

Quantifying multi-taxon functional change on tropicalising reefs for conservation.

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The candidate confirms that the work submitted is their own, except where work which has formed part of jointly authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

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Abstract

Coral reef ecosystems are undergoing community reassembly due to climate-induced range shifts, thermal stress events and localised disturbances such as coastal development, threatening reefs worldwide. The ecological processes that drive species and community shifts, and the functioning of resultant ecosystems is poorly understood, presenting a challenge for climate-resilient conservation management strategies. Here, I take a functional trait-based approach to understand and quantify functional change on Japanese coral reef ecosystems to inform conservation plans.

Urban reefs experience elevated levels of anthropogenic stressors, resulting in turbid, marginal conditions. It is unclear how urban reef ecosystems are structured at the community and functional level, and how they will respond to future disturbance events. Chapter two of this thesis quantifies how the functioning of a tropical urbanised reef has changed between 1975 and 2018 in Nakagusuku Bay, Okinawa, Japan. I identified widespread reef fish and coral genera community turnover, but functional space was maintained, suggesting the communities had retained ecosystem function.

Japan's coastal marine ecosystems form a tropical to temperate transition zone, where many high latitude reefs have undergone tropicalisation, with phase shifts from temperate to tropical species. Determining the winners and losers under further environmental change, and how to incorporate this into management is a key conservation priority. In Chapters three-five, I address this by classifying species into trait-based groups to understand and manage functioning. Chapter three explores how fish functional groups represent the within-group species. Species were found to have similar environmental drivers to that of their respective functional group, suggesting traits determine how species respond to the environment.

It is important to consider multiple taxa to understand how range shifts will affect the functioning of the whole ecosystem. Chapter four models the spatial distributions of fish, coral, echinoderm, mollusc and algae functional groups for now, and 2050 with climate change. Groups were found to have distinct tropical and sub-tropical distributions. Future predictions showed mixed responses to environmental change, with some tropical groups shifting poleward, some subtropical groups reducing in abundance, but also subtropical groups that remained stable, resulting in high latitude novel functional communities with enhanced functions.

Reserve networks based on current distributions may not remain effective in the future. In Chapter five, I outline a climate resilient framework for prioritising reefs for static and dynamic conservation management I use the predicted multi-taxon group distributions from Chapter four,

to identify areas for protection that would maximise ecosystem function, whilst considering range shifts.

Overall, this thesis provides an enhanced understanding of the functioning and protection of coastal reefs under ongoing climate change. Methods in this thesis could be applied to other localities along marine biogeographic transition zones, and be adapted for terrestrial ecosystems with latitudinal and altitudinal range shifts, improving evidence-based conservation action in a changing world.

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A Note on Style

Chapters two-five of this thesis have been written in manuscript format intended for publication. I am lead author on all data chapters, but I acknowledge contributions of co-authors by using terms ‘we’ and ‘our’ throughout these chapters. General Introduction and Discussion represent my sole work, and terms ‘I’ and ‘my’ are therefore used throughout. Chapters two- five follow classic manuscript format with introduction, methods, results and discussion.

Chapter One - General introduction

1.1 Background

Since the late 1800s, anthropogenic activities have caused the global mean temperature to rise by almost 1°C degree, with up to a 4°C rise in temperature expected by the end of the century (Hobday and Pecl 2014; Terry P Hughes *et al.*, 2018). This rapid warming and its associated climatic change poses a threat to biodiversity that is expected to soon overtake habitat loss as the major cause of species extinctions (Arneth *et al.*, 2020). The detrimental effects of climate change are most apparent in the oceans, which absorb over 90% of excess heat trapped by greenhouse gases and over 25% of carbon dioxide emitted (Hobday and Pecl 2014; Levitus *et al.*, 2012; Le Quéré *et al.*, 2012). As a result, in the last century, the average global sea surface temperature (SST) has risen by 0.7 °C with a 30% increase in acidity (Huang *et al.*, 2017). Such changing conditions are reducing habitat suitability in the tropics for environmentally sensitive species, whilst allowing for the persistence of species in previously unsuitable high latitudes environments (Verges *et al.*, 2014; Wild *et al.*, 2011; Wernberg *et al.*, 2011). This global redistribution of marine species is restructuring ecological communities and causing irreversible phase shifts (Terence P Hughes *et al.*, 2007; Kumagai *et al.*, 2018). It is currently unclear how this community turnover will impact ecosystem functioning, but this must be understood to implement long term conservation management strategies (Vergés *et al.*, 2019).

As environmental conditions at low latitudes are becoming unfavourable for tropical communities, ocean warming drives poleward latitudinal species range shifts (Verges *et al.*, 2014; Pecl *et al.*, 2017; Pinsky, Selden and Kitchel, 2019). Temperature is one of the most important physical variables affecting the survival of ectotherms, as it is linked to metabolism, growth and reproduction (Feary *et al.*, 2014). High latitude regions experience enhanced seasonality, with the poleward range limit of many species determined by their ability to overwinter through cold conditions (Sommer *et al.*, 2014; Beger *et al.*, 2014; Leriorato and Nakamura 2019). Species persisting in such regions often have broad environmental niches to cope with the environmental variability (Tewksbury, Huey, and Deutsch 2008; Sunday, Bates, and Dulvy 2011; Stuart-Smith, Edgar, and Bates 2017). Their low latitude range limits form either due to heat stress thresholds, or due to competition with tropical organisms (Cahill *et al.*, 2014). Tropical organisms have much narrower environmental niches due to limited seasonality, but are more likely to be environmental specialists with high competitive advantages (Cahill *et al.*, 2013). With ocean warming, environmental temperature thresholds can be crossed, resulting in mortality and range contractions (Pinsky *et al.*, 2019). At the same time, reduced marginality in the subtropics, allows for the survival of tropical species in environments that were previously unfavourable, replacing or outcompeting the contracting resident species (Bates *et al.*, 2013). Individual species have

unique environmental tolerances, and thus range shift potential, with recorded differences in shift velocity and direction (Pinsky, Selden, and Kitchel 2019; Champion, Brodie, and Coleman 2021). This can result in community disassembly with local extinctions of contracting species, and reassembly with novel species combinations of persisting native species and range expanding species (Graham, Cinner, *et al.*, 2014). Such community turnovers can result in novel ecosystems, but whether this will also result in functional turnovers is a key research question to address when understanding the ecological impacts of climate change (Graham, Cinner, *et al.*, 2014; Pecl *et al.*, 2017; Vergés *et al.*, 2019).

The effects of climate change are particularly apparent on coral reefs, which provide critical habitat for a large diversity of species, and multiple ecosystem services, including food provision, coastal protection, and tourism (Eddy *et al.*, 2021). Coral reefs are increasingly degraded due to local anthropogenic disturbances such as intensive coastal development, pollution and overfishing (Heery *et al.*, 2018). Since the 1950's there has been an estimated 50% loss of global coral reef coverage (Eddy *et al.*, 2021; Bruno and Selig 2007; De'Ath *et al.*, 2012) with much of this loss attributed to local anthropogenic stressors (Hoegh-Guldberg, Pendleton, and Kaup 2019). Many persisting reefs have reduced ecosystem health, for example, in 2015 over 80% of fished reefs supported less than half their expected fish biomass (MacNeil *et al.*, 2015). Local human disturbances also reduce reef resilience to thermal stress events, increasing the chance of phase shifts towards algal dominated ecosystems (Cheal *et al.*, 2017; Adam *et al.*, 2021).

Resilience is defined as the capacity of the ecosystem to resist and adapt to disturbance to remain within a stable state (Mumby *et al.*, 2014; Ludwig, Walker, and Holling 1997). Elevated sea temperatures just 1°C above the average summer maxima can cause coral bleaching, and if this occurs for a prolonged period it can lead to extensive mortality (Kwiatkowski *et al.*, 2015; Magris, Heron, and Pressey 2015). On coastal reefs, these effects can be exacerbated by localised coastal development and urbanisation, which can alter environmental conditions through direct habitat destruction, as well as indirect effects such as increased turbidity and eutrophication (Heery *et al.*, 2018). The sensitivity of species to such environmental changes differs, resulting in community turnovers to generalist resilient species, or those that colonise areas post disturbance (Stuart-Smith *et al.*, 2018, 2021; Pratchett, McWilliam, and Riegl 2020). Understanding if there are any similarities between these species, such as shared functional traits, could improve predictions of how ecosystems will respond to further environmental change (Aubin *et al.*, 2018; McLean *et al.*, 2019). Additionally, the conservation value of these communities is unknown as it is unclear if they will retain high levels of ecosystem functioning. (Hobbs, Higgs, and Harris 2009).

The resultant novel ecosystems from coastal development and climate-induced range shifts are unlikely to be reversed back to their original state due to ongoing environmental change, increased human coastal populations and associated ecological feedback mechanisms (Graham, Cinner, *et al.*, 2014; Hobbs *et al.*, 2006). Yet, such disturbed and changeable reefs could become increasingly important for species as their ranges contract elsewhere (Soares 2020; Beger *et al.*, 2014). Additionally, if species on disturbed reefs are preadapted to further environmental change, they could be targeted for conservation management (Soares 2020). However, most current conservation and resource management strategies do not account for future change, often discounting such reefs in conservation plans, and targeting stable areas (Reside, Butt, and Adams 2018). It is also unknown if these ecosystems will retain their current ecological functions, presenting significant challenges for conservation management (Hobbs, Higgs, and Harris 2009). Strategies are needed to integrate novel communities and range shifts into conservation management that incorporate long-term predictions and prioritise functioning. To do this effectively, the underlying processes regulating these shifts, and the conservation value of these novel ecosystems must fully be understood (Williams and Graham 2019). The research in this thesis addresses these challenges by focussing on understanding the ecosystem functioning of Japanese coral reefs and high latitude coral communities under environmental change, and developing strategies to integrate these findings into long-term conservation plans.

1.2 Range shifts, novel ecosystems and the tropicalisation of high latitude reefs

It is estimated that 25-85% of marine species have altered their ranges in some format due to climate change (Melbourne-Thomas *et al.*, 2021), with these range shifts occurring rapidly at an average rate of 70km per decade (Poloczanska *et al.*, 2013). Marine communities are primarily composed of ectotherms, with temperature strongly influencing their behaviours, fitness and distributions (Cereja 2020; Rubalcaba *et al.*, 2020). Physiological performance is regulated through aerobic and anaerobic metabolic pathways, which strongly depends on oxygen availability (Rubalcaba *et al.*, 2020; Deutsch *et al.*, 2015). Different species have different minimum temperature thresholds at which these processes can occur (Bennett *et al.*, 2021; Donaldson *et al.*, 2008). With ocean warming, locations that were historically too cold can support vital metabolic rates, with population increases via migration or recruitment resulting in expansions at the leading latitudinal edge (Bates *et al.*, 2014; Gervais, Champion, and Pecl 2021). However, although increasing water temperatures speeds up these pathways, it also reduces dissolved oxygen supply, with a loss of equilibrium impairing physiological processes (Deutsch *et al.*, 2015; Neuheimer *et al.*, 2011). When this equilibrium temperature threshold is crossed, it results in reductions in reproduction, increased mortality, local species extinctions and thus range

contractions (Bates *et al.*, 2014; Gervais, Champion, and Pecl 2021). This results in directional poleward range shifts, that can further facilitate further shifts in other species through changes in biotic and abiotic conditions (Yamano, Sugihara, and Nomura 2011; Bates *et al.*, 2014).

Range shifts of multiple species are particularly noticeable along biogeographic transition zones which have high community turnover due to environmental filtering along gradients of rapidly changing abiotic conditions (Horta e Costa *et al.*, 2014; Golla *et al.*, 2020; Sommer *et al.*, 2014). Ecological communities in such areas are host to unique assemblages of species that are surviving at their range margins (Beger *et al.*, 2014; Gaudin *et al.*, 2018). Across marine tropical to temperate transition zones, communities can be composed of an overlap of tropical coral and associated species, as well as sub-tropical and temperate macroalgal communities (Beger *et al.*, 2014; Bridge *et al.*, 2014; Floyd *et al.*, 2020). High latitude coral communities in such areas experience marginal conditions such as large seasonal temperature ranges, lower levels of solar radiation, and lower levels of aragonite which is required for reef growth (Beger *et al.*, 2014; Muir *et al.*, 2015; Kleypas 2015; Yara *et al.*, 2012). These reefs occur in areas where major currents that originate in the tropics bring warm water to higher latitudes, transporting the larval stages of tropical species (Verges *et al.*, 2014; Beger *et al.*, 2014; Leriorato and Nakamura 2019). With warming oceans, and the strengthening of these currents under climate change, high latitude reefs are experiencing an influx of tropical species (Booth *et al.*, 2007; Abe *et al.*, 2021; Yamano, Sugihara, and Nomura 2011). This process, known as tropicalisation, is a global phenomenon, with notable examples in Australia, South Africa and Japan (Yamano, Sugihara, and Nomura 2011; Lloyd *et al.*, 2012; Nakamura *et al.*, 2013; Beger *et al.*, 2014; Feary *et al.*, 2014; Horta e Costa *et al.*, 2014; Vergés *et al.*, 2016; Kumagai *et al.*, 2018; Ross *et al.*, 2021; Grillo *et al.*, 2021).

High latitude reefs across the globe have experienced similar stages of the tropicalisation process, suggesting they may be driven by the same underlying mechanisms (Fig. 1.1) (Verges *et al.*, 2014). These stages can be described using the ‘ball in cup analogy’ and the theory of alternative stable states (Fig 1.1) (Lamothe, Somers, and Jackson 2019; Ling *et al.*, 2015). Ecological communities can be represented by the ball in a cup, within a landscape of multiple states. The depth of the cup represents the energy required for the ball to shift into a different state (Ling *et al.*, 2015; Lamothe, Somers, and Jackson 2019), and for ecological communities, the severity of disturbances to initiate a regime shift. If the ball shifts into a new deeper cup, it is unlikely to naturally shift back due to ongoing feedback mechanisms, and is known as an alternative stable state (Lamothe, Somers, and Jackson 2019; Ling *et al.*, 2015) (Fig 1.1). On high latitude reefs, many species exist at their leading and contracting range edges, so small changes in environmental conditions can result in rapid ecosystem shifts (Beger *et al.*, 2014). Tropical species are first recorded as annual vagrants at high latitudes, which are then recorded over-wintering, creating new ecological

interactions as they permanently co-inhabit with existing species (Figueira and Booth 2010; Verges *et al.*, 2014; Vergés *et al.*, 2019). The community reaches a tipping point, often due to disturbances, pushing the community into an alternative state. On high latitude reefs, prolonged heat waves cause physiological stress and disease, resulting in mortality of temperate species such as kelps, with cascading mortalities for kelp-associated communities (Wernberg *et al.*, 2012; Kumagai *et al.*, 2018). Population increases in herbivorous urchins and tropical herbivorous fishes prevent the re-establishment of kelp, opening up areas for the settlement of tropical coral larvae (Wernberg *et al.*, 2012; S. Bennett *et al.*, 2015; Vergés *et al.*, 2019; Coni *et al.*, 2021). Once established, corals can alter the structural complexity and morphology of the seafloor through the creation of calcareous habitat facilitating the shifts of further tropical species (Yamano *et al.*, 2012), with such feedback mechanisms maintaining the ecosystem in its tropicalised stable state (Graham, Jennings, *et al.*, 2014; Vergés *et al.*, 2019) (Fig 1.1).

Tropicalisation is a complex multi-faceted process, affecting species within multiple taxa across different trophic levels in contrasting ways. Tropicalised ecosystems have been found to support a higher diversity of fish species, perhaps due to enhanced niche availability from coral structures (Smith *et al.*, 2021). But, as kelps are lost, so are important nursery habitats for many temperate fish, with potential for extinction lags (Vergés *et al.*, 2019; Smith *et al.*, 2021). Warm adapted grazing sea urchins are increasing in abundance, facilitating coral establishment (Coni *et al.*, 2021), yet in areas intensively grazed by limpets, corals are completely absent (Ling, Barrett, and Edgar 2018). Additionally, range shifts of tropical Holothurians (Nishihama, Yamana, and Yoshimura 2020), Zoanthids (González-Delgado *et al.*, 2018) and Gastropods (Nimbs and Smith 2018) have been recorded along tropical to temperate transition zones. Although these records are isolated and limited, that is likely to be because such taxa are highly understudied (Floyd *et al.*, 2020). However, multi-taxon shifts could unlock novel trophic pathways, or have cascading ecological effects with widespread socio-economic consequences (Cheung *et al.*, 2012; Sudo *et al.*, 2022). Understanding how tropicalisation affects the community as a whole, including understudied species, is a key conservation priority (Vergés *et al.*, 2019; Floyd *et al.*, 2020).

Ecosystem transformations from kelp to coral dominated reefs can occur rapidly within a few decades (Verges *et al.*, 2014). Kelp beds form critical habitats for commercially and ecologically valuable fish and shellfish and losses of these temperate ecosystems can thus lead to local extinctions, losses in biodiversity, and the resulting collapse of certain fisheries (Kiyomoto *et al.*, 2013; Wernberg *et al.*, 2016; Smith *et al.*, 2021). Ecosystem services that temperate and sub-tropical communities provide could either be lost or replaced (Sudo *et al.*, 2022; Madin *et al.*, 2012). However, tropicalising species may also provide new ecosystem services, including novel food sources and tourism opportunities such as coral-reef related diving activities (Madin *et al.*, 2012; Verges *et al.*, 2014). Tropicalised locations could also become increasingly critical for the

persistence of range expanding species, where their previous habitat has become environmentally unsuitable due to thermal stress (Beger *et al.*, 2014). Thus, there is an increased need for conservation management actions that protect such ecosystems and the functioning that provides these services (Arafeh-Dalmau *et al.*, 2021), whilst also protecting the ecosystem services provided by temperate systems.

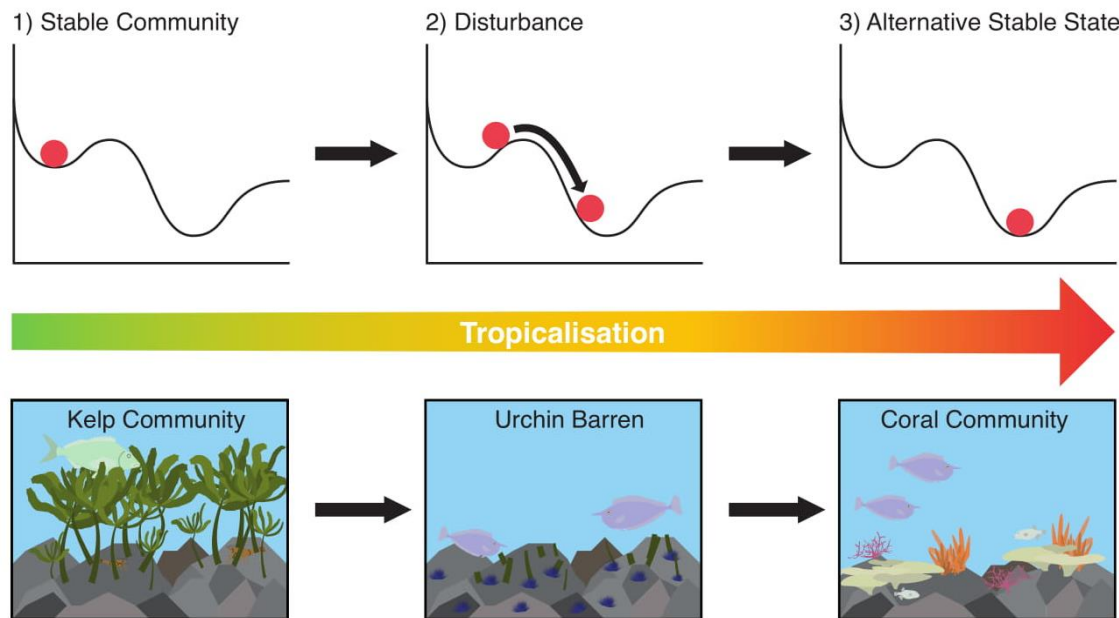


Figure 1.1 Tropicalisation constitutes an ecosystem shift from a kelp to a coral community under climate change. Ecosystem shifts can be described with the “Ball in cup” analogy of alternative stable states (top panel). The ball represents a particular community within a landscape representing all possible states (Lamothe, Somers, and Jackson 2019). The depth of the cup represents the amount of environmental change needed to shift to a new state. Disturbances result in these thresholds being crossed, resulting in displacement of the ball, and a shift to a new state. This state has a deeper cup due to feedback mechanisms, so it is difficult to shift back to the original state. Bottom panel: One of the typical tropicalisation pathways of high latitude rocky macro-algal beds is driven by stepwise kelp mortality, increased herbivory, and the influx of tropical species which alter the benthic structure.

1.3 A functional approach to understanding community change

It is clear that tropicalisation results in widespread community turnover across multiple trophic levels, but it is still largely unknown how this will affect whole ecosystem functioning (Vergés *et al.*, 2019). Ecosystem functioning is defined as the energy transformation and matter cycling regulated by living organisms (Ghilarov 2000; Boero and Bonsdorff 2007). Within the ecosystem, species interact with abiotic conditions, mediating rates of ecosystem processes such as

production, consumption and decomposition (Brandl *et al.*, 2019). Individual species can affect functioning if they are functionally distinctive in where they occur in the food web, how they acquire key resources, if they affect disturbance regimes and how they respond to environmental factors (Strayer 2012). Such unique species provide functions critical for ecosystem stability, yet, in high diversity systems, taxonomically distinct species can exhibit similar ecological functions (Guillemot *et al.*, 2011). This functional redundancy could buffer against the loss of ecosystem functioning resulting from anthropogenic and climate-induced community turnovers (Mouillot *et al.*, 2014). Additionally, with the formation of novel ecosystems through multi-taxon species turnovers, if the novel species share similar functions to those in the original community, there may be no functional losses (Rilov *et al.*, 2019; Zwart, Solomon, and Jones 2015). Thus, under such disturbances, understanding the changes in the type and number of functions is more ecologically informative than understanding species-based taxonomic change (Guillemot *et al.*, 2011).

In complex ecological systems, linking species and communities to ecosystem processes and functioning has been a long-standing challenge to ecologists (Funk *et al.*, 2017). However, over the past few decades, this challenge has been increasingly addressed using functional traits (Funk *et al.*, 2017). Functional traits can be physical, behavioural, biochemical or physiological, influencing how species interact within their biotic community and abiotic environment (McGill *et al.*, 2006). For example, traits related to where the species can persist such as habitat preference, tolerance to turbidity and wave exposure influence which other species they are likely to associate with, and traits such as trophic level and body size affect what the species can eat and what it can be eaten by, determining where it sits within food web (Cadotte *et al.*, 2015; Albouy *et al.*, 2011). Thus, traits are surrogates that operate in the absence of direct functional knowledge of how species empirically contribute to ecological processes (Bellwood *et al.*, 2019). Species with similar traits are likely to have similar functional roles within communities, and grouping such species together can account for functional redundancy when assessing community change under disturbance (Mouillot *et al.*, 2014; Anderson *et al.*, 2021). Such functional groups are manageable units that may be phylogenetically different yet share key functions allowing for enhanced understanding and management of function in complex and diverse systems such as coral reefs (Bellwood *et al.*, 2019; Anderson *et al.*, 2021, Thesis Chapter 3). However, the strength of the link between traits and certain functions can differ, and the functions themselves contribute unequally to ecosystem functioning, presenting a challenge to understand and link functional groups to functions they provide (Bellwood *et al.*, 2019).

Even without fully understanding the role of functional groups, they provide practical way to manage and prioritise for a diversity of functions without having to consider hundreds of different species (Anderson *et al.* 2021). Certain traits may also make species more susceptible to environmental change. Identifying if there are traits that are linked to range shift potential, or resilience to environmental change could provide information on the winners and losers under certain disturbances, and how this will affect ecosystem functioning (Hoey *et al.*, 2016). For example, corals with branching morphology are known to be more susceptible to thermal stress events than those with massive morphologies (Van Woesik *et al.*, 2011) and similar patterns could be identified across other taxa. Additionally, traits that capture high dispersal potential, such as reproductive strategy and pelagic larval duration could indicate species that have the capacity to disperse to new environments and range shift (Kumagai *et al.*, 2018). Species with generalist traits that survive across large depth ranges and are not habitat specific may be predisposed to persist in marginal conditions, enhancing shifting potential at the range edge (Stuart-Smith *et al.*, 2021). Yet, some traits such as large body size may provide beneficial adaptation to cold water or disturbed environments (Pörtner and Peck 2010), and specific traits linked to habitat specialisations may provide unique adaptation to change (D'Angelo *et al.*, 2015; Myers *et al.*, 2020). Thus, if traits can be linked to range shift potential, functional groups are likely to respond in similar ways to environmental disturbances, so without management whole groups of species, and the roles they provide could be lost.

If groups with some traits shift and others do not shift, it could result in functional mismatches with altered overall functioning, and potential cascading ecological effects through multiple functional groups. With tropicalisation, functional groups from one taxa, such as algae, are likely to be replaced by coral functional groups (Verges *et al.*, 2014), with similar changes across taxa of groups mediating critical functions such as herbivory. For example, shifts in dominance between temperate herbivorous urchins to tropical herbivorous fishes could retain the same level of functioning (Yeruham *et al.*, 2020), but if only looking at the fish it could seem like the functioning was being increased. Taking a multi-taxon trait-based approach more accurately indicates how reefs function before and after tropicalisation, or climate related disturbances. Thus, to assess and protect ecosystem functioning requires stepping away from phylogenetic and taxon specific approaches, protecting functions regardless of the species and groups that provide them (Guillemot *et al.*, 2011).

1.4 Conservation planning under climate change

The most common way of conserving coral reefs is through the creation of marine protected areas (MPAs) (Hargreaves-Allen, Mourato and Milner-Gulland, 2017). Well-designed MPAs can effectively reduce environmental degradation, and maintain or increase species diversity and richness by preventing fishing and other anthropogenic disturbances (Bennett and Dearden, 2014). MPAs are often created after a systematic planning process which aims to maximise the protection of set biodiversity features whilst minimising socio-economic impacts and cost (Makino *et al.*, 2015). They have been shown to increase biodiversity (Ferreira *et al.*, 2022), maintain high fish biomass (McClure *et al.*, 2020), support populations of threatened species (Albano *et al.*, 2021) and protect processes critical to sustained ecosystem function, such as the regulation of macroalgae on coral reefs (Mumby *et al.*, 2021). Thus, some well-designed MPA networks have also been shown to have increased resilience to climate disturbances (Bates *et al.*, 2019). In tropical areas, they maintain higher levels of coral coverage and associated biodiversity (Selig and Bruno 2010), and in temperate areas, protection can slow tropicalisation by minimising the effects of climate and anthropogenic disturbances on kelp habitats (Bates *et al.*, 2013). However, as such rapid environmental change threatens marine ecosystems, critical thermal thresholds are being crossed even in protected areas (Bruno, Côté, and Toth 2019). Habitats that are currently protected are likely to become vulnerable in the future due to species range shifts (Carpenter *et al.*, 2008).

Systematic conservation planning often assumes that the targeted biodiversity features are stable, not considering the effects of climate change and range shifts (Wilson *et al.*, 2020). However, increasing sea surface temperatures (SSTs) can result in faster growth rates, shortening planktonic larval duration and altering larval connectivity (Lima *et al.*, 2021; Andrello *et al.*, 2015). This can cut off areas from source populations, leaving MPAs isolated and reducing their ability to recover after disturbance (Álvarez-Romero *et al.*, 2017). Static MPA management often focuses on individual target organisms, not taking an ecosystem approach considering functioning. However, environmental conditions in current MPAs could exceed the level at which target organisms can survive (Alagador, Cerdeira, and Araújo 2014). For example, with increased frequent thermal stress events and bleaching related mortality (UNEP 2020), MPAs designated to protect coral communities may no longer fulfil their conservation objective (Fredston-Hermann, Gaines, and Halpern 2018). This static management approach is unlikely to protect ecosystem function in the long-term, as the target areas for specific organisms could be areas that experience the highest functional losses. Thus, there is an enhanced need to consider adaptive management strategies that are temporally cost-effective, whilst maintaining functioning ecosystems (Wilson *et al.*, 2020).

As climate change increasingly threatens marine ecosystems, static management strategies have been developed to select MPAs that will be least affected by climate-related disturbances and future ecosystem instability. Many planners use a risk spreading approach where multiple spatially separate areas are protected for each biodiversity feature (Magris, Heron, and Pressey 2015). Yet, this is not cost effective as either the overall total area protected has to be increased to cover multiple large reserves, or the protection is split between multiple small areas which could minimise survival chances (Fredston-Hermann, Gaines, and Halpern 2018). There is also no indication of whether or not all the areas will be negatively affected by climatic change. An alternative approach is to account for future environmental stressors using modelled predictions (Wilson *et al.*, 2020). Using downscaled climate projections, global coral reef futures exhibit predicted high local scale variation in environmental stability and bleaching probability (van Hooidek *et al.*, 2016). Thermal refugia areas with the least predicted environmental change are often targeted as conservation priority areas as they are likely to be more resilient to climate change, maximising the chance of community stability and reef persistence (Iwamura *et al.*, 2010; Magris, Heron, and Pressey 2015; Wilson *et al.*, 2020). However, as the effects of climate change increase, many such refugia areas are still likely to cross environmental thresholds (Dixon *et al.*, 2022), especially when targeting areas within set geographic boundaries, such as individual country jurisdictions. For example, countries such as Japan lie along biogeographic transition zones which are predicted to experience high levels of environmental change and associated community turnovers (Sudo *et al.*, 2022). In such areas, the optimal habitats for many species are likely to geographically change and this should be accounted for in conservation plans (Vergés *et al.*, 2019).

Dynamic conservation plans consider future conditions and allow for shifting reserve networks that track target species and communities (Alagador, Cerdeira, and Araújo 2014; Tittensor *et al.*, 2019). These reserves can be gazetted before shifts, so species have somewhere protected to shift into, and degazetted when they become redundant as target features continue to shift elsewhere (Alagador, Cerdeira, and Araújo 2014). Such conservation plans require detailed quantitative information on current and future species distributions, which can be determined using models that correlate species occurrence data with environmental variables to predict habitat suitability across landscapes (Elith and Leathwick 2009; Guisan and Thuiller 2005; Melo-Merino, Reyes-Bonilla, and Lira-Noriega 2020). Developing accurate models requires large amounts of information, which is often only available for well-studied species and taxa. A systematic review of marine SDM research found that over 25% the 236 publications reviewed were focussed on marine fish, with only one publication developing SDMs for echinoderms (Robinson *et al.*, 2017). Thus, conservation plans that have been developed using such methods focus largely on a few well-known species within a single taxon. However, broader approaches have been developed

which track climate velocity by prioritising environmental ecoregions (Makino *et al.*, 2015, 2014). For example, ecoregions have been used for a proxy for types of tropical and sub-tropical coral communities with different thermal affinities in the absence of species data to ensure that a target percentage of these ecoregions remain protected and connected through time and space (Makino *et al.*, 2014). In reality, large areas of such coarse ecoregions could be unsuitable for the target ecological communities, having the wrong environmental conditions such as turbidity and depth. The broad temperature ecoregions are also unrealistic for more fine scale conservation priorities, and do not capture information on ecosystem functioning and biodiversity of corals and associated taxa. Prioritising for the protection of functional groups provides a solution to incorporate sustained function into conservation plans, without needing vast amounts of information for all the component species within each community (Anderson *et al.*, 2021). In this thesis, I develop novel methods to integrate functional group distribution models into conservation management strategies.

1. 5. Japanese marine ecosystems as a system for understanding range shifts

The Japanese islands span almost continuously over 20° in latitude, ranging from tropical to temperate climates. From around 24°N to 35°N the East Coast is highly influenced by the northwards flowing Kuroshio Current, with a continuous latitudinal tropical to temperate environmental gradient (Yara *et al.*, 2012). As one of the strongest warm-water currents in the world, the current facilitates the larval dispersal of tropical species and pushes warm waters to higher latitudes, enabling the occurrence of the world's northernmost coral communities (Yamano *et al.*, 2012). Increasingly warm waters along this current due to climate change has allowed for the poleward range expansions of tropical species, and national records collected over 80 years indicate that tropical corals are expanding northwards at a rate of up to 14 km per year (Yamano, Sugihara, and Nomura 2011). Shifts from sub-tropical to tropical coral communities have been recorded in Kushimoto (33.47°N) (Nomura 2009) and from kelp dominated to coral dominated habitats in Shikoku (33° N) (Kumagai *et al.*, 2018; Verges *et al.*, 2014; Denis *et al.*, 2013), as well as influxes and establishment of tropical fish species at high latitudes (Nakamura *et al.*, 2013).

Japanese tropical reefs have been subject to multiple mass bleaching events, reducing coral cover by up to 85% in the tropics (Chen *et al.*, 2015). Additionally, Japan is a densely populated country with over 125 million people (United Nations Population Division 2019). Over 90% of this population live in urban areas (United Nations Population Division 2018), the majority of which lay along the coast (Hinrichsen 1999). Many of the coastal marine ecosystems around Japan have experienced high levels of anthropogenic disturbances related to urbanization and coastal

development (Matsushima and Ferreira 2022). Thus, the multiple drivers of climate and anthropogenic disturbance coupled with the detailed records of tropicalisation, along with the continuous geographic latitudinal gradient make Japan a good ecological study system for understanding how such marine ecosystems may look and function in the future (Makino *et al.*, 2014). Improved knowledge of ecosystem functional and community change across threatened marine ecosystems could inform climate resilient conservation management plans for Japanese reef communities.

1.6. PhD research aim, objectives, and chapters

Overview

Novel ecosystems are increasingly forming across the globe due to anthropogenic disturbances and climate-induced range shifts. This process is particularly apparent across biogeographic transition zones such as the tropical to temperate gradient spanning Japan's east coast. Here, the environments are changing rapidly, with high latitude communities undergoing tropicalisation due to climate induced range shifts (Yamano, Sugihara, and Nomura 2011; Abe *et al.*, 2021; Verges *et al.*, 2014), and low latitude tropics experiencing thermal stress events and other environmental disturbances (Loya *et al.*, 2001; Masucci and Reimer 2019). Yet, it is currently unclear how climate change will continue to affect species distributions and interactions, and the wider role this will play in the overall ecosystem functioning across the area. This is a knowledge gap that must be addressed in order to improve ecosystem protection.

Understanding the drivers of climate-induced community turnover, and the functional value of resulting novel ecosystems would allow for enhanced biodiversity protection, and the continued provision of ecosystem services beneficial to human populations. Well placed MPAs could allow for the persistence of sub-tropical/temperate species (Bates *et al.*, 2013), as well as facilitating shifts for species that are threatened in the tropics (Makino *et al.*, 2014). Therefore, under the rapid rates of climatic change and associated predicted species extinctions, it is critical that a conservation framework is developed that has clear objectives for how to manage climate change effects with conflicting environmental goals. Here, I overview how each of my data chapters (Chapters two to five) aim to address these knowledge gaps.

Chapter Two- A community and functional comparison of coral and reef fish assemblages between four decades of coastal urbanisation and thermal stress.

Chapter two focuses on understanding how Japanese marine ecosystems have changed functionally through time, in response to multiple anthropogenic stressors. Data on fish species and coral genera occurrence, as well as depths were collected in 1975 across tropical Nakagusuku Bay, Japan (26°N) and the sites were resampled in 2018. Over 43 years, the marine environment has been subject to anthropogenic impacts, with localised disturbances such as coastal landfilling, pollution, and fishing as well as prolonged mass bleaching events. I compare how the community and functional compositions have changed between the time periods, and identify site-based change across a coastal disturbance gradient. Additionally, I assess if benthic corals have shifted depths to more favourable habitats, and quantify the habitat generalisation of the fish communities pre- and post-disturbance.

Chapter Three- Systematic spatial variation of fish functional group abundances across a biogeographical transition zone.

Chapter three focuses on understanding the drivers of fish functional group distributions across Japan's tropical to temperate biogeographic transition zone. I build novel mixed effect distribution models for fish functional groups using abundance survey data collected across Japan's latitudinal gradient (24°N-35°N). The models are also developed for species with enough survey data, allowing me to compare the group level environmental responses to the within-group species environmental responses. I identify if the groupings are accurately representing the species, and use the models to predict functional group distributions to understand how ecosystem functions change across the gradient.

Chapter Four- Predicting changes in multi-taxon reef functioning under climate change.

Reef diversity cannot be represented by just fish, so I therefore extend the functional group approach from Chapter three across multiple taxa including fish, algae, corals, molluscs and echinoderms. I aim to understand how the ecosystem functioning of tropical to temperate coral communities differ spatially and temporally. To do this, I develop functional group based distribution models for these multi-taxon functional groups using ensemble models for now, and for 2050. I assess functional group range shifts and quantify changes in functioning over time.

Chapter Five- Integrating climate change and ecosystem functioning into dynamic spatial conservation planning.

In this Chapter, I develop a conservation framework that accounts for range shifting, with a static approach where reserve locations do not change over time, a dynamic approach where reserves are sequentially designated and gazetted to track range shifts, and a hybrid approach, with combined static and shifting dynamic reserves. Using the multi-taxon functional group distributions from Chapter four, I apply this framework with different scenarios to fulfil the conservation objectives of facilitating tropicalisation, slowing tropicalisation and maximising the protection of all functions. I compared the scenario outputs using a novel functional change metric, and assess the capacity of selected the reserve networks to maximise ecosystem functioning under tropicalisation and range shifts.

1.7 References

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Chapter Two - A community and functional comparison of coral and reef fish assemblages between four decades of coastal urbanisation and thermal stress.

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2.0 Abstract

1. Urbanised coral reefs experience anthropogenic disturbances caused by coastal development, pollution and nutrient runoff, resulting in turbid, marginal conditions in which only certain species can persist. Mortality effects are exacerbated by increasingly regular thermal stress events, leading to shifts towards novel communities dominated by habitat generalists and species with low structural complexity.
2. There is limited data on the turnover processes that occur due to this convergence of anthropogenic stressors, and how novel urban ecosystems are structured both at the community and functional level. As such, it is unclear how they will respond to future disturbance events.
3. Here, we examine the patterns of coral reef community change, and determine whether ecosystem functions provided by specialist species are lost post-disturbance. We present a comparison of community and functional trait-based changes for scleractinian coral genera and reef fish species assemblages subject to coastal development, coastal modification, and mass bleaching between two time periods, 1975-6 and 2018, in Nakagusuku Bay, Okinawa, Japan.
4. We observed an increase in fish habitat generalists, a dominance shift from branching to massive/ sub-massive corals and increasing site-based coral genera richness between years. Fish and coral communities significantly reassembled, but functional trait-based multivariate space remained constant, indicating a turnover of species with similar traits. A compression of coral habitat occurred, with shallow (<5m) and deep (>8m) coral genera shifting towards the mid-depths (5-8m).
5. We show that although reef species assemblages altered post disturbance, new communities retained similar ecosystem functions. This result could be linked to the stressors experienced by urban reefs, which reflect those that will occur at an increasing frequency globally in the near future. Yet, even after shifts to disturbed communities, these fully functioning reef systems may maintain high conservation value.

2.1 Introduction

Coral reefs are severely threatened by anthropogenic disturbances and climate change, with a significant loss of global coral cover recorded in the last few decades (Hughes *et al.*, 2018). As well as losses associated with increasingly frequent and severe global mass coral bleaching events (Hughes, Anderson, *et al.*, 2018; Sully *et al.*, 2019), coastal urbanisation threatens water quality, water fluxes, and sustainability of extractive use for nearshore coral reefs (Masucci and Reimer, 2019). Such disturbances result in reassembly of communities, with the turnover of certain species, taxa, and functional groups (Nyström *et al.*, 2008; Stuart-Smith *et al.*, 2018). Disturbed communities often have reduced structural complexity, losing the capacity to maintain diversity and altering trophic structure (Cruz *et al.*, 2018). The loss of microhabitats can cause communities to become homogenised and dominated by habitat generalists (Wilson *et al.*, 2008; Stuart-Smith *et al.*, 2021). The loss of complexity is especially pronounced on urban reefs (Januchowski-Hartley *et al.*, 2020), but its effects on trait communities and functioning remain poorly known.

As the human population increases, coastal zones are experiencing rapid rates of urbanisation, resulting in land reclamation, artificial rocky habitats for flood prevention and the building of harbours and piers (Heery *et al.*, 2018). The marine environment can further be altered by increased sedimentation, nutrient run off and the introduction of toxic heavy metals and organic contaminants (Pollock *et al.*, 2014). These processes threaten reef building corals by increasing turbidity, disease prevalence, and reducing coral reproduction (Browne, 2012). Yet, scleractinian coral reefs can still be found adjacent to established tropical and subtropical urban areas (Hongo and Yamano, 2013). These turbid urban reefs differ in composition to offshore reefs, but there is limited data to understand the turnover processes that occur due to urbanisation (Heery *et al.*, 2018). Furthermore, it is unknown if these ecosystems are structurally and functionally unique, and how they will respond to further environmental stress (Heery *et al.*, 2018). It has been suggested that species persisting in marginal conditions may be preadapted to be resilient to further stressors such as bleaching events (Sofonia and Anthony, 2008; Guest *et al.*, 2016).

Mass bleaching events caused by prolonged periods of thermal stress have occurred with increasing frequency in the last four decades (Hughes *et al.*, 2018), with differential responses to thermal stress exhibited by coral genera (Kim *et al.*, 2019). In Japan, live coral cover was reduced by 85% in some areas due to severe bleaching events that started in 1998, mostly killing branching coral morphologies such as *Acropora* sp. (Loya *et al.*, 2001). Post-bleaching, Japanese coral communities have been dominated by massive (boulder) and encrusting morphologies, and thermally susceptible branched corals have almost completely disappeared (Loya *et al.*, 2001). However, branching and plating colonies experienced differing degrees of bleaching mortality, suggesting factors other than coral morphology also affect survival. For example, corals found

across a large depth range are likely to be habitat generalists, pre-adapted to survive under a range of thermal conditions (Bongaerts and Smith, 2019; Chow *et al.*, 2019). Shallow specialists thrive under high light levels, high wave energy and low sediment deposition, but if disturbance alters these conditions, survival is less likely (Chow *et al.*, 2019). Deeper corals may be able to repopulate shallow areas after mortality (Smith *et al.*, 2014; Holstein *et al.*, 2015), particularly if they have a high dispersal capacity (Graham, Baird and Connolly, 2008).

Corals that survive disturbance events and those that repopulate degraded reefs may have similar functional traits (Chow *et al.*, 2019). Traits can determine a species abiotic tolerances, as well as biotic interactions such as competition, feeding and predation (Hébert, Beisner and Maranger, 2015). Thus, they are linked to ecosystem functioning, which considers how interactions between the biological assemblages of the system determine critical processes such as energy flow, and community properties such as resilience (Reiss *et al.*, 2009). If disturbances favour specific traits, the mortality of whole groups of species with different unique traits could occur, reducing the capacity of the ecosystem to function (Siwicka, Thrush and Hewitt, 2020). For example, on tropical reefs, zooxanthellate corals are the habitat builders, and the structural complexity of the reef can determine the abundance and diversity of reef associated species (Darling *et al.*, 2017). Corals with complex morphologies provide shelter and nursery habitats for reef fish (Hamilton *et al.*, 2017). If all branching corals are lost, these fishes may also be lost from the reef.

Diverse fish communities perform a multitude of functions, and their resilience to both fishing and coral habitat degradation have been linked to the functional traits of the component species (Streit, Cumming and Bellwood, 2019). For example, herbivorous fishes help prevent phase shifts from coral to algal dominated ecosystems and are critical in maintaining a functioning reef community (Edwards *et al.*, 2014). Furthermore, they provide prey to larger fish species that provide top-down predation, keeping the ecosystem in equilibrium (Valdivia, Cox and Bruno, 2017). A healthy, diverse reef system supports fish species with a wide range of specialised functional niches (Mouillot, Villéger, *et al.*, 2014). However, similar to corals, shifts to more generalised fish communities have been observed in degraded systems (Richardson *et al.*, 2018; Stuart-Smith *et al.*, 2021). This indicates reduced ecosystem functioning, feeding back to further coral losses (Richardson *et al.*, 2018). Thus, the resilience of coral reef ecosystems to disturbances is not only related to the corals themselves, but the interactions among species and taxa. Therefore, it is also important to understand how fish communities and their functions change with disturbance to help understand future community resilience and ecosystem change.

The coastline and reefs of Okinawa Island, Japan, present a good model system to study the combined impacts of urbanisation (Masucci and Reimer, 2019) and climate stress (Hongo and

Yamano, 2013) on coastal coral reefs. Okinawa's coasts have supported ports and naval bases since World War Two, creating extensive disturbances particularly in the bays on the southeast coast. In the post-war period, after Okinawa reverted from US occupation to Japan in 1972, the Japanese government invested heavily in Okinawa's development, supporting the farming and manufacturing industries, large-scale construction projects, and tourism. Development resulted in a population boom, and from 1955-1990, the population of Okinawa prefecture increased by 53% from 800,000 to 1.22 million people (Kuwahara, 2012; Tada, 2016). Currently, Okinawa Prefecture has a population of 1.45 million, and attracts over 10 million tourists per year (Aizawa, 2014; Hifumi *et al.*, 2020). The economic development from the 1970s led to rapid coastal development, with an acceleration in dredging, landfilling and terrestrial run-off (Japan Coral Reef Society, 2004; Omori, 2011; Masucci and Reimer, 2019). This has resulted in the creation of turbid urbanised reefs with high levels of suspended sediments and reduced water transparency (Hongo and Yamano, 2013). However, the long-term community changes of these urban reef are not well known.

Here we examine the changes in community and functional composition of corals and reef fish in Nakagusuku Bay, Okinawa, Japan between two time periods, 1975-6 and 2018. These 43 years span the majority of the years of Okinawa's extensive coastal development, as well as four global mass coral bleaching events. We determine whether anthropogenic disturbances have resulted in the reassembly of coral and fish communities. To understand the reassembly processes we explored: 1) the change in coral genera coverage, and the average depths of coral genera occurrence, 2) the change in coral and fish community composition and richness, 3) fish community homogenisation and 4) changes in functional trait-based community space. Under ongoing climate change, and with the ongoing increase in the global human population, turbid urbanised reefs may become increasingly dominant. Quantifying changes that occur in these reef communities is critical to understand how currently more 'pristine' reefs may look in the future, and how urbanised reefs may continue to change.

2.2 Methods

2.2.1 Study site and survey locations

Surveys were conducted across Nakagusuku Bay, Okinawa, Japan (26.25°N 127.84°E) in 1975-6 and repeated in 2018 (Fig. 2.1). Nakagusuku Bay covers multiple marine habitats, including coral reefs, seaweed beds and tidal mudflats. It forms a large part of an Ecologically or Biologically Significant Marine Area identified by the Ministry of Environment, and it is home to multiple endemic species (Japan Coral Reef Society, 2004). The bay has an average depth of

10-15m, covers 220 km², and faces east, and thus is impacted by yearly tropical typhoons (Rudolph, Blake and Brand, 1975). During World War Two, it was used as a major port, but significant development of the surrounding coastline did not occur until Okinawa was returned to Japan in 1972 (Kuwahara, 2012). The bay is now surrounded almost completely by urban areas, and includes a large US naval base, a natural gas power plant, and multiple large areas of reclaimed land (Masucci and Reimer, 2019).

Initial surveys were conducted between 1975-6 (Yamazato and Nishihara, 1977) on patch reefs in the northern half of Nakagusuku Bay. Yamazato and Nishihara (1977) reported an accurate topographical map including reef shape, depth contours and the relation of sites to the coastline and other sites that enabled us to replicate the surveys (Supplementary Fig. S2.1a, b). To resample the reef sites, we determined their co-ordinates by georeferencing the original maps with available satellite imagery. As each of the small patch reefs had a distinctive shape and was surrounded by areas of bare sand seafloor, they could be accurately located by boat sonar imagery when at the coordinate location. Three of the sites investigated in 1975-76 were found to be landfilled in 2018 (Fig. 2.1).

2.2.2 Coral surveys

Between December 1975 to April 1976, species and abundance of hermatypic corals present were recorded by visual observation during SCUBA dives at each major habitat (reef, reef slope, reef base/ bottom), of which depth was recorded. To calculate coral species percentage cover, 1x1m quadrats were set at 1-3 points per site covering the major reef habitats and depth range. In the case of shallow reefs, the quadrat was set only on reefs, or only reefs and bottoms, and in the case of deeper reefs, the quadrats were also set at some reef slopes. The depth, coral species, number of colonies and percentage coverage within the quadrat was recorded. Photographs of representative reefs at some of the sites were also captured (Supplementary Fig. S2.1c).

The surveys were repeated between June-October 2018 at 16 of the remaining sites. These sites were selected as they were also the location of fish surveys in 1975-6 and are still accessible by boat. Sites ranged from shallow near-shore sites with a maximum depth of 1.8 m, to offshore reef crest sites with a maximum depth of 36 m. Twenty 1x1m quadrats were randomly placed across depths matching those of the original surveys for each site. A photograph was taken of the whole quadrat to estimate live coral cover, and then of each colony within the quadrat. Using these

images, corals were identified to genus level using Indo Pacific ID guides and coral cover was determined using CPCe software (Kohler and Gill, 2006).

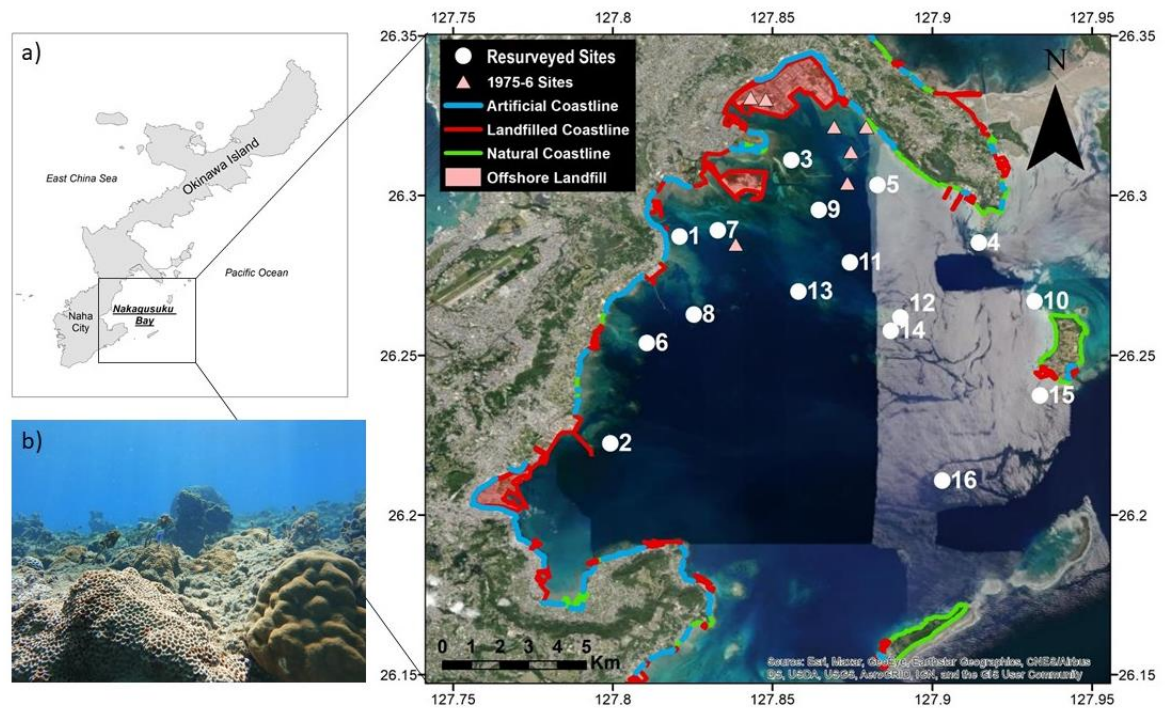


Figure 2.1. a) Map of Nakagusuku Bay and its position on Okinawa Island. Sites that were surveyed in 1975-6 and then resurveyed in 2018 are represented with a solid white circle and numbered according to distance from the coastline of the main island. Sites that were only surveyed in 1975 represented with a pink triangle. Colours represent coastline development as of 2018, much of which occurred after 1977 (Masucci and Reimer, 2019). **b)** Photograph of a typical coral reef site (site 12) in 2018 showing a predominance of massive and encrusting corals.

2.2.3 Fish Surveys

Fish surveys were also conducted between September 1975 to February 1976 at 31 sites, 23 of which were the same as the coral sites described above (Arasaki and Ida, 1977). A 50 m transect was extended from the shallowest point of the reef to the deepest point in a random direction. The width of the transect was not recorded. Fish species abundance observed whilst swimming along the transect were recorded, as well as the depths and the reef profiles of the surveys. Survey dives lasted 30-75 minutes, but it is unclear if the transect surveys lasted the whole length of the dive. Sub-benthic and cryptic species were not recorded as their observability is low using these methods.

Between July- October 2018, replicate fish surveys were conducted alongside coral surveys. Fish surveys were not conducted at two of the sites where coral data were collected (sites two and six) due to weather-related constraints. We recorded five 2 x10 m video transects, at the maximum, middle and minimum depths of those of the original surveys, resulting in 15 transects per site. Videos were recorded whilst swimming at a constant speed close to the edge of the reef slope, or the top of the reef, depending on topography of the site. After each 10 m transect, we then swam 10m without recording to avoid double counts between transects. The individual (alive and dead) reef structures were often small, so the transect length was chosen to allow for replicates whilst avoiding surveying over bare sandy bottom. Fish were identified to species level from videos, species present at each site was recorded.

2.2.4 Data Analyses

All analyses were conducted using R (R Core Team, 2020) and all plots were constructed using the R package ‘ggplot2’ (Wickham, 2011). Prior to any analyses the 1970s scleractinian coral genera and fish species were verified using online repositories and species and genera were reassigned to their current correct names if needed. If a fish species had been split into multiple new species, these names were then checked in the FishBase online database (www.fishbase.org) and the species with the most appropriate geographical range was selected. Similarly, for taxonomic splitting of scleractinian coral genera, genera were checked against the Japanese Ministry of Environment coral surveys (Japan Coral Reef Society, 2004), and the most appropriate genus was selected according to range.

2.2.5 Coral coverage and depth change

Using the scleractinian coral quadrat data, we calculated total coral coverage per site (mean percentage coverage across the site-specific quadrats), mean genus abundance per site, and relative abundance of each coral genera across both time points. The relationship between change in coral coverage and distance from Okinawa Island’s coastline was explored using a linear model. Distance from coastline was taken to be a proxy from distance from urbanisation and anthropogenic development, as the main Island’s coastline has become largely non-natural since 1977 (Masucci and Reimer, 2019). A two-way ANOVA was performed to determine the effect of survey year and coral genera on the depth at which coral colonies were found. We also calculated the average genus depth value across all sites for both years, and coral genera were categorised into three depth categories: ‘shallow’ <5 m, ‘medium’ 5-8 m and ‘deep’ >8 m groups.

2.2.6 Coral genera and fish species community analyses

Whilst the methods in 1975/6 are well described, the exact sampling effort was not reported. Differences in sampling efforts could compound our results in such a way that we cannot be sure whether differences in trait communities are due to community transformation or survey methods. To compare sampling effort between time periods, we performed individual- based rarefaction analyses with extrapolation using the ‘iNEXT’ R package (Hsieh, Ma and Chao, 2016). We plotted extrapolated species accumulation curves and sample coverage (sample completeness), based on 1975-6 and 2018 incidence data across the whole study area, for coral genera and fish species. To explore accumulation patterns across sites, we also plotted site-based accumulation curves for coral genera and fish species richness for 1975-6 and 2018 using the ‘specum’ function from the R ‘Vegan’ package (Oksanen *et al.*, 2019). Sites were added in a random order over 100 permutation, and genus and species richness was calculated per site for scleractinian coral and fish, respectively, for both time periods (1975-6 and 2018).

We conducted multiple statistical analyses to assess if the communities had changed between the years. All community analyses were conducted using the R package ‘vegan’ (Oksanen *et al.*, 2019). We applied a paired t-test to site-based richness values for both coral and fish to test if the difference between years was statistically significant. To visualise the changes in fish and coral communities at each site between years, we conducted a Principal Component Analyses (PCA). Presence and absence data was used for both corals and fish in order to compare between taxa. We then ran a PERMANOVA on the Bray-Curtis dissimilarity matrices using the ‘adonis2’ function to test for significant differences between communities and years. Finally, we used the ‘simper’ function to run a post-hoc test to explore which species/ genera were driving these differences.

2.2.7 Fish community generalisation

To explore if fish communities became more generalised in 2018 compared to 1975-76, we used a species generalisation index (SGI) calculated from a dataset of global fish surveys in relation to benthic habitat classes (for detailed methods see Stuart-Smith *et al.*, 2021). SGI data was available for 242 species out of a total of 306 species observed in our surveys. Species that did not have SGI data were excluded for this part of the analysis. The SGIs are an indicator of fish habitat niche, with larger values corresponding to a larger niche and thus a more generalist species (Stuart-Smith *et al.*, 2021). The community generalisation index (CGI) of each site was calculated using the mean SGIs of fish species present for both years (Stuart-Smith *et al.*, 2021). To see if

there was a significant increase in CGI between the years, we analysed the CGIs of the sites using a paired sample t-test.

2.2.8 Functional trait-based community space

We created trait databases for all our surveyed fish species and coral genera to understand how the Nakagusuku Bay communities had changed functionally. An array of morphological, behavioural and phenological traits were selected to represent functional niche, and thus roles within the ecosystem. For fish, we selected the following traits: maximum length, depth range, trophic level, behavioural aggregation, water column position, spawning mode and parental mode. These traits infer what the species can eat, where they can survive, and how specialised their ecology is, which can be critical parameters when identifying drivers of community change (Mouillot, Vileger, *et al.*, 2014; Nock, Vogt and Beisner, 2016). Traits were collated from online databases including FishBase as well as from extensive literature searches for local endemic species. For scleractinian corals, traits were downloaded at the species level from the Coral Traits database (<https://coraltraits.org/>) (Madin *et al.*, 2016) for all species present in Japan as based on Ministry of Environment surveys (Japan Coral Reef Society, 2004). The mean of the continuous numeric traits was calculated for each genus, and for categorical traits, the value that occurred the most was selected. We used the traits coloniality, maximum corallite width, typical growth form, water clarity preference, wave exposure preference, sexual system, larval development, growth rate, oocyte size, and depth range.

The function ‘gowdis’ from the ‘FD’ package was used to compute the Gower dissimilarity matrix from the species/genera by trait matrices (Laliberté, E., Legendre, P., Shipley, 2014). We used the Gower dissimilarity index because our trait data contained a mix of categorical and continuous traits and contained missing values for rarer species and genera. We then ran a Principal Coordinate Analysis (PCoA) on the distance matrices using a Cailliez correction to visualise traits in multivariate space. By plotting the PCoA values of the overall community, and then the 1975-76 and 2018 communities separately, we aimed to identify if there had been a shift in trait space. We conducted this analysis comparing both the species/genera present across the whole bay between the years, and for individual sites between the years. We then calculated individual hull areas for each site for both time periods using the function ‘areapl’ from the ‘splanx’ package (Bivand *et al.*, 2002) and analysed the change in area between years using a paired sample t-test.

2.3 Results

2.3.1 Coral cover community change

Live coral percentage cover in 1975-6 ranged from a minimum of 1% at site 15 to a maximum of 56% at site 2, and in 2018 ranged from a minimum of <1% at site 3 to a maximum of 48% at site 16. Eight of the sites (site 2, 3, 4, 5, 6, 7, 12, 14) experienced a decline in coral coverage, with the remaining eight sites (1, 8, 9, 10, 11, 13, 15, 16) experiencing an increase (Fig. 2.2c). In general, as the site's distance from Okinawa Island increased, so did the change in coral coverage ($R^2=0.13$, $F(1,14)= 3.29$, $p=0.09$) (Supplementary Fig. S2.2). The exceptions to this pattern were site one, which increased in coverage but was closest to the coast, and sites 12 and 14 which had much higher losses in coverage.

Although coral genera richness appeared to increase or be maintained across all the sites except site 15 (Fig. 2.3b), there was a shift in dominance from coral genera with branching growth forms to ones with massive growth forms (Fig. 2.2a). *Acropora* corals accounted for 25% of the corals surveyed in 1975-6 but dropped to 4% in 2018. *Porites* corals accounted for 20% of the corals in 1975-6 and increased to 24% in 2018. The top five genera with the largest increases in relative abundance all had massive growth forms: *Dipsastraea* (+10%), *Cyphastrea* (+7%), *Astreopora* (+6%), *Favites* (+5%) and *Porites* (+4%). Four out five of the genera with the largest decreases in relative abundance had branching growth forms; *Acropora* (-21%), *Stylophora* (-3%), *Seriatopora* (-2%) and *Pectinia* (-1%).

2.3.2 Coral depth distribution analyses

The average depths at which each coral genera was found differed significantly (ANOVA: $F=12.835$, $df=45,4218$, $p<0.001$). Overall, the change in depth between the years 1975-6 was found to be insignificant (ANOVA: $F=0.830$, $df=1,4218$, $p=0.326$) but the interaction term between year and genera was found to be significant (ANOVA: $F=4.116$, $df=30, 4218$, $p< 0.001$). The overall pattern suggests that coral genera that were once more abundant at shallower depths <5 m shifted deeper, and genera that were more abundant at deeper depths >8 m shifted shallower (Fig. 2.2b). Corals that had a medium average depth between 5 to 8 m in the 1970s have largely remained at similar depths in the 2018 survey. When categorising genera by their average depths (shallow= <5m, medium=5-8m and deep>8m) in 1975-6 nine genera were found to be shallow, 11 medium, and 18 deep. In 2018 this distribution shifted to eight shallow, 22 medium, and nine deep genera.

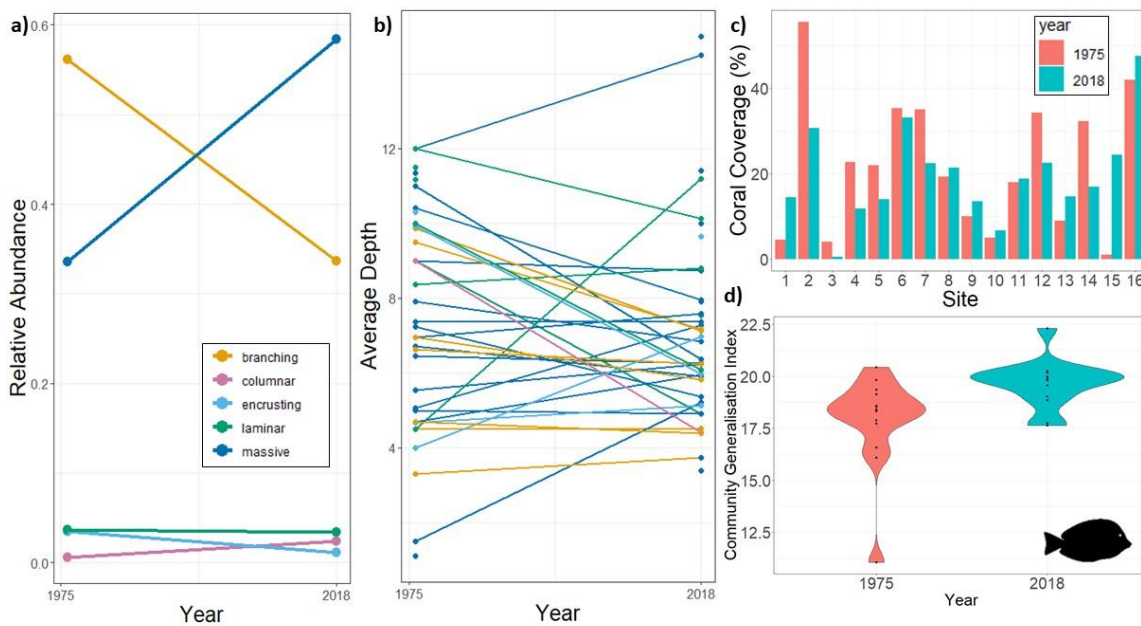


Figure 2.2. Summary of community reassembly in Nakagusuku Bay, showing **a)** Change in coral relative abundances between the years 1975-6 and 2018 calculated across all sites for the main coral growth forms, **b)** Changes in the average depth at which each coral genus was found in the years 1975-6 and 2018. Each line represents a coral genus, coloured by its most common growth form. **c)** Changes in average percentage coral coverage at each of the sites in the years 1975-6 and 2018. **d)** Change in the fish community generalisation index between the years 1975-6 and 2018 across all sites.

2.3.3 Coral genera and fish species community analyses

Results from the extrapolated rarefaction analyses showed that sample coverage estimates were similar for both years, with coral estimates being 97.6% and 99.7% and fish estimates being 89.8% and 92.1% for 1975-6 and 2018 respectively (Supplementary Fig. S2.3). This result supports the notion that we likely succeeded in replicating sampling strategies and effort adequately, generating a comparable sample. Thus, differences in community composition are highly likely to be attributable to community change rather than sampling protocol.

The richness of coral genera across all sites significantly increased between 1975-6 and 2018 ($t = -5.83$, $df=14$, $p<0.01$), with an increase at 14 of the 15 sites (Fig. 2.3b). However, across the whole bay, total coral genera richness only increased from 38 to 40, and when taking into account the slightly different sampling efforts, there was no overall change in richness (Supplementary Fig. S2.3f). In contrast, fish species richness decreased at 10 of the 14 of the sites but overall

changes between years was non-significant ($t=1.54$, $df=13$, $p=0.15$) (Fig. 2.3d). Between the years, the total number of fish species remained stable at 198, and extrapolations of richness to full sample coverage, confirmed that there was no significant difference in richness between years (Supplementary Fig. S2.3e). Site-based accumulation curves for fish genera and coral species were stable in both periods, and showed similar slopes, although the curves from 1975-6 had larger confidence intervals, suggesting that in the past, richness was more variable across sites (Supplementary Fig. S2.4). For both fishes and corals, the patterns in richness between sites remained similar across the years (Fig. 2.3). The sites with a higher richness in the 1970s generally still had a higher richness in 2018. Both the fish and coral PCAs revealed that community composition was distinctly different between 1975-6 and 2018, with two distinct clusters (Fig. 2.3a,c). The sites clustered similarly for the 1975-6 coral and fish cluster, and the 2018 fish clusters, with sites 12, 15 and 16 seeming to have more unique compositions. The 2018 sites for coral were more closely clustered together, suggesting potential homogenisation of coral communities.

Coral communities differed significantly between the years at each site (PERMANOVA: $F=7.94$, $R^2=0.21$, $p<0.01$) (Fig. 2.3a, Supplementary Table S2.1.). The SIMPER analyses did not identify any genera that significantly drove these changes. *Turbinara* accounted for the highest percentage of dissimilarity at 5%, followed by *Astreopora* (4.9%), *Psammocora* (4.4%), *Astrea* (4.3%), and *Pavona* (4.1%) (see Supplementary Table S2.3 for full list).

Fish communities also differed significantly between years (PERMANOVA: $F=5.53$, $R^2=0.17$, $p<0.01$) (Fig. 2.3c, Supplementary Table S2.2.). The results from the SIMPER analyses showed that there were no characteristic species or groups that were driving these changes. For example, *Acanthurus nigrofuscus* accounted for the highest percentage of dissimilarity between the years at 1.3% followed by *Ctenochaetus binotatus* (1.1%), *Sargocentron rubrum* (1.1%), *Meiacanthus sp.* (1.1%), *Chaetodon plebeius* (1.1%), *Siganus virgatus* (1%) (see Supplementary Table S2.4. For full list). However, considering there were a total of 309 species surveyed overall, and 65 of these species accounted for 50% of the variation between the years, there were still disproportional effects.

Overall, there was a significant increase in the community generalisation index (CGI) between the 1975-6 and 2018 ($t = -2.72$, $df=13$, $p=0.02$). The fish community transitioned to contain more habitat generalists at 10 of 14 sites (Fig. 2.2d), and the remaining sites only had a small decrease in CGI (i.e signs of a shift in the community consistent with specialisation). There appeared to be no spatial patterns in CGI change.

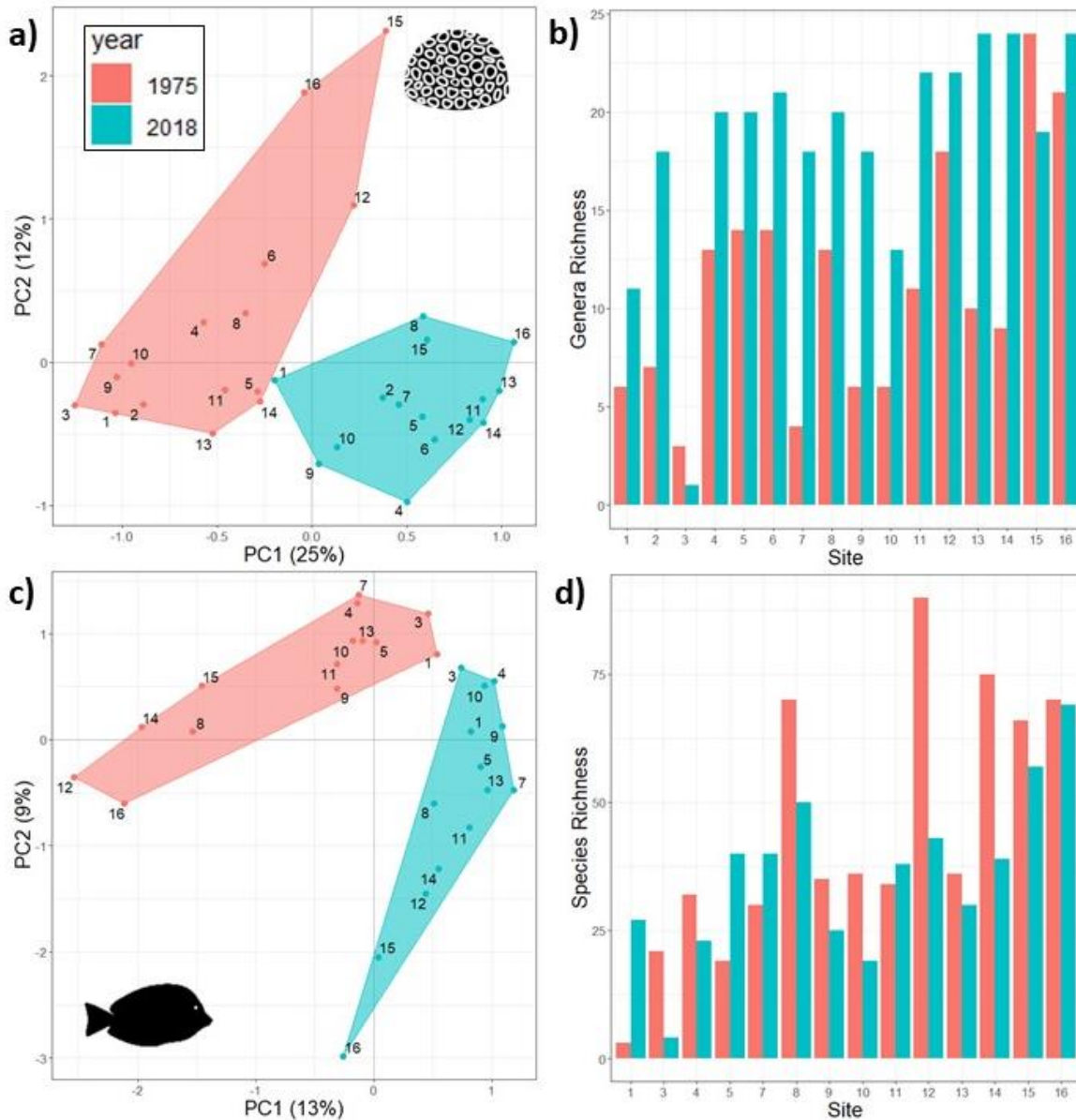


Figure 2.3. Summary of species and genera community changes for fish and coral across individual sites in Nakagusuku Bay, Okinawa. Sites are numbered according to distance from the coastline of the main island. **a)** Principal component analyses of coral genera present at each site for the years 1975-6 and 2018. **b)** Number of coral genera present at each site for the years 1975-6 and 2018. **c)** Principal component analyses of fish species present at each site for the years 1975-6 and 2018. **d)** Fish species richness at each site for the years 1975-6 and 2018.

2.3.4 Functional Trait based community space

When using PcoA to visualise the changes in the overall bay-wide coral community trait structure over time, the first two PcoA axes cumulatively explained 28.6% of the overall inertia (Fig. 2.4 a,b). The trait space was slightly altered by the loss of the genera *Mycedium* and *Cynaria* in 2018, and the addition of the genera *Trachyphyllia*, *Heteropsammia* and *Plerogyra*. Between the surveys, genera turnover occurred evenly across the trait space. The hull area of the coral trait space of individual sites increased slightly overall ($t=-2.6$, $df=15$, $p=0.02$) with only two sites (1 and 10) showing a shift in space (Supplementary Fig. S2.5a, b). Similarly, when using PcoA to visualise how the overall fish community trait structure has changed over time, the first two PcoA axes cumulatively explained 9.1% of the projected inertia (PcoA 1 = 5.3% and PcoA 2= 3.8%) (Fig. 2.4c, d). Between 1975 and 2018 there was very little change in trait space, and species turnover seems to be spread evenly across the space. When looking at the individual sites, site one experienced a large increase in trait space, and site three experienced a large decrease (Supplementary Fig. S2.6a, b). However, the rest of the sites stayed largely the same, the overall change in trait space hull area between the years was not significant ($t=0.39$, $df=13$, $p=0.70$). Species that were present in 1975-6 and then lost in 2018 that contributed to a contraction of trait space included *Epinephelus quoyanus*, *Epinephelus cyanopodus*, *Epinephelus fasciatus*, *Canthigaster janthinoptera*, *Koumansetta hectori* and *Aeoliscus strigatus*. Species that were gained in 2018 compared to 1975-6 that expanded the trait space included *Chromis alleni*, *Chromis ovatiformes*, *Pomacentrus nigromarginatus*, *Lutjanus gibbus*, *Lutjanus bohar* and *Gnathodentex aureolineatus*.

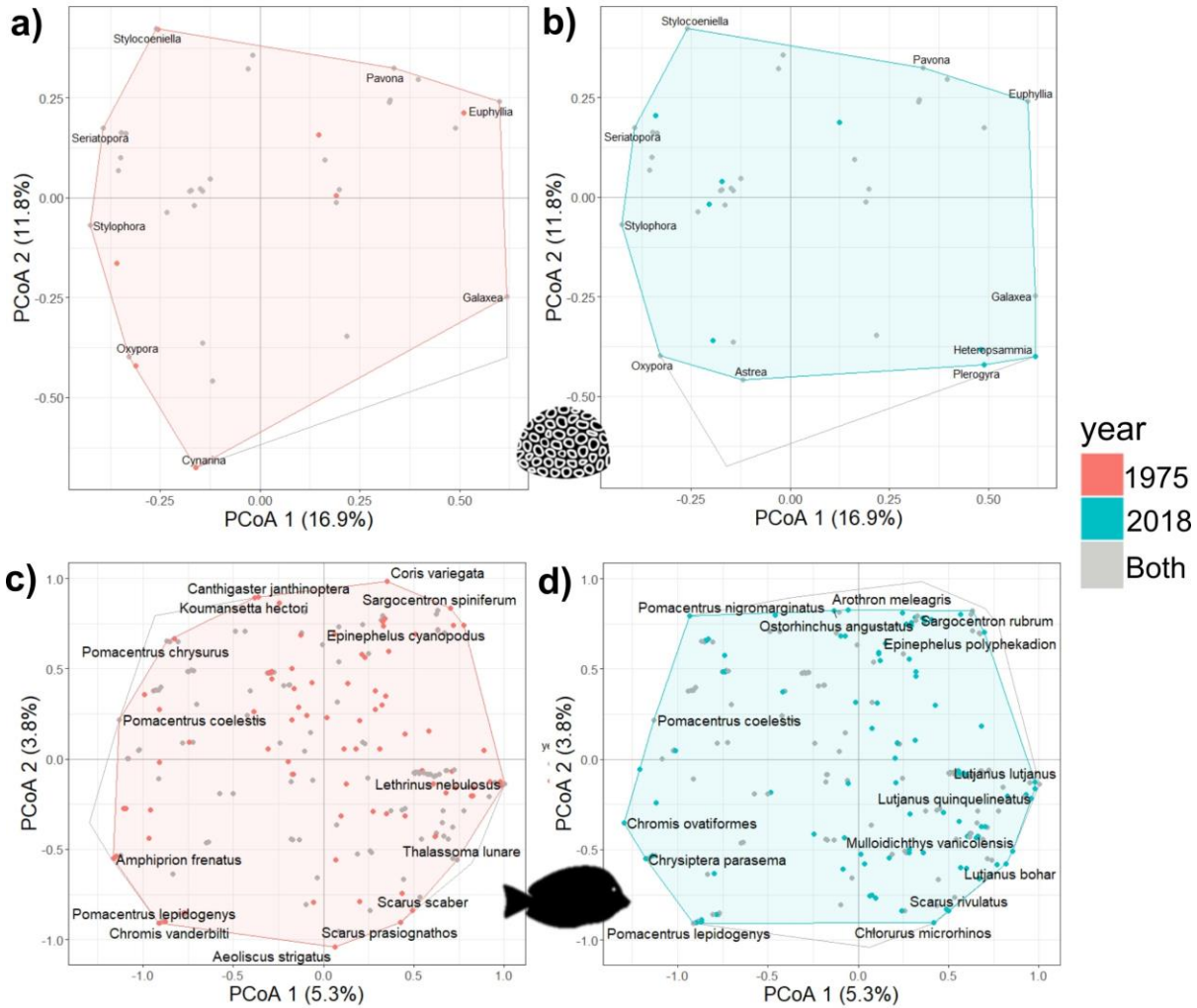


Figure 2.4. Summary of changes in functional trait space in Nakagusuku Bay, Okinawa between 1975-2018. **a)** Gower distance-based principal coordinate analyses (PCoA) of coral traits present across the whole study area for 1975-6. **b)** PCoA based on the Gower distances of coral traits for 2018. **c)** PCoA based on the Gower distances of fish traits for 1975-6. Points represent individual fish species. **d)** PCoA based on the Gower distances of fish traits for 2018. Grey convex hull represents overall site wide trait space across both years, coloured hull represents year specific trait space. Coloured points represent species or genera present only in the corresponding year, whereas grey points represent species or genera present across both study years.

2.4 Discussion

Over the past four decades, the coral reef communities of Nakagusuku Bay have been subject to the effects of extensive anthropogenic disturbances, most noticeably coastal development and three global bleaching events. Thus, we expected a loss of coral cover, a reduction in genera and species richness, and a community shift towards more stress-tolerant species that would be associated with a loss of ecosystem functions. By contrast, we discovered that while a significant change in fish and coral community compositions occurred over time, the range of functions remained stable. The overall community shift across the bay was characterised by a turnover of species and genera across the entire functional trait space, not a shift to groups with similar traits and associated contraction of trait space. However, we found that the fish communities have become dominated by habitat generalists, indicating a homogenisation of the habitat association trait, which was not considered in our trait-space analysis. We observed uneven declines in coral coverage, with associated inconsistent patterns in richness changes of both fish and coral. Our results also indicate ‘depth compression’ in corals, and a shift in dominance from branching to massive/ submassive coral morphologies. Our results support the hypothesis that the combined anthropogenic stressors of urban coral reefs alter community structure towards more generalist species, with specific findings of local depth shifts. But, thus far, these stressors do not appear to have resulted in a loss of ecosystem function.

Coral coverage declined at half of the sites. These sites were predominantly located near to landfilled areas and non-natural sections of the bay’s coastline. This geographic pattern suggests that coral coverage in the bay may be highly susceptible to such localised anthropogenic impacts. In contrast, all but one of the sites experienced a uniform increase in coral genera richness, although bay wide richness remained stable. This increase could be explained by the observed shift in dominance from genera with branching to massive growth forms. Die offs of branching corals have been recorded globally as a result of bleaching events, and thus the loss of branching corals at our sites due to thermal stress could have allowed for the recruitment of a more diverse array of less competitive, yet more disturbance resilient genera which already persisted within the bay but in lower abundances (Adjeroud *et al.*, 2018). However, although sampling effort was predicted to be comparable between the years across the whole bay, a level of uncertainty remains because detailed sampling methods were not reported in 1975 and despite our best efforts to take this into account with rarefaction analyses, we may have sampled differently in 2018.

Sites that increased in coral cover and richness did not increase in fish richness. Site specific reductions in fish species richness could be linked to the shifts in coral morphologies (Darling *et al.*, 2017). Branching corals are more structurally complex than massive corals, so their loss at our sites may have reduced habitat availability for more specialised fish species (Richardson *et*

al., 2018), as indicated by a significant increase across sites in the community generalisation index. The sites also experienced significant shifts in fish species composition. Generalist species such as *Acanthurus nigrofuscus*, *Ctenochaetus binotatus* and *Siganus virgatus* had very high SGIs, and the SIMPER analyses indicated that an increase in their presence across sites from 1975-6 to 2018 (Stuart-Smith *et al.*, 2021).

Significant shifts in coral community composition between the years appear to be driven by the introduction of genera with species known to have tolerance to turbidity and bleaching such as *Turbinaria*, *Astreopora*, and *Psammocora* (Marshall and Baird, 2000). Although these genera were present at some sites in the 1970's, they were recorded across more sites in 2018. It is not possible to quantify with our data whether bleaching events or local disturbances are driving such shifts, as that would require time series data for ecological and environmental variables. However, our results match patterns observed on Singapore's urban turbid reefs over a 27 year continuous time series analysis, which attributed community change to both thermal stress events and turbidity (Guest *et al.*, 2016). These reefs also experienced community turnover, although there was no evidence of shifts from branching to more stress tolerant species, possibly due to these shifts occurring prior to the beginning of monitoring. Most noticeably, Singapore's reefs underwent a 'reef compression' (Guest *et al.*, 2016), and we mirror this finding in Nakagusuku bay, with coral genera that were found deeper on average in the 1970s shifting shallower in 2018, and those found at shallower depths in 1975-76 shifting deeper. This phenomenon could be attributed to the effects of thermal stress events and bleaching, which are more pronounced in the shallows, resulting in higher mortality rates in the shallows (Guest *et al.*, 2016; Chow *et al.*, 2019). Deeper colonies may be thermally protected from bleaching, yet increased turbidity levels due to local stressors may reduce light levels past the critical point for phototrophic organisms (Browne, 2012). Our corroborative finding of 'reef compression' suggests these types of community shifts could be typical for coastal coral reefs exposed to urbanisation (Guest *et al.*, 2016). With continuing coastal urbanisation and thermal stress events, reef compression could continue to reduce suitable habitat area for coral reef species. If such compression occurs at a wider scale, it could result in significant losses of coral reef ecosystems, and the species which depend on them.

Although community composition changed, the overall trait space for both fish and coral remained similar between the years. There was a turnover of species and genera, but these were lost and gained evenly across the trait space. Corals had high sample coverage between the years, with the recorded total richness being similar to the predicted total richness with extrapolated rarefaction curves. This pattern suggests that the observed turnovers captured the actual change in the community over this time period. However, fish had lower sample coverage between the years. When extrapolated to full coverage for both years, species richness increased. Although

the total richness was not significantly different between years, these additional species may have increased the fish functional trait spaces. However, our current results indicate that for both fish and coral, species and genera that were lost were replaced with species and genera with similar traits. The turnover of taxa with similar traits suggests that their functional roles remained (McWilliam *et al.*, 2020), inferring the maintenance of ecosystem functioning across the whole study area between the years (Mouillot *et al.*, 2013). However, the trait-based analyses also did not account for abundance. This could be important as for example, *Acropora* was once the dominant coral genus, but has now been reduced to just 4% of the total coral colonies surveyed. Although there are some remnant colonies, they will not be providing as much of the important functions as they once did (McWilliam *et al.*, 2020). Yet, in terms of reef resilience, these remnant populations may be critical for the recovery of reefs post-disturbance for both coral and fish (Kayal *et al.*, 2018).

Trait space constancy could indicate that at the time of the original survey in 1975-76 the study area was already subject to human disturbances. Corals and fish with unique traits that could only survive in 'pristine' environments may have already been lost by the mid 1970s due to the impacts of World War Two, leaving a suite of more generalist species (Omori, 2011). Under further degradation, we may not have observed further shrinkage, as if the initial trait-based shift had already occurred, this new community in 1975-76 may have been more resilient to further disturbances. Alternatively, for fish, trait space could have been maintained due to a shift from clear water reef specialists to sandy or mud bottom turbid specialists, especially in sites with a high loss of coral coverage (Brandl *et al.*, 2016). This implies that functional losses are not linearly linked to disturbance gradients.

It must be noted that due to the historical nature of the 1975-6 dataset, we updated survey methods in 2018 to increase robustness and statistical power for potential future surveys. Details of the original survey sites were meticulously recorded (Yamazato and Nishihara, 1977), allowing us to resample the exact locations. However, historical coral surveys were not carried out along transects, but with visual observation survey dives across representative reef habitats (reef, reef slope and reef base). In 2018, we used quadrat methodology, standardising our survey area, and allowing us to calculate percentage cover. In 1975-6, a small number of quantitative quadrat surveys, were conducted with these same methods with much fewer replicates. Historical fish surveys were carried out across a transect length of 50m, matching our individual transect lengths in 2018. However, observability would have been influenced by transect width, swim speed and visibility, details of which were not recorded. As the sites were all based on small patch reefs, it is likely that the original surveys covered a relatively large area in comparison to overall reef size, capturing an accurate representation of the communities. To ensure the exact reefs were included,

and to increase the future repeatability of the surveys, we used standardised sampling procedures and increased replicate numbers of surveys across the same reefs. Both historical and current surveys sampled reef communities on singular dives lasting about 60 minutes, suggesting similar sampling efforts, and this was verified by the high similar sample coverage predictions in the rarefaction analysis (Supplementary Fig. S2.3). Abundance results would be more sensitive to sampling effort, but we only compared presence/absences of taxa, except for coral percentage cover where the quadrat method was directly comparable. Presence/ absence data is well used in community ecology, especially in temporal studies, as they show species losses and gains, providing insight into changing ecological processes (Legendre, 2019).

Temporal comparisons are difficult where the historical sampling process was not described in enough detail, as differences may be attributable to methods rather than community change. We accounted for this to the best of our ability by performing statistical tests to show sampling effort, supporting the validity of our approach. Furthermore, our results show that many species were not observed in 2018, despite predicted equal or higher sampling efforts (Supplementary Table S2.1, Table S2.2.). If our findings were due to differences in methods, we would expect to find the same species that were recorded in the 1970's, plus additional species with the increased sampling effort. Contrastingly, we found that seven coral genera and 107 fish species were not recorded in 2018, suggesting they truly disappeared from our sites. The loss of a large proportion of taxa strengthens the case for disturbance induced community turnover, and reduces the likelihood that the results were due to altered sampling protocols. However, working with historical data holds challenges related to how scientific methods and technology have changed over time. Given the differences in our methods, we acknowledge that species richness differences between historical and modern surveys may be due to challenges with comparing fish data from different surveys, relating to observer errors, potential differences in sampling efforts, or site differences, despite our best efforts to minimise and avoid such issues. Comparability issues such as these are a common when using older survey data collected before the introduction of standardised sampling methods (Tingley and Beissinger, 2009). However, such data should not be discounted for science, as it provides an invaluable resource for understanding community change and shifting historical baselines (Richards *et al.*, 2008).

Our research highlights that urban turbid reefs such as those in Nakagusuku Bay may have underlying resilience to disturbances, as we did not observe large losses in fish and coral richness, and coral coverage was maintained across most sites. This could be a relic due to extinction lag, with low abundances of species that survived through disturbances persisting in unfavourable conditions with reduced growth, survival, and reproduction (Graham *et al.*, 2007). Shifts to communities dominated by massive and sub-massive corals could be an early indicator of a

tipping point to an alternate stable state (Mellin *et al.*, 2019). Corals with this growth form are still vulnerable to longer term, severe thermal stress events, which are predicted to recur at an increasing frequency in the near future. If these corals experience high levels of mortality, they are unlikely to be able to recover due to their slow growth rates and reproductive strategies (Darling *et al.*, 2012). However, reefs may be able to survive at mid-depths, maintaining ecosystem functions and providing remnant populations for post-disturbance recovery. Disturbed reefs may have reduced structural complexity, but our results indicate that the corals and associated fish species are continuing to provide critical functional roles. Thus, under urbanisation and thermal stress, coral reef communities are likely to be significantly altered but not disappear completely (Robinson *et al.*, 2019). The shifts towards urban turbid reefs is becoming increasingly common worldwide (Heery *et al.*, 2018), and these functioning reef systems may have overlooked or underappreciated conservation value.

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2.6 Supplementary Materials for Chapter Two

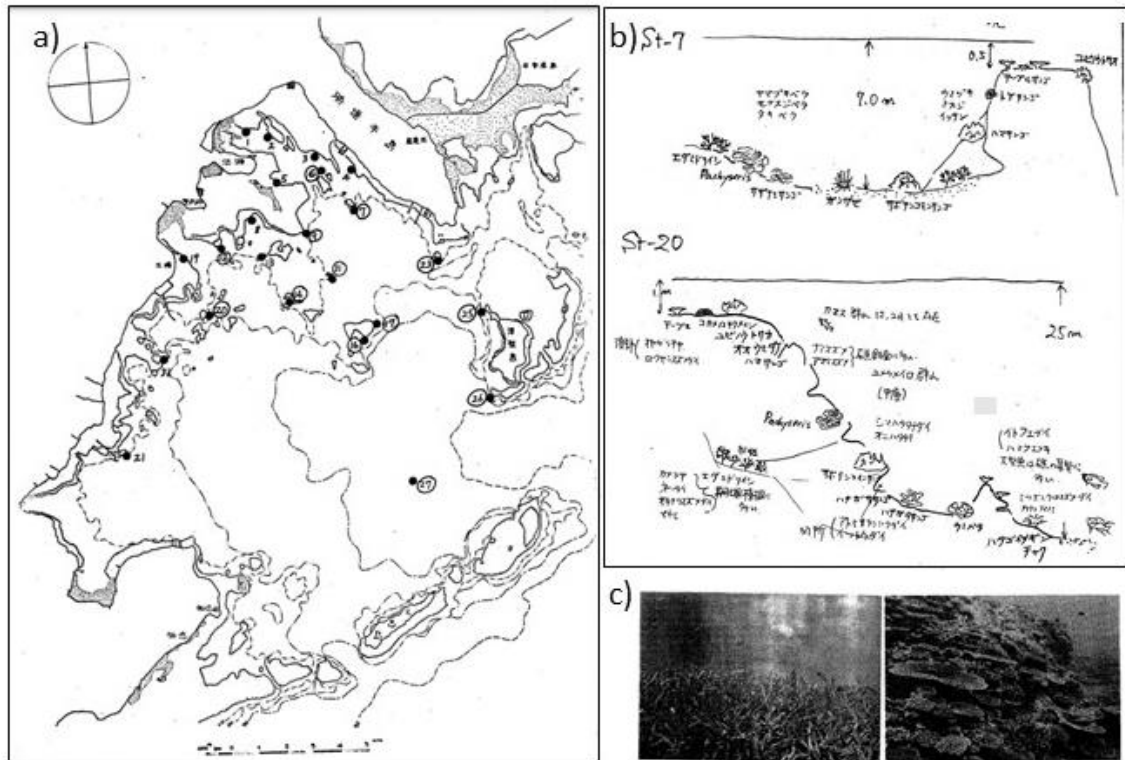


Figure S2.1 a) Original survey site map from Yamazato and Nishihara (1977). This map was georeferenced and used to determine GPS co-ordinates of each site for replicate surveys in 2018. Sites names were changed in 2018 to reflect distance from the Okinawa main island. b) Diagrams of Site 7 (now Site 5) and Site 20 (now Site 8) showing distinctive topography, depth and representative coral genera present in 1977 (Yamazato and Nishihara 1977). Such diagrams were available for each of the sites that resurveyed, enabling accurate relocation of survey sites. c) Images taken of coral assemblages in Nakagusuku Bay during 1975-6 (Yamazato and Nishihara, 1977). Images show dominance of plating and branching corals, which have significantly reduced in coverage in the present day.

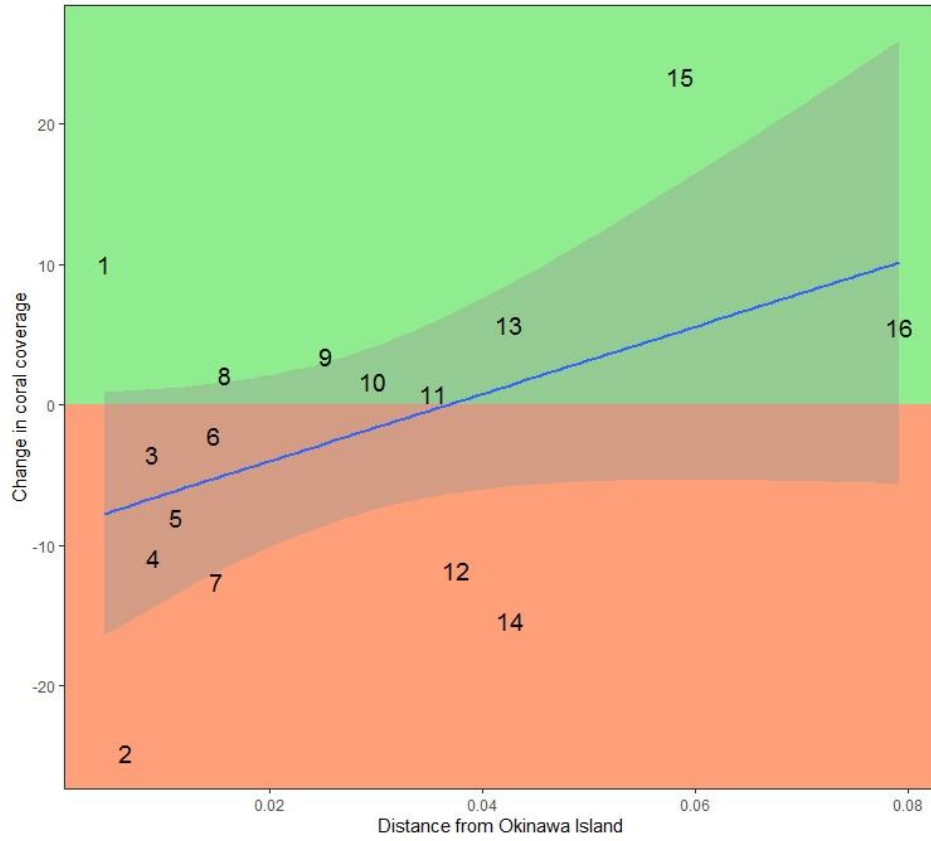


Figure S2.2) Relationship between site distance from Okinawa main island coastline and change in coral coverage between 1975-6 and 2018. Line shows linear model with 95% confidence intervals ($R^2=0.13$, $F(1, 14)= 3.29$, $P=0.09$). Numbers indicate site names.

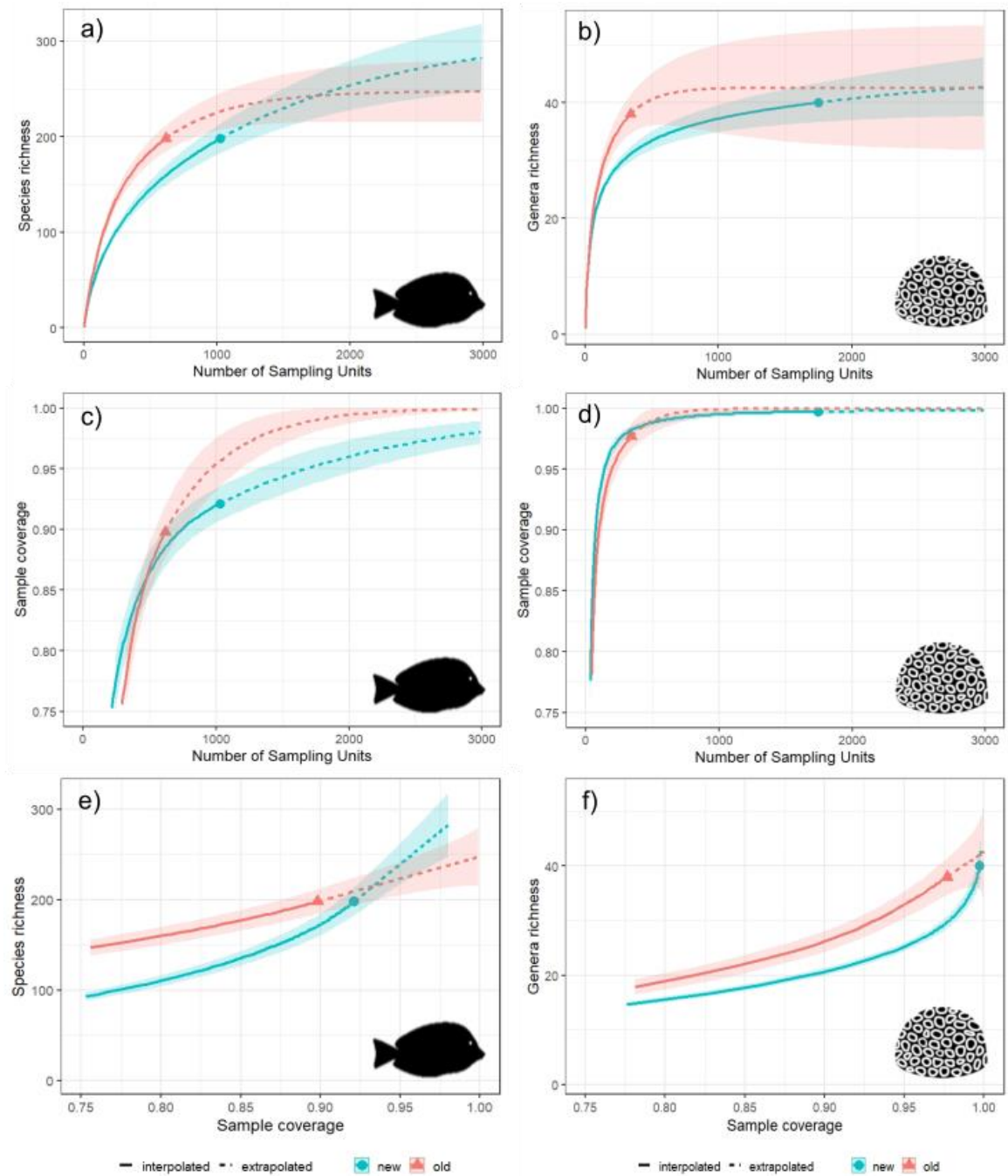


Figure. S2.3) Rarefaction (solid line segment) and extrapolation (dotted line segments) sampling curves with 95% confidence intervals (shaded areas) for the fish species and coral genera. **a, b)** Sample size – based curves for fish species and coral genera, **c, d)** Sample completeness curves based on fish species and coral genera, **e, f)** Coverage-based curves for fish species and coral genera.

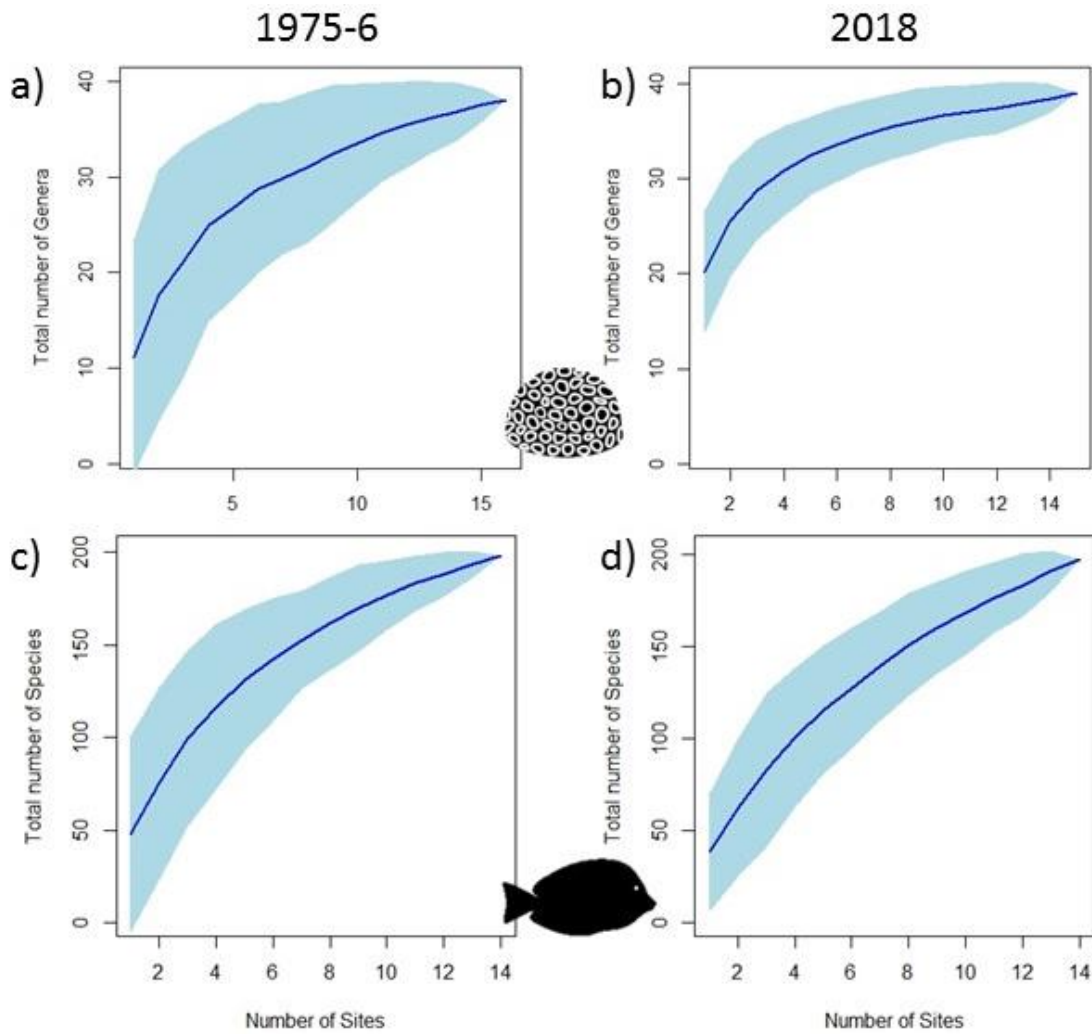


Figure S2.4) Genera and species richness accumulation curves produced by sequentially adding sites in a random order and calculating total richness, run over 100 permutations. Light blue bands represent 95% confidence intervals. **a)** Coral genera richness accumulation curve for 1975-6. **b)** Coral genera richness accumulation curve for 2018. **c)** Fish species richness accumulation curve for 1975-6. **d)** Fish species richness accumulation curve for 2018.

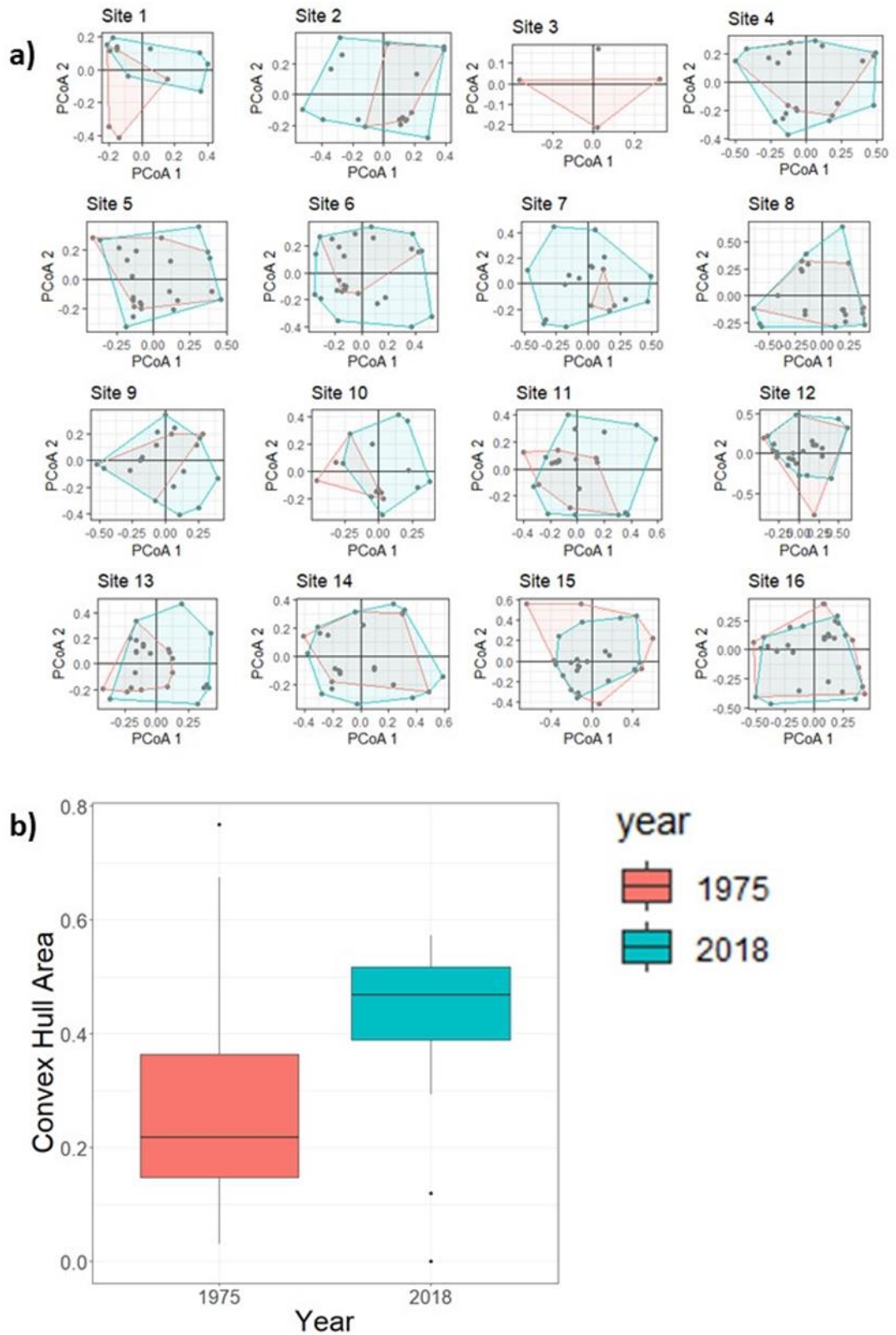


Figure S2.5. a) Gower distance-based principal coordinate analyses (PCoA) of coral traits present across each study site. Trait space for 1975-6 is represented by the pink polygon, and trait-space for 2018 is represented by the blue polygon. Grey dots represent individual coral genera. **b)** Boxplot of the site-based trait-space polygon hull areas for 1976-6 and 2018.

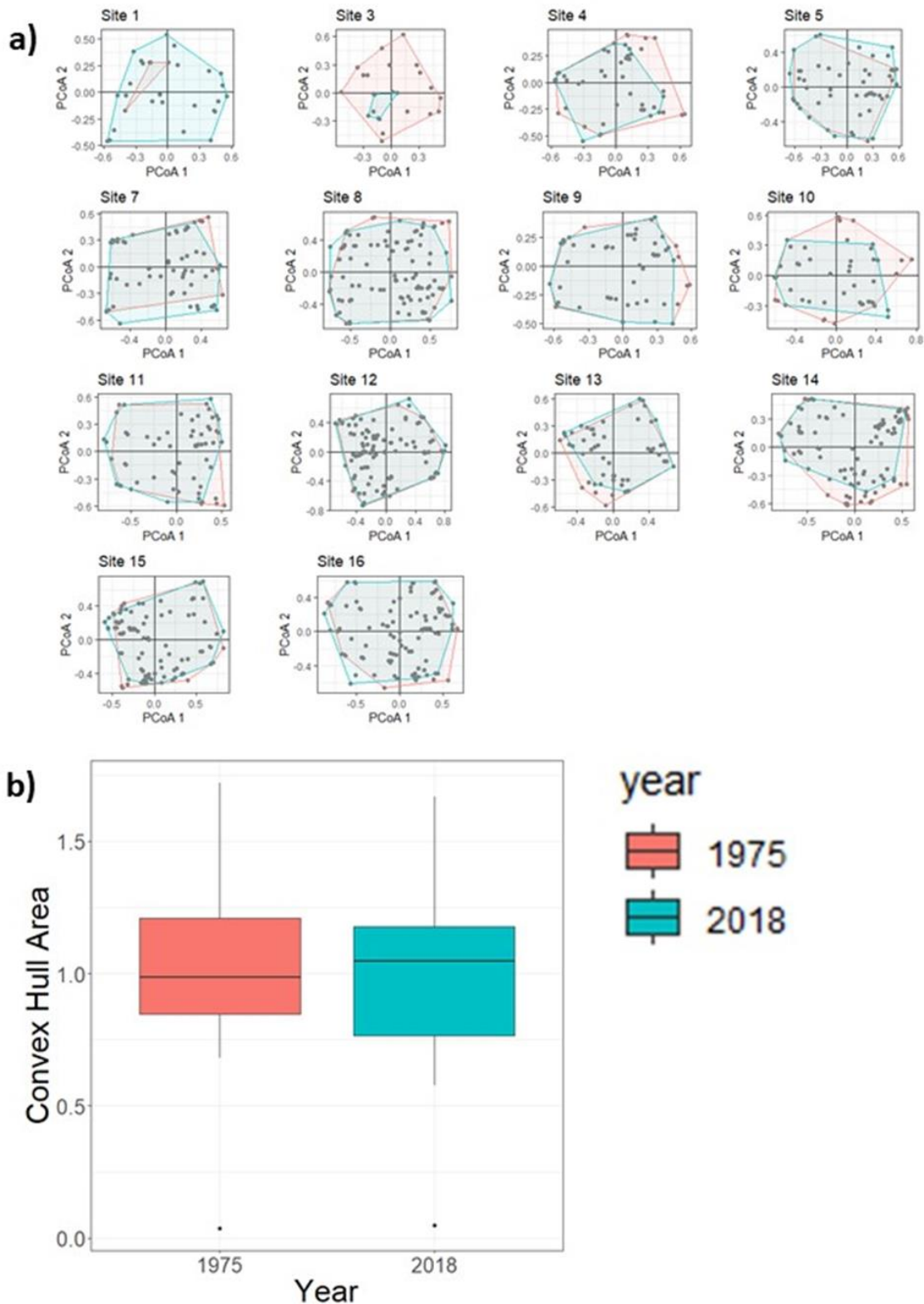


Figure S2.6. a) Gower distance-based principal coordinate analyses (PCoA) of fish traits present across each study site. Trait space for 1975-6 is represented by the pink polygon, and trait-space for 2018 is represented by the blue polygon. Grey dots represent individual fish species. **b)** Boxplot of the site-based trait-space polygon hull areas for 1976-6 and 2018.

Table S2.1. Coral genera recorded in 1975-6 only, both 1975-6 and 2018, and 2018 only at 16 sites across Nakagusuku Bay.

Recorded 1975-6 only	Recorded 1975-6 and 2018	Recorded 2018 only
<i>Coelastrea</i>	<i>Acropora</i>	<i>Alveopora</i>
<i>Cynarina</i>	<i>Astrea</i>	<i>Coscinaraea</i>
<i>Danafungia</i>	<i>Astreopora</i>	<i>Heteropsammia</i>
<i>Lithophyllon</i>	<i>Cyphastrea</i>	<i>Leptoria</i>
<i>Merulina</i>	<i>Dipsastraea</i>	<i>Leptoseris</i>
<i>Mycedium</i>	<i>Echinophyllia</i>	<i>Plerogyra</i>
<i>Sandalolitha</i>	<i>Echinopora</i>	<i>Symphyllia</i>
	<i>Euphyllia</i>	<i>Trachyphyllia</i>
	<i>Favites</i>	
	<i>Fungia</i>	
	<i>Fungiidae_family</i>	
	<i>Galaxea</i>	
	<i>Goniastrea</i>	
	<i>Goniopora</i>	
	<i>Hydnophora</i>	
	<i>Leptastrea</i>	
	<i>Lobophyllia</i>	
	<i>Montipora</i>	
	<i>Oulastrea</i>	
	<i>Oxypora</i>	
	<i>Pachyseris</i>	
	<i>Pavona</i>	
	<i>Pectinia</i>	
	<i>Platygyra</i>	
	<i>Pocillopora</i>	
	<i>Porites</i>	
	<i>Psammocora</i>	
	<i>Seriatopora</i>	
	<i>Stylocoeniella</i>	
	<i>Stylophora</i>	
	<i>Turbinaria</i>	

Table S2.2. Reef fish species recorded in 1975-6 only, both 1975-6 and 2018, and 2018 only at 14 sites across Nakagusuku Bay.

Recorded 1975-6 only	Recorded both years	Recorded 2018 only
<i>Acanthurus bariene</i>	<i>Abudefduf sexfasciatus</i>	<i>Abudefduf septemfasciatus</i>
<i>Acanthurus triostegus</i>	<i>Abudefduf vaigiensis</i>	<i>Acanthurus blochii</i>
<i>Aeoliscus strigatus</i>	<i>Acanthurus lineatus</i>	<i>Acanthurus maculiceps</i>
<i>Amblygobius phalaena</i>	<i>Acanthurus olivaceus</i>	<i>Acanthurus nigricauda</i>
<i>Amphiprion clarkii</i>	<i>Amblyglyphidodon curacao</i>	<i>Acanthurus nigrofuscus</i>
<i>Amphiprion ocellaris</i>	<i>Amblyglyphidodon leucogaster</i>	<i>Anampses geographicus</i>
<i>Amphiprion perideraion</i>	<i>Amphiprion frenatus</i>	<i>Arothron meleagris</i>
<i>Amphiprion sandaracinos</i>	<i>Balistoides conspicillum</i>	<i>Arothron nigropunctatus</i>
<i>Anampses caeruleopunctatus</i>	<i>Bodianus loxozonus</i>	<i>Balistapus undulatus</i>
<i>Anampses meleagrides</i>	<i>Caesio caeruleaurea</i>	<i>Balistoides viridescens</i>
<i>Atrosalarias holomelas</i>	<i>Caesio cuning</i>	<i>Bodianus izuensis</i>
<i>Aulostomus chinensis</i>	<i>Caesio teres</i>	<i>Calotomus japonicus</i>
<i>Bodianus axillaris</i>	<i>Canthigaster valentini</i>	<i>Caranx melampygus</i>
<i>Bodianus perditio</i>	<i>Centropyge ferrugata</i>	<i>Centropyge bispinosa</i>
<i>Canthigaster janthinoptera</i>	<i>Centropyge vrolikii</i>	<i>Cephalopholis argus</i>
<i>Centropyge bicolor</i>	<i>Chaetodon argentatus</i>	<i>Cephalopholis boenak</i>
<i>Centropyge tibicen</i>	<i>Chaetodon auriga</i>	<i>Cephalopholis leopardus</i>
<i>Cephalopholis urodeta</i>	<i>Chaetodon baronessa</i>	<i>Chaetodon auripes</i>
<i>Cetoscarus ocellatus</i>	<i>Chaetodon ephippium</i>	<i>Chaetodon guentheri</i>
<i>Chaetodon bennetti</i>	<i>Chaetodon kleinii</i>	<i>Cheilinus chlorourus</i>
<i>Chaetodon citrinellus</i>	<i>Chaetodon lunula</i>	<i>Cheilinus fasciatus</i>
<i>Chaetodon melannotus</i>	<i>Chaetodon lunulatus</i>	<i>Cheilio inermis</i>
<i>Chaetodon plebeius</i>	<i>Chaetodon ornatissimus</i>	<i>Cheilodipterus intermedius</i>
<i>Chaetodon reticulatus</i>	<i>Chaetodon speculum</i>	<i>Chlorurus microrhinos</i>
<i>Chaetodon ulietensis</i>	<i>Chaetodon vagabundus</i>	<i>Choerodon jordani</i>
<i>Chaetodon xanthurus</i>	<i>Chaetodontoplus mesoleucus</i>	<i>Chromis albicauda</i>
<i>Cheilodipterus macrodon</i>	<i>Cheilinus trilobatus</i>	<i>Chromis alleni</i>
<i>Cheilodipterus quinquelineatus</i>	<i>Chlorurus bowersi</i>	<i>Chromis delta</i>
<i>Cheiloprion labiatus</i>	<i>Chlorurus sordidus</i>	<i>Chromis notata</i>
<i>Chromis lepidolepis</i>	<i>Choerodon fasciatus</i>	<i>Chromis ovatiformes</i>
<i>Chromis ovatiformis</i>	<i>Choerodon schoenleinii</i>	<i>Chromis xanthura</i>

<i>Chromis</i> sp.	<i>Chromis atripes</i>	<i>Chrysiptera parasema</i>
<i>Chromis vanderbilti</i>	<i>Chromis chrysur</i>	<i>Chrysiptera starcki</i>
<i>Chromis viridis</i>	<i>Chromis flavomaculata</i>	<i>Chrysiptera unimaculata</i>
<i>Chromis weberi</i>	<i>Chromis fumea</i>	<i>Cirrhilabrus katherinae</i>
<i>Chromis xanthochira</i>	<i>Chromis margaritifera</i>	<i>Coris batuensis</i>
<i>Chrysiptera biocellata</i>	<i>Chromis ternatensis</i>	<i>Coris dorsomacula</i>
<i>Chrysiptera</i> sp.	<i>Chrysiptera cyanea</i>	<i>Coris gaimard</i>
<i>Cirrhilabrus temminckii</i>	<i>Chrysiptera glauca</i>	<i>Ctenochaetus binotatus</i>
<i>Cirrhitichthys aprinus</i>	<i>Chrysiptera rex</i>	<i>Ctenochaetus striatus</i>
<i>Cromileptes altivelis</i>	<i>Cirrhilabrus cyanopleura</i>	<i>Dascyllus trimaculatus</i>
<i>Ctenochaetus strigosus</i>	<i>Diploprion bifasciatum</i>	<i>Diagramma pictum</i>
<i>Dascyllus aruanus</i>	<i>Epinephelus merra</i>	<i>Dischistodus prosopotaenia</i>
<i>Dascyllus reticulatus</i>	<i>Forcipiger longirostris</i>	<i>Epibulus insidiator</i>
<i>Diademichthys lineatus</i>	<i>Gomphosus varius</i>	<i>Epinephelus polyphekadion</i>
<i>Ecsenius bicolor</i>	<i>Halichoeres prosopeion</i>	<i>Forcipiger flavissimus</i>
<i>Elagatis bipinnulata</i>	<i>Hemigymnus fasciatus</i>	<i>Gnathodentex aureolineatus</i>
<i>Epinephelus cyanopodus</i>	<i>Heniochus chrysostomus</i>	<i>Halichoeres chrysur</i>
<i>Epinephelus fasciatus</i>	<i>Labroides bicolor</i>	<i>Halichoeres nebulosus</i>
<i>Epinephelus quoyanus</i>	<i>Labroides dimidiatus</i>	<i>Halichoeres scapularis</i>
<i>Fistularia commersonii</i>	<i>Lutjanus vitta</i>	<i>Heniochus varius</i>
<i>Halichoeres hortulanus</i>	<i>Meiacanthus kamoharai</i>	<i>Labrichthys unilineatus</i>
<i>Halichoeres leucurus</i>	<i>Naso lituratus</i>	<i>Lutjanus bohar</i>
<i>Halichoeres melanocheir</i>	<i>Nemateleotris magnifica</i>	<i>Lutjanus fulviflamma</i>
<i>Halichoeres trimaculatus</i>	<i>Neoglyphidodon melas</i>	<i>Lutjanus gibbus</i>
<i>Hemigymnus melapterus</i>	<i>Neoglyphidodon nigroris</i>	<i>Lutjanus lutjanus</i>
<i>Heniochus acuminatus</i>	<i>Paraluteres prionurus</i>	<i>Lutjanus quinquelineatus</i>
<i>Heniochus monoceros</i>	<i>Parapercis pacifica</i>	<i>Macolor niger</i>
<i>Heniochus singularius</i>	<i>Parupeneus barberinoides</i>	<i>Mulloidichthys vanicolensis</i>
<i>Iniistius dea</i>	<i>Plagiotremus tapeinosoma</i>	<i>Myripristis hexagona</i>
<i>Koumansetta hectori</i>	<i>Plectorhinchus chaetodonoides</i>	<i>Naso hexacanthus</i>
<i>Labracinus</i> sp.	<i>Plectropomus leopardus</i>	<i>Neoniphon sammara</i>
<i>Labropsis manabei</i>	<i>Pomacanthus semicirculatus</i>	<i>Neopomacentrus cyanomos</i>
<i>Lethrinus nebulosus</i>	<i>Pomacentrus bankanensis</i>	<i>Neopomacentrus violascens</i>
<i>Lutjanus kasmira</i>	<i>Pomacentrus brachialis</i>	<i>Oplegnathus punctatus</i>

<i>Meiacanthus</i> sp.	<i>Pomacentrus chrysurus</i>	<i>Ostorhinchus angustatus</i>
<i>Myripristis murdjan</i>	<i>Pomacentrus coelestis</i>	<i>Ostorhinchus endekataenia</i>
<i>Naso brevirostris</i>	<i>Pomacentrus lepidogenys</i>	<i>Paracaesio xanthura</i>
<i>Nematalosa japonica</i>	<i>Pomacentrus moluccensis</i>	<i>Parapercis clathrata</i>
<i>Ostorhinchus ishigakiensis</i>	<i>Pomacentrus nagasakiensis</i>	<i>Parapercis hexophtalma</i>
<i>Ostorhinchus properuptus</i>	<i>Pomacentrus philippinus</i>	<i>Parupeneus barberinus</i>
<i>Ostracion cubicus</i>	<i>Pomachromis richardsoni</i>	<i>Parupeneus multifasciatus</i>
<i>Ostracion meleagris</i>	<i>Ptereleotris evides</i>	<i>Parupeneus spilurus</i>
<i>Oxymonacanthus longirostris</i>	<i>Pygoplites diacanthus</i>	<i>Plagiotremus rhinorhynchos</i>
<i>Paracirrhites arcatus</i>	<i>Sargocentron rubrum</i>	<i>Plectorhinchus lessonii</i>
<i>Paracirrhites forsteri</i>	<i>Scarus ghobban</i>	<i>Pomacanthus sexstriatus</i>
<i>Parapercis cylindrica</i>	<i>Scolopsis bilineata</i>	<i>Pomacentrus alexanderae</i>
<i>Parupeneus crassilabris</i>	<i>Siganus argenteus</i>	<i>Pomacentrus amboinensis</i>
<i>Parupeneus cyclostomus</i>	<i>Siganus virgatus</i>	<i>Pomacentrus nigromarginatus</i>
<i>Parupeneus indicus</i>	<i>Sufflamen chrysopterum</i>	<i>Pomacentrus vaiuli</i>
<i>Pervagor melanocephalus</i>	<i>Symphorus nematophorus</i>	<i>Prionurus scalprum</i>
<i>Plagiotremus laudandus</i>	<i>Thalassoma hardwicke</i>	<i>Pseudodax moluccanus</i>
<i>Platax pinnatus</i>	<i>Thalassoma lunare</i>	<i>Pseudojuloides elongatus</i>
<i>Plectroglyphidodon dickii</i>	<i>Thalassoma lutescens</i>	<i>Ptereleotris microlepis</i>
<i>Plectroglyphidodon lacrymatus</i>	<i>Zanclus cornutus</i>	<i>Pterocaesio marri</i>
<i>Pomacanthus imperator</i>	<i>Zebrasoma scopas</i>	<i>Rhinecanthus rectangulus</i>
<i>Pomacentrus</i> sp.	<i>Zebrasoma velifer</i>	<i>Sargocentron spinosissimum</i>
<i>Pomachromis</i> sp.		<i>Scarus chameleon</i>
<i>Pseudocaranx dentex</i>		<i>Scarus festivus</i>
<i>Pseudocheilinus hexataenia</i>		<i>Scarus forsteni</i>
<i>Pterocaesio tile</i>		<i>Scarus fuscocaudalis</i>
<i>Pterois lunulata</i>		<i>Scarus globiceps</i>
<i>Rhinecanthus aculeatus</i>		<i>Scarus hypselopterus</i>
<i>Sargocentron spiniferum</i>		<i>Scarus ovifrons</i>
<i>Scarus prasiognathos</i>		<i>Scarus rivulatus</i>
<i>Scarus scaber</i>		<i>Scarus rubroviolaceus</i>
<i>Scarus</i> sp.		<i>Scarus schlegeli</i>
<i>Siganus puellus</i>		<i>Scolopsis affinis</i>
<i>Siganus unimaculatus</i>		<i>Scolopsis lineata</i>

<i>Stethojulis interrupta</i>	<i>Scolopsis monogramma</i>
<i>Synodus variegatus</i>	<i>Stegastes altus</i>
<i>Syphraena</i> sp.	<i>Stegastes fasciolatus</i>
<i>Thalassoma amblycephalum</i>	<i>Stegastes nigricans</i>
<i>Thalassoma janseni</i>	<i>Stegastes obreptus</i>
<i>Thalassoma trilobatum</i>	<i>Stegastes punctatus</i>
<i>Trachyrhamphus serratus</i>	<i>Stethojulis trilineata</i>
<i>Zebrasoma flavescens</i>	<i>Thalassoma quinquevittatum</i>
	<i>Upeneus tragula</i>

Table S2.3. SIMPER analyses of average presence/ absence of coral genera contributing to differences (Bray-Curtis distance) between 1975-6 and 2018 at 16 sites across Nakagusuku Bay.

Genera	Mean 1975-6	Mean 2018	Consistency ratio	Cumulative contribution
<i>Turbinaria</i>	0.063	0.867	1.825	0.052
<i>Astreopora</i>	0.250	1.000	1.534	0.101
<i>Psammocora</i>	0.250	0.867	1.325	0.146
<i>Astrea</i>	0.063	0.733	1.422	0.189
<i>Pavona</i>	0.250	0.733	1.188	0.229
<i>Favites</i>	0.438	0.933	1.069	0.267
<i>Galaxea</i>	0.375	0.800	1.130	0.304
<i>Trachyphyllia</i>	0.000	0.600	1.151	0.341
<i>Pachyseris</i>	0.250	0.667	1.144	0.377
<i>Lobophyllia</i>	0.125	0.600	1.117	0.411
<i>Stylophora</i>	0.563	0.467	0.942	0.444
<i>Leptastrea</i>	0.188	0.533	0.987	0.476
<i>Goniastrea</i>	0.563	1.000	0.849	0.508
<i>Seriatopora</i>	0.438	0.533	0.962	0.540
<i>Pocillopora</i>	0.563	0.667	0.924	0.572
<i>Dipsastraea</i>	0.563	1.000	0.843	0.603
<i>Platygyra</i>	0.375	0.400	0.898	0.632
<i>Hydnophora</i>	0.313	0.400	0.869	0.662
Fungiidae_family	0.125	0.467	0.923	0.689

<i>Cyphastrea</i>	0.625	1.000	0.746	0.717
<i>Coscinaraea</i>	0.000	0.400	0.791	0.741
<i>Montipora</i>	0.750	0.800	0.699	0.764
<i>Stylocoeniella</i>	0.313	0.067	0.677	0.783
<i>Lithophyllon</i>	0.375	0.000	0.757	0.803
<i>Oulastrea</i>	0.063	0.267	0.627	0.821
<i>Pectinia</i>	0.188	0.200	0.660	0.838
<i>Leptoria</i>	0.000	0.267	0.587	0.854
<i>Oxypora</i>	0.063	0.200	0.542	0.868
<i>Fungia</i>	0.125	0.133	0.521	0.881
<i>Echinopora</i>	0.125	0.133	0.531	0.893
<i>Symphyllia</i>	0.000	0.200	0.488	0.906
<i>Echinophyllia</i>	0.188	0.067	0.537	0.917
<i>Leptoseris</i>	0.000	0.200	0.491	0.928
<i>Goniopora</i>	0.063	0.133	0.453	0.939
<i>Coelastrea</i>	0.125	0.000	0.369	0.948
<i>Danafungia</i>	0.125	0.000	0.372	0.955
<i>Euphyllia</i>	0.063	0.067	0.359	0.961
<i>Merulina</i>	0.125	0.000	0.375	0.967
<i>Mycedium</i>	0.125	0.000	0.375	0.973
<i>Acropora</i>	0.938	1.000	0.252	0.978
<i>Porites</i>	0.938	1.000	0.252	0.983
<i>Plerogyra</i>	0.000	0.067	0.262	0.987
<i>Alveopora</i>	0.000	0.067	0.263	0.991
<i>Heteropsammia</i>	0.000	0.067	0.263	0.994
<i>Sandalolitha</i>	0.063	0.000	0.256	0.997
<i>Cynarina</i>	0.063	0.000	0.257	1.000

Table S2.4. SIMPER analyses of average presence/ absence of fish species contributing to differences (Bray-Curtis distance) between 1975-6 and 2018 at 14 sites across Nakagusuku Bay.

Species	Mean 1975-6	Mean 2018	Consistency ratio	Cumulative contribution
<i>Acanthurus nigrofuscus</i>	0.000	0.857	1.632	0.014
<i>Ctenochaetus binotatus</i>	0.000	0.714	1.221	0.025
<i>Sargocentron rubrum</i>	0.714	0.071	1.152	0.036
<i>Meiacanthus</i> sp.	0.714	0.000	1.331	0.047
<i>Chaetodon plebeius</i>	0.714	0.000	1.252	0.058
<i>Siganus virgatus</i>	0.286	0.786	1.087	0.069
<i>Ctenochaetus strigosus</i>	0.643	0.000	0.719	0.079
<i>Abudefduf sexfasciatus</i>	0.214	0.714	1.066	0.090
<i>Chrysiptera rex</i>	0.357	0.714	0.928	0.100
<i>Thalassoma lutescens</i>	0.786	0.357	1.014	0.110
<i>Scarus rivulatus</i>	0.000	0.643	1.147	0.120
<i>Stegastes altus</i>	0.000	0.643	1.144	0.129
<i>Chrysiptera cyanea</i>	0.286	0.571	0.878	0.139
<i>Meiacanthus kamoharai</i>	0.500	0.214	0.883	0.148
<i>Halichoeres prosopion</i>	0.500	0.143	0.610	0.158
<i>Parupeneus multifasciatus</i>	0.000	0.571	1.011	0.167
<i>Zebrasoma velifer</i>	0.214	0.571	0.947	0.176
<i>Sufflamen chrysopterum</i>	0.571	0.429	0.846	0.184
<i>Labroides dimidiatus</i>	0.571	0.714	0.822	0.193
<i>Scolopsis bilineata</i>	0.286	0.500	0.859	0.201
<i>Coris batuensis</i>	0.000	0.429	0.545	0.210
<i>Pomacentrus moluccensis</i>	0.714	0.571	0.766	0.218
<i>Chromis margaritifer</i>	0.429	0.500	0.889	0.226
<i>Pomacentrus coelestis</i>	0.286	0.429	0.804	0.234
<i>Chaetodon auriga</i>	0.143	0.357	0.517	0.242
<i>Chaetodon citrinellus</i>	0.500	0.000	0.867	0.250
<i>Pomacentrus brachialis</i>	0.500	0.143	0.855	0.258
<i>Zanclus cornutus</i>	0.714	0.714	0.704	0.266
<i>Pomacentrus lepidogenys</i>	0.500	0.429	0.922	0.274
<i>Chlorurus sordidus</i>	0.143	0.500	0.894	0.281

<i>Chlorurus bowersi</i>	0.071	0.500	0.900	0.289
<i>Epinephelus fasciatus</i>	0.500	0.000	0.904	0.296
<i>Chaetodon lunulatus</i>	0.786	0.714	0.691	0.304
<i>Pomacentrus nagasakiensis</i>	0.357	0.214	0.751	0.311
<i>Chromis chrysur</i>	0.500	0.214	0.920	0.319
<i>Amphiprion frenatus</i>	0.429	0.214	0.790	0.326
<i>Choerodon schoenleinii</i>	0.143	0.357	0.702	0.333
<i>Amblyglyphidodon curacao</i>	0.357	0.357	0.820	0.340
<i>Parupeneus barberinoides</i>	0.071	0.357	0.678	0.347
<i>Plagiotremus laudandus</i>	0.500	0.000	0.893	0.354
<i>Neoglyphidodon nigroris</i>	0.429	0.071	0.807	0.361
<i>Plagiotremus rhinorhynchos</i>	0.000	0.357	0.654	0.368
<i>Thalassoma lunare</i>	0.429	0.071	0.761	0.375
<i>Chaetodon vagabundus</i>	0.286	0.214	0.684	0.382
<i>Parapercis pacifica</i>	0.357	0.071	0.691	0.388
<i>Pomachromis richardsoni</i>	0.357	0.286	0.766	0.395
<i>Cheilodipterus quinquelineatus</i>	0.429	0.000	0.738	0.402
<i>Pomacentrus alexanderae</i>	0.000	0.429	0.776	0.408
<i>Canthigaster valentini</i>	0.429	0.143	0.815	0.414
<i>Gomphosus varius</i>	0.357	0.286	0.813	0.421
<i>Scarus ghobban</i>	0.286	0.286	0.748	0.427
<i>Abudefduf vaigiensis</i>	0.286	0.286	0.761	0.433
<i>Hemigymnus fasciatus</i>	0.357	0.286	0.820	0.439
<i>Centropyge vrolikii</i>	0.357	0.214	0.761	0.445
<i>Epinephelus merra</i>	0.357	0.214	0.771	0.451
<i>Oxymonacanthus longirostris</i>	0.429	0.000	0.787	0.457
<i>Lutjanus fulviflamma</i>	0.000	0.286	0.393	0.463
<i>Acanthurus lineatus</i>	0.357	0.214	0.763	0.469
<i>Zebrasoma scopas</i>	0.286	0.286	0.762	0.475
<i>Cheilodipterus macrodon</i>	0.357	0.000	0.656	0.481
<i>Pomacentrus philippinus</i>	0.357	0.214	0.799	0.486
<i>Thalassoma hardwicke</i>	0.286	0.143	0.632	0.492
<i>Pomacentrus chrysurus</i>	0.286	0.071	0.616	0.497
<i>Pseudocheilinus hexataenia</i>	0.357	0.000	0.647	0.502

<i>Chaetodon argentatus</i>	0.357	0.143	0.730	0.508
<i>Amblyglyphidodon leucogaster</i>	0.357	0.143	0.726	0.513
<i>Caesio teres</i>	0.071	0.286	0.609	0.518
<i>Scarus scaber</i>	0.429	0.000	0.807	0.524
<i>Chaetodon kleinii</i>	0.286	0.143	0.671	0.529
<i>Heniochus monoceros</i>	0.357	0.000	0.646	0.534
<i>Scarus sp.</i>	0.214	0.000	0.333	0.539
<i>Epinephelus cyanopodus</i>	0.357	0.000	0.686	0.544
<i>Halichoeres trimaculatus</i>	0.357	0.000	0.676	0.549
<i>Amphiprion clarkii</i>	0.357	0.000	0.674	0.554
<i>Pomacanthus semicirculatus</i>	0.071	0.286	0.616	0.558
<i>Parupeneus barberinus</i>	0.000	0.286	0.536	0.563
<i>Synodus variegatus</i>	0.286	0.000	0.587	0.568
<i>Rhinecanthus aculeatus</i>	0.286	0.000	0.595	0.572
<i>Halichoeres hortulanus</i>	0.286	0.000	0.546	0.577
<i>Naso brevirostris</i>	0.286	0.000	0.556	0.581
<i>Ostorhinchus sp.</i>	0.286	0.000	0.574	0.585
<i>Diademichthys lineatus</i>	0.214	0.000	0.488	0.590
<i>Ostracion cubicus</i>	0.286	0.000	0.573	0.594
<i>Pervagor melanocephalus</i>	0.286	0.000	0.592	0.598
<i>Bodianus loxozonus</i>	0.286	0.143	0.710	0.602
<i>Labroides bicolor</i>	0.286	0.143	0.710	0.606
<i>Heniochus chrysostomus</i>	0.286	0.071	0.635	0.610
<i>Scarus schlegeli</i>	0.000	0.286	0.570	0.614
<i>Centropyge tibicen</i>	0.357	0.000	0.727	0.618
<i>Parupeneus spilurus</i>	0.000	0.214	0.473	0.622
<i>Cheilinus trilobatus</i>	0.071	0.214	0.506	0.626
<i>Plagiotremus tapeinosoma</i>	0.214	0.071	0.520	0.630
<i>Chromis ternatensis</i>	0.286	0.071	0.539	0.633
<i>Halichoeres scapularis</i>	0.000	0.143	0.260	0.637
<i>Neoglyphidodon melas</i>	0.143	0.143	0.528	0.641
<i>Forcipiger longirostris</i>	0.286	0.071	0.661	0.645
<i>Chromis xanthura</i>	0.000	0.214	0.468	0.648
<i>Ostorhinchus properuptus</i>	0.214	0.000	0.456	0.652

<i>Caesio caeruleaurea</i>	0.143	0.071	0.450	0.655
<i>Parapercis clathrata</i>	0.000	0.214	0.481	0.659
<i>Stegastes obreptus</i>	0.000	0.214	0.482	0.663
<i>Chromis viridis</i>	0.286	0.000	0.586	0.666
<i>Plectroglyphidodon dickii</i>	0.286	0.000	0.586	0.670
<i>Halichoeres chrysus</i>	0.000	0.214	0.486	0.673
<i>Chrysiptera glauca</i>	0.071	0.143	0.426	0.677
<i>Naso lituratus</i>	0.071	0.214	0.546	0.680
<i>Chaetodon speculum</i>	0.214	0.071	0.546	0.683
<i>Cheilinus chlorourus</i>	0.000	0.214	0.491	0.687
<i>Aulostomus chinensis</i>	0.214	0.000	0.461	0.690
<i>Fistularia commersonii</i>	0.214	0.000	0.461	0.693
<i>Paraluteres prionurus</i>	0.143	0.143	0.535	0.696
<i>Diploprion bifasciatum</i>	0.214	0.071	0.546	0.700
<i>Chaetodon reticulatus</i>	0.214	0.000	0.449	0.703
<i>Scarus prasiognathos</i>	0.286	0.000	0.618	0.706
<i>Balistoides viridescens</i>	0.000	0.214	0.494	0.709
<i>Caesio cuning</i>	0.143	0.143	0.545	0.712
<i>Halichoeres nebulosus</i>	0.000	0.143	0.365	0.715
<i>Pomacentrus amboinensis</i>	0.000	0.143	0.365	0.718
<i>Chaetodon baronessa</i>	0.214	0.071	0.564	0.721
<i>Siganus argenteus</i>	0.143	0.071	0.462	0.724
<i>Choerodon fasciatus</i>	0.143	0.143	0.555	0.727
<i>Balistoides conspicillum</i>	0.071	0.143	0.462	0.730
<i>Chromis atripes</i>	0.214	0.071	0.572	0.733
<i>Myripristis murdjan</i>	0.214	0.000	0.475	0.736
<i>Ctenochaetus striatus</i>	0.000	0.214	0.491	0.739
<i>Scarus chameleon</i>	0.000	0.214	0.491	0.741
<i>Cirrhilabrus cyanopleura</i>	0.143	0.143	0.553	0.744
<i>Chromis flavomaculata</i>	0.214	0.071	0.573	0.747
<i>Chromis alleni</i>	0.000	0.214	0.491	0.750
<i>Acanthurus olivaceus</i>	0.143	0.071	0.464	0.753
<i>Chromis fumea</i>	0.071	0.143	0.463	0.755
<i>Labropsis manabei</i>	0.214	0.000	0.486	0.758

<i>Plectropomus leopardus</i>	0.143	0.071	0.456	0.761
<i>Ptereleotris evides</i>	0.143	0.071	0.457	0.763
<i>Chaetodon ephippium</i>	0.071	0.071	0.357	0.766
<i>Epinephelus quoyanus</i>	0.143	0.000	0.392	0.768
<i>Chaetodontoplus mesoleucus</i>	0.143	0.071	0.462	0.771
<i>Parapercis hexophtalma</i>	0.000	0.143	0.376	0.773
<i>Dischistodus prosopotaenia</i>	0.000	0.143	0.376	0.776
<i>Siganus puellus</i>	0.214	0.000	0.513	0.778
<i>Siganus unimaculatus</i>	0.214	0.000	0.513	0.781
<i>Chaetodon lunula</i>	0.143	0.071	0.460	0.783
<i>Dascyllus trimaculatus</i>	0.000	0.143	0.346	0.785
<i>Pomacentrus vaiuli</i>	0.000	0.143	0.363	0.788
<i>Bodianus perditio</i>	0.214	0.000	0.510	0.790
<i>Cirrhilabrus temminckii</i>	0.214	0.000	0.510	0.792
<i>Paracirrhites arcatus</i>	0.214	0.000	0.510	0.795
<i>Paracirrhites forsteri</i>	0.214	0.000	0.510	0.797
<i>Symphorus nematophorus</i>	0.071	0.071	0.334	0.799
<i>Amphiprion perideraion</i>	0.214	0.000	0.512	0.802
<i>Pomacentrus bankanensis</i>	0.143	0.071	0.481	0.804
<i>Cephalopholis boenak</i>	0.000	0.143	0.357	0.806
<i>Chaetodon guentheri</i>	0.000	0.143	0.385	0.808
<i>Lutjanus quinquelineatus</i>	0.000	0.143	0.386	0.811
<i>Thalassoma janseni</i>	0.143	0.000	0.383	0.813
<i>Chromis albicauda</i>	0.000	0.143	0.387	0.815
<i>Zebrasoma flavescens</i>	0.143	0.000	0.386	0.817
<i>Chromis xanthochira</i>	0.143	0.000	0.387	0.819
<i>Pygoplites diacanthus</i>	0.143	0.071	0.481	0.821
<i>Arothron meleagris</i>	0.000	0.143	0.387	0.823
<i>Scarus hypselopterus</i>	0.000	0.143	0.387	0.825
<i>Stegastes nigricans</i>	0.000	0.143	0.387	0.827
<i>Cetoscarus ocellatus</i>	0.143	0.000	0.383	0.830
<i>Acanthurus triostegus</i>	0.143	0.000	0.384	0.832
<i>Gnathodentex aureolineatus</i>	0.000	0.143	0.387	0.834
<i>Chaetodon ulietensis</i>	0.143	0.000	0.375	0.835

<i>Plectorhinchus chaetodonoides</i>	0.071	0.071	0.342	0.837
<i>Coris dorsomacula</i>	0.000	0.143	0.389	0.839
<i>Chaetodon bennetti</i>	0.143	0.000	0.376	0.841
<i>Anampses caeruleopunctatus</i>	0.143	0.000	0.377	0.843
<i>Chromis lepidolepis</i>	0.143	0.000	0.377	0.845
<i>Dascyllus aruanus</i>	0.143	0.000	0.377	0.847
<i>Epibulus insidiator</i>	0.000	0.143	0.381	0.849
<i>Cephalopholis argus</i>	0.000	0.143	0.383	0.851
<i>Chromis ovatifformes</i>	0.000	0.143	0.386	0.853
<i>Pomacentrus nigromarginatus</i>	0.000	0.143	0.386	0.854
<i>Cirrhilabrus katherinae</i>	0.000	0.143	0.391	0.856
<i>Forcipiger flavissimus</i>	0.000	0.143	0.394	0.858
<i>Scarus forsteni</i>	0.000	0.143	0.394	0.860
<i>Ecsenius bicolor</i>	0.143	0.000	0.401	0.861
<i>Koumansetta hectori</i>	0.143	0.000	0.401	0.863
<i>Centropyge ferrugata</i>	0.071	0.071	0.381	0.865
<i>Nemateleotris magnifica</i>	0.071	0.071	0.381	0.866
<i>Canthigaster janthinoptera</i>	0.143	0.000	0.401	0.868
<i>Aeoliscus strigatus</i>	0.071	0.000	0.260	0.869
<i>Amblygobius phalaena</i>	0.071	0.000	0.260	0.871
<i>Heniochus acuminatus</i>	0.071	0.000	0.260	0.873
<i>Ostorhinchus ishigakiensis</i>	0.071	0.000	0.260	0.874
<i>Trachyrhamphus serratus</i>	0.071	0.000	0.260	0.876
<i>Parupeneus cyclostomus</i>	0.143	0.000	0.401	0.878
<i>Neoniphon sammara</i>	0.000	0.071	0.248	0.879
<i>Chaetodon melannotus</i>	0.143	0.000	0.402	0.881
<i>Chaetodon xanthurus</i>	0.143	0.000	0.402	0.882
<i>Chaetodon ornatissimus</i>	0.071	0.071	0.383	0.884
<i>Lutjanus vitta</i>	0.071	0.071	0.383	0.885
<i>Chromis ovatifformis</i>	0.143	0.000	0.400	0.887
<i>Halichoeres leucurus</i>	0.143	0.000	0.400	0.888
<i>Hemigymnus melapterus</i>	0.143	0.000	0.400	0.890
<i>Platax pinnatus</i>	0.143	0.000	0.400	0.891
<i>Plectroglyphidodon lacrymatus</i>	0.143	0.000	0.400	0.893

<i>Bodianus izuensis</i>	0.000	0.071	0.253	0.894
<i>Choerodon jordani</i>	0.000	0.071	0.253	0.896
<i>Anampses meleagrides</i>	0.143	0.000	0.402	0.897
<i>Stegastes punctatus</i>	0.000	0.071	0.256	0.899
<i>Upeneus tragula</i>	0.000	0.071	0.256	0.900
<i>Amblygobius</i> sp.	0.071	0.000	0.265	0.901
<i>Chrysiptera</i> sp.	0.071	0.000	0.265	0.903
<i>Rhinecanthus verrucosus</i>	0.071	0.000	0.265	0.904
<i>Chlorurus microrhinos</i>	0.000	0.071	0.256	0.905
<i>Oplegnathus punctatus</i>	0.000	0.071	0.256	0.907
<i>Ptereleotris microlepis</i>	0.000	0.071	0.256	0.908
<i>Pterois lunulata</i>	0.071	0.000	0.266	0.909
<i>Arothron nigropunctatus</i>	0.000	0.071	0.259	0.911
<i>Cheilinus fasciatus</i>	0.000	0.071	0.259	0.912
<i>Cheilio inermis</i>	0.000	0.071	0.259	0.913
<i>Iniistius dea</i>	0.071	0.000	0.267	0.914
<i>Nematalosa japonica</i>	0.071	0.000	0.267	0.916
<i>Halichoeres melanochir</i>	0.071	0.000	0.267	0.917
<i>Acanthurus bariene</i>	0.071	0.000	0.268	0.918
<i>Chrysiptera biocellata</i>	0.071	0.000	0.268	0.919
<i>Lutjanus kasmira</i>	0.071	0.000	0.268	0.921
<i>Parapercis cylindrica</i>	0.071	0.000	0.268	0.922
<i>Pseudocaranx dentex</i>	0.071	0.000	0.268	0.923
<i>Labrichthys unilineatus</i>	0.000	0.071	0.263	0.924
<i>Ostorhinchus angustatus</i>	0.000	0.071	0.263	0.925
<i>Pomacanthus sexstriatus</i>	0.000	0.071	0.263	0.927
<i>Acanthurus nigricauda</i>	0.000	0.071	0.263	0.928
<i>Balistapus undulatus</i>	0.000	0.071	0.263	0.929
<i>Naso hexacanthus</i>	0.000	0.071	0.263	0.930
<i>Prionurus scalprum</i>	0.000	0.071	0.263	0.931
<i>Scarus festivus</i>	0.000	0.071	0.263	0.932
<i>Stethojulis trilineata</i>	0.000	0.071	0.263	0.933
<i>Thalassoma quinquevittatum</i>	0.000	0.071	0.263	0.934
<i>Cephalopholis leopardus</i>	0.000	0.071	0.263	0.935

<i>Lutjanus lutjanus</i>	0.000	0.071	0.263	0.937
<i>Neopomacentrus cyanomos</i>	0.000	0.071	0.263	0.938
<i>Ostorhinchus endekataenia</i>	0.000	0.071	0.263	0.939
<i>Pseudodax moluccanus</i>	0.000	0.071	0.263	0.940
<i>Sargocentron spinosissimum</i>	0.000	0.071	0.263	0.941
<i>Chromis notata</i>	0.000	0.071	0.265	0.942
<i>Chrysiptera parasema</i>	0.000	0.071	0.265	0.943
<i>Epinephelus polyphekadion</i>	0.000	0.071	0.265	0.944
<i>Neopomacentrus violascens</i>	0.000	0.071	0.265	0.945
<i>Scarus ovifrons</i>	0.000	0.071	0.265	0.946
<i>Scolopsis monogramma</i>	0.000	0.071	0.265	0.947
<i>Abudefduf septemfasciatus</i>	0.000	0.071	0.266	0.948
<i>Acanthurus blochii</i>	0.000	0.071	0.266	0.949
<i>Acanthurus maculiceps</i>	0.000	0.071	0.266	0.950
<i>Caranx melampygus</i>	0.000	0.071	0.266	0.951
<i>Chromis delta</i>	0.000	0.071	0.266	0.952
<i>Coris gaimard</i>	0.000	0.071	0.266	0.953
<i>Diagramma pictum</i>	0.000	0.071	0.266	0.954
<i>Kyphosus pacificus</i>	0.000	0.071	0.266	0.955
<i>Lutjanus gibbus</i>	0.000	0.071	0.266	0.956
<i>Pterocaesio marri</i>	0.000	0.071	0.266	0.957
<i>Rhinecanthus rectangulus</i>	0.000	0.071	0.266	0.958
<i>Scolopsis affinis</i>	0.000	0.071	0.266	0.959
<i>Scolopsis lineata</i>	0.000	0.071	0.266	0.960
<i>Stegastes fasciolatus</i>	0.000	0.071	0.266	0.961
<i>Anampses geographicus</i>	0.000	0.071	0.268	0.962
<i>Calotomus japonicus</i>	0.000	0.071	0.268	0.962
<i>Chaetodon auripes</i>	0.000	0.071	0.268	0.963
<i>Chromis yamakawai</i>	0.000	0.071	0.268	0.964
<i>Chrysiptera starcki</i>	0.000	0.071	0.268	0.965
<i>Macolor niger</i>	0.000	0.071	0.268	0.966
<i>Mulloidichthys vanicolensis</i>	0.000	0.071	0.268	0.967
<i>Paracaesio xanthura</i>	0.000	0.071	0.268	0.968
<i>Plectorhinchus lessonii</i>	0.000	0.071	0.268	0.969

<i>Pseudojuloides elongatus</i>	0.000	0.071	0.268	0.969
<i>Scarus fuscocaudalis</i>	0.000	0.071	0.268	0.970
<i>Bodianus axillaris</i>	0.071	0.000	0.273	0.971
<i>Chromis vanderbilti</i>	0.071	0.000	0.273	0.972
<i>Ostracion meleagris</i>	0.071	0.000	0.273	0.973
<i>Parupeneus crassilabris</i>	0.071	0.000	0.273	0.974
<i>Sargocentron spiniferum</i>	0.071	0.000	0.273	0.975
<i>Stethojulis interrupta</i>	0.071	0.000	0.273	0.975
<i>Amphiprion ocellaris</i>	0.071	0.000	0.273	0.976
<i>Cromileptes altivelis</i>	0.071	0.000	0.273	0.977
<i>Dascyllus reticulatus</i>	0.071	0.000	0.273	0.978
<i>Elagatis bipinnulata</i>	0.071	0.000	0.273	0.979
<i>Heniochus singularius</i>	0.071	0.000	0.273	0.980
<i>Labracinus</i> sp.	0.071	0.000	0.273	0.980
<i>Lethrinus nebulosus</i>	0.071	0.000	0.273	0.981
<i>Pomacanthus imperator</i>	0.071	0.000	0.273	0.982
<i>Pomacentrus</i> sp.	0.071	0.000	0.273	0.983
<i>Pomachromis</i> sp.	0.071	0.000	0.273	0.984
<i>Syphraena</i> sp.	0.071	0.000	0.273	0.984
<i>Trimma caudomaculatum</i>	0.071	0.000	0.273	0.985
<i>Centropyge bispinosa</i>	0.000	0.071	0.270	0.986
<i>Cheilodipterus intermedius</i>	0.000	0.071	0.270	0.987
<i>Chrysiptera unimaculata</i>	0.000	0.071	0.270	0.988
<i>Heniochus varius</i>	0.000	0.071	0.270	0.988
<i>Lutjanus bohar</i>	0.000	0.071	0.270	0.989
<i>Myripristis hexagona</i>	0.000	0.071	0.270	0.990
<i>Scarus globiceps</i>	0.000	0.071	0.270	0.991
<i>Scarus rubroviolaceus</i>	0.000	0.071	0.270	0.991
<i>Atrosalarias holomelas</i>	0.071	0.000	0.273	0.992
<i>Cheiloprion labiatus</i>	0.071	0.000	0.273	0.993
<i>Parupeneus indicus</i>	0.071	0.000	0.273	0.994
<i>Thalassoma trilobatum</i>	0.071	0.000	0.273	0.995
<i>Amphiprion sandaracinos</i>	0.071	0.000	0.274	0.995
<i>Centropyge bicolor</i>	0.071	0.000	0.274	0.996

<i>Cephalopholis urodeta</i>	0.071	0.000	0.274	0.997
<i>Chromis</i> sp.	0.071	0.000	0.274	0.997
<i>Chromis weberi</i>	0.071	0.000	0.274	0.998
<i>Cirrhitichthys aprinus</i>	0.071	0.000	0.274	0.999
<i>Pterocaesio tile</i>	0.071	0.000	0.274	0.999
<i>Thalassoma amblycephalum</i>	0.071	0.000	0.274	1.000

Chapter Three - Systematic spatial variation of fish functional group abundances across a biogeographical transition zone.

Katie M Cook, Mark Miller, James D Reimer, Brigitte Sommer, Masami Obuchi, Masaru Mizuyama, Hiroki Kise, Maria Beger

3.0 Abstract

Aim

Understanding the drivers of current and future species distributions and ecosystem processes is critical for effective ecosystem management. However, species with critical ecosystem functions are often data deficient or rare, and excluded from quantitative analyses that support conservation action. Here, we group reef fish species by functional traits and model group abundance distributions using environmental variables. We examine if group level environmental responses represent within-group species level responses, if these responses differ among groups, and implications of predicted group distributions for ecosystem functioning under climate change.

Location

Kuroshio region, southern Japan

Methods

We used abundance survey data for 390 fish species and seven morphological and physiological traits to categorise fishes into twelve functional groups. A generalised linear mixed model was trained for fifty species across nine functional groups using environmental predictors. Models were rebuilt using functional groups to compare group-level environmental responses to within-group species responses and predict group distributions across space.

Results

Environmental predictors for species were similar to those of their respective functional group for all but one group, suggesting traits determine how species respond to their environment, and our groupings appropriately represented the species. Groups showed differing responses to the environmental variables, resulting in predicted tropical, subtropical/temperate, and cosmopolitan abundance distributions. Groups consisted of unique trait combinations, suggesting areas with different group compositions were functionally dissimilar. Subtropical communities currently consist of fewer groups that are strongly tied to minimum temperature and diffuse attenuation.

Main Conclusions

Future changes in environmental conditions may result in functional community reassembly under climate change, with losses of groups and their functions, functional mismatches, and novel communities with reduced functioning. Our trait-based grouping approach allows for inclusion of rare or data deficient species and provides ecologically informative outputs to facilitate future monitoring and evidence-based management and conservation actions.

3.1 Introduction

Pervasive anthropogenic disturbances including climate change, fishing and coastal development are causing the rapid degradation of marine environments (Halpern *et al.*, 2015; McCauley *et al.*, 2015; Lotze *et al.*, 2017). These disturbances are threatening unique species and communities, resulting in global biodiversity losses and the reduction of ecosystem services (Jones, 2011; Defries and Nagendra, 2017). Ongoing conservation efforts aim to mitigate these losses, but management actions require careful planning as conservation funds are limited (Mcintosh *et al.*, 2017). Making ecologically informed decisions is particularly challenging when taking an ecosystem-wide approach to protection, as vast amounts of spatially explicit information for multiple species is required (Robinson *et al.*, 2017). Frequently, species distribution models (SDMs) are used to extrapolate survey data across a landscape based on environmental drivers of species distributions, such as temperature and substrate type (Elith and Leathwick, 2009; Kearney and Porter, 2009; Muscatello, Elith and Kujala, 2021). SDMs typically use presence only or presence-absence data, due to the difficulty of collating abundance data (Yu, Cooper and Infante, 2020), and so are unable to distinguish between observations of vagrant individuals and high abundance population cores. However, understanding these abundance distributions is vital for improved management strategies under ongoing climate change (Loboda *et al.*, 2018; Prober *et al.*, 2018; Tittensor *et al.*, 2019; Baranov *et al.*, 2020).

Mapping accurate species distributions is becoming increasingly important due to the increased prevalence of climate-induced range shifts. Globally, species are expanding their ranges to higher latitudes and altitudes to follow suitable environmental conditions (Thuiller, 2004; Hole *et al.*, 2009; Verges *et al.*, 2014; Bonebrake *et al.*, 2017). In the marine realm, poleward range shifts are occurring rapidly due to ocean warming and high dispersal capacity of organisms along oceanic currents (Sorte, Williams and Carlton, 2010). Range shifts of multiple species can result in dramatic community turnover with large ecological and socioeconomic consequences (Pech *et al.*, 2017). This effect is especially notable along biogeographical transition zones, where tropical, subtropical and temperate species overlap at the edges of their environmental tolerances (Beger *et al.*, 2014; Verges *et al.*, 2014; Sanford *et al.*, 2019). Here, small shifts in range edge populations may drive ecosystems past tipping point thresholds, altering the environment to facilitate further

range shifts in other species (Wernberg *et al.*, 2016). For example, range expanding scleractinian coral species could establish to provide structure and habitat allowing coral associated species to settle, with feedback mechanisms resulting in widespread community turnover (Yamano, Sugihara and Nomura, 2011; Graham *et al.*, 2014). As such, along the coasts of South Africa, Australia, Japan, Oman, North America and Brazil, high latitude reef communities have become increasingly tropicalized over the last few decades, with abundance shifts from temperate to tropical taxa including reef fishes and habitat forming species such as seaweeds (Yamano, Sugihara and Nomura, 2011; Lloyd *et al.*, 2012; Nakamura *et al.*, 2013; Beger *et al.*, 2014; Feary *et al.*, 2014; Horta e Costa *et al.*, 2014; Vergés *et al.*, 2016; Kumagai *et al.*, 2018; Smith *et al.*, 2020; Ross *et al.*, 2021). In Japan, there have even been shifts from kelp to coral-dominated systems on some high-latitude reefs (Yamano, Sugihara and Nomura, 2011; Kumagai *et al.*, 2018; Vergés *et al.*, 2019).

To track and predict range and ecosystem shifts, we need to determine current species range boundaries, while also determining how species are spatially distributed within their range. The majority of research using SDMs use models built using presence only, or in rarer cases, presence-absence data (Beger and Possingham, 2008; Johnston *et al.*, 2015). Due to limited availability of species abundance data at large spatial scales, many SDM studies use data obtained from global databases such as GBIF that collate occurrence data from multiple sources such as citizen science, fisheries and scientific surveys (Flemons *et al.*, 2007). Models built using such data can be spatially biased, due to geographically uneven sampling effort, and differing experimental designs (Beck *et al.*, 2014; Melo-Merino, Reyes-Bonilla and Lira-Noriega, 2020). SDMs using abundance or density data are scarce, because combining data from multiple sources needs to account for differences in survey methods, and large scale individual surveys are often economically unfeasible (Jones, 2011). However, incorporating abundance in SDMs can increase accuracies of predictions towards the range edge where occasional vagrant records do not necessarily represent established populations. However, small yet viable range-edge populations of range shifting species could have disproportionately large ecological effects, so it is important that they are predicted accurately (Lindström *et al.*, 2013; Hargreaves and Eckert, 2019). This issue is especially relevant when modelling species distributions across subtropical reefs. Here, tropical, subtropical and temperate species co-exist, but each species may be more dominant in abundance where they are more suited to their environment. Observed changes in density or abundance within the range may provide an early indication of range contraction or expansion (Jarema *et al.*, 2009; Waldock *et al.*, 2019) and enable natural resource managers to proactively plan for future species redistributions (Melbourne-Thomas *et al.*, 2021).

Conducting surveys across biogeographical transition zones presents a further challenge, with species likely to be recorded at a small number of sites as their abundance tails off across a gradient of rapidly changing environmental conditions (Golla *et al.*, 2020). As such, rarer species are often data deficient and excluded from analyses, with little known about their distributions (Beger *et al.*, 2020; Zhang *et al.*, 2020). However, rare species often possess unique combinations of functional traits, with 98% of reef fish species that have the most distinct trait combinations found to be regionally rare (Mouillot *et al.*, 2013). These species are likely to provide important roles critical for continued ecosystem function (Mouillot *et al.*, 2013). Ecosystem functioning is described as the biological, chemical and physical mechanisms that support the maintenance of ecosystems (Brockerhoff *et al.*, 2017). Functions such as primary production and decomposition result from the interactions between species with certain functional roles (Brockerhoff *et al.*, 2017). Species also provide specific direct functions such as reef fish that remove algal turf to allow for coral settlement (Bellwood *et al.*, 2019). If species that provide unique functional roles, or contribute to large scale ecosystem processes can no longer persist due to unfavourable environmental conditions, overall functioning may be reduced, ultimately leading to ecosystem collapse (McWilliam *et al.*, 2020; Tebbett *et al.*, 2021). Rarer species can also help to regenerate degraded ecosystems (Baho *et al.*, 2017). For example, following a reef phase-shift to macro-algae, the batfish *Platax pinnatus* provided macro-algal herbivory functions in reef regeneration that more common reef herbivores were unable to provide (Bellwood, Hughes and Hoey, 2006; Mouillot *et al.*, 2013). Rare species can contribute more functional diversity than common ones, and they may also have specialist adaptations making them be pre-adapted to be resilient to environmental change (Jain *et al.*, 2014; Chapman, Tunnicliffe and Bates, 2018). Thus, these species are valuable to conservation beyond that of preserving biodiversity, and modelling and considering their distributions is important in ecosystem-based management (Ellingsen, Hewitt and Thrush, 2007).

One strategy to include data deficient rare species into distribution models is to classify them into groups that have enough records to build viable SDMs (Gourlet-Fleury *et al.*, 2005; Dunstan, Foster and Darnell, 2011). Rare species are often grouped taxonomically by genus or family, but taking a functional approach to species group is more ecologically informative. Many functional roles are shared by groups of species with similar functional traits, such as body length, diet and reproductive strategy (Miller *et al.*, *In revisions* ; Voigt, Perner and Hefin Jones, 2007; Engemann *et al.*, 2016; Anderson, Houk, Miller, Cuetos-Bueno, *et al.*, 2021). Grouping species by their traits may indicate broad functional niches (Voigt, Perner and Hefin Jones, 2007). Losses of species within these functional groups may have minimal impacts to ecosystem functioning, but losses of whole groups may result in the transitioning of the ecosystem to an alternate state (Newbold *et al.*, 2020). Thus, distribution models for these groups may provide clear, practical outputs for

ecosystem management, where all species, even those that are rare, can be included in management strategies. However, creating distribution models for groups only makes sense if species within groups respond similarly to the environmental conditions (Anderson, Houk, Miller, Cuetos - Bueno, *et al.*, 2021), so that the group level model reflects their distributions and response to environmental change.

Predicting how functional groups are distributed across space provides important insights into how species range shifts might affect ecosystem functioning (Voigt, Perner and Hefin Jones, 2007). Here we determine functional groups for Japanese tropical and subtropical reef fishes, and compare species-level and group-level SDMs to determine how future range shifts might influence ecosystem functioning. Using these groups, we explore three main questions: (1) Do the functional group level responses to environmental variables accurately represent respective species level responses?, (2) Do the responses to environmental variables differ among groups?, and (3) Do abundance distributions of different functional groups vary the tropical to temperate biogeographical transition zone? With ongoing climate change, accurately predicting how the species and functional composition of the ecological communities along biogeographical transition zones will be altered by range shifts is an urgent conservation priority. Incorporating a functional approach into distribution modelling using the methods we present here produces ecologically informative outputs, informing future strategies that target the protection of processes and functions, not just individual species themselves.

3.2 Methods

Fish surveys were undertaken at 31 sites along Japan's east coast in the boreal summers of 2015 and 2016, in areas with known scleractinian coral communities. Sites spanned a gradient from the tropical coral reefs of Iriomote Island (24°N), to Tateyama's temperate high latitude reefs (35 °N) (Fig. 3.1). All surveys were conducted at 8-10m depth, with the exception of Tateyama, where corals predominantly occurred at shallow depths to five metres. At each site, surveys were conducted along 3-5 replicate belt transects measuring 25m long and 5m wide. The abundance of reef associated non-cryptic fish species was recorded *in-situ*. At each site, the abundance of species was taken to be the average of the replicate transects. If species were not recorded at a site, they were assumed to be absent and given an abundance of zero.

To classify functional groups for all 390 fish species recorded in our surveys, we determined values for seven traits using the online database FishBase (www.fishbase.de) and through literature searches. The traits were maximum length, depth range, water column position, trophic

level, pelagic larval duration, parental mode and aggregation. These traits were selected as those most ecologically informative for range-shifting (Table 3.1). Gower-distances were calculated between species using the trait values, and hierarchically clustered using the ‘average’ method to create a dendrogram. We identified the optimal numbers of clusters (functional groups) whilst accounting for cluster stability. To do this, we ran a 1000 iteration bootstrap analysis of the original data by removing 5% of the data randomly, and recalculating the distance matrix during each iteration to determine the silhouette width, the Jaccard similarity index and the Rand matching index for two to 30 clusters. The optimal number of clusters was selected using the average silhouette width and index values averaged across all runs to incorporate cluster stability (Miller *et al.*, In revisions). The optimal clusters were then numbered, and species within the cluster were assigned the functional group number.

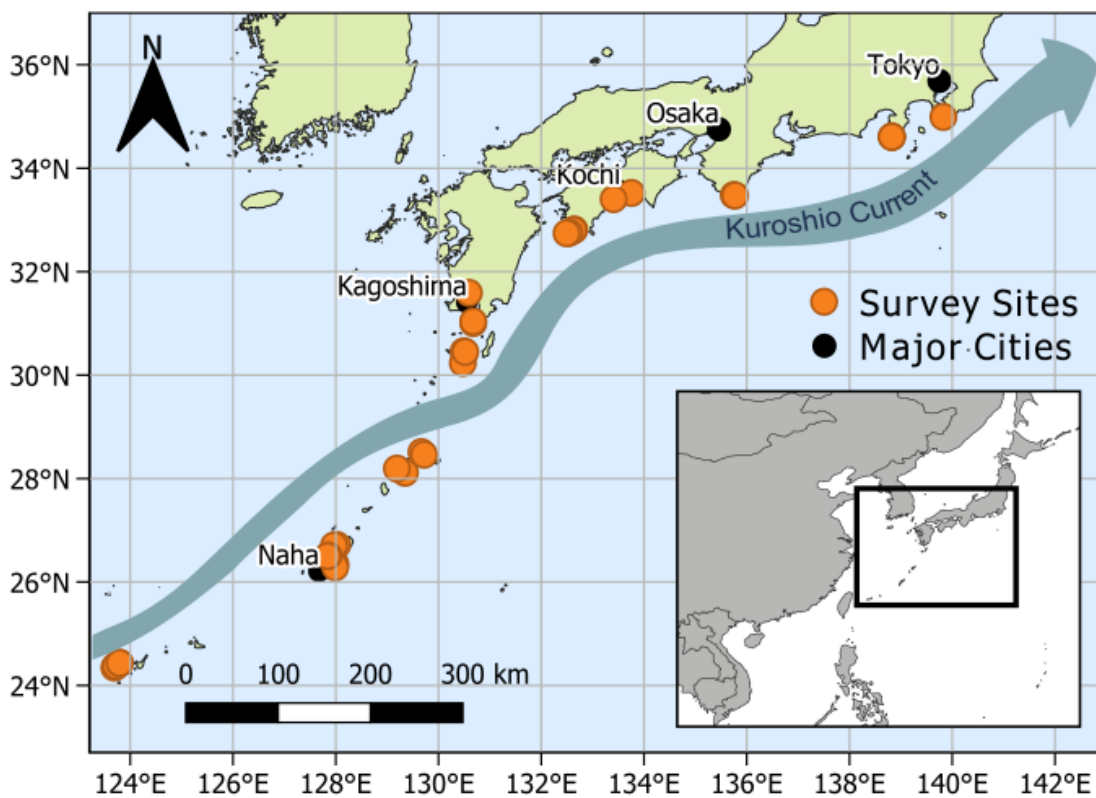


Figure 3.1. Map of study area along Japan’s Pacific coast, showing scleractinian community survey locations (orange circles) in the Kuroshio region and the path of the Kuroshio Current.

Table 3.1. List of fish traits used in this analysis and their ecological relevance to ecosystem functioning, niche determination and range shift potential.

Trait	Ecological relevance
Trophic level	Determines ecological niche, and affects ecosystem functioning through trophic interactions and networks (Mouillot, Villéger, <i>et al.</i> , 2014; Anderson, Houk, Miller, Cuetos-Bueno, <i>et al.</i> , 2021)
Water column position	Influences the prey available and impacts vertical nutrient transfer (Mouillot, Villéger, <i>et al.</i> , 2014)
Parental mode	A key component of life history strategies that affect species demography. Links to dispersal potential, affecting range shift potential (Olden, Poff and Bestgen, 2006; Feary <i>et al.</i> , 2014).
Aggregation	Determines the ability to escape predation and impacts local nutrient cycling and resource availability (Mouillot, Villéger, <i>et al.</i> , 2014; Anderson, Houk, Miller, Cuetos-Bueno, <i>et al.</i> , 2021).
Maximum length	Constrains mouth gape, affecting predator-prey relationships. Also linked to growth, with smaller fish having a faster growth rate, and temperature tolerance (Mouillot, Villéger, <i>et al.</i> , 2014). Larger fish are also thought to have more range shift potential as their size may increase the chance of successful establishment at a new location (Luiz <i>et al.</i> , 2012; Feary <i>et al.</i> , 2014).
Depth range	Species with a large depth range may be more tolerant to changing environmental conditions (Graham <i>et al.</i> , 2011).
Pelagic larval duration	A surrogate for dispersal potential in species; species with longer PLDs can be carried further by oceanic currents, increasing their potential to establish in novel environments (Selkoe and Toonen, 2011).

3.2.1 Model development

All data preparation and analyses were conducted using the R programming language (R Core Team, 2020). Environmental data layers for sea surface temperature range (°C), minimum sea surface temperature (°C), mean dissolved oxygen at mean depth ($\mu\text{mol}/\text{m}^3$), mean diffuse attenuation (K_{d490} , m^{-1}), mean chlorophyll ($\text{mg}\cdot\text{m}^{-3}$), surface current velocity (m^{-1}) and mean light at bottom ($\text{E}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$) were downloaded from the BioOracle database (Tyberghein *et al.*, 2012; Assis *et al.*, 2018) at a resolution of 5 arcmin using the SDM predictors R package (Bosch, 2016). Light at bottom was derived from photosynthetically available radiation (PAR), diffuse attenuation (K_{d490}) and depth (Z) using:

$$\text{Light at bottom} = \text{PAR} \times \exp(-K_{d490} \times Z)$$

These environmental variables were selected as they are known to particularly influence species distributions along tropical to temperate gradients. At higher latitudes, conditions are more variable than in the tropics, with considerably lower winter minimum temperatures and photosynthetically available radiation due to the angle of the earth (Kleypas, Mcmanus and Menez, 1999; Beger *et al.*, 2014). This can limit the growth of phototrophic benthic producers, which some reef fish species depend on for survival (Kleypas, Mcmanus and Menez, 1999). Furthermore, highly specialised reef fish species may struggle to persist under such environmental and seasonal variability, limiting their northward range margins (Munday *et al.*, 2008). Current velocity at the large scale of our environmental data can be a proxy for connectivity, especially for tropicalisation of temperate reefs (Kumagai *et al.*, 2018). Some species may rely on the Kuroshio Current, a warm water poleward current (Fig. 3.1), for larval transport to higher latitudes (Soeparno *et al.*, 2012). Areas adjacent to the current with high current velocity may be highly connected to source reefs, with regular influxes of tropical species, as well as species from surrounding reefs after disturbance events (Soeparno *et al.*, 2012). Changes in oxygen concentration can alter microbial processes, predator prey dynamics, fecundity and growth, and this has been found to result in fish distribution shifts (Meyer-Gutbrod *et al.*, 2021). Finally, diffuse attenuation can affect foraging success in visually foraging species (Aarflot, Dalpadado and Fiksen, 2020), and is known to affect the distribution of fish species (Whitton *et al.*, 2020).

All environmental data outside of the prediction area were masked out using the ‘raster’ package (Hijmans, 2021). The prediction area comprised of areas in the ‘Central Kuroshio’ and ‘South Kuroshio’ marine ecoregions (Spalding *et al.*, 2007) within 10 km from the coastline, with a minimum pixel depth of less than 500m derived from Bio-Oracle (Tyberghein *et al.*, 2012; Assis *et al.*, 2018). Survey sites were evenly spaced throughout this area to capture environmental variability across the latitudinal gradient. We calculated correlations between the variables, to reduce collinearity within the models. For pairs with high correlations ($r > 0.7$) we removed the variable deemed to be less ecologically relevant (Zuur, Ieno and Elphick, 2010). The remaining environmental variables were minimum temperature, diffuse attenuation, dissolved oxygen, and current velocity.

3.2.2 Abundance distribution models

To compare if species responses to environmental variables match their respective functional group response, we built two models, one with species abundance as the response variable (i.e. ‘species model’) and the other with functional group abundance as the response variable (i.e. ‘functional group model’). First, to build the ‘species model’, data deficient species that were

observed at ten or fewer sites were removed from the data (Beger and Possingham, 2008). To predict the abundance of the remaining species, we used a generalised linear mixed model (GLMM) using a Poisson error structure and a log link function. GLMMs take into account the hierarchical data structure by considering two types of variables, the fixed and the random effects (Coelho, Infante and Santos, 2020). Here, we used species abundance with a rounded square root*100 transformation (to fit the assumptions of a Poisson distribution) as the response variable and the standardised environmental variables as the fixed predictor variables. Environmental variables were standardised using the ‘scale’ function which subtracts the variable mean and divides by the standard deviation. Species was used as a random effect variable, with uncorrelated random intercepts and random slopes of the environmental variables within species (see Supplementary for model syntax). This allowed us to extract species level coefficients from the overall model to understand whether species-environment relationships varied among species. All models were fit using the ‘glmer’ function from the ‘lme4’ package (Bates *et al.*, 2014) and were checked for singularity, over dispersion and zero inflation using the RStats and DHARMA packages (Hartig, 2017).

Second, to build the comparative ‘functional group model’, we refitted a GLMM using all the data, including the previously excluded rarer species. The model had the same fixed effects, but with the functional group as the random effect variable. Functional group level model coefficients were extracted, so that they could be compared to the within functional group species level coefficients. As the species model was built using more abundant species, these species may have highly influenced the model, making the comparisons non-independent. Thus, we iteratively removed the comparison species (that occurred in both model types) from the data, rebuilt the functional group GLMM, and extracted the functional group level coefficients. This approach allowed us to identify whether the functional groups were representing the species level response to the environmental variables.

3.2.3 Spatial functional group abundance distributions

We used the functional group coefficients from the GLMM fit using all of the species data, with group as the random effect, to predict group level abundances across the prediction area. To assess model fit, we resampled the data using cross validation, removing three random ‘test’ sites iteratively across 1000 runs, training the model on the remaining site data. Model abundance predictions were compared to the observed test site abundance. Root mean square error (RMSE), normalised root mean square error (RMSE divided by the data range) (NRMSE), and Pearson’s correlations between the observed and predicted data were calculated for each functional group.

Model predictions were then plotted as rasters across the study area to determine functional group distributions.

3.3 Results

3.3.1 Survey results and functional group classification

Fish surveys identified a total of 390 species, which were found to cluster into 12 functional groups (FGs) (Supplementary Fig. S3.1). Groups were given representative names according to their dominant trait characteristics (Table 3.2). Groups had differing abundances (Supplementary Fig. S3.2), and abundance-based density across latitude showed that the core range of each group differed, with some groups spanning a larger latitudinal range than others (Figure 3.2).

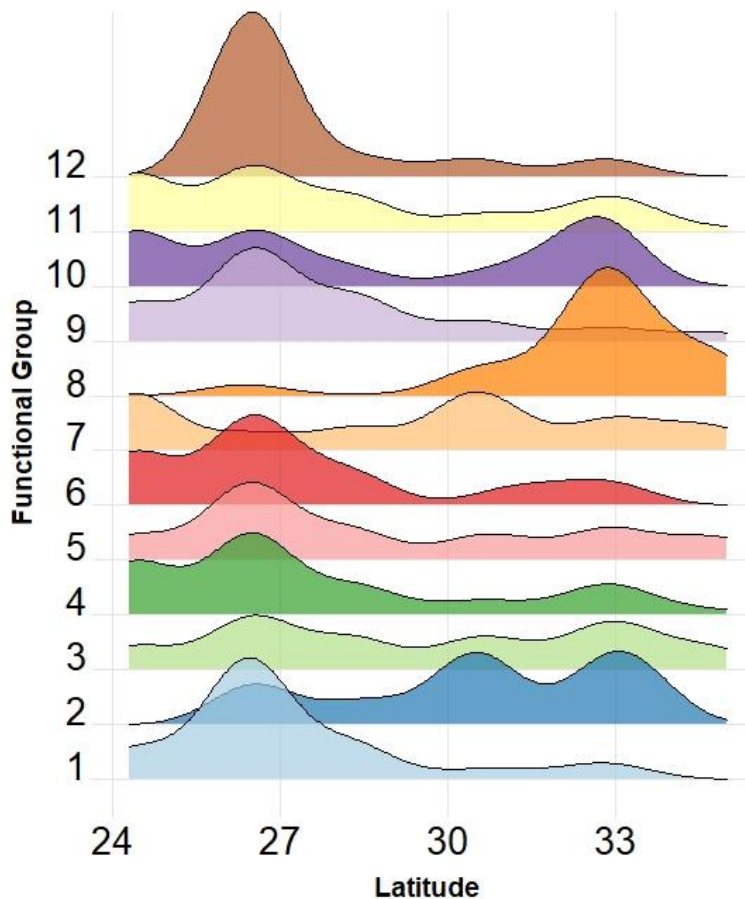


Figure 3.2. Abundance-based density distributions of reef fish functional groups across the latitudinal span of the Kuroshio region in southern Japan.

Table 3.2. Functional groups of Japanese reef fish and their trait-based characteristics.

Functional Group (FG)	Number of species in group	Group name	Trait based characteristics	Example representative species
1	n=24	Social small planktivores	Planktivores, aggregate in groups and schools, nesters, small depth range, small size, short PLD	<i>Chromis viridis</i>
2	n=4	Social large planktivores	Planktivores, aggregate in groups, reef pelagic position, reproductive scatterers, large depth range, larger size, long PLD	<i>Acanthurus mata</i>
3	n=110	Benthic paired scatterers	High and low trophic level, benthic position, reproductive scatterers	<i>Centropyge ferrugata</i>
4	n=138	Upper benthic large harem food generalists	Upper benthic position, high and low trophic level, large size, reproductive scatterers	<i>Choerodon azurio</i>
5	n=31	Solitary small benthic short dispersers	Solitary, benthic position, nesters, small size, short PLD	<i>Pseudoblennius cottoides</i>
6	n=13	Cnidarian-associated small short dispersers	Solitary, demersal position, nesters, small depth range, small size, short PLD	<i>Amphiprion ocellaris</i>
7	n=11	Solitary large piscivores	Piscivores, solitary, reproductive scatterers, large depth range, large size, long PLD	<i>Aprion virescens</i>

8	n=15	Benthic small brooding predators	Predators, aggregate in groups, benthic position, brooders and live bearers, small depth range, small size	<i>Sebastes inermis</i>
9	n=11	Solitary upper benthic omnivores	High trophic level, solitary, upper benthic position, nesters,	<i>Pterogobius elapoides</i>
10	n=6	Paired sneaky Omnivores	Aggregate in pairs, sub-benthic position, reproductive scatters	<i>Chaetodontoplus septentrionalis</i>
11	n=22	Paired sneaky demersal predators	High trophic level, solitary and aggregate in pairs, demersal position, reproductive scatterers	<i>Neoniphon argenteus</i>
12	n=3	Social sub-benthic planktivores	Planktivores, sub-benthic, reproductive scatterers, large depth range, long PLD	<i>Myripristis vittata</i>

3.3.2 Environmental abundance models

Fifty species (Supplementary Table S3.1) were observed at more than ten sites, and these data were used to fit the overall mixed effect model, taking into account species level abundances. All species from groups seven, ten and twelve were recorded at ten sites or fewer and so species in these groups were not used for comparative analyses between species and FGs.

The fixed effects of environmental variables oxygen concentration, diffuse attenuation and current velocity were found to significantly affect overall fish abundance, with minimum temperature found to have no effect as the confidence interval of the model coefficient overlapped zero (Supplementary Fig. S3.3). The random effect variation of the environmental variables significantly deviated from zero for all variables across species (Fig. 3.3). Conditional variation for current velocity, diffuse attenuation and minimum temperature included positive and negative values, suggesting species respond differently to these environmental variables. For example, in relation to other species, *Chrysiptera rex* and *Chromis flavomaculata* had the lowest negative

variance value for current velocity. These species reproduce with demersal eggs that adhere to the substrate, and so areas with high current may be unfavourable as it would disrupt their reproductive process. On the contrary, *Thalassoma lunare* had the highest positive conditional variance for current velocity. This species is known to have an exceptionally long pelagic larval duration of almost two months (Brothers, Williams and Sale, 1983), suggesting it relies on currents for widespread dispersal. Similarly, tropical species such as *Pomacentrus philippinus* had a highly positive conditional variance for minimum temperature, with subtropical species such as *Thalassoma cupido* having a highly negative conditional variance, confirming that they favour colder waters. The temperate species *Meiacanthus kamoharai* had a highly negative conditional variance for diffuse attenuation, with diffuse attenuation known to decrease at high latitudes. Conditional variance values for oxygen concentration were generally close to zero, suggesting most fish species respond similarly to this environmental variable.

The GLMM model fit using all data for all groups had significant fixed effects for all environmental variables except minimum temperature (Supplementary Fig. S3.4). The random effect variation deviated from zero for most of the environmental variables across groups (Fig. 3.4). FG2, FG8 and FG12 had negative conditional variances for minimum temperature, suggesting these may exist at higher latitudes. FG2 and FG12 also had negative conditional variances for diffuse attenuation, which also decreases at higher latitudes, with FG8 having zero conditional variance. Variance values for current velocity were also highly positive or negative depending on group, suggesting that the functional groups favour areas of differing current. Oxygen concentration variances also differed across groups (Fig. 3.4).

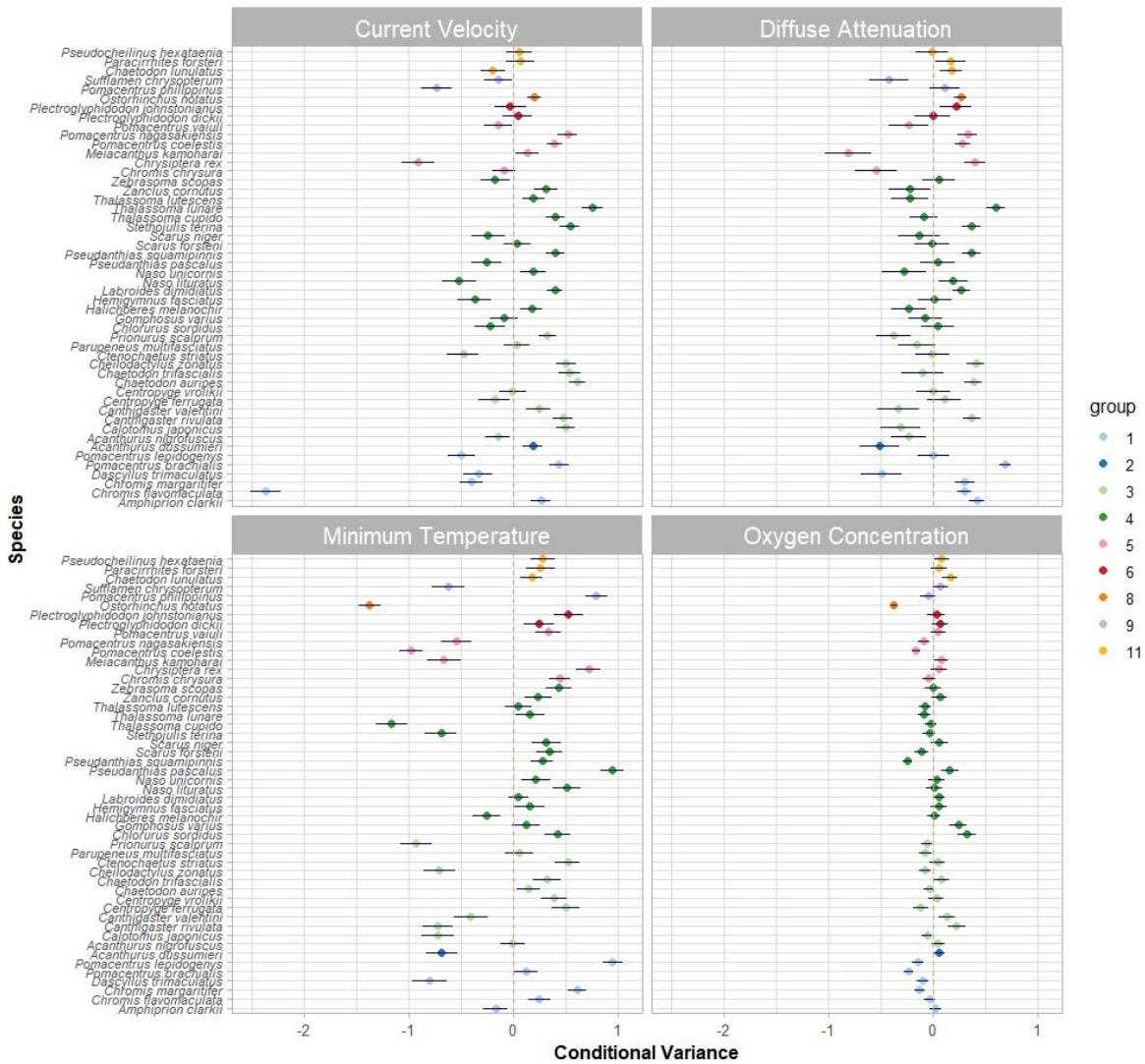


Figure 3.3. Random effect conditional variances from the fish species abundance mixed effect model with 95% confidence intervals.

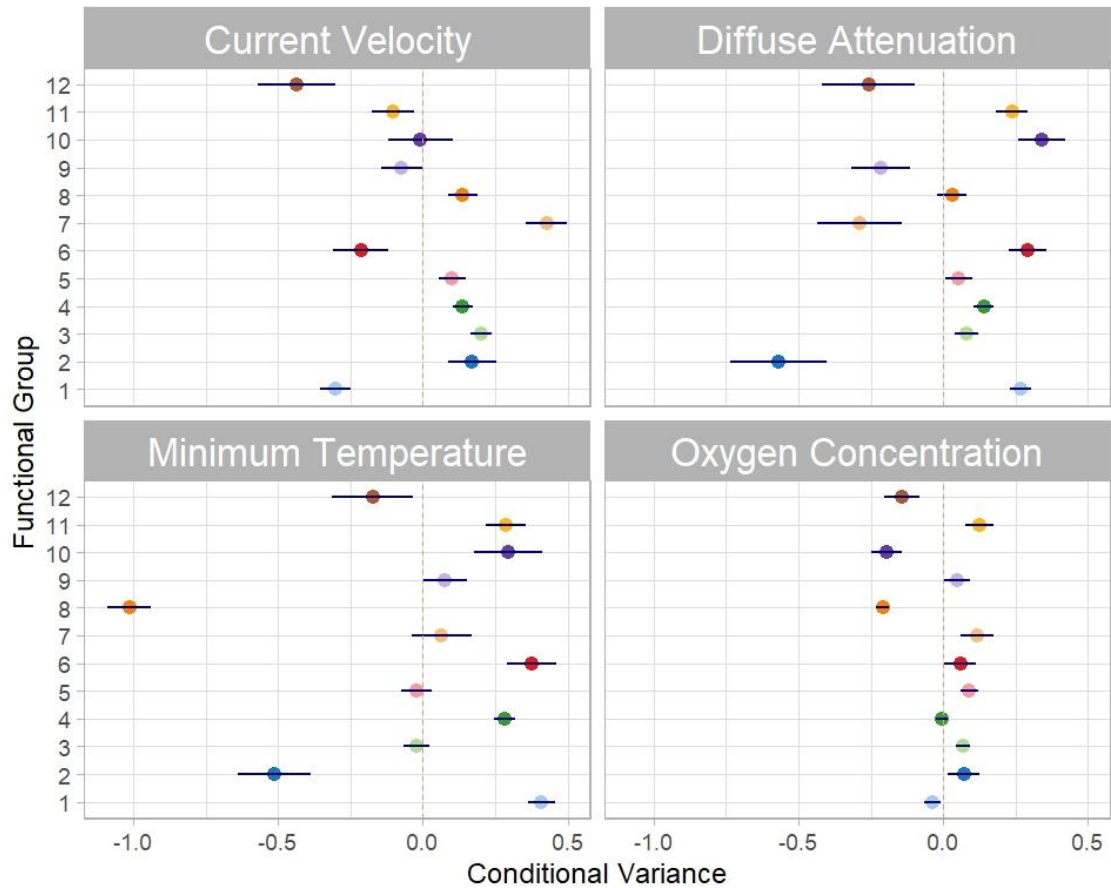


Figure 3.4. Random effect conditional variances from the fish functional group based mixed effect model with 95% confidence intervals.

3.3.3 Comparisons between species and functional group models

Nine of the twelve functional groups had enough individual species data to make comparisons. The similarities between species and group conditional variances differed among groups and environmental variables (Fig. 3.3, Fig. 3.4). For example, all the comparison species in FG1 had negative variances for oxygen concentration (except one with zero variance) (Fig 3.3) and this was reflected in the group conditional variance (Fig. 3.4). Yet, for FG3 the oxygen concentration variances were split between negative and positive for within-group species (Fig. 3.3), but positive for the overall group (Fig. 3.4). When models were rebuilt independently from the comparison species, the overall environmental coefficients for seven of the functional groups (FG 1, 3, 4, 5, 6, 9 and 10) were similar to those extracted from the respective species (Fig. 3.5). For FG1 and FG5, group coefficient values were within the interquartile range of the species coefficient values for all environmental variables, except for diffuse attenuation, where the group coefficient values still lay within the species coefficient value total range. This pattern matched FG3 and FG4, except that the environmental variable in the total range was dissolved oxygen.

For FG6 and FG11, all group level environmental coefficients lay within the range of species level environmental coefficients, except dissolved oxygen. The group coefficients for diffuse attenuation and temperature lay within the species range for group nine, but current and dissolved oxygen did not. For FG2 and FG8, the groups and species coefficients did not overlap (Fig. 3.5).

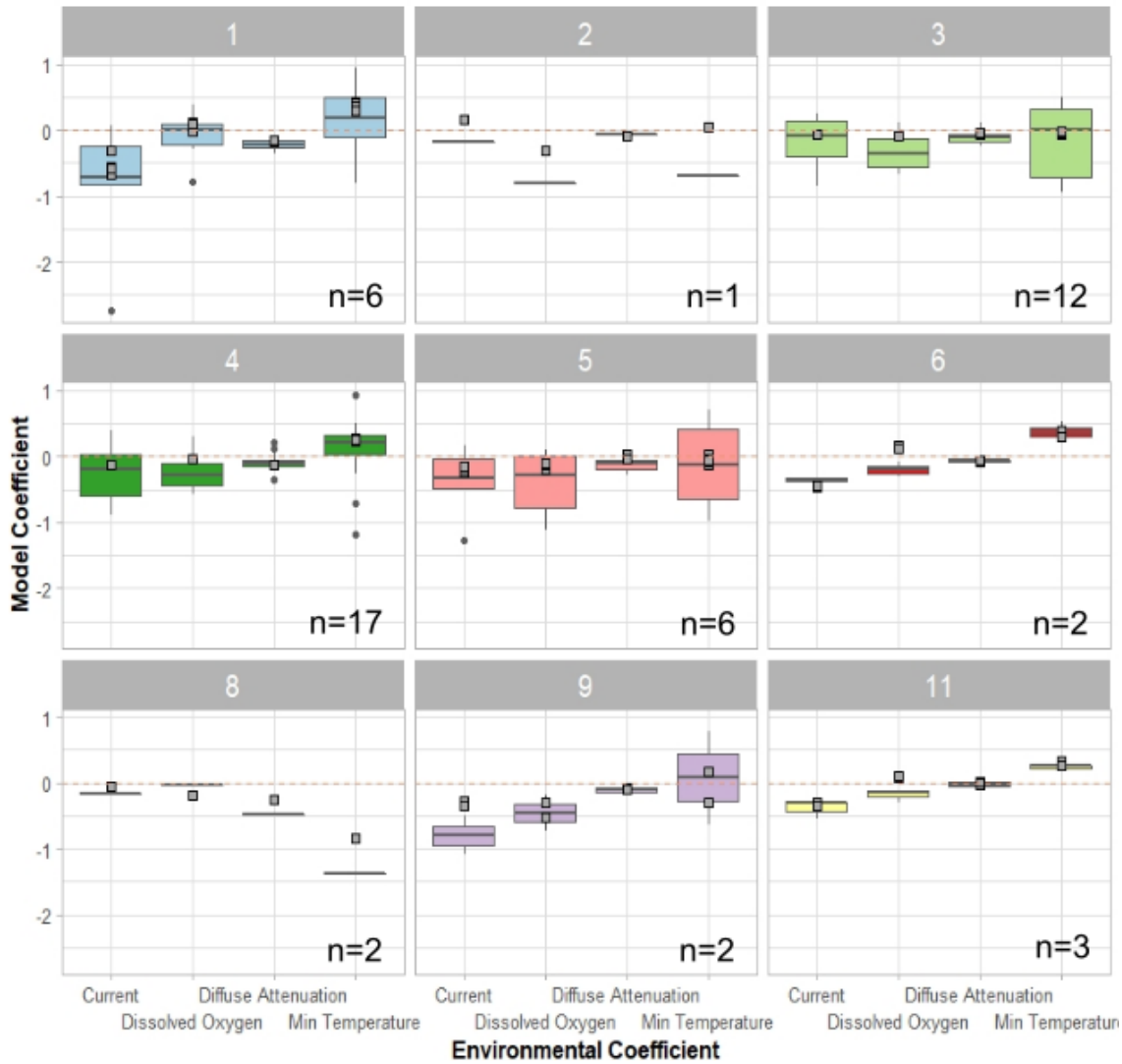


Figure 3.5. Environmental model coefficient ranges for surveyed fish species (boxplots) and their respective functional groups (coloured square dots). Numbers of species tested for each group are shown in the plots. Functional group models were retrained by iteratively removing the comparison species, to ensure the group models were independent from the species models, hence the multiple points for groups.

3.3.4 Spatial distribution models

When comparing cross-validated model predictions across 1000 runs, mean RMSE values were low relative to their total abundance for all groups except for FG2, FG8 and FG12. Mean Pearson's correlations varied between the groups, being higher than 0.25 for all groups except FG2 and FG5. The error for FG2 and FG8 was high, and FG2 also had a low the correlation value (Table 3.3). High error and low Pearson's values for groups were likely to be due to the means of the 1000 iterations being skewed by outliers. If functional groups were only found at few sites, such as FG12 which was recorded at seven sites (Supplementary Fig. S3.2), removal of three sites for cross-validation would have removed a large proportion of the data for these groups. Thus, for these iterations, the models would have been fit using very little data. For example, the histogram of the RMSE for the individual runs for FG2 showed that these outliers with large errors skewed the mean (Supplementary Fig. S3.5). When comparing observed and predicted abundance values for the full model with all study sites, all groups had low RMSE values relative to their total abundance, with NRMSE values lower than 0.3 and high positively correlated Pearson's correlation coefficients (Supplementary Table S3.2).

Predicted abundance distributions for FG1, FG4, FG9 and FG12 were skewed towards the lower latitudes, with the highest abundances around Okinawa prefecture's tropical islands, and sharp abundance declines towards mainland Japan (above 30°N) (Fig. 3.6). Abundance predictions for FG6, FG7 and FG11 were mostly higher in the tropics, with pockets of high abundances in the subtropics. FG3 and FG5 had a predicted tropical-subtropical distribution, tailing off towards the temperate edge of the prediction area. FG2 and FG8 were predicted to have strongly subtropical-to-temperate distributions (Fig 3.6).

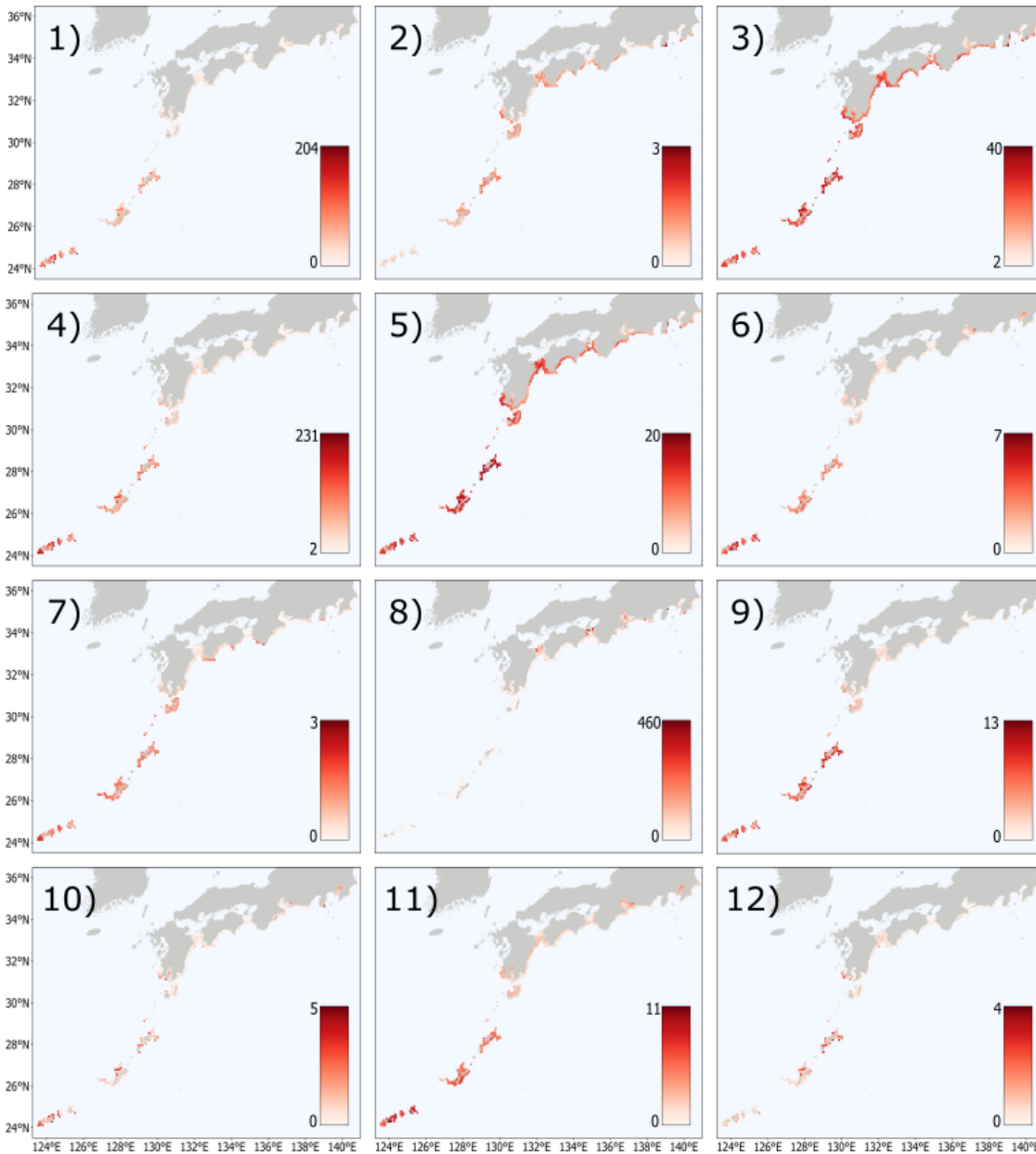


Figure 3.6. Reef fish functional group (1-12) distribution plots predicted using environmental raster layers and the functional group based generalised mixed model across our study area. Red colour intensity represents predicted abundances, with maximum values for each of the twelve functional groups given at the top of each bar.

Table 3.3. Mean root mean square error (RMSE), mean normalised root mean square error (NRMSE) and mean Pearson's correlations for cross validation of three independent sites removed iteratively across 1000 runs.

<i>Functional group</i>	<i>Mean RMSE</i>	<i>Mean NRMSE</i>	<i>Mean Pearson's Correlations</i>
<i>1</i>	37.78977	0.532102	0.698329
<i>2</i>	4.818463	2.564241	-0.03317
<i>3</i>	8.017497	0.423107	0.45585
<i>4</i>	51.24776	0.46005	0.586921
<i>5</i>	10.12324	0.542343	0.215231
<i>6</i>	1.708479	0.427597	0.531061
<i>7</i>	1.133674	0.468729	0.270531
<i>8</i>	30.55684	0.884568	0.41704
<i>9</i>	2.463985	0.292667	0.757376
<i>10</i>	0.800411	0.426488	0.403462
<i>11</i>	2.326023	0.352185	0.651935
<i>12</i>	5.159396	2.618118	0.338422

3.4 Discussion

Understanding how climate change alters ecosystem dynamics remains a challenge due to the high levels of data deficiency of component species. Our results show that when taking into account hierarchical data structure, functional group responses to our environmental variables represent species level responses for the majority of groups. This suggests that our functional grouping approach provides ecologically relevant information for conservation management purposes and helps overcome data deficiency. Specifically, grouping functionally similar data deficient species allowed for their inclusion into our spatial abundance models, producing outputs that can be incorporated in spatial planning and other spatially explicit management decisions.

The model agreement between species and functional group abundance models varied among the functional groups. Some functional groups, especially FG1 (social small planktivores) and FG4 (upper benthic large haremic food generalists), matched the environmental responses of their respective species better than others. We infer that these groups are more environmentally constrained, compared to groups such as FG3 (benthic paired scatters) and FG5 (solitary small benthic short dispersers) whose species show broad environmental preferences. Environmentally constrained groups varied in size, with FG4 composed of 138 species, and FG1 composed of 24 species, and so these links to environmental variables are unlikely to be due to group size. However, FG2 (social large planktivores) only had one model comparison species, and the group only comprised of four species in total. Using the current methods, the comparison species was removed to independently refit the functional group model for cross-validation. Therefore, this would have removed a large amount of the information used to build the group model, potentially leading to a large difference between the comparison functional group level and the overall functional group model. Thus, this independent cross validation for model comparisons might not be appropriate for communities comprised of small functional groups containing few species.

Our results suggest that the morphological and physiological traits that we chose to represent ecological functions determines how some functional groups respond to their environment, and where they can persist. We did not include any traits directly linked to environmental preference (such as thermal affinity) when categorising groups, yet, each functional group showed strong and differing responses to environmental variables (Fig 3.5). The models thus provided unique predicted spatial distributions for each functional group, allowing practitioners to consider range shifts and functional transformation of reefs in spatial conservation. Groups generally separated into tropical, subtropical-to-temperate, and cosmopolitan distributions. As each group was derived from a unique suite of traits, this suggests that areas with distinct group compositions are functionally dissimilar (Villéger, Novack-Gottshall and Mouillot, 2011), with dissimilarities increasing across the latitudinal gradient. Consistent with patterns previously identified for reef fish across larger scales (Stuart-Smith *et al.*, 2013), our predictions show that tropical areas have more group overlap and higher functional diversity. Subtropical-to-temperate functional communities are composed of fewer functional groups, and thus these regions have lower functional diversity, but these few groups may be relatively more influential to the ecological processes occurring in these areas (Stuart-Smith *et al.*, 2013). However, it must be noted that these results apply only to fish assemblages associated with scleractinian coral communities, which currently only occur in few regions in the sub-tropical and temperate areas of Japan (Beger *et al.*, 2014), compared to being much more ubiquitous in the tropics (Japan Coral Reef Society, 2004). We hypothesise that the inclusion of surveys and species from non-coral habitats along this transition zone might lead to an increase the functional diversity at high latitudes and dilute

the latitudinal pattern observed for coral habitats in our study, an important area for future research.

Environmental conditions in the Kuroshio region are predicted to change rapidly under projected climate change scenarios, especially as the strengthening poleward Kuroshio Current brings increasingly warm water to high latitudes (Zhang *et al.*, 2020). Some of our groups showed strong relationships with environmental variables, which suggests that functional turnover could increase in the future if these groups track their ideal environmental conditions, as has already been recorded for other taxa along Japan's Pacific coast, including scleractinian corals and macroalgae (Yamano, Sugihara and Nomura, 2011; Abe *et al.*, 2021). Range contractions of specific groups could result in the loss of important functions that these groups provide, being replaced with functions from range expanding groups currently only in the tropics. For example, FG8 (benthic small brooding predators), is mainly distributed in subtropical areas. The group has a negative relationship with minimum temperature, so increasing future SSTs will likely result in range contractions. This group might be replaced with currently tropical groups such as FG1 (planktivores, aggregate in groups and schools, nesters, small depth range, small size, short PLD) and FG4 (upper benthic position, high and low trophic level, large size, reproductive scatterers). New groups might inhabit different parts of the reef and have different food preferences, thus not replacing the functional roles of the contracted species, resulting in overall functional losses.

Functional groups are also likely to respond differently to environmental change. Habitat generalists are known to expand faster than specialists (Platts *et al.*, 2019), and some functional groups could be dependent on specific habitats such as coral reefs (Stuart-Smith *et al.*, 2021). Uneven responses to climate change could result in a functional mismatch in some communities (Damien and Tougeron, 2019). Some tropical groups, which currently co-occur with a high diversity of other functional groups, may expand or shift their ranges, whilst others may not. In areas where range expansions occur, these expanding groups may replace contracting subtropical groups, which are currently less functionally diverse but more influential to functional diversity. Thus, the new groups may fill a smaller functional niche than the contracting group resulting in an overall loss of ecosystem functions.

The predicted influential subtropical groups, such as FG2 (social large planktivores) and FG8 (benthic small brooding predators), and their respective species, were recorded at fewer sites. Furthermore, FG7 (solitary large piscivores), FG10 (paired sneaky omnivores) and FG12 (social sub-benthic planktivores) did not have any species with enough records to model. This suggests that if monitoring and management plans were based on more common ubiquitous species, whole groups of species and their critical functions may be excluded from conservation actions. In

general, our results emphasise the challenges in conducting surveys and modelling across biogeographical transition zones. A total of 340 of the 390 species we recorded were observed at fewer than 10 sites, suggesting that the majority of species surveyed were potentially rare or are locally range restricted. Species such as *Chaetodon nippon*, which are listed to have a subtropical distribution on FishBase (Froese and Pauly, 2021), were only present at four of the central mainland sites, and tropical species such as *Amphiprion frenatus* (Froese and Pauly, 2021) were only present at six of the southern sites. However, species such as these whose range edges are likely to be within our study area may be the ones that will show range shifts, with range edge expansions and contractions visibly tracking environmental change (Poloczanska *et al.*, 2013; Robinson *et al.*, 2015). Thus, excluding these species in monitoring might falsely imply that climate change is not impacting ecosystems through distribution shifts. In contrast, the fifty species which we were able to train models for were more ubiquitously distributed across our study area. As these species were found across a larger range of latitudes, range shifts may occur outside of the localised study area, increasing monitoring challenges.

Widespread functional turnover may not just occur in areas where functional groups are completely gained and lost due to climatic shifts but also due to changes in abundance (Baranov *et al.*, 2020). For ubiquitously distributed groups with pockets of high abundance such as FG5 (solitary small benthic short dispersers), abundance predictions within our study area may be more important to when monitoring the impacts of climate change. Currently, our predictions show that FG5 is abundant around Okinawa Island, which would not be possible to identify if only predicting presence/ absence ranges. Yet, within-range abundance changes have the potential to significantly alter ecological communities, with dominance and competition eventually resulting in the loss or reduction of other previously functionally important groups (Liang *et al.*, 2018). For example, the abundance of functional groups such as FG5 within the northern edge of our study area (Fig. 3.6) may currently be controlled by competition with native temperate fishes at the trailing range edge (Coni, Booth and Nagelkerken, 2021), but future abundance increases skewed positively towards the higher latitudes, possibly suggesting widespread turnover under a tipping point of disturbance (Vye *et al.*, 2020).

However, it must be noted that our results can only inform management of large-scale biogeographic patterns and shifts, as the scale of the environmental layers used was 5arcmin (~9 km²) (Assis *et al.*, 2018). Due to Japan's tectonically active geography, it has a very narrow continental shelf, with much of the coastline rapidly dropping to depths unsuitable for shallow water reef species. Thus, a large proportion of each cell may be unsuitable for shallow reef species, and our results should only be considered for areas directly adjacent to the coast. Results could

be further refined with habitat suitability information, including information on bottom substrate accurate bathymetry, and with finer-scale data layers that may become available in the future.

To summarise, we show that our trait-based grouping approach allows for the inclusion of rare or data deficient species, whilst providing functionally informative outputs for monitoring and management. Our abundance-based approach is beneficial for investigating distributions at regional scales, such as the Kuroshio region of southern Japan, enabling the identification of environmental niches at scales relevant to the management of range shifts. As our functional groups had differing, yet significant, responses to environmental variables, our results increase the understanding of current and future functional community composition, facilitating spatially coherent approaches to designing conservation management strategies.

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3.6 Supplementary Materials for Chapter Three

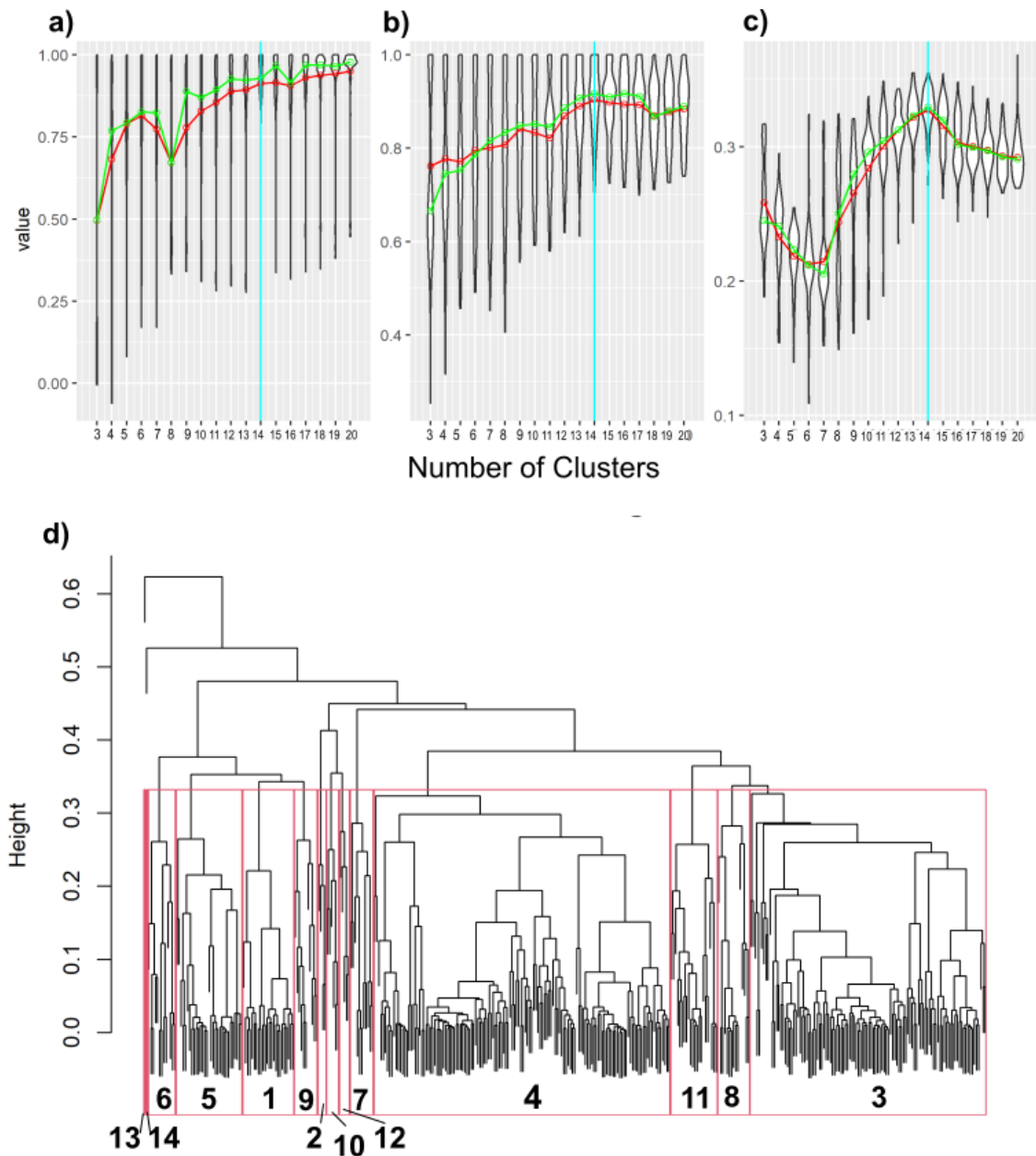


Figure S3.1. **a-c)** Choice of optimal number of clusters (functional groups) based on 1000-iteration 5% subsample bootstrap of Gower trait distance matrix (seven functional traits for 390 fish species). Red points and line are mean values, green points and line are median, **a)** Rand matching Index, **b)** Jaccard similarity index, **c)** average silhouette width, blue line is optimal number of clusters chosen (14), from 3-30 clusters. **d)** Dendrogram generated from the same Gower trait distance matrix, using the ‘average’ method to visualise the 14 functional groups (red boxes). For analyses, two groups (13 and 14) were excluded as they only contained one species, leaving a total of 12 functional groups.

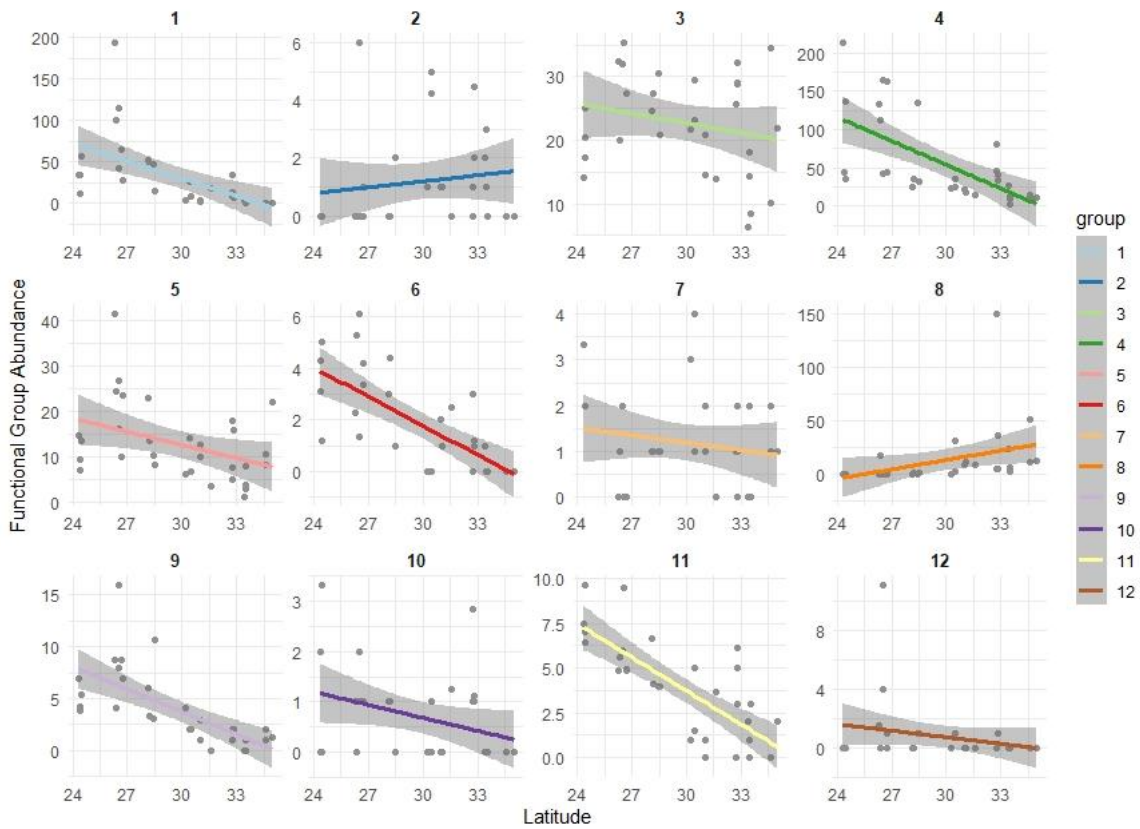


Figure S3.2. Functional group abundances plotted against latitude. Lines show linear models with 95% confidence intervals.

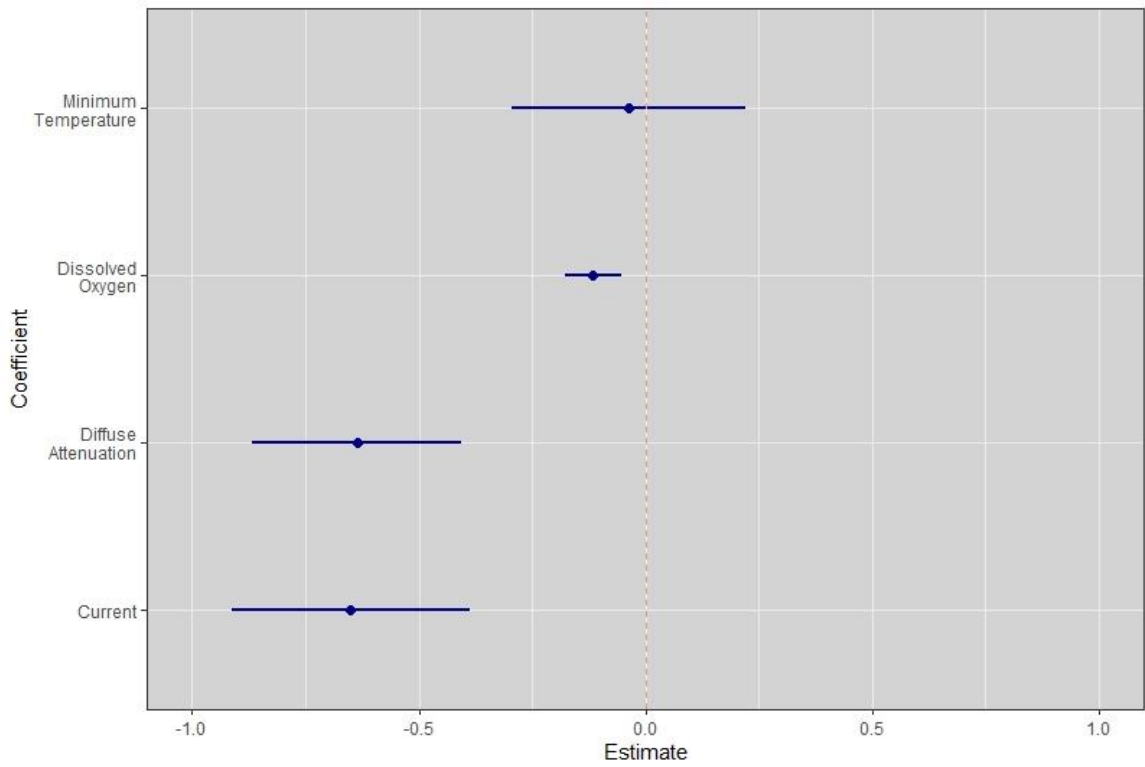


Figure S3.3. Fixed effect environmental variable coefficients with 95% confidence intervals for the species based mixed effect model.

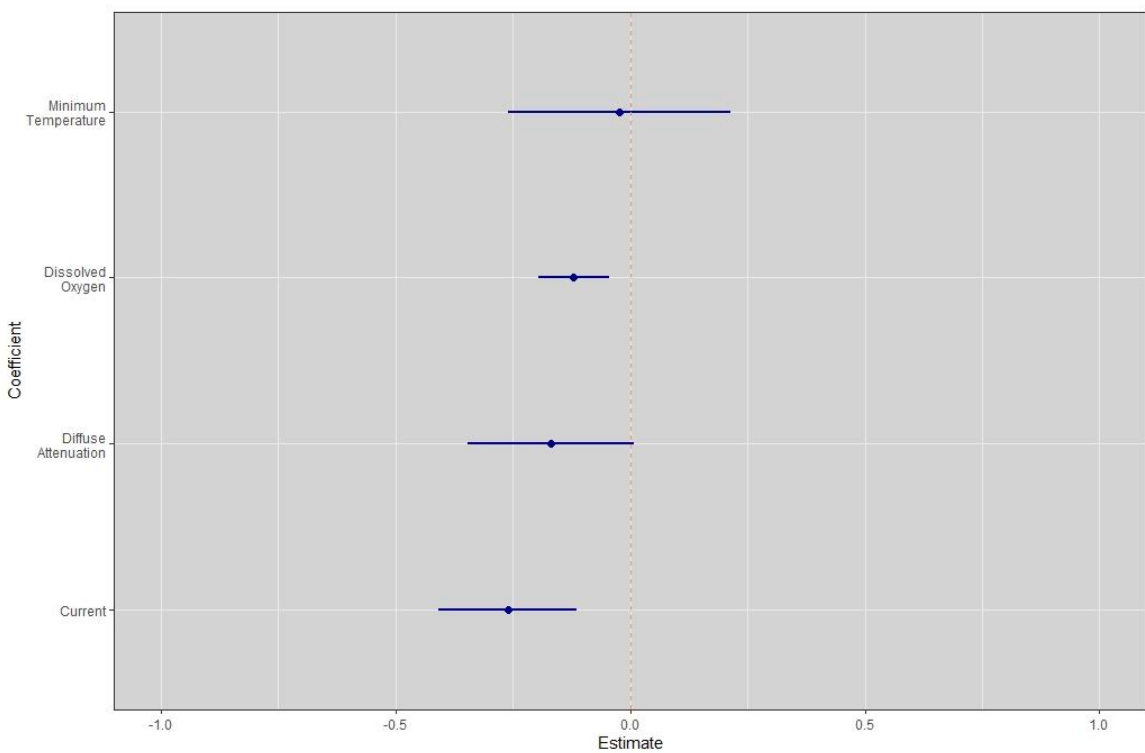


Figure S3.4. Fixed effect environmental variable coefficients with 95% confidence intervals for the functional group based mixed effect model.

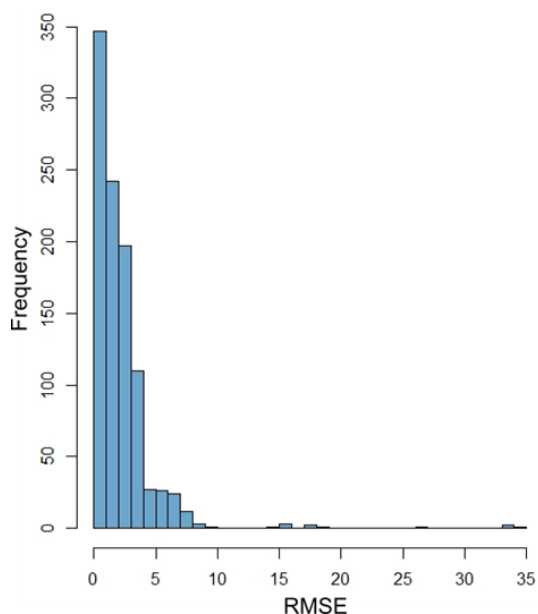


Figure S3.5. Histogram of RMSE across 1000 runs when iteratively removing three sites to cross validate models for functional group two.

Table S3.1. Model fish species recorded at >10 sites.

<i>Species</i>	<i>Number of sites present</i>
<i>Acanthurus dussumieri</i>	14
<i>Acanthurus nigrofuscus</i>	19
<i>Amphiprion clarkii</i>	19
<i>Calotomus japonicus</i>	15
<i>Canthigaster rivulata</i>	12
<i>Canthigaster valentini</i>	11
<i>Centropyge ferrugata</i>	14
<i>Centropyge vrolikii</i>	17
<i>Chaetodon auripes</i>	18
<i>Chaetodon lunulatus</i>	18
<i>Chaetodon trifascialis</i>	12
<i>Cheilodactylus zonatus</i>	12
<i>Chlorurus sordidus</i>	12
<i>Chromis chrysur</i>	15
<i>Chromis flavomaculata</i>	11
<i>Chromis margaritifer</i>	18
<i>Chrysiptera rex</i>	14
<i>Ctenochaetus striatus</i>	15
<i>Dascyllus trimaculatus</i>	13
<i>Gomphosus varius</i>	15
<i>Halichoeres melanochir</i>	19
<i>Hemigymnus fasciatus</i>	12
<i>Labroides dimidiatus</i>	30

<i>Meiacanthus kamoharai</i>	13
<i>Naso lituratus</i>	12
<i>Naso unicornis</i>	11
<i>Ostorhinchus notatus</i>	12
<i>Paracirrhites forsteri</i>	12
<i>Parupeneus multifasciatus</i>	17
<i>Plectroglyphidodon dickii</i>	11
<i>Plectroglyphidodon johnstonianus</i>	11
<i>Pomacentrus brachialis</i>	14
<i>Pomacentrus coelestis</i>	16
<i>Pomacentrus lepidogenys</i>	13
<i>Pomacentrus nagasakiensis</i>	11
<i>Pomacentrus philippinus</i>	14
<i>Pomacentrus vaiuli</i>	16
<i>Prionurus scalprum</i>	16
<i>Pseudanthias pascalus</i>	12
<i>Pseudanthias squamipinnis</i>	13
<i>Pseudocheilinus hexataenia</i>	17
<i>Scarus forsteni</i>	18
<i>Scarus niger</i>	12
<i>Stethojulis terina</i>	12
<i>Sufflamen chrysopterum</i>	14
<i>Thalassoma cupido</i>	13
<i>Thalassoma lunare</i>	11
<i>Thalassoma lutescens</i>	20
<i>Zanclus cornutus</i>	15
<i>Zebrasoma scopas</i>	15

Table S3.2. Root mean square error (RMSE), normalised root mean square error (NRMSE) and Pearson's correlation values between observed and fitted mixed effect model values for each fish functional group.

Functional group	RMSE	NRMSE	Pearson's correlation
1	40.75636	0.218182	0.780186
2	3.127325	0.205745	0.239265
3	8.110394	0.22782	0.454032
4	35.94156	0.206798	0.561784
5	18.55792	0.258467	0.514091
6	2.214555	0.225975	0.540272
7	0.935	0.23375	0.60918
8	30.99237	0.154191	0.774535
9	11.49142	0.242435	0.738452

10	1.06227	0.245139	0.591634
11	1.794411	0.289421	0.790699
12	1.227323	0.181826	0.675427

Model syntax for the a) species based generalised linear mixed model (GLMM) and b) functional group based GLMM using package ‘*lme4*’ in RStudio. All environmental predictor variables were standardised, and abundance response variables were transformed to fit the poisson distribution.

```
a) species GLMMM <- glmer(species abundance ~
  temp_min+
  o2+
  da+
  current+
  (1 | Species) +
  (0 + temp_min.| Species) +
  (0 + o2 | Species) +
  (0 + da | Species) +
  (0 + current | Species) ,
  data = species_data , family = poisson(link = "log"))
```

```
b) Group GLMM <- glmer(group abundance ~
  temp_min +
  o2+
  da+
  current+
  (1 | group) +
  (0 + temp_min | group) +
  (0 + o2 | group) +
  (0 + da | group) +
  (0 + current | group) ,
  data =grouped_data , family = poisson(link = "log"))
```

Chapter Four - Predicting changes in multi-taxon reef functioning under climate change.

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4.0 Abstract

Environmental and ecological changes along tropical to temperate transition zones exemplify ecological systems experiencing the effects of poleward range shifts. On subtropical high latitude reefs, range expansions of tropical species are resulting in benthic turnovers from macro-algae to coral, with associated community change. Only tropical species with certain functional traits may be able to persist in marginal high latitude conditions, but they could replace functionally diverse native species, resulting in communities with reduced functioning. Here, we take a multi-taxon functional group approach to answer two main questions: (1) Are the distributions of functional groups in all taxa driven by similar environmental factors? (2) Do the functional groups within and between taxa respond similarly to environmental change?

Surveys were conducted at 31 reefs with scleractinian coral communities along Japan's east coast from 24-35°N, recording the abundance of fish, echinoderm, mollusc and algae species and coral genera percentage cover. We classified the species into within-taxon functional groups based on their morphological, physiological and life history traits, yielding 35 groups across the five taxa. We then built abundance-based distribution models for the functional groups for the near past (2015) based on environmental factors, and predicted group abundances for 2050 under the CMIP5 RCP8.5 climate scenario.

We found that functional group distributions of all taxa had distinct tropical, sub-tropical and cosmopolitan distributions. We only observed the expected range shifting behaviours of increased abundances of tropical groups at high latitudes, and reduced abundances of sub-tropical groups in four tropical and five subtropical groups. We identified seven other behaviours, including groups that stayed stable (n=5), and groups that increased everywhere (n=5), with these behaviours exhibited across all taxa. Thus, our results predicted that although future high latitude communities undergo functional turnovers, they will maintain a high diversity of functional groups, making them appropriate targets for climate-resilient conservation management plans.

4.1 Introduction

Across the globe, increasing temperatures due to human-induced climate change are resulting in species range shifts as they track their ideal abiotic conditions (Donelson *et al.*, 2019). Range shifts have been recorded in all taxa, from large mobile species to small sessile invertebrates (Pecl *et al.*, 2017). The majority of these shifts are to higher altitudes or latitudes, and 75% of marine range shifts occur in a poleward direction (Sorte, Williams and Carlton, 2010). This is resulting in the reassembly of existing communities, and the formation of ecosystems with novel climates and species compositions (Miller and Bestelmeyer, 2016). However, it is unclear if reassembly alters ecosystem functioning, and if it will continue to occur, posing issues for conservation management (Clement and Standish, 2018).

Range shifts are occurring an order of magnitude faster in the ocean than on land (Sorte, Williams and Carlton, 2010). The ranges of marine organisms are more closely aligned to their thermal tolerances (Hastings *et al.*, 2020, Sunday *et al.*, 2012). This may be because the ocean has few barriers such as roads, rivers and mountains which hinder terrestrial dispersal (Figueira and Booth, 2010). Marine species often also have pelagic larval life stages, so even those with benthic sessile adult forms can be transported long distances by oceanic currents (Bani *et al.*, 2021), increasing the chances of rapid range shifts (Feary *et al.*, 2014). Such warm water currents facilitate poleward range shifts (Madin *et al.*, 2012), impacting communities along biogeographical transition zones (Beger *et al.*, 2014; Verges *et al.*, 2014). At high latitudes, many species are existing at the edge of their environmental tolerances, so small changes in abiotic conditions, such as increasing sea temperatures under climate change, can result in large scale ecosystem turnover (Fogarty *et al.*, 2017). These subtropical areas are considered marginal environments for scleractinian corals and tropical associated species, with high seasonality, low light availability, low aragonite saturation, low temperatures and high competition with macro-algae (Tuckett and Wernberg, 2018). Species that persist in such marginal conditions often have sub-tropical affinities and are habitat generalists with broad niche requirements (Tuckett and Wernberg, 2018). Climate change is causing the environments to warm, allowing for increased coral coverage, increased habitat complexity and the survival of more tropical species, through a process known as tropicalisation (Verges *et al.*, 2014).

The tropicalisation of high latitude reefs is a global phenomenon, and widespread shifts from macroalgae beds to novel coral dominated ecosystems have been recorded in South Africa, Australia and Japan (Schleyer, Kruger and Celliers, 2008; Beger *et al.*, 2014; Verges *et al.*, 2014; Kumagai *et al.*, 2018; Smith *et al.*, 2020). With range shifts, high latitude reefs could become refugia for species threatened by climate change at their tropical range margins (Beger *et al.*, 2014). However, it is unclear how these communities will continue to change, where future

tropicalisation will occur and what impacts this will have on ecosystem functioning (Vergés *et al.*, 2019). Ecosystem functioning is defined as the flux of energy and nutrients throughout ecosystems, which is quantified through rates of consumption, production and decomposition (Topor *et al.*, 2019). The capacity of an organism to contribute towards such processes is linked to its functional traits. Traits influence survival, growth, reproduction and consequently overall fitness (Poorter *et al.*, 2008). They can be physical, behavioural, biochemical and phenological/temporal and can be used to define a species functional role (Cadotte, Carscadden and Mirotnick, 2011). Traits influence the ability of an organism to persist in its environment as they influence competitiveness and responses to abiotic conditions (Sommer *et al.*, 2014a). As climate change alters ecological filters, new communities may form with different trait combinations (Muler *et al.*, 2018). For example, range shifting fish species at high latitudes have larger body size, high swimming behaviour and pelagic larval life stages, and are habitat generalists with high dispersal capacity (Feary *et al.*, 2014). Similarly, invasive species have been found to be functionally similar generalists, which outcompete specialist native species (Funk *et al.*, 2016). Thus, under tropicalisation, if the subtropical range contracting species have specialist functions and are replaced by generalist tropical species, this could result in the loss of local and global ecosystem functions.

Taking a species based approach to understanding the ecological processes which regulate ecosystems is challenging due to the many complex interactions (Bellwood *et al.*, 2019). Additionally, records are often not available for rare or data-deficient species, which can disproportionately contribute towards functioning (Mouillot *et al.*, 2013; Dee *et al.*, 2019). Species in high diversity systems often share similar functional traits and life strategies, inferring that they share environmental niches, and thus provide the same functional roles (Blaum *et al.*, 2011). The resulting functional redundancy means that individual species can be lost with little change to ecosystem functioning (Guillemot *et al.*, 2011). Grouping these species together, and understanding the functional turnovers of these groups could provide valuable information about how functions are gained, conserved, or lost (Bellwood *et al.*, 2019; Pacioglu *et al.*, 2020).

Across tropical to temperate gradients, reef fish functional groups have been found to fall into distinct thermal guilds, being distributed in either tropical, sub-tropical or cosmopolitan areas (Chapter three). It is unclear such spatial patterns can be generalised across other taxa. In tropical and temperate reef systems, corals and macro-algae provide habitat (Wernberg, Kendrick and Toohey, 2005; Darling *et al.*, 2017), and fish and macroinvertebrates including molluscs and echinoderms cycle nutrients and energy flow through herbivory (Brandl *et al.*, 2019; Magdalena Zarzyczny *et al.*, 2022), the removal of detritus (Wolkenhauer *et al.*, 2010; Netchy *et al.*, 2016) and through complex multi-taxon trophic networks (Casey *et al.*, 2019). Relationships between

functional traits and environmental gradients have been identified for coral (Sommer *et al.*, 2014), algae (Stelling-Wood, Poore and Gribben, 2021) and molluscs (Floyd *et al.*, 2020) suggesting that the distributions of trait-based functional groups for these taxa may also exhibit thermal guilds. Yet, despite being important reef herbivores (Zarzyczny *et al.*, 2022), echinoderm traits are not well studied (Rojas-Montiel *et al.*, 2020) and it is unknown if trait distributions differ across latitudinal gradients.

If functional thermal guilds are identified in all taxa, it is not known if groups within and across taxa will have similar responses to climate change. For example, will poleward range shifts to high latitudes occur for all tropical groups, with contractions in all subtropical groups regardless of taxa, or could losses occur across whole taxa, and with gains across others? If all groups shift poleward, this could suggest that high latitude reefs will gain new tropical functions through range expansions, but lose the unique functions that the contracting subtropical groups provide. However, expanding groups from one taxon could fill the functional roles of contracting groups from another. For example, as habitat forming kelps decline due to thermal stress, they can be replaced by range expanding corals which provide novel structural habitats (Tuckett *et al.*, 2017; Kumagai *et al.*, 2018). Herbivory processes have also been recorded shifting from echinoderms to herbivorous tropical fishes under tropicalisation (Yeruham *et al.*, 2020). However, range shifts have been found to be multi-directional, and some species do not experience shifts (Goatley and Bellwood, 2014; Pinsky, Selden and Kitchel, 2019). As the functional groups have different traits, they are likely to have unique functional niches, suggesting that range expanding groups may be able to co-exist with resident natives (Pacioglu *et al.*, 2020). In this case, high latitude reefs could experience increased functioning, with current records of co-existing range shifting tropical groups and persisting native groups on Australia's tropicalising reefs (Zarco-Perello *et al.*, 2020; Smith *et al.*, 2021). In such cases, this could be due to an extinction debt (Kuussaari *et al.*, 2009), and it is unclear if these groups will be able to co-exist in the future.

Here, we develop functional group-based distribution models for fish, coral, algae, molluscs and echinoderms for now and 2050 under climate change, and use these to predict and quantify the functional change across Japan's marine tropical to temperate transition zone. We aim to answer two main questions: (1) Are the distributions of functional groups in all taxa driven by similar environmental factors? and (2) Do the functional groups within taxa respond similarly to environmental change, or are there shared patterns of distribution change across multi-taxon groups? Improved knowledge on how the functioning of high latitude systems will change, will allow for better informed climate-resilient management plans for areas of environmental instability.

4.2 Methods

4.2.1 Study Region

The Japanese coastline ranges from tropical to temperate marine ecosystems which are highly influenced by the Kuroshio Current, the strongest northwards flowing boundary current in the world (Sudo *et al.*, 2022). This brings warm waters to high latitudes, allowing for the survival of scleractinian coral communities, with the most northern coral community in the world being located in Japan (Yamano *et al.*, 2012). Spanning over 20° in latitude, the islands form stepping-stones along a gradual environmental gradient which facilitates dispersal (Yamano, Sugihara and Nomura, 2011). Range expansions in the region have been well studied, with coral species found to be shifting 14km per year northwards, resulting in local phase shifts from temperate to subtropical ecosystems in the last few decades (Yamano, Sugihara and Nomura, 2011; Verges *et al.*, 2014; Kumagai *et al.*, 2018). During summer 2015 and summer 2016, we surveyed 31 sites across a latitude of 24-35°N, spanning the tropical – temperate environmental gradient for Japanese coral communities (Fig. 4.1). Sites were chosen to accurately encompass the types of shallow water coral communities found along this gradient, from tropical coral reefs at Japan's southernmost Islands, to one of Japan's highest latitude scleractinian coral communities in Tateyama 35°N (Mizerek *et al.*, 2016).

4.2.2 Survey Methods

At each site, we surveyed along three to five replicate belt transects of 25m length and varying widths depending on taxa. Site depths ranged from 8-10m except at the highest latitude site in Tateyama where corals only occurred at 3-5m depth. For the corals, we took 25 benthic photographs of approximately 1-1.5m width along each transect, and identified scleractinian coral genus abundance (percentage cover) using CPCE software (Kohler and Gill, 2006). Macro-algal abundance was identified to species level where possible (with some identified to genus only) along belts transect with a width of 2m. The abundance of reef-associated fish species were recorded along transects with a width of 5m, laying the transect tape whilst swimming to avoid fish disturbance. We measured species abundance of epifaunal molluscs along the transects using a belt width of 1m, focussing on visible macro- molluscan species. Mollusc bases were photographed to aid identification where required. Echinoderms, which included starfish (Asteroidea), sea urchins (Echinoidea) and sea cucumbers (Holothuroidea) were recorded along the transects with a belt width of 2m, and searches were conducted to attempt to capture cryptic echinoderms.

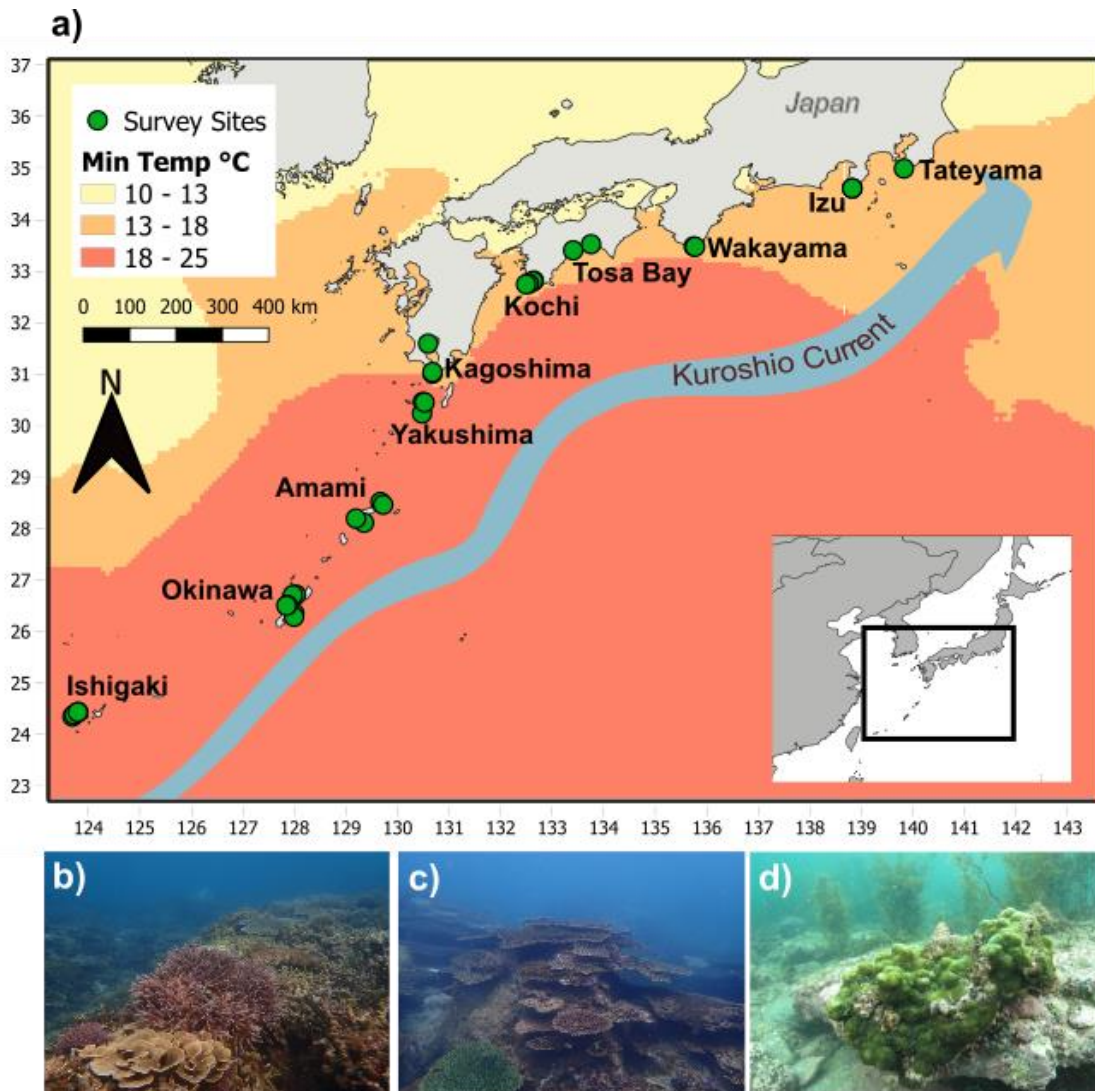


Fig 4.1. **a)** Map showing the survey sites (green dots), area names, and the path of the Kuroshio current. The background colours represent minimum sea surface temperature isotherms derived from BioOracle (Assis *et al.*, 2018). The temperature bands indicate tropical (18-24°C), sub-tropical (13-18°C) and temperate (10-13°C) coral reef habitat classifications as defined by (Makino *et al.*, 2014). **b)** A typical Okinawan tropical reef at 27°N with high diversity of reef building corals. **c)** A typical sub-tropical reef in Kochi at 33°N with dominant plating *Acropora* species attached to rocky substrate **d)** A high latitude reef community in Tateyama at 35°N where kelps and corals co-exist on rocky substrate.

4.2.3 Trait-Based Analyses

A comprehensive species trait database was created for fish, algae, molluscs and echinoderms. Values for fish, mollusc, algae and echinoderm traits were gathered from online data sources such as Florabase (<https://florabase.dpaw.wa.gov.au>), SeaLife Base (www.sealifebase.ca), FishBase

(www.fishbase.org) (Froese and Pauly, 2021) and The Fish Database of Taiwan (<http://fishdb.sinica.edu.tw>) (Shao, 2022), as well as through extensive literature searches for Japanese endemics. If multiple trait values were available for individual species, the value that was collected in Japan, or geographically closer to Japan was selected. In the occasional cases where data was found to be unavailable after searching, genus level data was used. As the coral survey data was collected to genus level, species present in Japan for the recorded genera were determined using a Japanese hermatypic coral species list (Japan Coral Reef Society, 2004). Traits were collated from the Coral Traits Database (Madin *et al.*, 2016) for all these species. To determine a single value for each trait per genus, the mean of the continuous traits was calculated. For the categorical traits, the category value that was the most abundant was selected.

Morphological, physiological, behavioural and life history traits were selected that would capture the species ecological and functional roles within the community (Floyd *et al.*, 2020; Anderson *et al.*, 2021, Chapter three). These traits were broadly similar across taxa, such as depth range and size, but with some taxa specific traits such as support mechanism for the algae (Table 4.1). To cluster species into functional groups, for each taxon, the functional trait values for each species were used to calculate Gower distances, which were then hierarchically clustered using the ‘average’ method. To determine cluster stability, we iteratively removed 5% of the species data randomly over 1000 runs, and recalculated the distance matrix during each iteration to determine the silhouette width, Jaccard similarity index and the Rand matching index for two to 30 clusters. We selected the most stable number of clusters using the average silhouette value, and index values. Outlier groups that contained only one species were excluded from analyses, and the clusters were labelled as functional groups (Miller *et al. in revisions*). Corals were also clustered into groups with this method, but the groups were less robust as they were based on genus level data. Thus, the corals were grouped by morphological types defined as ‘growth form typical’ on coraltraits.org (Madin *et al.*, 2016). The ‘submassive’ category was combined into the ‘massive’ group and ‘branching open’, ‘branching closed’, ‘corymbose’ ‘digitate’ and ‘hispidose’ categories were combined into a ‘branching’ group. Trait values for each coral morphological group were still collated to assess overall group functions.

Functional groups of all taxa were plotted against latitude to explore environmental patterns prior to developing distribution models (Supplementary Fig. S4.1-S4.5).

Table 4.1. Traits used to categorise species in functional group for algae, molluscs, fish and echinoderms, with the trait categories or numeric units. Coral were categorised into groups by their growth forms (in bold), but within each growth forms, the traits listed in the table for corals were assessed.

<i>Taxa</i>	<i>Trait</i>	<i>Units / Categories</i>
Coral	Growth form	Massive, branching, tables or plates, columnar, encrusting
Coral	Corallite size	Numeric (mm)
Coral	Max depth	Numeric (m)
Coral	Growth rate	Numeric (mm)
Coral	Coloniality	Colonial, solitary, both
Coral	Larval development	Brooder, spawner
Coral	Reproductive strategy	Gonochore, hermaphrodite
Coral	Wave exposure	Exposed, protected, both
Coral	Water clarity	Clear, turbid, both
Algae	Maximum height	Numeric (cm)
Algae	Depth range	Numeric (m)
Algae	Holdfast morphology	Bulbous, conical, crustose, discoid, rhizoidal
Algae	Support Mechanism	Calcified, corticated, low support, symbiotic support
Algae	Substrate preference	Generalist, epiphytic, specialist epiphyte, rocky, sandy, rocky or epiphytic, rocky or sandy
Algae	Tidal zone	Intertidal, intertidal/subtidal, subtidal
Algae	Reproductive strategy	Asexual spores, dioecious, dioecious with long/multiple fertile periods, fragmentation and spores/ propagules/ gametes, fragmentation/ vegetative spread, monoecious- not self-fertilising, monoecious- self fertilising.
Mollusc	Maximum size	Numeric (cm)
Mollusc	Depth range	Numeric (m)

Mollusc	Shell morphology	Bivalve, conical, cowry shape, fusiform, globose, heliciform, no shell, trochiform, whelk shape, worm like
Mollusc	Mobility	Crawling, mobile, sessile
Mollusc	Reef position	Benthic, sub-benthic, generalist
Mollusc	Tidal zone	Intertidal, intertidal/subtidal, subtidal
Mollusc	Habitat preference	Generalist, coral rubble, soft sediment, coral rubble/ sand, hard substrate, live coral, macroalgae/ rocky, rocky, rocky/ coral rubble, rocky/ sandy, rocky/ live coral
Mollusc	Trophic level	Herbivore, predator, grazer, deposit feeder/ grazer/ detritivore, deposit feeder/ grazer/ herbivore, , grazer/ deposit feeder, grazer/ detritivore, predator/ grazer, suspension feeder/ grazer
Fish	Maximum length	Numeric- (cm)
Fish	Depth range	Numeric- (m)
Fish	Pelagic larval duration	Numeric- (Days)
Fish	Aggregation	Groups, pairs, schools, solitary
Fish	Water column position	Demersal, sub-benthic, benthic, upper benthic, reef pelagic, pelagic
Fish	Parental mode	Nesters, demersal, brooders, live bearers, scatters
Fish	Trophic level	Predator, piscivore, planktivore, omnivore, corallivore, herbivore, detritivore
Echinoderm	Maximum length	Numeric- (mm)
Echinoderm	Depth range	Numeric- (m)
Echinoderm	Spines	Yes, no
Echinoderm	Aggregation	Gregarious, solitary
Echinoderm	Trophic level	Carnivore, corallivore, planktivore, omnivore, herbivore, detritivore, small invertebrate specialist

Echinoderm	Mating system	Sexual, sexual and asexual
Echinoderm	Tidal zone	Intertidal/shallow, subtidal
Echinoderm	Exposure	Exposed, protected, exposed or protected

4.2.4 Environmental data

Environmental variables were downloaded into R (R Core Team, 2020) using the ‘sdmpredictors’ (Bosch, 2016) and ‘raster’ packages (Hijmans, 2020) from the Bio-ORACLE online database (<http://www.bio-oracle.org/>) (Tyberghein *et al.*, 2012; Assis *et al.*, 2018). All data was available at a spatial resolution of 5 arcmin, which were produced by statistically downscaling monthly average climate data obtained from satellite and in-situ observations from the period of 2000-2014 (Assis *et al.*, 2018). The variables used were minimum sea surface temperature, maximum surface current velocity, mean surface salinity, surface chlorophyll and mean bottom light at the minimum depth. Surface variables were chosen as the environmental data is relatively coarse-scale with pixels covering a range of different depths. Coral communities at high latitudes only exist in relatively shallow areas where the conditions are more likely to be similar to the surface. The minimum sea surface temperature was used as winter water temperatures is thought to be one of the main barriers to further range expansion for tropical species (Kleypas, Mcmanus and Menez, 1999). Another barrier for expansion is solar radiation, which declines towards the poles due to day length and angle (Muir *et al.*, 2015). To capture this, we included the variable bottom light which was calculated using depth dependant exponential function based on photosynthetically active radiation (PAR) and diffuse attenuation coefficient (Kd490):

$$\text{Light at bottom} = \text{PAR} \times \exp(-Kd490 \times Z)$$

Where z= depth (Assis *et al.*, 2018).

Chlorophyll concentration can be a proxy for water quality, high concentrations represent increased nutrification (Cleary *et al.*, 2016). Chlorophyll is rapidly taken up by phytoplankton communities which alter the natural nutrient environment, and increase susceptibility of corals to bleaching and affect the abundance and community structure of reef associated marine taxa (Collie, Wood and Jeffries, 2008; D’Angelo and Wiedenmann, 2014; Cleary *et al.*, 2016). Current velocity affects rates of plankton delivery, as well as detrital production and can be used as a proxy for the connectedness of ecosystems (Carr *et al.*, 2011; Hata *et al.*, 2017). Areas with high current velocity are likely to be on the path of the Kuroshio Current, with higher levels of tropical

species recruitment (Uchiyama *et al.*, 2018). Finally, we included salinity as many marine organisms exhibit firm survival limits to high and low salinity environments (Hoegh-guldberg and Smith, 1989; Berkelmans, Jones and Schaffelke, 2012).

Future temperature, salinity and current velocity layers for 2040-50 projected under the RCP 85 business as usual climate change scenario were downloaded from Bio-ORACLE. These layers were created by averaging data from coupled atmosphere-ocean general circulation models provided by the CMIP 5 including the models CCSM4, HadGEM2-ES and MIROC5 (Assis *et al.*, 2018).

4.2.5 Spatial Abundance Models

Using the environmental and survey data, spatial abundance models were created for each functional group to predict their abundance across space for the present, and for future climate scenarios. Abundance based models more accurately predict species occurrences than presence/absence models, making the results more appropriate for conservation planning and management (Johnston *et al.*, 2013). Furthermore, it may be possible to identify key areas of change before full range shifts occur. Species may still have a similar overall range but at range edges their abundances may increase where conditions are more favourable, and decrease where they are less favourable before they cease to exist there (Bates *et al.*, 2014).

The abundance of each functional group along each transect was calculated by totalling the abundance of species within that group. The mean abundance of each functional group was then calculated across the five transects to give the average abundance at each site. The environmental variables were extracted from the GPS points of each site using the 'extract' function (Hijmans, 2021). The variance inflation factor (VIF) of the variables was calculated using the 'vifstep' function (Naimi *et al.*, 2013) to check for collinearity, and no variables were excluded. Generalised linear models (GLMs), generalised additive models (GAMs) and random forest (RF) algorithms were then constructed using ~80% training data (n=25) and ~20% test data (n = 6). For algae, molluscs, fish and echinoderms the GLMs and GAMs were fitted with negative binomial errors and the log link function (McCullagh and Nelder, 1989). Stepwise model selection was implemented based on AIC values. For the corals, as the data was collected in percentage cover, this was converted to proportions and a beta regression was used instead of a GLM using the 'betareg' function (Cribari-Neto and Zeileis, 2010). Similarly, GAMs were fitted with the beta regression family (betar) (Wood, 2017). All GAMs were implemented using the MGCV package (Wood, 2017) and we specified the maximum degrees of freedom as five for each individual smoothing component.

Random Forests are a machine learning technique that is robust to overfitting and are known recognised to produce high quality predictive models (Mi *et al.*, 2017). We used the R package ‘random forest’ (Liaw, *et al.*, 2018) and using the training data, we constructed each model 1000 times for each functional group and validated it against the test data using the root mean square error (RMSE) and Pearson’s correlations. The RMSE and Pearson’s correlation values of the 1000 runs were then averaged, to determine one average value for each model.

GLM, GAM and RF models were then fit using data from all of the sites (n=31). An ensemble model was created for each functional group, including the models with at least one significant ($p < 0.05$) predictor variable, an average RMSE that was smaller than half the range of the data and an average Pearson’s correlation value above 0.25. If the models did not fit these criteria then they were not included in the ensemble, with the ensemble being created with only the two other models. For some groups only one model fit the criteria, thus only a single model was used for the final outputs. In the ensembles, the models were weighted by their average RMSE and Pearson’s correlation value in the ensemble. The ensemble models were then used to predict the abundance of each functional group across space for each 9km² raster pixel using the predict function within the SDM R package (Naimi and Araújo, 2016). We predicted within the central Kuroshio and South Kuroshio ecoregions from WWFs marine ecoregions of the world (Spalding *et al.*, 2007), masking out areas over 30km from the coastline. These ecoregions do not extend latitudinally past the data sites and are highly influenced by the Kuroshio Current (Sudo *et al.*, 2022). They were merged, and edited within ArcMap (ESRI, 2011) to exclude areas that are likely to differ significantly in environmental conditions such as the Seto Inland Sea, and the Izu oceanic Islands. Thus, we are predicting within abiotically similar areas of known coral ecosystems.

To predict the future spatial abundances of functional groups we ran the same models using values for the environmental variables projected under the RCP8.5 ‘business as usual’ climate scenario for 2050. To find the change over time for each functional group, we subtracted the current predicted abundance from the future predicted abundance for all groups. We then extracted the coordinates of each raster pixel, and plotted the change in abundance for each pixel against latitude, and identified patterns in abundance change. Abundance change patterns across groups were visualised using principal co-ordinate analyses, inputting latitude, longitude, functional groups of all taxa, and the predicted abundance change for each pixel.

4.3 Results

4.3.1 Functional group classification

A total of 392 fish, 92 mollusc, 107 algae and 58 echinoderm species, as well as 59 coral genera and morpho-genera were recorded in our surveys. The fish species were found to cluster most appropriately into 12 functional groups. Algae species clustered into five functional groups, mollusc species clustered into seven functional groups and echinoderm species clustered into five functional groups. The coral genera were split into six morphological types, hereby known as functional groups. Functional groups of all taxa were shown to have varying patterns in abundance change across latitude (Supplementary Fig. S4.1-4.5).

4.3.2 Performance of spatial abundance models

The abundance of each functional group was found to be dependent on unique sets of the environmental variables (Table 4.2). However, sea surface temperature was a significant predictor for all groups where the generalised additive or generalised linear models had appropriate fits. Model predictive ability varied between the functional groups and between the different statistical modelling approaches (Supplementary Table S4.1). Averaged over all groups, GLMs had the poorest performance based upon Pearson's correlations between observed and modelled abundances (0.24), followed by GAMs (0.34) then Random Forests (RF) (0.45). GAMs had the highest average Root Mean Square Error (RMSE), followed by GLMs and then RFs. The predictive capacity of the models for six of the functional groups (coral FG2 and FG3, fish FG 10, mollusc FG5 and echinoderm FG2 and FG4) was not high enough to continue modelling these groups. Thus, they were excluded from further analyses.

Table 4.2. Root mean square error (RMSE) and Pearson's correlations between predictions from training data and observed values from test data for each functional group for the models that were used for further analyses. Blank grey rows indicate the groups with high model error or low predictive capacity which were excluded from further analyses. Dots represent if the environmental variables were included in the ensemble model as significant predictors for the generalised linear models and generalised additive models. Light was only included as a predictor variable for the phototrophic groups (Corals and Algae).

<i>Functional Group (FG)</i>	<i>Model</i>	<i>RMSE</i>	<i>Pearson's</i>	<i>SST</i>	<i>Current</i>	<i>Salinity</i>	<i>Chlorophyll</i>	<i>Light</i>
Coral FG1	Ensemble	0.05	0.74	•	•	•	•	•
Coral FG2	Not enough data to model							
Coral FG3	Not enough data to model							
Coral FG4	Ensemble	0.02	0.43	•	•			
Coral FG5	Ensemble	0.07	0.54	•	•	•	•	
Coral FG6	Ensemble	0.16	0.25	•	•	•	•	
Algae FG1	Random Forest	2.01	0.57					
Algae FG2	Random Forest	5.68	0.37					
Algae FG3	Ensemble	5.21	0.59			•		
Algae FG4	Random Forest	0.31	0.59					
Algae FG5	Random Forest	3.09	0.93					
Mollusc FG1	Random Forest	30.06	0.41					NA
Mollusc FG2	Ensemble	9.81	0.73	•				NA
Mollusc FG3	Ensemble	10.83	0.47	•	•	•	•	NA

Mollusc FG4	Random Forest	12.46	0.5					NA
Mollusc FG5	Not enough data to model							
Mollusc FG6	Ensemble	14.46	0.62					NA
Mollusc 7	Random Forest	1.88	0.48					NA
Fish FG1	Ensemble	41.12	0.66	•	•	•	•	NA
Fish FG2	Random Forest	3.03	0.25					NA
Fish FG3	Random Forest	8.66	0.34					NA
Fish FG4	Ensemble	38.19	0.51	•				NA
Fish FG5	Ensemble	14.35	0.58		•		•	NA
Fish FG6	Ensemble	2.44	0.50		•	•	•	NA
Fish FG7	Ensemble	1.05	0.44	•	•	•		NA
Fish FG8	Random Forest	38.62	0.38					NA
Fish FG9	Ensemble	7.15	0.81	•	•			NA
Fish FG10	Not enough data to model							
Fish FG11	Ensemble	1.33	0.73	•	•			NA
Fish FG12	Random Forest	1.14	0.53					NA
Echinoderm FG1	Random Forest	108.13	0.45					NA
Echinoderm FG2	Not enough data to model							

Echinoderm FG3	GAM	1.75	0.46	•	•	NA
Echinoderm FG4	Not enough data to model					
Echinoderm FG5	Random Forest	4.11	0.41			

4.3.3 Model predictions

Spatial predictions from the models suggest that the functional groups of all taxa split into tropical (higher abundances below the 18-degree isotherm), subtropical (higher abundances above the 18 degree isotherm) (Fig. 4.1) or cosmopolitan distributions (Fig 4.2, Table 4.3, Supplementary Fig. S4.6 - S4.10). All predictions for coral groups were tropically distributed, except table/plating corals (coral FG6) which had higher subtropical abundances. In contrast, all algae FGs were found to be sub-tropically distributed except FG1. Mollusc group distributions were mixed; FG3 was tropical, FG2, FG4 and FG6 were subtropical, FG1 and FG7 were cosmopolitan, with high abundances around the tropical/ subtropical boundary. For the fish groups, FG2 and FG8 had subtropical distributions, with the remainder of the groups having tropical distributions except FG7 which was cosmopolitan. Echinoderm FG1 and FG5 were found to be more abundant in the subtropics, and FG5 had a cosmopolitan distribution.

When assessing how the functional group abundances were predicted to change between the two time periods across our study region, we identified nine tropicalisation behaviours (Fig. 4.3, Fig. 4.4, Table 4.3). The patterns were: **1) Decrease at high latitudes:** Algae FG2 and FG5, Mollusc FG2 and FG6, Fish FG8. **2) Decrease everywhere:** Coral FG4 and FG5, Algae FG3, Fish FG7, Echinoderm FG1. **3) Decrease in the tropics, increase at high latitudes:** Coral FG1 and FG6, Algae FG1, and Echinoderm FG5. **4) Increase at mid and high latitudes:** Mollusc FG1, Fish FG3 and FG4. **5) Increase everywhere:** Mollusc FG3, Fish FG5, FG9 and FG11, Echinoderm FG3. **6) Increase in the tropics:** Fish FG1 and FG6, Echinoderm FG3. **7) Stays the same:** Algae FG4, Mollusc FG4 and FG7, Fish FG2 and FG12. (Fig 4.3, Fig. 4.4, Table 4.4.).

The principal component analyses identified spatial similarities in functional group change across and within groups (Fig. 4.4)

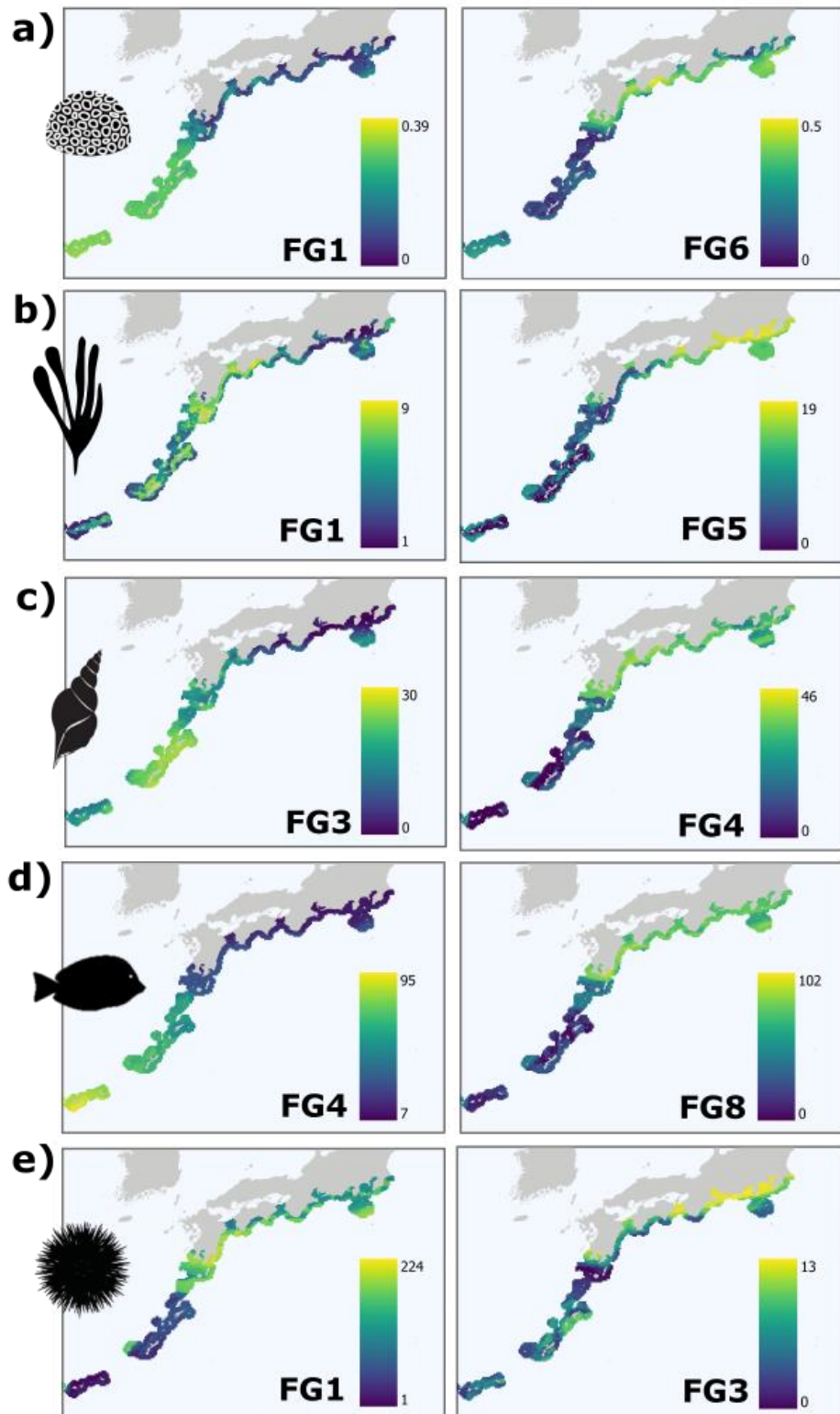


Figure 4.2. Examples of functional group (FG) spatial distributions predicted for 2015 using ensemble models. The colour gradient represents abundance gradients for all groups except corals where the gradient represents percentage cover. **a)** Coral FG1 (tropical) and FG6 (subtropical), **b)** Algae FG1 (cosmopolitan) and FG5 (subtropical), **c)** Mollusc FG3 (tropical) and FG4 (subtropical), **d)** Fish FG4 (tropical) and FG8 (subtropical), **e)** Echinoderm FG1 (subtropical) and FG3 (cosmopolitan).

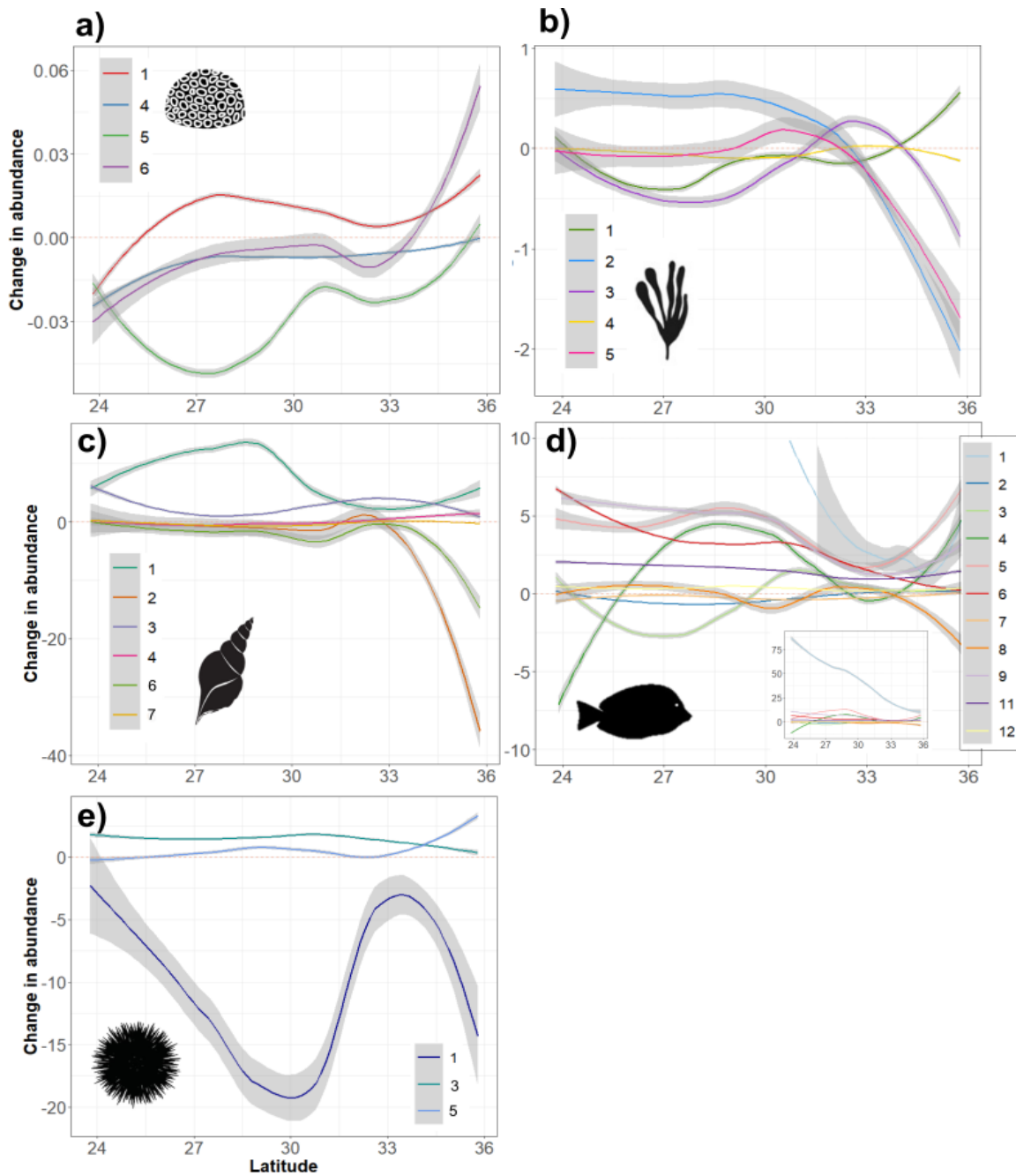


Figure 4.3. Predicted change in abundance for 2050 under the RCP8.5 climate scenario plotted against latitude using LOWESS smoothing for functional groups of **a)** Corals, **b)** Algae, **c)** Molluscs, **d)** Fishes and **e)** Echinoderms. Functional group one for fish had a larger change in abundance which is presented in the inset plot.

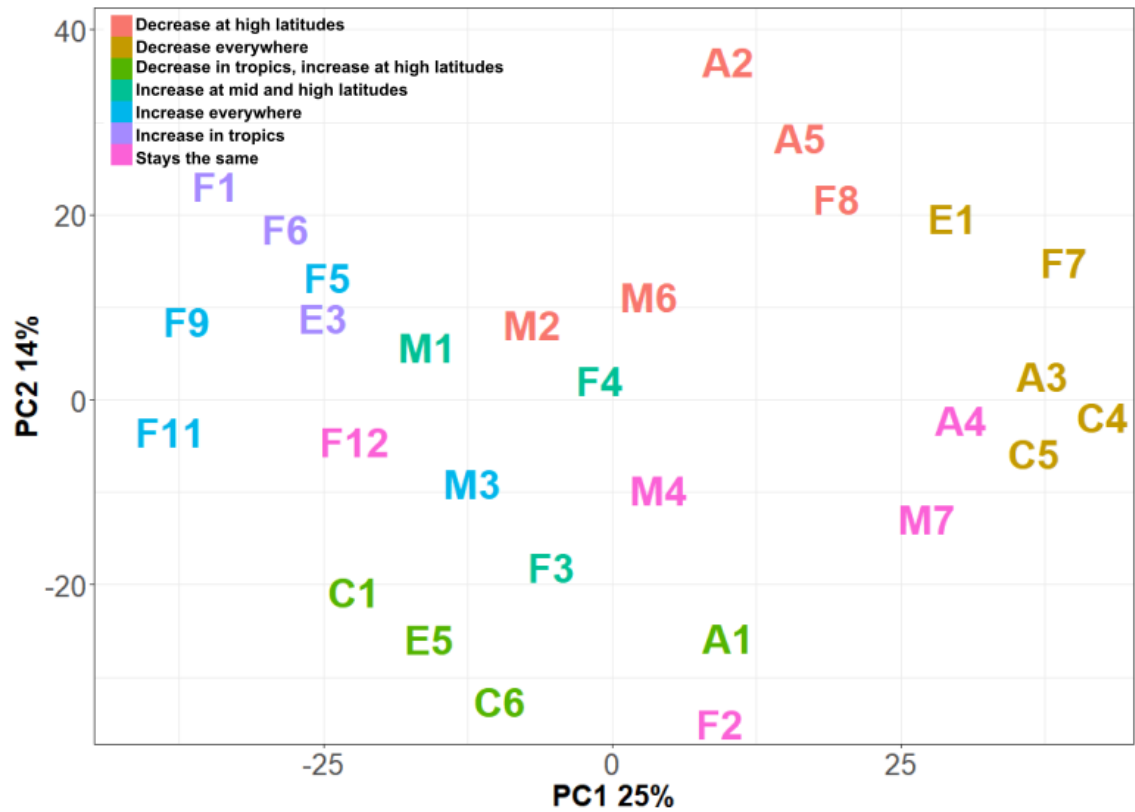


Figure 4.4. Principal component analyses (PCA) of predicted functional group change in abundance between now and 2050 for all pixels within 30km of the coastline within our study area. Each text label represents a functional group. Labels beginning with C= coral, A=algae, M=mollusc, F=fish and E=echinoderm, with the number representing the functional group within the taxa. Labels are coloured by their tropicalisation behaviours (Figure 4.3).

Table 4.3 Modelled functional groups for all taxa, with their trait characteristics and modelled current abundance distributions. Groups with a higher predicted abundance south of the 18°C sea surface temperature isotherm were categorised as tropical, and those with a higher abundance north of the isotherm were categorised as subtropical. Tropicalisation behaviours were determined from predicted change in abundance for 2050 under the RCP8.5 climate change scenario.

<i>Functional Group and Characteristics</i>	<i>Current distribution</i>	<i>Tropicalisation Behaviour</i>
Coral FG1- Branching , Clear water habitat with broad wave exposure, small max depth. Mostly hermaphroditic with spawning and brooding. Fast growth rate and small corallites.	Tropical	Decrease in tropics, increase at high latitudes

Coral FG2- Columnar , Broad water clarity and wave exposures, medium max depth. Mostly hermaphroditic spawner. Medium growth rate, small corallite width.	Not enough data	
Coral FG3- Encrusting , Broad water clarity and wave exposure, small max depth. Spawner and brooder. Slow growth rate and medium corallites.	Not enough data	
Coral FG4- Laminar , Predominantly clear water and protected to broad wave exposure, large max depth. Spawner. Medium growth rate and corallite size.	Tropical	Decreases everywhere
Coral FG5- Massive , Predominantly clear water, protected to broad wave exposure, medium max depth. Spawner. Slow growth rate with large corallites.	Tropical	Decreases everywhere
Coral FG6- Tables/Plates , Clear water with broad wave exposures, large max depth. Hermaphroditic spawner. Fast growth rate and small corallites.	Subtropical	Decrease in tropics, increase at high latitudes
Algae FG1- Small height, crustose/discoid/conical holdfast, all support types including symbiotic. Large depth range, rocky habitat. Mostly asexual reproduction	Cosmopolitan	Decrease in tropics, increase at high latitudes
Algae FG2- Medium height, rhizoidal holdfast, all support types. Very large depth range, substrate generalist, asexual fragmentation and spores/propagules gametes	Subtropical	Decreases at high latitudes
Algae FG3- Medium height, discoid holdfast, all support types. Large depth range, Rocky habitat, multiple reproductive types	Subtropical	Decreases everywhere
Algae FG4- Very small height, rhizoidal holdfast, medium depth range, sandy intertidal habitat, dioecious reproduction.	Subtropical	Stays the same
Algae FG5- Very large height, conical holdfast, corticated support. Small depth range rocky subtidal habitat. Multiple reproductive types.	Subtropical	Decreases at high latitudes

Mollusc FG1- Large size, bivalve. Crawling, benthic, habitat generalist, all tidal zones, medium depth range. Herbivore.	Cosmopolitan	Increase at mid and high latitudes
Mollusc FG2- Large size. Mobile, benthic, hard substrate, mostly subtidal, medium depth range. Low trophic level generalist	Subtropical	Decreases at high latitudes
Mollusc FG3- Small size. Sessile, sub-benthic, habitat specialist, mostly subtidal, medium depth range. High trophic level generalist.	Tropical	Increases everywhere
Mollusc FG4- Medium size, elongate shell. Crawling, benthic, hard substrate habitat, all tidal zones, large depth range. Grazer	Subtropical	Stays the same
Mollusc FG5- Large size. Crawling, benthic, hard substrate, mostly intertidal, small depth range. Grazer.	Not enough data	
Mollusc FG6- Large size, trochiform shell. Sessile, benthic, rocky habitat, mostly subtidal, medium depth range. Low trophic level generalist.	Subtropical	Decrease at high latitudes
Mollusc FG7- Small size. Sessile, benthic, rocky habitat, mostly intertidal, small depth range. Grazer.	Cosmopolitan	Stays the same
Fish FG1- Small size. Demersal/ upper benthic habitat, small depth range. Nesters, short PLD. Aggregates in groups/ schools. Planktivores.	Tropical	Increase in tropics
Fish FG2- Large size. Reef pelagic habitat, large depth range. Scatterers, long PLD. Aggregates in groups. Planktivore/ detritivore.	Subtropical	Stays the same
Fish FG3- Medium size. Benthic habitat, medium depth range. Scatterers, medium PLD. High and low trophic level.	Tropical	Increase at mid and high latitudes
Fish FG4- Large size. Upper benthic habitat, medium depth range. Scatterers, medium PLD. Diet generalist.	Tropical	Increase at mid and high latitudes

Fish FG5- Small size. Benthic habitat, small depth range. Nesters, short PLD. Solitary. High trophic level.	Tropical	Increase everywhere
Fish FG6- Small size. Demersal habitat, small depth range. Nesters, short PLD. Solitary. Omnivore.	Tropical	Increase in tropics
Fish FG7- Very large size. All habitats, large depth range. Scatters, medium PLD. Solitary. Piscivore.	Cosmopolitan	Decrease everywhere
Fish FG8- Small size. Benthic habitat, medium depth range. Brooders/ live bearers, large PLD, Groups/ schools. Predator.	Subtropical	Decrease at high latitudes
Fish FG9- Medium size. Upper benthic habitat, large depth range. Nesters, medium PLD. Solitary. High trophic level.	Tropical	Increase everywhere
Fish FG10- Medium size. Sub-benthic habitat, medium depth range. Scatterers, medium PLD. Pairs. Herbivore/ corallivore.	Not enough data	
Fish FG11- Medium size. Demersal habitat, medium depth range. Scatterers, medium PLD. Pairs/solitary. High trophic level.	Tropical	Increase everywhere
Fish FG12 - Medium size. Sub-benthic habitat, large depth range. Scatterers, long PLD. Groups/ schools. Planktivore.	Tropical	Stays the same
Echinoderm FG1- Small size, spines. Protected subtidal habitat generalist, intermediate depth range. Both gregarious and solitary. Sexual mating system. Low trophic level generalist.	Subtropical	Decrease everywhere
Echinoderm FG2- Small size, spines. Exposed and protected intertidal/shallow hard substrate habitat generalist, intermediate depth range. Gregarious. Sexual mating system. Herbivore.	Not enough data	

Echinoderm FG3- Large size, no spines. Protected, subtidal caves, crevices and living coral habitat, large depth range. Solitary. Sexual mating system. Planktivore.	Cosmopolitan	Increase in tropics
Echinoderm FG4- Medium size, no spines. Exposed intertidal/ shallow habitat generalist, intermediate depth range. Solitary. Sexual and asexual mating. Generalist diet.	Not enough data	
Echinoderm FG5- Large size, no spines. All exposures, subtidal rocky/reef habitat generalist, small depth range. Solitary. All mating systems. Omnivore.	Subtropical	Decrease in tropics, increase at high latitudes

4.4 Discussion

With ongoing global change, it is inevitable that poleward range shifts will continue to occur along tropical to temperate transition zones, causing community turnovers and phase shifts (Bonebrake *et al.*, 2017). Understanding how these communities function, and how this will be altered with further change is a priority for effective climate-resilient ecosystem management. Our results suggest that currently across the environmental gradient, taxa contribute unequally to overall functioning, and with climate change, the dominant taxa providing specific functions could be altered. Across all taxa, there were distinct sub-tropical, tropical, and cosmopolitan functional group distributions (hereby discussed as thermal guilds), but the proportion of groups within each thermal guild differed between taxa. The majority of the fish and coral functional groups were tropical, compared to molluscs, algae and echinoderms which were mostly subtropical or cosmopolitan (Table 4.3). Each group was predicted to have a different response to environmental change, yet there were shared projected response behaviours within and across taxa, including patterns of range expansion, contraction, and poleward shifts. These behaviours indicate that by 2050, there will be functional community turnovers across the tropical to temperate gradient, with novel combinations of range shifting and native persisting groups, with potential functional mismatches and associated management implications.

The distinct thermal guilds for functional groups of all taxa, and the tail of abundances across the environmental gradient (Fig 4.2, Supplementary Fig. S4.1 - S4.5) suggest that environmental filtering is determining the distribution of these groups (Sommer *et al.*, 2014). Currently, the

dominant habitat forming taxa are corals in the tropics (Graham, 2014; Darling *et al.*, 2017) and macroalgae in the subtropics (Wernberg *et al.*, 2011). Our current predictions support this as the majority of coral functional groups were predicted to be tropical, with mostly sub-tropical algae groups (Table 4.3). Our predictions found that at high latitudes, fish groups were predominantly piscivores (FG7), planktivores (FG2) and predators (FG8), whereas the subtropical and cosmopolitan invertebrate mollusc and echinoderm functional groups (mollusc FG1, FG2, FG4, FG6 and FG7, and echinoderm FG1, FG3 and FG5) were predominantly herbivorous. This supports findings that fishes on high latitude reefs exhibit less herbivory pressure than on tropical reefs, instead feeding at higher trophic levels (Longo *et al.*, 2019), with herbivorous functional roles at high latitudes being filled by invertebrates (Barrientos, Piñeiro-Corbeira and Barreiro, 2022; Zarzycny *et al.*, 2022). In contrast, in the tropics, there were nine tropical fish functional groups that covered all trophic levels, compared to only four invertebrate groups (Table 4.3). We could not fit models for one mollusc group (FG5) and two echinoderm groups (FG2, FG3) but plots of the raw abundance data against latitude (Supplementary Fig. S4.3 and S4.5) suggest that these groups have higher abundances in the subtropics, strengthening this pattern. It could also be that cryptic functional groups of echinoderms and molluscs are present in the tropics but were not observed during surveys due to difficulty spotting them within complex reef structures (Sloan, 1982; Bouchet *et al.*, 2002; Alexander, 2013). However, cryptic fish species were also likely to have been missed during our surveys (Willis, 2001), and these fish could be in additional functional groups (Depczynski and Bellwood, 2005), further increasing fish functional diversity in the tropics. Thus, our results show the taxa mediating such functional roles change across the environmental gradient, with potential shifts between the taxa providing these roles in the future.

Given extensive records of poleward range shifts (Sorte, Williams and Carlton, 2010; Melbourne-Thomas *et al.*, 2021), we hypothesised that tropical groups would reduce in abundance in the tropics, and increase at high latitudes, and that subtropical groups would contract from our study region. The behaviours we predicted were more complex, with patterns of range, expansion, contraction, and shifting, as well as stable abundances (Table 4.3). On the whole, eight subtropical and cosmopolitan groups declined in abundance at high latitudes (algae FG2, FG3 and FG5, mollusc FG2 and FG6, fish FG7 and fish FG8 and echinoderm FG1) whilst eight tropical groups increased at high latitudes (coral FG1, mollusc FG3, fish FG1, FG3, FG4, FG5, FG9, FG11). Seven cosmopolitan or subtropical groups either stayed the same or increased at high latitudes (coral FG6, algae FG1, mollusc FG1, FG4, FG7, fish FG2, echinoderm FG5). In total, the future high latitude communities were predicted to be composed of native subtropical and range expanding functional groups, with the same number of overall functional groups. This result that tropical range expanders do not always displace sub-tropical natives has been found for tropicalising reefs in eastern and western Australia for fish (Zarco-Perello *et al.*, 2020; Smith *et*

al., 2021), but only for current observations that could be due to extinction debt (Kuussaari *et al.*, 2009). Our results predict that persistence of native species also occurs across multiple taxa and into the future, suggesting long-term maintenance of functioning in novel communities.

High latitude sites in the future were predicted to support an increased diversity of non-habitat forming groups (rising from 12 to 13 FGs), which could be supported by increased habitat complexity, and enhanced niche space due to an algal to coral phase shift (Vergés *et al.*, 2019; Lanham, Poore and Gribben, 2020). Our results predict that the benthic turnovers at high latitudes from macro-algae to branching corals that are currently occurring (Yamano, Sugihara and Nomura, 2011; Kumagai *et al.*, 2018) will continue in the future. We found that at high latitudes, subtropical algae groups (algae FG2, FG3 and FG5) are predicted to decrease in abundance, with increases in branching and tables/plating corals (Coral FG1 and FG6). However, massive and laminar corals (coral FG4 and FG5) are predicted to decrease everywhere in in the future. Thus, tropicalised high latitude coral assemblages will have reduced functional diversity compared to current tropical reefs, potentially reducing the capacity to support associated species (Brandl *et al.*, 2019; Magel *et al.*, 2019; Benkwitt, Wilson and Graham, 2020). Yet, branching and plating corals are known to be the most structurally complex (Richardson, Graham and Hoey, 2020), so are likely to still be able to provide the functions found on tropical reefs (Graham and Nash, 2013).

The functional distinctness of each group increases the chance of co-existence between range shifting and native groups (Pacioglu *et al.*, 2020; Smith *et al.*, 2021), but it also means that range contractions would result in the loss of the functions that contracting groups provides (Vergés *et al.*, 2019). However, contrasting environmental responses of other taxa that have niche similarities, could reduce functional losses (Wilcox, Schwartz and Lowe, 2018; Vergés *et al.*, 2019). At high latitudes, predicted replacement of macro-algae by corals is likely to maintain the habitat forming functional role (Vergés *et al.*, 2019). Similarly, although we predicted range contractions of benthic low trophic level generalists (mollusc FG2, FG6 and echinoderm FG1), we also predicted range expansions and abundance increases in omnivorous echinoderms (FG5) and fish (FG4) which could maintain such functional roles (Zarzyczny *et al.*, 2022). Such changes have been observed on tropicalising reefs in western Australia, where historically herbivory was attributed to urchins, and is now attributed to tropical rabbit fish (Zarco-Perello *et al.*, 2017). Proportionally, fish had the most range expanding groups, with the least functional losses, suggesting that functioning on high latitude sites may become more similar to our current tropical reefs where fish are the most functionally diverse. Current studies on the functioning of tropicalising high latitude reefs have largely been on fish (Bates *et al.*, 2013; Coni *et al.*, 2021; Smith *et al.*, 2021), with similar findings of more winners than losers (Zarco-Perello *et al.*, 2020; Smith *et al.*, 2021). However, our results show that only exploring functional changes in one

taxon can provide an unbalanced indication of functional change under tropicalisation, highlighting the importance of multi-taxon studies.

In the tropics, although we predicted that the abundance of some tropical or cosmopolitan groups will increase (Fish FG1 and FG6, Echinoderm FG3) or remained stable (Mollusc FG7, Fish FG2 and FG12), when considering the contracting groups, the communities were predicted to have reduced functional diversity. However, we only surveyed tropical reef sites in relatively good health, so we may not have captured whole disturbance specialist functional groups that could colonise the area (Graham *et al.*, 2014; Moreno-Borges, López and Clemente, 2022). Additionally, the Kuroshio Current could allow for potential range shifts of species with higher thermal tolerances into our tropical study region from equatorial areas (Chaudhary *et al.*, 2021; Sudo *et al.*, 2022). The likelihood of this could be low as tropical species have been found to be less limited by abiotic factors (Schemske *et al.*, 2009). In contrast, at the northern edge of our study area, the Kuroshio current curves away from the coastline resulting in rapid temperature drops at higher latitudes (Sudo *et al.*, 2022). Thus, on the east coast of Japan, sub-tropical and cosmopolitan contracting groups that we identified to be declining are unlikely to be able to shift northwards (Sudo *et al.*, 2022). These groups contain the large macro-algae, temperate fishes, and urchins which are targeted for fisheries (Kiyomoto *et al.* 2013), so may be targets for management strategies. Such strategies could target areas of stable abundances within the region to minimise economic losses.

The tropicalisation patterns identified in this research are broad biogeographic patterns and at the finer scale, functional groups are likely to be limited by substrate type and localised changes in environmental conditions such as increased turbidity from coastal development (Heery *et al.*, 2018). Additionally, we only explored responses of functional group abundance to abiotic components and did not consider biotic components such as competition and facilitation of range shifts. Biotic interactions are known to be more important in the tropics, allowing for the maintenance of higher species and functional diversity (Schemske *et al.*, 2009). The tropical coral and sub-tropical algae groups were strongly tied to the abiotic conditions, yet the others had more mixed responses to the environment, and this could be because their distributions are more determined by competitive exclusion and facilitation masking environmental patterns (Ludt *et al.*, 2015; Chow *et al.*, 2019; Koffel, Daufresne and Klausmeier, 2021). This is not something we could capture in our surveys, but further studies including biotic variables could further increase model accuracy (Leach, Montgomery and Reid, 2016). Finally, abundance declines and range contractions could be limited through phenotypic plasticity (Camp *et al.*, 2018), with shifting resource use and physiological adaptations to unfavourable environmental conditions enhancing

survival potential at range margins (Gibbin *et al.*, 2017; Munday, Donelson and Domingos, 2017; Donelson *et al.*, 2019; Putnam, 2021), minimising functional losses of contracting groups.

Even considering such caveats, our research is the first that we know of to predict multi-taxon range shifts in tropicalising areas to provide an indication of future ecosystem functioning. Our results support current findings that within taxa, traits are mediated by environmental filtering, resulting in unique tropical and sub-tropical functional community compositions. Our predictions of range expansions of tropical functional groups, and persistence of native groups suggest that future communities will have novel functioning, but functional diversity will remain similar. Losses of sub-tropical functions could be minimised by expansions of similar functional groups in different taxa, showing the importance of assessing multi-taxon functional change. To summarise, our findings suggest high latitude tropicalising reefs will retain high ecosystem functions making them suitable for targets for conservation of reef species under climate change.

4.5 References

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4.5 Supplementary Materials for Chapter Four

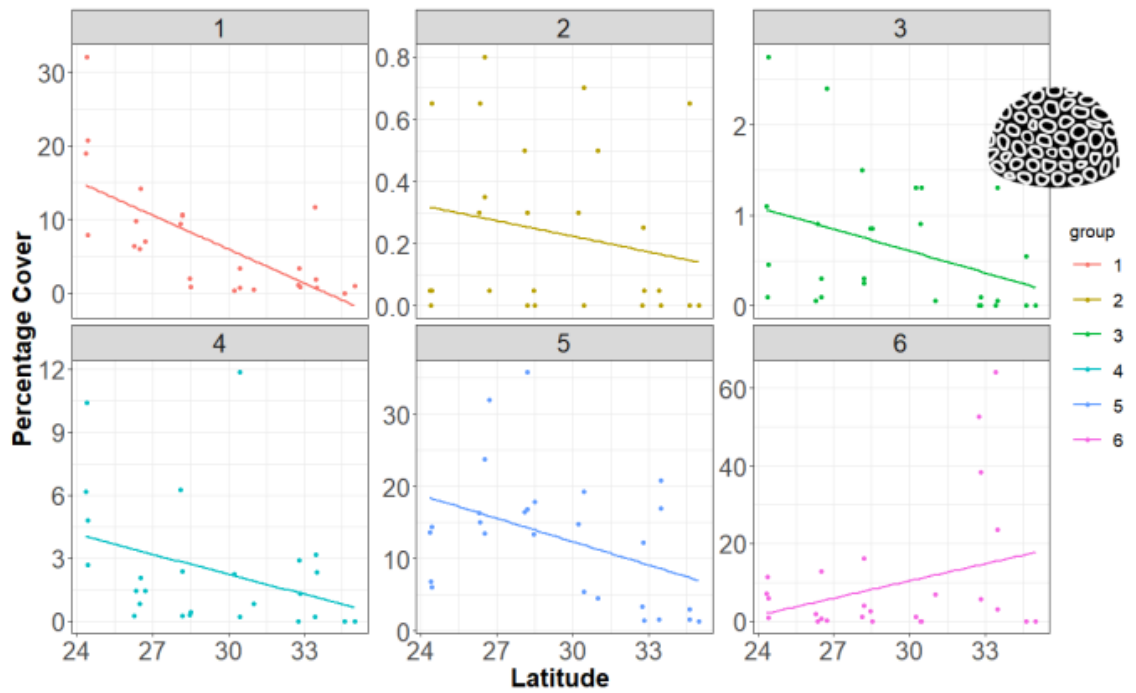


Figure S4.1. Total percentage cover of coral functional groups 1-6 plotted against latitude. Lines show linear models.

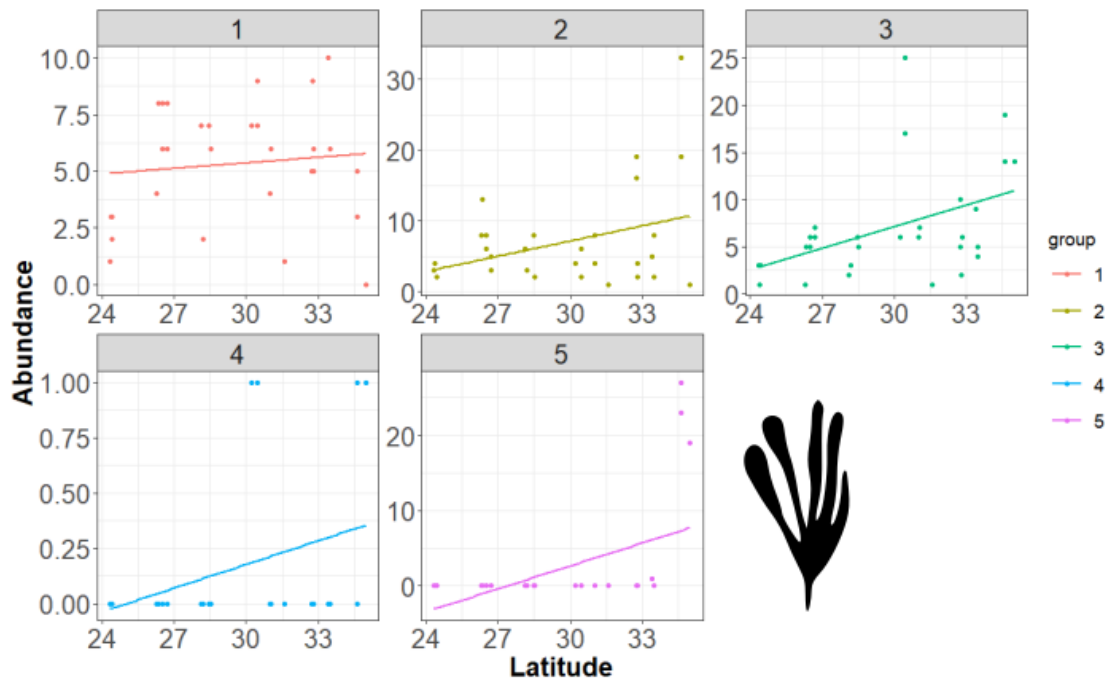


Figure S4.2. Total abundance of algae functional groups 1-5 plotted against latitude. Lines show linear models.

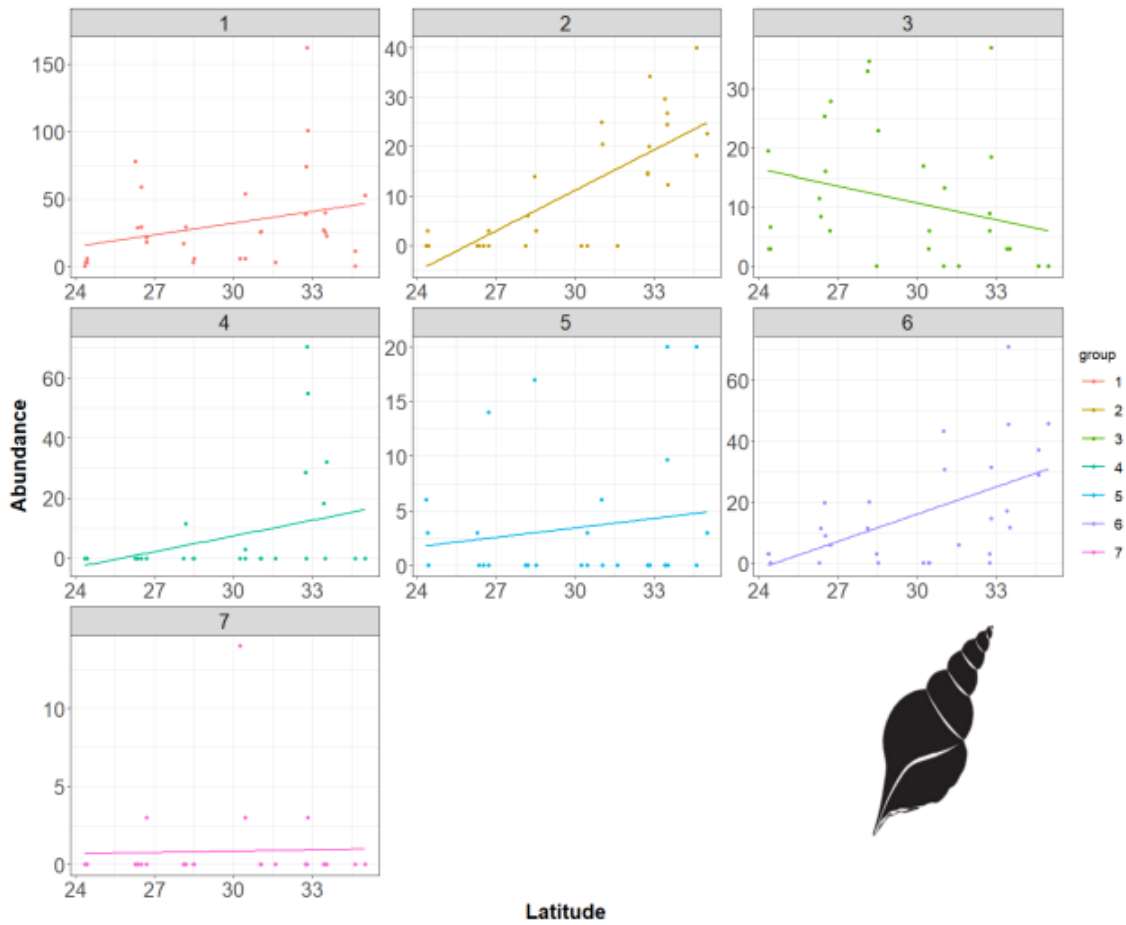


Figure S4.3. Total abundance of mollusc functional groups 1-7 plotted against latitude. Lines show linear models.

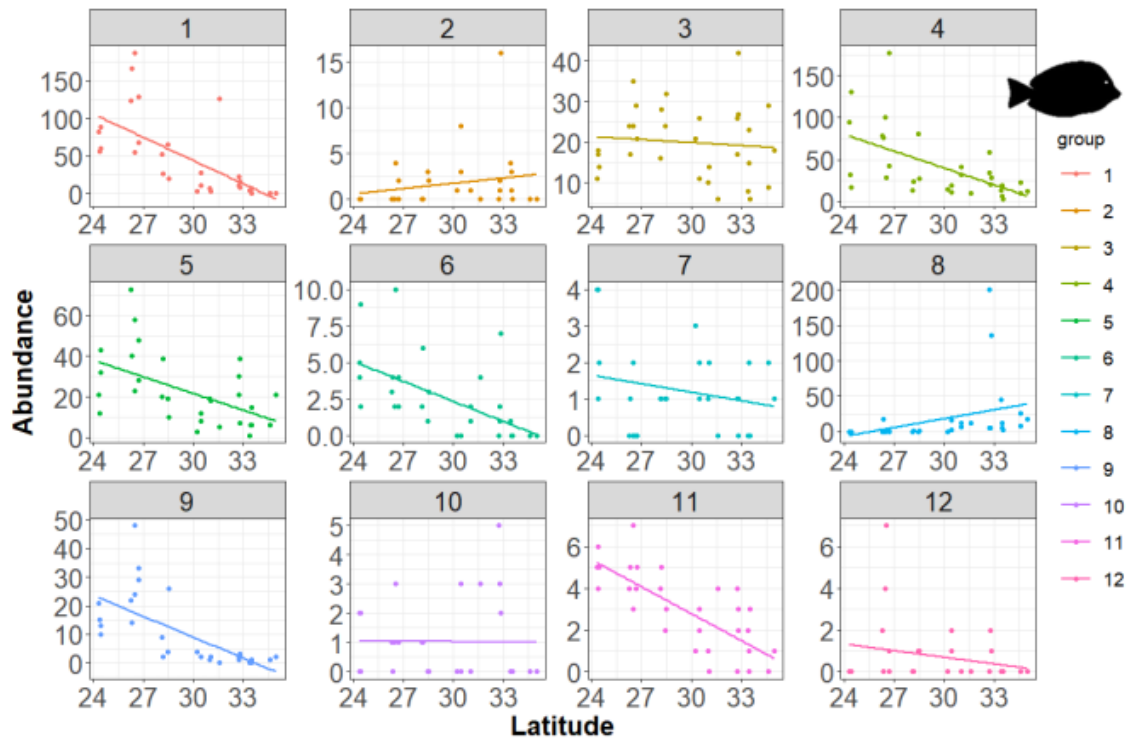


Figure S4.4. Total abundance of fish functional groups 1-12 plotted against latitude. Lines show linear models.

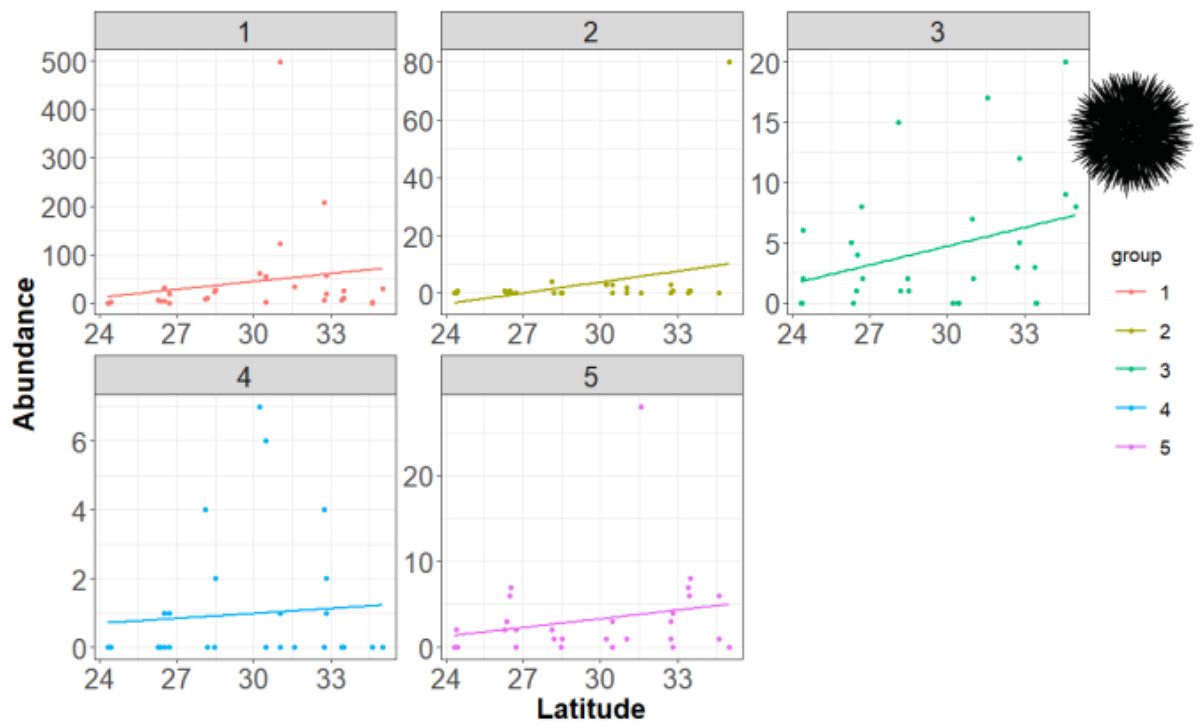


Figure S4.5. Total abundance of echinoderm functional groups 1-5 plotted against latitude. Lines show linear models.

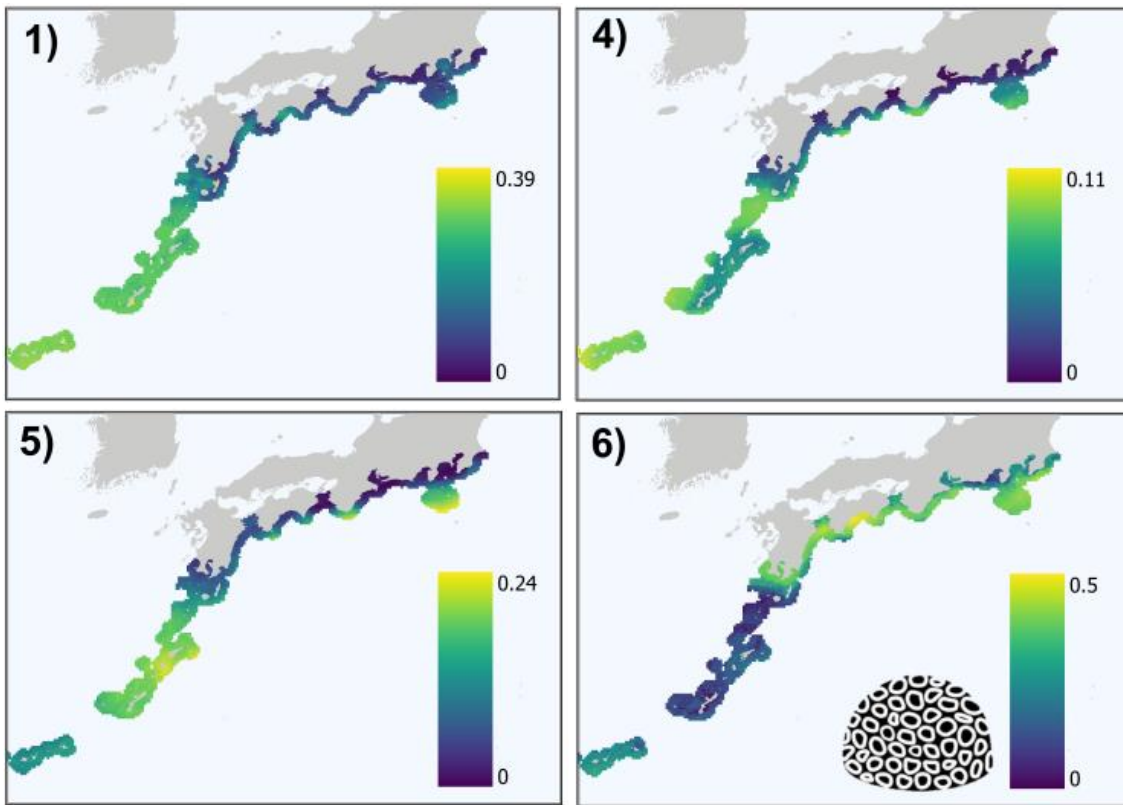


Figure S4.6. Abundance of coral functional groups (the number in the corner of the panel) for 2015 across the study area predicted using a combination of generalised additive models, generalised linear models and random forest algorithms.

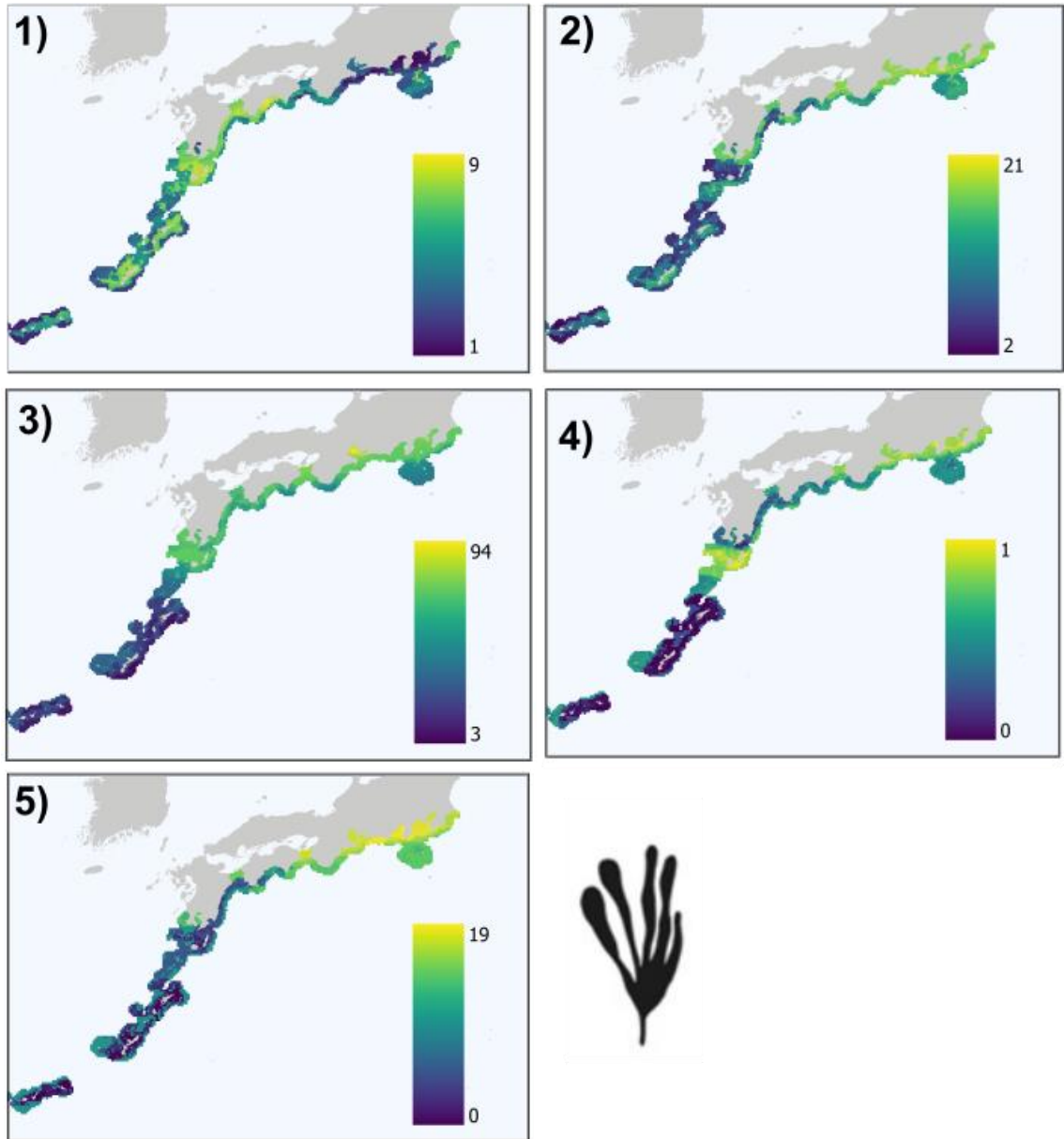


Figure S4.7. Abundance of algae functional groups (the number in the corner of the panel) for 2015 across the study area predicted using a combination of generalised additive models, generalised linear models and random forest algorithms.

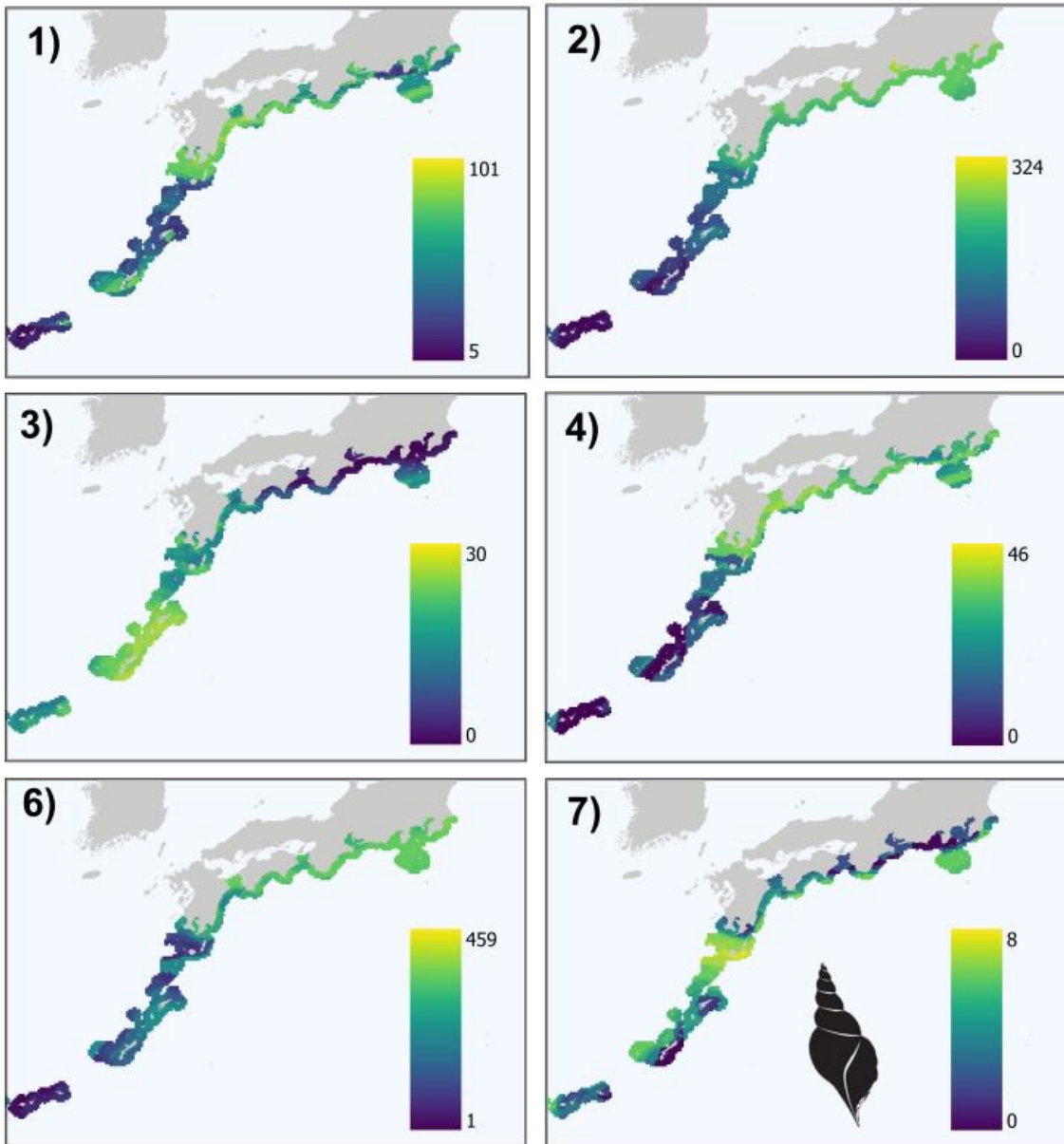
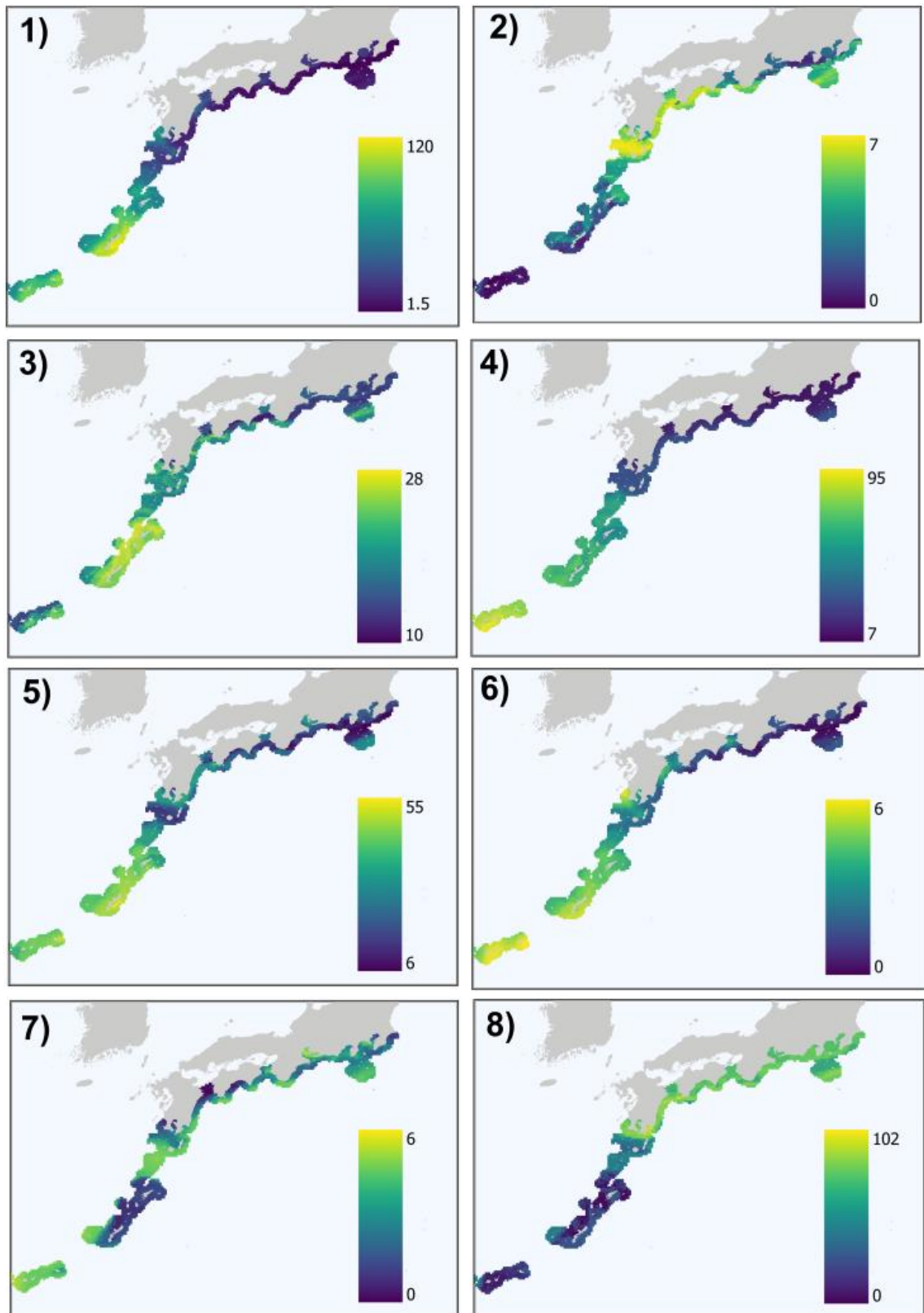


Figure S4.8. Abundance of algae functional groups (the number in the corner of the panel) for 2015 across the study area predicted using a combination of generalised additive models, generalised linear models and random forest algorithms. The abundance for functional group five could not be predicted as the models were found to have low predictive capacity during cross validation.



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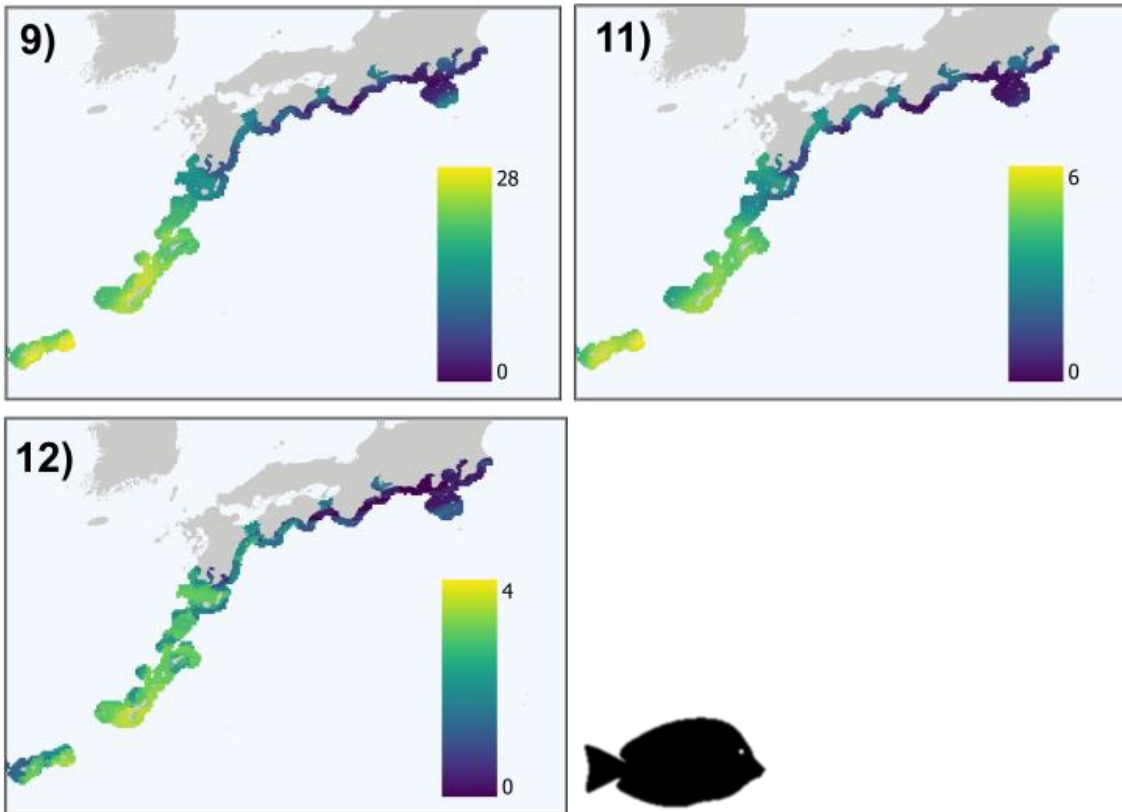


Figure S4.9. Abundance of fish functional groups (the number in the corner of the panel) for 2015 across the study area predicted using a combination of generalised additive models, generalised linear models and random forest algorithms. The abundance for functional group ten could not be predicted as the models were found to have low predictive capacity during cross validation.

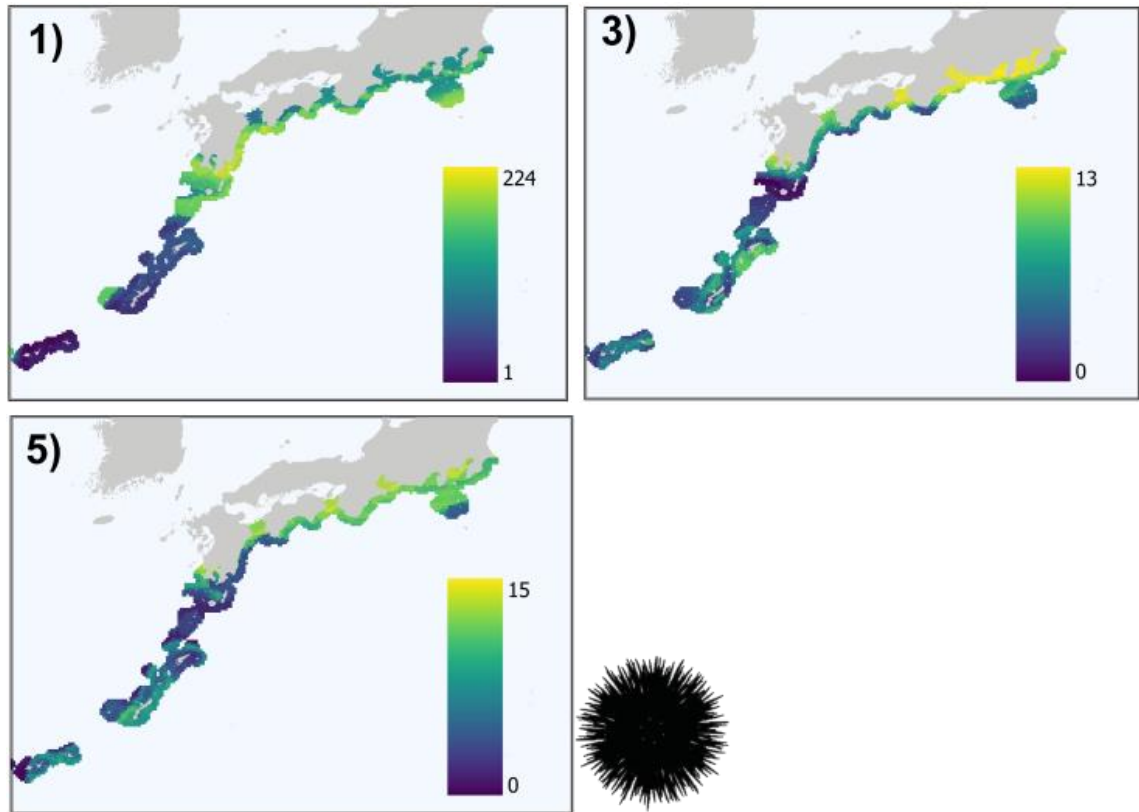


Figure S4.10. Abundance of echinoderm functional groups (the number in the corner of the panel) for 2015 across the study area predicted using a combination of generalised additive models, generalised linear models and random forest algorithms. The abundance for functional groups two and four could not be predicted as the models were found to have low predictive capacity during cross validation.

Table S4.1. Average Root mean square error (RMSE) and Pearson's correlations between predictions from 1000 runs of training data (80%) and observed values from test data (20%) for each functional group for best fit generalised linear, generalised additive and random forest models. Results in bold indicate models with significant predictor variables, small error and appropriate predictive capacity (Pearson's correlation >0.25).

Functional group	Model	RMSE	Pearson's
Coral FG1	GLM: abundance ~ sst ($p < 0.001$)	0.06	0.65
	GAM: abundance ~ sst ($p < 0.001$) + current ($p = 0.05$)	0.07	0.62
	+ salinity ($p = 0.04$) + chlorophyll ($p = 0.20$) + light ($p = 0.15$)	0.05	0.73
	RF:		
Coral FG2	GLM: Null model	0.008	-0.25
	GAM: abundance ~ sst ($p = 0.335$)	0.02	-0.22
	RF:	0.008	-0.39

Coral FG3	GLM: ~ Null model	0.01	-0.04
	GAM: ~sst(p=0.335)	0.02	-0.12
	RF:	0.009	0.16
Coral FG4	GLM: abundance ~ sst (p<0.001) + current (p=0.0117)	0.02	0.44
	GAM: abundance ~ sst (p=0.005)	0.03	0.40
	RF:	0.03	0.35
Coral FG5	GLM: abundance ~ sst (p=0.008) + current (p=0.02) + salinity (p<0.01) + chlorophyll (p=0.05)	0.07	0.65
	GAM: abundance ~ sst (p=0.04) + current (p=0.008) + salinity (p=0.002)	0.07	0.64
	RF:	0.07	0.62
Coral FG6	GLM: Null model	0.15	-0.45
	GAM: abundance ~ sst (p<0.01) + current (p=0.08) + salinity (p=0.03) + chlorophyll (p=0.12)	0.17	0.26
	RF:	0.15	0.26
Algae FG1	Glm: abundance ~sst (p=0.0106)+ salinity (p=0.0840) + chlorophyll (p=0.1342)	3.08	-0.11
	GAM: ~ sst (p=0.13) + salinity (p=0.0992)	2.45	0.45
	RF:.,	2.02	0.57
Algae FG2	GLM: abundance ~ sst (p=0.0102) + salinity (p=0.1064)	10.48	-0.0003
	GAM: abundance ~ sst (<0.001) + current (p<0.001) + salinity (p<0.001) + chlorophyll (p=0.007) + light (p<0.05)	12315.1	0.20
	RF:	5.77	0.36
Algae FG3	GLM: abundance ~ salinity (p=0.002)	6.22	0.40
	GAM: abundance ~ sst (p<0.005) + chlorophyll (p<0.05)	47.52	0.40
	RF:	4.36	0.57
Algae FG4	GLM: abundance ~ salinity (p=0.0508)	Inf	0.10
	GAM: abundance ~ sst (p=0.447)	Inf	0.30
	RF:	0.31	0.61
Algae FG5	GLM: all p values 0.999	Inf	0.89
	GAM: ~sst (p=1) + salinity (p=1) +chlorophyll (p = 1)	Inf	0.85
	RF:	3.05	0.95
Mollusc FG1	GLM: abundance ~ sst (p=0.0002) + current (p=0.042) + chlorophyll (p=0.030)	42.68	0.19
	GAM: abundance ~ sst (p=0.002)	296.65	0.17
	RF:	29.30	0.43
Mollusc FG2	GLM: abundance ~ sst (p<0.0001)	13.98	0.69
	GAM: abundance ~ sst (p=0.003) + salinity (p=0.47)	6.02+e07	0.53
	RF:	10.11	0.75

Mollusc FG3	GLM: abundance ~ sst (p=0.001) + chlorophyll (p<0.001)	12.23	0.45
		26.27	0.34
	GAM: abundance ~ sst (p=0.025) + current (p=0.026) + salinity (p=0.004) RF:	12.69	0.45
Mollusc FG4	GLM: abundance ~ sst (p<0.0001) + current (p<0.0001) + salinity (p=0.01) + chlorophyll (p<0.0001)	Inf	0.25
		Inf	0.27
	GAM: abundance ~sst(p=0.2)+current(p=0.4)+salinity(p=0.155) RF:	12.69	0.56
Mollusc FG5	GLM: null model	7.23	-0.06
	GAM: abundance ~ sst (p=0.6)	2.12e03	-0.09
	RF:	6.52	-0.002
Mollusc FG6	GLM: abundance ~sst (p<0.001) + salinity (p=0.080)	5.38e+04	0.54
		12.81	0.46
	GAM: abundance ~ sst (p<0.0001) RF:	14.46	0.68
Mollusc FG7	GLM: abundance ~ sst (p=0.126) + current (p=0.022) + salinity (p=0.001) + chlorophyll (p=0.016)	3.05e+39	-0.10
		Inf	0.23
	GAM: ~sst(p=0.4) RF:	1.92	0.51
Fish FG1	GLM: abundance ~sst (p=0.1641) + current (p=0.0251) +s salinity (0.1462) + chlorophyll (p<0.0001)	42.34	0.62
		1.72e+02	0.79
	GAM: abundance ~ sst (p=0.141) + current (p<0.0001) + chlorophyll (p=0.01) RF:	39.19	0.68
Fish FG2	GLM: abundance ~ sst (p=0.0514) + chlorophyll (p=0.113)	4.29	-0.25
		1.98e+04	0.28
	GAM: abundance ~sst (p=0.189) + current (p=0.018) + salinity (p=0.119) + chlorophyll (p=0.118) RF:	3.04	0.25
Fish FG3	GLM: abundance ~sst (p=0.146)	9.48	-0.12
	GAM: abundance ~ sst (p=0.218)	10.45	0.06
	RF:	8.49	0.36
Fish FG4	GLM: abundance ~ sst (p<0.0001)	36.01	0.51
		41.11	0.44
	GAM: abundance ~sst (p<0.0001) RF:	37.99	0.48
Fish FG5	GLM: abundance ~current (p=0.083) + chlorophyll (p=0.096)	16.44	0.44
		52.12	0.47
	GAM: abundance ~sst (p=0.008) + chlorophyll (p<0.001) RF:	14.29	0.59

Fish FG6	GLM: abundance ~ current (p=0.07) + salinity (p=0.10) + chlorophyll (p=0.016)	2.46	0.48
	GAM: abundance ~ sst(p=0.047) + current (p=0.28) + salinity (p=0.323) + chlorophyll (p=0.005)	6.54e+07	0.34
	RF:	2.58	0.46
Fish FG7	GLM: abundance ~sst (p=0.002) + current (p=0.146) + salinity (p=0.073)	1.22	0.41
	GAM: abundance ~sst(p=0.001) + current (p=0.024)	1.45e+03	0.40
	RF:	0.93	0.41
Fish FG8	GLM: abundance ~ sst (p=0.001) + current (p=0.065) + salinity (p=0.121) + chlorophyll (p=0.003)	180.73	0.34
	GAM: abundance ~sst (p=0.004) + chlorophyll (p=0.73)	9.76e+06	0.37
	RF:	39.17	0.38
Fish FG9	GLM: abundance ~sst (p<0.0001) + current (p=0.002)	9.36	0.70
	GAM: ~ sst (0.052) + chlorophyll (p=0.623)	8.91	0.74
	RF:	6.06	0.73
Fish FG10	GLM: abundance ~sst (p=0.002) + chlorophyll (p=0.004)	3.71	0.36
	GAM: abundance ~sst (p=0.31) + salinity (p=0.017) + chlorophyll (p=0.06)	1.27e+03	0.15
	RF:	1.34	0.16
Fish FG11	GLM: abundance ~ sst (p=0.044) + current (p<0.007)	1.37	0.71
	GAM: abundance ~ sst (p=0.084)+ current (p=0.007)	1.32	0.74
	RF:	1.35	0.86
Fish FG12	GLM: abundance ~ sst (p=0.081) + chlorophyll (p=0.042)	42.43	0.13
	GAM: abundance ~ sst (p=0.068)	1.75e+17	0.29
	RF:	1.14	0.53
Echinoderm FG1	GLM: abundance ~ sst (p=0.0001)+ current (p=0.09) + salinity (p=0.042) + chlorophyll (p<0.05) - didn't use (high RMSE)	172.96	0.35
	GAM: ~sst(p=0.155)+salinity(p=0.0442)	3.35	0.51
	RF:	e+07	0.49
Echinoderm FG2	GLM: abundance ~chloropyll (p<0.01)	77.78	
	GAM: abundance ~sst (p=0.76) + chlorophyll (p<0.01)	8.22	-0.21
	RF:	38.35	-0.09
Echinoderm FG3	GLM: abundance ~ sst (p<0.01) + current (p=0.07)	8.02	-0.15
	GAM: abundance ~sst (p=0.045) + current (p=0.04) + salinity (p=0.14) + chlorophyll(p=0.11)	96.06	0.226
	RF :	3.13+e04	0.36
Echinoderm FG4	GLM: abundance ~ sst (p=0.06) + chlorophyll (p=0.06)	5.24	0.33
	GAM: abundance ~sst(p=0.032)	69776.85	-0.20
	RF:	5.11e+18	0.46
		1.75	0.2

Echinoderm	GLM: abundance ~sst (p=0.007) + chlorophyll	5.45	-0.07
FG5	(p=0.05)	6.67	-0.04
	GAM: abundance ~sst (p=0.89) + current (p=0.01) + salinity (p=0.19)	4.42	0.40
	RF:		

Chapter Five- Designing static- dynamic conservation areas to manage range shifting of multi-taxon functional groups.

Katie M Cook, Mark Miller, James D. Reimer, Masaru Mizuyama and Maria Beger

5.0 Abstract

Climate change drives the poleward range shifts of tropical species, resulting in a transformation of high latitude reef ecosystems. Such tropicalisation can lead to habitat shifts from benthic macro-algae to tropical coral dominated systems, and associated community and functional changes. Tropicalisation creates a conservation dilemma. As thermal stress events threaten tropical communities at low latitudes, these novel high-latitude communities will be valuable for the survival of tropical species. Yet, the temperate communities they replace are also ecologically important. Thus, conservation plans need to account for the conflicting objectives of facilitating and delaying tropicalisation, whilst considering temporal change and ecosystem functioning.

Here we develop an area-based conservation framework that integrates traditional static marine management areas and shifting dynamic reserves for contrasting conservation objectives. We test the framework quantitatively for 29 functional groups across five taxa along Japan's Kuroshio coast, comparing the conservation benefit to manage changes associated with tropicalisation. Using predicted abundances of multi-taxon trait-based functional groups of fish, corals, molluscs, algae and echinoderms for the recent past (2015) and 2050, we identified priority conservation areas for static, dynamic and hybrid static-dynamic approaches for three objectives: facilitate tropicalisation, slow tropicalisation and protect all functional groups.

We calculated the total functional change across all groups between the two time periods and used this to assess the selected reserve networks. For all conservation objectives, the dynamic and hybrid approaches selected areas that had higher total functional change than the static scenario, suggesting the networks would be more effective at maintaining ecosystem functioning. The hybrid approach selected similar areas to the dynamic approach, with a high capacity to protect for functioning, yet required fewer shifting reserves, providing a practical solution for long-term protection. Thus, we demonstrate a flexible concept and quantitative-based methodology that could be adapted across the globe to improve climate-resilient conservation planning.

5.1 Introduction

Coastal marine environments are threatened by global climate change and local anthropogenic stressors that include over fishing, pollution, and habitat destruction (Cabral *et al.*, 2019; Cordier, Poitelon and Hecq, 2019; Link and Watson, 2019). The resulting ecosystem transformations require careful strategic management to protect biodiversity and natural resources (Pinheiro *et al.*, 2019). In particular, climate change causes global community turnover and species redistributions due to range shifts of multiple taxa, including turnovers of habitat engineers and associated species (Bonebrake *et al.*, 2017; Pecl *et al.*, 2017; Pinsky, Selden and Kitchel, 2019; Champion, Brodie and Coleman, 2021). Over the past few decades, poleward range shifts to higher latitudes have been frequently recorded across the globe (Yamano, Sugihara and Nomura, 2011; Pinsky, Selden and Kitchel, 2019; Sanford *et al.*, 2019; Gervais, Champion and Pecl, 2021). Most marine species have a pelagic life stage, with few physical barriers to dispersal, and narrow thermal tolerances, allowing them to live close to their thermal maximum (Donelson *et al.*, 2019, Pinsky *et al.*, 2019, Sunday *et al.*, 2012). Thus they track their environmental conditions more closely than their terrestrial counterparts, and range shift rate is expected to increase under intensifying climatic change (Lenoir *et al.*, 2020). These range shifts are likely to have widespread ecological implications, as shifting species have the potential to outcompete endemic residents, alter ecosystem functioning, and drive irreversible phase shifts (Pinsky, Selden and Kitchel, 2019; Vergés *et al.*, 2019). However, such ecological shifts are difficult to capture in conservation planning and protected area policies, and current strategies take a permanent and static approach to area-based management (Beger *et al.*, 2014; Makino *et al.*, 2014; Tittensor *et al.*, 2019). This is a challenge that must be addressed so that conservation management remains ecologically and economically effective over the coming decades.

The most widely used form of marine spatial management is through the creation of marine protected areas (MPAs) (Ban *et al.*, 2019). MPAs are geographically designated marine areas which are regulated and managed to fulfil set conservation objectives, often restricting certain activities such as commercial resource extraction and habitat destruction (Laffoley *et al.* 2019). MPAs are increasingly designed with objective-driven systematic conservation planning, a process to maximise ecological representation, whilst reducing opportunity and management costs (Álvarez-Romero *et al.*, 2018). The planning process can be approached in two ways, using fine filter approaches, that prioritise protection of specific species, or coarse filter approaches that aim to protect aggregations of species or habitats that are likely to maintain overall biodiversity and ecosystem processes (Tingley, Darling and Wilcove, 2014). Ideally, the selected reserve, or MPA network should represent the full variety of biodiversity, enhancing ecological processes, and minimising environmental threats, with this protection persisting into the future (Margules

and Pressey, 2000). Traditionally, to enhance persistence, MPAs were often designed to be large and well connected to maintain viable populations of target species or communities (Metcalf *et al.*, 2015). However, given rapid range shifts, MPAs could become ineffective if the target features cease to exist in the reserve network (Tittensor *et al.*, 2019).

When taking a coarse filter approach to protect habitats, designating protection to an area could increase climate resilience, helping to slow range shift induced community turnovers (Stuart-Smith *et al.*, 2013). For example, along tropical to temperate biogeographic transition zones, ecosystems are experiencing tropicalisation, a process where a previously temperate or subtropical community becomes dominated by tropical range expanding species (Verges *et al.*, 2014; Vergés *et al.*, 2019). Temperate and sub-tropical macro-algal communities are already globally threatened due to climate-related disturbances such as heatwaves and increased herbivory from heightened abundances of grazing urchins and fishes (Wernberg *et al.*, 2012; Krumhansl *et al.*, 2016; Filbee-Dexter and Wernberg, 2018; Smale, 2020). Tropicalisation threatens these ecosystems further with increased competition from range shifting species, and increased grazing from tropical herbivores (Verges *et al.*, 2014; Wernberg *et al.*, 2016; Kumagai *et al.*, 2018). Protection of stable macroalgal communities could maintain high levels macroalgal cover with increased abundances of predators which feed upon the grazing herbivores (Bates *et al.*, 2017; Eisaguirre *et al.*, 2020). This could also increase recovery potential after extreme events, and slow invasions from tropical species as they may not be able to compete with established native species (Bates *et al.*, 2017, 2019). Thus, protection may be critical for the survival of threatened temperate and sub-tropical communities, especially in cases where temperate and sub-tropical species cannot range shift themselves due to geographical limitations (Wernberg *et al.*, 2011). However, protection could also enhance ecosystem turnover by allowing range shifting herbivorous species to increase in abundance. Increased herbivory is likely to reduce the competitiveness of macroalgae, and suppress recovery from climate disturbances (Zarco-Perello *et al.*, 2021), facilitating the establishment potential of benthic tropical corals (Verges *et al.*, 2014). In this instance, these reefs may become important refuges for range extending species whose original habitat might have become climatically unsuitable at lower latitudes (Beger *et al.*, 2014). Protecting such areas may facilitate range shifts to higher latitudes, increasing survival potential. With such conflicting cases, the processes occurring in these ecosystems must be fully understood before management decisions, which must have clearly defined conservation objectives related to climate-induced range shifts.

There are currently various conservation planning strategies that address climate-induced range shifts. Yet, as a relatively novel field, these strategies have been proposed as theoretical frameworks without being practically applied (Tittensor *et al.*, 2019; Wilson *et al.*, 2020). Static

strategies such as (Makino *et al.*, 2015) rely on designating MPAs that will continue to be effective in the future using information from the current time period. Range shifts could be slowed, attempting to maintain habitats and ecological communities in their current state, by prioritising climatically stable refugia (Carter *et al.*, 2020; Davis, Champion and Coleman, 2021). Range shifts could also be facilitated through static protection of current and future habitat and ensuring connectivity between them (Makino *et al.*, 2015; Wilson *et al.*, 2020). Designating tall MPAs across large latitudinal ranges spanning biogeographical boundaries following the path of climate velocity could allow for more within reserve shifts (Fredston-Hermann, Gaines and Halpern, 2018), and MPA networks along latitudinal coastlines could form stepping-stones for shifting species, acting like terrestrial migration corridors to facilitate shifts (Fredston-Hermann, Gaines and Halpern, 2018; Tittensor *et al.*, 2019). Such large-scale networks increase the chances of multiple species being protected within and at the edge of their ranges, and would allow for species to shift into already protected areas, but for most reefs the large-scale MPAs required to support these ideas are socio-economically not feasible. Additionally, both the refugia and biogeographic approaches do not directly maximise biodiversity protection and provide conflicting conservation outcomes that either facilitate or slow tropicalisation but this is rarely explicitly addressed.

Quantitative strategies to inform conservation management require spatially explicit data sets. As such, conservation planning often relies on species distribution models (SDMs) which combine observational data and environmental variables to predict spatio-temporal species distributions (Chapter two and three). SDMs can predict future distributions using climate projections, allowing for strategies that prioritise areas that remain suitable long term (Welch *et al.*, 2020; Wilson *et al.*, 2020). Distributions from different time periods can also be used to inform dynamic conservation strategies, which sequentially designate reserves as species shift into them, and degazette them when they no longer contribute to conservation targets (Alagador, Cerdeira and Araújo, 2014; Welch *et al.*, 2020). However, the requirement to regularly change and update legislation is likely to be impractical for nationally managed MPAs, given the large amount of stakeholder consultations, political discussion, and other resources needed to designate protection (Moilanen *et al.*, 2014; D'Aloia *et al.*, 2019; Ortuño Crespo *et al.*, 2020). This approach would also be difficult to implement for a range of species which would likely be shifting at different rates (Pinsky *et al.*, 2013). As SDMs require large amounts of data to build accurate predictive models, data deficient species that possess unique functional traits may be excluded (Mouillot *et al.*, 2013) and consequently not included in conservation considerations.

It is currently unclear how novel tropicalised communities will function (Vergés *et al.*, 2019), but it is likely that protecting a diverse range of functional trait combinations will increase chances

that important functional roles are fulfilled or replaced with ecosystem turnovers (Jacob *et al.*, 2020). Maximising species diversity is likely to capture functional diversity (Brandl *et al.*, 2019), yet highly biodiverse systems have high levels of functional redundancy, where multiple species in certain communities contribute similar functional roles (Guillemot *et al.*, 2011; Mouillot *et al.*, 2014). Focussing on protecting ecosystem functions regardless of the species that contribute them could increase cost efficiency, whilst maximising functional potential (Guillemot *et al.*, 2011). Additionally, in areas with rapid environmental change experiencing tropicalisation, it may not be possible to conserve species sensitive to warming, but if these species are replaced by species with similar functions, critical ecosystem processes may be continued (Rilov *et al.*, 2019). One approach is to classify species with similar functional traits into functional groups, as they are likely to be contributing similar functional roles (Newbold *et al.*, 2020). These functional groups can be targeted for management (Nyström *et al.*, 2008; Cheal *et al.*, 2013; Anderson *et al.*, 2021) to ensure that a diversity of groups are comprehensively protected to sustain key ecosystem functions (Soliveres *et al.*, 2016; Newbold *et al.*, 2020). If the functional groups in tropical, sub-tropical, and temperate communities differ, ensuring that a proportion of each functional group is protected could maximise chances of successful establishment, and thus tropicalisation, or ecosystem stability, depending on the desired conservation objective.

Range shifting can theoretically be addressed by an integrated hybrid conservation strategy that couples permanent ‘static’ protected areas in locations that retain their conservation value long-term with temporary ‘dynamic’ conservation areas that shift optimally for each assessed time period (D’Aloia *et al.*, 2019; Tittensor *et al.*, 2019). However, this proposed strategy is not yet supported by a practical conservation framework, nor has it been tested with ecological objectives in an existing system. Here, we develop a novel framework that underpins a hybrid conservation planning strategy with explicit range-shifting objectives, whilst accounting for maintained multi-taxon function. Using abundance distributions of multi-taxon reef-associated functional groups predicted under climate change, we then apply the framework to identify and compare areas for static, dynamic and hybrid protection across the Japanese Kuroshio marine region. Our approach maximises the conservation of ecosystem function by utilising a coarse filter approach to capture the range-shifting of diverse functional groups that fulfil critical ecosystem roles. We address three main questions 1) Does adding a dynamic aspect to conservation plans enhance range shifting potential? 2) How does the reserve network change given three different ecological scenarios which facilitate tropicalisation (by protecting tropical groups), slow tropicalisation (by protecting sub-tropical and temperate groups), and protect everything (protecting all groups)? 3) How do the areas selected alter when taking a static, dynamic and hybrid approach to protection? We demonstrate a flexible method to achieve effective and lasting conservation of marine ecosystem functioning. The approach can be applied to different marine and terrestrial

environments, being integrated into existing reserve networks to enhance the long-term protection of threatened ecosystems.

5.2 Conservation framework

We develop a methodological framework to apply coupled dynamic and static conservation strategies (the hybrid strategy) to identify optimal MPA networks that remain effective under current and future climatic conditions (Fig. 5.1). The framework integrates quantitative distribution information, such as current and future outputs of ecological niche models. It outlines target-based strategies that can be used with differing ecological scenarios to facilitate range shifts and tropicalisation, to slow tropicalisation and to protect everything. Protecting a proportion of tropical functional group ranges in a connected reserve network can facilitate tropicalisation as species have increased survival in the protected areas, using them as stepping stones whilst range shifting (Fredston-Hermann, Gaines and Halpern, 2018). Protecting sub-tropical groups can slow range shifts, and thus tropicalisation by increasing the fitness of sub-tropical and temperate species, allowing them to outcompete range shifting vagrants (Bates *et al.*, 2013). Prioritising for all functional groups is a broad approach that maximises overall functioning, without supporting or slowing the turnover processes. We demonstrate using this framework, applying Japanese coral reefs as a case study.

5.3 Methods

5.3.1 Conservation planning analyses

We conducted conservation planning analyses using Marxan (Ball and Possingham, 2000). To create the input files, we split the focal area (see below) into planning units (PUs) which were assigned biological values (conservation features) and costs. Marxan uses a simulated annealing algorithm to identify the complementary sets of PUs, i.e., a MPA network, that meets conservation feature protection targets, whilst minimising overall costs (Ball and Possingham, 2000). We implemented prioritisation analyses based upon our methodological framework (Fig 5.1.) across three conservation objectives, to 1) Facilitate tropicalisation, 2) Slow tropicalisation, and 3) Protect all functional groups. All analyses were conducted using the R programming language (R Core Team, 2020), with additional spatial data preparation and visualisation being conducted in ArcGiS (ESRI, 2011) and QGIS (QGIS.org, 2022). Prior to any analyses, all spatial layers were projected into the Mercator projection.

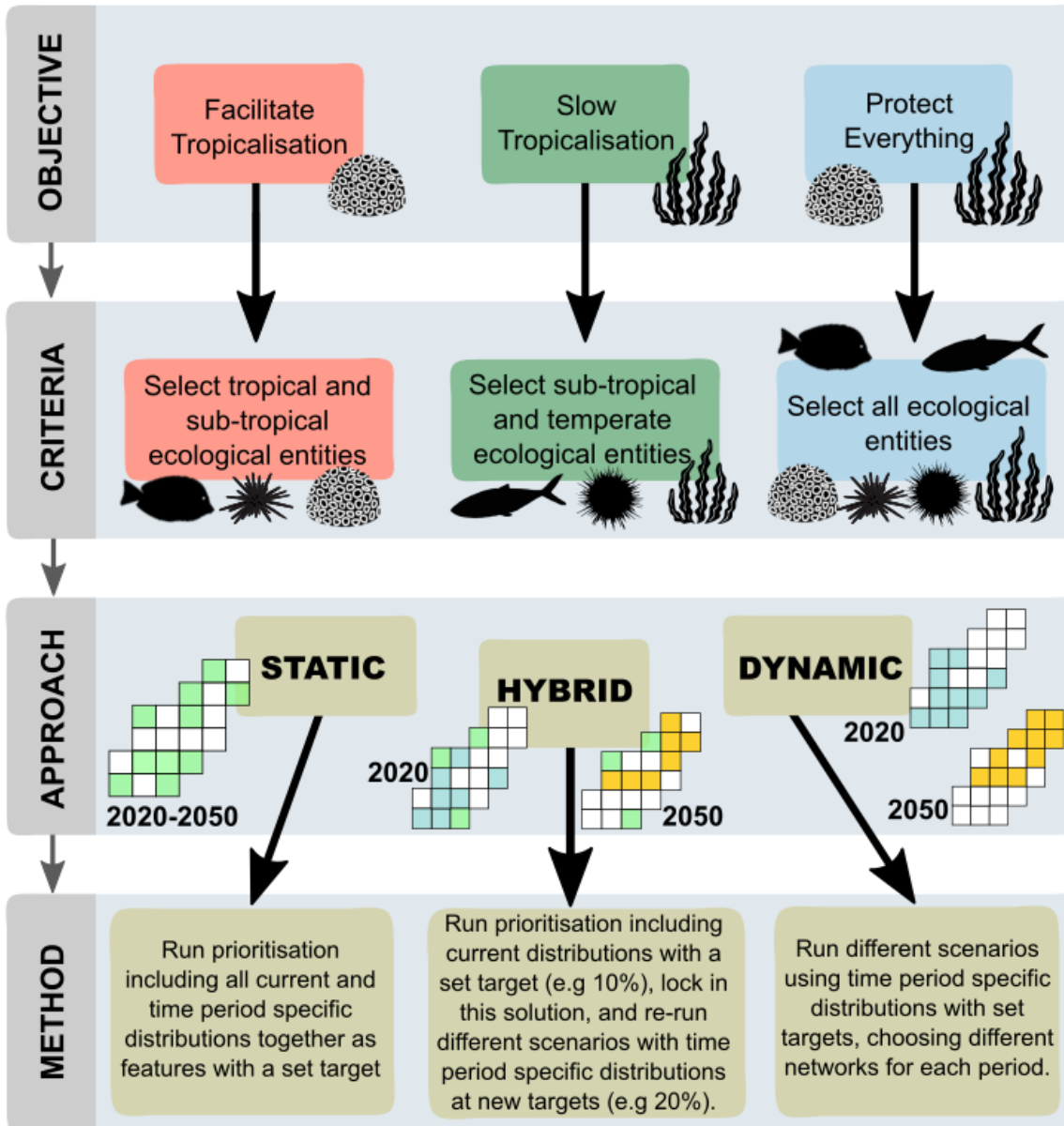


Figure 5.1. Schematic diagram of three possible static, hybrid and dynamic approaches for conservation planning that integrates climate-induced range shifts into conservation planning. The approaches taken can meet three conservation objectives, to facilitate tropicalisation, to slow tropicalisation and to protect all conservation features.

5.3.2 Study system: Japan's Kuroshio Coast

Our study area encompassed the Central Kuroshio and South Kuroshio Marine ecoregions (Spalding *et al.*, 2007) (Fig. 5.2). These ecoregions cover the range of scleractinian coral reefs and coral communities along Japan's East Coast. The coastline and islands form a stepping stone chain of habitats along a tropical to temperate gradient, facilitating the dispersal of species to higher latitudes (Yamano, Sugihara and Nomura, 2011). Furthermore, the ecosystems are strongly influenced by the poleward Kuroshio current, and have undergone climate-induced tropicalisation and community change in the past few decades (Yamano, Sugihara and Nomura, 2011; Kumagai *et al.*, 2018; Abe *et al.*, 2021). High latitude reef communities have undergone benthic community shifts (Yamano, Sugihara and Nomura, 2011), from macro-algal to coral communities, and tropical corals have experienced large-scale bleaching events and degradation (Loya *et al.*, 2001; Omori, 2011), increasing the need for objective driven conservation management.

We first established habitat areas where tropical and temperate reefs exist. We downloaded benthic and geomorphic distribution maps from the Allen Coral Atlas (Allen Coral Atlas, 2022) and the WCMC (United Nations Environment Programme- World Conservation Monitoring Center., 2021), excluding the sand category, for our study area. The reef data was merged together with distribution maps of seaweed beds, coral reefs, and mangroves from the National Surveys on the Natural Environment (Biodiversity Center of Japan, 2021) to create an overall reef substrate map. To create the planning units, we then created a fishnet with a 4.5km² resolution that covered the reef substrate map. With the exception of Izu Oshima, we removed the Izu archipelago, because the islands were likely to have highly variable environmental conditions and we had no species records to accurately model biological features. The final planning unit layer had a total of 1418 planning units.

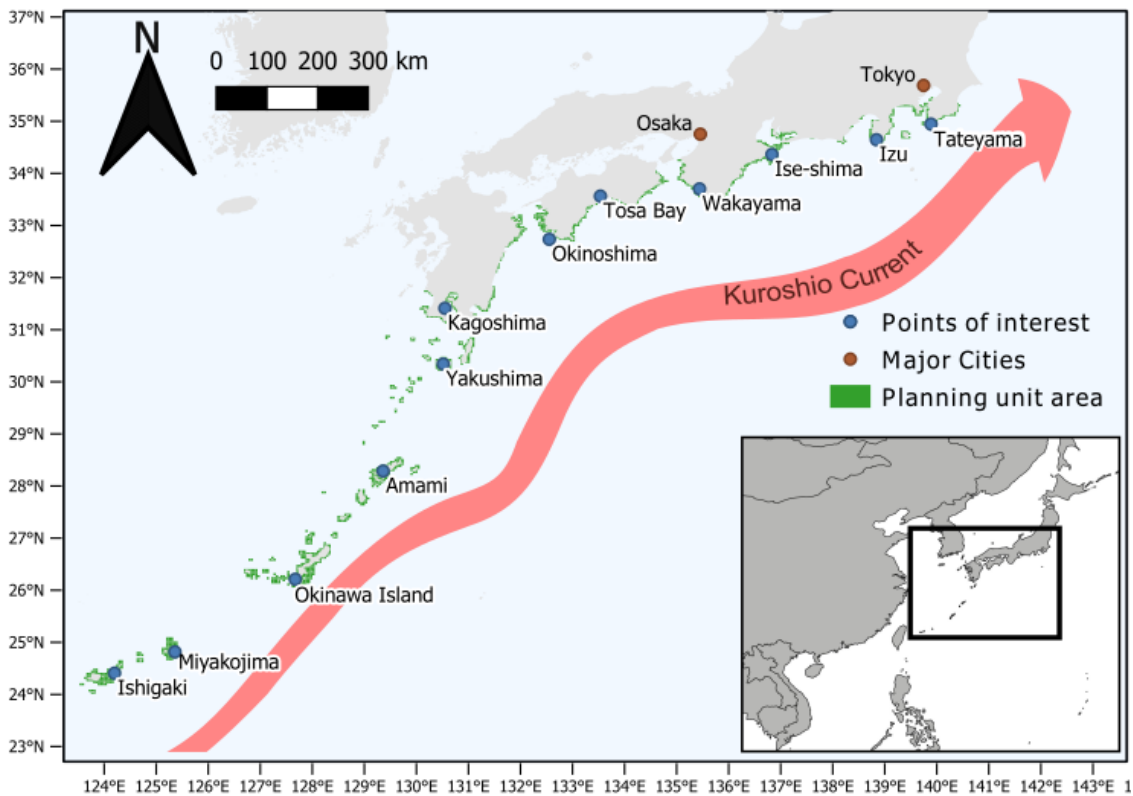


Figure 5.2. Map of the Kuroshio region along Japan's east coast used as the case study area, showing the path of the Kuroshio current in red. Blue circles indicate locations of interest, brown circles show the location of major cities for reference, and the green area shows the planning unit area for conservation planning analyses.

5.3.3 Biological conservation features

We used multi-taxon functional groups as our biological conservation features to allow for the inclusion of rarely observed species, and to allow the prioritisation of diverse functions. During 2015-16 we surveyed 32 coastal coral community and reef sites spanning 24°N-34°N, and recorded the abundance of non-cryptic coral, fish, algae, mollusc and echinoderm species on three replicate transects of 25m length, and at 8m depth (Chapter three and Chapter four). We collated trait databases containing morphological, physiological and life history traits such as body size, reproductive mode and habitat preference for all survey species using information from online databases and primary literature (Madin *et al.*, 2016; Froese and Pauly, 2021). Species were categorised into functional groups according to traits using cluster analyses (Miller *et al.*, In revision; Anderson *et al.*, 2021, Chapter three, Chapter four).

Site-based functional group abundances, and values for the environmental variables minimum sea surface temperature, mean current velocity, mean salinity, mean chlorophyll and bottom light were used to develop abundance based distribution models for now (representing survey years, i.e., 2015/16), and also for 2050 using the environmental variables projected under RCP 8.5 business as usual scenario. Environmental variables were downloaded from Bio-Oracle (Tyberghein *et al.*, 2012; Assis *et al.*, 2018) at a resolution of 5arc min (~9km²). For each group, we trained generalised linear and generalised additive models, as well as random forest machine learning algorithms, and combined these into an ensemble model weighted by predictive accuracy. Using the ensemble model, we predicted the current and future abundances of four coral, eleven fish, five algae, six mollusc and three echinoderm functional groups across our study area. Functional group abundance distributions were found to be tropical n=12, subtropical/temperate n=12, or cosmopolitan n=5. For detailed methods on biological surveys, functional group categorisation and model fitting see Chapter four.

The coastline of Japan is highly complex, and some narrow inlets and bays were excluded from the marine environmental data layers, and thus model predictions, as they were largely covered by land. To ensure that we had biological values in such areas, we used the function ‘disaggregate’ from the R ‘Raster’ package (Hijmans, 2021) to double the resolution of the predicted abundance distribution layers, so each raster cell was roughly 4.5km². These datasets were exported to QGIS and we interpolated the missing values using the ‘fill no data’ tool with a maximum search of five pixels. Abundance values were rounded to the nearest integer.

The PU layer spatially matched the raster grid, and PUs were assigned the respective functional group relative abundances as the input conservation features. To calculate relative abundances, the functional group abundances were multiplied by the proportion of hard substrate coverage in each PU.

5.3.4 Cost data

We used human population as a proxy for opportunity costs as it can indicate fishing pressure as well as environmental disturbance (Makino *et al.*, 2014, 2015). To identify the cost of each PU, we calculated the average population within a 10km radius from its centroids. Population data was obtained from Japanese government statistics (Portal Site of Official Statistics of Japan, 2020), and contained current and projected population values for 2050 per 1km cell. Thus, we were able to calculate a current and projected 2050 cost value for each PU (Supplementary Fig. S5.1). PU’s with an average population of less than four were assigned a population of four to avoid automatic selection of extremely low-cost (zero cost) areas in the spatial planning analyses.

5.3.5 Conceptualising tropicalisation benefit to benchmark Marxan scenarios

Using our decision framework (Fig. 5.1) we analysed scenarios for static, dynamic and hybrid approaches across three conservation objectives that facilitate tropicalisation, slow tropicalisation, and protect everything (Table 5.1). We chose an overall target of 30% protection for each conservation feature as this is a global target for protected area coverage by 2030 (Dinerstein *et al.*, 2019). For all scenarios, we ran Marxan 100 times, to determine the selection frequency for each PU in the final solution for each run.

For the static approach, we used all conservation features from both years and the current cost values. For the dynamic approach we ran Marxan twice, firstly with the current conservation features and current cost to determine the reserve network for now, and then re-ran it with future conservation features, and future costs to determine the reserve network for the future. For the hybrid approach, we selected the best solution from static target percentage runs ranging from 5-30%, locked these in so they would be included in the final solution, and re-ran Marxan using time-period specific values to identify the dynamic network for the remaining percentage to make an overall protection of 30%. For example, given a hybrid scenario where 10% of the solution was static, the other 20% would be dynamic. We selected the static-dynamic ratio value where the total functional change reached an asymptote. We assessed how our scenarios differed according to their total functional change achieved across all selected PUs (Equation 1). The functional change was calculated as the predicted total relative change in abundance for each functional group for each planning unit (Supplementary Figure S5.2):

$$\text{Total functional change} = \sum_{i=1}^n (\sum_{j=1}^m (\Delta A_{i,j})) / n \quad \text{Eq.1}$$

Where n is number of selected PUs i , $\Delta A_{i,j}$ is the normalised relative abundance change in each functional group j in i .

We also calculated the positive functional change, with the same formula, but only summing the functional group planning units with positive change in abundance, and similarly the functional losses by only considering the planning units for each functional group that had abundance losses, converting these abundances into positive values and summing them together. Analysing the functional changes enabled us to assess if the scenarios and approaches were prioritising PUs for protection that had high overall total changes in abundance across all functional groups between now and 2050. Planning units with high overall abundance change were likely to be those that were experiencing the most community change, and thus tropicalisation.

Table 5.1. Table showing the input conservation features for each conservation planning scenario. For the hybrid scenarios, Marxan was run twice, once with features and targets values in the upper part of the respective table row (in bold), and then re-run locking in the best solution of the initial run, with the values in the lower part of the respective table row.

Scenario Name	Conservation feature types	Input feature times	Input cost	Feature targets	Locked in planning units	Time period useful for
Facilitate tropicalisation static	Tropical distributed functional groups	now, 2050	now	30%	None	2015-2050
Slow tropicalisation static	Sub-tropical and temperate distributed functional groups	now, 2050	now	30%	None	2015-2030
Protect all static	All functional group abundances	now, 2050	now	30%	None	2015-2050
Facilitate tropicalisation dynamic now	Tropically distributed functional groups	now	now	30%	None	2015
Facilitate tropicalisation dynamic future	Tropically distributed functional groups	2050	2050	30%	None	2050
Slow tropicalisation dynamic now	Sub-tropical and temperate distributed functional groups	now	now	30%	None	2015
Slow tropicalisation dynamic future	Sub-tropical and temperate distributed groups	2050	2050	30%	None	2050
Protect all dynamic now	All functional groups	Now	now	30%	None	2015

Protect all dynamic future	All functional groups	2050	2050	30%	None	2050
Facilitate tropicalisation hybrid now	Tropical functional groups	now, 2050 now	Now Now	10% 20%	Lock-in	2015
Facilitate tropicalisation hybrid future	Tropical functional groups	now, 2050 2050	Now 2050	10% 20%	Lock-in	2050
Slow tropicalisation hybrid now	Temperate and subtropical groups	now, 2050 now	Now Now	10% 20%	Lock-in	2015
Slow tropicalisation hybrid future	Temperate and subtropical groups	now, 2050 2050	Now 2050	10% 20%	Lock-in	2050
Protect all hybrid now	All groups	now, 2050 now	Now Now	10% 20%	Lock-in	2015
Protect all hybrid future	All groups	now, 2050 2050	Now 2050	10% 20%	Lock in	2050

5.4 Results

5.4.1 Differences in tropicalisation benefit between the hybrid scenarios

To make up the 30% overall protection target for the hybrid scenario, we included and locked-in the networks selected for a 10% static target, and re-ran the analyses using an additional 20% dynamic target using the time-period specific data. When iteratively running different ratios of locked-in static, and additional dynamic networks, increasing the dynamic proportion of the network increased the total functional change for the future scenarios (Fig. 5.3). The increase in total functional change according to the static/dynamic ratio differed when different functional groups were inputted into the analyses for each of the three conservation objectives (facilitate tropicalisation, slow tropicalisation and protect everything). For the subtropical functional groups,

the increase tailed off at 20% suggesting this was an appropriate cut-off value for the static/dynamic ratio within the hybrid scenarios (Fig. 5.3). Changing the amount of static locked in reserves appeared to have little difference in total functional change for the scenarios that facilitate tropicalisation.

For all conservation objectives, including a dynamic reserve network aspect at any proportion in the hybrid solution reduced the selected reserve networks' total functional change for the present day analyses compared to the static solution, but increased the functional change significantly in the future (Fig. 5.3, Fig. 5.4). The reduction in functional change for the current period compared to the static network was smaller than the increase in future benefit, suggesting a net gain in the capacity to facilitate range shifts and account for climate change. Similarly, including a dynamic protection aspect also maximised positive functional change (Supplementary Fig. S5.3) and minimised functional losses in the future (Supplementary Fig. S5.4). When comparing the dynamic and hybrid total functional change values for both time periods, they were largely similar.

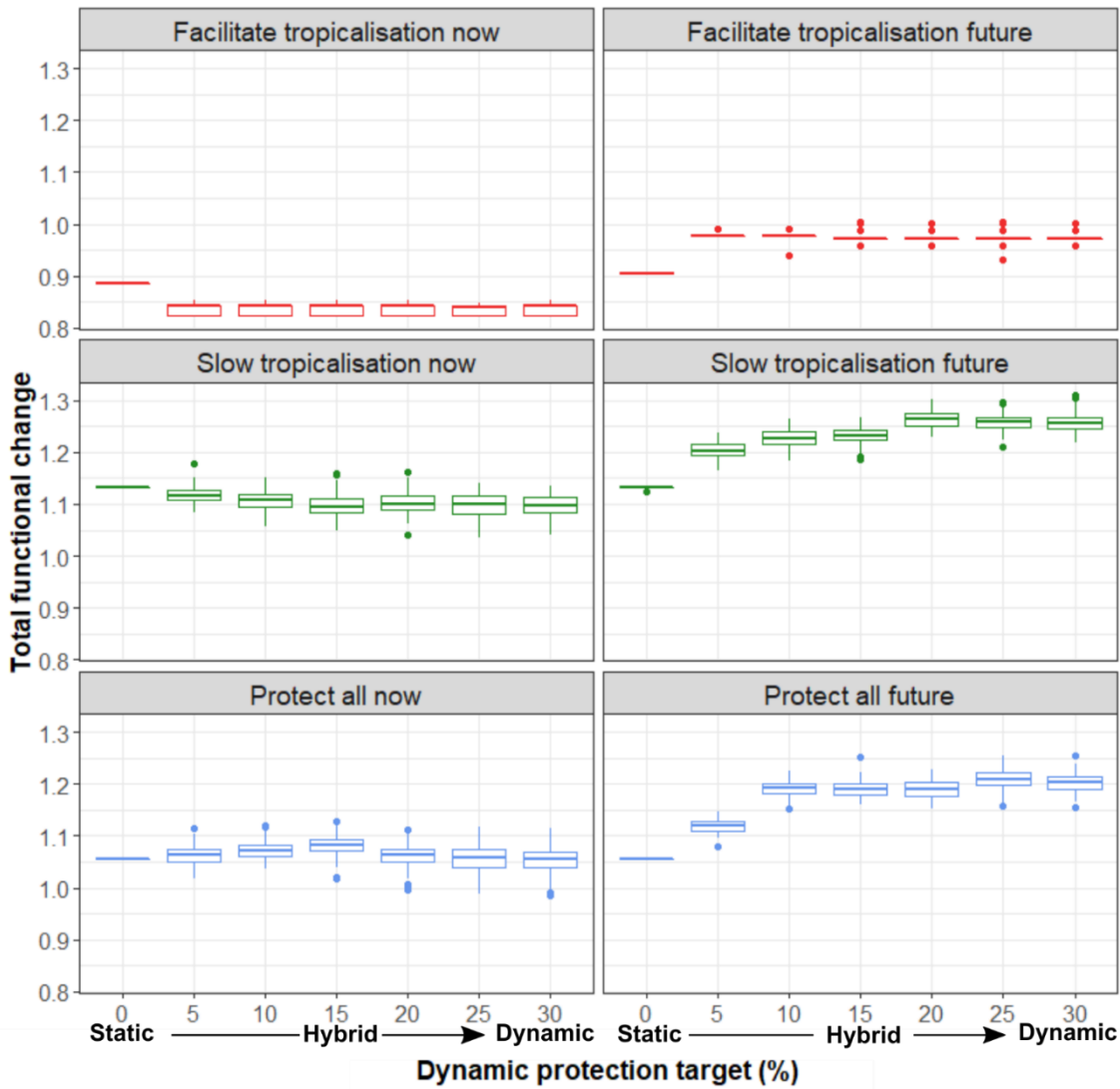


Figure 5.3. Boxplots indicating the range of total functional change across the 100 Marxan runs for the now and future (2050) hybrid scenarios for each conservation objective - Facilitate tropicalisation, Slow tropicalisation and Protect all functional groups. All scenarios were run with a total protection target of 30%, but the X axis shows the dynamic target percentage, with the remainder of the 30% target being inputted with a static target percentage (e.g., at a dynamic protection target of 5%, 25% of the remaining protection target would be static).

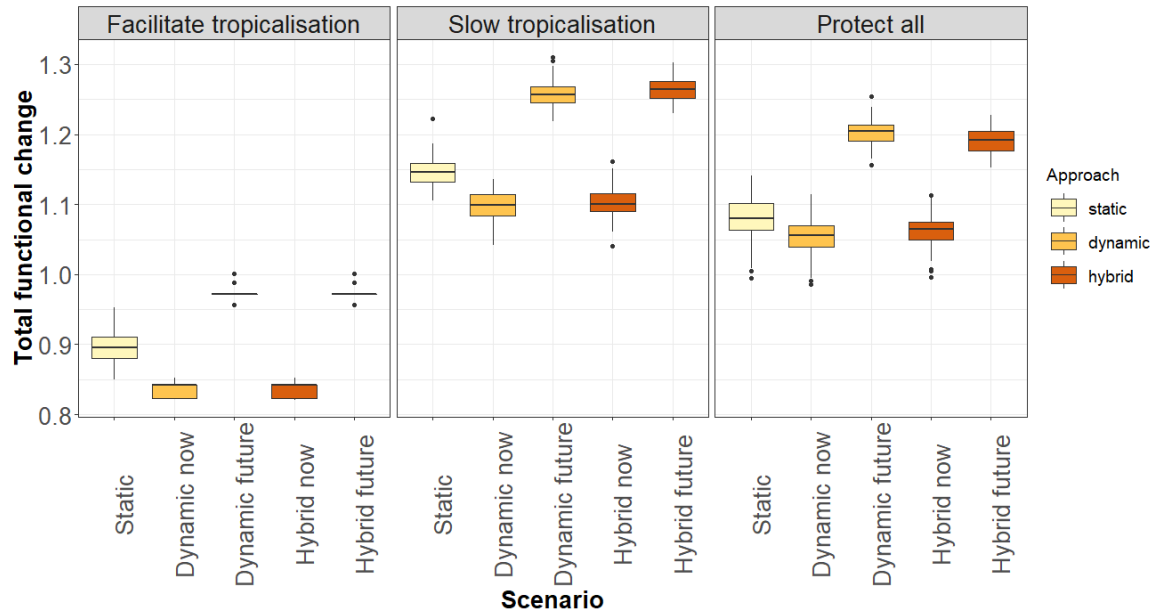


Figure 5.4. Boxplots comparing the range of total functional change across the 100 Marxan runs between the static, dynamic and hybrid approaches across the three conservation objectives to Facilitate tropicalisation, Slow tropicalisation and to Protect all functional groups.

5.4.2 Spatial selection of protected areas

The spatial configuration of selected planning units for the reserve networks differed for static, dynamic and hybrid approaches across the three conservation objectives (Fig. 5.5). The differences in spatial selection of planning units was more affected by conservation objective than by the time period and the approach (static, dynamic and hybrid). For all objectives, the areas selected for protection in using the static approach seemed to be the most spatially similar to the areas selected using dynamic approach from the current time period (dynamic now). Similarly, there was very little visual difference between the hybrid and dynamic scenarios of the same time period for each conservation objective.

5.4.3 Scenarios that support tropicalisation

When planning with a conservation objective to facilitate tropicalisation by prioritising protection for tropical functional groups, the PUs with high selection frequencies were mainly in the southern tropical areas for all static, dynamic and hybrid scenarios (Fig 5.5a). For the static, the hybrid now and dynamic now scenarios, the highest latitude planning units selected were around Okinoshima Island, Kochi Prefecture (see Fig. 5.2 for site locations). For 2050, both the dynamic and hybrid future scenarios had further PUs selected around this area, as well as planning units selected at

increasingly higher latitudes around the Northern end of Tosa Bay and the Ise-shima peninsula. Within the tropical areas, the selection frequency of PUs around Amami, the islands north of Yakushima, and Kagoshima also increased for future scenarios. Outputs for the lowest latitude tropical areas appeared largely to be the same for all scenarios.

5.4.4 Scenarios that slow tropicalisation

The slow tropicalisation objective scenario which prioritised protection of subtropical and temperate groups had PUs with high selection frequencies across the whole range of the planning area. Within the sub-tropics, there were pockets of PUs with high selection frequencies around the Izu Peninsula, Ise-shima peninsula, just north of Tosa Bay, around Okinoshima and along the west coast of shikoku, and also around Kagoshima (Fig 5.5b). Between the now and 2050 scenarios, there was not much spatial change of selected PUs in these areas, except for a few additional PUs with high selection frequency around Okinoshima. In the tropics, PUs around Ishigaki and Miyakojima were highly selected in all scenarios. However, between the two time periods, there was a reduction in PUs with high selection frequency around Okinawa Island, with PUs around Amami more likely to be selected in 2050. For PUs around the Islands between Amami and Yakushima, the selection frequency decreased in the future.

5.4.5 Scenarios that protect all functional groups

The areas with high selection frequency PUs for scenarios with the objective to protect all functional groups appeared to be similar to those of the slow tropicalisation objective scenarios. Between the now and 2050 scenarios, there were slight reductions in selection frequency around northern Okinawa Island, and increases around Southern Amami (Fig 5.5c). Between the dynamic scenarios, there were reductions in selection frequency around the islands between Amami and Yakushima between the years, but these reductions were not as noticeable for the hybrid scenarios. Visually, there appeared to be little difference between the dynamic and hybrid scenarios. There were also noticeable increases in planning units selected around Okinoshima for both future scenarios. PU selection around tropical Ishigaki and surrounding islands was lower for the static scenario than any of the hybrid and dynamic scenarios which had similar PUs selected around this area.

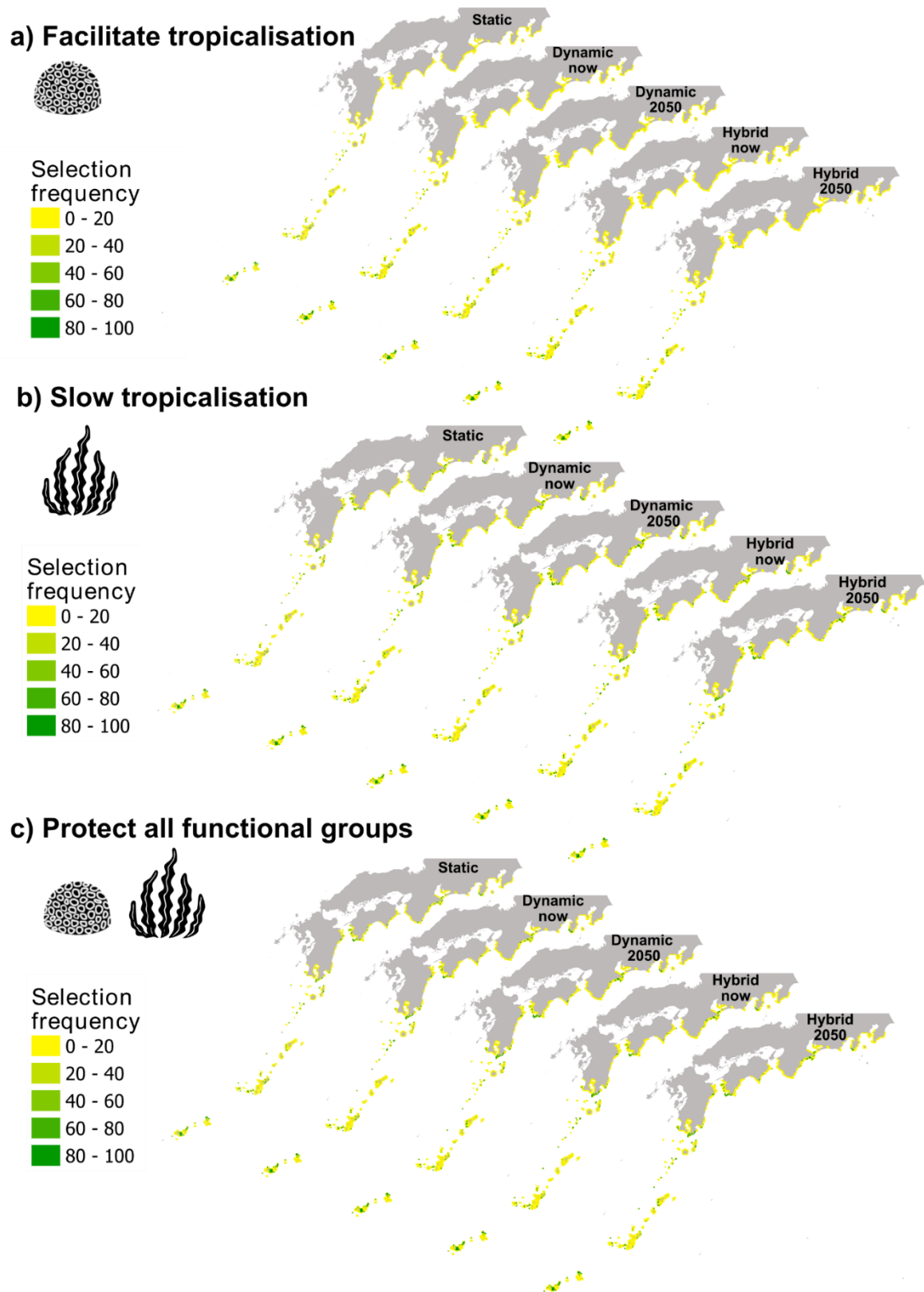


Figure 5.5. Maps showing the selection frequency of planning units for 100 Marxan runs across the different scenarios for the objectives **a)** Facilitate tropicalisation, **b)** Slow tropicalisation and **c)** Protect all functional groups.

5.5 Discussion

Here we present a methodological framework to mitigate the effect of climate-induced range shifts on tropicalising biogeographical transition zones. This study demonstrates how combining static and dynamic protected area elements in a marine protected area network can significantly increase the conservation benefit for reef functioning across multiple taxa. The necessity for such hybrid reserve networks has been previously discussed (D'Aloia *et al.*, 2019; Tittensor *et al.*, 2019), but here we develop and test a replicable objective-based framework that integrates past and future distributions of 29 functional groups across five taxa. The framework is novel in three ways, firstly, it uses a biodiversity driven metric (the total functional change) to compare prioritisation outcomes, secondly, it considers the conservation of multiple taxa and ecosystem function through the prioritisation of functional groups, and finally, it applies a climate resilient approach that incorporates a static reserve network along with dynamically reserves that track range shifts. Our results suggest that for the hybrid network, a 10% static and 20% dynamic ratio (totalling 30% overall protection) maximised the protection of functioning, yet this is likely to differ between case studies and can be flexibly changed to maximise functional protection. Our framework provides a coarse scale systematic approach to determine long-term ecologically effective management actions and all, or parts of this framework could be adapted to be applied across different realms.

We compared the outputs of our prioritisation scenarios by assessing if the networks were selecting locations with high or low climate-induced functional turnover by calculating the total functional change across the networks. This allowed us to compare between scenarios using a metric relevant to our conservation objectives. Traditional conservation planning analyses often assess and compare prioritised reserve networks using the overall cost of the network, or the size of the network (i.e., the number of planning units selected for protection) e.g. (Proudfoot, Devillers and Brown, 2020; Christodoulou, Griffiths and Vogiatzakis, 2021; Plumptre *et al.*, 2021). These broad metrics are linked to efficiency, but they not provide any information about how reserves meet specific ecological objectives (Magris *et al.*, 2018), and do not assess the effectiveness of protection whilst considering temporal change to communities and ecosystem function. Especially in the context of range shifts, smaller reserve networks with fewer planning units might be cost effective, but they have increased chance of species shifting out of protected areas due to range shifts (Alagador, Cerdeira and Araújo, 2014). Evaluating reserve network prioritisation outputs using independent biological data has been explored to account for connectivity (White *et al.*, 2014), but we are the first, to our knowledge to develop and implement an approach to compare performance of reserves in the context of range shifts and functional change.

When assessing the total functional change across all approaches and conservation objectives, the future dynamic and hybrid scenarios had the highest values, followed by the static scenarios, with the present day dynamic and hybrid scenarios having the lowest functional change (Fig 5.4). The present-day dynamic scenarios are equivalent to standard conservation management, as the conservation feature and cost inputs are only based on current information, and with no future climate-induced effects. Thus, we show that including future distribution predictions in any static or dynamic capacity increases the chance that the selected areas for prioritisation will maintain high functional diversity, and thus inferred high levels of ecosystem functioning. The functional change was similar for the dynamic and hybrid scenarios. As the hybrid approach has fewer shifting reserves, but retains the capacity to protect functioning, it provides a practical solution without sacrificing effectiveness.

When prioritising to protect tropical functional groups and facilitate tropicalisation, the selected reserve networks had lower total functional change compared to the objective to protect all functional groups, and the objective to slow tropicalisation. The spatial selection of areas when protecting tropical functional groups was largely around Japan's tropical islands further south than Kagoshima, with the majority of change between time periods occurring within the tropical areas, with protection shifting from the low latitude islands of Ishigaki and Okinawa, to around Amami Island (Fig 5.5a). Very few PUs were selected in areas such as Okinoshima, Wakayama and Tateyama which are known (Yamano *et al.*, 2012; Abe *et al.*, 2021) and predicted (Supplementary Fig. S5.2) to be tropicalising the most, thus reducing the tropicalisation benefit. Yet, the changes with the tropics are likely to be accounting for within range changes in abundance, which are likely to have ecological impacts (Weiskopf *et al.*, 2020). The extension of the reserve network into small pockets of high latitude areas, without the contraction away from the southern reefs may reflect findings that range contractions occur slower than range extensions (Poloczanska *et al.*, 2013). It is possible that with a longer time period (e.g., up to 2100), there may be more visual shifts in the reserve network away from the tropics towards high latitudes, but such predictions would have high uncertainty.

The conservation objectives to protect all functional groups and to slow tropicalisation by protecting subtropical and temperate groups had visually similar results, with large pockets of PUs selected around known tropicalising areas (Denis *et al.* 2013, Kumagai *et al.* 2018, Nomura 2009). Our functional groups were created from species identified during surveys that targeted tropical reefs, as well as high latitude coral communities which are known to have increasing coral cover. Thus, the functional groups we categorised as subtropical due to having increased abundances at higher latitudes could be largely formed of species that actually drive tropicalisation. This could also explain why the tropicalisation benefit was highest when

protecting these sub-tropical groups, compared to the tropical group scenarios. However, the total functional change value accounted for both reductions in functional group abundance as well as increases. When just assessing the negative abundance changes for functional groups the slow tropicalisation scenario had the lowest functional losses (Supplementary Fig. S5.4). This may be because these areas had already experienced range contractions from truly temperate groups such as those that survive in macro-algal dominated habitats, and our baseline was shifted (Muldrow, Parsons and Jonas, 2020). Adding data to this analysis from surveys conducted at temperate sites without any coral coverage may capture additional truly temperate functional groups. Prioritising for just these groups within the slow tropicalisation scenario could select stable refugia sites with low future changes in abundance, lowering tropicalisation benefits.

Some of the subtropical groups were also found at low abundances in the tropics, potentially driving the selection of tropical areas in the scenarios with the ‘slow tropicalisation’ objective. Even with low abundances, these areas could have been selected in the final solutions because many of the tropical islands south of mainland Japan are sparsely populated, with very low PU protection cost (Supplementary Fig. S5.1). Temperate mainland areas such as Tateyama are nearer to high population cities, reducing their chance of PU selection. Habitats in these areas are more likely to be subject to coastal development, pollution and direct destructive activities (Heery *et al.*, 2018). Yet, rural communities are more likely to rely upon fishing to generate food and income, so the surrounding areas may actually have higher levels of fishing pressure (Teh *et al.*, 2020). However, Japan has an aging population, that is predicted to experience a 24% population decline by 2050 (Tsunoda and Enari, 2020). The effects of this decline are expected to be particularly severe in rural areas, and in 2018 39% of fishers were over 65 with predicted significant reductions in rural fishing pressure in the near future (Chen *et al.*, 2018; Teh *et al.*, 2020; Tsunoda and Enari, 2020). These effects were considered in our dynamic and hybrid scenarios which used future population projections for 2050. Even still, using a combination of measured anthropogenic disturbances, as well as true values of fishing pressure could increase the accuracy of conservation plans.

Many of Japan’s current protected areas are non-centrally managed by local fishery co-operatives (Yagi *et al.*, 2010). Though not protected by national laws, these community-based self-imposed no take zones are often established seasonally, and known to be effective at preventing fishing activities for varying durations throughout the year (Yagi *et al.*, 2010). Such community-based protection could incorporate the dynamic aspect of the hybrid strategy, with static reserves being designated as official strict MPAs to keep reserves connected (D’Aloia *et al.*, 2019). Although we did not include any biogeographic aspect within the conservation prioritisation analyses, the selected output networks were spread evenly in a stepping stone formation across the whole study

area, suggesting the bio-geography of the reserve networks would account for appropriate connectivity (Fredston-Hermann, Gaines and Halpern, 2018). The exception to this was the tropical scenario, where the output networks were spread across only the tropical areas, but they were still spread evenly across this smaller range. Changing the static, dynamic, or hybrid approach appeared to have no effect on the connectivity between the reserves. For each conservation objective, the reserve networks selected in the hybrid and dynamic scenarios appeared visually similar for each time period, suggesting the majority of the 10% static areas were already included in both the time periods for the dynamic results. However, if this analysis was repeated across a different study area, or with more time periods, there could be more differences in the hybrid and dynamic approaches, and this is something that should be explored further.

We demonstrate that including a dynamic aspect to long-term conservation planning increases the capacity of the reserve network to account for climate-induced ecosystem change. By prioritising for diverse functions across multiple conservation objectives, management plans designed in this way may have increased capacity to protect ecosystem function and ensure it is maintained in the future. However, this study demonstrates this framework and is not an implementable conservation plan. Such a plan would require including existing protected areas, incorporating better socioeconomic data such as fine scale fishing pressure, and biological data from temperate ecosystems. Yet, whilst we acknowledge the limitations, our novel framework can be adapted to be used across the globe to improve conservation management of threatened ecosystems under climate change.

5.6 References

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5.7 Supplementary Materials for Chapter Five

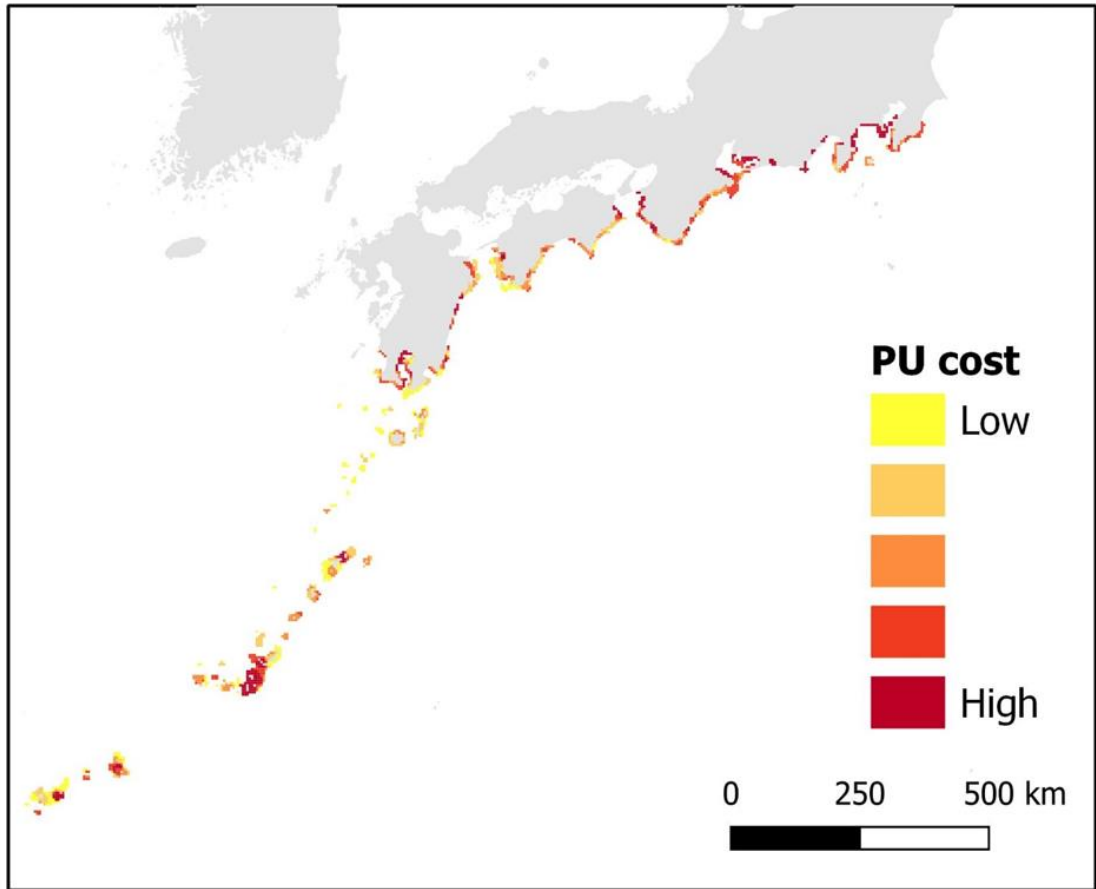


Figure S5.1. Relative cost of planning units for 2020 calculated using the average population (Portal Site of Official Statistics of Japan, 2020), in a 10km buffer around each planning unit.

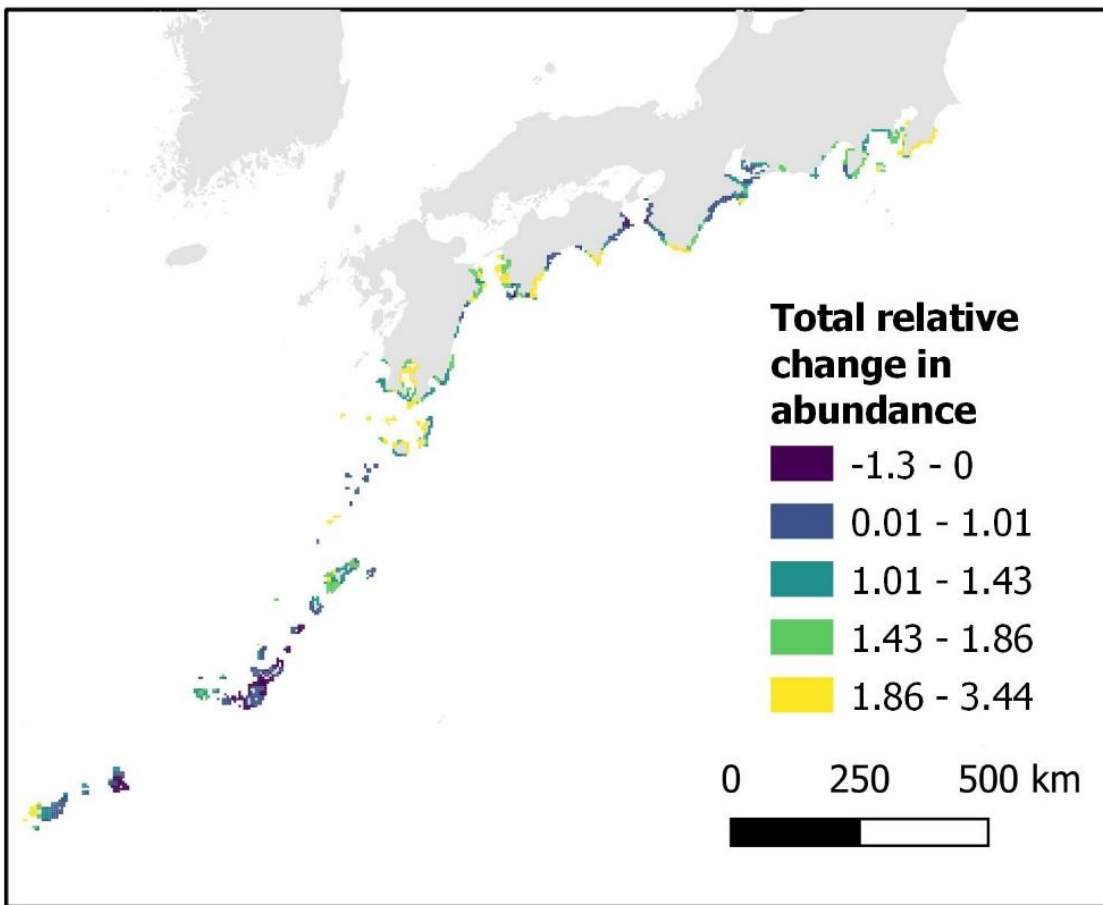


Figure S5.2. Total predicted change in relative abundance between now and 2050 for each planning unit summed across all functional groups (n= 29) of five taxa.

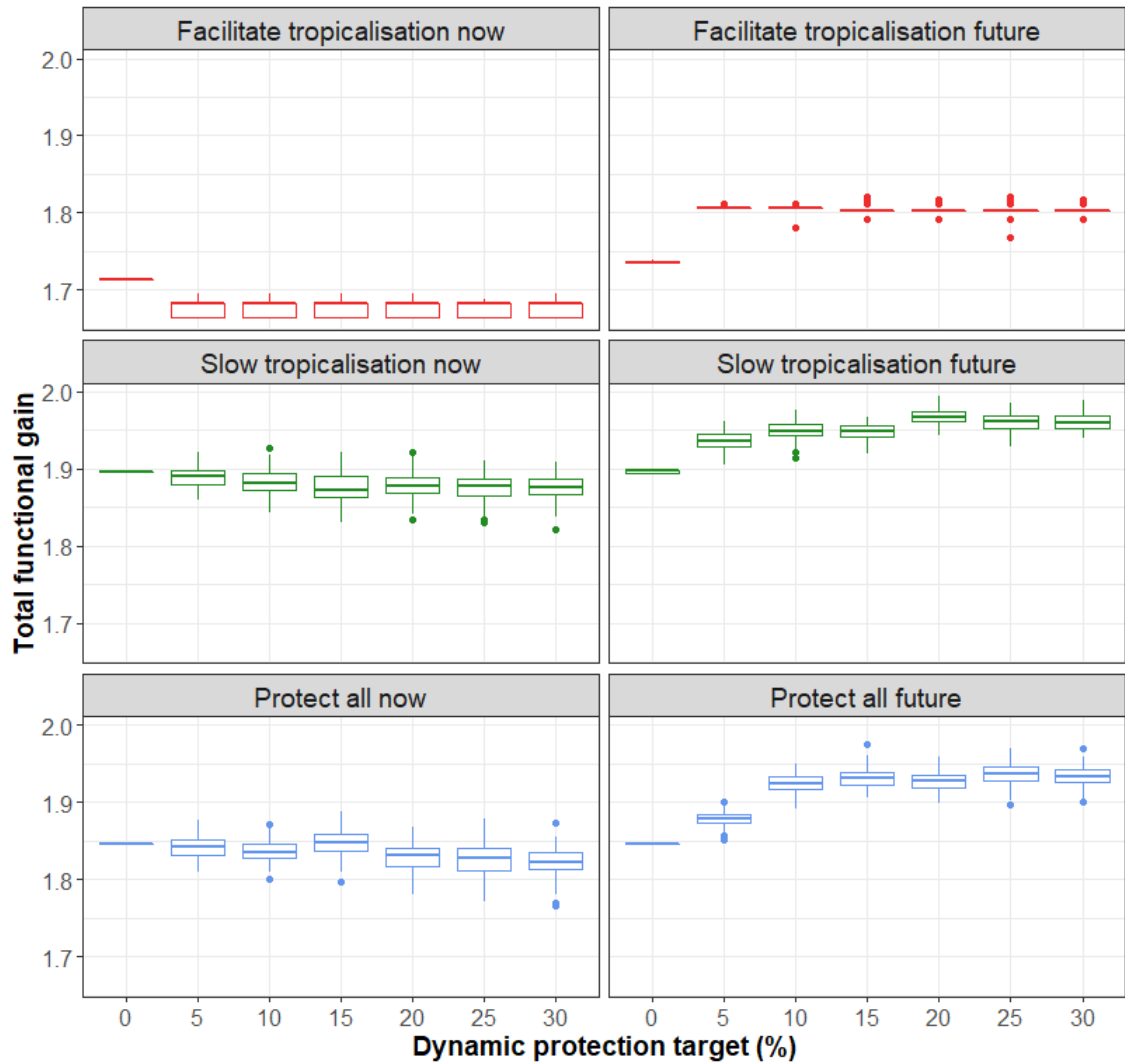


Figure S5.3. Boxplots indicating the range of total functional gain (summing only positive abundance change across functional groups) for conservation area portfolios from 100 Marxan runs for the now and future (2050) hybrid scenarios for each conservation objective - Facilitate tropicalisation, slow tropicalisation and protect all functional groups. All scenarios were run with a total protection target of 30%, but the X axis shows the dynamic target percentage, with the remainder of the 30% target being inputted with a static target percentage (e.g., at a dynamic protection target of 5%, 25% of the remaining protection target would be static).

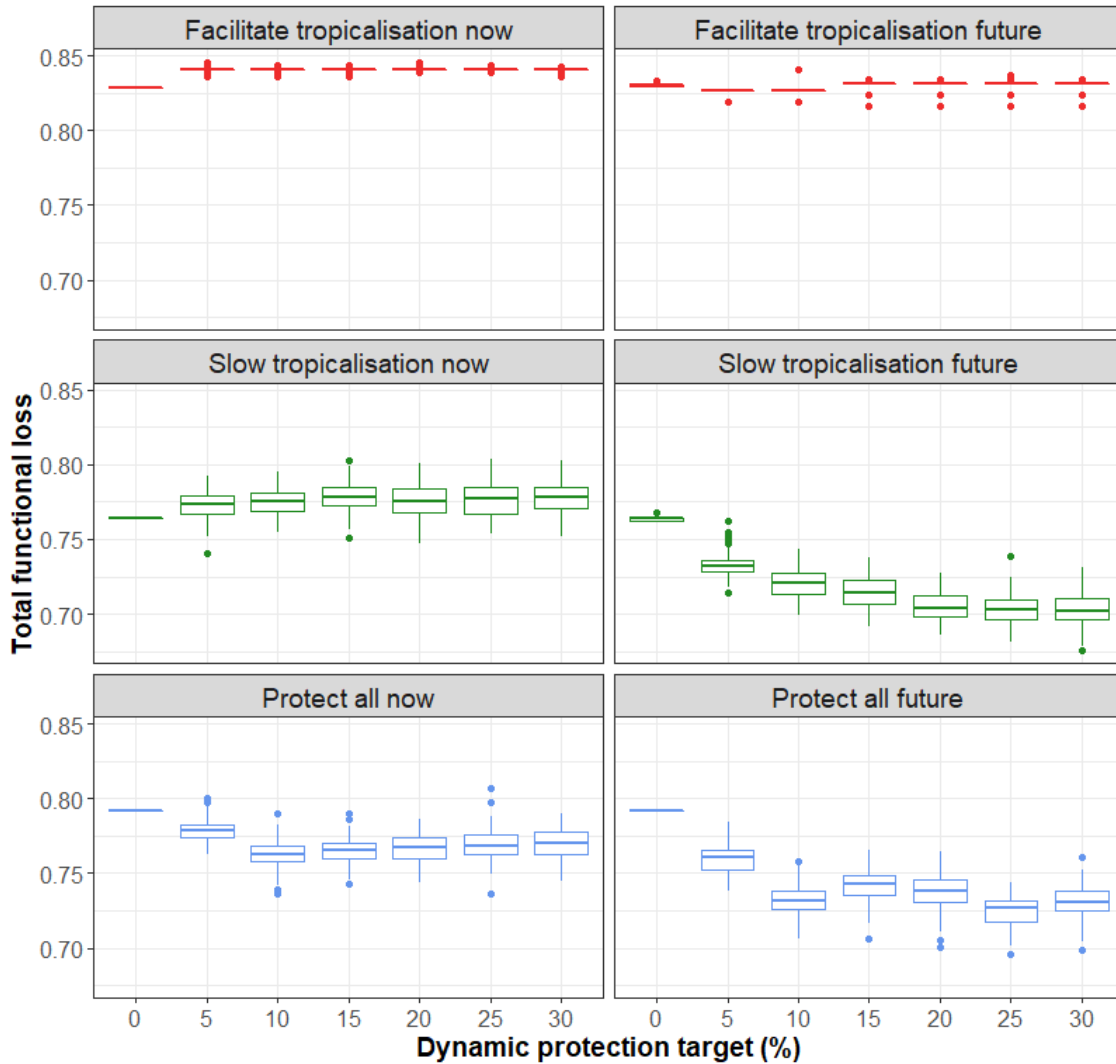


Figure S5.4. Boxplots indicating the range of total functional loss (summing negative abundance change across functional groups) negative tropicalisation benefits across the 100 Marxan runs for the now and future (2050) hybrid scenarios for each conservation objective - Facilitate tropicalisation, slow tropicalisation and Protect all functional groups. All scenarios were run with a total protection target of 30%, but the X axis shows the dynamic target percentage, with the remainder of the 30% target being inputted with a static target percentage (e.g., at a dynamic protection target of 5%, 25% of the remaining protection target would be static).

Chapter Six - General discussion

6.1 Research Summary

The research presented in this thesis aimed to understand the ecosystem functioning of urbanised and tropicalising coral communities, and to predict functional change for informed conservation management. In this thesis, I have demonstrated that ecosystem functioning changes across tropical to temperate transition zones, as trait-based functional groups of multiple taxa had distinct tropical, sub-tropical and cosmopolitan distributions. In the tropics, with localised disturbances, ecosystem functioning was retained, but this finding is unlikely to reflect the future functioning of communities across the latitudinal gradient. Under further predicted environmental change, some of the groups exhibited expected poleward range expansions. Yet, some did not change in abundance, there were only a few range contractions, and some groups even increased in abundance in the tropics. These complex responses highlight that climate-induced community turnover is not as clear as a replacement of sub-tropical groups with tropical ones, and there is likely to be co-existence of range expanding and native functional groups. This process could have consequences for certain functions and related services, so I developed a dynamic conservation framework which targeted different combinations of functional groups depending on three conservation objectives, to facilitate tropicalisation, to slow tropicalisation and to protect all functional groups. Taking a dynamic approach with shifting reserves enhanced the network's ability to maximise the protection of functions, regardless of the conservation objective, increasing the chance of maintaining fully functioning ecosystems under environmental change.

6.2 Chapter Overview

Following on from the general introduction, Chapter two explored the temporal changes in functioning of reef fish and coral communities across tropical Nakagusuku bay between 1975 and 2018. Despite high levels of disturbances and widespread community turnovers, the overall functional trait space was maintained, with even turnovers of species across the space (Cook *et al.*, 2022). Although there were not functional losses, there were dominance shifts from branching to massive coral morphologies, a depth compression of corals towards the mid-depths, and an overall generalisation of the fish communities, indicating redistribution of traits across the bay in response to environmental change. The rest of my thesis contrasts these functional changes from localised urbanisation with those attributable to environmental gradients and tropicalisation. In Chapter three, I used a functional group approach to quantify how reef fish functions are

distributed across space. Functional group-based distribution models revealed that there were distinctive sub-tropical, tropical and cosmopolitan group distributions, implying that functioning changes across the environmental gradient.

In Chapter four, I combined the spatial and temporal aspects of the previous chapters and predicted multi-taxon functional group distributions through space, and determined how these distributions would change in 2050 under climate change. Similar to reef fishes, corals, algae, echinoderms and molluscs were found to have functional groups with distinct thermal affinities. Predicted future group shifts indicated that there will be community reassembly, reduced abundances of the sub-tropical groups at high latitudes, and range extensions of the tropical functional groups by 2050. As these groups were composed of different trait combinations, this turnover indicates there will be a change in overall functioning. Finally, in Chapter five, the multi-taxon functional group predictions were used to identify priority areas for conservation management through a framework that allowed static, or dynamic and hybrid shifting protection. The conservation objectives were to facilitate tropicalisation, slow tropicalisation, and to protect all functional groups. For all objectives, including a shifting dynamic aspect to protection increased the capacity of the reserve network to protect areas that had maintained or increased levels of ecosystem functioning, illustrating the need for dynamic manage strategies to safeguard future functioning.

6.3 Differences in functioning between the tropics and subtropics.

Across tropical to temperate transition zones, it is clear that range shifts will continue to alter community composition under ongoing climate change (Verges *et al.*, 2014; Kumagai *et al.*, 2018) (Chapters three and four). There is an increasing need to bridge the knowledge gap between communities and functioning to understand how these novel ecosystems might function in the future (Pecl *et al.*, 2017; Vergés *et al.*, 2019). Chapters two to four indicate that tropical and sub-tropical ecosystems currently function in a different way. In the tropics, I found that 43 years of local disturbances and climate change did not result in functional losses across Nakagusuku bay (Chapter 2). There was high species turnover, but the species that were lost were replaced with species with similar functions, maintaining overall functioning. This finding suggests that these communities have high functional redundancy, where many species are contributing the same functional roles (Mouillot *et al.*, 2013). Thus, with tropicalisation and poleward range contractions, functional space could be maintained at low latitude sites, even in disturbed areas. However, urbanised communities may be pre-adapted to environmental change or marginal conditions (Burt *et al.*, 2020), or these communities could have a shifted baseline (Muldrow,

Parsons and Jonas, 2020), with community turnovers and reductions in functions prior to the original surveys in the 1970's. Thus, the responses of these urbanised communities to disturbance may not reflect those of typical tropical reefs.

The functioning of Nakagusuku bay was maintained through species turnover, and there was very little change to overall diversity, potentially through colonisations of disturbance specialists, or expansions of more low latitude species. However, for reef fish, I found that species in shallow waters exhibit distributional patterns, falling into distinct tropical and temperate thermal guilds (Chapter three), supporting the findings of Stuart-Smith, Edgar and Bates (2017). Although we are seeing range shifts across tropical to temperate transition zones (Verges *et al.*, 2014), it is unclear if there will be similar shifts within the tropical region. In the tropics, species are more likely to be constrained by competition, not minimum temperatures (O'Brien and Scheibling, 2018), so there could be fewer poleward range shifts within already tropical areas to replace range contractions, with associated functional losses. Instead, it is likely that generalist species that were limited by biotic competition by habitat specialists could increase in abundance within their range (Stuart-Smith *et al.*, 2021). This would result in the community being formed of a few generalist species, which ultimately may reduce functional redundancy, enhancing the vulnerability of these ecosystems to environmental change (Araújo *et al.*, 2020).

In comparison, the results from Chapters three and four indicate that under range shifts, subtropical high latitude communities could have increased ecosystem functioning. I found that the functional groups in subtropical ecosystems differed from those in the tropics, and this was true for all taxa. My results in Chapter four suggest that the functional groups respond differently to the environment, and it is not as simple as all the subtropical groups contracting and being replaced by tropical groups. Although I predicted that some sub-tropical functional groups will contract and become locally extinct at high latitude sites, others remain, or increase in abundance even with influxes of tropical functional groups, which could indicate overall increased functional space. Currently, sub-tropical ecosystems are known to have lower functional diversity (Araújo *et al.*, 2020), with species filling broad functional roles across few functional niches (Saupe *et al.*, 2019). This is potentially due to the resource limitations of species living in such marginal conditions (McWilliam *et al.*, 2018). The results from Chapters three and four support these findings, as there were fewer functional groups across all taxa that were distributed in the subtropics for the current time period. However, as high latitude environments become less marginal, more functional niches could arise, allowing for tropical and sub-tropical species to co-exist with more winners than losers, and this has been found for reef fish in tropicalising communities in Australia (Smith *et al.*, 2021). The predicted increase in coverage of tropical

corals in Chapter four, suggests habitats will become more complex, supporting more new functional niches.

New functional niches are likely to be filled by range expanding tropical groups composed of unique functional traits, reducing the chance of direct competition with resident natives (Smith *et al.*, 2021). However, I still predicted range contractions of certain functional groups that were more constrained by environmental conditions, such as the group containing large macroalgae such as kelps, which are declining due to heat stress (Wernberg *et al.*, 2016). Additionally, competition between taxa in different functional groups could accelerate turnover processes and cause local extinctions, with recorded range expansions of herbivorous tropical rabbit fish in the Mediterranean found to contribute towards the collapse of resident herbivorous sea urchins (Yeruham *et al.*, 2020). Thus, even if there are more winners than losers in one taxon, this may not extrapolate across multiple taxa, and doing so could produce misleading hypotheses. My results from Chapter four highlight the importance of considering multiple functional groups, as I predicted few fish functional group declines across the latitudinal gradient, yet the findings were more mixed for the other groups, especially for algae and molluscs. In particular, the results predict benthic turnovers, from kelps to corals, supporting real life observations from tropicalising systems in Australia and Japan (Verges *et al.*, 2014; Kumagai *et al.*, 2018; Smith *et al.*, 2021). Thus, even if some species co-exist, the ecosystems are unlikely to retain all functions, especially those linked to temperate kelp beds, resulting in socio-economic losses (Pecl *et al.*, 2019). To protect such functions and associated ecosystem services, in Chapter five, I developed a conservation framework with objective based management.

6.3 Conservation implications

The conservation framework developed in Chapter five allowed for systematic conservation planning that could be adapted to meet three objectives, to facilitate tropicalisation by prioritising the protection of tropical functional groups, to slow tropicalisation by protecting sub-tropical and temperate functional groups, and to maximise the functional potential of the reserve network by protecting all functional groups. Facilitating tropicalisation could be beneficial for conservation of tropical species that are thermally stressed at low latitudes so that they can persist at higher latitude thermal refugia sites (Makino *et al.*, 2014). However, although average sea surface temperatures are predicted to rise, amidst unpredictable climate change, there could be increased extreme events such as long term cold spells (Wang, Liu and Lee, 2010; Leriorato and Nakamura, 2019). In Japan, high latitude reef communities rely on warm water from the Kuroshio current, which has a variable path (Tanaka, Ikeda and Masumoto, 2004). If the path of the current shifts away from the coastline, the coastal communities can experience extreme cold events, causing

cold coral bleaching, and mortality of corals and species that are persisting at their cold range edge (Lerriorato and Nakamura, 2019). In Tosa Bay, central Japan, an extreme cold event occurred during the winter of 2018, resulting in mortality of more than 90% of corals and an 80% reduction in species richness in the bay, with the majority of losses in range shifting species (Lerriorato and Nakamura, 2019). Currently, the corals persisting in the sub-tropics have been found to have adaptations and enhanced resilience to such disturbances (Higuchi, Yuyama and Agostini, 2020). In Chapter four, I predicted turnover abundance increases in tropical corals, which may not have such adaptations to cold stress. This highlights the potential instability of such areas as refuges for low latitude species (Higuchi, Yuyama and Agostini, 2020). However, given that the hybrid conservation approach discussed in Chapter five maintains some protection of the current species range, these areas could perhaps be important source populations, for recovery after such disturbances.

The proposed high latitude refugia are also not immune to warm thermal stress events, with records of warm water bleaching on South African (Celliers and Schleyer, 2002), Australian (Kim *et al.*, 2019) and Japanese (Kumagai and Yamano, 2018) high latitude reefs. In Australia, the bleaching was recorded only in some sub-tropical endemics (Kim *et al.*, 2019), and in Japan and South Africa it is not stated if the bleached corals were endemics, so it is unclear if shifting tropical groups adapted to areas with higher average temperatures will also be affected in the future. Additionally, even with thermal stress related mortalities and disturbances, I have shown that functioning can be maintained at the mid-depths (Chapter two, Cook *et al.* 2022). Such depth shifts could work in a similar way to latitudinal shifts, providing additional refuges within already protected areas (MacDonald, Jones and Bridge, 2018). Currently, similar functional turnover processes occur across depth gradients, with deeper areas becoming increasingly marginal, and thus supporting species with broader functional niches (MacDonald, Jones and Bridge, 2018; MacDonald *et al.*, 2019). Although on disturbed reefs I found evidence of depth compressions (Chapter two), on undisturbed, less turbid reefs, there may be more of a depth expansion as deeper areas become more thermally suitable, but such shifts are yet to be recorded or predicted globally. The likelihood of such depth shifts is particularly viable in Japan which has steep topography, with large coastal depth gradients. Thus, the availability of new functional niches across depths may enhance functioning, if such shifts occur, as there could additionally be latitudinal range shifts of species with new functions in the shallow areas. However, this is only likely in the tropics for phototropic organisms and associated communities, as currently at high latitudes, species are limited to shallow areas by low levels of solar radiation (Muir *et al.*, 2015) which will not change in the future.

I used a 4.5km² planning unit resolution in Chapter five, based upon 9km² modelled data (Chapters three and four), to develop conservation plans. This coarse resolution does not reflect the fine scale habitat heterogeneity of marine ecosystems, especially those influenced by local disturbances, such as the communities across Nakagusuku Bay which differed across a disturbance gradient of a few kilometres (Chapter two, Cook et al. 2022). However, protecting such large planning units would enhance the possibility of depth shifts, and shifts within the planning units between heterogenous habitat types (Fredston-Hermann, Gaines and Halpern, 2018). Additionally, the broader scale allowed me to understand and infer large biogeographic patterns and processes occurring with range shifts. Yet, the research in Chapters three and four, as well as the associated management strategy in Chapter five could be developed further by developing models with finer scale environmental data, and extending the study sites to more temperate and tropical areas to fully understand these range shifts. Furthermore, taking conservation action requires input from multiple stakeholders and careful socio-economic considerations, so my conservation framework, and suggested reserve network is a starting point for climate-resilient management, and such further detailed research is required before implementation of plans.

6.4 Is the functional group approach appropriate?

In Chapter three, I demonstrated that for reef fish, functional group responses to environmental variables represented the within-group species level responses, suggesting that grouping the species and modelling their distributions provided information on ecosystem functioning with species range shifts. I inferred that this would also apply for other taxa, so also used this approach for corals, algae, molluscs and echinoderms in Chapters four and five. Fish are one of the most well studied taxa on coral reefs, especially for functional research, with detailed knowledge about many traits at species level (Froese and Pauly, 2021). For fish, information on how specific traits relate to mechanistic processes, such as herbivory is widely discussed (e.g., Green and Bellwood, 2009; Bellwood *et al.*, 2019; Siqueira, Bellwood and Cowman, 2019), allowing me to make informed decisions when selecting which traits to include in the grouping process. However, excluding corals, the other taxa included in my research are significantly less studied, and only information for certain traits was available. This was especially true for molluscs and echinoderms, where trait-data was often only available at the genus level. Yet, I was still able to select multiple functionally informative traits, such as tidal zone and habitat preference (Floyd *et al.*, 2020) for the clustering. Even if some of the data was missing, or at genera level, each of the functional groups still had unique trait values, indicating each group had unique functional roles.

In contrast, due to the difficulty of identifying corals to species level without genetic tests (Ladner and Palumbi, 2012), they were surveyed *in situ* at genus level. At the genus level, trait values showed no stable clusters, so I grouped corals by their morphological types, as these have been linked to functioning (Darling, McClanahan and Côté, 2013). Distinctive trait values were identified between morphological types, suggesting that morphological groupings were also functionally informative. Despite these limitations, including multiple taxa, not just fish and corals, provides an indication of how overall ecosystem functioning will be affected by climate change. My research is the first to develop such multi-taxon groups, and predict their distributions and how they will change. The functional group approach that I have developed allows for the analyses and management of complex multi-species and multi-trait information (Bellwood *et al.*, 2019; Anderson *et al.*, 2021), providing a practical approach that could be applied elsewhere.

6.5 Global applications

Stepping away from species, and assessing functional community change allows for comparisons of how climate change will affect ecosystems across geographic locations with different taxonomic compositions. For example, the Eastern coastline of Australia is also experiencing tropicalisation (Verges *et al.*, 2014; Smith *et al.*, 2021), so the methodology throughout this thesis could be applied to Australian survey data to identify if there are also unique tropical and sub-tropical functional groups, and to compare the trait values of these groups with those in Japan. The Japanese coastline is highly fished (OECD, 2021), with low abundances of target species, potentially opening up niche space for co-existence between native and range shifting groups (Chapters three to five) or masking functional changes with local disturbances (Chapter two). Thus, my results may not apply across coastlines with less human disturbance, and this is something that would be interesting to compare.

Although there are other tropicalising high latitude reefs along biogeographic transition zones, Japan is unique in that the Kuroshio Current curves away from the coastline at round 35°N, resulting in a rapid drop in temperature north of where this occurs (Sudo *et al.*, 2022). This means that with climate-induced community turnovers, sub-tropical communities are unlikely to be able to shift beyond this oceanographic barrier, enhancing the need for conservation objectives that slow tropicalisation, (Chapter five) so such communities can persist. However, in other tropicalising sites, including Eastern Australia, Western Australia and South Africa, the currents span the whole coastline, with more gradual temperature shifts between sub-tropical and temperate areas. In such areas, the sub-tropical communities themselves may be able to shift to higher latitudes, threatening more temperate areas. In such cases, the conservation framework

from Chapter five could be adapted to include further or different conservation objectives. The ‘slow tropicalisation’ objective could be split into two separate objectives, one to protect subtropical functional groups, and the other to protect temperate groups which have limited shifting capacity due to continental shelf edges. The conservation framework is broad and easily adaptable to different realms and localities, and such ideas could also be used to dynamically include species range shifts, and protect biodiversity, as opposed to functions.

6.6 Future directions

The research presented in this thesis could be developed to further understand climate change, range shifts and ecosystem functions in multiple ways. Firstly, when I assessed how functional group distributions would change in Chapters three and four, I did not consider depth shifts, but these were found to be significant when assessing the impacts of local disturbances (Cook *et al.*, 2022). Understanding and integrating depth and latitudinal shifts together may improve predictions on how functioning changes geographically for conservation management. Secondly, in Chapter two, I assessed how functional trait space changed across time, but I did not categorise the species into functional groups as I did for Chapters three to five. Future work could integrate these approaches, by grouping the species in Nakagusuku bay, and continuing to survey the sites to see how the groups change over time at such a localised scale. Additionally for conservation management in Japan, high latitude coral reef communities also occur along the West Coast (Yamano *et al.*, 2012). This coastline is influenced by the weaker Tsushima current, and there are no significant records of tropicalisation related phase shifts along this coast. However, under climate change, these areas could increase in environmental suitability, resulting in tropicalisation, so research could be conducted to see if these areas may be similarly suitable for conservation management, and to predict how the communities might change. Similarly, comparing how multi-taxon functional groups are distributed and change along other tropicalising coastlines could help to understand if this is a global pattern, with wider conservation implications. Finally, to develop the most accurate conservation plans for Japan, the research from Chapters three to five could be repeated with further taxa, such as soft corals, as well as increased spatial and temporal resolution.

6.7 Final Conclusions

It is becoming increasingly clear that protecting all species will not be possible due to ongoing and worsening anthropogenic disturbances. With functional redundancy, where species share similar functional roles, communities can lose individual species and continue to function in a

similar way. Thus, a realistic and efficient conservation goal is to ensure that organisms supporting critical patterns and processes are safeguarded, regardless of their unique taxonomies. In this thesis, I presented evidence that it is possible for communities to experience species losses due to local disturbances, yet maintain overall functioning, supporting the step away from taxonomic conservation. My research suggests that future predicted climate-induced community phase shifts will result in large scale functional turnovers over biogeographic gradients, requiring dynamic management strategies to account for such ecosystem instability. My work is the first that I know of, that integrates a multi-taxon trait-based approach to predict functional change, and to apply this directly to develop a novel dynamic conservation management strategy. This flexible strategy is an ecosystem-based management framework that can be adapted to be used globally to prioritise and conserve the functioning of healthy ecosystems.

6.8 References

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