Adriano Guido Fossati

Unravelling fish communities' structures in tropical to temperate reefs of eastern Australia

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Supervisors:

Jorge Assis

Co-supervisor

Catherine J.S. Kim

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Declaração de autoria de trabalho

Declaro ser o(a) autor(a) deste trabalho, Unravelling fish communities' structures in tropical to temperate reefs of eastern Australia, que é original e inédito. Autores e trabalhos consultados estão devidamente citados no texto e constam da listagem de referências incluída.

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I. Abstract

Anthropogenic climate stress events are increasing in frequency and severity, threatening marine environments. Higher temperatures alter habitats of aquatic species, which cope by shifting their ranges poleward to more suitable conditions, referred to as tropicalisation. However, the resulting changes in species, functional group biomass, and thermal affinities are variable, with uncertainties remaining around primary drivers of change. Here, I characterise the structure and temporal changes in communities' composition, trait-based functional group biomass, and community thermal affinity. I use fish biomass records from 2010-2023 across 33 eastern Australian reefs along a tropical to temperate environmental gradient. Fish community structure is assessed using hierarchical clustering and recursive partitioning with regression trees to infer how environmental conditions (sea surface temperature, primary productivity, wave height, distance to mainland and southern oscillation index) drive the clustering structure. The main community assembly process is assessed using the Dispersal Niche Continuum Index. Functional groups are defined clustering five fish traits, whereas the surveys' Community Thermal Index is calculated by averaging the thermal mid-points of each species weighted by their mean biomass. Finally, a generalised additive model is applied to quantify the contribution of the same environmental conditions to the changes in the community thermal index. Contrary to expectations, clear tropicalisation patterns are absent at the community level, with limited changes in tropical species biomass. However, communities' thermal affinities show some increase over time at similar latitudes, suggesting a progression of some tropical species polewards, driven mainly by the harshness of the previous winter as well as distance to land and wave height. Overall, communities display a certain stability in composition, despite the domination of dispersal assembly processes. These results highlight the importance of integrating various spatial resolutions in analyses with extended time series fish biomass data to better detect, predict, and protect marine communities' alterations under global climate change.

II. Sumário (Portuguese Abstract)

Os eventos de stress climático antropogénico estão a aumentar em frequência e severidade, ameaçando os ambientes marinhos. As temperaturas mais elevadas alteram os habitats das espécies aquáticas, que respondem mudando as suas áreas de distribuição em direção aos polos, onde as condições são mais adequadas, um fenómeno conhecido como tropicalização. A região leste da Austrália é caracterizada por um longo gradiente latitudinal de zonas de transição, com comunidades heterogéneas sensíveis a mudanças na sua composição. Estas mudanças são intensificadas pela Corrente Leste Australiana, que liga as comunidades de peixes através da dispersão de larvas de peixes. A redistribuição de características importantes, como a herbivoria, foi identificada como um fator de alteração drástica nos ecossistemas, com desflorestação significativa em regiões temperadas. Em todo o mundo, vários estudos destacaram uma progressão em direção a habitats estruturalmente simplificados, que, por sua vez, simplificam a estrutura de características e a cadeia trófica das comunidades de peixes.

Para identificar a função dos ecossistemas e caracterizar as mudanças nas comunidades de peixes, a atribuição de grupos funcionais com base no agrupamento de características de espécies tem sido reconhecida como fundamental. Este método evita análises específicas de espécies, ao mesmo tempo que fornece uma avaliação mais completa da estrutura e das mudanças no ecossistema. Além disso, a biomassa dos peixes oferece um método poderoso para avaliar a estrutura ecológica das comunidades, ligando diretamente as características funcionais ao tamanho corporal, que reflete de forma previsível vários processos ecológicos importantes. As tendências de biomassa em todo o globo parecem apresentar alta variabilidade, mas, em geral, observa-se uma redução no tamanho dos peixes, particularmente em níveis tróficos mais elevados. Esta perda de peixes de grande porte pode ter efeitos desproporcionais nos ecossistemas, uma vez que desempenham papéis ecológicos chave, como a bioerosão, a regulação do crescimento de algas e a regulação das populações de presas. Todas estas mudanças na estrutura e composição das comunidades são provavelmente impulsionadas pela temperatura, um efeito amplamente conhecido em grandes escalas espaciais e temporais. No entanto, parâmetros oceanográficos importantes, incluindo, mas não se limitando, à Temperatura da Superfície do Mar (SST), Produtividade Primária (PP), vento, Corrente Leste Australiana (EAC), altura das ondas (WH), Índice de Oscilação Sul (SOI) e suas interações, são provavelmente impulsionadores importantes das comunidades de peixes na região leste da Austrália.

Os efeitos das mudanças climáticas nas ocorrências de espécies no leste da Austrália, na biomassa de grupos funcionais e nas afinidades térmicas parecem ser variáveis, com incertezas remanescentes sobre os principais impulsionadores destas mudanças. Por isso, neste estudo, o meu objetivo é avaliar o efeito das mudanças climáticas nas comunidades de peixes, detetar padrões de tropicalização e seus efeitos no funcionamento dos ecossistemas. Para al, utilizo registos de peixes coletados entre 2010 e 2023 através de censos subaquáticos em 33 recifes tropicais a temperados no leste da Austrália. Em cada local, as abundâncias e os tamanhos de todas as espécies de peixes não crípticos de recife foram registados ao longo de transectos de 25 ou 50 metros de comprimento por cinco metros de largura a uma profundidade de oito a dez metros, com três a cinco réplicas. A partir do tamanho registado dos peixes, a biomassa (B) foi estimada como ($B = a^*(\text{tamanho do peixe})^b$), com os parâmetros morfométricos "a" e "b" de cada espécie individual recuperados do FishBase.

Apliquei análises de agrupamento multivariadas para entender a composição e a rotatividade da comunidade. Utilizei a técnica de particionamento recursivo com árvores de regressão para inferir como as condições ambientais impulsionam a estrutura do agrupamento. Do Serviço de Informação Marinha da União Europeia (Copernicus), recuperei dados de séries temporais para a Temperatura da Superfície do Mar, Produtividade Primária, Altura das Ondas, distância da costa e Índice de Oscilação Sul para cada um dos locais estudados. Identifico o processo de montagem da comunidade usando o Índice de Continuidade Nicho-Dispersão (DNCI). Esta metodologia fornece um índice único e comparável que pode avaliar se o mecanismo de montagem da comunidade é dominado por nichos ou por dispersão. O DNCI é baseado no método PER-SIMPER, derivado do SIMPER, uma abordagem de modelo nulo que identifica o processo de montagem da comunidade a partir da percentagem de similaridade composicional dos grupos comunitários. Valores positivos de DNCI indicam que a comunidade biológica estudada é dominada por montagem de nicho, enquanto valores negativos indicam dominação por dispersão. Além disso, valores absolutos elevados indicam uma maior força do respetivo processo de montagem. Para identificar os grupos funcionais do meu estudo, agrupei cinco características de espécies conhecidas por serem afetadas pelas mudanças climáticas e pela sua relevância no efeito das espécies no ecossistema: agregação, tamanho corporal, faixa de profundidade, dieta e associação ao habitat. Selecionei o número ideal de agrupamentos (Grupos Funcionais) com base numa inspeção da silhueta média bootstrap e calculei o índice de similaridade de Jaccard e o índice de correspondência de Rand. Para quantificar a mudança na afinidade térmica das comunidades ao longo do tempo, computei o Índice Térmico da

Comunidade (CTI) para cada censo. Recuperei as ocorrências globais de todas as 583 espécies do GBIF.org e combinei a temperatura média da superfície do mar encontrada nas suas ocorrências. Finalmente, obtive o índice térmico da comunidade por levantamento, aplicando a média ponderada nas médias de temperatura das espécies, utilizando a respetiva biomassa média. Utilizando os mesmos dados ambientais de séries temporais, avaliei, através de um modelo aditivo generalizado, os impulsionadores da afinidade térmica das comunidades.

Descobri que a tropicalização das comunidades de peixes parece ter ocorrido nos últimos 14 anos no leste da Austrália, com sinais de expansão em direção aos polos das espécies tropicais, aumentando a afinidade térmica da comunidade. Este aumento na afinidade térmica é impulsionado principalmente pela severidade do inverno anterior e pela altura das ondas, que limitam a expansão em direção aos polos das espécies de peixes. A distância da costa foi identificada como um fator que intensifica a tropicalização, provavelmente destacando o efeito da Corrente Leste Australiana nos recifes exteriores. Por outro lado, ao nível da comunidade, encontrei uma certa estabilidade na composição ao longo do tempo, com as comunidades de peixes agrupando-se claramente em zonas de transição Tropical, Subtropical e Temperada. Esta estabilidade mantém-se mesmo numa escala mais detalhada com oito grupos comunitários, apesar de algumas comunidades bem ligadas serem dominadas por processos de montagem de dispersão. Sob mudanças climáticas, a tropicalização das comunidades de peixes deveria levar a um aumento da biomassa de espécies associadas aos trópicos em direção aos polos. Aqui, em contraste, observei mudanças limitadas na biomassa, com apenas alguns grupos funcionais seguindo esta expectativa. Estes grupos funcionais abrangem uma ampla gama de funções ecológicas, reforçando ainda mais a variabilidade da resposta das comunidades de peixes às mudanças climáticas. Além disso, a reação das espécies a efeitos climáticos variáveis seria específica a cada espécie, o que poderia mascarar os padrões de tropicalização nas biomassas dos grupos funcionais.

Estes resultados destacam a importância de integrar várias resoluções nas análises com dados de biomassa de peixes em séries temporais mais longas para melhor detetar, prever e proteger as alterações nas comunidades marinhas sob as mudanças climáticas globais.

III. Keywords

Climate change, marine biodiversity, ecology, fish traits, tropicalisation

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VI. Abbreviations

CTI: Community Thermal Index

DNCI: Dispersal Niche Continuum Index

EAC: Eastern Australian Current

FG: Functional Group

PP: Primary Productivity

SST: Sea Surface Temperature

SOI: Southern Oscillation Index

WH: Wave Height

VII. General Introduction

Anthropogenically driven climate change is a phenomenon undeniably increasing in recent years (Calvin et al., 2023; Holbrook et al., 2020; Rockström et al., 2009). It affects ecosystems both on land and sea with serious consequences likely to increase in occurrence in the near future (Stuart-Smith et al., 2017). Fishes are at the forefront of these changes, suffering directly from sea surface temperature (SST) increase, which causes redistribution to more suitable ranges (Chen et al., 2011; Pinsky et al., 2013). This dispersal is easier in water than on land (Heath et al., 2012; Poloczanska et al., 2013). However, it is still unclear how fish communities, key actors in marine ecosystem functioning, are affected and could adapt to climate change.

As ocean temperatures rise, fish communities move polewards in the attempt to stay within their preferred thermal range (Mahony et al., 2017; Pecl et al., 2017). The consequence of such population redistribution patterns is an advance of tropical species into more temperate regions, a process defined as tropicalisation (Beger et al., 2014; Vergés & Steinberg, 2014; Yamano et al., 2011). Its effect on ecosystems is important as community member changes affect trophic networks, cohabitation, and whole ecosystem functioning (Scheffers et al., 2016). When such changes happen in regions already under climatic or anthropogenic pressure, major failures in trophic cascade could happen (Kingsbury et al., 2020; Pagès et al., 2018; Perry et al., 2005).

Communities from overlapping ecoregions present different species assemblages that combine into transition zones (Horta e Costa et al., 2014). These zones are sensitive due to the heterogeneity in community composition (Rijnsdorp et al., 2009). Thus, with an increase in tropical species polewards associated with tropicalisation, we might experience drastic changes in ecosystem equilibriums (Miller et al., 2023; O'Connell et al., 2023; Vergés & Steinberg, 2014). This issue is especially a growing concern in eastern Australia, characterised by an extensive latitudinal span and an important gradient of transition zones, putting at risk many different fish communities (Vergés et al., 2016).

With recent ocean warming, various studies highlighted a progression towards structurally simplified habitats, also resulting in simplified trait structure and trophic chain of fish communities (Bosch et al., 2022; Rijnsdorp et al., 2009; Silva et al., 2023). However, changes within communities in trait composition and their subsequent change in biotic interactions are not well understood, with many uncertainties around the interactions with climate-mediated factors (Donelson et al., 2019; Vergés et al., 2019). In tropical to temperate transitions zones such as eastern Australia, important trait redistributions, such as increased herbivory, seem to play a crucial role in reshaping marine communities (Zarzyczny et al., 2022). Indeed, herbivory pressure is essential for reef ecosystems functioning, as it regulates the algal cover (Steneck, 2020). If not confined, this pressure can become harmful as it happened with the expansion of tropical herbivores into temperate algal forests resulting in important deforestation in eastern Australia (Vergés et al., 2016; Vergés & Steinberg, 2014). In the same region, planktivores were found not relocating polewards with a biomass decline across all thermal affinities, drastically altering pathways of ecologically important energy flows (Truong et al., 2017). Predator-prey interactions are still mostly unexplored and their response to tropicalisation remains unanswered, further highlighting the uncertainty around the capacity of local fish communities to reorganise following tropical invasions (Smith et al., 2021).

Fish community characterisation has always come with challenges to capture the effect of changes on the ecosystem. However, it has been recently acknowledged that functional group (FG) assignment based on species traits clustering is key to identify ecosystem functions (Bellwood et al., 2019; Nyström, 2006; Reiss et al., 2009). This method not only avoids species-specific analyses but also provides a more complete evaluation of ecosystem structures and changes (Hooper et al., 2005; Hughes et al., 2017; Mouillot et al., 2014; Yeager et al., 2017). In addition, functional groups' multidimensional trait space defines the fundamental functional niche as it reflects the space where the population can be maintained (Brandl et al., 2019). This helps identify and understand the processes associated with the re-organisation of fish communities, especially from tropicalisation effects under changing biotic and abiotic conditions, constraining the realised functional niche (Brandl & Bellwood, 2014; Díaz et al., 2013; Lavorel et al., 2008; Violle et al., 2007; Worm et al., 2006).

Fish biomass offers a powerful method to assess the ecological structure of communities, linking functional traits directly to body size, the latter predictably reflecting a number of important ecological processes (Brown, 2014; Taylor et al., 2014; West et al., 2001). Fish biomass changes around the world seem to show variability, intrinsically linked with some differences in location and climatic conditions. Nevertheless, studies seem to agree that under anthropogenic pressures, we observe a reduction in fish size, particularly at higher trophic levels, shortening the trophic chain (Geraldi et al., 2019; Robinson et al., 2017; Seguin et al., 2023; Silva et al., 2023). Such loss of large-bodied fishes could have disproportionate effects on ecosystems. Indeed, large fishes carry key ecological roles such as bioerosion or regulation of algal growth through herbivorous feeding (Bellwood et al., 2012; Edwards et al., 2014), and controlling the stability of prey populations by predation (Britten et al., 2014; Rooney et al., 2006). Communities affected by this reduction in size might be less stable (Blanchard et al., 2012; Rochet & Benoît, 2012), experiencing higher turnover due to faster growth rates in smaller individuals (Brown et al., 2004), and could be more sensitive to climate change (Jennings & Blanchard, 2004). However, the magnitude of the effect on overall community structure, its variability around the world, and the temporal aspect of change remains to be clarified (Booth et al., 2011)

In the attempt to characterise the impact of climatic conditions on fish community changes, many different biotic and abiotic drivers have been identified (Day et al., 2018). While the effect of temperature is well-known at large spatial and temporal scales, it might hinder other important factors shaping fish communities (Wilson et al., 2010). Major oceanographic parameters including, SST, Primary Productivity (PP), wind, Eastern Australian Current (EAC), wave height (WH), and Southern Oscillation Index (SOI), and their interactions are likely to be important drivers of fish communities in Eastern Australia. However, their impact could be expected to be variable as different eco-physiological tolerances in fish species will influence their capacity to redistribute (Fowler et al., 2018; Rijnsdorp et al., 2009). Even more so, as with such a large ecosystem, fish communities would differ substantially with latitude. Thereby, the effect and magnitude of environmental conditions on fish communities remain highly variable worldwide, and the eastern Australian communities' response remains to be clarified (Donelson et al., 2019).

Eastern Australia's tropical to temperate reefs are characterised by a long latitudinal span, composed of a gradient of ecoregions (Ridgway & Hill, 2009; Suthers et al., 2011). Deeply influenced by the Eastern Australian Current, fish communities are well connected by enhanced species dispersal (Booth et al., 2007; Fowler et al., 2018; O'Connell et al., 2022). Tropical fish larvae entrained from lower latitudes can be dispersed over many degrees polewards into temperate ecoregions (Vergés & Steinberg, 2014). However, while the EAC is capable of such dispersals, the suitability of reef conditions remains a major component for the recruitment, settlement, and survival of fishes, presumably limiting tropicalisation advances (Castro et al., 2020; Vergés et al., 2019).

In this study, I aim to evaluate the effect of climate change on fish communities, detect tropicalisation patterns, and the effects on ecosystem functioning, using fish biomass records from 2010-2023 across 33 tropical to temperate eastern Australian reefs. I first characterise the structure and temporal changes in communities' composition to assess if significant changes are detectable at the community level. I model what environmental conditions are drivers of community change and identify major assembly processes. Secondly, communities are split into trait-based functional groups and biomass evolution over time in regard to species thermal affinities is assessed for tropicalisation patterns. Lastly, a generalised additive model is applied to quantify environmental conditions contribution to the Community Thermal Index changes. Considering previous findings, latest climatic trends, and recent evolution of oceanographic conditions in eastern Australia, I expect to detect some tropicalisation patterns in fish communities. Some variations in community composition should be detectable, here hypothesised to be driven by sea surface temperatures, distance to mainland, primary productivity, and eventually SST of the previous winter (Clark et al., 2020; Horta e Costa et al., 2014). With regards to biomass change in functional groups, I expect to detect an increase in tropical-associated species biomass towards temperate regions, corresponding to a tropicalisation trend. The community thermal index can be expected to decrease with latitude, reflecting the natural temperature gradient. With tropical species progressing polewards under warming sea surface temperatures, I expect communities' thermal affinity to increase with time at similar latitudes. Characterising fish communities' tropicalisation and their drivers will be essential to better understand, predict, and protect marine ecosystems under climate change.

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Unravelling fish communities' structures in tropical to temperate reefs of eastern Australia

Adriano G. Fossati[1,2]

Supervisor

Jorge Assis[3,4]

Co-supervisor

Catherine J. S. Kim[2,5,6]

Collaborator

Maria Beger[7,8]

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[1] Faculty of Science and Technology, University of Algarve, Campus de Gambelas, 8005-139 Faro, Portugal
[2] School of Earth and Atmospheric Sciences, Queensland University of Technology, Brisbane, QLD 4000, Australia
[3] Centre of Marine Sciences, CCMAR, University of Algarve, Campus de Gambelas, 8005-139 Faro, Portugal
[4] Faculty of Bioscience and Aquaculture, Nord Universitet, Postboks 1490, Bodø, Norway
[5] Centre for Data Science, Queensland University of Technology, Brisbane, QLD 4000, Australia
[6] Resilience Centre, Queensland University of Technology, Brisbane, QLD 4000, Australia
[7] School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds LS2 9JT, UK
[8] Centre for Biodiversity Conservation Science, School of the Environment, The University of Queensland, Brisbane, QLD 4072, Australia

1. Abstract

Anthropogenic climate stress events are increasing in frequency and severity, threatening marine environments. Higher temperatures alter habitats of aquatic species, which cope by shifting their ranges poleward to more suitable conditions, referred to as tropicalisation. However, the resulting changes in species, functional group biomass, and thermal affinities are variable, with uncertainties remaining around primary drivers of change. Here, I characterise the structure and temporal changes in communities' composition, trait-based functional group biomass, and community thermal affinity. I use fish biomass records from 2010-2023 across 33 eastern Australian reefs along a tropical to temperate environmental gradient. Fish community structure is assessed using hierarchical clustering and recursive partitioning with regression trees to infer how environmental conditions (sea surface temperature, primary productivity, wave height, distance to mainland and southern oscillation index) drive the clustering structure. The main community assembly process is assessed using the Dispersal Niche Continuum Index. Functional groups are defined clustering five fish traits, whereas the surveys' Community Thermal Index is calculated by averaging the thermal mid-points of each species weighted by their mean biomass. Finally, a generalised additive model is applied to quantify the contribution of the same environmental conditions to the changes in the community thermal index. Contrary to expectations, clear tropicalisation patterns are absent at the community level, with limited changes in tropical species biomass. However, communities' thermal affinities show some increase over time at similar latitudes, suggesting a progression of some tropical species polewards, driven mainly by the harshness of the previous winter as well as distance to land and wave height. Overall, communities display a certain stability in composition, despite the domination of dispersal assembly processes. These results highlight the importance of integrating various spatial resolutions in analyses with extended time series fish biomass data to better detect, predict, and protect marine communities' alterations under global climate change.

2. Introduction

Anthropogenically driven climate change is a phenomenon undeniably increasing in recent years with serious consequences for marine ecosystems (Calvin et al., 2023; Holbrook et al., 2020; Rockström et al., 2009; Stuart-Smith et al., 2017). Suffering directly from sea surface temperatures (SST) increase, fish tend to redistribute polewards to more suitable ranges (Chen et al., 2011; Pinsky et al., 2013), a process defined as tropicalisation (Beger et al., 2014; Vergés & Steinberg, 2014; Yamano et al., 2011). With the heterogeneity in community composition of those affected zones (Rijnsdorp et al., 2009), changes will affect trophic networks, cohabitations, and whole ecosystem functioning (Miller et al., 2023; O'Connell et al., 2022; Scheffers et al., 2016; Vergés & Steinberg, 2014).

Many fish communities are at risk in eastern Australia, characterised by an important gradient of transition zones (Vergés et al., 2016). Deeply influenced by the Eastern Australian Current (EAC), fish communities are well connected by enhanced species dispersal (Booth et al., 2007; Fowler et al., 2018; O'Connell et al., 2022). Tropical fish larvae entrained from lower latitudes can be dispersed over many degrees polewards into temperate ecoregions (Vergés & Steinberg, 2014). Important trait redistributions, such as increased herbivory, seem to play a crucial role in reshaping marine communities (Zarzyczny et al., 2022). If not confined, the algal cover regulative pressure can become harmful as it happened with the expansions of tropical herbivores into temperate algal forests resulting in important deforestation (Steneck, 2020; Vergés et al., 2016; Vergés & Steinberg, 2014). In the same region, planktivores were found not shifting poleward with a biomass decline across all thermal affinities, drastically altering pathways of ecologically important energy flows (Truong et al., 2017). With recent ocean warming, various studies highlighted a progression towards structurally simplified habitats, simplifying in return the trait structure and trophic chain of fish communities (Bosch et al., 2022; Rijnsdorp et al., 2009; Silva et al., 2023). However, changes within communities in trait composition and their subsequent change in biotic interactions are not well understood, with many uncertainties still laying around the interactions with climate-mediated factors (Donelson et al., 2019; Vergés et al., 2019).

It has been recently acknowledged that functional group (FG) assignment based on species traits clustering is key to identify ecosystem functions and characterise changes in fish communities (Bellwood et al., 2019; Nyström, 2006; Reiss et al., 2009). This method not only avoids species-specific analyses but also provides a more complete evaluation of ecosystem structures and changes (Hooper et al., 2005; Hughes et al., 2017; Mouillot et al., 2014; Yeager et al., 2017). In addition, functional groups' multidimensional trait space defines the fundamental functional niche as it reflects the space where the population can be maintained (Brandl et al., 2019). This helps identify and understand the processes associated with the re-organisation of fish communities, especially from tropicalisation effects under changing biotic and abiotic conditions, which constrains the realised functional niche (Brandl & Bellwood, 2014; Díaz et al., 2013; Lavorel et al., 2008; Violle et al., 2007; Worm et al., 2006).

Fish biomass offers a powerful method to assess the ecological structure of communities, linking functional traits directly to body size, which reflects predictably a number of important ecological processes (Brown, 2014; Taylor et al., 2014; West et al., 2001). Fish biomass changes around the world seem to show variability, intrinsically linked with some differences in location and climatic conditions. Nevertheless, studies seem to agree that under anthropogenic pressures, we observe a reduction in fish size, particularly at higher trophic levels, shortening the trophic chain (Geraldi et al., 2019; Robinson et al., 2017; Seguin et al., 2023; Silva et al., 2023). Such loss of large-bodied fishes could have disproportionate effects on ecosystems as they carry key ecological roles such as bioerosion, algal growth regulation, and regulation of prey populations (Bellwood et al., 2012; Britten et al., 2014; Edwards et al., 2014; Rooney et al., 2006). Affected communities might be less stable (Blanchard et al., 2012; Rochet & Benoît, 2012), experiencing higher turnover due to faster growth rates in smaller individuals (Brown et al., 2004), and could be more sensitive to climate change (Jennings & Blanchard, 2004). However, the magnitude of the effect on overall community structure, its variability around the world, and the temporal aspects of change remains to be clarified (Booth et al., 2011)

While the effect of temperature is well-known at large spatial and temporal scales, it might hinder other important factors shaping fish communities (Day et al., 2018; Wilson et al., 2010). Major oceanographic parameters including, SST, Primary Productivity (PP), wind, EAC, wave height (WH), and Southern Oscillation Index (SOI), and their interactions are likely to be important drivers of fish communities in Eastern Australia. However, their impact could be expected to be variable as different eco-physiological tolerances in fish species will influence their capacity to redistribute (Fowler et al., 2018; Rijnsdorp et al., 2009). Even more so, as with such a large ecosystem, fish communities would differ substantially with latitude. Thereby, the effect and magnitude of environmental conditions on fish communities remain highly variable worldwide, and the eastern Australian communities' response remains to be clarified (Donelson et al., 2019).

In this study, I aim to evaluate the effect of climate change on fish communities, detect tropicalisation patterns, and the effects on ecosystem functioning, using fish biomass records from 2010-2023 across 33 tropical to temperate eastern Australian reefs. I first characterise the structure and temporal changes in communities' composition to assess if significant changes are detectable at the community level. I model environmental conditions as drivers of community change and identify major assembly processes. Secondly, communities are split into trait-based functional groups and biomass evolution over time in regard to species thermal affinities is assessed for any tropicalisation patterns. Lastly, a generalised additive model is applied to quantify the contribution of environmental conditions to the Community Thermal Index (CTI) changes. I expect to detect some tropicalisation patterns in fish communities, with some variations in community composition, here hypothesised to be driven by SST, distance to mainland, PP, and eventually SST of the previous winter (Clark et al., 2020; Horta e Costa et al., 2014). With regards to biomass change in functional groups, I expect to detect an increase in tropical-associated species biomass towards temperate regions, corresponding to a tropicalisation trend. The community thermal index can be expected to decrease with latitude, reflecting the natural temperature gradient, but increase over time at similar latitudes as tropical species progress polewards. Characterising the tropicalisation of fish communities and the environmental drivers will be essential to better understand, predict, and protect marine ecosystems under climate change.

3. Methods

Visual census fish surveys were conducted across 33 sites in eastern Australia between 2010 and 2023 during Austral summer and winter (Figure 1, Table S1). Not all sites were surveyed every year due to logistical, weather, or COVID-19 constraints. At each site, abundances and sizes of all non-cryptic reef fish species were recorded along 25 or 50 meters long per five-meter-wide belt transects at eight to ten meters deep, with three to five replicates. From the recorded fish size, the biomass B was estimated as:

Equation 1: $(B = a * fish\ size^{b})$

with the individual species' a and b morphometric parameters retrieved from FishBase (Froese & D. Pauly, 2024). To account for differences in survey transect length, number, and repetitive efforts, the data was standardized per unit of area (B/m2) (Miller et al., 2023).

Communities' clustering, environmental drivers, and main assembly processes:

I applied multi-variate cluster analysis to understand community composition and turnover, and its environmental drivers. Using the R *vegan* package (v2.6-6.1, Oksanen et al. 2024), I square-root transformed the standardised biomass to create a survey by species matrix used to compute the Bray-Curtis dissimilarities. The two latter are used with the *NbClust* package (v3.0.1, Charrad et al., 2014) to assess the optimal number of clusters using the k-means clustering algorithm to group fish communities by their similarity across the latitudinal gradient. This analysis shows whether there is a continuous turnover on the gradient (many clusters), a high community turnover between communities (few clusters), or no turnover (all communities are in one group). The contribution of ecologically relevant environmental conditions to our community clusters was assessed using recursive partitioning and regression trees with the *rpart* package (v4.1.23, Therneau & Atkinson, 2023).

The environmental variables analysed are recovered time series data at each study site's exact location or nearest available tile from E.U. Copernicus Marine Service Information (http://marine.copernicus.eu/). I obtained monthly mean data from 2010 to 2022, at ¼ grid resolution, for two abiotic variables and their respective standard deviation from the Global Ocean Ensemble Physics reanalysis (https://doi.org/10.48670/moi-00024), SST and Wave Height. I computed winter average SST from monthly means and assigned it to sites following the corresponding winter to reflect the effect of the previous winter temperatures found to be driving the structure of fish communities (Clark et al., 2020; Horta e Costa et al., 2014). In addition, I downloaded Primary Productivity with its respective standard deviation from the Copernicus Global Ocean Colour database (https://doi.org/10.48670/moi-00281) providing daily values from 2010 to 2024 at four kilometres square resolution. Daily data is averaged monthly to match the survey's occurrences. Finally, I recovered southern oscillation index values from the NOAA data platform (https://www.ncei.noaa.gov/access/monitoring/enso/soi, 08/08/24). I did not include Chlorophyll-a as it was highly correlated with PP (r=0.94, p < .001).

To assess the drivers of the distinct fish assemblage mechanisms, I used the Dispersal-Niche Continuum Index (DNCI) which provides a quantitative and comparable index that can assess whether a community assembly mechanism is niche assembly or dispersal-dominated. DNCI is based on the PER-SIMPER method (Gibert & Escarguel, 2019) that derives itself from SIMPER, a null model approach identifying the community assemblage process from the compositional similarity percentage of community groups (Clarke, 1993). PER-SIMPER

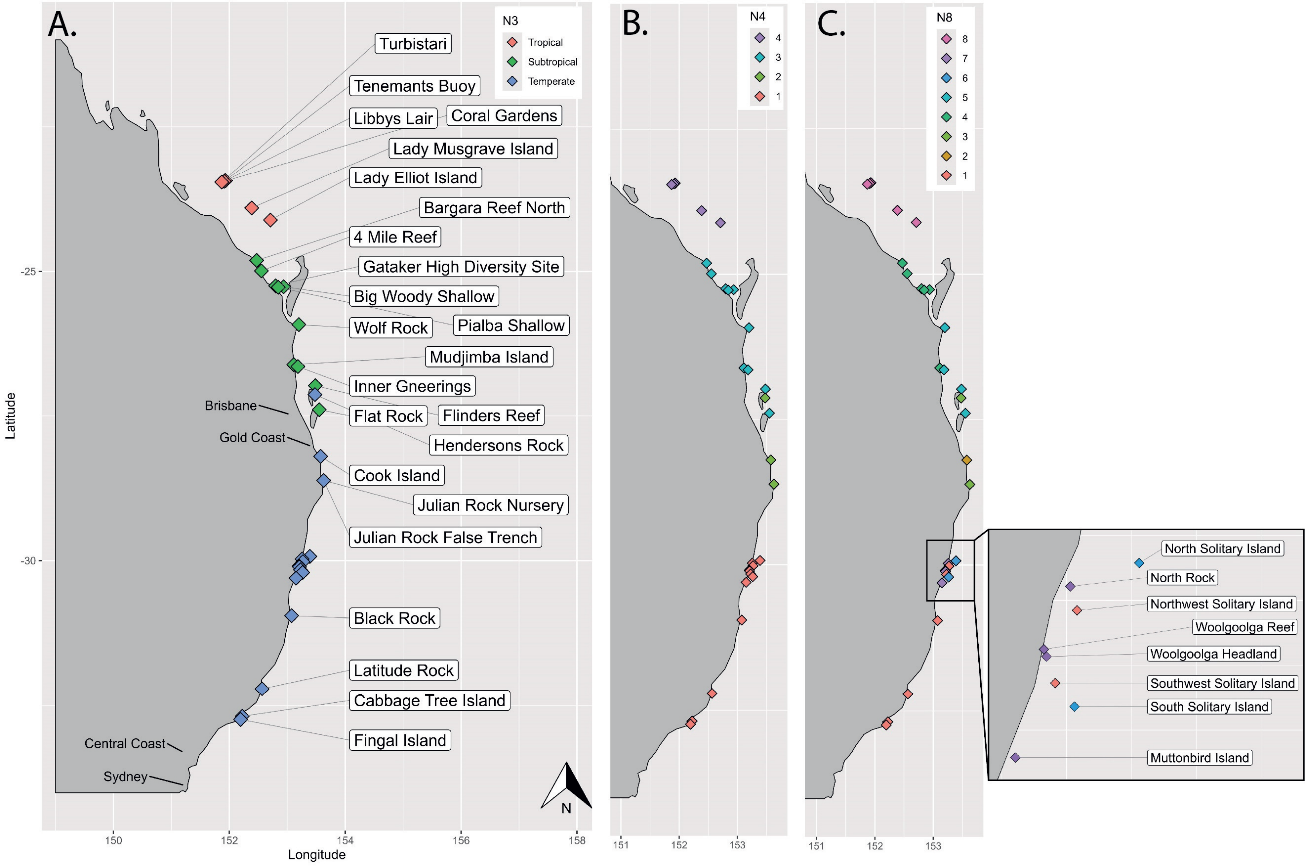

Figure 1: Maps of communities clustering result. *Fish communities (diamonds) grouped in transition zones using biomass rendered three possible clustering solutions. A) Is identified as the optimal clustering solution with three transition zones: Tropical, Subtropical, and Temperate. B) Is the second-best solution with four clusters, and C) with eight clusters.*

consists of a permutation algorithm applied to a site-by-taxa matrix, restraining sequentially the rows (niche assembly, i.e. site-specific processes dominated), columns (dispersal assembly, i.e. species-specific processes dominated), and both (joint assembly). It generates three null models that are compared to the detected empirical profile (Gibert & Escarguel, 2019). This simple comparison is limited in interpretation as it highlights only the best matching profile, but not the driving force. DNCI remediates to it by subtracting the standard effect size of the niche model metric from the dispersal model. With this new computation, the strength of assembly processes is directly quantifiable and comparable, using both presence/absence or biomass data. Positive DNCI values indicate that the biological studied community is dominated by a niche assembly, and negative ones by a dispersal, whereas high absolute values indicate a greater strength of the respective assembly process (Vilmi et al., 2021).

Trait-based functional groups:

I applied Miller et al., 2023 methodology to identify functional groups representing fundamental functional niche space of the study time span. With the *cluster* package (v2.10, Maechler et al., 2023), the Gower distance was calculated between five species' traits known to be affected by climate change and for their relevance in species effect on the ecosystem (Beauchard et al., 2017; Mouillot et al., 2014): aggregation, body size, depth range, diet, and habitat association (Table S4). Fish traits were inferred from FishBase (Froese & D. Pauly, 2024) and completed or adjusted from field observations (Anderson et al., 2022; Miller et al., 2023, Beger, unpublished data). The optimal number of functional group clusters was selected based on an inspection of the bootstrapped average silhouette. The Jaccard similarity index and Rand matching index were calculated with the *clue* package (v0.3-65, Hornik, 2023). The trait composition of each FG was visualised with word clouds, where the size of a word scales with its importance to categorise a group using the *ggwordcloud* package (v0.6.2, Le Pennec & Slowikowski, 2024).

Community thermal affinities and environmental drivers:

To quantify communities' thermal affinity change over time, I computed the Community Thermal Index for every survey (Stuart-Smith et al., 2017). The global occurrences of all 583 species were recovered from GBIF.org (https://doi.org/10.15468/dl.at9eea) using the *rgbif* package (v3.8.0, Chamberlin et al., 2024) and matched the temperature midpoint of sea surface temperatures found at their occurrences using packages *sdmpredictors* and *raster* (respectively v0.2.15, Bosch & Fernandez, 2023, and v3.6-26, Hijmans, 2023). The midpoint was chosen as it is less sensitive to species distribution across different temperature ranges (Stuart-Smith et al., 2015). Finally, I obtained the CTI per survey applying the weighted mean to the species midpoints using the respective mean biomass. This measure is a useful proxy to detect the response from communities to environmental extreme thermal conditions as it directly reflects their turnover (Burrows et al., 2019).

I referred to the environmental data previously recovered from Copernicus Marine service to assess drivers of communities' thermal affinity, building a General Additive Model (GAM) with the *mgcv* package (v1.9-1, Wood, 2011). CTI is used as a response variable, whereas monthly SST, average SST of the preceding winter (SSTWin), WH, and logged distance to mainland are used as smooth fixed effect explanatory variables. I fine-tuned the smooth effects using the *tune* package (v1.2.1, Kuhn, 2024) with all combinations of GCV.CP and REML methods, and trained the model with cross-validation using the caret package (v6.0-94, Kuhn& Max, 2008).

4. Results

Communities' transition zones, environmental drivers, and main assembly processes:

The fish communities showed distinct clustering, where the best model identified three clusters: tropical, subtropical, and temperate zones (Fig 1A), with four and eight clusters statistically identified as suitable (Fig. 1B and 1C). All solutions present as ecologically sensible given previous papers (Malcolm & Ferrari, 2019; Miller et al., 2023) and show stability with community composition being attributed to the same cluster over time, even at finer resolution with eight transition zones (Figure 1C).

The site distance to mainland is identified by the recursive partitioning and regression tree as the most relevant parameter to the clustering solution, accounting for 29.7% of the relative importance. Of smaller importance, primary productivity and wave height account for 9.7% and 9.1% of the variance, respectively, followed by SST of the preceding winter, accounting for 7.8%. Finally, together explaining 91.3% of the total variance, the monthly SST accounts for 5.3% (Fig. S2). Distance to mainland is the most relevant variable, defining the Tropical cluster with sites sitting on the outer reef of the GBR (>=47km), and the middle reef sites of the Subtropical cluster (>20km, <47km). The rest of the sites closer than 20km from shore are mainly defined by primary productivity and wave height, with Subtropical sites differing from Temperate ones by their low PP (<1065 mg m-2 day-1) in low wave height conditions (<0,83m), and their high PP (>1151 mg m-2 day-1) in high wave (>=0.83m). The Temperate cluster is completed by southern sites characterised by high wave height (>=0.83m) in low temperatures (<26°C) (Fig. S3).

I discover that the communities are mostly driven by a dispersal assembly process, with all three pairs of communities' transition zones displaying a negative DNCI value, independently of the transformation of the input data (Table 1). The pair Temperate-Subtropical zones shows the most negative index value (Presence/Absence: -73.29), indicating that it is under the highest dispersal assembly process out of the three communities clusters pairs. In contrast, the two pairs including the Tropical cluster show a similar smaller magnitude of DNCI values but are still negative (P/A: -16.75, and -14.54, respectively). This indicates that the Tropical communities are indeed under a dominating dispersal assembly process but are more under the effect of the niche assembly process than the Subtropical and Temperate communities.

Table 1: Dispersal Nice Continuum Index (DNCI) summary table*. DNCI and confidence intervals present the comparison by pairs of study site clusters for each combination of data entry: Biomass per meter square, logarithmic transformation of the B/m^2, and data transformed in presence-absence format. Negative DNCI values indicate a domination of the dispersal assembly process, whereas positive DNCI values indicate a niche assembly dominating process behind community dissimilarities among site clusters. The magnitude of the absolute values corresponds to the strength of the dominating process. DNCI values close to zero indicate a similar effect of both dispersal and niche assembly processes on the distributions.*

Pair of clusters		**B/m^2**		**log10(B/m^2)**		**P/A**	
Sites 1	Sites 2	DNCI	CI.DNCI	DNCI	CI.DNCI	DNCI	CI.DNCI
Temperate	Subtropical	-2090.18	284.90	-17.27	1.44	-73.29	2.14
Temperate	Tropical	-972.87	785.44	-13.42	2.23	-16.75	1.29
Subtropical	Tropical	-527.69	88.34	-10.22	2.16	-14.54	1.80

Trait-based functional groups biomass:

I classify fish communities of the eastern Australia Tropical to Temperate gradient in the eight most represented functional groups containing 87% of the study fish species (an additional 19 rarer FG complete the communities). Diet accounted for most of the influence on clustering, driving for 78.6% (from the multinomial random forest, Darling et al., 2012) of the delimitations in FGs, with depth range (9.1%), aggregation (7.3%), habitat association (3.1%), and body size (1.9%) contributing far less. Word clouds visualise the trait characterisation of each functional group. Notably, similar diet can be found in different FGs, highlighting the importance of the traits clustering when looking at ecosystem functioning as various functions can be displayed within a trait (Fig. 2C). The dominance of thermal guilds in each region follows an expectable pattern, with subtropical and temperate species dominating the southern sites and tropical species being more abundant in low latitudes for most of the functional groups. The biomass evolution over time does not follow a tropicalisation pattern, with the biomass of most FG thermal guilds staying stable, particularly in Temperate communities (Fig 2A). This is to the exception of the biomass of tropical species in the FG15 which seems to increase in all three clusters, with FG5 and FG21 showing the same trend but only in the Subtropical sites. Moreover, these increases are linked with decreases in the biomass of subtropical and temperate species. Temperate species even ceases to be detected in the surveys of Subtropical sites after 2013 in both FG3 and FG21. This all suggests some sort of tropicalisation signal with a progression of some species polewards despite a general stable trend.

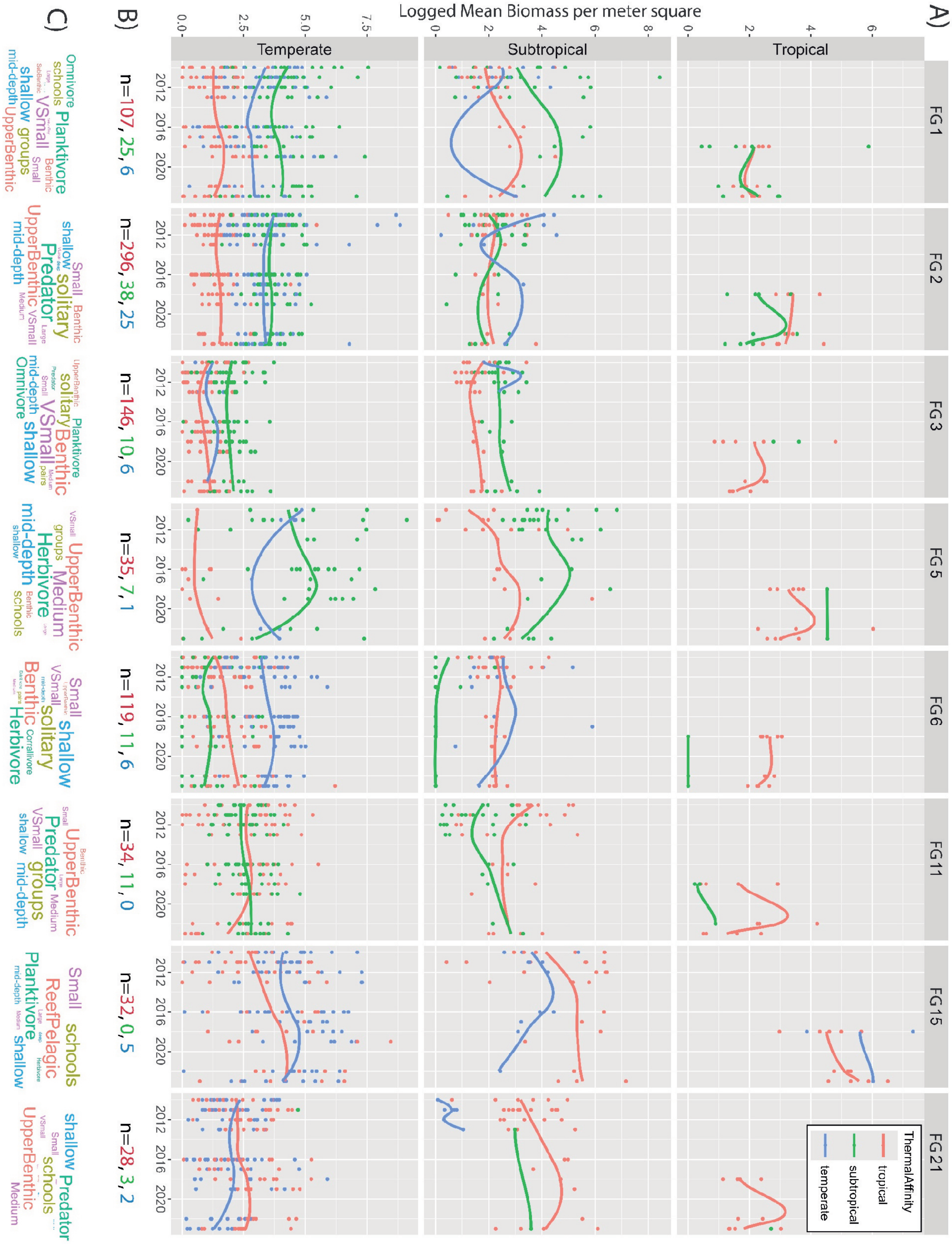
A)
Logged Mean Biomass per meter square
Tropical
Subtropical
Temperate
0
2
4
6
8
0.0
2.5
5.0
7.5
FG 1
FG 2
FG 3
FG 5
FG6
FG11
FG15
FG21
2012
2016
2020
ThermalAffinity
tropical
subtropical
temperate
B)
n=107, 25, 6
n=296, 38, 25
n=146, 10, 6
n=35, 7, 1
n=119, 11, 6
n=34, 11, 0
n=32, 0, 5
n=28, 3, 2
C)
Omnivore Planktivore schools VSmall Small Benthic shallow groups mid-depth UpperBenthic
Small Benthic shallow solitary Predator Large UpperBenthic VSmall mid-depth Medium
UpperBenthic Planktivore Predator solitary Small VSmall Benthic mid-depth Medium pairs Omnivore shallow
VSmall UpperBenthic groups Medium Herbivore mid-depth Benthic shallow schools Large
Small UpperBenthic shallow VSmall mid-depth solitary Benthic pairs Corrallivore Herbivore Medium
Small Benthic UpperBenthic Large Predator Medium VSmall groups shallow mid-depth
Small schools ReefPelagic Large Herbivore Planktivore mid-depth Medium Shallow
shallow Predator VSmall Small schools UpperBenthic Medium

Figure 2: Change in Functional Groups' biomass over time in each transition zone. *A) Eight most represented Functional Groups logged Mean Biomass per meter square change over time facetted in transition zones and divided by thermal affinity guilds of Tropical species (red), Subtropical (green), and Temperate (blue). Loess smooth lines (span = 1) visualizing FGs biomass evolution are fitted on all the data. B) Number of species per thermal affinity guilds for each functional group (same colour code as smooth lines). C) Word clouds defining traits characteristics of functional groups, with the size of words showing the relative importance of a trait, and colours denoting traits: diet = cyan, habitat association = red, body size = pink, aggregation = green, depth range = blue, parental mode = brown.*

Community thermal affinities and environmental drivers:

There is an increase in thermal affinities represented by the CTI across most of the sites over time up to about 1°C (Table 2). In addition, the CTIs are decreasing with an increase in latitude, reflecting the temperature gradient along the coast of Australia. Some variability is detected around the Solitaries Islands and the latitudinal CTI gradient does not exactly match this gradient anymore. North and South Solitary Islands display the highest increase of CTI over time in the region. They are also the furthest from mainland, sitting on the outer reef (Fig. 1). Closest to land, North Rock, Woolgoolga Reef and Headland, all display lower CTI increase over time in the Solitaries, with Northwest and Southwest Solitary Islands having an intermediate CTI increase, witting on the middle reef. Thus, it seems there is an offshore increasing gradient in CTI around the Solitaries Islands.

Table 2: Community thermal index for every study survey over time. *Sites are organized latitudinally. Summer and winter surveys of the same site are highlighted in between two thicker horizontal black lines. Colors illustrating CTI values from lower (green) to higher (red).*

Surveys	**2010**	**2011**	**2012**	**2013**	**2016**	**2017**	**2018**	**2019**	**2022**	**2023**
Tenemants Buoy Win	NA	NA	NA	NA	NA	NA	24.9	NA	NA	25
Libbys Lair Win	NA	NA	NA	NA	NA	NA	26.5	NA	26.4	26.1
Coral Gardens	NA	NA	NA	NA	NA	NA	NA	NA	26.5	26.7
Turbistari Win	NA	NA	NA	NA	NA	NA	26.5	NA	26.4	26.3
Lady Musgrave Win	NA	NA	NA	NA	NA	NA	26.4	NA	NA	NA
Lady Elliot Island Win	NA	NA	NA	NA	NA	NA	24.6	NA	NA	NA
Bargara Reef North Win	24.5	NA	NA	NA	NA	NA	NA	NA	NA	NA
4 Mile Reef Win	25.9	NA	NA	NA	NA	NA	NA	NA	NA	NA
Gataker High Diversity Site Win	24.5	NA	NA	NA	NA	NA	NA	NA	NA	NA
Big Woody Shallow Win	25.8	NA	NA	NA	NA	NA	NA	NA	NA	NA
Pialba Shallow Win	24.5	NA	NA	NA	NA	NA	NA	NA	NA	NA
Wolf Rock Sum	NA	24.2	NA	NA	NA	NA	NA	NA	NA	NA
Wolf Rock Win	24.9	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mudjimba Island Shallow Win	NA	24.6	NA	NA	NA	NA	NA	NA	NA	NA
Mudjimba Island Sum	NA	23.5	NA	24.1	NA	NA	NA	NA	NA	NA
Mudjimba Island Win	23.8	23.2	24	NA	NA	NA	NA	NA	NA	24.4
Inner Gneerings Sum	NA	25.1	25.7	23.2	NA	NA	NA	NA	NA	NA
Inner Gneerings Win	NA	22.5	23.9	NA	NA	NA	NA	NA	NA	24.1
Flinders Reef Sum	NA	24.6	25.3	24.9	24.7	NA	NA	NA	NA	NA
Flinders Reef Win	24.3	24.7	25.5	NA	25	23.1	24.5	26.5	26.2	25.6
Hendersons Rock Sum	NA	22.4	NA	NA	NA	NA	NA	NA	NA	NA
Flat Rock Sum	NA	23.9	NA	NA	NA	NA	NA	NA	NA	NA
Flat Rock Win	23.7	NA	NA	NA	NA	NA	NA	NA	NA	25.3
Cook Island Sum	NA	21.7	22.1	21.7	22.1	NA	NA	NA	NA	NA
Cook Island Win	22.1	22	21.9	NA	22.3	22.4	23.4	22	NA	22.2
Julian Rock Nursery Sum	21.7	22.4	22	21.7	22.2	NA	NA	NA	NA	NA
Julian Rock Nursery Win	21.1	20.6	21	NA	NA	NA	22.3	23	23.6	24.9
Julian Rock False Trench Sum	NA	21.8	NA	NA	21.6	NA	NA	NA	NA	NA
Julian Rock False Trench Win	21.3	NA	NA	NA	NA	NA	NA	NA	21.9	22.9
North Solitary Island Sum	21.9	22.3	22.5	22.6	23.1	NA	NA	NA	NA	NA
North Solitary Island Win	22.5	21.9	21.1	NA	21.3	22.1	22.8	23.3	22.4	22.9
North Rock Sum	NA	NA	NA	NA	20.8	NA	NA	NA	NA	NA
North Rock Win	21.5	NA	NA	NA	20.6	NA	NA	NA	20.7	21.6
Northwest Solitary Island Sum	20.8	NA	22.2	21.2	21.1	NA	NA	NA	NA	NA
Northwest Solitary Island Win	21.2	21.6	21.1	NA	20.7	21.8	20.3	20.5	20.7	21.5
Woolgoolga Reef Sum	NA	NA	NA	NA	20.5	NA	NA	NA	NA	NA
Woolgoolga Reef Win	NA	NA	NA	NA	21.2	20	NA	NA	NA	20.9
Woolgoolga Headland Sum	NA	NA	NA	NA	20.8	NA	NA	NA	NA	NA
Woolgoolga Headland Win	22.3	NA	NA	NA	20.4	20.4	NA	NA	20.5	NA
Southwest Solitary Island Sum	21	20.7	19.6	19.7	21.2	NA	NA	NA	NA	NA
Southwest Solitary Island Win	20.9	21.6	21.4	NA	20	20.8	20.1	21.4	22.6	21.6
South Solitary Island Sum	NA	21	NA	NA	21.9	NA	NA	NA	NA	NA
South Solitary Island Win	NA	NA	NA	NA	21.6	22.6	21.8	21.3	20.8	23.9
Muttonbird Island Win	NA	19.2	NA	NA	NA	NA	NA	NA	NA	NA
Black Rock Sum	20.7	21.4	20.4	20.7	NA	NA	NA	NA	NA	NA
Black Rock Win	21.7	20	19.8	NA	NA	21.4	21.8	22.3	21	20.9
Latitude Rock	NA	20.8	NA	NA	NA	NA	NA	NA	NA	NA
Cabbage Tree Island Sum	NA	20.3	NA	NA	NA	NA	NA	NA	NA	NA
Fingal Island Sum	NA	20.6	NA	NA	NA	NA	NA	NA	NA	NA

The GAM explains for 63% of the data variability (Table 3). The community thermal index almost increases by one unit for each additional degree in the preceding winter average SST (slope = 0.94, p value = < .001). Distance to mainland is also positively driving CTI, with an approximate increase by one degree every 15km offshore (logged in the model, slope = 2.69, p value = <.001, $e^{2.69}$ = 14.731km). With an increase in wave height, the CTI decreases (slope = - 4.41, p value = < .001) (Table 3). The sea surface temperature and the primary productivity of the survey month do not significantly impact the CTI in the GAM.

Table 3: General additive Model (GAM) summary. *CTI was used as our response variable with SST, SST of the preceding winter, wave height, logged distance to mainland and PP as our response environmental variables fitted as smoothed fixed effects.*

Component	**Term**	**Estimate**	**Std Error**	**t-value**	**p-value**	
A. parametric coefficients	(Intercept)	22.389	0.095	234.480	0.0000	***
B. smooth terms	s(DisLandLog)	2.696	3.405	25.780	0.0000	***
	s(SSTWint)	0.945	1.000	15.796	0.0001	***
	s(WaveHeight)	- 4.408	5.593	7.494	0.0000	***
	s(SST)	0.001	1.001	0.002	0.9756	
	s(PP)	0.583	2.992	0.928	0.4119	

Signif. codes: 0 <= '***' < 0.001 < '**' < 0.01 < '*' < 0.05

Adjusted R-squared: 0.618, Deviance explained 0.630

5. Discussion

There is evidence of tropicalisation of fish species in eastern Australia in the last 14 years based on increasing community thermal affinities (Table 2). However, at the community level the clustering shows a clear Tropical, Subtropical, and Temperate transition zones clustering indicating that are stable through time (Fig. 1). Under climate change, tropicalisation of fish communities should lead to a poleward increase in biomass of tropical associated species (Miller et al., 2023; Vergés et al., 2016; Vergés & Steinberg, 2014). Here, in contrast, there are limited changes in biomass with only a few functional groups following this expectation (Fig. 2). This highlights the variability of responses from fish communities to climate change and the difficulty of capturing clear trends within the natural variations.

Community structure and assembly processes stability over out study time:

At the community level, transition zone delimitation is constant over time suggesting stable community compositions. The drivers of this community clustering correspond to previous studies of major latitudinal gradients, identifying the distance from land as a main driver of fish community compositions (Dubuc et al., 2023; Patterson & Swearer, 2007). Even more so in eastern Australia with the EAC impacting biotic conditions predominantly of outer reefs (Booth et al., 2007; Ridgway & Hill, 2009; Suthers et al., 2011). Supported by previous studies (Booth et al., 2011; Fowler et al., 2018; O'Connell et al., 2022), this major current seems to have a dispersal impact on all our three transition zones' broader structure, as highlighted by negative DCNI values. The dispersal assembly process is generally common between communities at this geographic scale, especially with an important environmental heterogeneity between zones (Arellano et al., 2016; Ford & Roberts, 2018; Jones et al., 2006). However, the EAC is particularly important for larvae dispersal, playing a major role in the survival and adaptability of fish species (Castro et al., 2020; Patterson & Swearer, 2007; Vergés et al., 2019). Dispersal is key indeed, but for some long-term settlement, suitable environmental conditions, and moreover, suitable habitat is necessary (Harriott & Banks, 2002; Nakamura et al., 2013).

The latitudinal span of the sites displays clear transition zones characterised by different habitat conditions. Highlighted by higher DNCI values, the Tropical communities show more influence from the niche assembly process than the Subtropical and Temperate, which suggests they consist of a different environment than the southernmost clusters. This corresponds to the habitat characteristics gradient of eastern Australia with Tropical regions displaying heterogenous benthic cover with coral reefs, whereas Subtropical and Temperate reefs display more turf mat reefs, rocky-dominated reefs, and kelp forests (Castro et al., 2020). Thus, tropical habitat specialist species might be unable to find suitable reefs in more temperate regions, preventing their polewards tropicalisation (Stuart-Smith et al., 2021).

Lack of clear functional group biomass change at the community level:

To aim for a more complete ecosystem understanding, analyses based on ecosystem functioning are key (Hughes et al., 2017; Mouillot et al., 2014; Reiss et al., 2009; Yeager et al., 2017). In that regard, I identified functional groups sharing similar ecological functions by clustering major fish traits. The biomass of FGs shows little to no change over time in most of the thermal guilds and transition zones (Fig. 2). This is particularly the case in the Temperate cluster, which also encompasses most sites (n=16). Some site-specific biomass changes or finer scale competition might be masked as the identity of functional groups changes through environmental filtering with latitude (Kingsbury et al., 2020; Sommer et al., 2014). Unexpectedly, most of the FGs in Tropical sites seem to have experienced a decline in biomass from 2022 to 2023. This eventually could be linked with the mass coral bleaching in 2022 that affected mostly the central GBR, and the variable regional consequences of such event on fish communities (Graham et al., 2007; Richardson et al., 2018; Vessaz et al., 2022; Wismer et al., 2019). The recent and short time frame of survey effort in Tropical sites (2018 to 2023) must be acknowledged, making it difficult to detect longer-term clear biomass trends. The short time frame and small sample size also make it more sensitive to outliers such as a single medium-sized temperate species (*Kyphosus sydneyanus*) in FG15 accounting for most of the biomass variation in the tropical region. Additional surveys in the tropical sites will identify if this biomass decline was a singular event due to climatic perturbations, or if the fish communities are recovering. Only FG5, FG15, and FG21 seem to show some detectable increase in tropical species in the Subtropical region. They are characterised by respectively, medium-sized upper benthic herbivores, schools of small reef pelagic planktivores, and schools of predators in the upper benthic. Those FGs cover a wide range of ecological functions, further supporting the variability of response from fish communities to climate change. In addition, species reaction to variable climatic effects would be species-specific, which could mask tropicalisation patterns in functional groups biomass.

Communities' thermal affinities affected by climatic conditions:

There is a clear decrease in community thermal index with latitude (Table 2). This latitudinal gradient corresponds to the expectation as the CTI directly reflects the thermal affinity of community species (Burrows et al., 2019). With higher temperatures up north, species would display a higher thermal affinity, resulting in a higher index. Notably, the CTI seems to increase in most of the sites over time, suggesting that a polewards redistribution of species in response to changing environment is indeed happening despite some stability at the community level. This tropicalisation is not driven by the current month SST but rather by the preceding winter conditions. It is indeed unlikely that temperatures within the same months would drive species distribution as dispersal and redistribution would take time. This finding is supported by previous studies that highlighted the harshness of the winter as a major limitation factor from tropical species' poleward expansion, rather than an assistance from mild summers (Buyse et al., 2022; Henriques et al., 2007; Horta e Costa et al., 2014). Distance to mainland is also found to be significantly positively affecting CTI, which corresponds to the anticipated ecological impact of the EAC, increasing temperature, and affecting dispersal (Dubuc et al., 2023; Ridgway & Hill, 2009). Wave exposure and height are considered to be important factors shaping assemblages of reef fish communities as they affect species swimming capacities and energy supply (Bellwood & Wainwright, 2001; Floeter et al., 2007; Nunes et al., 2013; White & Warner, 2007). Thus, wave exposure is believed to affect the composition of communities, shaping survival by predation, and energetical limitations. In my general additive model, I observe a significant decrease in the thermal affinity of communities with an increase in wave height, possibly highlighting that tropical-associated species prefer sheltered reefs.

Despite our satisfactory and expected CTI trends, the resolution of the thermal affinity detection could be further improved. Indeed, the GBIF database contains some bias in measurements and a very broad resolution. Alternative databases such as Reef Life Surveys, with good coverage and higher resolution in Eastern Australia, could further improve our understanding of the community thermal affinity changes.

My study identifies some indications of stability in community structures and compositions over 14 years in eastern Australia. Whereas this is due to our choices of analyses, or if there is indeed some stability in the communities in our time frame remains to be elucidated in further studies. Species re-distributions effectively increasing CTI over time do not clearly reflect in FG biomass changes, eventually caused by a lack of sensitivity due to FGs large species numbers. With winters becoming milder and milder due to climate change, tropical-associated fish species will be able to survive at higher latitudes, altering ultimately the structure of communities. This highlights the major implications future climate change could have on fish communities, with a massive poleward expansion of tropical-associated species altering temperate ecosystems. The effects of such species distribution changes remain to be clearly unravelled to understand the implications for ecosystems functioning and plan adequate measures of conservation.

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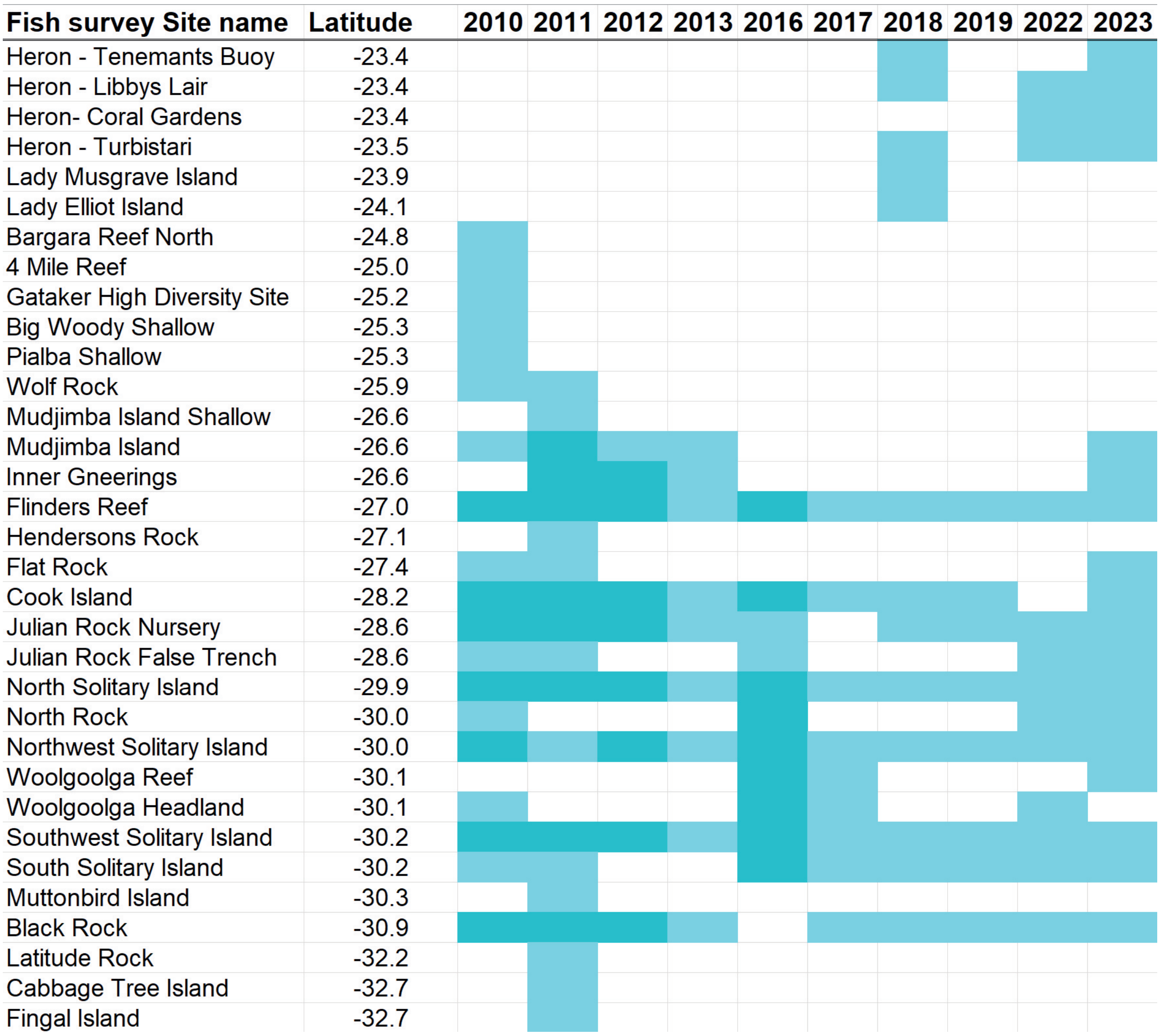
7. Supplementary material:

Table S1: Surveying effort every year per study site. Light blue represents one survey during that year. Dark blue represents two. Sites are organized latitudinally.



Fish survey Site name	Latitude	2010	2011	2012	2013	2016	2017	2018	2019	2022	2023
Heron - Tenemants Buoy	-23.4							▨			▨
Heron - Libbys Lair	-23.4							▨		▨	▨
Heron- Coral Gardens	-23.4									▨	▨
Heron - Turbistari	-23.5							▨		▨	▨
Lady Musgrave Island	-23.9							▨			
Lady Elliot Island	-24.1							▨			
Bargara Reef North	-24.8	▨									
4 Mile Reef	-25.0	▨									
Gataker High Diversity Site	-25.2	▨									
Big Woody Shallow	-25.3	▨									
Pialba Shallow	-25.3	▨									
Wolf Rock	-25.9	▨	▨								
Mudjimba Island Shallow	-26.6		▨								
Mudjimba Island	-26.6	▨	■	▨	▨						▨
Inner Gneerings	-26.6		■	■	▨						▨
Flinders Reef	-27.0	■	■	■	▨	■	▨	▨	▨	▨	▨
Hendersons Rock	-27.1		▨								
Flat Rock	-27.4	▨	▨								▨
Cook Island	-28.2	■	■	■	▨	■	▨	▨	▨		▨
Julian Rock Nursery	-28.6	■	■	■	▨	▨		▨	▨	▨	▨
Julian Rock False Trench	-28.6	▨	▨			▨				▨	▨
North Solitary Island	-29.9	■	■	■	▨	■	▨	▨	▨	▨	▨
North Rock	-30.0	▨				■				▨	▨
Northwest Solitary Island	-30.0	■	▨	■	▨	■	▨	▨	▨	▨	▨
Woolgoolga Reef	-30.1					■	▨				▨
Woolgoolga Headland	-30.1	▨				■	▨			▨	
Southwest Solitary Island	-30.2	■	■	■	▨	■	▨	▨	▨	▨	▨
South Solitary Island	-30.2	▨	▨			■	▨	▨	▨	▨	▨
Muttonbird Island	-30.3		▨								
Black Rock	-30.9	■	■	■	▨		▨	▨	▨	▨	▨
Latitude Rock	-32.2		▨								
Cabbage Tree Island	-32.7		▨								
Fingal Island	-32.7		▨								

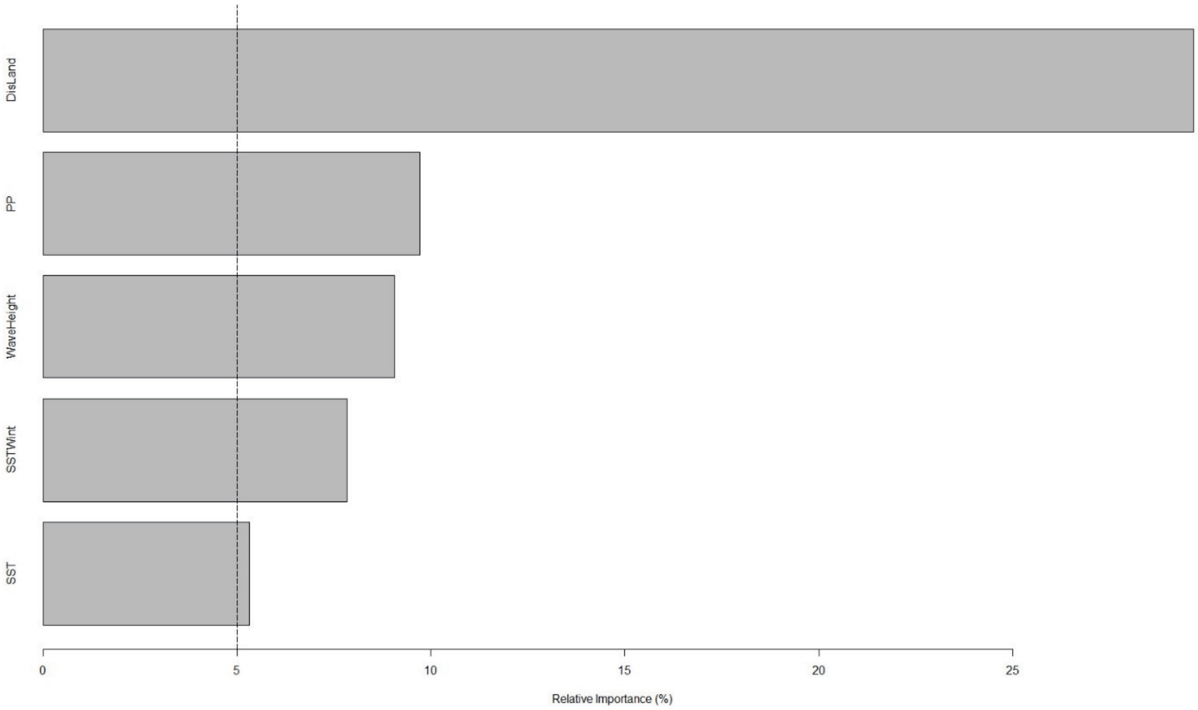


Figure S2: Environmental variables relative contribution in percentage to communities clusters delimitation.

Figure S3: Regression tree of environmental variables clusters decision.

Table S4: Fish species trait definition.

Trait (type)	Trait level	Definition
Body Size (continuous)	4.4 - 450	Maximum tail length recorded in the core range, in cm
Depth range (continuous)	3 – 200	The difference between the deepest and shallowest depths at which a species occurs, in m
Diet (categorical)	Piscivore	Feed on other fishes
	Predator	Predates on a range of animals including macro/microfauna predators
	Planktivore	Feeds on phyto- and/or zooplankton
	Omnivore	Feeds on a mix of flora and fauna
	Corallivore	Obligate corallivore, feeding on scleractinian or octo corals
	Herbivore	Feeds exclusively on plants, includes grazers, farmers, scrapers, and browsers
	Detritivore	Feeds on detritus and plants
Aggregation (ordinal)	Schools	Tends to form schools
	Groups	Usually seen in small groups of 3 to 10 individuals
	Pairs	Typically occur in pairs
	Solitary	Solitary
Position (categorical)	Pelagic	Pelagic species who occasionally venture near a reef
	Reef pelagic	Pelagic fast swimmers that move well above the reef, but typically found near to a reef
	Upper Benthic	Mobile and changeable distance away from the benthos but with substantial associating with the reef matrix
	Benthic	Living closely associated with the benthic substrate, or swimming within a few cm of the bottom
	Demersal	Living on benthic substrate, usually lying on it
	Sub-benthic	Living within crevices, caves, or holes within the reef matrix