ecological studies of coral reefs were greatly enhanced by the advent of SCUBA diving in the 1950s, but the capacity to study reefs at depths >30 m is still limited [9]. Consequently, important questions surrounding the spatial extent, biodiversity and ecological significance of deeper reef habitats remain unresolved [10]. Overcoming this knowledge gap requires the development of new methods that enable more rapid collection of ecological data from deeper habitats. Ideally, such methods would also be broadly applicable across a range of depths and sampling regions.

Standardized methods in empirical data collection for benthic communities in marine ecosystems were developed in the 1970s primarily in conjunction with the increased use of SCUBA (e.g. [11]). The line intercept transect (LIT), adapted from terrestrial vegetation studies, has been widely used for coral reef studies (e.g. [12]). In this method, a transect line of a set length is placed along a reef, and the identification of each species under the line is recorded along with the distance it occupies. The LIT provides a precise estimate of abundance (i.e. coral cover and density), making it well suited to examination of temporal or spatial trends in the abundances of species. LITs, however, are not appropriate for all ecological questions or locations. For example, the length of time taken to complete a suitable number of replicate 10 m transects (typically ≥5) makes LITs impractical in depths >15 m, below which safe bottom times for divers become severely limiting factors for SCUBA based surveys. Furthermore, because of the time required to conduct 10 m LITs, the amount of replication achieved may result in under-sampling of rare and incidental species or events. Consequently, LITs are limited in their application according to habitat and ill equipped to address questions that require the detection of rare events or species.

A fundamental tenet of ecology is that the distribution of species is not random in time or space [13], and understanding how these non-random patterns are created and maintained is a major ecological goal [14]. The mechanisms generating patterns, such as species richness gradients, are now investigated using increasingly complex statistical analyses [15, 16], which require extensive and precise data [17]. Computationally demanding analyses, such as sample-based rarefaction, enable estimates of species richness at standardized levels of sampling effort; however, data for such analysis requires large sample sizes, consistent sampling methodology and data independence [17–19]. The logistical restrictions imposed by LITs make them ineffective for addressing these questions in most situations. Consequently, little suitable data exists, or is being collected, to investigate fundamental ecological phenomena on coral reefs using these statistical techniques.

Here, we present a novel sampling technique more suitable than LITs for estimating species richness (Alpha diversity) and abundance on coral reefs: the point count transect (PCT). The method is derived from a well-established technique in avian ecology, the point count distance transect [20, 21]. Point sampling techniques are popular for monitoring songbirds, primarily for examining species richness and diversity [22]. The detectability and mobility of different bird species is highly variable, resulting in continued refinement and calibration of this method (e.g. [20]). We adapted the point transect framework to the marine environment by conducting point counts of a constrained number of individuals at stations located along a transect. Rather than timed counts (as per the point count distance transect), we utilized point counts of a predetermined number of colonies at each station. Although taxonomically complex, surveying

corals presents fewer detectability problems (i.e. audible detection, mobility, cryptic behavior) than surveying birds, substantially reducing the main source of methodological error [23]. Moreover, standardizing the number of colonies sampled in each count controls for effort, ensuring a repeatable and efficient sampling unit. We compared the effectiveness and time efficiency of the PCT method to traditional LIT surveys for estimating species richness at the same reef site at Lizard Island, Australia. We compared 1) total species richness estimated from a standardized sample size, 2) species accumulation rate per unit effort (per additional individual, and per minute), and 3) species abundance distributions, to reveal detectability bias towards rare and incidental species.

Methods

Point Count Transect Survey Method

A linear transect of a specified length (in this case 50 m) is randomly deployed within the study site, with count stations located at regular intervals (in this case every 10 m) along the transect line (Fig 1A). The transect length, and the spacing of count stations is highly flexible, depending on the research objective. For example, a study of species richness over depth could use a vertical transect up a reef slope, with count stations at bathymetric, rather than distance intervals. In that case the transect length would be variable depending on the reef profile, as would the linear distance between count stations, but the survey principle remains the same. An initial

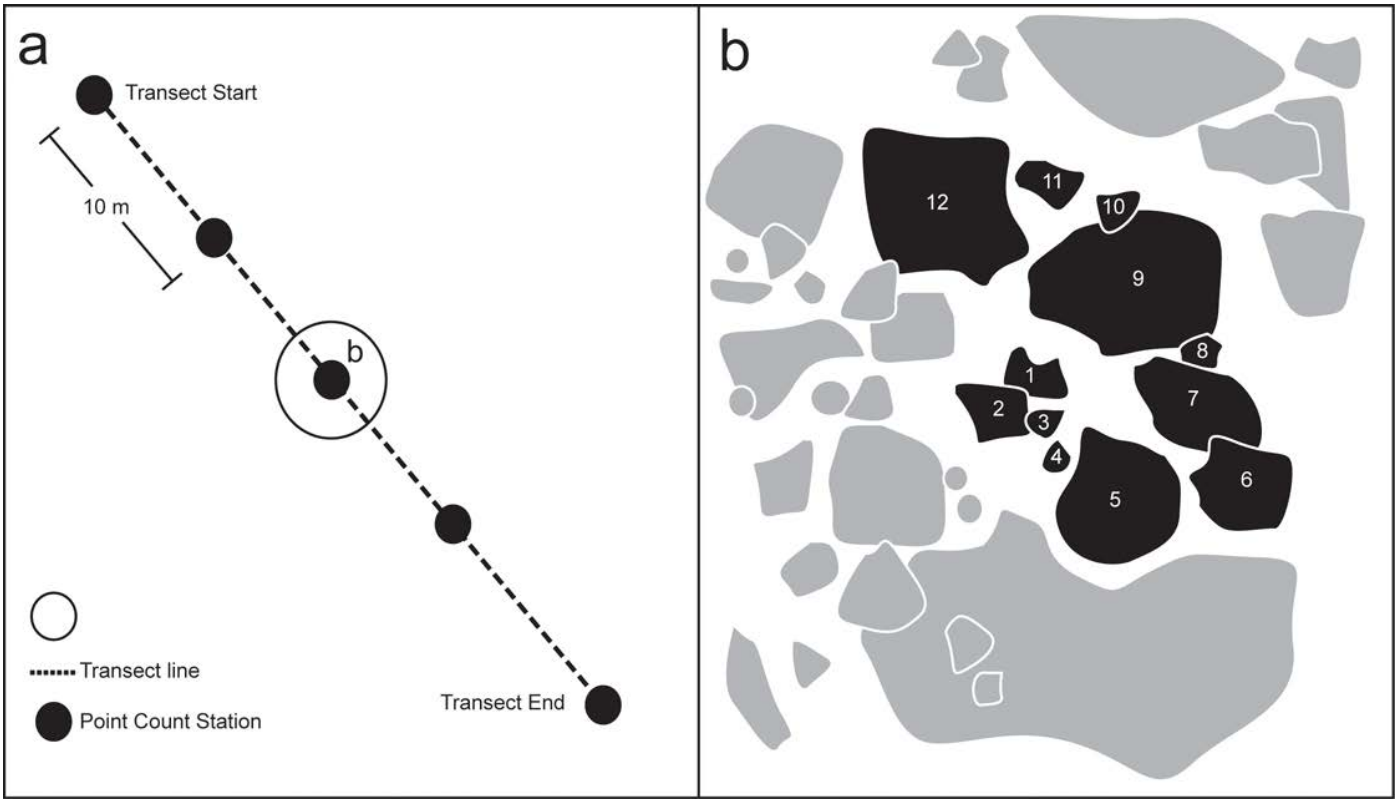

Fig 1. PCT Sampling Scheme. a) overview of transect with count stations, b) one count sample (12 colonies). Shaded shapes represent recorded colonies, with numbers representing the progressive sampling order. Directionality of the count progression (in this case counterclockwise) is flexible, but should be decided prior to the study.

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coral colony situated on a consolidated section of reef substrate suitable for coral habitation is chosen and identified at each sampling station. The nearest neighboring colony to the initial colony is then chosen as the next in the survey (Fig 1B). Successive colonies are identified such that the sampling area expands outwards in an approximately counterclockwise spiral shape from the initial colony (Fig 1B). The directionality of the expanding spiral should remain consistent, but either counterclockwise or clockwise can be chosen. As this method details reef-building coral occurrence patterns, areas known to be unsuitable for habitation, or which exclude the vast majority of species (eg. sand dunes, unconsolidated rubble banks) are not targeted. This is in contrast to existing area-based methods (eg. LIT) which often invest significant resources sampling areas of unsuitable habitat, which yields little relevant data. Additionally, the stipulation to survey suitable habitat, even when colonies are rare or absent, is an important measure of sampling effort, and represents a record of range limits, environmental filters, or other environmental factors influencing species range distributions. The requirement for types of habitat suitable for surveys can be expanded or restricted based on the research question. For a study focusing on species richness of *Acropora* spp. for example, areas of sand can be avoided, while a study focusing on *Fungia* spp. may only target sand areas. Colonies < 5 cm diameter were not recorded in this study due to difficulties consistently identifying juvenile corals to species level [24].However, the minimum size of recorded colonies will be dictated by the taxonomic expertise of the surveyor. For instance, if fragments are collected for genetic analysis, or if the locally extant species are easily differentiated, this size limit may be significantly lower. After a pre-determined number of colonies is recorded at each station (in this case 12), the surveyor moves to the next sampling station (in this case located 10 m along the transect). Twelve colonies were selected at each sampling station for this study as experience suggested that this was the maximum number reliably recorded by the observer in ~5 minutes. This value should be determined prior to the start of the survey, and be suited to the question asked. The currency in this survey method is the individual colony, grouped into count stations, which allows for the number of individuals to be chosen to suit the research question and location of the study. For instance, the research question in this case focused on time efficiency at each site, in a species rich region, so a short test revealed the maximum number of individuals reliable recorded in the chosen time limit (12 colonies in 5 minutes). In regions where coral density and/or richness is lower (such as the Caribbean, or East Pacific) a smaller number may be more suitable. Conversely, where time restrictions are not so severe, a larger number of colonies can be recorded at each sampling station. For this study, average colony densities allowed this number to be successfully recorded at each site, but to account for regions where colony densities are low, only colonies with at least part of the colony occurring within a two metre radius of the initial start colony are recorded. Colonies are countable as long as part of the colony occurs within the two metre radius. Where individual colonies extend beyond the sampling area, the size is recorded, but this is not deducted from the sampling area. If the pre-determined number of colonies cannot be found, the sampling will stop when the area is exhausted. For each colony, the species, water depth (to the nearest 0.1 m, corrected to lowest astronomical tide), maximum diameter and its perpendicular width (to the nearest 5 cm) are recorded. Species are identified *in situ* where possible, or with reference to a high-resolution image.

Comparing the Methods

Comparative surveys were conducted along the upper reef slope of 'Big Vickies' reef, Lizard Island, Australia (145.44° E, 14.683° S). No permit was required from the Great Barrier Reef Marine Park Authority (GBRMPA) due to the limited impact (non-extractive) nature of the

research, conducted under the accreditation of James Cook University. Only visual surveys were conducted, and no endangered or protected species were collected or manipulated. Transects to be used for both methods were laid end to end along the reef slope where there was contiguous hard substrata between 2 and 4 m depth. Nineteen replicate 10 m LITs surveys were conducted, covering the same linear reef area as the PCT while representing a sampling intensity significantly greater than the three to five transect recorded in most studies. In addition to species identity, we recorded the time taken to complete each transect. We then conducted 4 PCTs of 50 m in length (containing 6 count stations per transect at 10 m intervals) as described above overlying the same reef area. The time taken to complete each survey was recorded.

The efficiency of the two methods was compared through the rate at which new species were observed against both time invested and the number of colonies surveyed. Species accumulation curves [15] were used to compare estimates of alpha diversity from each method. Differences in sampling effort were accounted for using species accumulation curves extrapolated to a sample size of 50 samples (~600 individuals) through rarefaction using the program EstimateS [25]. Curves were used to compare the rate of increase (indicating the rate of observing new species) and the number of species recorded at a common sample size (468 individuals). The average time taken to increase the sample size by one individual was used to compare the time efficiency of each method. Species abundance distributions (SADs) were calculated to detect and display sampling bias towards or against rare species. Results are presented as mean ± 95% CI, unless otherwise stated.

Results and Discussion

Species Accumulation and Abundance

A total of 234 colonies were recorded on the LITs, compared to 288 colonies during the PCTs. A mean of 12.3 colonies were recorded for each 10 m LIT, compared to the 12 colonies sampled for each station of the PCT. PCTs recorded 85 species in 120 minutes, compared to the 41 in 171 minutes for the LIT. The rate of species detection was faster for the PCT and mean estimated species richness higher for any given sample size (Fig 2). This difference was even greater when comparing species richness for any given sampling time (Fig 3). Importantly, estimates of total site species richness did not converge with the PCT species accumulation curve when extrapolated using rarefaction (Fig 2). At a comparable sample size (468 individuals), the estimated species number was substantially lower for the LIT (52.83, 95% CI: 41.13–64.53) than the PCT (100.99, 95% CI: 88.5–113.49). This disparity was even greater when time invested was accounted for (LIT: 42.85 95% CI: 35.44–50.27, PCT: 100.3 95% CI: 88.08–112.51 for 189 minutes) (Fig 3). The number of species recorded by PCT after sampling 288 colonies (83 species) was also substantially higher than the estimated total species richness after sampling 600 colonies using LIT (56 species). Although both methods showed an asymptotic accumulation curve, the projected estimates of total species richness between the methods were substantially different. Even with increased effort LITs are likely to underestimate the number of species present far more than comparable PCTs.

The SADs revealed that 41 of the 44 species recorded in PCTs but not in LITs were rare (observed $\leq$ 3 times; Fig 4). This indicates that the cause of the disparity between richness estimates was the failure of LITs to detect rare species (Fig 4). Both methods indicated similar abundances among common species, but LITs consistently failed to detect rare species even though the number of replicate transects used at Big Vickies reef (n = 19) was considerably higher than the usual number of replicates used to characterize coral assemblages at any particular site (e.g. [26, 27]). The cause of this chronic lack of detection of rare species by the LIT is

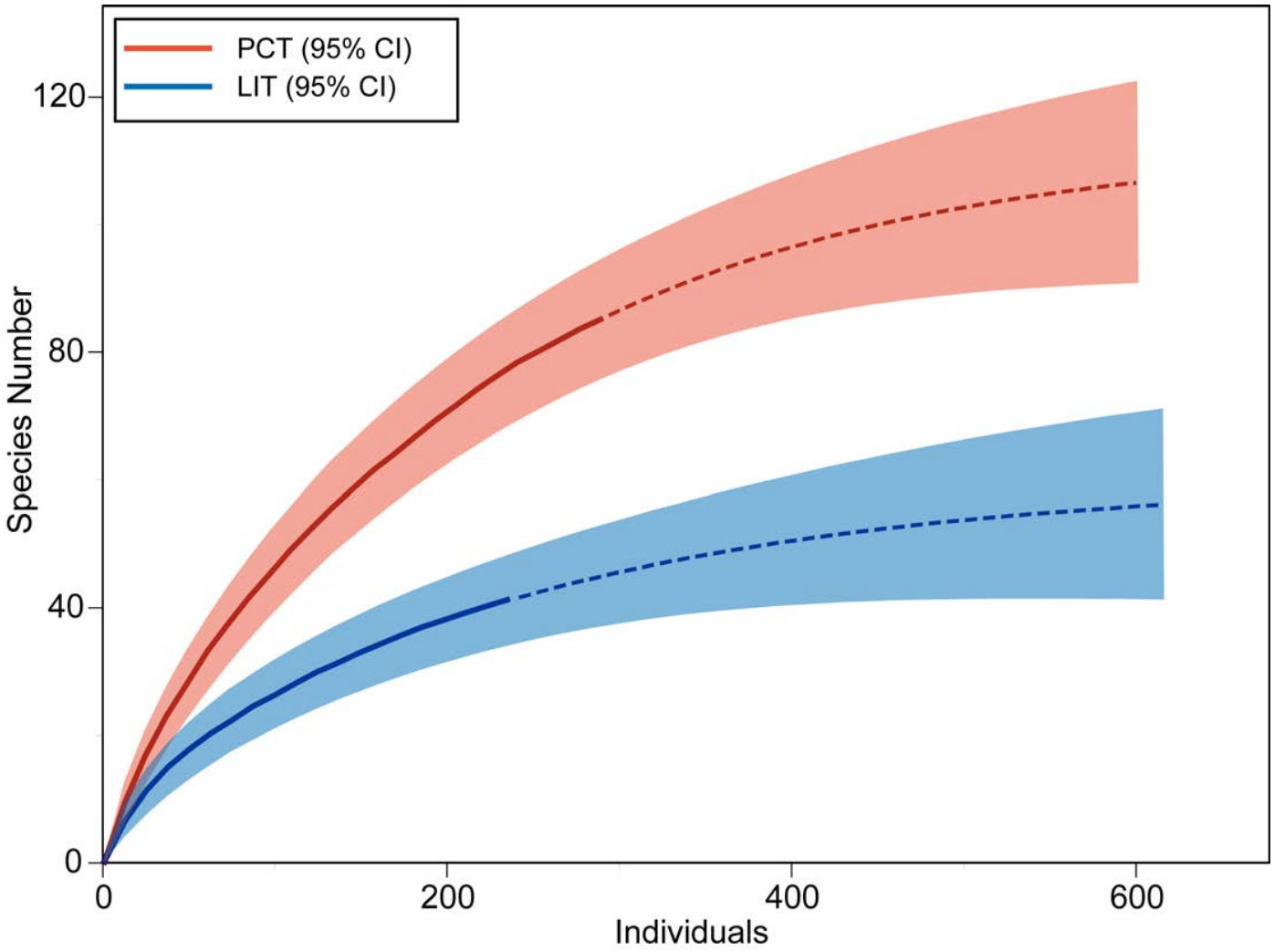

Fig 2. Species Accumulation Curves For PCT And LIT (by individuals added). Species richness (y axis) by number of individual colonies sampled (x axis). Solid lines represent observed species richness, dashed lines show projected species richness rarefied to ~600 individuals, with corresponding 95% CI intervals (shaded area).

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likely due to the practical limitations of the method. Coral reef habitats are complex environments, with many microhabitats within a small region. The LIT method can only detect species that can be covered by a stationary line from above, and the application of the transect line is almost always unable to follow the reef contours precisely, missing most of the complex habitat. In theory, the LIT should not under-represent rare species, but the practical limitations of deploying the method in coral reefs causes errors. The real-world limitations of sampling methodologies are an important consideration, but are often overlooked in favour of theoretical justifications. Given the importance of detecting rare species for many ecological studies, we suggest that PCTs can be a more effective method of surveying coral assemblages than LITs.

The PCT was developed to assess patterns of species richness and meta-community structure along steep environmental gradients (e.g. depth) on coral reefs. These types of research questions do not require metrics of absolute abundance such as coral cover, which can be

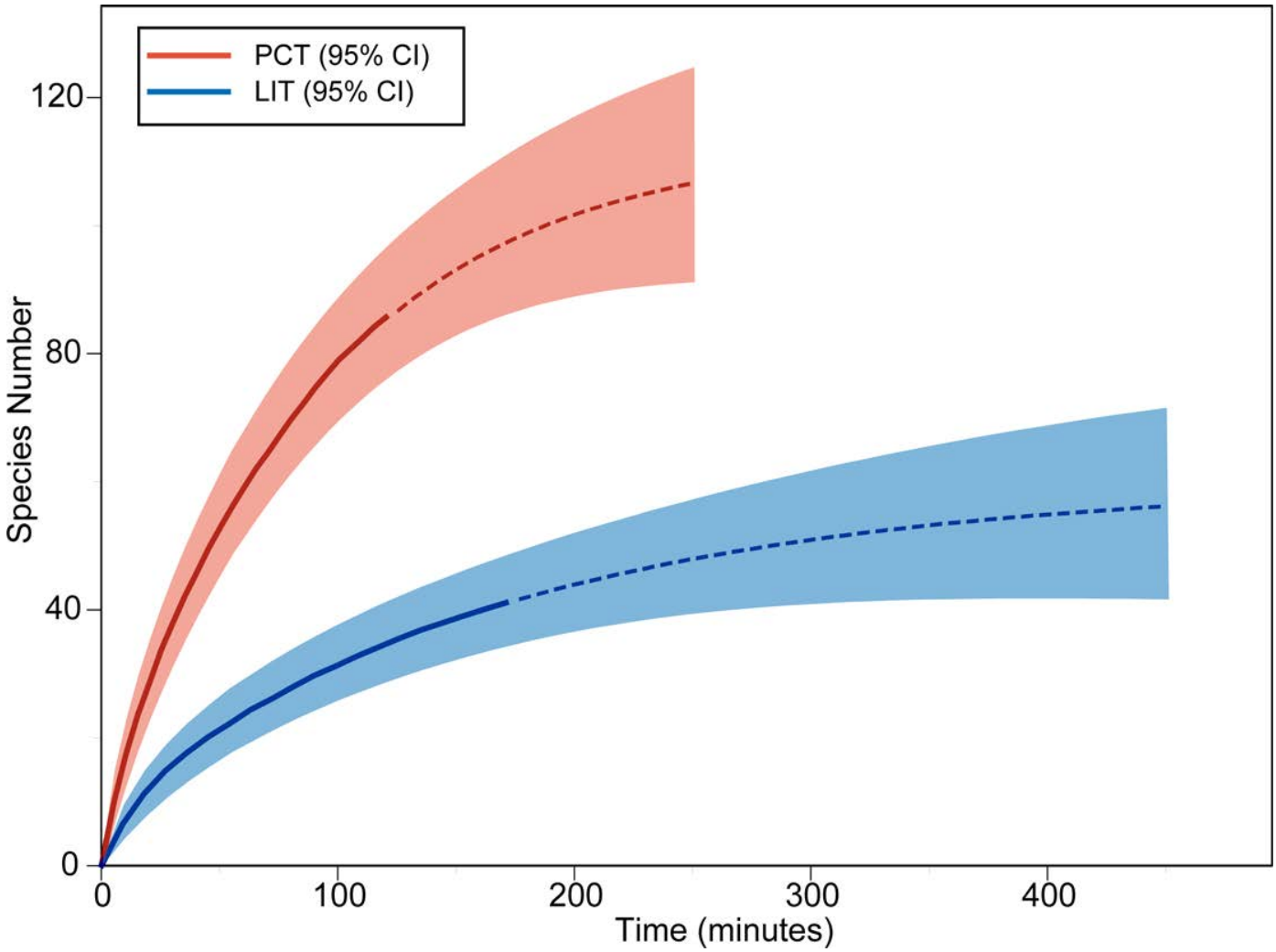

Fig 3. Species Accumulation Curves For PCT And LIT (by time invested). Species richness (y axis) by number of minutes invested in sampling (x axis). Solid lines represent observed species richness, dashed lines show projected species richness rarefied to ~600 individuals, with corresponding 95% CI intervals (shaded area).

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effectively obtained using LITs. As a result, the PCT represents a complementary data collection technique, rather than a replacement. The sensitivity of the PCT to rare and incidental species allows insight into the poor detection by the LIT, but emphasizes rapid capture of richness at the expense of absolute abundance measures. Using the PCT without considering its own strengths and weaknesses to a specific research question will likely result in an equally erroneous result as misuse of the LIT. Where detection of rare species is important, we propose the PCT as a robust and time-efficient method of collecting ecological data on coral reefs. This method will be particularly effective for examining questions such depth-diversity gradients, where the amount of survey time is greatly restricted. While this protocol was tested in a highly species rich habitat, with high coral abundance, it is applicable to any environment. The flexibility of the methodological framework allows for adjustment to specific systems, and questions.

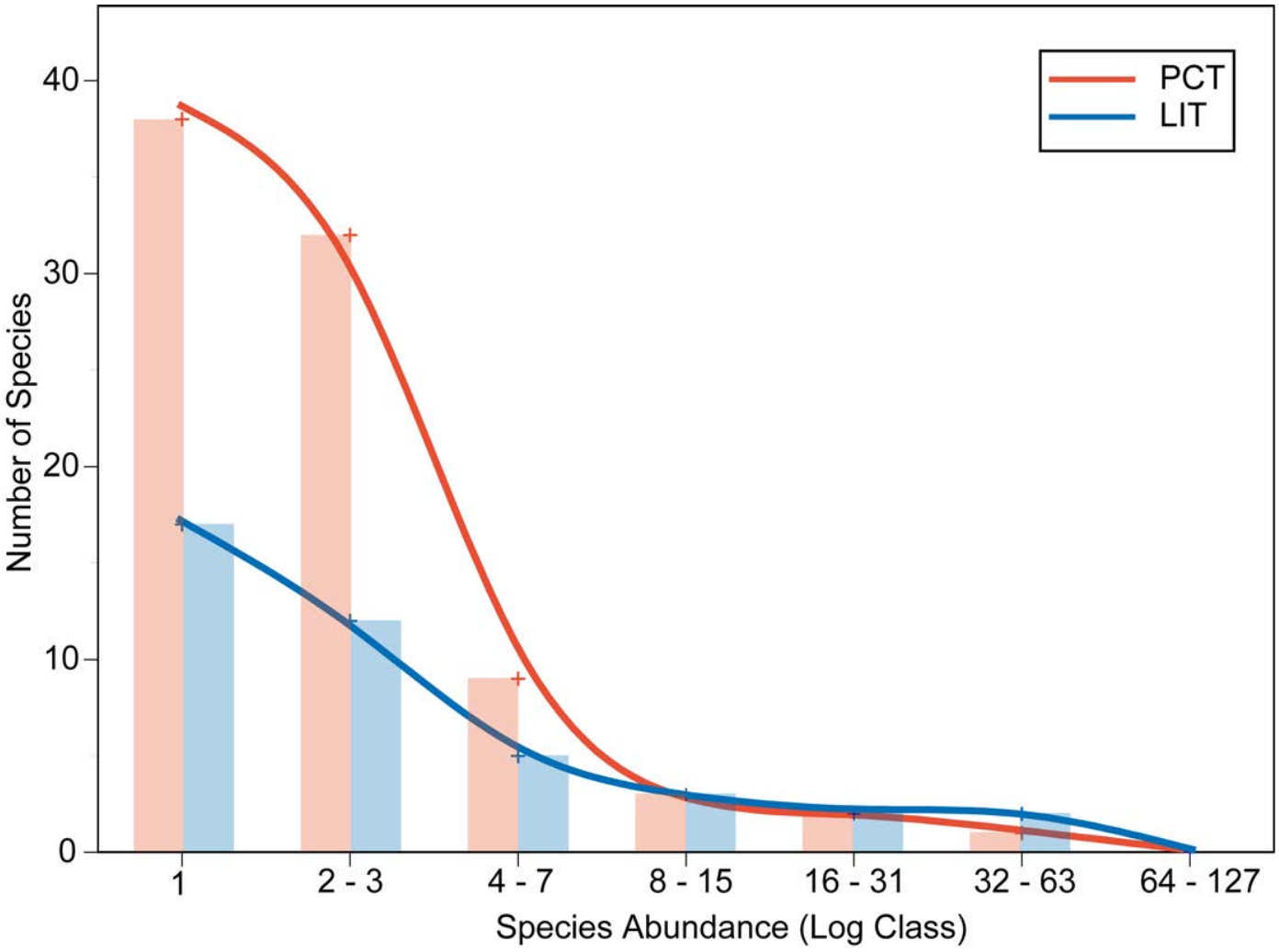

Fig 4. Species Abundance Distribution (SAD) Of PCT (red) and LIT (blue). Frequency bins as per Gray et al. [28] (1, 2–3, 4–7, 8–15. . .).

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Our results also highlight the importance of collecting field data using methods appropriate for the question being asked to avoid error in interpreting findings. For example, estimating species richness of a particular site using species accumulation curves requires samples to have no detectability bias towards or against any given species [17]. Bias against rare species may confound results, and can be difficult to quantify unless the extent of the bias is known. The sensitivity of such analysis to sampling error and bias is well established (e.g. [8]), yet basic errors continue to occur [6, 17].

Coral reef ecologists should continue to develop new and improved methodologies to overcome logistical constraints, and improve the precision and scope of available data. Establishing the real-world strengths and weaknesses of various methodologies enables more researchers to make a more informed decision when collecting data. Methods such as the PCT can complement existing techniques, enabling researchers to better match data collection to suit the desired analysis.

Supporting Information

S1 File. Sampling data for LIT and PCT, with EstimateS analysis outputs.
(XLSX)

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Author Contributions

Conceived and designed the experiments: TER AHB. Performed the experiments: TER. Analyzed the data: TER. Wrote the paper: TER TB JC AHB.

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