Downloaded from orbit.dtu.dk on: Sep 22, 2021

DTU Library

The biogeography of Scleractinian reef corals: Evidence from beta diversity

Maginnis, Neil

Publication date:
2020

Document Version
Publisher's PDF, also known as Version of record

Link back to DTU Orbit

Citation (APA):
Maginnis, N. (2020). *The biogeography of Scleractinian reef corals: Evidence from beta diversity*. DTU Aqua.

General rights
Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

DTU Aqua
National Institute of Aquatic Resources

The biogeography of Scleractinian reef corals

Evidence from beta diversity

Neil Maginnis

PhD Thesis

The biogeography of Scleractinian reef corals: Evidence from beta diversity

PhD Thesis

Neil Maginnis

Principal supervisor:

Martin Lindegren

Co-supervisor:

Sally Keith

Assessment Committee:

Brian MacKenzie, DTU Aqua

Maria Dornelas, University of St Andrews

Janne Soininen, University of Helsinki

Preface

This thesis was submitted as part of the requirements to fulfil the Doctor of Philosophy Degree (PhD) at the Technical University of Denmark (DTU). The thesis was supervised by Dr. Martin Lindegren and co-supervised by Dr. Sally Keith. In addition, external research stays were carried out at the University of Lancaster, England, in collaboration with Dr. Keith, at James Cook University, Australia, in collaboration with Prof. Andrew Baird, Prof. Sean Connolly and Associate Professor Mia Hoogenboom.

The research presented was carried out at the Centre for Ocean Life, a VKR center for excellence funded by the Villum Foundation, at the National Institute of Aquatic Resources (DTU Aqua) in Kongens Lyngby between April 2017 and August 2020. This PhD thesis was funded by the Villum Foundation through a grant awarded to Dr. Martin Lindegren (grant number: 13159). Additional funding was received from the Otto Mønsteds Fond for conference participation.

Acknowledgements

I am deeply grateful to my supervisors Martin Lindegren and Sally Keith for their support over the years. Martin put his faith in me when he recruited me, and has been unwaveringly supportive throughout the PhD. I'd also like to thank Martin for the freedom he has given me in developing this thesis, his enthusiasm and his bigger-picture perspective. Writing my Master thesis with Sal back in 2015 & 2016 was the confirmation I needed to pursue a career in academia. Sal took me on as a research assistant following my thesis and it was Sal that initially put me in touch with Martin. With Martin and Sal I've always felt certain that my supervisors were on my side. Their guidance has challenged me, developed my thinking and improved me as a scientist. During the PhD I have been lucky enough to have research stays at Lancaster University and James Cook University. I'd like to thank Sal, Knud, Nick, Christina and Andrew for their hospitality.

Spending the last three years at the Centre for Ocean Life has been stimulating and enjoyable. In being part of the Centre, and the larger DTU Aqua group, I have been lucky to have wonderful friends and colleagues. Thank you to you all, in particular my office mates past and present, the writing group and the Friday-bar faithful. It has been a pleasure to spend this time with you. Thank you, Louise, for your help with the Danish summary. By now I feel like I should have done it myself, but alas, no. Thank you too, Lilian and Rikke, for patiently helping me with numerous administrative tasks that I couldn't navigate through. A special mention goes to Aurore and Marie, for your support these last few months.

Life in Copenhagen wouldn't be what it is, without my friends outside of work. I look forward to seeing you again soon! A big thank you goes to Helena, for your support and understanding over these last few months. I promise never to be so one-dimensional again!

The final thank you is reserved for my family. This thesis is dedicated to you, and to the memory of dad.

Summary

Across the globe, hundreds of millions of people and even greater numbers of marine organisms depend on coral reef ecosystems. However, these ecosystems are increasingly harmed by human activities that are transforming the environment in a variety of ways. Corals are particularly vulnerable to these changes, with many reefs having lost over half of their coral cover in the last three decades. These trends threaten people's livelihoods and even the continued existence of many species.

Implementing effective conservation action with limited resources requires prioritisation. Prioritisation, however, depends on knowledge of how organisms will respond to the various pressure placed on them and which of those are most destructive. Experiments offer one avenue to pursue such understanding, but developing an experimental understanding of coral ecology is hindered by the richness of corals, their phenotypic plasticity, their diversity of traits and the numerous ways that the environment is being modified. Moreover, certain factors may have influences that are only detectable at very large spatio-temporal scales, and which are essentially impossible to manipulate experimentally. Biogeography constitutes an alternative method to understanding the factors that are most limiting to corals. Biogeographers take a broad-scale approach to understanding biodiversity, exploring patterns in the distribution of life and the structure of assemblages and relating them to putative drivers. Identifying what generates these present-day patterns provides an indication of the factors most relevant to the ecology of the organisms and may improve predictions of the impacts and responses of organisms and ecosystems to future climate change.

The work presented in this thesis applies such a biogeographic approach to reef-building corals. In Chapter 3, I attempt to identify the key factors generating differences in species composition (i.e., beta diversity) of coral assemblages across oceans basins and spatial scales. To achieve this objective I assess the influence and relative importance of a number of variables, including environmental conditions, dispersal limitations and geographic factors on global patterns of coral beta diversity. My results demonstrate that Indo-Pacific and Atlantic corals respond to similar factors, especially dispersal limitation, sea surface temperature and nutrient concentrations. Previous large-scale analyses of coral diversity

have typically failed to identify a strong influence of dispersal limitation, but the integration of realistic estimates of coral connectivity into this analysis reveals that it is a key determinant of coral distributions and beta diversity. The influence of environmental factors are particularly apparent at small spatial scales, whereas the size of reef areas emerges as an important factor at large spatial scales.

Chapter 4 builds on the conclusions from the third chapter and explores the influence of dispersal limitation on coral assemblages in more detail. The life-history traits of organisms dictate how they interact with their environment and in this chapter I investigate how different modes of reproduction (i.e., spawning of gametes and brooding larvae), with different long-range dispersal abilities, may affect the biogeography of corals. I begin by investigating the consequences of different reproductive modes on the range sizes of corals using permutation tests. I then determine how the structure of coral assemblages change across distance depending on the mode of reproduction. My results do not show that species' range sizes differ significantly between reproductive groups, despite a tendency for spawning corals to have larger ranges. However, the spatial structure of assemblages does differ significantly between reproductive groups. Assemblages of corals that brood larvae are more dissimilar across space than assemblages of broadcast spawning corals, which display greater spatial overlap. These results suggest that differences in dispersal ability resulting from distinct reproductive strategies influences large-scale biogeographic patterns.

This thesis demonstrated that dispersal limitation is an important challenge for corals, suggesting that there may be a delay, or even a failure, to track suitable environmental conditions under climate change. This problem may not be of equal importance to all coral species, since species with spawning reproduction appear to be less dispersal limited. Managers may therefore need to focus extra attention on brooding corals. In addition, the primary environmental factors that influence coral distributions (i.e., temperature and nutrient concentrations) are strongly impacted by human activities and worsening conditions are virtually guaranteed. The importance of coral reef area at very broad scales emphasises the necessity of coordinated and decisive action to limit the multiple stresses being placed on coral reef ecosystems to halt the degeneration and destruction of these precious places.

I hope that this thesis will be inspiring to other researchers and prove useful in tackling one the most pressing matters of our time, namely the preservation of coral reefs.

Dansk resumé

Menneskeskabt aktivitet påvirker miljøet og livet på jorden på mange forskellige måder, specielt koraller er sårbare over for disse forandringer. Det er særligt bekymrende, da mange organismer er afhængige af sunde koralrev og dertilhørende økosystemer. Derudover er hundrede af millioner af mennesker direkte afhængige af et sundt og produktivt koralrev. At implementere effektiv bevarelse og beskyttelse af korallerne kræver en prioritering af ressourcer. Denne prioritering afhænger af den viden der er om organismerne og hvordan de reagerer på de forskellige påvirkninger.

Eksperimenter kan give sådan en forståelse af korallers økologi, men dette bliver udfordret af den store diversitet der er inden for koraller, såsom deres høje fænotypiske plasticitet og deres evne til at interagere med fotosyntetiserende alger. Den store diversitet giver en forskel imellem korallerne, endvidere bliver de også påvirket forskelligt afhængig af miljøforhold. Derudover, er der visse faktorer der kan have indflydelse som kun er synlige på en stor skala, dette er umuligt at gengive eksperimentelt. Biogeografi giver en anden alternativ metode til forståelse af, hvilke faktorer der er mest begrænsende for koraller. Biogeografi bruger en bred tilgang til at forstå diversiteten. Dette giver mulighed for at undersøge mønstre i udbredelse af livet, samt strukturer og formodede underliggende årsager i plante og dyresamfund. At identificere hvad der genererer disse nutidige mønstre, kan hjælpe med at lokalisere de mest relevante faktorer for organismerne og deres økologi. Dette kan hjælpe med at forudsige korallers fremtidig respons på klimaforandring.

Denne afhandling gør brug af den biogeografiske metode, for at få en bedre forståelse af revformende koraller. I det tredje kapitel forsøger jeg, at svare på følgende spørgsmål: ”Hvad er de grundlæggende nøglefaktorer der genererer koral beta diversitet?”. Her sammenligner jeg påvirkningen af en række forskellige faktorer, de miljømæssige faktorer, udbredelse og geografiske faktorer og hvordan det påvirker globale mønstre af koral beta diversitet. Jeg udfører denne analyse over en bred række af faktorer for at sikre en omfattende forståelse. Indo-Stillehavs og Atlantiske koraller reagerer ens på de samme faktorer, især udbredelses begrænsning, havoverflade temperaturer og næringskoncentrationer. Påvirkning af miljøfaktorer er tilsyneladende mest tydelig ved lille skala, hvor det ved stor skala ser ud til at tilgængelig rev areal er af større betydning. Undersøgelser på stor skala har ofte ikke kunnet identificere en påvirkning af begrænset

spredning hos koraller. Men ved at integrere resultatet af en realistisk model af koral sammenhæng i denne analyse, afsløres det som en af nøglefaktorerne for at bestemme koral udbredelse og beta diversitet.

Det fjerde kapitel bygger på konklusionerne fra det første kapitel. Her undersøges det mere dybdegående hvad betydningen af begrænset spredning har for sammensætningen af koraller. Organismernes egenskaber såsom livshistorie afgør hvordan de interagerer med deres miljø. I dette kapitel undersøger jeg konsekvenserne af de forskellige reproduktions metoder og hvordan det påvirker korallers biogeografi. Jeg begynder med at undersøge hvordan forskellige reproduktions strategier har konsekvens for udbredelsen for koraller. Dette gør jeg ved at lave en permutation test. Jeg undersøger da hvordan sammensætningen af koraller varierer på tværs af afstand, afhængig af deres reproduktions strategi. Arternes udbredelsesområde ændres ikke signifikant mellem reproduktions strategier. Men strukturen af koral sammensætningen ændres efter deres reproduktions sammensætning. Sammensætningen af koraller der avler larver er mere forskellig i forhold til de koraller der reproducerer sig via gydning med æg og sæd frit i vandet. Sidstnævnte udviser dog større variation i artssammensætning grundet større udbredelsesevne.

Denne afhandling demonstrerer at begrænset udbredelsesevne er en betydelig udfordring for koral økologi, dette indikerer at der muligvis er forsinkelser eller endda fejlagtig sporing af optimale klimaforhold for koraller. Dette problem er dog ikke af lige stor betydning for alle koralarter. Da arter med gydning reproduktion tilsyneladende er mindre påvirket af udbredelses begrænsning. Derfor er det nødvendigt at være ekstra opmærksom på koraller der ikke gyder frit i vandet men har larver internt, når det kommer til bevarings og beskyttelses arbejde. De primære miljøfaktorer der påvirker udbredelsen af koraller er faktorer som havoverflade temperaturer og næringskoncentrationer. Disse to faktorer er højst påvirkelige af menneskelig aktivitet og vil i fremtiden blive yderligere påvirket i negativ retning. Vigtigheden af revhabitater til koraller bliver tydelig på stor skala, dette understreger behovet for kordineret og afgørende handling, for at begrænse stress på koral økosystemer og hindre nedbrydelse og ødelæggelse af disse dyrebare steder.

Jeg håber at denne afhandling vil inspirere andre forskere. Mest af alt håber jeg, at disse resultater kan være brugbare til at tackle en af de mest presserende udfordringer i vores tid, særligt bevaringen af koralrev.

Contents

1

Introduction

1.1 Biogeography

The spatial distribution of life

It has long been apparent that life on Earth is unevenly distributed. Early naturalists documenting these large-scale patterns marvelled at the diversity of life in the tropics and discovered that there is order in the way the distribution of life varies (von Humboldt 1949, Dawin 1859, Wallace 1869). Species richness varies systematically along latitudinal (Hillebrand 2004), altitudinal (Shmida and Wilson 1985), and depth (Rex 1973) gradients, amongst others. These acts, of documenting large-scale spatial patterns of biodiversity and attempting to understand them, constitute the science of Biogeography (Lomolino et al. 2006).

The existence of consistent patterns in the distribution of life imply the presence of causal processes and have inspired the development of a multitude of hypothesise to explain them (Willig et al. 2003). Endeavours to identify processes underpinning biogeographic patterns led to numerous breakthroughs. For instance, from studies on the distributions of fossils came conclusions that the Earth's climate was not constant, that species could go extinct, and eventually the theory of continental drift (Lomolino et al. 2006). Perhaps more notably, both Darwin and Wallace's ideas on evolution were stimulated by observations about the distribution of species: Darwin by observations of morphological variation of finches and tortoises across the Galapagos archipelago (Darwin 1859); Wallace by his studies on the Malay Peninsula (Wallace 1869). Biogeography has therefore been foundational to breakthroughs that have revolutionised our understanding of the world.

Biogeography is as important as ever as we move forward into the Anthropocene, since it can provide significant insight into the potential consequences of human-driven environmental change on the natural world. This knowledge can guide effective conservation interventions and may help to change human behaviour at a societal level. One example of an important insight from biogeography is the species-area relationship – larger areas support more species than smaller areas (Rosenweig 1995). This lesson from biogeography is highly topical today as human activities fragment species ranges and divide population into smaller, more isolated groups. As the processes that generate and maintain them many key biogeographical patterns are still unresolved, it is likely that the continued endeavours of biogeographers will yield further insights. A recent survey of ecologists to identify 100 fundamental knowledge-gaps highlighted several biogeographical themes, including influences on diversity at different scales, the relative importance of deterministic versus stochastic processes in controlling diversity, and the role of dispersal limitation (Sutherland et al. 2013). This knowledge is particularly lacking in the marine realm, which has typically trailed behind the terrestrial realm due to the practical difficulties in obtaining necessary data.

When placed into a geographical context, all aspects of biodiversity, commonly defined as **"the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic systems and the ecological complexes of which they are part; this includes diversity within species between species and of ecosystems"** (Heywood and Watson, 1995) are the subject matter of biogeography. Modern biogeography confronts patterns in the distribution of genes (Miraldo et al. 2016), traits (Beukhof et al. 2019, McWilliam et al. 2018) and evolutionary lineages (Marske et al. 2011). This breadth is important, because it recognises diversity at multiple levels of organisation. However, these multiple facets of diversity are rarely studied in tandem due to logistical constraints. The most thoroughly researched aspect of biodiversity by far, perhaps due to its relative ease of study, is species richness (Chase and Knight 2013). Whilst we have learnt a lot from this work, it is imperative that biogeography moves towards quantifying and understanding more complex patterns that can help us to disentangle underlying processes.

One of the biggest limitations of focusing on species richness is that it is often correlated with multiple hypothesised drivers, making it difficult to draw conclusions about their roles in shaping the observed patterns (Gotelli et al. 2009). Moreover, species richness cannot differentiate between regions that have the same number of species yet very different species composition, which could be indicative of different structuring mechanisms. These limitations mean that the knowledge that can be gained from species richness has reached a plateau. To test and develop biogeographical theory further, biogeographers are increasingly adopting alternative approaches in their attempts to understand how ecological processes generate biodiversity patterns. One approach that can yield more nuanced information and therefore has greater potential to reveal underlying mechanisms is the study of beta diversity (Anderson et al 2011). I therefore focus on beta diversity patterns throughout this thesis.

Moving forwards with beta diversity

Beta-diversity is a useful measure that can provide key insights to inform conservation strategies (Socolar et al 2016), for example by identifying otherwise hidden biodiversity loss occurring through biotic homogenization (Keith et al 2009). Beta diversity was originally formulated as **"the extent of change of community composition, or degree of community differentiation, in relation to a complex gradient of environment, or a pattern of environment"** (Whittaker 1960). The original definition, however, was furnished with several examples that differ conceptually from each other (Anderson et al. 2011). Subsequently, a proliferation of redefinitions, modifications and various indices followed, that measure diverse phenomena (reviewed in Tuomisto 2010) and offer different conclusions from the same data (Koleff et al. 2003). Despite confusion and inconsistency around the concept and formulation of beta diversity, it has proven popular among ecologists. Two key reasons for beta diversity's popularity are 1) that the amount of differentiation between assemblages determines how diversity scales from local to regional scales (Whittaker 1960), and 2) changes in assemblage structure along gradients provide an excellent means to infer processes shaping the distribution of biodiversity (Keith et al. 2011). Throughout this thesis, centred on the large-scale biogeography of corals, I define beta diversity as the dissimilarity in the presence of species between pairs of plots (i.e., geographical locations). Although there is still some debate about the correct use of the term beta diversity (see Tuomisto 2010), this approach is particularly suitable for relating assemblage dissimilarities to physical distances or environmental dissimilarity (Vellend 2001). Due to the importance of clearly defining my use of the concept throughout the thesis, I explain further below.

More specifically, I adopt Sørensen's distance as the measure of beta diversity since it has an intuitive formulation (Sørensen 1948). I calculate this distance as 1 – Sørensen similarity, where Sørensen similarity is the number of species mutually present in two assemblages, divided by the average number of species present (Vellend 2001). The formula for calculating Sørensen's distance is given by: $1 - 2a/(2a + b + c)$ (Legendre and Legendre 2012, Figure 1).

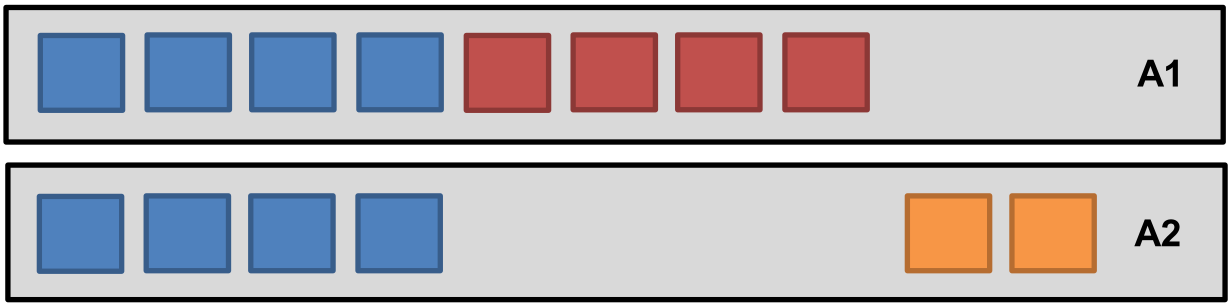


Figure 1. Schematic illustration of two species assemblages, A1 and A2. Colours indicate terms in the equation for Sørensen's distance: blue boxes indicate shared species, *a;* red boxes are species only present in assemblage A1 and represent *b*; orange boxes are species only present in assemblage A2 and represent *c*.

Sørensen's distance is measured on a scale of zero to one, where a score of zero represents assemblages of identical composition and one indicates that assemblages have no species in common. Baselga (2010) introduced a framework which treats beta diversity as the sum of two distinct components, termed turnover and nestedness (See Figure 2). Turnover in the Baselga framework is represented by Simpson's distance (Simpson, 1943), which is similar to the Sørensen distance. Like the beta diversity turnover is also calculated from a similarity index and bounded by zero and one. The only difference is that the number of mutually present species is divided by the number of species present in the least speciose assemblage. The result of this small difference in formulation is that Sørensen distance (beta diversity) is sensitive to differences in species richness between sites or assemblages whereas Simpson dissimilarity (turnover) is not and instead reflects strict species replacement. The second component of the Baselga framework is nestedness, which is the concept of one assemblage being a subset of the other. According to Baselga (2010), nestedness can be calculated as the difference between overall beta diversity and turnover, or Sørensen distance minus Simpson distance.

The decomposition of beta diversity into turnover and nestedness components is an appealing concept to ecologists as the two indices identify different ways in which assemblages can differ across space or time. Species replacement (turnover) and ordered species loss/gain (nestedness) likely result from different processes, hence decomposing beta diversity in this way improves our ability to infer causal processes structuring species assemblages (Baselga 2010).

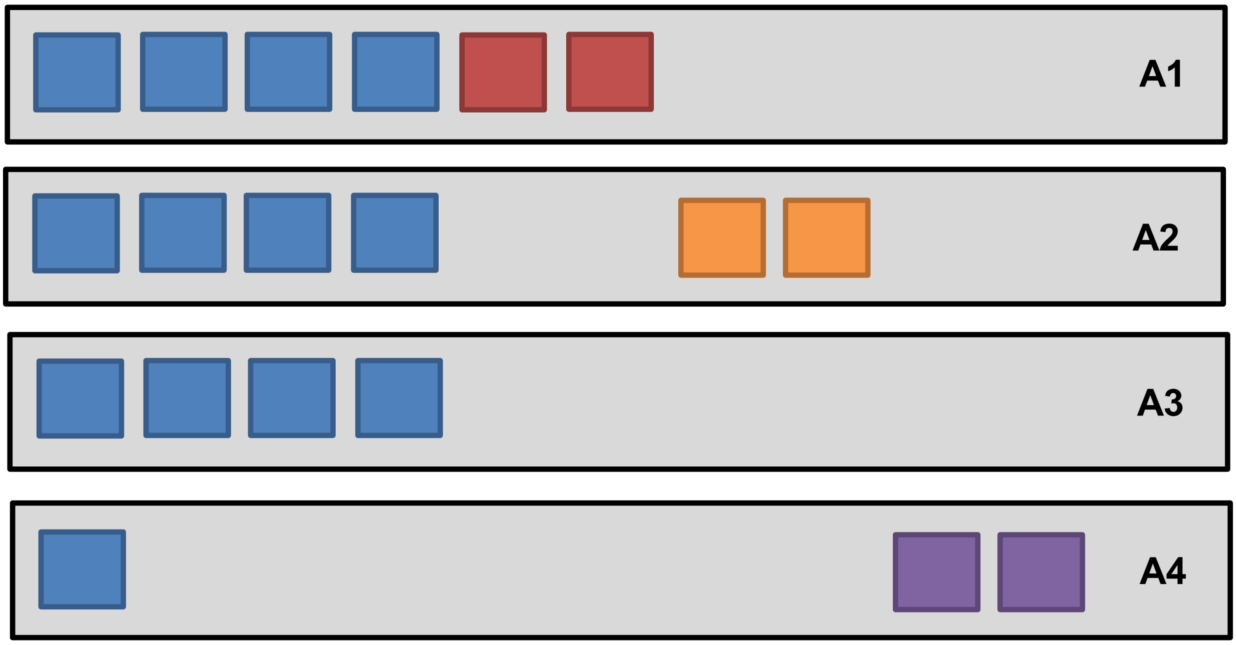


Figure 2. Schematic illustration of turnover and nestedness components of beta diversity. Hypothetical assemblages all display beta diversity. Assemblages A1 and A2 have equal species richness and are therefore not nested. However both assemblages contain species not present in the other, indicating turnover. A3 contains no unique species and has few species than A1 and A2, resulting in nestedness. A4 displays both nestedness and turnover. It contains 2 unique species but is of lower species richness than A1-3 whilst sharing 1 species with them.

Similar to the general concept of beta diversity, the meaning of these decomposed elements is also subject to potential confusion due to the use of differing terminology. For instance, other authors have preferred to use the terms *broad sense turnover* to describe pairwise dissimilarities that capture total compositional change (i.e. Jaccard or Sørensen), and *narrow sense turnover* to describe strict species replacement (i.e. Simpson distance) (e.g. Magurran et al. 2019). Given the varying uses of the terms beta diversity and turnover there is a clear potential for misunderstanding to arise. To avoid confusion, I adopt the Baselga (2010) framework and use his terminology throughout this thesis.

1.2 Corals and coral reefs

The importance of coral reefs

Coral reefs are one of Earth's iconic ecosystems. They are a source of wonder to people around the world, known for their beauty and the stunning abundance and diversity of life they support. Despite covering a minute fraction of the ocean surface area (between 0.1% (Spalding and Grenfell 1997) and 0.25% (Costanza et al. 1997)) it is estimated that at least one third of all marine species inhabit coral reefs during at least one life stage (Reaka-Kudla 1997, Fisher et al. 2015). In addition to being extremely diverse, coral reefs turn otherwise low-productivity waters into highly productive ecosystems (Sheppard et al. 2017). This enhanced productivity means coral reefs play a critical role in the lives of many local communities by providing protein-rich food and essential micronutrients (Hicks et al, 2019). More generally, coral reefs also support livelihoods, as well as providing protection against waves and coastal erosion (Wilkinson 2000). Furthermore, coral reefs form an important part of the cultural and spiritual heritage of many coastal populations (Wilkinson 2000).

Coral reefs are limited to warm, sunlit waters of the tropics and subtropics. Their development is a complicated process involving the activity of numerous different organisms (Sheppard et al. 2017), but the most important reef builders are the hard corals known as the Scleractinians. Corals are ecosystem engineers (Jones et al. 1994) whose growth transforms their environment and creates a complex living space and provide food resources for a myriad of other reef organisms including fish and invertebrates. After the death of a coral, its calciferous skeleton is partially or completely eroded by physical and biological processes. Some of the material produced may be consolidated into the substratum, before creating suitable substratum for the settlement and growth of future generations of corals. When consolidation exceeds erosion, this cycle leads to the gradual accumulation of a reef from the remnants of coral skeletons. Because corals grow radially from their attachment on the sea-floor, reefs develop upwards towards the sea surface, altering the structural, chemical and physical properties of the area.

Corals

Over 1,600 species of Scleractinian corals are known to science (Hoeksema and Cairns 2020). Historically, corals have been classified as hermatypic, meaning reef-forming, or ahermatypic corals; a separation largely dependent on the presence of symbiotic photosynthetic algae (zooxanthellae) within the coral. Reef and non-reef building corals differ substantially in their ecology. Of the known species, 837 species are reef-building corals (Huang 2012), and, due to their essential role for the wider ecosystem, I focus exclusively on reef-building corals in this thesis. Hereafter, the term “coral” refers specifically to reef-forming corals.

In addition to their beauty and their fundamental position in the coral reef ecosystem, corals have a number of fascinating characteristics. For instance, many corals are clonal and modular, meaning that they are composed of repeating units, termed “polyps”, which are genetically identical. The morphology of polyps reflects the membership of corals to the Cnidaria, a phylum of animals displaying radial symmetry and possessing cnidocytes – specialised stinging cells that deliver toxins into prey and potential predators (Tardent 1995). Coral polyps feature a mouth surrounded by tentacles upon which the stinging cnidocytes are located. The mouth leads to a central body cavity, within which zooplankton prey captured by the armed tentacles are digested. Each polyp is encapsulated and protected by a calcium carbonate “cup”, or corallite, within which it can retract to avoid predation.

One of the most distinctive and ecologically important characteristic of corals is the symbiotic relationship with photosynthetic algae called zooxanthellae within coral tissues. This relationship is the key to enabling productive coral reefs to establish and thrive in otherwise unproductive waters. Zooxanthellae are protected within the coral and receive carbon and nitrogen which they use to produce amino acids, carbohydrates and fatty acids during photosynthesis. Corals also benefit because a large proportion of these products are released to the coral polyps (Muscatine et al. 1981), enhancing the growth of the colony (Davies 1984). The ability to obtain nutrients via photosynthetic symbionts or through predation is supplemented by a capability for the direct uptake of dissolved nutrients (Houlbreque and Ferrier-Pages 2009). Together, these abilities permit coral species to adopt a range of different strategies to obtain the energy and nutrients they need to survive, grow and reproduce (Muscatine and Porter 1977). As they grow, the basal tissues secrete additional calcium carbonate, causing polyps to grow upwards from the base of the colony. The growing polyps divide via asexual reproduction in a process known as “budding” that adds additional units to the colony and causes the colony to increase in size. The location of budding and degree of separation between polyps influence the overall shape of the coral that develops, leading to a multitude of different growth forms. It is extraordinary that simple variations in budding are able to generate the astonishing array of forms that corals exhibit (Sheppard et al. 2017).

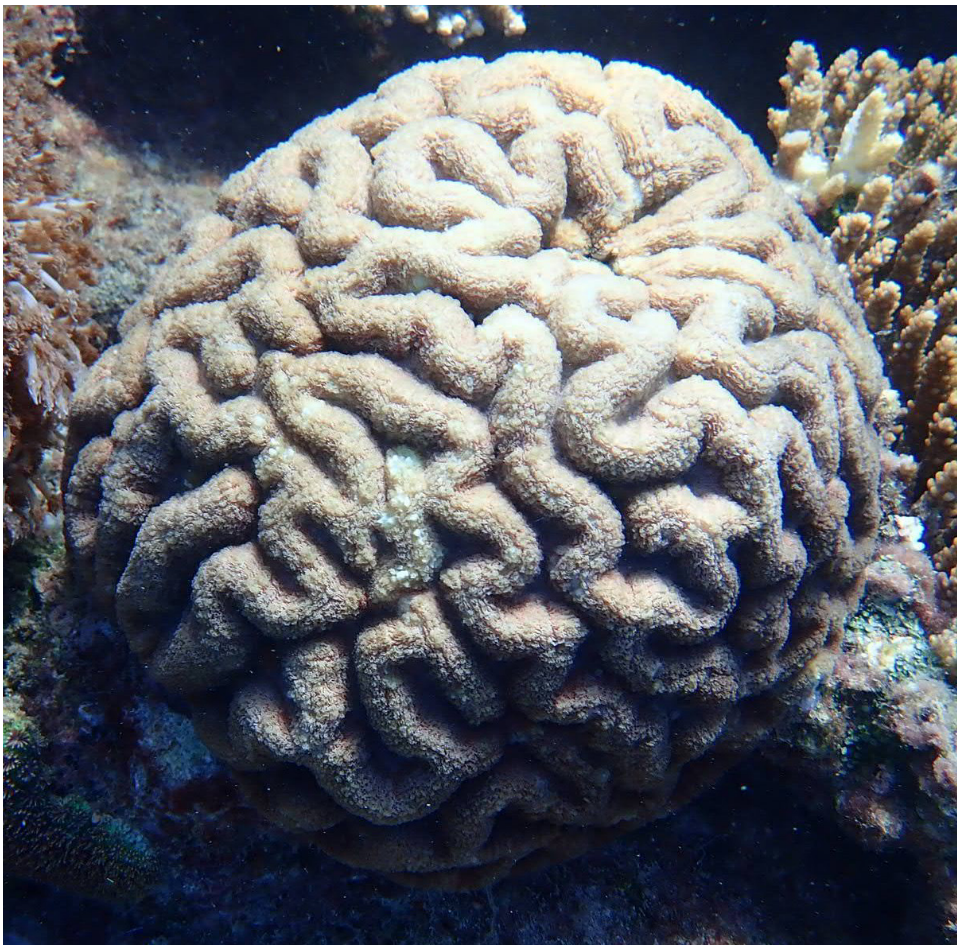
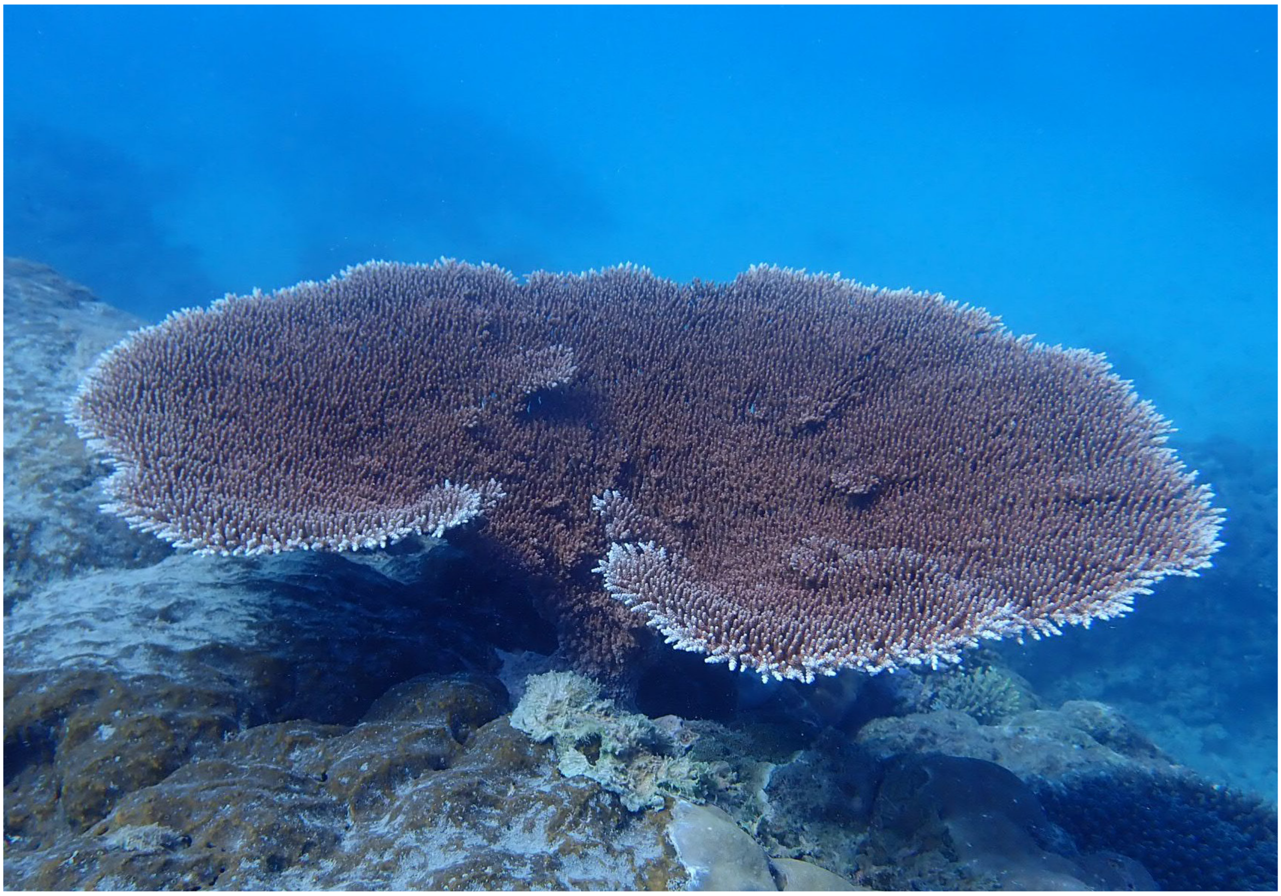


Figure 3. Coral colony morphologies can exhibit a variety of growth forms that results to a large degree in the location of polyp budding and the degree of separation that develops between polyps. *Above*: A massive colony (note the even small corals are termed massive if they display this solid, mound-shaped morphology). *Below left*: A foliacious coral. *Below right*: Branching corals can develop dense thickets. *Overleaf*: A large tabular coral.



Coral distributions

Whilst the symbiotic relationship with zooxanthellae is critical to the ecological success of reef corals, it simultaneously restricts corals to the limited amount of sea-floor that receives sunlight. Combined with their narrow temperature niche (generally 20C – 29C), and salinity niche (33 – 36 ppt), this requirement is one of the main reasons why coral reefs cover such a small proportion of the global oceans (Sheppard et al. 2017). Shallow water habitat occurs on continental shelves and around oceanic islands and sea mounts in limited amounts. As a result, patches of potential coral habitat can be separated by hundreds or thousands of kilometres, placing a pressure on corals to disperse vast distances. Sexual reproduction is the primary mechanism through which corals traverse these vast distances. Although there are different reproductive strategies in corals, all sexual reproduction involves a pelagic planula larval stage. Whilst coral larvae are poor swimmers (Hata et al. 2017), in optimal conditions they can live for several months (Graham et al. 2008). Even in the absence of effective swimming, long residence times in the water column, known as pelagic larval duration, and the activity of tides and ocean currents allow coral larvae to travel long distances (Harrison et al. 1984; Wood et al. 2014).

In spite of the great distances that can separate coral reefs, many species have very large geographic ranges (Hughes et al. 2002) suggesting that long-distance dispersal events occur sufficiently often to be ecologically important. Nonetheless, despite the dispersal and colonisation capabilities of corals, the dramatic differences that exist in the composition of regional species pools strongly suggest that it is not a fully open system i.e., not everything can get everywhere (Keith et al, 2013). Illustrating this, the centre of coral reef diversity in the Indo-Pacific, the “coral triangle”, is home to 605 species (Veron 2009), whereas the Caribbean, home to the most diverse reefs in the Atlantic Ocean, supports around 60 species, an order of magnitude fewer (Karlson and Cornell 1998). Further regional differences occur within ocean basins. For instance, in the Indo-Pacific, species richness declines both longitudinally and latitudinally away from the centre of diversity (see figure 4), whilst coral reefs in Hawai’i and in the Red Sea exhibit unusually high endemism (Hughes et al. 2002).

The global distributions of corals have changed over time. Scleractinia first emerged in the Triassic era, more than 200 million years ago (Stanley 2003) during which time the centre of diversity has shifted. In the last 50 million years, the centre of diversity has moved east from a West Tethyan hotspot, roughly encompassing the modern day Mediterranean and Persian Gulf, to its present location encompassing central and eastern Indonesia, the Philippines and Papua New Guinea (Renema et al. 2008, Veron et al. 2009). However, despite persisting through more than 200 million years, corals are increasingly harmed by human activities to the extent that over one third of coral species are now considered threatened (Carpenter et al. 2008).

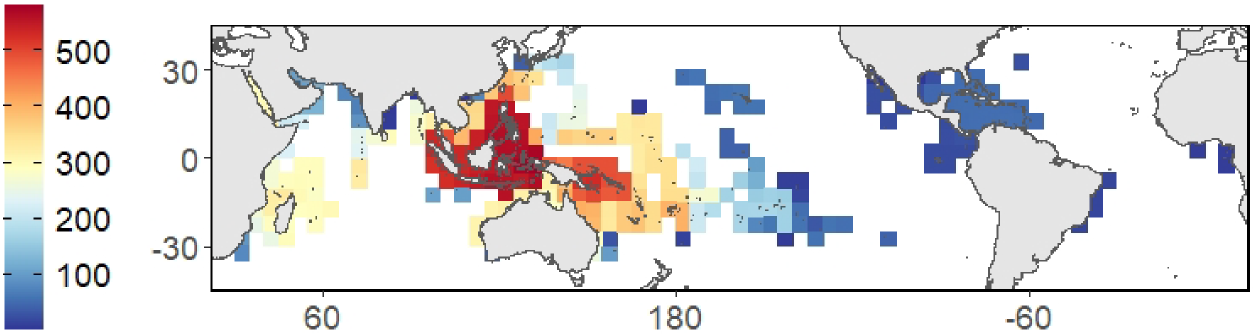


Figure 4. Map of coral reef locations and species richness (IUCN 2016). Warm colours indicate high species richness while cool colours indicate low species richness.

1.3 The Anthropocene

A new epoch

Agriculture, construction, resource extraction, and the deliberate targeting of species, compounded by increased spreading of pathogens and alien species, have resulted in the loss, fragmentation and modification of natural ecosystems (See Barnosky et al. 2011). Humans extract between 20 – 40% of the solar energy that is captured in organic material by land plants (Vitousek et al. 1986) and industrialisation has led to enormous emissions of greenhouse gasses and the modification of nutrient cycles. The consequence of all these changes is that today's ecosystems are transformed to such an extent that they represent novel ecosystems (Hobbs et al. 2006). Rockstrom et al. (2009) identified nine planetary boundaries that mark the limits of the "safe operating space" for humanity. They concluded that humanity has exceeded three of these boundaries; atmospheric CO_2 concentration, changes to the global nitrogen cycle and rate of biodiversity loss. The consequence of our actions (and collective inaction) is that we are now in the midst of two simultaneous crises, a climate crisis and a biodiversity crisis.

The effects on planet Earth of climate change and other human-driven distortions is so great that geologists have identified a new geological epoch called the Anthropocene (Lewis and Maslin 2015). That humankind has generated its own epoch bears testimony to the breadth and scale of our impact.

Climate change

The burning fossil fuels and other anthropogenic emissions, have caused a dramatic increase in the concentration of atmospheric CO_2 relative to pre-industrialisation levels. As a result, concentrations have risen from 277 ppm prior to industrialisation to 407 ppm (Joos and Spahni 2008, Dlugokencky and Tans 2018). Such high CO_2 concentrations have not been seen for several million years (Bala 2013), and the result is an increase in the global mean surface temperature of $0.87^{\circ}C$ since the pre-industrial period (IPCC 2018). Oceans have absorbed a significant proportion of the released CO_2 (IPCC 2019), mitigating some of the warming effect of carbon emissions, but causing the oceans to become more acidic. In addition to increases in global mean ocean temperatures and acidity, climate change has also caused sea level rise, increased frequency and duration of heatwaves, increased frequency of extreme weather events such as drought and heavy rain, and changes to ocean circulation (IPCC 2019).

Such profound changes to the abiotic environment inevitably impact marine life with widespread distributional shifts occurring in diverse groups of organisms (Hoegh-Guldberg and Bruno 2010, Poloczanska et al. 2013) and alterations in food webs and ecosystem functioning (Lotze et al. 2019, Pecl 2017). Even under the most optimistic forecasts the ocean is predicted to warm further by 2100, exacerbating the changes observed to date and further stressing organisms and ecosystems, particularly coral reefs (IPCC 2018, IPCC 2019).

The global biodiversity crisis

Most of the earth’s surface is impacted by human activities (Sanderson et al. 2002, Halpern et al. 2008). Even the small fragment of wild areas that remain are not entirely free from human influence since the consequences of anthropogenic climate change act diffusely (Jones et al. 2018). Thus, humans have impacted every part of the surface of the earth and even the deepest parts of the ocean floor reveal the influence of human activity (Chiba et al. 2018). For many organisms, human pressures reduce population size, alter geographic distributions, increase risk of extinction (Brown and Maurer 1989; Walther et al. 2005) and change behaviour (Tucker et al 2018; Keith et al 2018). Causes can be direct, through the targeted or accidental killing of individuals and the destruction of habitat (Lewis and Maslin 2015), or indirect, such as increased rarity of resources (Wilcove 1987) or interference with growth or reproductive output. Smaller populations have less adaptive potential and are more vulnerable to extinction (Willi et al. 2006).

Alarm over the declining state of biodiversity saw the adoption of the United Nations Convention on Biological Diversity in 2002, where world leaders made commitments to slow the rate of biodiversity loss (UNEP 2002). Despite indications of increasing responses to the challenge faced, ecological trends between 2002 and 2010 revealed increased pressures and subsequent losses of biodiversity (Butchart et al. 2010). Of greatest worry is that current extinction rates exceed the background rate by orders of magnitude suggesting that the Earth is may be entering into a sixth mass extinction event (Barnosky 2011).

1.4 Corals in the Anthropocene

Vulnerability to anthropogenic change

The vulnerability of a given species to anthropogenic change is dependent not only on its sensitivity to the particular stresses being placed upon it, but also on the degree of exposure to stressors, often linked to the overlap between its habitat and human activities (Cinner et al. 2018). Whilst some species may actually benefit from global change, others will be negatively affected (McKinney and Lockwood, 1999). Although there is disagreement as to the balance of “winners and losers” and the overall pattern of abundance change (McKinney and Lockwood 1999, Dornelas et al., 2019), reef corals appear to be both particularly sensitive to anthropogenic change and highly exposed to human influences (Cinner et al. 2018).

Climate impacts

Increased ocean temperatures and marine heatwaves are the stressors of corals that elicit the most visible and well-documented consequences. These factors combine to create physiologically stressful conditions for the coral that destabilise its symbiosis with zooxanthellate algae. Exposure to elevated temperature over sufficiently long time periods causes coral bleaching, where corals eject their zooxanthellate symbionts. This process is damaging and sustained bleaching often results in reduced growth and substantial mortality (Hughes et al. 2017b). In mass bleaching events, bleaching affects many corals over a large spatial extent. Repeated mass bleaching events affecting regions greater than 1,000 km in extent was unknown prior to the 1980s, but since 1998 three global scale bleaching events have occurred (Hughes et al 2017b). Smaller scale bleaching events also occur and compound global bleaching events, impacting reefs before they have had time to recover. The fastest growing coral species may require 10 to 15 years to recover, whilst corals with slower life-histories need multiple decades (Hughes et al. 2018a). Recent estimates suggest that as of 2018, reefs are typically affected by bleaching every six years, preventing full recovery and resulting in degraded reefs with transformed assemblages (Hughes et al. 2018b) and reduced structural complexity (Robinson et al. 2019). Structural complexity is critically important to coral reef ecosystems. It is strongly related to fish density and biomass as well as being linked to the proper functioning of multiple ecosystem services (Graham and Nash 2013). Recent work has found that structural complexity even facilitates the settlement of coral larvae (Hata et al. 2017), which may explain why reefs with greater structural complexity tend to show better recovery following major bleaching (Graham et al. 2015). Structural losses as a result of bleaching can therefore have devastating impacts on the entire ecosystem and dependent communities.

“Death by a thousand cuts”

In addition to their sensitivity to climate change, corals’ requirement for shallow water means that they typically overlap with human settlements and therefore a range of more local stressors. For instance, pollution, destructive fishing practices and over-harvesting damage coral reef ecosystems (McManus et al. 1997, Bellwood et al., 2004), intensifying the effects of ocean warming and acidification. Nitrogen loading of the coastal zone has increased by about 80% worldwide (MEA 2005), promoting the growth of macroalgae that compete with corals for space and produce allelopathic chemicals that harm coral growth (Rasher et al. 2011). Corals are adapted to low nutrient environments and typically outcompete macroalgae when nutrient concentrations are low, but eutrophication tips the balance in favour of algae (Fabricius et al. 2005). Nutrient loading is also believed to promote the abundance of Crown-of-thorns starfish (COTS; Birkeland 1982), which prey on corals and have been responsible for large reductions in coral cover on the Great Barrier Reef (De’ath et al. 2012). Nutrient loading also acts together with overfishing to destabilise coral reef ecosystems because the depletion of COTS predators (Sweatman 2008) and herbivorous fishes removes top-down control on macroalgal and COTS abundances. Finally, the introduction of invasive species alters the composition of reef communities, illustrated by the decline in prey species of the Indo-Pacific lionfish following its introduction into the Western Atlantic (Green et al. 2012). The consequences of these multiple stressors are described as “death by a thousand cuts” (Hughes et al. 2017a). This is demonstrated by the long term decline of the Great Barrier Reef, where coral cover is estimated to have declined by 50% between 1985 and 2012 (De’ath et al. 2012). The combined effect of these various human pressures can result in large-scale alteration of the structure and functioning of these ecosystems, termed phase-shifts, where the system becomes stably dominated by macroalgae (Hughes 1994, Graham et al. 2015).

In recognition of the dire climate change situation that the world is facing, world leaders at the 2015 United Nations Climate Change Conference in Paris agreed upon an ambitious target of limiting climate change to “well below 2^{o}C[…] and to pursue efforts to limit the temperature increase to 1.5°C” (UNFCCC 2015). Unfortunately, backtracking on commitments and delayed implementation mean that we are someway off reaching this target. Even if the terms of the Paris Agreement are met and global warming is limited to 1.5°C, there is a very high probability that tropical corals will suffer from severe, and to a significant degree irreversible, impacts, with significant local extinctions and loss of area (IPCC 2019). Under the most optimistic projection, the forecasted warming of coral reef provinces between 2010 and 2100 will be roughly equivalent to the warming of the previous century (Hughes et al. 2017a). Should emission reductions be less aggressive, the consequences will be much worse than the bleak outlook just described.

Understanding coral futures in the Anthropocene

One of the primary challenges in understanding, and reliably predicting, the consequences of anthropogenic change on ecosystems lies in the fact that multiple aspects of the environment are changing simultaneously. Particularly relevant for corals are the expected increases in temperature and nutrient concentrations, although these increases are unlikely to be equally large or proceed at the same rate across all locations. Also highly relevant are projections of changes in ocean circulation and losses in reef area (IPCC 2019). It is difficult to know which of these aspects will have the greatest impact on corals, or how their effects will interact (Harvey et al. 2013). Experiments offer one avenue to answer these questions but few manipulate more than a single factor (Korell et al. 2020). Additionally, experiments may struggle to capture the complexity of real-world systems and face the challenge that long-term changes are hard to replicate under laboratory or mesocosm settings (Connell 1974). As an alternative, or as a complement to experiments, a biogeographic approach can provide valuable insights as to how biodiversity is generated, maintained and might respond to natural and human factors. The goal of such work is a set of generalisable ecological rules that apply across taxa or ecosystems (Lawton 1999). Biogeographical knowledge can then inform management and conservation actions (Whittaker et al 2005).

1.5 Aims of the thesis

The overarching goal of this thesis is to contribute to our understanding of the key factors explaining the biogeography of corals. To pursue this, I explore spatial patterns of distributions and assemblages across the Indo-Pacific and Atlantic oceans, also investigating the effect of changing the spatial grain of analysis. I gather data on a number of environmental variables, the size of reef areas and estimates of dispersal limitation from connectivity and distance, and combine this data with information on coral traits and published maps of coral distributions.

In Chapter 3, I attempt to determine the key factors influencing global coral beta diversity and how their relative influence is linked to the spatial grain of analysis. In this extensive investigation, I specifically address the following questions:

1. What are the key factors determining global patterns of beta diversity in corals?
2. Are the key factors and their relative importance similar across ocean basins?
3. How does the spatial grain of analysis affect the relative importance and shape of the relationship between key factors and coral beta diversity?

In Chapter 4, I examine the role of dispersal limitation in greater depth, exploring the influence of coral reproductive mode on coral range size and coral assemblage structure. I partition beta diversity into turnover and nestedness components and relate the decay of coral assemblages to spatial distances across the Indo-Pacific ocean basin. In order to shed light on whether a spawning life-history supports greater long-distance dispersal than a brooding strategy I ask:

1. To what extent can the reproductive mode of corals predict their range size?
2. Does beta diversity increase more rapidly with distance in brooding corals than spawning corals?
3. Do assemblages of spawning corals exhibit reduced turnover and greater nestedness across distance than brooding corals?

2

Synopsis

Beta diversity measures variation in species' identities between sites (Anderson et al. 2011). Investigating how beta diversity is generated and maintained can illuminate the underlying mechanisms that structure species assemblages. Ultimately, beta diversity provides a means to study a key question in community ecology, namely, why do species assemblages differ from one another (Vellend 2010). Through relating differences in assemblage composition to dissimilarities or distances of potential drivers, we are able to reveal the key factors structuring assemblages (Vellend 2001). Potential drivers of beta diversity include environmental conditions, dispersal limitation as well as characteristics of the organisms themselves, i.e. species traits. Biodiversity loss is accelerating in the Anthropocene due to habitat degradation and climate change (Butchart et al. 2010, Barnosky et al. 2011) and improved understanding of the mechanisms structuring species assemblages would provide valuable information about how species and ecosystems may respond.

In this thesis, I study the beta diversity of corals, an important group of organisms (Wilkinson 2000) severely threatened by Anthropogenic change (Carpenter 2008, IPCC 2019). To develop a robust understanding of the factors determining global patterns in coral beta diversity, I explore coral beta diversity across both the Indo-Pacific and Atlantic basins, and across multiple spatial scales.

In Chapter 3, I attempt to elucidate the key factors associated with contemporary patterns of coral beta diversity and determine how their relative importance changes across ocean basins and spatial scales. Numerous factors have been hypothesised to drive coral biogeographic patterns, yet the key determinants and their relative importance are still debated. Uncertainty is particularly acute regarding the influence of dispersal limitation owing to the difficulty of measuring it. I tackle this problem by combining coral species distributions with data on a number of potential predictors, including environmental conditions, reef area and modelled estimates of coral connectivity. I extract occurrences for all Scleractinian species across both the Indo-Pacific and Atlantic Ocean basins from published range maps

(IUCN 2016). The environmental predictors include data of sea surface temperature (SST), together with nutrient concentrations and light penetration depth. Modelled estimates of global connectivity (Wood et al. 2014) are used to estimate dispersal limitation between sites, and are supplemented with distance-based estimates of dispersal limitation.

To determine the key variables influencing coral beta diversity and their relative importance, I iteratively model Atlantic and Indo-Pacific coral beta diversity across a range of spatial scales using generalised dissimilarity modelling. I use a backward variable selection procedure across all scales to identify the key variables that predict coral beta diversity at each scale. I then combine this information to select a subset of variables that are the most import factors for coral beta diversity overall. Finally, the relative importance of the various factors and their response to changes in grain size is determined using variation partitioning and I-spline curves.

I found that variables representing dispersal limitation, SST and nutrient concentrations were important factors predicting beta diversity in both Indo-Pacific and Atlantic coral assemblages. Critically, dispersal limitation was an important factor in both ocean basins, particularly in the Indo-Pacific where it was the most important factor. The size of reef area also emerged as an important factor at large grains of analysis. Grain size affected variation in both the response and predictor variables with the predictive utility factors responding differently to the changing scale. Environmental factors and reef area displayed opposing responses to changes in grain, with environmental factors being important at fine scales but declining in importance with increasing grain size. The importance of dispersal limitation was less affected by changes in the scale of analysis.

These results have implications for the conservation of corals. All of the variables determining and maintaining coral beta diversity are likely to change in the Anthropocene (IPCC 2019). Concerted efforts to combat climate change, improve water quality and protect reef habitat over large areas are of paramount importance to protect coral reefs. The finding that dispersal limitation is a key determinant of coral beta diversity contrasts to previous findings from large-scale biogeographic analysis of marine biogeography (Keith et al. 2013, Luiz et al. 2013, Mora et al. 2012), and emphasises the importance of developing realistic models of dispersal. In particular, the finding underlines the need to conserve connected dispersal pathways to support corals ability to track suitable environmental conditions.

Chapter 4 builds on the findings of Chapter 3 by investigating the influence of a fundamental trait on the dispersal ability of corals. Many marine organisms that are unable to disperse as adults have a pelagic larval life stage with the potential to travel long distances (Cowen 2000). Different strategies for producing such planula larvae have long been thought to influence the dispersal potential of marine taxa (e.g. Thorson 1950), with the release of gametes into the water column, termed broadcast spawning, likely to result in wider dispersal than a strategy where larvae are brooded internally until ready to settle. In Chapter 4, I investigate whether the dispersal consequences of different reproductive modes of corals (i.e., brooding vs broadcast spawning) generate differences in their large-scale biogeography with respect to species range sizes and assemblage structure across distance.

First, I investigate how different reproductive modes affect the range sizes of corals using permutation tests. To test the hypotheses that weaker dispersal ability in brooding corals results in smaller geographic ranges relative to spawning corals, I combine range maps (Hughes et al. 2013) with trait data on coral reproductive mode (Madin et al. 2016, McWilliam et al. 2018). For every species were trait data is available I calculate the range as the extent of occurrence (Gaston 1991). I then applied a permutation procedure to compare the observed differences in range size between the groups against a null distribution of possible differences in range size that assumes no difference between brooding and spawning corals.

Second, to reveal the influence of reproductive mode on the structure of coral assemblages across space, I fit distance-decay models for brooding and spawning assemblages separately. I decompose beta diversity into turnover and nestedness components (Baselga 2010) and model the distance-decay relationships of all three measures of assemblage dissimilarity. Turnover and nestedness result from different processes (Baselga 2010), and modelling these components separately provides more clarity of how reproductive strategy influences the processes structuring assemblages across space. To capture potential nonlinearities in the relationships between distance and dissimilarity, I repeat the fitting of decay curves with the addition of a quadratic distance term.

Although there was a trend for larger range size in spawning corals relative to corals that brood larvae, the relationship is not significant. Nonetheless, distance-decay relationships for beta diversity, turnover and nestedness differed significantly between groups. Beta diversity and turnover increased more rapidly in brooders than spawners, whereas nestedness was lower in brooders and tended to decline with distance. The addition of a quadratic distance term did not affect the rank order of brooder and spawner distance-decay relationships, and the shape of beta diversity and turnover decay curves remained broadly similar. However, the quadratic term revealed a parabolic relationship between nestedness and distance for both reproductive modes, potentially indicating problems in the formulation of nestedness.

These results suggest that brooding and spawning strategies may result in differing long-distance dispersal ability and biogeographic patterns in corals with important implications for their conservation and management under climate change. Overall, the thesis highlights important challenges in the conservation of corals, with consideration of dispersal differences between coral species an additional factor that needs to be accounted for in the establishment of marine protected areas. In Chapter 5, I elaborate on these findings, before proposing potentially fruitful research avenues in Chapter 6.

3

Cross-scale determinants of global beta diversity in reef corals

Neil Maginnis, Sally Keith, Michael Borregaard, Martin Lindegren

Abstract

Aim: The key determinants of coral assemblage structure and their relative importance are still debated, particularly the influence of dispersal limitation. Our aim was to elucidate the key factors associated with contemporary patterns of coral beta diversity and determine how their relative importance changes across ocean basins and spatial scales.

Location: All known reef locations in the Indo-Pacific and Atlantic Ocean basins (34° S - 34° N), aggregated at spatial scales ranging from 1° - 10° resolution.

Methods: We combined coral species distributions with data on a number of potential predictors, including environmental conditions, reef area and modelled estimates of coral connectivity. We then applied a Generalised Dissimilarity Modelling (GDM) framework to model coral beta diversity in response to the above-mentioned predictors across ocean basins and spatial scales. Backwards variable selection, variation partitioning and I-spline curves were used to assess the relative importance and shape of response curves.

Results: Contemporary patterns of beta diversity of Indo-Pacific and Atlantic coral assemblages were primarily explained by variables related to dispersal limitation, sea surface temperature and nutrient concentrations. Reef area was also influential in the Indo-Pacific, but not the Atlantic. Dispersal limitation displayed the strongest relationship with beta diversity in the Indo-Pacific, whilst Atlantic coral beta diversity responded more strongly to environmental variables. Environmental variables generally decreased in importance with larger grain size, whereas reef area increased in importance. Dispersal limitation was robust to spatial grain.

Main conclusions: Dispersal limitation acts as a constraint on corals and may prevent them from tracking suitable environmental conditions in the Anthropocene. Concerted efforts to combat climate change, improve water quality and halt the degradation and loss of coral reefs are critically important.

3.1 Introduction

Corals form the cornerstone of coral reefs, a staggeringly diverse ecosystem home to one third of all marine species (Fisher et al. 2015), but one that is highly threatened by human activities (IPBES 2019). Assemblages of corals and coral reef associated organisms exhibit pronounced geographical differences in species richness and composition, often with striking concordance amongst taxa (Tittensor et al. 2010, Paulay, 1990, Roberts et al. 2002, Palumbi 1997, Keith et al 2013, Lindegren et al. 2018). For example, both corals and reef fish show a global maximum in diversity, expressed either in terms of taxonomic or functional (trait) richness, in the Indo-Australian Archipelago, with declines occurring both latitudinally and longitudinally away from this biodiversity hotspot (Veron, 1995, Stuart Smith et al. 2013, McWilliam et al. 2018). Because of these parallels across taxa, corals provide an excellent opportunity to explore one of the longest standing questions in ecology and conservation, namely understanding the factors determining the diversity and composition of communities (Sutherland et al. 2012).

Large-scale biogeographic analyses have typically focused on species richness (Chase and Knight 2013). However, such an approach cannot effectively discriminate between different assemblages of similar species richness. This reduces its power to resolve between factors determining broad-scale diversity patterns, especially since such patterns are typically also confounded by collinearity. Potentially owing to these issues, energy input (Fraser and Currie 1996), reef area (Bellwood and Hughes 2001) and enhanced dispersal along ocean currents (Connolly et al. 2002) have variously been highlighted as the key determinants of coral species richness patterns. Utilising beta diversity, commonly defined as the extent of change in community composition (Whittaker 1960) may allow us to resolve some of the uncertainty around the factors suggested to determine coral biogeography, since it considers species identity and can distinguish between equally rich assemblages whose composition differ. The literature on coral beta diversity has served to identify coral faunal provinces (Keith et al. 2013) and demonstrated that differences in assemblage composition do not follow the predictions of neutral theory (Dornelas et al. 2006). Rather, beta diversity patterns are suggested to result from environmental heterogeneity (Dornelas et al. 2006) or differences in geological history (Keith et al. 2013, Leprieur et al. 2016). Geological history influences patterns of dispersal and likelihood of colonization success (Keith et al. 2013), together with speciation and extinction probabilities (Leprieur et al. 2016). Although the above authors have either explored, integrated or acknowledged the influence of dispersal limitation, none were able to include a realistic model of coral dispersal to test its impact. Hence, the importance of dispersal limitation to coral beta-diversity may be underestimated in comparison to other hypothesised factors. Furthermore, studies on marine diversity and biogeography, including corals, are often conducted in different regions or at different spatial scales, precluding unbiased comparisons across studies (Barton et al. 2013, Chase and Knight 2013).

Consequently, whilst progress has been made in identifying a candidate set of variables plausibly shaping coral beta diversity and biogeography at large, a great deal of uncertainty still remain regarding their relative importance and potential cumulative impacts across spatial scales and ocean basins. To counter this knowledge gap we combined global observational data on coral species occurrences, environmental conditions and reef area with a novel representation of dispersal limitation estimated from a global model of coral connectivity (Wood et al. 2014). Subsequently, we used generalised dissimilarity modelling (GDM) to investigate the single, or combined effects of candidate variables on coral beta diversity across a range of spatial scales in both the Atlantic and Indo-Pacific, with the aim of answering the following research questions:

1. What are the key factors determining global beta diversity of corals?
2. Are the key factors and their relative importance similar across ocean basins?
3. How does the spatial grain of analysis affect the relative importance and shape of the relationship between key factors and coral beta diversity?

3.2 Material and Methods

Coral beta diversity across spatial scales

To determine the global composition and beta diversity of reef building corals we extracted occurrences for all Scleractinian species across both the Indo-Pacific and Atlantic Ocean basins from published maps (IUCN 2016). All data were initially extracted to the same 1/6° grid grain used in the coral connectivity model of Wood et al. (2014), but to examine the effects of changing spatial grain, the analysis was performed across a range of grains spanning 1° - 10°. After updating the species data to the latest taxonomy, we eliminated corals lacking photosynthetic symbionts using trait data accessed from the Coral Trait Database (https://coraltraits.org). Thereafter, we determined Presence-Absences of the retained species for each grid cell across all spatial grains in both ocean basins. To calculate beta diversity between coral assemblages, we compared the species composition of grid cells of the same grain size on a pairwise basis using the Sørensen’s distance as our metric for beta diversity.

Environment, dispersal limitation and reef area

To represent environmental conditions potentially influencing coral beta diversity we extracted raster layers for a range of variables that have been found, or proposed, to affect the ecology or biogeography of corals (Table 1). We initially selected four variables covering different components of sea surface temperature (herafter SST). SST range and SST mean are proxies for environmental stability and available energy, whilst monthly maximum and minimum SST were included to represent extreme high and low temperature that can impact coral growth and survival (Coles and Jokiel 1978, Glynn 1977). Since high nutrient concentrations promote macroalgal growth, which compete with corals for light and space (McCook et al. 2001), we also included global data on nitrate and phosphate concentrations. Furthermore, corals show differing affinities to light intensity and tolerances of turbidity (Siebeck 1988, Loya 1976). Hence, we included photosynthetically active radiation (PAR) and diffusive attenuation (DA) in our analysis. Following Couce et al. (2012) we also used PAR and DA to estimate the maximum light penetration depth. Salinity was also included, as corals are known to vary in their ability to osmoregulate (Sheppard, 1988). To measure the influence of dispersal limitation between reefs we calculated two measures, Isolation by Distance (IBD) and Isolation by Resistance (IBR). IBD was calculated as the shortest path through the water between all pairs of grid cells containing reefs, whilst IBR was derived from a biophysical model of coral connectivity with empirically derived parameters for larval life history (Wood et al. 2014). Since stepping-stone dispersal may be critical to species’ long range dispersal we treated reefs as interconnected nodes in basin-wide networks (Saura et al. 2013). Using the strength of connection between locations, we calculated the lowest cost route through the network for all reef pairs. Finally, to estimate reef area, we combined high resolution bathymetry data (Sbrocco and Barber 2013) with the 1/6 degree reef cells. We treated ocean areas of 30m or less as being suitable for coral occupation and therefore extracted the total area within each reef cell above this depth. After checking for cross-correlation among candidate variables, we omitted DA and minimum SST from the analysis as their correlation with other variables exceeded 0.75.

Model setup and variable selection

To determine the key variables influencing coral beta diversity and their relative importance, we iteratively modelled Atlantic and Indo-Pacific coral beta diversity across a range of spatial scales using generalised dissimilarity modelling (GDM) (Ferrier et al., 2002). GDM is an approach that allows a single response matrix, in this case of pairwise Sørensen dissimilarities in species composition, to be modelled as a function of a set of explanatory variables. It additionally accounts for two forms of non-linearity: 1) variation in the rate of compositional turnover along environmental gradients, and 2) non-linearity between ecological distance and observed compositional dissimilarity which results from dissimilarity being bounded between 0 and 1. Monotonic I-splines were used to determine

Table 1. Variables used as candidate predictors of coral beta diversity. Data type is described together with data source and the method of data aggregation from 1/6^{o} resolution.

Data layer	Aggregation	Source
Mean annual SST	Mean	Sbrocco and Barber (2013)
SST of the warmest month	Mean	Sbrocco and Barber (2013)
Annual range in SST	Mean	Sbrocco and Barber (2013)
SST of the coldest month	Mean	Sbrocco and Barber (2013)
Mean Nitrate concentration	Mean	Assis et al. (2017)
Mean Phosphate concentration	Mean	Assis et al. (2017)
Mean Diffusive attenuation	Mean	Tyberghein et al. (2012)
Mean PAR	Mean	Tyberghein et al. (2012)
Light penetration depth	Mean of $\frac{ln(PAR_{Cell}/5Em^{-2}d^{-1})}{DA_{Cell}}$	This paper, utilising Tyberghein et al. (2012)
Mean Salinity	Mean	Assis et al. (2017)
Reef area	Sum	Wood et al. (2014)
Isolation by distance	Calculated at all grains	This thesis
Isolation by resistance	Sum prior to network shortest path calculations	This thesis, utilising Wood et al. (2014)

the shape of the relationships between beta diversity and each of the explanatory variables and the importance determined using maximum likelihood estimation (See Ferrier et al. 2002 and Ferrier et al. 2007 for more details).

We identified the most important predictors of global coral beta diversity across spatial scales using a backwards selection procedure. Treating Atlantic and Indo-Pacific models separately, we applied a permutation procedure to the models at every spatial scale. After iteratively eliminating the variable explaining the least variation in beta diversity, we grouped models of every scale according to the number of predictor variables present and constructed boxplots of the deviance explained by the models. We then determined the number of variables required to generate a model with good performance across scale by means of the elbow criteria, i.e., visually identifying the number of variables where a further model reduction causes performance to decline sharply. To allow for comparison between the Indo-Pacific and the Atlantic models, we selected the same number of variables in both basins. Extracting and tabulating the variables from models with this optimal number of variables allowed us to determine the variables that occurred most frequently across scales and effectively explained the observed variation in coral beta diversity at all spatial grains in both basins. Due to the lack of sufficient data points available in the Atlantic at lower grains, we restricted our analysis to 1 ° to 5° in this basin. We reran the analysis at all scales with this subset of variables before partitioning the variance attributable to environmental conditions, reef area and dispersal limitation and combinations thereof. To explore how the relationship to coral beta diversity differs across variables and spatial grain we extracted and plotted the fitted I-splines from each model.

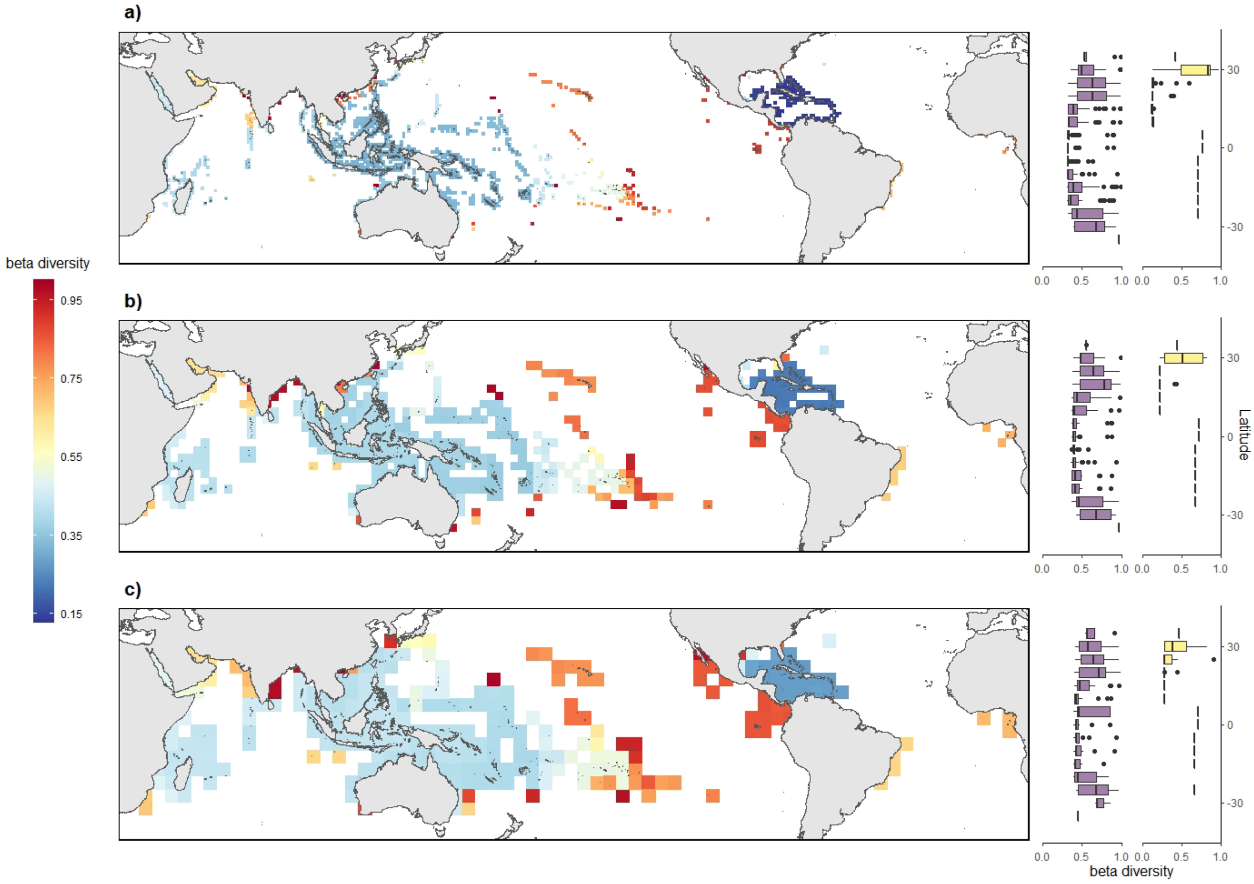


Figure 1. Mean pairwise beta diversity of corals across ocean basins and spatial grain. a) 1°, b) 3°, c) 5°. Boxplots show the latitudinal distribution of mean pairwise beta diversity. Purple boxes represent Indo-Pacific beta diversity, yellow boxes Atlantic.

3.3 Results

Global patterns of coral beta diversity

Coral assemblages in the Indo-Pacific generally exhibit greater mean pairwise dissimilarity in species composition compared to Atlantic coral assemblages (Figure 1, Table 2). However, Atlantic assemblages exhibit greater variation in beta diversity, indicated by a higher standard deviation of beta diversity in this ocean basin. Mean beta diversity exhibits an increasing trend with increasing spatial grain in both ocean basins. However, the standard deviation of beta diversity is largely constant across grain (Table 2). In the Indo-Pacific Ocean, the coral assemblages that are generally most similar to other coral assemblages are located in the Central Indo-Pacific, indicated by minimal average pairwise beta diversity in this region (Figure 1). Mean beta diversity rises only slightly across the Indian Ocean and in the Red Sea, whilst assemblages become markedly different across Polynesia, indicated by increasing beta diversity values in this region. Beyond the wide divide of the Eastern Pacific barrier, coral assemblages are highly distinct, with mean pairwise beta diversity values that are consistently high. There is a trend for increasing beta diversity values at higher latitudes, though this is skewed in a northerly direction in the Atlantic. Variation in species composition in the Atlantic primarily occurs between the Caribbean, Brazilian and West African regions (Figure 1).

Determinants of coral beta diversity

Our backward model selection procedure revealed considerable alignment between ocean basins in terms of the variables retained in the final models. Variables representing dispersal limitation, SST and nutrient concentrations featured heavily in models for both the Indo-Pacific and Atlantic and the Atlantic model exclusively contained variables of this type. Interestingly, reef area was not present in the final model for the Atlantic, whereas it was present in the Indo-Pacific model, which also contained a variable for light penetration depth. Although there are strong parallels between basins in terms of the broader type of variables selected, there are some differences between basins in terms of the specific variables retained (see Figure 3, Table S1 for details). Our model selection was robust to the stochasticity inherent in the permutation procedure, indicated by the fact that variables selected in three-, four- and five-variable models are sequentially nested. Three variable models were outperformed by four and five variable models which differed little in deviance explained (Figure S1). However, since maximum SST and light penetration depth occurred equally often as the final variable in the four variable model for the Indo-Pacific (Table S1) it was necessary to include a fifth variable. The final models from the variable selection procedure explained a large proportion of the observed variation in pair-wise beta diversity in the Indo-Pacific (42 – 54%) and Atlantic (77 – 85%) across all spatial grains (Table 2). Furthermore, the model predictions generate realistic overall patterns of coral beta diversity across broad-scales (Figure S2). However, models for the Indo-Pacific slightly overestimated beta diversity in more similar (β_{Sor} < 0.5) assemblages and slightly underestimated beta diversity in less similar (β_{Sor} > 0.5) assemblages (Figure S4). Many of the more distinct assemblages, where beta diversity is underestimated occur in peripheral or higher latitude locations such as the Hawaiian archipelago and fringe regions of Polynesia (Figure S2). Models built from dispersal limitation or environmental conditions alone are able to reproduce some aspects of coral beta diversity patterns. For example, locations where the observed beta diversity exceeds values predicted from dispersal limitation alone, particularly in some high latitude locations, are better predicted by modelled environmental effects and reef area. However, neither models of environmental effects, nor reef area predict the observed beta diversity in the Central Eastern Pacific, which is instead best predicted by dispersal limitation. Finally, a model based on reef area alone fails to produce recognisable coral beta diversity patterns.

Table 2. Coral beta diversity in the Indo-Pacific and Atlantic ocean basins. Beta diversity of cells is presented as minimum, maximum, mean and S.D. of pairwise dissimilarities. Variance explained (%) by the final model in each ocean is calculated separately at every spatial grain.

	Grain size	N	Mean	SD	Variation explained
Indo-Pacific	1°	1057785	0.426	0.279	42.2
	2°	255255	0.476	0.284	42.1
	3°	105111	0.499	0.287	43.1
	4°	55278	0.510	0.287	45.2
	5 °	33153	0.538	0.287	49.5
	6 °	20910	0.550	0.291	48.9
	7 °	14365	0.549	0.285	43.6
	8 °	10153	0.560	0.288	48.8
	9 °	7021	0.555	0.283	47.5
	10 °	5460	0.567	0.295	53.7
Atlantic	1°	26335	0.223	0.327	84.7
	2°	5995	0.319	0.362	84.9
	3°	2278	0.359	0.355	83.6
	4°	1326	0.391	0.370	84.6
	5 °	630	0.435	0.361	77.0

Relative importance of variables across spatial grain

Variance partitioning indicates that dispersal limitation was the most important factor influencing coral beta diversity in the Indo-Pacific, particularly at coarser spatial grains. By contrast, environmental factors were the most important predictors of coral beta diversity patterns in the Atlantic. Because at least 36.7% of explained variance was shared between two or more variables across all analyses, more nuanced conclusions on the relative importance of variables are uncertain. Nonetheless, some trends emerged in the Indo-Pacific. There was a clear increase in the importance of reef area with increasing spatial grain (Figure 2). At fine spatial grains the contribution of reef area to model performance was negligible, but at the coarsest grain its importance equalled, or even exceeded that of environmental variables. Conversely, the explained variation directly attributable to environmental conditions and variation shared between environment and other variables showed declining trends with increasing spatial grain. Dispersal limitation exhibited no trend across grain, and explained the largest proportion of variation at all grain sizes.

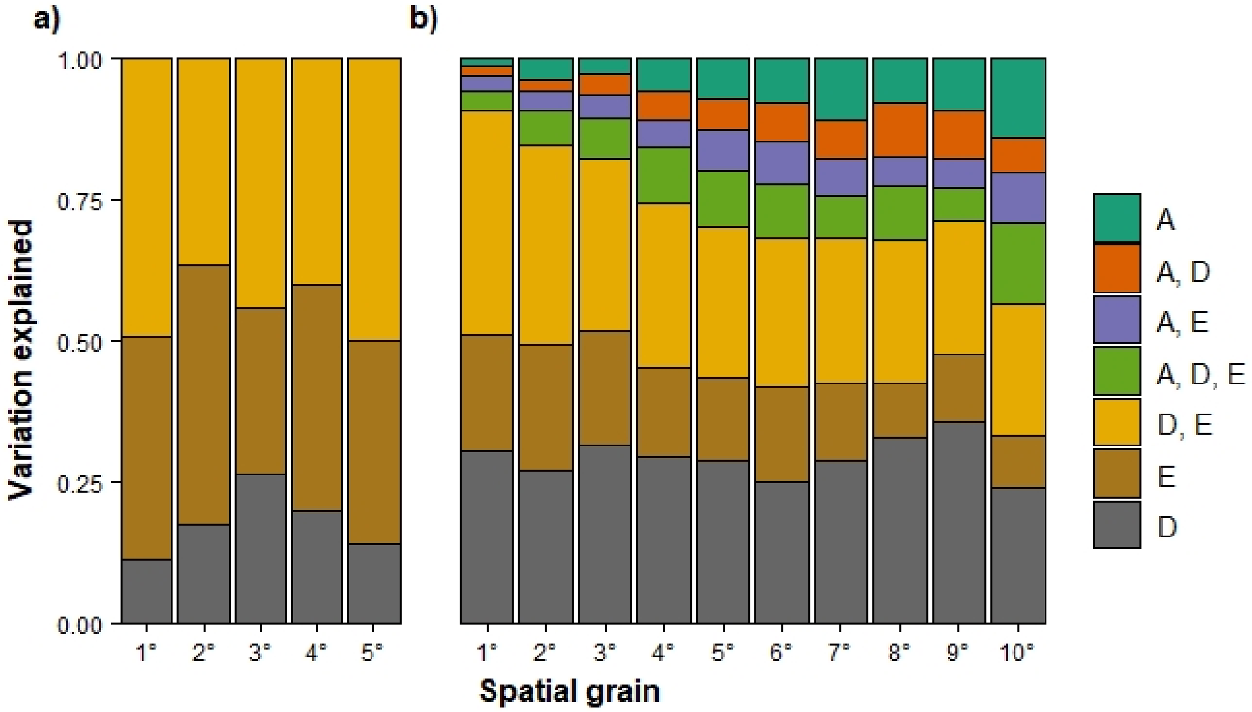


Figure 2. Variance partitioning demonstrating the proportion of explained variance attributable to the variables predicting coral beta diversity across spatial grain in a) the Atlantic, and b) the Indo-Pacific. Legend initials refer to the single and combined effect of the following set of variables: A = Reef Area; D = Dispersal Limitation; E = Environment.

The effects of spatial grain on beta diversity response curves

The relationship between the selected set of predictors and coral beta diversity are described by the I-spline curves produced by the final models at each spatial grain in both ocean basins (Figure 3). The overall height reached by each response curve indicates its relative importance compared to other predictor variables. Furthermore, the shape of the response curves illustrate the rate of change in beta diversity along the entire gradient of observed predictor values, where steeper gradients indicate a more rapid transition in assemblage composition. In general, relationships between coral beta diversity were rather alike for similar variables, whilst differing markedly between variable types. For instance, the response of beta diversity to dispersal limitation, characterized by either IBD (Atlantic) or IBR (Indo-Pacific) were represented by linear (or slightly non-linear) positive relationships (Figure 3a, f). Temperature, either expressed in terms of mean- (Atlantic) or maximum SST (Indo-Pacific) were characterised by saturating curves (Figure 3b, g), and nutrient concentrations, expressed in terms of nitrate- or phosphate concentrations displayed exponential increases (Figure 3c, i, h). Moreover, explaining the overall pattern in variance partitioning, different variable types showed contrasting patterns in their response to changes in spatial grain. Whilst the overall shape of the response curves were generally robust to changes spatial grain, the slope and maximum height of the curves (corresponding to the rate of change in composition and relative importance of the variable, respectively), differed between spatial grains in some variables. This was particularly apparent in the response curves of mean and maximum SST (Figure 3b, d) whose asymptotic height was greatest at finest spatial grains and relatively low at coarse grains. Contrastingly, reef area was unimportant at the finest grains but exceeded the importance of maximum SST in the Indo-Pacific at the coarsest grain. Dispersal limitation was the single most important predictor across all spatial grains in the Indo-Pacific and the most important factor in the Atlantic at coarser grain sizes. Estimates of dispersal limitation span a greater range of values at finer grain sizes, but the shape and height of all the response curves were similar over the range of values present at every grain size. It is important to note that the values of predictor variables where marked changes in composition occur were generally unaffected by grain size (i.e., the location of gradients in response curves were unchanged), indicating that the biologically relevant range of values was consistently detected across grain size. Exceptions to this rule can occur when a change in grain size affects the range of values a predictor varies over, as with dispersal limitation, as well as maximum SST and reef area in the Indo-Pacific. In these cases, the change in grain extended or compressed the range of values over which compositional change occurred, with corresponding impact on variable importance. Greater range in the predictors resulted in increased variable importance.

Histograms overlaying the response curves reveal the frequency with which values of a particular variable were recorded. The interaction between the frequency of observations and the associated gradient in beta diversity provides additional information about the generality of a variables influence. When large bars (i.e. many observations) occur over a range of values associated with a steep gradients in the response curves, the variable is of general importance, whereas if the majority of observations are associated with shallow or flat response curves, the influence of the predictor is more restricted in its geographic influence. Compositional dissimilarity resulting from dispersal limitation occurred frequently in the Indo-Pacific but less commonly in the Atlantic. Mean and maximum SST, were typically recorded within a band of values that are not associated with beta diversity in corals, and whilst low temperatures can cause considerable compositional change, these are rare for coral reefs as a whole. The pattern exhibited by SST, whereby considerable change in composition coincides with limited observations, was repeated across all temperature and nutrient variables (Figure 3b, c, g, h, i, j). Depth of light penetration was the only environmental variable that differed from this pattern. This was associated with coral beta diversity at values between 0 - 30m and 70 – 110m depth, values which occur with relatively frequently (Figure 3e). Finally, the degree of confidence in the response curves also differs along the range of values observed in each variable. Where the numbers of observations are limited the shape of the response curve should be treated with some caution. Nonetheless, despite this uncertainty, the shape of the fitted curves are typically highly consistent for each variable across scale, and where differences in spatial grain lead to differences in the asymptotic heights of response curves, these show a consistent pattern with changing grain size. The consistency was mirrored across ocean basin and across similar types of variable, providing confidence that the overall patterns uncovered by our model are reliable.

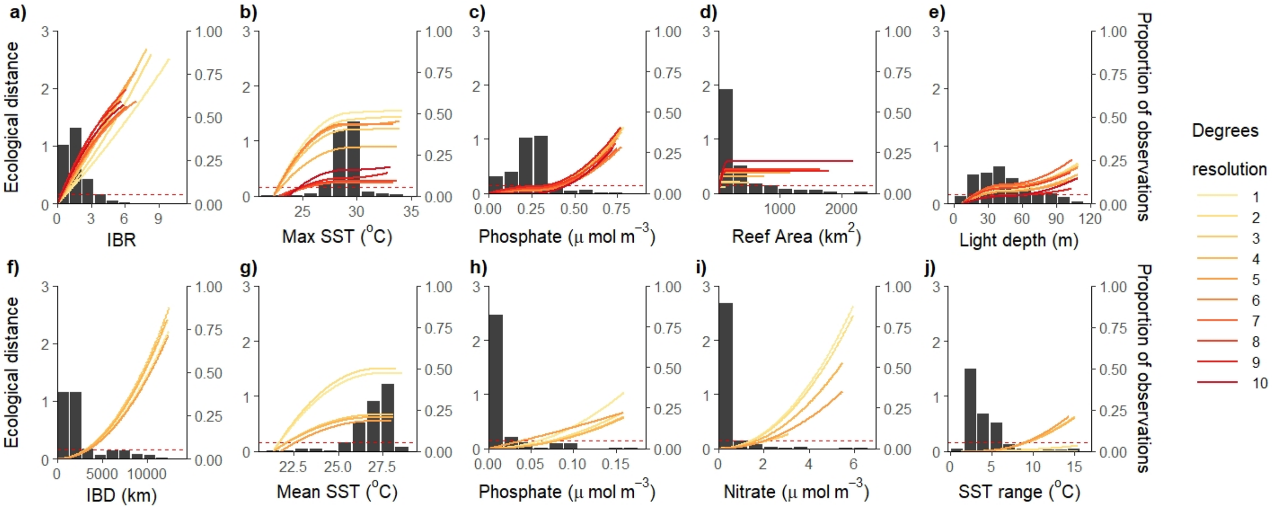


Figure 3. I-Splines response curves illustrating the partial effects of selected predictor variables on coral beta-diversity in the Indo-Pacific (top) and Atlantic (bottom) across spatial grains (given by colours ranging from yellow to red). The shape of each function indicates how the rate of change in composition varies along the entire range of values (i.e., gradient) of each predictor variable. The maximum height reached by each response curve indicates the total amount of compositional change associated with that variable (i.e., relative varible importance), holding all other variables constant. Histrograms show the underlying distribution of predictor values along each gradient.

3.4 Discussion

Understanding the factors determining the diversity and composition of assemblages remains a key challenge in ecology (Sutherland et al. 2012). This knowledge is especially urgent in coral reef ecosystems whose unique and staggering diversity of life (Fisher et al. 2015) are severely threatened by anthropogenic change (IPCC 2019). A candidate set of variables plausibly determining coral biogeographic patterns has previously been identified, however uncertainty regarding their relative importance across spatial scales and ocean basins remains, in particular relating to the role of dispersal limitation. We show for the first time that coral dispersal is the best predictor of coral beta diversity patterns in the Indo-Pacific basin, followed by environmental conditions and lastly reef area. In contrast, coral beta diversity patterns in the Atlantic basin were best predicted by environmental conditions with a lesser role for dispersal. We document opposing influences of changes in spatial grain on the importance of environmental variables and reef area, whereas dispersal limitation was important across scale. Our analysis constitutes the first attempt to understand the determinants of coral biogeography across ocean basins and spatial scales, considering environmental conditions, reef area and novel estimates of dispersal limitation. In doing so, we shed light on the relative importance of factors which have been invoked independently to explain coral diversity patterns. Below we elaborate on these findings in light of the existing literature and discuss the implications for the conservation of coral reef diversity in the Anthropocene.

Determinants of coral biogeography & beta diversity

Accumulating evidence (Cowen et al. 2000, Treml et al. 2008) suggests that marine systems are more “closed” than previously thought and that dispersal pathways can impact biogeographic patterns (Gaylord and Gaines 2000). This has not clearly emerged, however, in large-scale analyses that have lacked realistic parameterisations of larval biology and ocean currents (Keith et al. 2013, Luiz et al. 2013, Mora et al. 2012). Recent advancements in computing now permit global models of connectivity based on empirical larval dynamics (e.g. Wood et al. 2014). Our inclusion of a realistic model of coral dispersal (Wood et al. 2014) reveals dispersal limitation to be the most important variable explaining the large-scale patterns of coral beta-diversity across the Indo-Pacific. Specifically, the response curves indicate that dispersal limitation has a pronounced influence on beta-diversity over a broad range of values (Fig. 3a). Whilst our study underlines the utility of using realistic models of dispersal limitation, distance-based estimates proved adequate and were consistently selected ahead of connectivity-based estimates in the Atlantic. This could result from the influence of stochasticity at low levels of connectivity. Alternatively, it may reflect that different reproductive strategies of corals predominate the two ocean basins, namely broadcast spawning in the Indo-Pacific and brooding in the Atlantic (McWilliam et al. 2018). The different reproductive strategies have implications for dispersal patterns and colonisation success (Keith 2015) and future models of connectivity and dispersal limitation should be tailored to specific life-history traits.

The environmental factors that explain global patterns of coral beta diversity in our analysis, low SST, high concentrations of nutrients and depth of light penetration are also critical factors limiting the development of coral reefs (Kleypas et al. 1999, Couce et al. 2012). High temperatures, which have in recent years caused mass bleaching of coral, are currently only weakly implicated in broad-scale patterns of Indo-Pacific coral beta diversity. While environmental factors contribute to explaining the overall pattern of coral beta diversity in our analysis, their importance, particularly that of SST, is foremost evident in peripheral locations and marginal, high latitude reefs (Figure S3). Consequently, the contribution of environmental variables to coral beta diversity is likely due to the limiting conditions in these locations filtering out less hardy or highly specialised coral species (Bellwood and Hughes 2001). This is clearly illustrated by the response curves showing steeply increasing slopes at low SST and high nutrient concentrations. The greater role for environmental conditions that we find relative to previous investigations (Keith et al. 2013, Bellwood et al. 2005, but see Fraser and Currie 1996) may result from our global analysis encompassing a greater range of variation in both composition and environmental conditions. However, over the range of environmental conditions present on the majority of coral reefs, the largely flat response curves indicate that environmental variables are not limiting and therefore have little impact on coral beta-diversity (Figure 3 b, c, e, g-j). To that end, our global analysis is consistent with environmental conditions correlating poorly with the boundaries of coral faunal provinces (Keith et al. 2013) and confirm why environmental conditions are not required for diversification models to generate realistic patterns of beta diversity (Leprieur et al. 2016).

Larger areas support more individuals, more habitats and sustain fewer extinctions than smaller areas. Consequently, they typically harbour more species (Rosenweig 1995). Limited reef area on a regional scale likely contains fewer habitat types and supports smaller metapopulation sizes. Either case alone would be expected to result in impoverished assemblages relative to regions with greater reef area. Island biogeography states that both immigration and local extinction act together to determine the species richness of islands (MacArthur and Wilson 1967). Whilst larger area increases immigration (Rosenweig 1996), immigration is also influenced by dispersal pathways. Studies lacking an adequate representation of dispersal limitation may therefore overestimate the effect of area on diversity. Although we do find an effect of reef area in the Indo-Pacific, the fact that we also include dispersal may contribute to our finding of a weaker association between reef area and coral beta diversity compared to studies that exclude dispersal (Bellwood and Hughes 2001, Bellwood et al. 2005). Nonetheless, given the trend of increasing importance of reef area with larger spatial grain, even larger grain sizes could reveal greater importance of reef area than found here.

The effects of spatial grain

There are fundamental differences in the scale at which ecological processes act and, as such, a single scale may not illuminate diverse processes (Wiens 1989, Levin 1992). This is illustrated in our findings which demonstrate that changes in the spatial grain of analysis may alter the explanatory power and subsequently the relative importance of the variables. More specifically, the spatial grain influences the distribution and range of variation in both dependent and independent variables. Increasing grain size can obscure fine-scale variation in biological and environmental data, by merging distinct assemblages and diluting “extreme” environmental values through averaging across larger areas. Simultaneously, reef area estimations become more differentiated at larger grain sizes. In contrast to both of the above cases, the importance of dispersal limitation was relatively insensitive to changes in spatial grain. This is potentially the result of fine-scale dispersal barriers not limiting coral colonisation success over longer time-periods. Overly precise estimates may even be misleading when modelling stochastic processes such as dispersal. The final consequence of spatial grain’s differing effect on the variance of independent variables is a change in the relative importance of variables across scale. The effect of spatial scale may also be responsible for the difference between the Indo-Pacific and Atlantic models. The smaller extent of Atlantic corals restricted our analysis to grain sizes <5° in this ocean, conceivably precluding a role of reef area. Limited longitudinal extent also truncates the variation in dependent and independent variables i.e. Atlantic coral assemblages belong to just three clusters (Veron 2015), whilst dispersal limitation is reduced compared to the Indo-Pacific. Because latitudinal extent is not similarly constrained in the Atlantic, variation in variables such as mean SST is not affected in the same way which potentially promotes its relative importance. Our analysis illustrates the impact of spatial grain on coral biogeography and highlights the need to further explore the role of spatial extent and the interaction between spatial grain and extent in biogeographic analyses.

3.5 Conclusion

Our multi-scale approach has revealed that the variables determining and maintaining coral beta diversity are those likely to change in the Anthropocene. Habitat destruction is reducing or degrading coral reefs, temperatures are increasing globally in response to greenhouse gas emissions, and changes in land-use and poor management practises lead to eutrophication and proliferation of macroalgae (IPCC 2019, Fabricius et al. 2005). Finally, climate driven changes in ocean circulation are likely to interact with elevated temperatures impacting larval dispersal, and establishment (Figueirido 2014). The pronounced changes in composition observed between low and moderate temperatures provides support to predictions that sub-tropical coastal regions face tropicalisation (Cheung et al. 2012). Small increases in temperature could facilitate the establishment of numerous coral species, although the rate of establishment will likely be mediated by biotic interactions (Verges et al. 2014) and dispersal limitation. Dispersal limitation is geographically uneven, with areas downstream of currents experiencing less dispersal limitation and facing more rapid species range expansions (Baird et al. 2012). A future featuring widespread and repeated bleaching events can profoundly affect coral composition (Hughes et al. 2018b), creating a requirement for larval replenishment from external sources. This requirement may not be met if dispersal limitations prevent recolonisation. Therefore, preventing reefs from becoming isolated from potential sources of larvae by halting coral reef degradation and ensuring pathways for dispersal will therefore be essential to supporting reef recovery in the Anthropocene.

Our results have broader relevance beyond coral biogeography, since many other taxa are reliant on corals and demonstrate similar biodiversity patterns (Veron, 1995, Tittensor et al., 2010, Stuart Smith et al., 2013, Lindegren et al. 2018). They may or may not be sensitive to the same factors we find to determine coral beta diversity. Nonetheless, future changes in these variables will directly or indirectly affect the abundance and composition of coral associated organisms. Concerted efforts to combat climate change, improve water quality and halt destructive practices are of paramount importance to protect coral reefs, as well as the human societies and bewildering array of life that depend upon them.

Acknowledgements

N.M. received funding from VILLUM FONDEN research grant awarded to M.L. (grant number: 13159). S.A.K. also acknowledges support from VILLUM FONDEN (grant number: 10114). All authors would like to thank Sally Wood for providing the connectivity data.

3.6 Supplementary Material

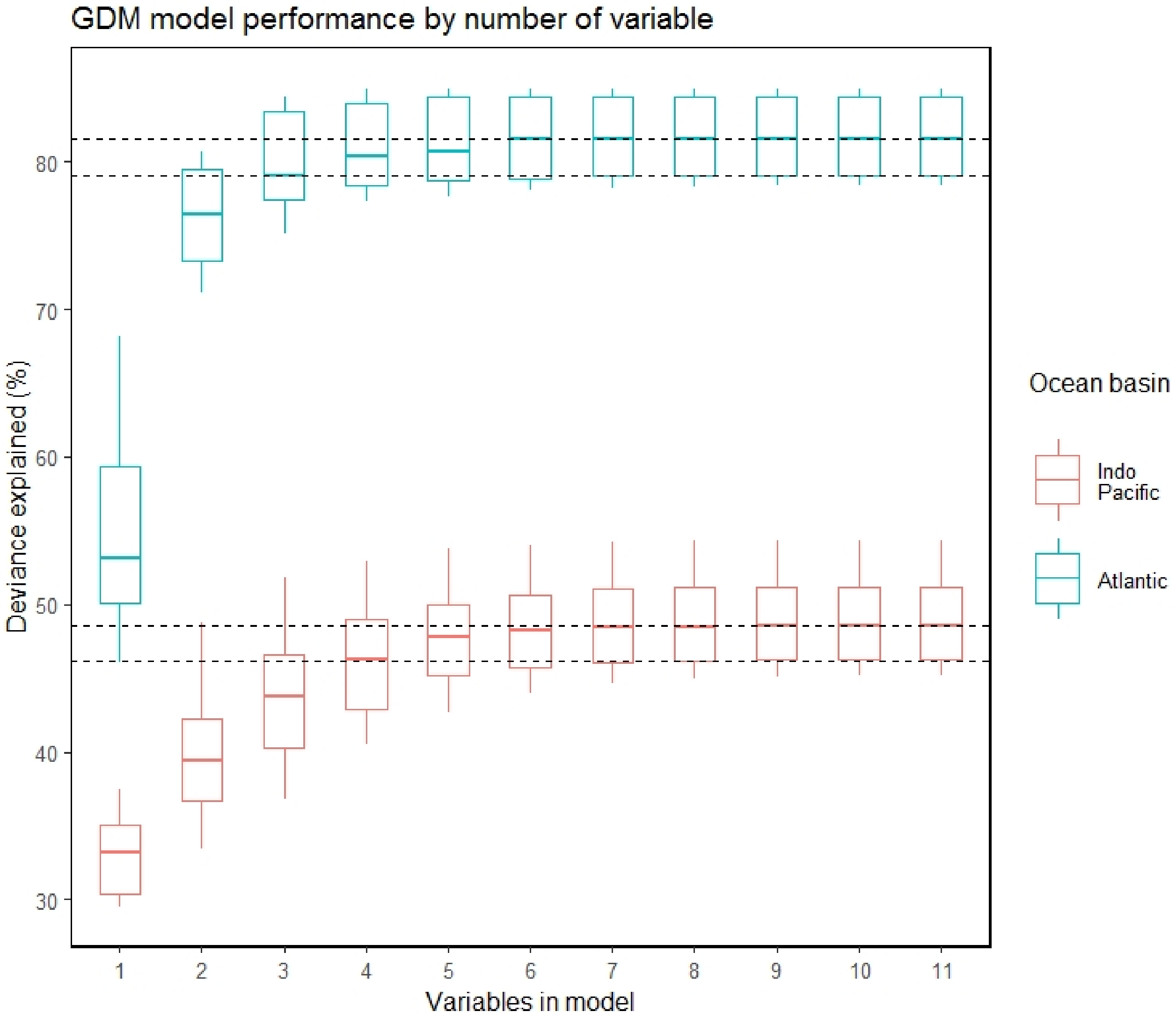


Figure S1. Boxplots of model performance. Variance explained by models at resolutions of 1° – 10° spatial scale, grouped according to the number of variables in the model. Each boxplot represents the spread of model performance of 10 models containing *n* variables at resolutions of 1° – 10° spatial scale. Dashed lines correspond to the median and 25th percentile of the boxplot for the full model, for comparison.

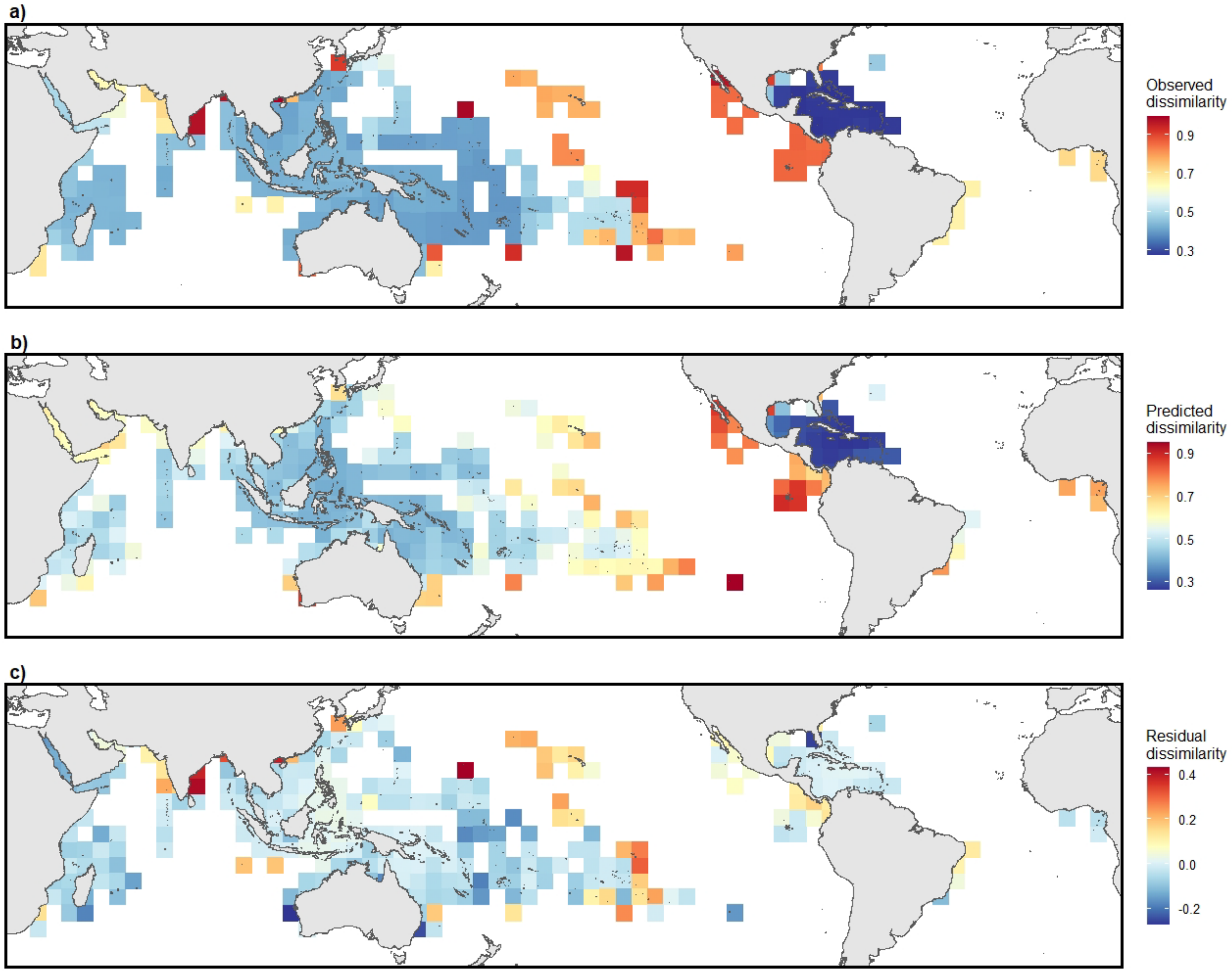


Figure S2 Comparison between observed patterns of beta diversity, models predictions and residuals. a) observed mean pairwise beta diversity; b) predicted mean pairwise beta diversity; c) residual mean pairwise beta diversity

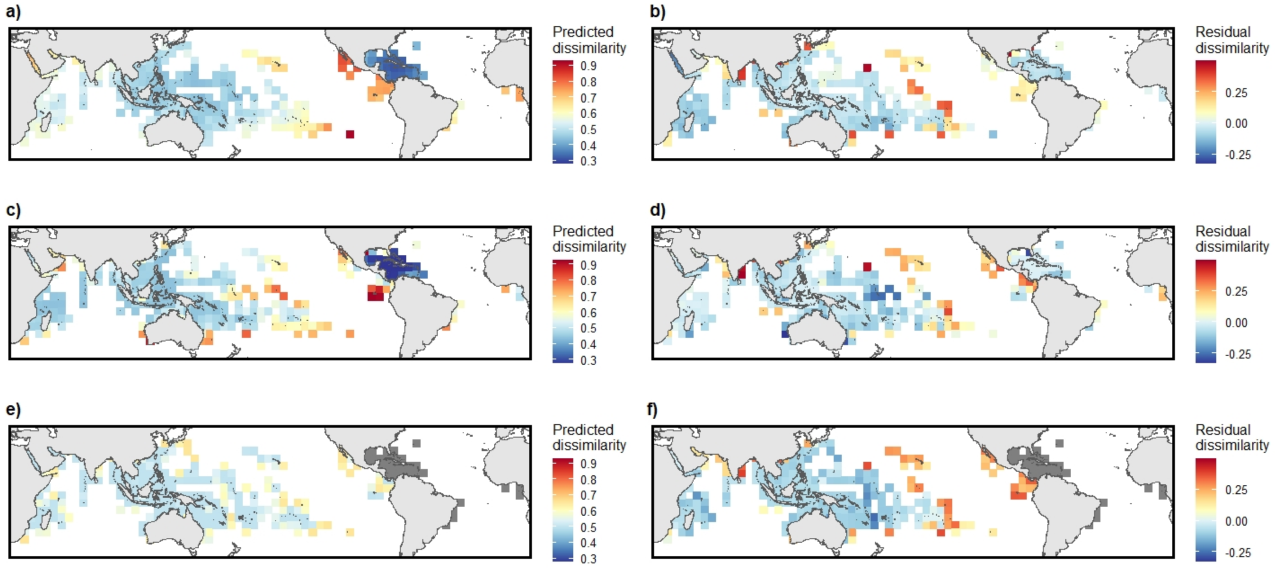


Figure S3. Model predictions (a, c, e) and residuals (b, d, f) from models containing only variables for dispersal limitation (a, b), environment (c, d) or habitat area (e, f).

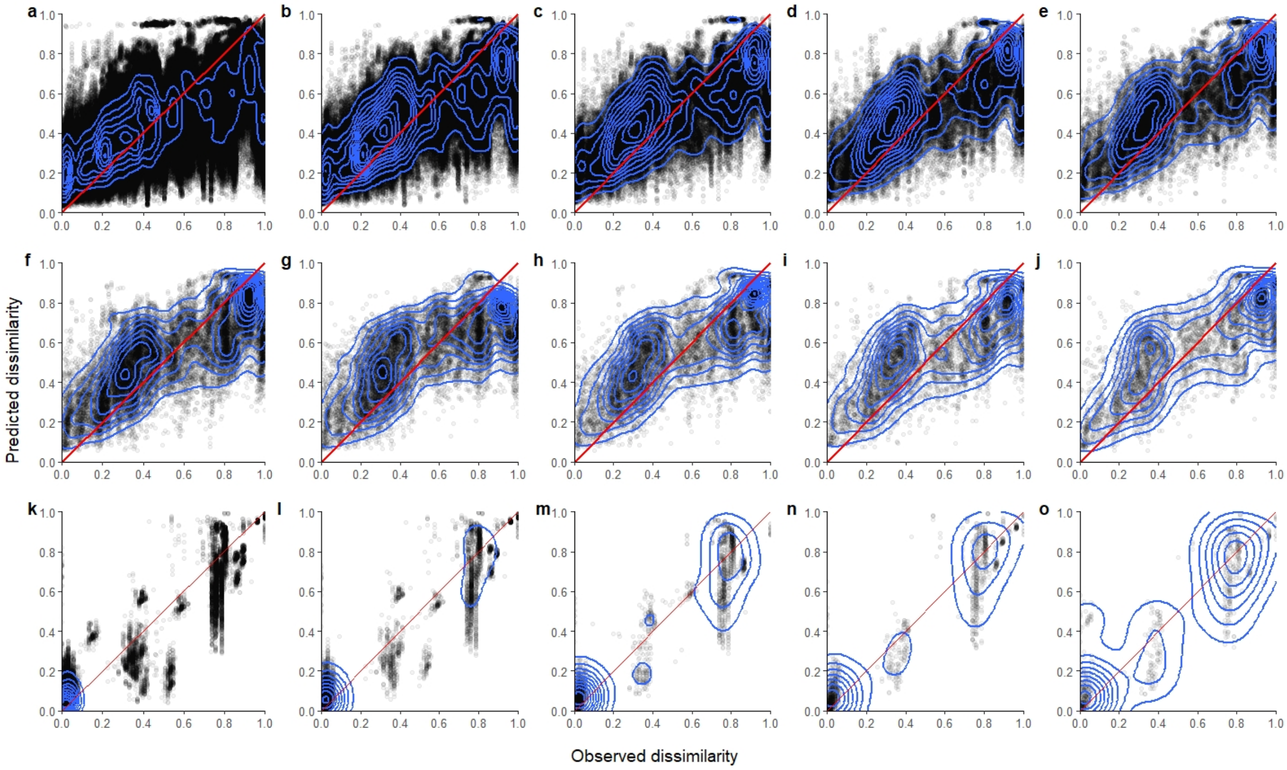


Figure S4. Observed vs predicted dissimilarity between communities. Points in black represent comparisons between assemblages with blue contour lines highlighting how the data cluster. Red lines indicate 1:1 correlation between observed and predicted dissimilarities. a-j: Indo-Pacific assemblages, scales 1 - 10°; k-o: Atlantic assemblages, scales 1 – 5 °.

Table S1 Selection of model variables. Grey boxes indicate variables not included in the model.

Numbers refer to the number of times a variable occurs in the best model containing *n* variables.

Each model represents a particular resolution so the maximum number of times a variable can occur is 10 for Indo-Pacific models and 5 for Atlantic models.

	3 variables		4 variables		5 variables	
Indo-Pacific	IBR	9	IBR	9	IBR	9
	Area	6	Phosphate	8	Phosphate	9
	Phosphate	5	Area	7	Light depth	9
	(SST max)	4	SST max	5	Area	7
	(Nitrate)	2	Light depth	5	SST max	6
Atlantic	IBD	5	IBD	5	IBD	5
	SST mean	5	SST mean	5	SST mean	5
	Nitrate	5	Nitrate	5	Nitrate	5
			Phosphate	4	Phosphate	5
			(Salinity)	1	SST range	4

4

The influence of reproductive traits on coral range sizes and distance-decay relationships

Neil Maginnis, Sally Keith, Martin Lindegren

Abstract

Aim: Understanding the influence of dispersal limitation on species distributions and community composition is limited by our inability to directly measure dispersal. Therefore, identifying traits acting as valid proxies for dispersal ability is highly desirable. We investigate whether the dispersal consequences of different reproductive modes of corals (i.e., brooding vs broadcast spawning) generate differences in their large-scale biogeography with respect to species range sizes and assemblage structure.

Location: Coral reefs of the Indo-Pacific (34° S - 34° N).

Methods: We estimated the range sizes of brooding and spawning corals and tested for significant differences between groups using permutation tests. We then fitted distance-decay models for beta diversity, turnover and nestedness of brooding and spawning assemblages to determine the extent and rate at which dissimilarity in species composition changes with increasing spatial distance. To capture potential nonlinearities in the statistical relationships between distance and dissimilarity, we repeated the fitting of decay curves with the addition of a quadratic distance term.

Results: Spawning corals display a trend for larger range sizes than brooding corals, but the difference is not significant. However, distance-decay relationships differ significantly between groups. In line with our hypotheses, beta diversity and turnover increase more rapidly across space in brooders than in spawners, whereas nestedness is lower in brooders. The addition of a quadratic term does not change these overall patterns, but reveals a parabolic relationship between nestedness and distance in both groups.

Main conclusions: Assemblages of spawning corals exhibit a greater degree of species overlap. This generates lower beta diversity and a higher degree of nestedness relative to brooders, which exhibit more rapid turnover with distance. Our results suggest that brooding and spawning strategies may result in differing long-distance dispersal ability and biogeographic patterns in corals with important implications for their conservation and management under climate change.

4.1 Introduction

The ability of organisms to disperse at different life stages, either passively or actively, is a key factor determining the distribution of life on Earth (Jønsson et al. 2016). Despite the importance of dispersal for the distribution, abundance and persistence of organisms (Wilson et al. 2009, Pulliam 2000, Campbell Grant 2010), significant uncertainties remain in determining the dispersal potential of species and its influence on broader biogeographical patterns (Sutherland et al. 2013). This lack of knowledge challenges our ability to predict species and community responses to climate change and to conserve biodiversity effectively. Coral reefs, Earth's most diverse marine ecosystems, are especially threatened by rising temperatures and are projected to suffer from extinctions and significant loss of area (IPCC 2019). Recent global bleaching events have already led to mass coral mortality and transformed coral assemblages (Hughes et al. 2018b) and the recovery of reefs depends critically on replenishment of larvae (Hughes et al. 2019). Differing dispersal abilities amongst coral species has the potential to impact their recolonisation following bleaching. Therefore, improved understanding of how dispersal abilities influence large-scale distribution and assemblage patterns of corals will enhance forecasts of the impact of future disturbance events, and the subsequent recovery of coral reefs.

Significant difficulties are associated with measuring dispersal directly, making the ability to predict species dispersal potential from readily measurable proxies one of the best ways to move forwards. Such proxies may be based on species characteristics (i.e., traits), informed by the Coral Trait Database , which includes morphological, physiological and reproductive traits (Madin et al. 2016a). Although many traits have the potential to influence dispersal ability – notably body size (Bradbury et al. 2008) – reproductive mode has often been proposed as a key trait influencing the dispersal ability and biogeography of marine taxa (Thresher 1991, Kinlan and Gaines 2003). Corals reproduce sexually through brooding larvae or spawning gametes into the water column. In brooding corals, fertilisation of eggs takes place internally and the larvae are retained within coral polyps until they are fully developed. When brooded larvae are released they are able to settle almost immediately, making them more likely to recruit locally (Figueiredo et al. 2013). Spawning corals, by contrast, release bundles of eggs and sperm into the water column where fertilization and development take place over several days (Baird 2001). Waves, tides and currents act continuously throughout this period, advecting passive gametes and the subsequent larvae from their point of origin. These larvae remain in the water column until they are competent to settle, after which time they metamorphose (in most cases) into a sedentary polyp. Consequently, the rate at which larvae develop and reach this competent phase affects how many are transported off the reef (Figueiredo et al. 2013), which is expected to influence the probability of long distance dispersal. Evidence shows clearly that these differences in reproductive strategy result in ecological differences, with a spawning strategy resulting in less genetic subdivision and greater temporal variability in recruitment compared to brooders (Hughes et al. 1999, Ayre and Hughes 2000, Underwood et al. 2009). However, whether and how these ecological differences also influence large-scale patterns of coral diversity remains unclear.

One way to gain insight into how reproductive mode affects biogeographic patterns is to explore changes in species composition through space, or distance-decay relationships (Nekola and White 1999; Soininen et al. 2007; Gomez-Rodriguez and Baselga 2018). Such relationships, which can be reformulated in terms of beta diversity, traditionally describe how compositional similarity declines with distance. Beta diversity is composed of turnover and nestedness components (Baselga 2010). Within this framework turnover refers to the replacement of species in assemblages whilst nestedness captures the property of one assemblage being a subset of another (Baselga 2012). Distance-decay relationships are often attributed to dispersal limitation (Baselga 2010, Qian 2009, Wetzel et al. 2012), but clear inference on the underlying processes responsible for generating beta diversity are complicated by the unseparated contributions of turnover and nestedness (Baselga 2010). Quantifying these two components simultaneously creates the opportunity to delve more deeply into the processes underlying the decay of assemblages with distance. Nestedness patterns are often attributed to greater dispersal abilities (Lomolino 1996), in which case spawner assemblages should display elevated nestedness if they disperse more effectively than brooders. In contrast, we expect brooders will occupy smaller ranges, which should result in non-overlapping ranges and higher turnover.

In order to shed light on the role of dispersal ability on large-scale patterns of coral assemblage composition, we match observational data of coral species ranges with reproductive trait data. Specifically, we investigate the influence of reproductive mode on species range sizes and hypothesise (H1) that spawners have larger geographic ranges than brooders, due to a greater long-distance dispersal ability. Subsequently, due to this elevated dispersal and expected larger range sizes, we hypothesise (H2) that assemblages of spawning corals will remain more similar in terms of species composition across space than assemblages of brooding corals, reflected by a shallower distance-decay curve. Finally, since nestedness patterns are often attributed to greater dispersal abilities (Lomolino 1996), spawner assemblages should display elevated nestedness if they disperse over large distances more effectively than brooders. Consequently, we hypothesise (H3) that spawners will exhibit reduced turnover and a greater degree of nestedness than brooders with increasing distance.

4.2 Methods

Data

To study the influence of reproductive mode on coral biogeography we combined spatial data of species' ranges and coral reef locations with trait data on the reproductive mode of corals. For coral species ranges, we accessed published maps for Indo-Pacific Scleractinian corals (Hughes et al. 2013), whilst data on coral reproductive mode were gathered from both the Coral Traits Database (Madin et al. 2016a) and McWilliam et al. (2018). The former source contains direct observations of species reproductive mode, whilst the latter also conducted trait infilling by assigning reproductive modes considering data from congeners. We used McWilliam et al. (2018) as our primary source, supplementing with trait data from the Coral Traits Database where additional data were available. Coral reef locations were taken from Wood et al. (2014). After aligning the respective datasets with the latest taxonomic information, we merged the ranges of synonymized species and excluded species that with the latest genetic detail have now been split into multiple species because it was not clear how to robustly separate the range data. This process returned range data for 34 brooding coral species and 567 spawning coral species across the Indo-Pacific.

Geographic range size differences

To test the hypotheses that brooding corals have smaller geographic ranges, we calculated range size as the Extent of Occurrence (EOO; Gaston 1991). For each coral species, we calculated the entire area within the range limits of the published range maps of Hughes et al. (2013). Following the recommendation of Gaston and Fuller (2009), we included in our calculation discontinuities in the occurrence of reef corals, such as ocean areas outside the photic zone. We then applied a permutation procedure to compare the observed differences in range size between the groups to a null distribution of possible differences in range size, assuming no difference between brooders and spawners. To achieve this, we randomly assigned species to the two reproductive groups 1000 times, maintaining the original number of species in each group. We then determined the probability of the observed pattern emerging by calculating the proportion of times the observed difference between the reproductive groups exceeded the null differences.

Distance-decay of coral assemblages

Distance-decay relationships have traditionally been calculated and presented in terms of similarities, but we believe the processes of turnover and nestedness are more intuitive when considered as dissimilarities. As such, we present our results as dissimilarities for greater interpretability. To determine the distance-decay patterns of coral assemblages, we overlaid range maps onto coral reef locations and presence/absence tables were generated for each locality under the assumption that species are present throughout the full extent of their range. We then constructed a 5° resolution grid encompassing the ranges of all species and aggregated the reef-level presence/absence data to this spatial scale. Using the reproductive trait data, the species composition of each grid cell was divided into brooder and spawner assemblages. For each group, we calculated pairwise dissimilarities between all grid cells. Using the Sørensen distance for beta diversity and its turnover and nestedness components (Baselga 2010), we generated three matrices of pairwise dissimilarities for both reproductive modes. Spatial distance between locations was calculated as the in-water distance between the centroids of grid cells, to account for land impeding dispersal.

After converting dissimilarities into similarities, we used negative exponential functions (Nekola and McGill 2014) to assess the relationship between assemblage structure and distance. We fitted exponential functions using Generalized Linear Models (GLM) with log link, where similarities were the response variable, spatial distance, x_D, was a predictor variable and errors assume a Gaussian distribution (Gomez-Rodriguez and Baselga 2018). To account for potential nonlinearities in the relationship between similarity and distance, we repeated our analysis including a squared term, x_D^2, for spatial distance. Our final models took the form:

$$Ln(1 - Y) = \alpha + x_D b_1; \qquad 1)$$

$$Ln(1 - Y) = \alpha + x_D b_1 + x_D^2 b_2; \qquad 2)$$

where Y is the pairwise dissimilarity of grid cells; either expressed in terms of overall beta diversity, turnover or nestedness. Following Gomez-Rodriguez and Baselga (2018), we then determined whether the fitted coefficients of the curves (i.e., α and b) differed significantly between spawning and brooding corals by conducting a bootstrapping procedure with 1000 iterations. The significance level was set at $p = 0.05$and p values of each parameter were calculated as the proportion of times that intercepts and slopes were larger for one of the reproductive groups. All analyses were performed in R version 4.0.0 (R Core Team 2020). We used functions from the *betapart* package (Baselga et al., 2018) to calculate dissimilarities and to fit the decay models.

4.3 Results

Geographic range size differences

Spawning corals exhibit both a greater breadth and greater variation in geographic range size compared to brooders (Table 1, Figure 1). Typical range sizes for both reproductive modes are large, with an overall mean for corals in excess of 4.4 x10^7 km^2. The majority of species have a geographic distribution over 1.0 x10^6 km^2 and whilst less than 3% of spawners have a smaller geographic extent, almost 12% of brooders fall below this level. At the other extreme, just under 12% of brooders have a geographic extent greater than 7.5 x10^7 km^2 compared to almost 24% of spawners. In both groups median range sizes fall below the mean, with distributions of geographic range size exhibiting strong right skew in both cases (Figure 1). The results of our permutation tests indicate that the difference in mean geographic range size between brooding and spawning corals is near not significant (p = 0.052).

Table 1 Geographic range sizes of Brooder and Spawner corals

	Geographic range area (km^2)				
	Minimum	Mean	Median	Maximum	S.D
Brooder	25,565	3.5 x10^6	3.1 x10^6	9.2 x10^6	3.0 x10^6
Spawner	12,018	4.5 x10^6	4.0 x10^6	1.4 x10^7	3.3 x10^6

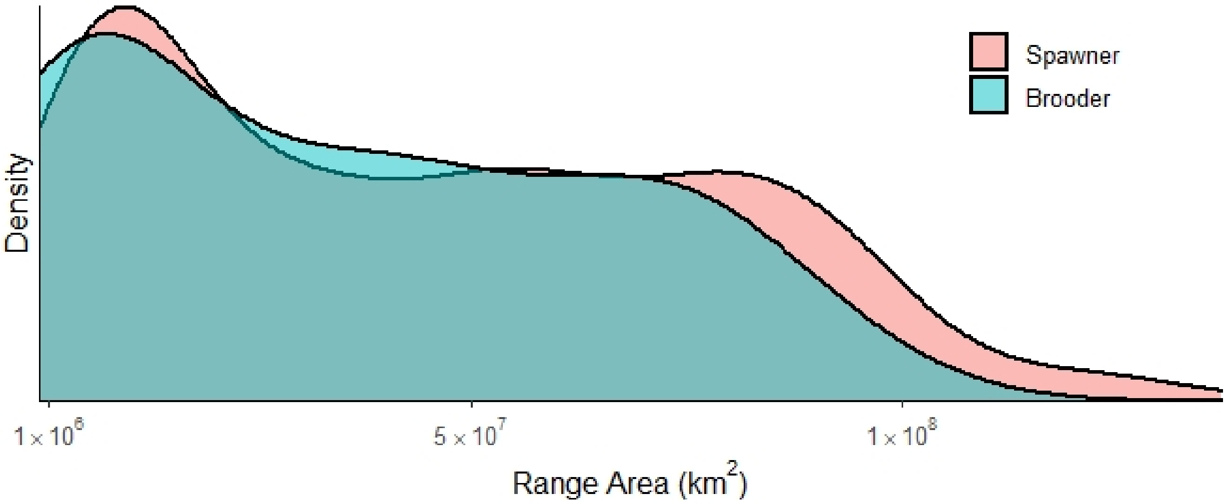


Figure 1. Density plot of coral range size grouped according to reproductive mode

Distance-decay relationships

The fitted distance-decay models demonstrated significant relationships between distance and all indices of coral assemblage dissimilarity for both spawning and brooding corals (Table 2). Beta diversity and turnover demonstrate a saturating or sigmoid response to increasing distance in both groups, irrespective of the inclusion of the squared distance term, x_D^2 (Figure 2a, b, d, e). Models of nestedness that exclude x_D^2 demonstrate a linear relationship with distance, positive for spawners and negative for brooders (Figure 2c). In models of nestedness that include the squared term, nestedness patterns are parabolic for both groups (Figure 2f). Notably, peak nestedness is lower and occurs earlier in brooders than in spawners. Although including a squared distance term only marginally improves overall model performance in terms of pseudo-r^2 values, it leads to lower AIC scores (Table 2). Hence, we focus on the results of those models below.

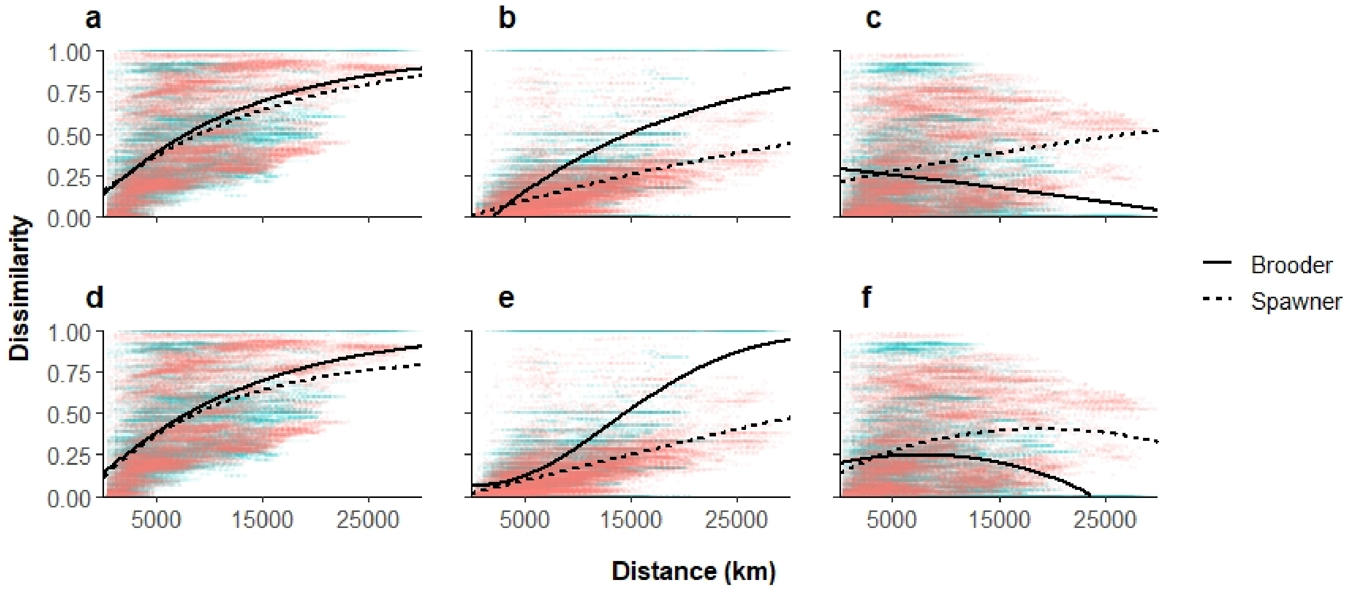


Figure 2 Distance-decay curves of brooder and spawner assemblages. Distance-decay of beta diversity, a) and d), turnover, b) and e) and nestedness c) and f) are modelled. Decay curves a), b) and c) are fitted with a single decay term whilst curves d), e) and f) also contain a quadratic term.

Table 2 Models of distance-decay relationships in coral assemblages displaying the fitted intercepts and slopes coefficients, together with their corresponding p values, as well as the pseudo r^2 and Akaike information criterion for each model. Reproductive mode is indicated by “Br” for brooders and “Sp” for spawners.

Dissimilarity	Model	Mode	α	b_1	b_2	p value	pseudo r^2	AIC
Beta diversity	Linear	Br	0.13	7.1 x10^{-5}		0.01	0.31	4866
		Sp	0.15	5.8 x10^{-5}		0.01	0.29	-1866
	Non-linear	Br	0.14	6.7 x10^{-5}	2.1 x10^{-10}	0.01	0.31	4864
		Sp	0.12	7.2 x10^{-5}	-8.1 x10^{-10}	0.01	0.30	-1980
Turnover	Linear	Br	-0.11	5.4 x10^{-5}		0.01	0.33	13260
		Sp	0.00	1.9 x10^{-5}		0.01	0.31	-43800
	Non-linear	Br	0.07	-4.5 x10^{-6}	3.3 x10^{-9}	0.01	0.36	11830
		Sp	0.02	1.5 x10^{-5}	1.8 x10^{-10}	0.01	0.31	-43850
Nestedness	Linear	Br	0.29	-9.9 x10^{-6}		0.01	0.03	-46
		Sp	0.21	1.7 x10^{-5}		0.01	0.06	286
	Non-linear	Br	0.20	1.7 x10^{-5}	-1.1 x10^{-9}	0.01	0.06	-934
		Sp	0.14	3.9 x10^{-5}	-1.0 x10^{-9}	0.01	0.07	-191

The bootstrapping procedure revealed that the distribution of parameter values from the fitted models differed significantly between brooders and spawners (Figure 3), with the exception of the squared term for nestedness (Figure 3i). The distribution of Intercepts of the beta diversity models were close to zero, with brooders showing slightly higher values compared to spawners (Figure 3). However, beta diversity of brooders increased more rapidly in response to distance and exceeded that of spawners over all distances (Figure 2d). This was despite spawners having a significantly larger $b_{\beta 1}$and resulted from the difference between the $b_{\beta 2}$ coefficients which was negative for spawners and positive for brooders (Figure 3b, c). Turnover in brooders exceeds that of spawners over all distances (Figure 2e). Initial turnover is higher in brooders, illustrated by an α_t that is slightly larger than that of spawners. Moreover, brooder turnover increases greatly at longer distances, owing to a much larger b_{t2} coefficient corresponding to the squared distance them x_D^2. Nevertheless, over a narrow range of shorter distances turnover of brooder and spawner assemblages is very similar. This is due to the coefficient b_{t1}, which is considerably smaller in brooders than in spawners. Despite the similar degree of turnover at short distances, the general pattern is clearly that turnover increases more rapidly in brooders than spawners with distance.

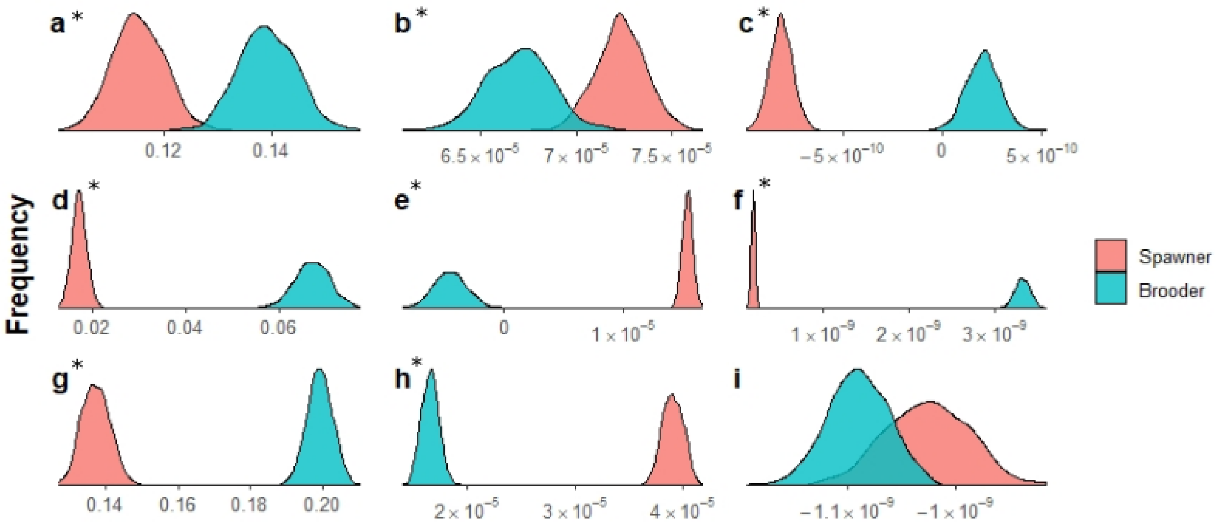


Figure 3 Bootstrap distributions of the parameters describing the distance-decay relationships of beta diversity (a, b, c), turnover (d, e, f) and nestedness (g, h, i). Intercepts (a, d, g), linear slopes (b, e, h) and quadratic slopes (c, f, i) are displayed from left to right. Significant differences (* for $p < 0.05$) between coefficients for brooders and spawners is indicated in each plot.

Both reproductive modes showed similar degrees of initial nestedness, with spawners having a slightly lower intercept α_n than brooders. Nestedness in both groups exhibits a parabolic relationship with distance, with nestedness increasing more rapidly in spawners than brooders, peaking later, and declining to a lesser degree following its peak. This was illustrated in a larger b_{n1} coefficient and a less negative b_{n2} coefficient for spawner assemblages than for brooding assemblages.

4.4 Discussion

Dispersal is a key factor affecting the distribution, abundance and persistence of populations (Wilson et al. 2009, Pulliam 2000, Campbell Grant 2010), yet its influence on species composition and diversity at large remains a key question in ecology (Sutherland et al., 2013). In this large-scale analysis of the effect on coral biogeography, we have investigated how reproductive mode influences species range sizes and the distance-decay of assemblages across the Indo-Pacific Ocean. We detect a strong trend for reproductive mode influencing coral range size, yet differences in range sizes between the ranges of brooding and spawning corals are not significant and do not firmly support our first hypothesis (H1). In contrast, the fitted distance-decay models provide compelling evidence that different reproductive strategies significantly influence large-scale patterns of coral beta diversity, turnover and nestedness, in support of H2 and H3. Below, we elaborate on our findings in light of the existing literature and discuss their implications for ecological research and conservation.

Coral range size

The size and location of species ranges are influenced by a variety of extrinsic and intrinsic factors. Extrinsic factors, such as continental boundaries and unsuitable environmental conditions can provide constraints to species ranges (Gaston 2000), whilst intrinsic factors determine how a species interacts with its environment and its ability to access and compete to exploit the available resources. Gaston (2003) concluded that for the majority of species, physical factors are limiting, in at least some parts of a species range. For Indo-Pacific corals, the physical factors appear primarily to be dispersal barriers (Maginnis et al, Chapter 1 *in prep*). Therefore, species with stronger dispersal abilities should be better able to overcome dispersal limitations, colonise suitable habitat, and expand their range. In corals, more larvae of spawners are expected to be transported off their natal reef, improving long distance dispersal and establishment outside the native range (Lockwood et al. 2005). Although Lester et al. (2007) argue that dispersal ability is not the primary determinant of range size, theory and evidence suggests that long distance dispersal is critical to colonisations and the rate of range expansions (Lester et al. 2007, Le Corre et al. 1997). Clearly, reproductive mode alone is not sufficient to explain the observed distribution of coral range sizes (Figure 1), but it does appear to be an important contributor. In a broad review of marine invertebrates, Gaston (2003) concluded that there was significant support of reproductive mode influencing species range size. However, contrary evidence exists and the topic is much debated (e.g. Johannesson 1988).

The relationship between range size and reproductive mode, which approaches significance, indicates that a spawning strategy may infer long-distance dispersal advantages leading to larger range sizes. Caution against drawing such a conclusion is prudent in light of the fact that, across taxa, the best supported factor relating to range size appears to be abundance (Gaston 2003). Many of the dominant corals on reefs are broadcast spawners (Knowlton 2001, Hughes et al. 2019), and their higher abundance may be responsible for their wider distributions. Furthermore, most combinations of environmental conditions are rather uncommon (Gaston, 2003). Spawners are the more speciose group so are more likely to occupy niches that occur more frequently on reefs. Finally, other traits that interact with reproductive strategies, such as growth rate and environmental tolerance, may serve to explain observed differences in distributions and range sizes. Species that cross the East Pacific Barrier will contribute significantly to range size estimates and are disproportionately characterised by the presence of photosynthetic symbionts in their larvae. These factors are all potentially capable of causing differences in species ranges that correlate with dispersal mode. Hence, we advocate further research on these aspects to better understand the underlying traits and mechanisms contributing to species distributions and range sizes of corals.

Distance-decay relationships

Assemblages ultimately result from the overlap of individual species ranges. Consequently, all factors that influence range size and location are plausibly capable of generating some degree of distance-decay relationship if they vary with distance. Nonetheless, dispersal limitation is very commonly invoked to explain distance-decay relationships (e.g. Condit et al.

2002, Qian 2009, Wetzel et al. 2012), likely because few alternatives are expected to vary so consistently with distance. Expanding upon traditional distance-decay of similarity by also considering the turnover and nestedness components of beta diversity (Baselga 2010) and their relation to spatial distances can provide additional insights into the underlying processes structuring species assemblages (Soininen et al. 2018) and strengthen conclusions drawn from distance-decay relationships. For example, turnover can result from diversification dynamics (Aranda et al. 2013), whereas patterns of nestedness have implicated dispersal limitation in North European trees and beetles (Svenning and Skov 2007, Baselga 2010).

In support of our second hypothesis (H2), spawning corals species demonstrated more similar assemblage structure across distance than brooding corals, as illustrated by a shallower distance-decay curve. This contrast between brooding and spawning coral assemblages across space agrees with expectations of differing dispersal abilities in these groups. The decomposition of Sørensen dissimilarity into its turnover and nestedness components revealed further differences in the spatial structure of brooder and spawner assemblages. Whereas differences between beta diversity curves were quite small across all distances, turnover and nestedness patterns differed substantially between groups of brooders and spawners.

In agreement with H3, spawners display a lower rate of turnover combined with a greater degree of nestedness relative to brooders. Lower rates of turnover and lower overall beta diversity in spawning corals provide a signal that improved dispersal abilities are manifested in spawner assemblages that are more homogenous and nested across space than those of brooders (Figure 4). The greater level of nestedness indicates that when differences between assemblages do occur in spawners, it is more commonly the result of species loss/gain rather than replacement. Elevated nestedness is typically associated with better dispersal abilities (Lomolino 1996), since it requires that at least one species is capable of occupying both sites being compared.

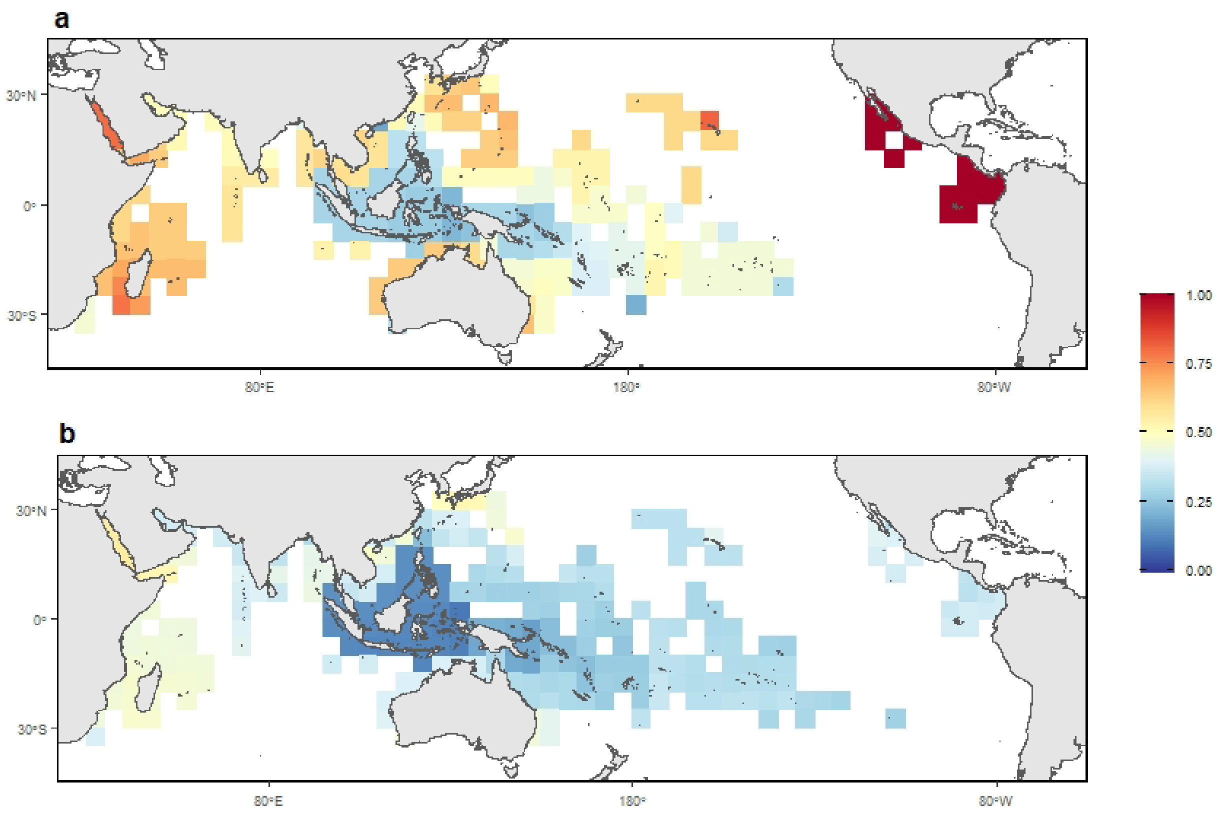


Figure 4. Turnover as a proportion of overall beta diversity for a) Brooding corals and b) Spawning corals. Warm colours indicate that beta diversity primarily results from turnover whilst cold colours indicate that nestedness dominates beta diversity. Displayed values are mean values calculated from pairwise beta diversity and pairwise turnover.

When these sites are separated by great distances, it demands dispersal that is sufficiently long-range and common to cross barriers and maintain gene flow between disparate populations. Recent papers have shown that turnover is typically the dominant component of beta diversity patterns (Soininen et al. 2018, Antão et al. 2018). Interestingly, brooding corals, with their smaller ranges, conform to this typical pattern, whereas spawning corals do not. We hypothesised that the divergent nestedness patterns observed between the two groups is the result of dispersal differences, but the greater richness of spawners is a more parsimonious explanation. Calculations of turnover, however, are not influenced by differences in species richness and this difference between brooders and spawners is very plausibly the result of dispersal ability.

Our analysis has provided support for the influence of different reproductive strategies on the dispersal ability of corals. Although we observe a trend for different species range sizes and significantly different distance-decay relationships of brooders and spawners, we have noted that reproductive mode is just one relevant factor influencing coral distribution and alternative factors and traits could underlie the observed patterns. Some authors have concluded that reference to life history traits is too simplistic approach to explain patterns of distribution (Hidas et al. 2007). However, compelling evidence exists that the presence of zooxanthellae in larvae is an important precondition for corals to cross the East Pacific Barrier and colonising the East Pacific region (Baird et al. 2009), reinforcing that life history traits are informative in the analysis of biogeographic patterns. The challenge lies in identifying the relevant traits and understanding how they interact, not only with other life history traits but also with the abiotic environment (Madin et al, 2016b). For example, the development rate of spawned larvae and subsequent retention on the natal reef is negatively related to egg size (Figueiredo et al. 2013). Development rate has previously been found to influence the probability of corals crossing broad-scale biogeographic barriers (Keith et al. 2013). Furthermore, development rate is affected by temperature and will likely alter in the Anthropocene with consequences for recruitment and dispersal of spawning corals (Figueiredo et al. 2014). Further work is required to understand how traits and life history strategies determine the current biogeographic patterns of corals and how they will respond in the Anthropocene, but these results in combination with the new findings we present here suggest that coral traits are useful proxies for understanding dispersal ability and its effects on coral biogeography at large.

In this study, we introduced a quadratic distance term, allowing distance-decay relationships to vary in a curvilinear and non-monotonic manner. Doing so revealed parabolic relationships between nestedness and distance that, to our knowledge, have not previously been documented in the biogeographic literature. Such relationships could reflect either a mid-domain effect (Colwell and Hurrt, 1994), or the nonmetric nature of the nestedness measure. A mid-domain effect, which describes declining species richness away from the centre of a bounded domain, could feasibly generate a peak in nestedness at intermediate distances. However, peaks in nestedness at notably different distances in brooders and spawners are not expected from a mid-domain effect alone. Instead, the observed pattern is most likely to arise as a result of the idiosyncratic behaviour of the nestedness metric itself. Under the Baselga (2010) construction, the nestedness measure is not a measure of nestedness, per se, but of how dissimilar two communities are because of nestedness (Murray and Baselga 2015). The measure is constrained to values less than one, but may approach one when assemblages share just a single species. But, if that shared species is lost, nestedness equals zero. Furthermore, as nestedness drops to zero, turnover rises immediately to one, irrespective of its prior value. This characteristic is problematic for the study of community assembly processes, unless these idiosyncratic behaviours can be used to ascertain additional information. In the case of nestedness, we observe that it peaks at shorter distances in brooders, indicating an increasing tendency for sites to have no shared species beyond that point. In spawners that distance is greater, again likely reflecting the differing dispersal abilities of these groups.

Adopting novel methodological frameworks, such as the decomposition of beta diversity (Baselga 2010) can help to improve our understanding of ecological processes. However, care should be taken to ensure that the behaviour of novel measures are properly understood and accounted for, so as to extract the maximum benefit from their use and to avoid spurious conclusions. The non-monotonic relationship of nestedness and beta diversity described by Carvalho et al. (2012) has typically been overlooked in analyses utilising the Baselga (2010) framework. This is potentially significant as the Baselga framework (2010) has been widely adopted and is regularly used to infer processes structuring assemblages. Non-monotonicity of nestedness has the potential to affect the influence accurate detection and interpretation of those processes, and we therefore urge further research into the modelling of nestedness across distance, including what curves best describe it, how it relates to life history traits and the influence of physical constraints on the ranges of focal organisms. Doing so could potentially improve our understanding of the processes underpinning community assembly and can be illustrated by the spatial scaling of nestedness components. Whilst it has been proposed that greater levels of nestedness may increase at larger scales (Soininen et al. 2018), Antão et al. (2019) found that nestedness was largely unperturbed by the spatial extent of the analysis. Our results, which demonstrate the non-linearity of nestedness patterns, suggest that this outcome may depend on the size and placement of species ranges relative to the boundaries and extent of the study area.

4.5 Conclusion

Brooding and spawning reproductive strategies are widespread among marine species. Understanding the consequences of different strategies is important to revealing the determinants of marine species distributions and assembly processes at large. This knowledge is urgently required, especially in highly threatened coral reef ecosystems, to predict species and community responses to climate change and to support effective conservation of biodiversity. Our results point to spawning strategies conferring greater dispersal ability relative to brooding strategies, but we caution that further investigation is required. These findings would imply that marine reserves should be designed along pathways and corridors of dispersal with spacing that reflects the dispersal limitations, particularly of brooding corals, to allow them to track suitable habitat in the Anthropocene. However, the probability of colonisation and establishment is not only dependent on dispersal pathways, but also on a sufficient number of offspring produced to ensure successful recruitment. It has recently become apparent that the recruitment of spawning corals is particularly sensitive to Allee effects (Hughes et al. 2000, Knowlton 2001, Hughes et al. 2019), and a reduction in the number of fertilised propagules would counter small benefits in the likelihood of long distance dispersal. This interaction illustrates the challenge of predicting future responses to climate change from contemporary patterns that arose under different conditions. To best conserve corals in the Anthropocene will require a combination different research approaches, including experiments and long-term monitoring, and urgent efforts to limit human impacts that affect the number and size of adult colonies, and the abundance of fertilised propagules.

Acknowledgements

N.M. received funding from VILLUM FONDEN research grant awarded to M.L. (grant number: 13159). S.A.K. also acknowledges support from VILLUM FONDEN (grant number: 10114). N.M. would like to thank Aurore Maureaud for her helpful comments on the manuscript.

5

Synthesis

5.1 Extended discussion

This thesis has investigated extrinsic and intrinsic factors that influence the biogeography of corals with a particular focus on beta diversity and the influence of dispersal. In this chapter I expand upon the results and methodology of the thesis, discussing their broader relevance and highlighting promising avenues for further research. I also discuss some potential shortcomings of the thesis and make proposals for how to address them.

The influence of dispersal

The present-day distributions of species are determined to a large degree by differences in the historical processes of origination, extinction and dispersal (Jablonski et al. 2006), and failing to account for the influence of dispersal can lead to incorrect conclusions about the processes generating gradients in diversity (Roy and Goldberg 2007). Jokiel and Martinelli (1992), writing on the subject of coral reef biogeography, complained that the role of dispersal was not “given adequate consideration before other factors are invoked”, which, in light of Roy and Goldberg’s findings, suggests that a number of conclusions made prior to that time regarding the generation of diversity gradient may be incorrect. However, the development and use of genetic analyses (Ayre and Hughes 2000) and sophisticated modelling approaches (e.g. Cowen 2000; Treml et al. 2008) have improved our understanding of the role of dispersal. Practical and computational limitations have hindered these approaches from being applied at the broadest scales, but the publication of a global model of coral connectivity (Wood et al. 2014) provided an ideal opportunity for me to explore the disconnect between a strong theoretical rationale for dispersal influencing large-scale marine biogeography versus limited empirical evidence (Mora et al. 2012, Luiz et al. 2013, Keith et al. 2013). The inclusion of this mechanistically underpinned model output in the analysis presented in Chapter 3 transforms our understanding of broad-scale coral biogeography and places dispersal limitation at the forefront of factors that need to be considered in ecological analyses and conservation management.

That finding led naturally to questions of whether all corals are equally dispersal limited and how species level traits could influence the dispersal capacity of corals. Davies et al. (2015) showed that genetic isolation-by-distance patterns of two corals species vary across Micronesia, which could plausibly result from differing dispersal abilities. Brooding and spawning strategies have long been hypothesised to influence the distributions of marine species (e.g. Thorsen 1950). Indeed, differences in recruitment patterns (Hughes et al. 1999) and genetic structure (Ayre and Hughes 2000) suggest that such reproductive modes could also affect the large-scale biogeography of corals. Chapter 4 provides evidence in support of this hypothesis. Significantly lower beta diversity and turnover in spawners and a trend for larger species range size indicate that they experience less dispersal limitation relative to brooders. A pelagic spawning strategy also supports the ability of tropical ray-finned fish to expand their range into temperate regions (Feary et al. 2014), suggesting that this trait influences biogeographic patterns across taxa.

Evidence that dispersal limitation structures assemblages is sometimes taken as evidence for neutral processes (e.g. Thompson and Townsend 2006). Although Hubbel's Unified Neutral Theory of Biodiversity (2001) has been a hugely influential development in the field of ecology, abundant evidence indicates that biological communities are not determined by such neutral processes (McGill 2003, Dornelas et al. 2006, Stanley Harpole and Tilman 2006). The assumption of equal dispersal ability among species may serve as a useful Null model, even if it is an assumption that does not reflect reality. The results presented within Chapter 3 show that dispersal limitation does indeed structure coral assemblages. That does not, however, imply neutrality, and Chapter 4 provides good evidence that dispersal limitation depends on species reproductive traits and is not neutral. Hence, intrinsic and extrinsic factors interact to determine the dispersal limitation of corals, with both aspects ultimately shaping the distributions and assemblage structure of corals.

Beta diversity

Beta diversity arises due to differences in the co-occurrence of species, determined here from the overlap in their ranges. A multitude of factors can plausibly limit a species range, but both biotic and abiotic factors are important, with physical factors limiting most species in at least some parts of their ranges (Gaston 2003). Biotic interactions can potentially have important influences on community assembly and patterns of diversity through processes of competition and predation (Adler et al. 2013, Kraft et al. 2015). Though these are unlikely to be dominant factors determining the distributions, and thereby beta diversity, of corals, it represents a weakness of this thesis that they have not been considered. One conceivable mechanism by which competitive exclusion could impact beta diversity is through limiting the expansion of species ranges. The influence of competitive exclusion is not immediately apparent when considering coral reefs, given the great diversity that can occur. For instance, individual reefs of the Bird's head peninsula of Indonesian Papua support up to 280 species ha^{-1} (Veron et al. 2009). However, this region is centrally located within the Indo-Pacific basin and well connected (Treml and Halpin 2012), and the supply of immigrants may overcome competitive exclusion. Elsewhere, where incoming larval supply is more limited, the struggle to establish may be more pronounced and the influence of competition greater.

Although there are conceivable mechanisms by which biotic factors impact patterns of beta diversity, physical factors appear to dominate over biotic factors, at least over the large spatial scales considered in this thesis. Over 40% of the variation can be explained through the physical factors identified in Chapter 3 (and c. 80% of variation in the Atlantic). Furthermore, it is highly unlikely that we have exhaustively captured the various physical processes influencing coral biogeography and, even amongst the factors that we do model, we were not able to integrate them into a model where each variable was utilised at its most relevant scale. Therefore, the actual contribution of physical factors to coral beta diversity may even be greater than documented here. The factors identified ultimately predict the location of species range edges. The results from this thesis imply that abiotic factors are the dominant factor determining the location of coral range limits, though the specific driver may vary between species (Sommer et al. 2018). The important roles of both dispersal limitation and reef area also illustrate the continued relevance of MacArthur and Wilson's Theory of Island Biogeography (1967), which has recently been applied to predict beta diversity of avifauna on islands (Lu et al. 2019).

Beta diversity decomposition

Decomposing beta diversity into turnover and nested has proven extremely popular with ecologists since first a framework was first proposed (Baselga 2010). Although I only adopt this framework in Chapter 4 it is possible to make some predictions for how the physical determinants of coral beta diversity from Chapter 3 relate to the processes of turnover and nestedness. The most straightforward case is reef area, which is almost certainly primarily associated with nestedness patterns (Lomolino et al. 2006). The species area relationship is the best supported pattern in ecology (Rosenweig 1995). Larger areas support more species than smaller areas. The reasons for this can include a greater diversity of habitats, as well as larger populations which are less vulnerable to extinction compared to smaller populations (Rosenweig 1995). Moreover, larger areas receive more immigrants than smaller areas (Lomolino, 1990). These various processes contribute to species richness being greater over larger areas than smaller areas. Therefore, differences in reef area are likely to be primarily associated with differences in richness.

The relationships between environmental conditions or dispersal limitation to turnover and nestedness are expected to be more complicated. In both cases, it is likely to be an issue of the amount environmental distance or dispersal limitation separating assemblages. For example, along an environmental continuum encompassing all of the niches of a taxa, there are likely to be both specialists and generalists. At extremes of the environmental continuum, specialist species may persist, but the majority of generalists will likely be excluded. A comparison of assemblages from both extremes of the continuum will therefore detect high, if not complete, turnover. High turnover is also evident when comparing an assemblage from extreme environments against one from the centre of the variable’s distribution. However, in conditions that are sub-optimal but not extreme some generalists may persist and turnover will be reduced relative to a more typical assemblage. Contingent on the number of generalists that persist in such a location, and the possibility of their co-occurrence with some specialists, a greater or lesser degree of nestedness is expected relative to the “typical” assemblage. The “sub-optimal” and the “extremist” assemblage may only be separated by a relatively short environmental distance, yet turnover and nestedness relative to “typical” assemblages can differ substantially. Nestedness in the “sub-optimal” assemblage gives way to turnover in the “extreme” assemblage. Similarly, dispersal limitations can conceivably lead to both turnover and nestedness in assemblages. Again, nestedness is expected to give way to turnover along gradients of dispersal limitation. Intermediate levels of dispersal limitation generate nestedness as species sequentially fail to colonise potential habitat (Darlington 1957). Eventually, in the same manner as along environmental continua, nestedness patterns give way to turnover when assemblages have no species in common. This outcome is also a function of time, with longer time-periods acting together with dispersal limitation to promote genetic drift, then speciation, which results in turnover. Greater time therefore reduces the distance at which dispersal limitation results in turnover.

These examples illustrate the challenge of reconciling beta diversity patterns with underlying processes. From these hypothetical cases it would seem that turnover would apparently dominate at greater distances with nestedness being more important at shorter distances, and these are indeed the patterns that we document for corals in Chapter 4. Typically, however, turnover dominates nestedness across distance (Wen et al. 2016, Soininen et al. 2018, Antao et al. 2019). The deviation from the typical pattern documented here could result from the use of species range maps which produce errors of commission in species occurrences, thereby suppressing turnover. On a single reef, a transect running perpendicular to the shoreline would certainly detect turnover in assemblage composition, but this biotic variation is not apparent in range map data. Other studies of distance-decay relationships have also used coarse distributional data (e.g. Wen et al. 2016). Therefore, alternative explanations could relate to specific characteristics of corals (e.g. their generally large range sizes) or context specific factors (e.g. the relative, broad-scale environmental homogeneity of the tropical Indo-Pacific in comparison to its vast extent) could also contribute to the divergence from the standard pattern.

It is worth emphasising that the examples given previously are simplifications, since environmental conditions vary along multiple axes, interacting with each other and the dispersal landscape. The hyper-dimensionality of environmental space and organisms niches (Colwell and Rangel 2009) naturally promotes turnover, since environment can vary on all axes simultaneously. Each changing variable compounds compositional change in an assemblage and drives it towards complete turnover. Moreover, dispersal is not a unidirectional process as conceptualised above, but multidirectional, supporting immigration from regions with different evolutionary histories. Clearly, even when considering the additional detail that turnover and nestedness provide, observed patterns can result from a multitude of processes which are difficult to disentangle. This does have implications for Chapter 4, since environmental factors could conceivably generate the observed patterns. It would therefore be prudent to examine the distance-decay relationships of brooding and spawning corals also with respect to environmental distance.

The Baselga framework (2010) is not without its critics (e.g. Schmera and Podani 2011, Almeida-Neto 2012), where the nestedness component in particular has come under focus (Almeida-Neto 2012, Carvalho et al. 2013). The suitability of the measure as a component of beta diversity is not completely clear. It is acknowledged that it doesn’t capture nestedness *per se*, but rather, dissimilarity derived from nestedness or nestedness resultant dissimilarity

(Baselga 2012). Moreover, the measure is the product of a dissimilarity and a similarity component (Baselga 2010), which makes predictions about its behaviour and scaling challenging (Soininen et al. 2018, Antao et al. 2019). One thing that is apparent in of distance-decay relationships measuring nestedness is a high level of noise (Svenning et al. 2011, Wen et al. 2015, Antao et al. 2019), which is also the case in Chapter 4. The noisy distance-decay of nestedness exhibits some parallels across studies, but it is unclear whether this reflects ecological processes or the formulation of the nestedness measure. In contrast to previous studies we found that nestedness across distance was best fitted by parabolic curves. There are two plausible explanations for why nestedness could behave in this way. The first is that many studies will encompass a bounded domain and exhibit a Mid-Domain Effect (Colwell and Hurtt 1994) with richness therefore peaking at intermediate distances. This would naturally generate a parabolic relationship between nestedness and distance. The second possibility is that while nestedness may initially increase with extent as hypothesised by Soininen et al. (2018), this overlooks the fact that nestedness is by construction non-monotonically related to total beta diversity (Carvalho et al. 2013). Eventually, across large enough scales, turnover is expected to be complete and as a result nestedness must equal zero. Soininen et al. (2018) report that pairwise nestedness patterns are invariant to spatial extent. It could be fruitful to revisit this finding in light of the potential impact of the non-metric quality of nestedness.

The problem with the strange behaviour of the nestedness index is not only the difficulty associated with interpreting it, but also that it leads to erroneous conclusions. For instance, Svenning et al. (2011) postulated that declining nestedness with geographic distance is consistent with recolonization from outside the study extent. However, given that turnover in that dataset sometimes equals one, the more plausible explanation for declining nestedness with distance is that an increasing number of sites have no shared species. An index that increases monotonically, measuring the process of losing shared species, would be more intuitive and may help to reveal ecological processes better than Baselga’s (2010) measure. The “percentage relativized nestedness” index purportedly avoids this problem (Podani and Schmera 2012), and it may be that exploring distance-decay of assemblages using indices other than Baselga’s (2010) nestedness measure proves more useful in uncovering ecological processes.

Effects of scale

One major concern with respect to scale in ecological analyses is that the shape of the relationship between predictor and dependent variables may change according to scale (Scheiner et al. 2000). This is clearly apparent in Chapter 3 where influences of environmental factors and reef area respond in opposing directions to changes to the grain of analysis. The ways in which scale can influence the analysis of biodiversity are varied, affecting both the measurement of biodiversity itself, and putative drivers. This complicates biogeographic analyses, and necessitates multi-scale approaches. Despite this clear need, multi-scale analyses are the exception rather than the norm (Chase et al. 2018). In Chapter 2 we used an iterative approach to uncovering the key determinants of coral beta diversity across scale that allowed important variables to emerge at their relevant scale. However, an optimal model would integrate each variable at its most relevant scale, i.e. SST and reef area would be included at 1° and 10° resolution, respectively. One approach for doing so may be convolution filtering (Nelson 2001), which could be applied to resample reef area to a fine-scale, whilst retaining broad-scale information. This step would still require identification of the most relevant scale for each variable. Iterating over large study extents, such as those featuring in this thesis, is computationally expensive and other authors may prefer to use theory to shortcut this step. However, using fewer steps between the extreme grain sizes would also reduce the computational demands and may reveal unexpected patterns that resorting to theory could miss.

The influence of scale depends on the choice of the dataset. Both the appropriate dataset and the appropriate scale are dictated by the research question & the study organism. Therefore, because scale influences biogeographical studies so fundamentally (e.g. Levin 1992), scale and data should be considered at the outset in the design of new research studies to ensure that the data used is suitable and the influence of scale can be understood. Below, I elaborate on the interactions between scale and data and discuss how the decisions made in this thesis influence the findings.

Spatial grain, together with spatial extent, are critical aspects of scale that determine the range and variation of biological and environmental data (Wiens 1989). A study design where an inappropriate grain or extent is used could fail to detect important processes due to lack of detectable variation. For practical reasons, extent and grain interact. A large extent can place computational, cost or time constraints on the minimum grain size. Overly large grain can result in loss of information (Rahbek 2005), therefore, excessively large study extents can also limit the variation of the data. Lack of variation due to insufficient extent are avoided in this thesis where the smallest extent is the breadth of the tropical Atlantic. However the very large extents used also dictated minimum grain sizes that concealed environmental and biotic variation by excluding the possibility of finer-grain analyses. Fine-scale environmental variation in factors including wave exposure, light, and turbidity is known to be important in the structuring of local communities (Dollar 1982, Tamir et al. 2019, van Woesik and Done 1997). However, such local structuring forces are not detectable in this analysis. Temporal scale also influences biogeographic analyses. The environmental data used here is an amalgamate of several years of satellite imagery (Tybergein et al. 2012, Assis et al. 2018) and prohibits the detection of environmental variability that, like fine scale variation in environmental conditions, is presumed to be an important determinant of coral assemblage composition (Dornelas et al. 2006).

Temporal variation in predictor variables would, nonetheless, not be expected to further out understanding of coral biogeography in this case, owing to the use of species range maps as the distributional data. Range maps, unless regularly updated, cannot show species response to short term phenomena, and even if they are regularly updated, responses would only be visible at the edges of the range. In addition to affecting the range and distribution of variables through sampling a subset of the available data (extent) or through the process of aggregating it (grain), changes in scale influence measures of biodiversity by interacting with species abundance patterns and sampling effort (Chase et al. 2018). The use of species range maps may initially seem to be inferior to alternatives such as abundance or occurrence data, since it necessarily disregards discontinuities within the perimeter of the range and results in errors of commission (Hurlbert and White 2005). However, whilst abundance data in particular may be more revealing of the niche preferences and demographic processes, range map data may be more suitable than other forms of distribution data for understanding the dynamics of species ranges (Hortal 2008). Moreover, abundance and occurrence data are likely to suffer from uncertainty due to insufficient sampling (MacKensie 2005, Hortal 2008). Insufficient sampling is a particular problem for corals, given the challenges associated with conducting fieldwork underwater, often by scuba diving, and often in isolated locations. Illustrating the under-sampling prevalent for most locations and species it has recently been argued that the IUCN red list status for most corals should be “data deficient” rather than “threatened” or “near-threatened” (Bridge et al. 2020). In that context, then, species range maps are a suitable dataset for attempting to identify global drivers of beta diversity, despite shrouding the influences of abundance patterns and sampling effects on overall patterns. The decision to use any data set represents a trade-off, and in the attempt to identify global drivers of biogeographic patterns, the decisions taken here are justifiable, e.g. the loss of detail at fine scales likely doesn’t affect our ability to detect the determinants of large-scale coral biogeography (but see Gotelli et al. 2010 for local scale processes influencing larger scale pattern).

Although there is an increasing focus on the scaling of beta diversity (Barton et al. 2013, Soininen et al. 2018, Antao et al. 2019), studies exploring how putative drivers of beta diversity respond to changes in scale are relatively uncommon. Martiny et al. (2011), exploring bacterial beta diversity, discovered a pattern that differs notably from that which I have documented. In that study, bacteria were dispersal limited on local scales, but at regional and continental scales dispersal limitation was not apparent and variation was exclusively explained by environmental variables (Martiny et al. 2011). This probably results from “scale” having very different meaning for different organisms. A challenge that is yet to be resolved is how to identify the “relevant” scale for particular organisms, especially since this can differ dramatically for an individual organism across life stages.

Evolutionary considerations

As discussed previously, evolutionary processes have major impacts on biogeographic patterns (Roy and Goldberg 2007), however these processes are largely unaccounted for in this thesis. Historically, much of the literature on biodiversity gradients has centered on whether they arise from differing rates of origination or extinction, so-called “cradles” and “museums” of diversity (e.g. Stebbins 1974, Mittelbach et al. 2007). Today, it is increasingly recognized that species ranges are not static (Roy and Goldberg 2007, Huang et al. 2018), and range expansions and shifts can have important influences on patterns of diversity. Irrespective of how gradients initially arise, limitations to range expansions are essential to maintaining them. In that light this thesis can be understood as primarily focusing on the processes that maintain beta diversity. However, by not considering evolutionary processes I risk promoting the importance of factors that correlate with differences in origination or extinction. Until recently, the phylogeny of corals has been poorly resolved, to the extent that one clade of the Scleractinian phylogeny was informally known as the “Bigmessidae”. However, recent improvements in resolving the phylogeny (e.g. Huang et al. 2011), may permit a Phylogeographic approach in future, accounting for these risks.

An alternative to the phylogenetic approach is to model origination and extinction processes together with factors limiting range expansions. This was the approach of Leprieur et al. (2016), who modelled habitat-driven diversification dynamics throughout geological time, combining estimates of reef area with distance-based dispersal limitation to generate realistic beta diversity patterns. This captures some of the key processes generating diversity gradients but risks overlooking other factors influencing the location of range limits. When mechanistic and statistical approaches identify the same processes generating an observed pattern it provides emphatic support of the findings. That both Chapter 3 and Leprieur et al. (2016) highlight reef area and dispersal limitation is reassuring and convincing. The results here also emphasise the influence of environmental factors on observed outcomes, especially at finer scales.

Differences in origination rates between coral genera have the potential to influence the patterns assemblage structure of brooding and spawning corals if this trait is phylogenetically conserved. Whilst Kerr et al. (2011) have shown that transitions between brooding and spawning occur throughout evolutionary time, a considerable degree of conservatism is present and indeed underpins the trait in-filling conducted by McWilliam et al. (2018). The fact that transitions between brooding and spawning modes do occur though, suggest that reproductive mode confers a selective advantage under specific conditions. One likely condition is isolation. The brooding strategy results in rapid settling of larvae and appears to promote local abundance and establishment (Keith et al. 2015) at the expense of longer-distance dispersal. Lord Howe Island, the world’s most southerly coral reef, receives only limited input of larvae from the Great Barrier Reef to the north and abundances of coral species there appear to be primarily governed by their local reproductive success. Ocean currents at Lord Howe Island are not particularly conducive to self-recruitment (Wood et al. 2014), typically sweeping larvae offshore. Species with rapidly developing larvae are disproportionately represented as a result, with brooders making up a far greater proportion of the community than at islands on the Great Barrier Reef (Keith et al. 2015). If isolation and local physical processes favour brooding strategies, as appears to be the case, we should expect that the transition from brooding to spawning more commonly originates in such locations. A species originating in such extreme isolation may not expand its range as rapidly as species originating elsewhere, which would imply that differences in the biogeography of brooders and spawners can arise from their evolutionary history in addition to their capacity from long range dispersal.

All ecology is driven by trade-offs (Litchman et al. 2013), and the benefit of improved establishment ability in brooders must result in a cost elsewhere. Corals would otherwise all eventually exhibit brooding strategies, whereas the opposite is closer to the truth (Baird et al. 2009). Our hypothesis was that the trade-off was between local abundance and long distance dispersal, but plausible alternative explanations exist. One such alternative is that long distance dispersal is largely equal among reproductive modes, but that mid-range dispersal and abundance is promoted in spawners relative to brooders – such a strategy is sub-optimal for spawning corals of Lord Howe Island where no habitat lies downstream, but spawners in well-connected habitat may record greater overall abundance. The relative merit of each strategy is therefore determined by the habitat mosaic in which the coral is situated. Abundance differences interact with inbreeding considerations in determining the relative fitness of brooding and spawning strategies. Spawners are expected to suffer less from inbreeding relative to brooders which promotes their fitness (Amos et al. 2001). The balance of benefits and costs of different trait combinations can be hard to quantify, however their consequences define the ecology of all organisms and determine to a large degree the abundance or rarity of species and their distributions. In the following section I discuss further the benefits and challenges associated with the trait-based approach.

The trait-based approach

Chapter 4 employed a trait-based approach to understand how organismal properties influence biogeography at large. In recent years ecologists have increasingly adopted trait-based approaches (McGill et al. 2006, Violle et al. 2007) in their attempts to identify general laws in ecology (Lawton 1999). One benefit of the trait-based approach is that it can serve to reduce the complexity of ecosystems. Instead of considering many different species, the trait-based approach considers individuals interacting through a few key traits (Kiørboe et al. 2018) leading to a mechanistic understanding of organisms and ecosystems. Traits are interrelated through life-history trade-offs, and an organism's particular suite of traits determines how it interacts with its abiotic and biotic surroundings (McGill et al. 2006). The mechanistic understanding based on key traits that cross taxa also allows for comparisons and reveal similarities between systems that have no species in common. For example, brooding and spawning reproductive modes are common in marine systems and studying their influence in one group can be informative in providing understanding of the ecology of another taxonomic group. The differing strategies appear to influence large-scale biogeographic patterns in corals, with brooding corals exhibiting greater turnover in assemblage composition across space. The trait-based approach allows us to make *a priori* predictions for how similar types of reproductive strategies will influences assemblage structure in other groups. However, cross-taxa generalisations may be challenging (Soininen et al. 2018) which perhaps illustrates one of the difficulties of the trait-based approach, namely, how to determine traits that are sufficiently specific that they are ecologically meaningful, and yet avoiding excessive specificity that they lose their generalisability across taxa. Other challenges include accounting for intraspecific variation in traits and the lack of trait coverage that exists across many species. For example, the majority of corals are functionally heterotrophic, acquiring energy and nutrients both from their photosynthetic symbionts and also from zooplankton prey. Whilst many aspects of coral ecology is determined by their gross morphology (Madin et al. 2014, Zawada et al. 2019), the interface is the coral tissue. This is particularly the case during predation where prey is captured on coral tentacles. Despite this, however, little data relates coral soft tissue with other traits (but see Precoda et al. 2020).

Corals as a model organism

Ecological systems are hugely complicated and the value of science lies in identifying general principles that apply broadly, thereby reducing this complexity. Therefore, in addition to the merits of studying corals for the sake of understanding and conserving them better, it is to be hoped that the findings of this thesis have broader relevance. Because of the number of other taxa that display similar patterns in diversity, corals represent a useful model organism for understanding marine biogeography. Like corals, reef fish, seagrasses, mangroves and benthic invertebrates such as bivalves, snails, lobsters, sea urchins, show declining richness away from a peak in the Indo-Australian Archipelago (Tittensor et al. 2010; Paulay, 1990; Roberts et al. 2002; Palumbi 1997). Broadly convergent patterns in diversity are likely the product of similar processes acting across these various taxonomic groups. The knowledge gained from coral biogeography may therefore apply to these other taxa, especially those which possess similar traits. *A priori* expectations for these organisms would be that environmental processes are the primary limiting factors at higher latitudes, habitat area will be important to species richness, and that dispersal limitation is a significant problem across the breadth of the Indo-Pacific.

The novel finding that coral beta diversity results primarily from dispersal limitation is likely relevant to biogeography more broadly. This finding has not been shown previously in the absence of a realistic model of dispersal limitation, underlining the importance of developing better tools for estimating and measuring dispersal (Hussey et al. 2015, Kays et al. 2015). The use of directional network models has also been shown to improve predictions of species composition patterns relative to time-distance models (Carvalho et al. 2015). We should not, therefore, disregard the potential influence of dispersal limitation on the basis of distance- or time-based analyses alone. Wherever possible ecologists should develop models of dispersal that consider ocean-currents, prevailing wind patterns and the resistance of the landscape.

There are limits, nonetheless, to the generality of the findings presented here. The vastness of the Indo-Pacific basin is unmatched in other biomes and, considering its extent, environmental conditions are *relatively* homogenous in comparison to other ecosystems (although boreal forests may be surprisingly similar in these regards). These factors may promote the importance of dispersal limitation, which may not necessarily be the primary factor in other domains where maximum distances are shorter. There, environmental or biotic factors may have stronger effects. This is demonstrated in Chapter 3 where beta diversity of Atlantic coral assemblages correlates more strongly with environmental conditions than with dispersal limitation. Nonetheless, one of the central findings of this thesis is that dispersal limitation is not equivalent to distance. Dispersal limitation results from the difficulty of traversing a landscape, which is organism and environment specific. Organisms with different life histories than corals are not subject to the same limitations. Therefore, even in smaller domains, dispersal history can be a significant problem. The dispersal limitation of bacteria over “local scales” (Martiny et al. 2011) reflects that relevant scales differ between organisms. Similarly, the capability for significant active dispersal in large fish as adults may mean that they are not dispersal limited as corals, even across the vastness of the Indo-Pacific. The influences of traits on biogeography are context-dependant (Soininen et al. 2018). Therefore, whilst the conclusions of this thesis may well apply more broadly, the properties of environment and the specific traits of the taxa in question must also be considered.

Management outlook

There is another sense in which corals can be viewed as a model organism. Coral reefs have been described as “the canary in the coal mine” in regards to their sensitivity to global warming (Brown and Ogden 1993). Corals may serve as a test case of humanities willingness and ability to act to stem climate change and environmental destruction.

Documented declines of coral abundance (Hughes et al. 2011) provide a vision of the fate likely to befall other organisms and ecosystems in the Anthropocene in the absence of dramatic action.

From a management and conservation perspective, the finding that dispersal is an important limiting factor for coral distributions is a troubling outcome. This is especially the case since corals are notable for their very large range sizes (Hughes et al. 2002) – if corals are dispersal limited, then, in the absence of better evidence, the conservative conclusion is that many other species are dispersal limited. This finding also presents a significant challenge, because dispersal is a process that we have historically struggled to measure. One positive finding in this thesis is that we were able to utilise modelled connectivity to predict coral beta diversity across a range of scales. Whilst this needs to be verified in other contexts, it suggests that dispersal models, once developed, can be scaled to the specific needs of managers.

This thesis did not demonstrate the effects of global warming or mass-bleaching on coral assemblages since the distribution data are composites of many years of reef surveys (Hughes et al. 2013, IUCN 2016) and lack the resolution to discern responses to recent climate change. Nonetheless, the results presented reassert the importance of minimising nutrient impacts to protect the amount of healthy coral reef. Moreover, these findings underline the necessity of doing everything possible to conserve healthy coral reef ecosystems over very large-scales. Finally, because corals are dispersal limited, establishing and enforcing protection of connected reefs along dispersal pathways will support coral in tracking suitable habitat under climate change.

5.2 Future directions

This thesis has touched upon several topics which could prove fruitful avenues of future research effort. These include theoretical questions related to the measurement of biodiversity and biodiversity change, together with more specific questions relating to the biogeography and physiology of corals.

Quantification of biodiversity change in space and time.

This thesis has highlighted the uncertainty around the origin and interpretation of turnover and nestedness components of beta diversity. As I acknowledged, these patterns may be related to the data type, study design or organismal properties. It would be worthwhile, therefpre, to develop a formal framework that makes predictions for how these different considerations could be expected to influence beta diversity. Understanding the patterns and underlying causes of beta diversity is important both across space but also over time (Magurran et al. 2019). Extending exploration of how turnover and nestedness covary in a temporal beta diversity framework (Tisseuil et al. 2012) would have useful applications in biological monitoring and ecological impact assessments and could take the form of temporal-decay relationships (Shimadzu et al. 2015). Although there are unique challenges associated with the application of beta diversity to time-series data (Magurran et al. 2019), confounding effects of species origination are less of a concern than in spatial beta diversity studies. Turnover and nestedness components of beta diversity may be more interpretable in a temporal beta diversity framework as a result. Changes in the absolute amount and ratios of turnover and nestedness could warn of impending phase-shifts or measure the impact and recovery from disturbances. Given the pressing need to document and understand biodiversity change, it is essential to extract the maximum information from available data sets. Further developing the application of beta diversity in both spatial and temporal settings will support these efforts.

The influence of isolation on coral assemblages

Dispersal is integral to the colonisation of new habitat, but dispersal alone does not ensure successful establishment. Therefore, future studies expanding on the findings presented here that also consider how traits relating to establishment influence assemblage structure would be particularly relevant to understanding the consequences of anthropogenic change. Habitat degradation and periodic mass-bleaching events on coral reefs are causing these ecosystems to become more fragmented and more isolated from potential larval sources. Whilst a great deal of research has understandably focused on the direct impacts of stressors on assemblage structure, we must look further at the effects of increasing isolation, which modify the selective pressures on corals and their fitness landscape. Certain traits, such as the development rate of larvae (A. Baird *Pers. Communication*), may be more likely to promote persistence in isolation. Identifying and quantifying the relative importance of different traits to the success of corals across a continuum of isolation could potentially reveal a trajectory of reefs in the Anthropocene.

Of particular interest is the potential mismatch between traits naturally selected under bleaching (i.e., winners and losers; Loya et al. 2001), traits that promote persistence in isolation, and those that support the tracking of suitable environmental conditions through space. For example, the relative abundance of coral species that spawn gametes versus corals that brood larvae has shifted substantially on the Great Barrier Reef in response to repeated mass bleaching events (Hughes et al. 2019), indicating differential susceptibility to current and future conditions. However, evidence from this thesis and evidence from coral reef fish (Feary et al. 2014) indicates that a brooding strategy is less suitable for tracking suitable climate via range expansion. Yet more evidence suggests that brooding corals are better at establishing in isolated locations where ocean currents limit self-recruitment (Keith et al. 2015). Considering likely future selection pressures on coral reefs may reveal “forbidden” areas of trait-space that are particularly likely to experience reduced fitness and abundance.

One example of a trait that could be under selection is more isolated locations is gross morphology. Coral reefs are dynamic ecosystems subject to frequent disturbance (Madin et al. 2014) and isolation could therefore be expected to select for corals that are particularly robust, since these will be less subject to stochastic events. Madin et al. (2014) applied a measure of colony shape to predict the annual mortality of different morphologies according to their size. Morphologies that suffer lower mortality as they grow would be expected to persist better in isolated locations than more fragile morphologies. However, in some fragile morphologies, particularly branching morphologies, fragmentation appears to be a important mode of asexual reproduction (Smith and Hughes 1999). Fragmentation occurs when parts of the coral break off from the larger colony, often as a result of wave stress. These fragments can sometimes reattach to the reef substrate, increasing the abundance of the species. Therefore, fragmentation could also be an important mechanism for establishing substantial populations in isolated locations. A relationship between mechanical strength and persistence of corals on isolated reefs could be expected to demonstrate a U-shaped curve. Consequently, future analyses to tease apart how spatial influences such as reef area and isolation interact with coral traits to impact assemblage structure will be valuable in predicting the consequences of anthropogenic change on corals.

Modelling coral investment strategy to understand niche space and physiological tolerance

Corals display a range a strategies for acquiring energy and nutrients, as described in the introduction to this thesis. Photosynthetic zooxanthellate symbionts provide energy-rich Carbon compounds to corals tissues, whilst predation of zooplankton delivers both Carbon and Nitrogen. The direct uptake of dissolved nutrients provides an alternative source of Nitrogen. The ability of a coral to harness these resources and the way in which they are subsequently invested is an important determinant of its niche breadth, its growth rate in different environments and potentially its tolerance of adverse conditions. The nutrient investment strategies of different coral species are of critical relevance in the Anthropocene because they ultimately determine the fluxes of, and requirements for, Carbon and Nitrogen. One example where human activities chronically distort these fluxes is nutrient enrichment, which increases availability of dissolved Nitrogen (Fabricius et al. 2005).

These trophic dynamics may be critical in mediating the response of corals to bleaching events. Carbon fluxes are acutely impacted during such events because zooxanthellae are expelled from the coral tissue. This loss of carbon-supplying symbionts starves corals of their largest energy source and, over extended periods, can be fatal (Anthony et al 2009). This process is the key mechanism underlying coral mortality associated with coral bleaching events. Interestingly, it appears that the susceptibility of corals to death during bleaching can be mediated by increased heterotrophic activity in some species (Grottoli et al. 2006, Hughes and Grottoli 2013). Additionally, corals living in highly turbid waters with elevated nutrient and plankton concentration have shown reduced bleaching and accelerated recovery (Camp et al. 2017). These cases illustrate how niches and traits that relate to heterotrophy could be important in determining how well corals are able to withstand Anthropogenic change.

One way to understand the potential importance of trophic strategies is to model coral growth across a range of possible investment strategies. The optimal strategy not only depends on the traits of the coral, but also on the biotic and abiotic gradients over which corals occur, including light, dissolved nutrients and abundance of zooplankton prey (Tamir et al. 2019, Fabricius et al. 2005, Liston 1990). In taking this approach, we can begin to develop a mechanistic understanding of how and why coral assemblages differ across gradients of depth and nutrients. Even more pressing is the need to understand why the outcome (mortality or recovery) for coral colonies differs following bleaching events, permitting greater predictions of their response to future climate change.

I propose a model based on an optimisation approach that treats the ideal trophic strategy for a coral with a particular morphology in a certain environment as an emergent property (Chakrabory et al. 2017). The model describes a single coral colony that acquires Carbon through photosynthesis, dissolved Nitrogen through direct uptake, and Carbon and Nitrogen through predation. In doing so, it necessarily simplifies the relationship between coral and photosynthetic symbionts, essentially treating the zooxanthellae as organelles within coral tissue. The overarching model structure is shown in Figure 1. Under the model formulation, corals invest in skeletal mass, together with the resource-harvesting traits of photosynthesis, predation and direct uptake of nutrients. Performance with respect to the differing traits varies according the level of investment in each. Tissue mass, which constrains the resource-harvesting traits, is assumed to scale with the skeleton in a manner that varies according to morphology. All investments incur direct costs in terms of the construction of the necessary machinery, whilst investments in the different resource-harvesting traits also incur maintenance costs via elevated respiration.

Following subtraction of these costs from inward fluxes, the optimal investment strategy is calculated following Liebig’s law of the minimum (Odum 1971) i.e. whichever is of more limited supply (Carbon or Nitrogen) will determine the amount each that is invested in biomass, with the remainder being excreted. In other words, some of the non-limiting nutrient is wasted since the organism lacks the capacity to utilise it. In this formulation, the optimal strategy is one that maximizes the supply of the limiting nutrient, therefore maximising the addition of biomass.

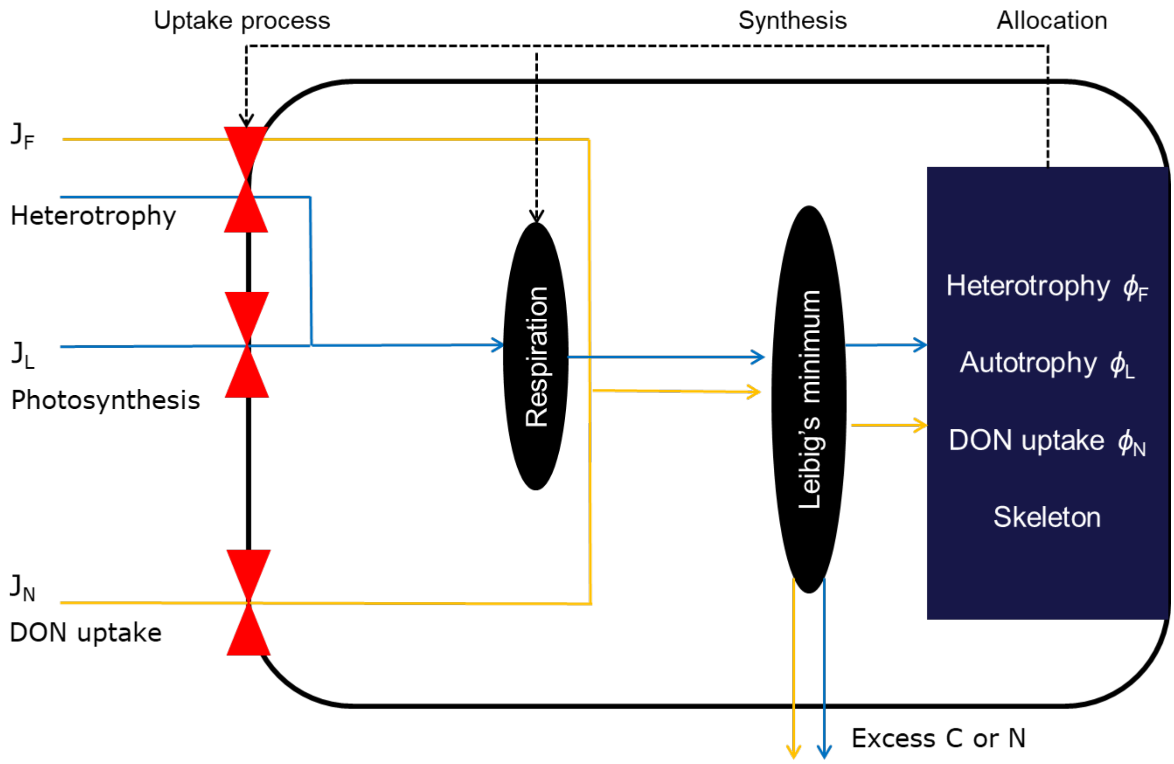


Figure 1. A schematic representation of the model showing how fluxes of Carbon (blue lines) and Nitrogen (yellow lines) are respired and combined to be allocated to structure and resource harvesting traits.

Such a model would allow identification of the ideal trophic strategy for a coral with a particular morphology under a range of different light, prey and nutrient concentrations. Once this has been identified, the model can readily be extended to reveal the Carbon shortfall that different corals experience during bleaching by removing symbionts from the model and thereby setting Carbon fluxes from this source to zero. As this model is theoretical, it would be useful to confront its predictions of trophic strategies with empirical data to determine if the mechanisms proposed within the model can plausibly generate observed outcomes. One possibility is the use of stable isotope data to quantify the origin of Carbon and Nitrogen in coral and zooxanthellae tissues across environmental gradients and through bleaching events. An alternative option is to test whether coral species that experience greater mortality in response to bleaching events are also those that the model predicts a greater carbon shortfall for in the absence of photosynthetic Carbon.

I believe this model could be useful in understanding coral zonation and assemblage structure. Perhaps even more importantly, it offers a method to predict the vulnerability of different corals to Anthropogenic change from a few key traits. Models such as this can potentially improve the accuracy of projections of coral mortality following bleaching events.

6

Bibliography

Adler, P. B., Fajardo, A., Kleinhesselink, A. R., & Kraft, N. J. B. (2013). Trait-based tests of coexistence mechanisms. *Ecology Letters*, *16*, 1294–1306. https://doi.org/10.1111/ele.12157

Almeida-Neto, M., Frensel, M. B., & Ulrich, W. (2012). Rethinking the relationship between nestedness and beta diversity: a comment on Baselga (2010). *Global Ecology and Biogeography*, *21*, 772–777.

Amos, W., Worthington Wilmer, J., Fullard, K., Burg, T. M., Croxall, J. P., Bloch, D., & Coulson, T. (2001). The influence of parental relatedness on reproductive success. *Proceedings of the Royal Society B: Biological Sciences*, *268*(1480), 2021–2027. https://doi.org/10.1098/rspb.2001.1751

Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., Sanders, N. J., Cornell, H. V., Comita, L. S., Davies, K. F., Harrison, S. P., Kraft, N. J. B., Stegen, J. C., & Swenson, N. G. (2011). Navigating the multiple meanings of β diversity: A roadmap for the practicing ecologist. *Ecology Letters*, *14*(1), 19–28. https://doi.org/10.1111/j.1461-0248.2010.01552.x

Antão, L. H., McGill, B., Magurran, A. E., Soares, A. M. V. M., & Dornelas, M. (2019). B-Diversity Scaling Patterns Are Consistent Across Metrics and Taxa. *Ecography*, *42*(5), 1012–1023. https://doi.org/10.1111/ecog.04117

Anthony, K. R. N., Hoogenboom, M. O., Maynard, J. A., Grottoli, A. G., & Middlebrook, R. (2009). Energetics approach to predicting mortality risk from environmental stress: A case study of coral bleaching. *Functional Ecology*, *23*(3), 539–550. https://doi.org/10.1111/j.1365-2435.2008.01531.x

Aranda, S. C., Gabriel, R., Borges, P. A. V., Santos, A. M. C., Hortal, J., Baselga, A., & Lobo, J. M. (2013). How do different dispersal modes shape the species-area relationship? Evidence for between-group coherence in the Macaronesian flora. *Global Ecology and Biogeography*, *22*(4), 483–493. https://doi.org/10.1111/geb.12008

Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E. A., & De Clerck, O. (2018). Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. *Global Ecology and Biogeography*, *27*(3), 277–284. https://doi.org/10.1111/geb.12693

Ayre, D. J., & Hughes, T. P. (2000). Genotypic diversity and gene flow in brooding and spawning corals along the great barrier reef, Australia. *Evolution*, *54*(5), 1590–1605. https://doi.org/10.1111/j.0014-3820.2000.tb00704.x

Baird, A. H. (2001). *The ecology of coral larvae: settlement patterns, habitat selection and the length of the larval phase* (Doctoral dissertation, James Cook University).

Baird, A. H., Sommer, B., & Madin, J. S. (2012). Pole-ward range expansion of Acropora spp. along the east coast of Australia. *Coral Reefs*, *31*(4), 1063. https://doi.org/10.1007/s00338-012-0928-6

Baird, Andrew H., Guest, J. R., & Willis, B. L. (2009). Systematic and Biogeographical

Patterns in the Reproductive Biology of Scleractinian Corals. *Annual Review of Ecology, Evolution, and Systematics*, *40*(1), 551–571. https://doi.org/10.1146/annurev.ecolsys.110308.120220

Bala, G. (2013). Digesting 400 ppm for global mean CO2 concentration. *Curr Sci*, *104*(11), 1471-1472.

Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., Mersey, B., & Ferrer, E. A. (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, *471*(7336), 51–57. https://doi.org/10.1038/nature09678

Barton, P. S., Cunningham, S. A., Manning, A. D., Gibb, H., Lindenmayer, D. B., & Didham, R. K. (2013). The spatial scaling of beta diversity. *Global Ecology and Biogeography*, *22*(6), 639–647. https://doi.org/10.1111/geb.12031

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, *19*(1), 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Baselga, A. (2012). The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography*, *21*(12), 1223–1232. https://doi.org/10.1111/j.1466-8238.2011.00756.x

Baselga A., Orme D., Villeger S., De Bortoli J. and Leprieur F. (2018). betapart: Partitioning Beta Diversity into Turnover and Nestedness Components. R package version 1.5.1. https://CRAN.R-project.org/package=betapart

Bellwood, D. R., & Hughes, T. P. (2001). Regional-scale assembly rules and biodiversity of coral reefs. *Science*, *292*(5521), 1532–1534. https://doi.org/10.1126/science.1058635

Bellwood, D. R., Hughes, T. P., Connolly, S. R., & Tanner, J. (2005). Environmental and geometric constraints on Indo-Pacific coral reef biodiversity. *Ecology Letters*, *8*(6), 643–651. https://doi.org/10.1111/j.1461-0248.2005.00763.x

Bellwood, D. R., Hughes, T. P., Folke, C., & Nyström, M. (2004). Confronting the coral reef crisis. *Nature*, *429*(6994), 827–833. https://doi.org/10.1038/nature02691

Beukhof, E., Frelat, R., Pecuchet, L., Maureaud, A., Dencker, T. S., Sólmundsson, J., Punzón, A., Primicerio, R., Hidalgo, M., Möllmann, C., & Lindegren, M. (2019). Marine fish traits follow fast-slow continuum across oceans. *Scientific Reports*, *9*(1), 17878. https://doi.org/10.1038/s41598-019-53998-2

Birkeland, C. (1982). Terrestrial runoff as a cause of outbreaks of Acanthaster planci (Echinodermata: Asteroidea). *Marine Biology*, *69*(2), 175–185. https://doi.org/10.1007/BF00396897

Bradbury, I. R., Laurel, B., Snelgrove, P. V. R., Bentzen, P., & Campana, S. E. (2008). Global patterns in marine dispersal estimates: The influence of geography, taxonomic category and life history. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1644), 1803–1809. https://doi.org/10.1098/rspb.2008.0216

Bridge, T. C. L., Luiz, O. J., Kuo, C. Y., Precoda, K., Madin, E. M. P., Madin, J. S., & Baird, A. H. (2020). Incongruence between life-history traits and conservation status in reef corals. *Coral Reefs*, *39*(2), 271–279. https://doi.org/10.1007/s00338-019-01885-7

Brown, B. E., & Ogden, J. C. (1993). Coral bleaching. *Scientific American*, *268*(1), 64–70. https://doi.org/10.1038/scientificamerican0193-64

Brown, J. H., & Maurer, B. A. (1989). Macroecology: The Division of Food and Space among

Species on Continents. *Science*, *243*, 1145–1150. https://doi.org/10.1017/CBO9781107415324.004

Butchart, S. H. M., Walpole, M., Collen, B., Van Strien, A., Scharlemann, J. P. W., Almond, R. E. A., Baillie, J. E. M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K. E., Carr, G. M., Chanson, J., Chenery, A. M., Csirke, J., Davidson, N. C., Dentener, F., Foster, M., Galli, A., … Watson, R. (2010). Global biodiversity: Indicators of recent declines. *Science*, *328*(5982), 1164–1168. https://doi.org/10.1126/science.1187512

Camp, E. F., Nitschke, M. R., Rodolfo-Metalpa, R., Houlbreque, F., Gardner, S. G., Smith, D. J., Zampighi, M., & Suggett, D. J. (2017). Reef-building corals thrive within hot-acidified and deoxygenated waters. *Scientific Reports*, *7*(1), 2434. https://doi.org/10.1038/s41598-017-02383-y

Campbell Grant, E. H., Nichols, J. D., Lowe, W. H., & Fagan, W. F. (2010). Use of multiple dispersal pathways facilitates amphibian persistence in stream networks. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(15), 6936–6940. https://doi.org/10.1073/pnas.1000266107

Carpenter, K. E., Abrar, M., Aeby, G., Aronson, R. B., Banks, S., Bruckner, A., ... & Edgar, G. J. (2008). One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science*, *321*(5888), 560-563.

Carvalho, J. C., Cardoso, P., Borges, P. A. V., Schmera, D., & Podani, J. (2013). Measuring fractions of beta diversity and their relationships to nestedness: A theoretical and empirical comparison of novel approaches. *Oikos*, *122*(6), 825–834. https://doi.org/10.1111/j.1600-0706.2012.20980.x

Carvalho, J. C., Cardoso, P., Rigal, F., Triantis, K. A., & Borges, P. A. V. (2015). Modeling directional spatio-temporal processes in island biogeography. *Ecology and Evolution*, *5*(20), 4671–4682. https://doi.org/10.1002/ece3.1632

Chakraborty, S., Nielsen, L. T., & Andersen, K. H. (2017). Trophic strategies of unicellular plankton. *American Naturalist*, *189*(4), E77–E90. https://doi.org/10.1086/690764

Chase, J. M., & Knight, T. M. (2013). Scale-dependent effect sizes of ecological drivers on biodiversity: Why standardised sampling is not enough. *Ecology Letters*, *16*(SUPPL.1), 17–26. https://doi.org/10.1111/ele.12112

Chase, J. M., McGill, B. J., McGlinn, D. J., May, F., Blowes, S. A., Xiao, X., Knight, T. M., Purschke, O., & Gotelli, N. J. (2018). Embracing scale-dependence to achieve a deeper understanding of biodiversity and its change across communities. *Ecology Letters*, *21*(11), 1737–1751. https://doi.org/10.1111/ele.13151

Cheung, W. W. L., Meeuwig, J. J., Feng, M., Harvey, E., Lam, V. W. H., Langlois, T., Slawinski, D., Sun, C., & Pauly, D. (2012). Climate-change induced tropicalisation of marine communities in Western Australia. *Marine and Freshwater Research*, *63*(5), 415–427. https://doi.org/10.1071/MF11205

Chiba, S., Saito, H., Fletcher, R., Yogi, T., Kayo, M., Miyagi, S., Ogido, M., & Fujikura, K. (2018). Human footprint in the abyss: 30 year records of deep-sea plastic debris. *Marine Policy*, *96*(August 2017), 204–212. https://doi.org/10.1016/j.marpol.2018.03.022

Cinner, J. E., Maire, E., Huchery, C., Aaron MacNeil, M., Graham, N. A. J., Mora, C., McClanahan, T. R., Barnes, M. L., Kittinger, J. N., Hicks, C. C., D'Agata, S., Hoey, A. S., Gurney, G. G., Feary, D. A., Williams, I. D., Kulbicki, M., Vigliola, L., Wantiez, L., Edgar, G. J., … Mouillot, D. (2018). Gravity of human impacts mediates coral reef conservation gains. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(27), E6116–E6125. https://doi.org/10.1073/pnas.1708001115

Coles, S. L., & Jokiel, P. L. (1978). Synergistic effects of temperature, salinity and light on the hermatypic coral Montipora verrucosa. *Marine Biology*, *49*(3), 187–195. https://doi.org/10.1007/BF00391130

Colwell, R. K., & Hurtt, G. C. (1994). Nonbiological gradients in species richness and a spurious Rapoport effect. *American Naturalist*, *144*(4), 570–595. https://doi.org/10.1086/285695

Colwell, Robert K., & Rangel, T. F. (2009). Hutchinson's duality: The once and future niche. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(SUPPL. 2), 19651–19658. https://doi.org/10.1073/pnas.0901650106

Condit, R., Pitman, N., Leigh, E. G., Chave, J., Terborgh, J., Foster, R. B., Núñez, P. V., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H. C., Losos, E., & Hubbell, S. P. (2002). Beta-diversity in tropical forest trees. *Science*, *295*(5555), 666–669. https://doi.org/10.1126/science.1066854

Connell, J.H. 'Field Experiments in Marine Ecology'. In *Experimental Marine Biology*, edited by R. Mariscal, 21–54. New York: Academic Press Inc, 1974.

Connolly, S. R., Bellwood, D. R., & Hughes, T. P. (2003). INDO-PACIFIC BIODIVERSITY OF CORAL REEFS : DEVIATIONS FROM A MID-DOMAIN MODEL. *Ecology*, *84*(8), 2178–2190.

Costanza, R., D'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R. V., Paruelo, J., Raskin, R. G., Sutton, P., & van den Belt, M. (1997). The value of the world's ecosystem services and natural capital. LK - https://royalroads.on.worldcat.org/oclc/4592801201. *Nature TA - TT -*, *387*(6630), 253–260. https://www-nature-com.ezproxy.royalroads.ca/articles/387253a0.pdf

Couce, E., Ridgwell, A., & Hendy, E. J. (2012). Environmental controls on the global distribution of shallow-water coral reefs. *Journal of Biogeography*, *39*(8), 1508–1523. https://doi.org/10.1111/j.1365-2699.2012.02706.x

Cowen, R. K., Lwiza, K. M. M., Sponaugle, S., Paris, C. B., & Olson, D. B. (2000). Connectivity of Marine Populations : Open or Closed ? *Science*, *287*(5454), 857–859.

Darlington, Philip J. (1957) *Zoogeography; the geographical distribution of animals*. Wiley

Darwin, C.1859. *On the origin of species by means of natural selection*. London: Penguin. OCLC: 803439483.

Davies, P. S. (1984). The role of zooxanthellae in the nutritional energy requirements of Pocillopora eydouxi. *Coral Reefs*, *2*(4), 181–186. https://doi.org/10.1007/BF00263571

Davies, S. W., Treml, E. A., Kenkel, C. D., & Matz, M. V. (2015). Exploring the role of Micronesian islands in the maintenance of coral genetic diversity in the Pacific Ocean. *Molecular Ecology*, *24*(1), 70–82. https://doi.org/10.1111/mec.13005

De'Ath, G., Fabricius, K. E., Sweatman, H., & Puotinen, M. (2012). The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(44), 17995–17999. https://doi.org/10.1073/pnas.1208909109

Dlugokencky, E., & Tans, P. (2018). Trends in atmospheric carbon dioxide, National Oceanic & Atmospheric Administration, Earth System Research Laboratory (NOAA/ESRL).

Dollar, S. J. (1982). Wave stress and Coral Community Structure in Hawaii. *Coral Reefs*, *1*, 71–81. https://doi.org/10.1016/B978-0-12-811963-1.00001-9

Dornelas, M., Connolly, S. R., & Hughes, T. P. (2006). Coral reef diversity refutes the neutral theory of biodiversity. *Nature*, *440*(7080), 80–82. https://doi.org/10.1038/nature04534

Dornelas, M., Gotelli, N. J., Shimadzu, H., Moyes, F., Magurran, A. E., & McGill, B. J. (2019). A balance of winners and losers in the Anthropocene. *Ecology Letters*, *22*(5), 847–854. https://doi.org/10.1111/ele.13242

Fabricius, K., De'ath, G., McCook, L., Turak, E., & Williams, D. M. B. (2005). Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. *Marine Pollution Bulletin*, *51*(1–4), 384–398. https://doi.org/10.1016/j.marpolbul.2004.10.041

Feary, D. A., Pratchett, M. S., J Emslie, M., Fowler, A. M., Figueira, W. F., Luiz, O. J., Nakamura, Y., & Booth, D. J. (2014). Latitudinal shifts in coral reef fishes: Why some species do and others do not shift. *Fish and Fisheries*, *15*(4), 593–615. https://doi.org/10.1111/faf.12036

Ferrier, S., Drielsma, M., Manion, G. & Watson, G. (2002) Extended statistical approaches to modelling spatial pattern in biodiversity in north-east New South Wales: II. Community level modelling. *Biodiversity and Conservation*, **11**, 2309–2338.

Ferrier, S., Manion, G., Elith, J., & Richardson, K. (2007). Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Diversity and Distributions*, *13*(3), 252–264. https://doi.org/10.1111/j.1472-4642.2007.00341.x

Figueiredo, J., Baird, A. H., & Connolly, S. R. (2013). Synthesizing larval competence dynamics and reef-scale retention reveals a high potential for self-recruitment in corals. *Ecology*, *94*(3), 650–659. https://doi.org/10.1890/12-0767.1

Figueiredo, J., Baird, A. H., Harii, S., & Connolly, S. R. (2014). Increased local retention of reef coral larvae as a result of ocean warming. *Nature Climate Change*, *4*(6), 498–502. https://doi.org/10.1038/nclimate2210

Fisher, R., O'Leary, R. A., Low-Choy, S., Mengersen, K., Knowlton, N., Brainard, R. E., & Caley, M. J. (2015). Species richness on coral reefs and the pursuit of convergent global estimates. *Current Biology*, *25*(4), 500–505. https://doi.org/10.1016/j.cub.2014.12.022

Fraser, R. H., & Currie, D. J. (1996). The Species Richness-Energy Hypothesis in a System Where Historical Factors Are Thought to Prevail : Coral Reefs Author (s): Robert H . Fraser and David J . Currie Published by : The University of Chicago Press for The American Society of Naturalists St. *Coral Reefs*, *148*(1), 138–159.

Gaston, K. J. (1991). How Large Is a Species ' Geographic Range ? Author (s): Kevin J . Gaston Published by : Wiley on behalf of Nordic Society Oikos Stable URL : http://www.jstor.com/stable/3545251 REFERENCES Linked references are available on JSTOR for this article : refer. *Oikos*, *61*(3), 434–438.

Gaston, K. J. (2000). Global patterns in biodiversity. *Nature*, *405*(6783), 220–227. https://doi.org/10.1038/35012228

Gaston, K. J. (2003). *The structure and dynamics of geographic ranges*. Oxford University Press on Demand.

Gaston, K. J., & Fuller, R. A. (2009). The sizes of species' geographic ranges. *Journal of Applied Ecology*, *46*(1), 1–9. https://doi.org/10.1111/j.1365-2664.2008.01596.x

Gaylord, B., & Gaines, S. D. (2000). Temperature or Transport ? Range Limits in Marine

Species Mediated Solely by Flow. *The American Naturalist*, *155*(6), 769–789. https://doi.org/0003-0147/2000/15506-0005$03.00

Glynn, P. (1977). Coral growth in upwelling and nonupwelling areas off the Pacific coast of Panama. *Journal of Marine Research*, *35*(3), 567–585.

Gómez-Rodríguez, C., & Baselga, A. (2018). Variation among European beetle taxa in patterns of distance decay of similarity suggests a major role of dispersal processes. *Ecography*, *41*(11), 1825–1834. https://doi.org/10.1111/ecog.03693

Gotelli, N. J., Anderson, M. J., Arita, H. T., Chao, A., Colwell, R. K., Connolly, S. R., Currie, D. J., Dunn, R. R., Graves, G. R., Green, J. L., Grytnes, J. A., Jiang, Y. H., Jetz, W., Kathleen Lyons, S., McCain, C. M., Magurran, A. E., Rahbek, C., Rangel, T. F. L. V. B., Soberón, J., … Willig, M. R. (2009). Patterns and causes of species richness: A general simulation model for macroecology. *Ecology Letters*, *12*(9), 873–886. https://doi.org/10.1111/j.1461-0248.2009.01353.x

Gotelli, N. J., Graves, G. R., & Rahbek, C. (2010). Macroecological signals of species interactions in the Danish avifauna. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(11), 5030–5035. https://doi.org/10.1073/pnas.0914089107

Graham, E. M., Baird, A. H., & Connolly, S. R. (2008). Survival dynamics of scleractinian coral larvae and implications for dispersal. *Coral Reefs*, *27*(3), 529–539. https://doi.org/10.1007/s00338-008-0361-z

Graham, N. A.J., & Nash, K. L. (2013). The importance of structural complexity in coral reef ecosystems. *Coral Reefs*, *32*(2), 315–326. https://doi.org/10.1007/s00338-012-0984-y

Graham, Nicholas A.J., Jennings, S., MacNeil, M. A., Mouillot, D., & Wilson, S. K. (2015). Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature*, *518*(7537), 94–97. https://doi.org/10.1038/nature14140

Green, S. J., Akins, J. L., Maljokic, A., & Cote, I. M. (2012). Invasive Lionfish Drive Atlantic Coral Reef Fish Declines. *PloS One*, *7*(3). https://doi.org/10.1371/Citation

Grottoli, A. G., Rodrigues, L. J., & Palardy, J. E. (2006). Heterotrophic plasticity and resilience in bleached corals. *Nature 2006 440:7088*, *440*(7088), nature04565. https://doi.org/10.1038/nature04565

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J. F., Casey, K. S., Ebert, C., Fox, H. E., Fujita, R., Heinemann, D., Lenihan, H. S., Madin, E. M. P., Perry, M. T., Selig, E. R., Spalding, M., Steneck, R., Watson, R. (2008). A global map of human impact on marine ecosystems. *Science*, *319*(5865), 948-952.

Harrison, P. L., Babcock, R. C., Bull, G. D., Oliver, J. K., Wallace, C. C., & Willis, B. L. (1984). Mass spawning in tropical reef corals. *Science*, *223*(4641), 1186-1189.

Harvey, B. P., Gwynn-Jones, D., & Moore, P. J. (2013). Meta-analysis reveals complex marine biological responses to the interactive effects of ocean acidification and warming. *Ecology and Evolution*, *3*(4), 1016–1030. https://doi.org/10.1002/ece3.516

Hata, T., Madin, J. S., Cumbo, V. R., Denny, M., Figueiredo, J., Harii, S., Thomas, C. J., & Baird, A. H. (2017). Coral larvae are poor swimmers and require fine-scale reef structure to settle. *Scientific Reports*, *7*(1), 1–9. https://doi.org/10.1038/s41598-017-02402-y

Heywood, V. H., & Watson, R. T. (1995). *Global biodiversity assessment* (Vol. 1140). Cambridge: Cambridge university press.

Hicks, C. C., Cohen, P. J., Graham, N. A. J., Nash, K. L., Allison, E. H., D'Lima, C., Mills, D. J., Roscher, M., Thilsted, S. H., Thorne-Lyman, A. L., & MacNeil, M. A. (2019). Harnessing global fisheries to tackle micronutrient deficiencies. *Nature*, *574*(7776), 95–98. https://doi.org/10.1038/s41586-019-1592-6

Hidas, E. Z., Costa, T. L., Ayre, D. J., and Minchinton, T. E. (2007). Is the species composition of rocky intertidal invertebrates across a biogeographic barrier in south-eastern Australia related to their potential for dispersal?. *Marine and Freshwater Research*, *58*(9), 835-842.

Hillebrand, H. (2004). On the generality of the latitudinal diversity gradient. *American Naturalist*, *163*(2), 192–211. https://doi.org/10.1086/381004

Hobbs, R. J., Arico, S., Aronson, J., Baron, J. S., Bridgewater, P., Cramer, V. A., Epstein, P. R., Ewel, J. J., Klink, C. A., Lugo, A. E., Norton, D., Ojima, D., Richardson, D. M., Sanderson, E. W., Valladares, F., Vilà, M., Zamora, R., & Zobel, M. (2006). Novel ecosystems: Theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography*, *15*(1), 1–7. https://doi.org/10.1111/j.1466-822X.2006.00212.x

Hoeksema, B. W.; Cairns, S. (2020). World List of Scleractinia. Accessed at http://www.marinespecies.org/scleractinia on 2020-07-28

Hoegh-Guldberg, O., & Bruno, J. F. (2010). The impact of climate change on the world's marine ecosystems. *Science*, *328*(5985), 1523–1528. https://doi.org/10.1126/science.1189930

Hortal, J. (2008). Uncertainty and the measurement of terrestrial biodiversity gradients. *Journal of Biogeography*, *35*(8), 1335–1336. https://doi.org/10.1111/j.1365-2699.2008.01955.x

Houlbrèque, F., & Ferrier-Pagès, C. (2009). Heterotrophy in tropical scleractinian corals. *Biological Reviews*, *84*(1), 1–17. https://doi.org/10.1111/j.1469-185X.2008.00058.x

Huang, D. (2012). Threatened reef corals of the world. *PLoS ONE*, *7*(3), 1–12. https://doi.org/10.1371/journal.pone.0034459

Huang, D., Goldberg, E. E., Chou, L. M., & Roy, K. (2018). The origin and evolution of coral species richness in a marine biodiversity hotspot*. *Evolution*, *72*(2), 288–302. https://doi.org/10.1111/evo.13402

Huang, D., Licuanan, W. Y., Baird, A. H., & Fukami, H. (2011). Cleaning up the "Bigmessidae": Molecular phylogeny of scleractinian corals from Faviidae, Merulinidae, Pectiniidae and Trachyphylliidae. *BMC Evolutionary Biology*, *11*(1). https://doi.org/10.1186/1471-2148-11-37

Hubbell, S. P. (2001). The unified neutral theory of biodiversity and biogeography (MPB-32) (Vol. 32). Princeton University Press.

Hughes, A. D., & Grottoli, A. G. (2013). Heterotrophic compensation: A possible mechanism for resilience of coral reefs to global warming or a sign of prolonged stress? *PLoS ONE*, *8*(11), 1–10. https://doi.org/10.1371/journal.pone.0081172

Hughes, T. P., Baird, A. H., Bellwood, D. R., Card, M., Connolly, S. R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J. B. C., Kleypas, J., Lough, J. M., Marshall, P., Nyström, M., Palumbi, S. R., Pandolfi, J. M., Rosen, B., & Roughgarden, J. (2003).

Climate change, human impacts, and the resilience of coral reefs. *Science*, *301*(5635), 929–933. https://doi.org/10.1126/science.1085046

Hughes, T. P., Baird, A. H., Dinsdale, E. A., Moltschaniwskyj, N. A., Pratchett, M. S., Tanner, J. E., & Willis, B. L. (1999). Patterns of recruitment and abundance of corals along the Great Barrier Reef. *Nature*, *397*(6714), 59–63. https://doi.org/10.1038/16237

Hughes, T. P., Baird, A. H., Dinsdale, E. A., Moltschaniwskyj, N. A., Pratchett, M. S., Tanner, J. E., & Willis, B. L. (2000). Supply-side ecology works both ways: The link between benthic adults, fecundity, and larval recruits. *Ecology*, *81*(8), 2241–2249. https://doi.org/10.1890/0012-9658(2000)081[2241:SSEWBW]2.0.CO;2

Hughes, T. P., Bellwood, D. R., Baird, A. H., Brodie, J., Bruno, J. F., & Pandolfi, J. M. (2011). Shifting base-lines, declining coral cover, and the erosion of reef resilience: Comment on Sweatman et al. (2011). *Coral Reefs*, *30*(3), 653–660. https://doi.org/10.1007/s00338-011-0787-6

Hughes, Terence P. (1994). Catastrophes , Phase Shifts, and Large-Scale Degradation of a Caribbean Coral Reef. *Science*, *265*(5178), 1547–1551.

Hughes, Terry P., Anderson, K. D., Connolly, S. R., Heron, S. F., Kerry, J. T., Lough, J. M., Baird, A. H., Baum, J. K., Berumen, M. L., Bridge, T. C., Claar, D. C., Eakin, C. M., Gilmour, J. P., Graham, N. A. J., Harrison, H., Hobbs, J. P. A., Hoey, A. S., Hoogenboom, M., Lowe, R. J., … Wilson, S. K. (2018a). Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science*, *359*(6371), 80–83. https://doi.org/10.1126/science.aan8048

Hughes, Terry P., Barnes, M. L., Bellwood, D. R., Cinner, J. E., Cumming, G. S., Jackson, J. B. C., Kleypas, J., Van De Leemput, I. A., Lough, J. M., Morrison, T. H., Palumbi, S. R., Van Nes, E. H., & Scheffer, M. (2017a). Coral reefs in the Anthropocene. *Nature*, *546*(7656), 82–90. https://doi.org/10.1038/nature22901

Hughes, Terry P., Bellwood, D. R., & Connolly, S. R. (2002). Biodiversity hotspots, centres of endemicity, and the conservation of coral reefs. *Ecology Letters*, *5*(6), 775–784. https://doi.org/10.1046/j.1461-0248.2002.00383.x

Hughes, Terry P., Connolly, S. R., & Keith, S. A. (2013). Geographic ranges of reef corals (Cnidaria: Anthozoa: Scleractinia) in the Indo-Pacific. *Ecology*, *94*(7), 1659. https://doi.org/10.1890/13-0361.1

Hughes, Terry P., Kerry, J. T., Álvarez-Noriega, M., Álvarez-Romero, J. G., Anderson, K. D., Baird, A. H., Babcock, R. C., Beger, M., Bellwood, D. R., Berkelmans, R., Bridge, T. C., Butler, I. R., Byrne, M., Cantin, N. E., Comeau, S., Connolly, S. R., Cumming, G. S., Dalton, S. J., Diaz-Pulido, G., … Wilson, S. K. (2017b). Global warming and recurrent mass bleaching of corals. *Nature*, *543*(7645), 373–377. https://doi.org/10.1038/nature21707

Hughes, Terry P., Kerry, J. T., Baird, A. H., Connolly, S. R., Chase, T. J., Dietzel, A., Hill, T., Hoey, A. S., Hoogenboom, M. O., Jacobson, M., Kerswell, A., Madin, J. S., Mieog, A., Paley, A. S., Pratchett, M. S., Torda, G., & Woods, R. M. (2019). Global warming impairs stock–recruitment dynamics of corals. In *Nature* (Vol. 568, Issue 7752, pp. 387–390). Nature Publishing Group. https://doi.org/10.1038/s41586-019-1081-y

Hughes, Terry P., Kerry, J. T., Baird, A. H., Connolly, S. R., Dietzel, A., Eakin, C. M., Heron, S. F., Hoey, A. S., Hoogenboom, M. O., Liu, G., McWilliam, M. J., Pears, R. J., Pratchett, M. S., Skirving, W. J., Stella, J. S., & Torda, G. (2018b). Global warming transforms coral reef assemblages. *Nature*, *556*(7702), 492–496. https://doi.org/10.1038/s41586-018-0041-2

Hurlbert, A. H., & White, E. P. (2005). Disparity between range map- and survey-based analyses of species richness: Patterns, processes and implications. *Ecology Letters*, *8*(3), 319–327. https://doi.org/10.1111/j.1461-0248.2005.00726.x

Hussey, N. E., Kessel, S. T., Aarestrup, K., Cooke, S. J., Cowley, P. D., Fisk, A. T., Harcourt, R. G., Holland, K. N., Iverson, S. J., Kocik, J. F., Flemming, J. E. M., & Whoriskey, F. G. (2015). Aquatic animal telemetry: A panoramic window into the underwater world. *Science*, *348*(6240), 1255642. https://doi.org/10.1126/science.1255642

IPBES (2019): Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. S. Díaz, J. Settele, E. S. Brondízio E.S., H. T. Ngo, M. Guèze, J. Agard, A. Arneth, P. Balvanera, K. A. Brauman, S. H. M. Butchart, K. M. A. Chan, L. A. Garibaldi, K. Ichii, J. Liu, S. M. Subramanian, G. F. Midgley, P. Miloslavich, Z. Molnár, D. Obura, A. Pfaff, S. Polasky, A. Purvis, J. Razzaque, B. Reyers, R. Roy Chowdhury, Y. J. Shin, I. J. Visseren-Hamakers, K. J. Willis, and C. N. Zayas (eds.). IPBES secretariat, Bonn, Germany. 56 pages.

IPCC, 2018: Summary for Policymakers. In: *Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty* [Masson-Delmotte, V., P. Zhai, H.-O. Pörtner, D. Roberts, J. Skea, P.R. Shukla, A. Pirani, W. Moufouma-Okia, C. Péan, R. Pidcock, S. Connors, J.B.R. Matthews, Y. Chen, X. Zhou, M.I. Gomis, E. Lonnoy, T. Maycock, M. Tignor, and T. Waterfield (eds.)]. In Press.

IPCC, 2019: Summary for Policymakers. In: *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate* [H.-O. Pörtner, D.C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, A. Alegría, M. Nicolai, A. Okem, J. Petzold, B. Rama, N.M. Weyer (eds.)]. In press.

IUCN (2016). The *IUCN Red List of Threatened Species. Version 2016-1*. http://www.iucnredlist.org. Downloaded on <15-07-2017>.

Jablonski, D., Kaustuv, R., Valentine, J., & W. (2006). Out of the Tropics : Evolutionary Diversity Gradient. *Science*, *314*(October), 102–106. https://doi.org/10.1126/science.1130880

Johannesson, K. (1988). The paradox of Rockall: why is a brooding gastropod (Littorina saxatilis) more widespread than one having a planktonic larval dispersal stage (L. littorea)?. *Marine biology*, *99*(4), 507-513

Jokiel, P., & Martinelli, F. J. (1992). The Vortex Model of Coral Reef Biogeography. *Journal of Biogeography*, *19*(4), 449–458. http://www.jstor.com/stable/2845572

Jones, C. G., Lawton, J. H., Shachak, M., & Organisms, M. (1994). Organisms as Ecosystem Engineers. *Oikos*, *69*(3), 373–386.

Jones, K. R., Klein, C. J., Halpern, B. S., Venter, O., Grantham, H., Kuempel, C. D., Shumway, N., Friedlander, A. M., Possingham, H. P., & Watson, J. E. M. (2018). The Location and Protection Status of Earth's Diminishing Marine Wilderness. *Current Biology*, *28*(15), 2506-2512.e3. https://doi.org/10.1016/j.cub.2018.06.010

Jønsson, K. A., Tøttrup, A. P., Borregaard, M. K., Keith, S. A., Rahbek, C., & Thorup, K. (2016). Tracking Animal Dispersal : From Individual Movement to Community Assembly and Global Range Dynamics. *Trends in Ecology & Evolution*, *31*(3), 204–214. https://doi.org/10.1016/j.tree.2016.01.003

Joos, F., & Spahni, R. (2008). Rates of change in natural and anthropogenic radiative forcing over the past 20 ,000 years. *Proceedings of the National Academy of Sciences*, *105*(5), 1425–1430.

Karlson, R. H., & Cornell, H. V. (1998). Scale-dependent variation in local vs. regional effects on coral species richness. *Ecological Monographs*, *68*(2), 259–274. https://doi.org/10.1890/0012-9615(1998)068[0259:SDVILV]2.0.CO;2

Kays, R., Crofoot, M. C., Jetz, W., & Wikelski, M. (2015). Terrestrial animal tracking as an eye on life and planet. *Science*, *348*(6240), aaa2478. https://doi.org/10.1126/science.aaa2478

Keith, S A, Baird, A. H., Hughes, T. P., Madin, J. S., & Connolly, S. R. (2013). Faunal breaks and species composition of Indo-Pacific corals: the role of plate tectonics, environment and habitat distribution. *Proceedings. Biological Sciences*, *280*(1763), 20130818. https://doi.org/10.1098/rspb.2013.0818

Keith, Sally A., Baird, A. H., Hobbs, J. P. A., Woolsey, E. S., Hoey, A. S., Fadli, N., & Sanders, N. J. (2018). Synchronous behavioural shifts in reef fishes linked to mass coral bleaching. *Nature Climate Change*, *8*(11), 986–991. https://doi.org/10.1038/s41558-018-0314-7

Keith, Sally A., Newton, A. C., Morecroft, M. D., Bealey, C. E., & Bullock, J. M. (2009). Taxonomic homogenization of woodland plant communities over 70 years. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1672), 3539–3544. https://doi.org/10.1098/rspb.2009.0938

Keith, Sally A., Newton, A. C., Morecroft, M. D., Golicher, D. J., & Bullock, J. M. (2011). Plant metacommunity structure remains unchanged during biodiversity loss in English woodlands. *Oikos*, *120*(2), 302–310. https://doi.org/10.1111/j.1600-0706.2010.18775.x

Keith, Sally A., Woolsey, E. S., Madin, J. S., Byrne, M., & Baird, A. H. (2015). Differential establishment potential of species predicts a shift in coral assemblage structure across a biogeographic barrier. *Ecography*, *38*(12), 1225–1234. https://doi.org/10.1111/ecog.01437

Kerr, A. M., Baird, A. H., & Hughes, T. P. (2011). Correlated evolution of sex and reproductive mode in corals (Anthozoa: Scleractinia). *Proceedings of the Royal Society B: Biological Sciences*, *278*(1702), 75–81. https://doi.org/10.1098/rspb.2010.1196

Kinlan, B. P., & Gaines, S. D. (2003). Propagule dispersal in marine and terrestrial environments: A community perspective. *Ecology*, *84*(8), 2007–2020. https://doi.org/10.1890/01-0622

Kiørboe, T., Visser, A., Andersen, K. H., & Browman, H. (2018). A trait-based approach to ocean ecology. *ICES Journal of Marine Science*, *75*(6), 1849–1863. https://doi.org/10.1093/icesjms/fsy090

Kleypas, J. A., McManu, J. W., & Mene, L. A. B. (1999). Environmental limits to coral reef development: Where do we draw the line? *American Zoologist*, *39*(1), 146–159. https://doi.org/10.1093/icb/39.1.146

Knowlton, N. (2001). The future of coral reefs. *Proceedings of the National Academy of Sciences*, *98*(10), 5419–5425. https://doi.org/10.1126/science.334.6062.1494-b

Koleff, P., Gaston, K. J., Lennon, J. J., Journal, S., May, N., Koleff, P., Gaston, K. J., & Lennont, J. J. (2003). Measuring Beta Diversity for Presence-Absence Data. *Journal of*

Animal Ecology, *72*(3), 367–382.

Korell, L., Auge, H., Chase, J. M., Harpole, S., & Knight, T. M. (2020). We need more realistic climate change experiments for understanding ecosystems of the future. *Global Change Biology*, *26*(2), 325–327. https://doi.org/10.1111/gcb.14797

Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2015). *Community assembly , coexistence and the environmental fi ltering metaphor*. 592–599. https://doi.org/10.1111/1365-2435.12345

Lawton, J. H. (1999). *Are There General Laws in Ecology ? Author (s): John H . Lawton Published by : Wiley on behalf of Nordic Society Oikos Stable URL : http://www.jstor.com/stable/3546712 Are there general laws in ecology ? 84*(2), 177–192.

Le Corre, V., Machon, N., Petit, R. J., & Kremer, A. (1997). Colonization with long-distance seed dispersal and genetic structure of maternally inherited genes in forest trees: A simulation study. *Genetical Research*, *69*(2), 117–125. https://doi.org/10.1017/S0016672397002668

Legendre, P., & Legendre, L. F. (2012). *Numerical ecology*. Elsevier.

Leprieur, F., Descombes, P., Gaboriau, T., Cowman, P. F., Parravicini, V., Kulbicki, M., Melian, C. J., De Santana, C. N., Heine, C., Mouillot, D., Bellwood, D. R., & Pellissier, L. (2016). Plate tectonics drive tropical reef biodiversity dynamics. *Nature Communications*, *7*(May), 1–8. https://doi.org/10.1038/ncomms11461

Lester, S. E., Ruttenberg, B. I., Gaines, S. D., & Kinlan, B. P. (2007). The relationship between dispersal ability and geographic range size. *Ecology Letters*, *10*(8), 745–758. https://doi.org/10.1111/j.1461-0248.2007.01070.x

Levin, S. A. (1992). The problem of pattern and scale in ecology. *Ecology*, *73*(6), 1943–1967.

Lewis, S. L., & Maslin, M. A. (2015). Defining the Anthropocene. *Nature*, *519*(7542), 171–180. https://doi.org/10.1038/nature14258

Lindegren, M., Holt, B. G., Mackenzie, B. R., & Rahbek, C. (2018). A global mismatch in the protection of multiple marine biodiversity components and ecosystem services. *Scientific Reports*, *8*. https://doi.org/10.1038/s41598-018-22419-1

Litchman, E., Ohman, M. D., & Kiørboe, T. (2013). Trait-based approaches to zooplankton communities. *Journal of Plankton Research*, *35*(3), 473–484. https://doi.org/10.1093/plankt/fbt019

Liston, P. W. (1990). *Spatial variability and covariability of chlorophyll and zooplankton on the Great Barrier Reef* (Doctoral dissertation, James Cook University).Lockwood, J. L., Cassey, P., & Blackburn, T. (2005). The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution*, *20*(5). https://doi.org/10.1016/j.tree.2005.02.004

Lomolino, M. V. (1990). The Target Area Hypothesis : The Influence of Island Area on Immigration Rates of Non-Volant Mammals. *Oikos*, *57*(3), 297–300. http://www.jstor.com/stable/3565957%0AREFERENCES

Lomolino, M. V. (1996). Investigating causality of nestedness of insular communites: selective immigrations or extinctions? *Journal of Biogeography*, *23*, 699–703.

Lomolino, M. V., B. R. Riddle, and James H. Brown. (2006). Biogeography, 3rd Edition. Sinauer Associates

Lotze, H. K., Tittensor, D. P., Bryndum-Buchholz, A., Eddy, T. D., Cheung, W. W. L., Galbraith, E. D., Barange, M., Barrier, N., Bianchi, D., Blanchard, J. L., Bopp, L., Büchner, M., Bulman, C. M., Carozza, D. A., Christensen, V., Coll, M., Dunne, J. P., Fulton, E. A., Jennings, S., … Worm, B. (2019). Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(26), 12907–12912. https://doi.org/10.1073/pnas.1900194116

Loya, Y. (1976). Effects of Water Turbidity and Sedimentation. *Bulletin of Marine Science, 26*(4), 450–466.

Loya, Y., Sakai, K., Yamazato, K., Nakano, Y., Sambali, H., & Van Woesik, R. (2001). Coral bleaching: The winners and the losers. *Ecology Letters*, *4*(2), 122–131. https://doi.org/10.1046/j.1461-0248.2001.00203.x

Lu, M., Vasseur, D., & Jetz, W. (2019). Beta diversity patterns derived from island biogeography theory. *American Naturalist*, *194*(3), E52–E65. https://doi.org/10.1086/704181

Luiz, O. J., Allen, A. P., Robertson, D. R., Floeter, S. R., Kulbicki, M., Vigliola, L., Becheler, R., & Madin, J. S. (2013). Adult and larval traits as determinants of geographic range size among tropical reef fishes. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(41), 16498–16502. https://doi.org/10.1073/pnas.1304074110

MacArthur, R. H., & Wilson, E. O. (2001). *The theory of island biogeography* (Vol. 1). Princeton university press.

MacKenzie, D. I. (2005). What are the issues with presence-absence data for wildlife managers?. *The Journal of Wildlife Management*, *69*(3), 849-860.Madin, J. S., Anderson, K. D., Andreasen, M. H., Bridge, T. C. L., Cairns, S. D., Connolly, S. R., Darling, E. S., Diaz, M., Falster, D. S., Franklin, E. C., Gates, R. D., Hoogenboom, M. O., Huang, D., Keith, S. A., Kosnik, M. A., Kuo, C.-Y., Lough, J. M., Lovelock, C. E., Luiz, O., … Baird, A. H. (2016). The Coral Trait Database, a curated database of trait information for coral species from the global oceans. *Scientific Data*, *3*, 160017. https://doi.org/10.1038/sdata.2016.17

Madin, J. S., Baird, A. H., Dornelas, M., & Connolly, S. R. (2014). Mechanical vulnerability explains size-dependent mortality of reef corals. *Ecology Letters*, *17*(8), 1008–1015. https://doi.org/10.1111/ele.12306

Madin, J. S., Hoogenboom, M. O., Connolly, S. R., Darling, E. S., Falster, D. S., Huang, D., Keith, S. A., Mizerek, T., Pandolfi, J. M., Putnam, H. M., & Baird, A. H. (2016). A Trait-Based Approach to Advance Coral Reef Science. *Trends in Ecology and Evolution*, *31*(6), 419–428. https://doi.org/10.1016/j.tree.2016.02.012

Magurran, A. E., Dornelas, M., Moyes, F., & Henderson, P. A. (2019). Temporal β diversity — A macroecological perspective. *Global Ecology and Biogeography*, *28*, 1949–1960. https://doi.org/10.1111/geb.13026

Marske, K. A., Leschen, R. A. B., & Buckley, T. R. (2011). Reconciling phylogeography and ecological niche models for New Zealand beetles: Looking beyond glacial refugia. *Molecular Phylogenetics and Evolution*, *59*(1), 89–102. https://doi.org/10.1016/j.ympev.2011.01.005

Martiny, J. B. H., Eisen, J. A., Penn, K., Allison, S. D., & Horner-Devine, M. C. (2011). Drivers of bacterial β-diversity depend on spatial scale. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(19), 7850–7854. https://doi.org/10.1073/pnas.1016308108

McCook, L. J., Jompa, J., & Diaz-Pulido, G. (2001). Competition between corals and algae on coral reefs: A review of evidence and mechanisms. *Coral Reefs*, *19*(4), 400–417. https://doi.org/10.1007/s003380000129

McGill, B. J. (2003). A test of the unified neutral theory of biodiversity. *Nature*, *422*(6934), 881–885. https://doi.org/10.1038/nature01583

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, *21*(4), 178–185. https://doi.org/10.1016/j.tree.2006.02.002

Mckinney, M. L., & Lockwood, J. L. (1999). Taxonomic and ecological enhancement of homogenization. *Tree*, *5347*(Table 1), 450–453. https://doi.org/10.1016/S0169-5347(99)01679-1

McManus, J. W., Nanola, C. L., Reyes, R. B., Kesner, K. N., & Mcmanus, J. W. (1997). Resource Ecology of the Bolinao Coral Reef System\rEffects of some destructive fishing methods on coral cover and potential rates of recovery. *Environmental Management*, *21*(1), 69–78. http://download.springer.com/static/pdf/276/art%253A10.1007%252Fs002679900006.pdf?originUrl=http%3A%2F%2Flink.springer.com%2Farticle%2F10.1007%2Fs002679900006&token2=exp=1491219173~acl=%2Fstatic%2Fpdf%2F276%2Fart%25253A10.1007%25252Fs002679900006.pdf%3For

McWilliam, M., Hoogenboom, M. O., Baird, A. H., Kuo, C. Y., Madin, J. S., & Hughes, T. P. (2018). Biogeographical disparity in the functional diversity and redundancy of corals. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(12), 3084–3089. https://doi.org/10.1073/pnas.1716643115

Millennium Ecosystem Assessment (2005). *Ecosystems and human well-being* (Vol. 5). United States of America: Island press.

Miraldo, A., Li, S., Borregaard, M. K., Florez-Rodriguez, A., Gopalakrishnan, S., Rizvanovic, M., Wang, Z., Rahbek, C., Marske, K. A., & Nogues-Bravo, D. (2016). Genetic diversity. *Science*, *353*(6307), 1532–1535. https://doi.org/10.1017/cbo9780511809002.006

Mittelbach, G. G., Schemske, D. W., Cornell, H. V., Allen, A. P., Brown, J. M., Bush, M. B., Harrison, S. P., Hurlbert, A. H., Knowlton, N., Lessios, H. A., McCain, C. M., McCune, A. R., McDade, L. A., McPeek, M. A., Near, T. J., Price, T. D., Ricklefs, R. E., Roy, K., Sax, D. F., … Turelli, M. (2007). Evolution and the latitudinal diversity gradient: Speciation, extinction and biogeography. *Ecology Letters*, *10*(4), 315–331. https://doi.org/10.1111/j.1461-0248.2007.01020.x

Mora, C., Treml, E. A., Roberts, J., Crosby, K., Roy, D., & Tittensor, D. P. (2012). High connectivity among habitats precludes the relationship between dispersal and range size in tropical reef fishes. *Ecography*, *35*(1), 89–96. https://doi.org/10.1111/j.1600-0587.2011.06874.x

Murray, K. A., & Baselga, A. (2015). Reply to Chen and Schmera : Partitioning beta diversity into replacement and nestedness- resultant components is not controversial. *Proceedings of the National Academy of Sciences*, *112*(52). https://doi.org/10.1073/pnas.1522279113

Muscatine, L., & Porter, J. W. (1977). Reef Corals: Mutualistic Symbioses Adapted to Nutrient-Poor Environments. *BioScience*, *27*(7), 454–460. https://doi.org/10.2307/1297526

Muscatine, L., R. McCloskey, L., & E. Marian, R. (1981). Estimating the daily contribution of carbon from zooxanthellae to coral animal respiration. *Limnology and Oceanography*, *26*(4), 601–611. https://doi.org/10.4319/lo.1981.26.4.0601

Nekola, J. C., & Mcgill, B. J. (2014). Scale dependency in the functional form of the distance decay relationship. *Ecography*, *37*(4), 309–320. https://doi.org/10.1111/j.1600-0587.2013.00407.x

Nekola, J. C., & White, P. S. (1999). The distance decay of similarity in biogeography and ecology. *Journal of Biogeography*, *26*(4), 867–878. https://doi.org/10.1046/j.1365-2699.1999.00305.x

Nelson, A. (2001). Analysing data across geographic scales in Honduras: detecting levels of organisation within systems. *Agriculture, ecosystems & environment*, *85*(1-3), 107-131.

Odum, E. P., & Barrett, G. W. (1971). *Fundamentals of ecology* (Vol. 3, p. 5). Philadelphia: Saunders.

Palumbi, S. R. (1997). Molecular biogeography of the Pacific. *Coral Reefs*, *16*(SUPPL. 1), 47–52. https://doi.org/10.1007/s003380050241

Paulay, G. (1990). Effects of Late Cenozoic Sea-Level Fluctuations on the Bivalve Faunas of Tropical Oceanic Islands Author (s): Gustav Paulay Published by : Cambridge University Press Stable URL : https://www.jstor.org/stable/2400967 bivalve faunas of tropical oceanic is. *Paleobiology*, *16*(4), 415–434.

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I. C., Clark, T. D., Colwell, R. K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R. A., Griffis, R. B., Hobday, A. J., Janion-Scheepers, C., Jarzyna, M. A., Jennings, S., … Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, *355*(6332). https://doi.org/10.1126/science.aai9214

Podani, J., & Schmera, D. (2012). A comparative evaluation of pairwise nestedness measures. *Ecography*, *35*(10), 889–900. https://doi.org/10.1111/j.1600-0587.2011.07319.x

Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., Brander, K., Bruno, J. F., Buckley, L. B., Burrows, M. T., Duarte, C. M., Halpern, B. S., Holding, J., Kappel, C. V., O'Connor, M. I., Pandolfi, J. M., Parmesan, C., Schwing, F., Thompson, S. A., & Richardson, A. J. (2013). Global imprint of climate change on marine life. *Nature Climate Change*, *3*(10), 919–925. https://doi.org/10.1038/nclimate1958

Precoda, K., Hardt, M. J., Baird, A. H., & Madin, J. S. (2020). Tissue biomass trades off with growth but not reproduction in corals. *Coral Reefs*, *39*(4), 1027–1037. https://doi.org/10.1007/s00338-020-01925-7

Pulliam, H. R. (2000). On the relationship between niche and distribution. *Ecology Letters*, *3*(4), 349–361. https://doi.org/10.1046/j.1461-0248.2000.00143.x

Qian, H. (2009). Beta diversity in relation to dispersal ability for vascular plants in North America. *Global Ecology and Biogeography*, *18*(3), 327–332. https://doi.org/10.1111/j.1466-8238.2009.00450.x

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rahbek, C. (2005). The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters*, *8*(2), 224–239. https://doi.org/10.1111/j.1461-0248.2004.00701.x

Rasher, D. B., Stout, E. P., Engel, S., Kubanek, J., & Hay, M. E. (2011). Macroalgal terpenes function as allelopathic agents against reef corals. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(43), 17726–17731. https://doi.org/10.1073/pnas.1108628108

Reaka-Kudla, M. L. (1997). The global biodiversity of coral reefs: a comparison with rain forests. *Biodiversity II: Understanding and protecting our biological resources*, *2*, 551.

Renema, W., Bellwood, D. R., Braga, J. C., Bromfield, K., Hall, R., Johnson, K. G., Lunt, P., Meyer, C. P., McMonagle, L. B., Morley, R. J., O'Dea, A., Todd, J. A., Wesselingh, F. P., Wilson, M. E. J., & Pandolfi, J. M. (2008). Hopping hotspots: Global shifts in marine biodiversity. *Science*, *321*(5889), 654–657. https://doi.org/10.1126/science.1155674

Rex, M. A. (1973). Deep-Sea Species Diversity: Decreased Gastropod Diversity at Abyssal Depths. *Science*, *181*, 1051–1053.

Riginos, C., Buckley, Y. M., Blomberg, S. P., & Treml, E. A. (2014). Dispersal Capacity Predicts Both Population Genetic Structure and Species Richness in Reef Fishes. *The American Naturalist*, *184*(1). http://dx.doi.org/10.5061/dryad.522cm.

Roberts, C. M., McClean, C. J., Veron, J. E. N., Hawkins, J. P., Allen, G. R., McAllister, D. E., Mittermeier, C. G., Schueler, F. W., Spalding, M., Wells, F., Vynne, C., & Werner, T. B. (2002). Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science*, *295*(5558), 1280–1284. https://doi.org/10.1126/science.1067728

Robinson, J. P. W., Wilson, S. K., & Graham, N. A. J. (2019). Abiotic and biotic controls on coral recovery 16 years after mass bleaching. *Coral Reefs*, *38*(6), 1255–1265. https://doi.org/10.1007/s00338-019-01831-7

Rockström, J., Steffen, W., Noone, K., Persson, Å., Chapin, F. S., Lambin, E., Lenton, T. M., Scheffer, M., Folke, C., Schellnhuber, H. J., Nykvist, B., de Wit, C. A., Hughes, T., van der Leeuw, S., Rodhe, H., Sörlin, S., Snyder, P. K., Costanza, R., Svedin, U., … Foley, J. (2009). Planetary boundaries: Exploring the safe operating space for humanity. *Ecology and Society*, *14*(2). https://doi.org/10.5751/ES-03180-140232

Rosenzweig, M. L. (1995). *Species diversity in space and time*. Cambridge University Press.

Roy, K., & Goldberg, E. E. (2007). Origination, extinction, and dispersal: Integrative models for understanding present-day diversity gradients. *American Naturalist*, *170*(SUPPL.). https://doi.org/10.1086/519403

Sanderson, E. W., Jaiteh, M., Levy, M. A., Redford, K. H., Wannebo, A. V, & Woolmer, G. (2002). The Human Footprint and the Last of the Wild. *BioScience*, *52*(10), 891–904.

Saura, S., Bodin, Ö., & Fortin, M. J. (2014). Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. *Journal of Applied Ecology*, *51*(1), 171–182. https://doi.org/10.1111/1365-2664.12179

Sbrocco, E. J., & Barber, P. H. (2013). MARSPEC: ocean climate layers for marine spatial ecology. *Ecology*, *94*(4), 979–979. https://doi.org/10.1890/12-1358.1

Scheiner, S. M., Cox, S. B., Willig, M., Mittelbach, G. G., Osenberg, C., & Kaspari, M. (2000). *Species richness , species – area curves and Simpson ' s paradox*. 791–802.

Schmera, D., & Podani, J. (2011). Comments on separating components of beta diversity. *Community Ecology*, *12*(2), 153–160. https://doi.org/10.1556/ComEc.12.2011.2.2

Shimadzu, H., Dornelas, M., & Magurran, A. E. (2015). Measuring temporal turnover in ecological communities. *Methods in Ecology and Evolution*, *6*(12), 1384–1394. https://doi.org/10.1111/2041-210X.12438

Sheppard, C. R. C. (1988). Similar trends, different causes: Responses of corals to stressed environments in Arabian Seas. *Proceedings of the 6th International Coral Reef Symposium* **3**:297 – 302.

Sheppard, C., Davy, S., Pilling, G., & Graham, N. (2017). *The biology of coral reefs*. Oxford University Press.

Shmida, A., & Wilson, M. V. (1985). Biological Determinants of Species Diversity. *Journal of Biogeography*, *12*, 1–20.

Siebeck, O. (1988). Experimental investigation of UV tolerance in hermatypic corals (Scleractinia). *Marine Ecology Progress Series*, *43*, 95–103. https://doi.org/10.3354/meps043095

Simpson, G. G. (1943). Mammals and the nature of continents. *American Journal of Science*, *241*(1), 1-31.

Smith, L., & Hughes, T. P. (1999). Experimental assessment of coral fragments. *Journal of Experimental Marine Biology and Ecology*, *235*, 147–164.

Socolar, J. B., Gilroy, J. J., Kunin, W. E., & Edwards, D. P. (2016). How Should Beta-Diversity Inform Biodiversity Conservation? *Trends in Ecology and Evolution*, *31*(1), 67–80. https://doi.org/10.1016/j.tree.2015.11.005

Soininen, J., Heino, J., & Wang, J. (2018). A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. *Global Ecology and Biogeography*, *27*(1), 96–109. https://doi.org/10.1111/geb.12660

Soininen, J., McDonald, R., & Hillebrand, H. (2007). The distance decay of similarity in ecological communities. *Ecography*, *30*(1), 3–12. https://doi.org/10.1111/j.0906-7590.2007.04817.x

Sommer, B., Beger, M., Harrison, P. L., Babcock, R. C., & Pandolfi, J. M. (2018). Differential response to abiotic stress controls species distributions at biogeographic transition zones. *Ecography*, *41*(3), 478–490. https://doi.org/10.1111/ecog.02986

Spalding, M. D., & Grenfell, A. M. (1997). New estimates of global and regional coral reef areas. *Coral Reefs*, *16*(4), 225–230. https://doi.org/10.1007/s003380050078

Stanley, G. D. (2003). The evolution of modern corals and their early history. *Earth-Science Reviews*, *60*, 195–225.

Stanley Harpole, W., & Tilman, D. (2006). Non-neutral patterns of species abundance in grassland communities. *Ecology Letters*, *9*(1), 15–23. https://doi.org/10.1111/j.1461-0248.2005.00836.x

Stuart-Smith, R. D., Bates, A. E., Lefcheck, J. S., Duffy, J. E., Baker, S. C., Thomson, R. J., Stuart-Smith, J. F., Hill, N. A., Kininmonth, S. J., Airoldi, L., Becerro, M. A., Campbell, S. J., Dawson, T. P., Navarrete, S. A., Soler, G. A., Strain, E. M. A., Willis, T. J., & Edgar, G. J. (2013). Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature*, *501*(7468), 539–542. https://doi.org/10.1038/nature12529

Stebbins, G. L. (2013). *Flowering plants: evolution above the species level*. Harvard University Press.

Sutherland, W. J., Freckleton, R. P., Godfray, H. C. J., Beissinger, S. R., Benton, T., Cameron, D. D., Carmel, Y., Coomes, D. A., Coulson, T., Emmerson, M. C., Hails, R. S., Hays, G. C., Hodgson, D. J., Hutchings, M. J., Johnson, D., Jones, J. P. G., Keeling, M. J., Kokko, H., Kunin, W. E., … Wiegand, T. (2013). Identification of 100 fundamental ecological questions. *Journal of Ecology*, *101*(1), 58–67. https://doi.org/10.1111/1365-2745.12025

Svenning, J. C., Fløjgaard, C., & Baselga, A. (2011). Climate, history and neutrality as drivers of mammal beta diversity in Europe: Insights from multiscale deconstruction. *Journal of Animal Ecology*, *80*(2), 393–402. https://doi.org/10.1111/j.1365-2656.2010.01771.x

Svenning, J. C., & Skov, F. (2007). Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? *Ecology Letters*, *10*(6), 453–460. https://doi.org/10.1111/j.1461-0248.2007.01038.x

Sweatman, H. (2008). No-take reserves protect coral reefs from predatory starfish. *Current Biology*, *18*(14), 598–599. https://doi.org/10.1016/j.cub.2008.05.033

Sørensen, T. (1948). "A method of establishing groups of equal amplitude in plant sociology based on similarity of species and its application to analyses of the vegetation on Danish commons". *Kongelige Danske Videnskabernes Selskab*. **5** (4): 1–34.

Tamir, R., Eyal, G., Kramer, N., Laverick, J. H., & Loya, Y. (2019). Light environment drives the shallow-to-mesophotic coral community transition. *Ecosphere*, *10*(9). https://doi.org/10.1002/ecs2.2839

Tardent, P. (1995). The cnidarian cnidocyte, a high-tech cellular weaponry. *BioEssays*, *17*(4), 351–362.

Thompson, R., & Townsend, C. (2006). A truce with neutral theory: Local deterministic factors, species traits and dispersal limitation together determine patterns of diversity in stream invertebrates. *Journal of Animal Ecology*, *75*(2), 476–484. https://doi.org/10.1111/j.1365-2656.2006.01068.x

Thorson, G. (1950). Reproductive and larval ecology of marine bottom invertebrates. *Biological reviews*, *25*(1), 1-45.

Thresher, R. E. (1991). Geographic Variability in the Ecology of Coral Reef Fishes: Evidence, Evolution, and Possible Implications. In *The Ecology of Fishes on Coral Reefs*. ACADEMIC PRESS, INC. https://doi.org/10.1016/b978-0-08-092551-6.50020-9

Tisseuil, C., Leprieur, F., Grenouillet, G., Vrac, M., & Lek, S. (2012). Projected impacts of climate change on spatio-temporal patterns of freshwater fish beta diversity: A deconstructing approach. *Global Ecology and Biogeography*, *21*(12), 1213–1222. https://doi.org/10.1111/j.1466-8238.2012.00773.x

Tittensor, D. P., Mora, C., Jetz, W., Lotze, H. K., Ricard, D., Berghe, E. Vanden, & Worm, B. (2010). Global patterns and predictors of marine biodiversity across taxa. *Nature*, *466*(7310), 1098–1101. https://doi.org/10.1038/nature09329

Treml, E. A., & Halpin, P. N. (2012). Marine population connectivity identifies ecological neighbors for conservation planning in the Coral Triangle. *Conservation Letters*, *5*(6), 441–449. https://doi.org/10.1111/j.1755-263X.2012.00260.x

Treml, E. A., Halpin, P. N., Urban, D. L., & Pratson, Æ. L. F. (2008). Modeling population connectivity by ocean currents , a graph-theoretic approach for marine conservation. *Landscape Ecology*, *23*, 19–36. https://doi.org/10.1007/s10980-007-9138-y

Tucker, M. A., Böhning-gaese, K., Fagan, W. F., Fryxell, J. M., Moorter, B. Van, Alberts, S. C., Ali, A. H., Allen, A. M., Attias, N., Avgar, T., Bartlam-brooks, H., Bayarbaatar, B., Belant, J. L., Bertassoni, A., Beyer, D., Bidner, L., Beest, F. M. Van, Blake, S., Blaum, N., … Rimmler, M. (2018). Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*, *469*(January), 466–469.

Tuomisto, H. (2010). A diversity of beta diversities : straightening up a concept gone awry . Part 1 . Defining beta diversity as a function of alpha and gamma diversity. *Ecography*, *33*, 2–22. https://doi.org/10.1111/j.1600-0587.2009.05880.x

Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F., & De Clerck, O. (2012). Bio-ORACLE: A global environmental dataset for marine species distribution modelling. *Global Ecology and Biogeography*, *21*(2), 272–281. https://doi.org/10.1111/j.1466-8238.2011.00656.x

Ulrich, W., Almeida-Neto, M., & Gotelli, N. J. (2009). A consumer's guide to nestedness analysis. *Oikos*, *118*(1), 3–17. https://doi.org/10.1111/j.1600-0706.2008.17053.x

Underwood, J. N., Smith, L. D., Oppen, M. J. H. Van, Gilmour, J. P., Applications, S. E., Jan, N., & Jim, N. (2009). Ecologically Relevant Dispersal of Corals on Isolated Reefs : Implications for Managing Resilience Published by : Ecological Society of America Ecologically relevant dispersal of corals on isolated reefs : for resilience implications managing. *Ecological Applications*, *19*(1), 18–29. http://dx.doi.org/10.1890/07-1461.1

UNEP (2002). Convention on Biological Diversity. *Conference of the Parties to the Convention on Biological Diversity: Sixth Meeting*

UNFCCC (2015) Adoption of the Paris Agreement. *Conference of the Parties on its twenty-first session*

Van Woesik, R., & Done, T. J. (1997). Coral communities and reef growth in the southern Great Barrier Reef. *Coral Reefs*, *16*(2), 103–115. https://doi.org/10.1007/s003380050064

Vellend, M. (2001). Do commonly used indices of β -diversity measure species turnover ? *Journal of Vegetation Science*, *12*, 545–552.

Vellend, M. (2010). Conceptual synthesis in community ecology. *Quarterly Review of Biology*, *85*(2), 183–206. https://doi.org/10.1086/652373

Vergés, A., Steinberg, P. D., Hay, M. E., Poore, A. G. B., Campbell, A. H., Ballesteros, E., Heck, K. L., Booth, D. J., Coleman, M. A., Feary, D. A., Figueira, W., Langlois, T., Marzinelli, E. M., Mizerek, T., Mumby, P. J., Nakamura, Y., Roughan, M., van Sebille, E., Gupta, A. Sen, … Wilson, S. K. (2014). The tropicalization of temperate marine ecosystems: Climate-mediated changes in herbivory and community phase shifts. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1789). https://doi.org/10.1098/rspb.2014.0846

Veron J. E. N., (1995). Corals in Space & Time. The Biogeography & Evolution of the Scleractinia. Cornell University Press

Veron, J. E. N., Devantier, L. M., Turak, E., Green, A. L., Kininmonth, S., Stafford-Smith, M., & Paterson, N. (2009). Delineating the Coral Triangle. *Galaxea, Journal of Coral Reef Studies*, *11*, 91–100.

Veron, J., Stafford-Smith, M., DeVantier, L., & Turak, E. (2015). Overview of distribution patterns of zooxanthellate Scleractinia. *Frontiers in Marine Science*, *2*(FEB), 1–19. https://doi.org/10.3389/fmars.2014.00081

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, *116*(5), 882–892. https://doi.org/10.1111/j.2007.0030-1299.15559.x

Von Humboldt, A. (1849). *Aspects of Nature, in Different Lands and Different Climates: With Scientific Elucidations. in 2 Vols*. Lea and Blanchard.

Vitousek, P. M., Ehrlich, P. R., Ehrlich, A. H., & Matson, P. A. (1986). Human Appropriation of the Products of Photosynthesis. *BioScience*, *36*(6), 368–373.

Wallace, A. R. (1869). *The Malay Archipelago: The Land of the Orangutan and the Bird of Paradise*. New York: Harper

Walther, G. R., Berger, S., & Sykes, M. T. (2005). An ecological “footprint” of climate change. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1571), 1427–1432. https://doi.org/10.1098/rspb.2005.3119

Wen, Z., Yang, Q., Quan, Q., Xia, L., Ge, D., & Lv, X. (2016). Multiscale partitioning of small mammal β-diversity provides novel insights into the Quaternary faunal history of Qinghai–Tibetan Plateau and Hengduan Mountains. *Journal of Biogeography*, *43*(7), 1412–1424. https://doi.org/10.1111/jbi.12706

Wetzel, C. E., de Bicudo, D. C., Ector, L., Lobo, E. A., Soininen, J., Landeiro, V. L., & Bini, L. M. (2012). Distance Decay of Similarity in Neotropical Diatom Communities. *PLoS ONE*, *7*(9), 10–11. https://doi.org/10.1371/journal.pone.0045071

Whittaker, R. H. (1960). Vegetation of the Siskiyou Mountains , Oregon and California Author (s): R . H . Whittaker Published by : Wiley on behalf of the Ecological Society of America Stable URL : https://www.jstor.org/stable/1943563 Ecological Society of America , Wiley are co. *Ecological Monographs*, *30*(3), 279–338.

Whittaker, R. J., Araújo, M. B., Jepson, P., Ladle, R. J., Watson, J. E. M., & Willis, K. J. (2005). Conservation biogeography: assessment and prospect. *Diversity and Distributions*, *11*(1), 3–23. https://doi.org/10.1111/j.1366-9516.2005.00143.x

Wiens, J. A. (1989). Spatial Scaling in Ecology Published by : British Ecological Society Stable URL : https://www.jstor.org/stable/2389612 Spatial scaling in ecology1. *Functional Ecology*, *3*(4), 385–397.

Wilcove, D. S. (1987). From fragmentation to extinction. *Natural Areas Journal*, 23-29.

Wilkinson, C. (2000). *Status of coral reefs of the world: 2000.* Australian Institute of Marine Science: Townsville. ISBN 0-642-32209-0. 363 pp

Willi, Y., Van Buskirk, J., & Hoffmann, A. A. (2006). Limits to the adaptive potential of small populations. *Annual Review of Ecology, Evolution, and Systematics*, *37*, 433–458. https://doi.org/10.1146/annurev.ecolsys.37.091305.110145

Willig, M. R., Kaufman, D. M., & Stevens, R. D. (2003). Latitudinal Gradients of Biodiversity: Pattern, Process, Scale, and Synthesis. *Annual Review of Ecology, Evolution, and Systematics*, *34*(1), 273–309. https://doi.org/10.1146/annurev.ecolsys.34.012103.144032

Wilson, J. R. U., Dormontt, E. E., Prentis, P. J., Lowe, A. J., & Richardson, D. M. (2009). Something in the way you move: dispersal pathways affect invasion success. *Trends in Ecology and Evolution*, *24*(3), 136–144. https://doi.org/10.1016/j.tree.2008.10.007

Wood, S., Paris, C. B., Ridgwell, A., & Hendy, E. J. (2014). Modelling dispersal and connectivity of broadcast spawning corals at the global scale. *Global Ecology and Biogeography*, *23*(1), 1–11. https://doi.org/10.1111/geb.12101

Zawada, K. J. A., Madin, J. S., Baird, A. H., Bridge, T. C. L., & Dornelas, M. (2019). Morphological traits can track coral reef responses to the Anthropocene. *Functional Ecology*, *33*(6), 962–975. https://doi.org/10.1111/1365-2435.13358