Dahlstroem, Ebba (2024) ***Species habitat use and functional diversity of clear-water mangrove habitats in north Queensland: how environmental conditions impact fish assemblages.*** **Masters (Research) Thesis, James Cook University.**

Access to this file is available from:
https://doi.org/10.25903/cm3e%2D6g87

Species Habitat Use and Functional Diversity of Clear-water Mangrove Habitats in north Queensland: How Environmental Conditions impact Fish Assemblages

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B.Sc., Science

Submitted in October 2024
For the degree of Master of Philosophy
In the College of Science and Engineering
James Cook University

Acknowledgements

I would like to express my gratitude to my primary supervisor, A. Prof. Nathan Waltham, and my secondary supervisor, Prof. David Bellwood, for their guidance, support, and encouragement throughout the course of my research. I also wish to acknowledge the support of James Cook University and Orpheus Island Research Station, where I conducted my field work. Their contribution has been vital to the completion of this research. I especially wish to thank Bec Tite, the station officer at OIRS at the time of my research, for her support and help with organizing my field work. I also want to thank my numerous volunteers, which made my field work both possible and enjoyable, and who put in many long hours snorkelling in, and wading through, mangrove forests to support my research. They also provided many good discussions, streamlining the field work and the data collection.

Lastly, I am very grateful to my partner, Remi Heraud, whose unwavering belief in me has provided continuous strength and encouragement. Remi's understanding has been invaluable throughout this journey, and I am eternally thankful for his constant support. I am also immensely grateful to my parents, Asa Nilsson Dahlstroem and Henrik Dahlstroem, for their unconditional support and for always encouraging me to pursue my dreams, no matter the obstacles.

I respectfully acknowledge the Traditional Owners of the lands on which this research was conducted. I pay my respects to the Bindal and Wulgurukaba Peoples of the Townsville area, and the Manbarra People of Orpheus Island. I honour their Elders past, present, and emerging, and recognize their continuing connection to land, sea, and community.

Habitat Use and Functional Diversity of Clear-water Mangrove Habitats in north Queensland

Statement of the Contribution of Others

Supervision	*Supervision*	*A.Prof. Nathan Waltham, Prof. David Bellwood*
Intellectual support	*Field work support*	*Bec Tite*
Financial support	*Research grant* *Field work*	*OIRS Morris Family Trust SRG* *A.Prof. Nathan Waltham*
Data collection	*In-field volunteers*	*Remi Heraud* *Samantha Crisp* *Lachlan Drane* *Cameron Owens-Gale* *Atlanta Simutanyi* *Tarryn O'Leary* *Ashley Scarlett Luke* *Sam Grierson* *Axel Broman*
Data collection	*Use of equipment*	*A.Prof. Nathan Waltham*

Habitat Use and Functional Diversity of Clear-water Mangrove Habitats in north Queensland

Abstract

Clear-water mangroves, characterised by their proximity to coral reefs and minimal terrestrial input, play a crucial role in the coastal ecosystem mosaic (CEM). However, research on these ecosystems, particularly in the Indo-Pacific, is limited compared to studies conducted in the Caribbean. The principal objectives of this study were to investigate the spatial and temporal patterns influencing fish community structure and utilisation within these mangroves, and to challenge existing paradigms such as the nursery habitat theory, which has largely been established based on previous research completed in Caribbean mangrove ecosystems.

The methodology employed in this research comprised the use of remote underwater videos (RUVs) deployed along six sites at Orpheus Island, Australia, to capture the presence, behaviour, and size structure of fish species occupying mangrove areas surrounding the island. These recordings, taken over multiple field trips, provide a comprehensive view of how different environmental factors, such as tidal regime (rising or falling), water depth (sorted into six depth levels, ranging from a few cm to >2 m), season (wet or dry), and substrate type (sand, mixed or rock), influence the composition of fish communities within the clear-water mangrove habitat. High-frequency water level data loggers deployed in the mangroves recorded the semi-diurnal tides defining clear-water mangrove habitat availability to fish.

The primary analysis involved a permutational multivariate analysis of variance (PERMANOVA), which was used to test the significance of the effects of environmental variables such as tidal regime, water depth, substrate type, and season on the composition of fish communities. To further investigate the ecological functions within the clear-water mangrove habitat, the study focused on multivariate functional diversity, which goes beyond species diversity by examining the roles species play within the ecosystem, and the relation between environmental variables and functional traits through RLQ, fourth-corner and Random Forest analyses. Functional traits were selected to represent various ecological roles, and these traits were used to calculate the functional diversity indices functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv). These indices provide a comprehensive picture of how species utilise available resources and how evenly those resources are distributed across the community.

The PERMANOVA results indicated that substrate type ($p < 0.01$) and season ($p < 0.01$) were significant factors shaping the fish assemblages within the mangroves. Sites with rock substrate exhibited higher species diversity and abundance compared

to sand substrates, and the dry season exhibited higher taxonomic and functional diversity than the wet season. Juvenile utilisation was significantly associated with sand substrate, as there may be more feeding opportunities and ability to migrate into the forest along a sloping gradient before larger predators can access the mangrove forest.

One of the contributions of this research is its challenge to the nursery habitat hypothesis, which posits that mangroves are critical nursery grounds for juvenile fish. The findings from Orpheus Island suggest a more complex picture, where the clear-water mangroves appear to function as transitional habitats, facilitating connectivity between coral reefs and other coastal environments. This is indicated by the high proportion of reef-associated species and the observation that many species utilise the mangroves at different life stages, for instance as small adults and not just as juveniles. Additionally, the study indicates that the possible role of Indo-Pacific clear-water mangroves as juvenile habitats is species-specific and context-dependent, influenced by factors such as substrate type, seasonality and depth.

This study showed that rays (Batoidea) shape the functional diversity of Indo-Pacific clear-water mangroves, particularly within sand substrates. Rays, characterised by their large body size and benthic feeding habits, occupy unique trophic niches not found in rock substrates. Their presence drives higher functional richness and divergence, as they fill ecological roles that are not easily replaced by other species. Excluding rays from the analysis led to a more homogenised trait space, particularly in the sand substrates, indicating their crucial role in contributing to complexity and resilience.

The sand substrate exhibited higher functional richness due to species belonging to the Batoidea, which were present at the edges of the trait space, contributing to greater functional richness and divergence. These species, along with smaller estuarine-associated planktivores, illustrate how environmental filtering supports species with distinct feeding strategies. In the clear-water mangroves with rock substrates, species were more evenly distributed within the trait space. The exclusion of rays from the functional diversity analysis reduced the functional richness in sand substrates, while having less impact on the rock substrate, emphasising the specialised ecological roles rays occupy in these environments. The study highlights the importance of preserving species that increase functional diversity and, by extension, ecosystem resilience. Their loss could reduce the ability of these ecosystems to maintain functionality, particularly under changing environmental conditions. The study also found complex relationships between environmental

variables and functional traits, indicating the substrate type and depth affect the size, size ratio and trophic level of the individuals present in the forest. The findings were in line with the foraging and refugia hypothesis, and found sand substrate to be associated with smaller and younger individuals with higher trophic levels.

The conclusions from this study emphasise the importance of clear-water mangroves as multifunctional habitats within the CEM. These habitats contribute to the biodiversity and ecological resilience of the region, supporting a diverse array of species by providing various ecological functions such as refuge, foraging grounds, and facilitating ontogenetic migrations. This study highlights the need for a more nuanced understanding of habitat use in clear-water mangrove ecosystems, particularly in the Indo-Pacific, where the environmental conditions differ from those in the Caribbean. It has important implications for the management and conservation of coastal ecosystems in the Indo-Pacific, and the findings suggest that conservation strategies should account for the unique traits, ecological roles and microhabitats within clear-water mangroves. Specifically, the study argues for a shift towards ecosystem-based management that recognise the interconnectedness of clear-water mangroves as part of broader habitats in the coastal mosaic. By protecting the entire seascape, rather than focusing on individual habitats, conservation efforts can better support the ecological functions and biodiversity of these critical environments.

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1. General Introduction

The coastal ecosystem mosaic (CEM) describes the interconnectedness of habitats within a seascape, which enables the utilisation of different resources by organisms (Sheaves, 2009). Among these habitats, intertidal mangrove forests link terrestrial, coastal and marine environments (Nagelkerken et al., 2008; Sheaves et al., 2024). However, research on mangrove forests in the Indo-Pacific region is faced with two challenges: firstly, studies conducted in the Caribbean are often used as a reference, despite notable dissimilarities between the two regions (Gillanders et al., 2003; Nagelkerken, 2007; Nagelkerken, 2009a; Semenuik & Cresswell, 2018; Stuthmann et al., 2022). Secondly, the existing research often focuses on the ecological benefits of mangroves for other habitats, such as fish population recruitment to coral reefs, rather than specifically examining the mangrove habitat in and for itself (Jones et al., 2010; Kulbicki et al., 2022; Martin et al., 2015; Nagelkerken, 2007; Paillon et al., 2013). As mangrove forests today are facing numerous threats, and the management and conservation of habitats in the seascape more often is focused on coral reefs, this study aims to highlight the importance of an often-overlooked habitat. Deforestation driven by urban expansion, agriculture, and aquaculture leads to the loss of these critical habitats, disrupting the complex web of life that depends on them (Abrantes et al., 2015). Additionally, pollution, climate change, and rising sea levels expedite the degradation of mangrove ecosystems, diminishing their capacity to act as natural buffers against coastal erosion (Sheaves et al., 2016). The loss of mangrove forests has far-reaching consequences, including a decline in biodiversity, particularly among species that are uniquely adapted to these environments (Magneville et al., 2022). The reduction in mangrove coverage not only threatens the species that inhabit and utilise these areas but also undermines the ecosystem services that support coastal communities and protect marine environments.

The results from studies conducted in the Caribbean establish a paradigm of high productivity and functionality of mangrove forests, but the paradigm cannot be readily translated to Indo-Pacific ecosystems due to substantial variations in environmental conditions, habitats, and species composition (Semenuik & Cresswell, 2018). Notably, most mangrove habitats investigated in the Caribbean are marine or clear-water mangroves, which are characterised by their proximity to coral reefs and minimal terrestrial input, whereas the Indo-Pacific lack sufficient research on this specific habitat, with emphasis instead placed on estuarine mangrove habitats which have more terrestrial influences affecting the turbidity and salinity (Wolanski et al., 2001). The divergence in habitat types between the two regions likely accounts for the disparities in outcomes and theories regularly reported between Caribbean and Indo-Pacific research (Nagelkerken, 2007; Nagelkerken, 2009a; Kulbicki, 2022).

Consequently, research targeting the marine or clear-water mangroves of the Indo-Pacific, and their role within the CEM, including ontogenetic and trophic migrations and habitat use, represent a relatively new field in mangrove habitat research. Additionally, adopting a focus on functional diversity, as opposed to biodiversity, provides a more comprehensive understanding of how the mangrove habitat is utilised by fish, particularly as functional diversity enables insights into resilience. Functional diversity enables us to understand the 'why' in relation to the 'how' and 'what'. With taxonomic biodiversity one may understand which species are present ('what'), and where and 'how' they are distributed how, but with the addition of functional diversity in relation to the environmental context one may understand 'why' they inhabit these areas. Resilience describes how ecosystems absorb and resist impacts, and tend to regenerate after a disturbance (Kulbicki et al., 2022; Sheaves et al., 2024).

To comprehend the significance of mangrove forests within the CEM and the broader coastal seascape, it is imperative to evaluate habitat use by establishing both biodiversity and functional diversity (Marre et al., 2019; Martin et al,.2015; Mumby, 2006). To understand these interactions, a paradigm shift in how to evaluate the functionality of an ecosystem, as well as how to define habitat boundaries in the CEM, is necessary owing to wide scale loss of coastal wetland habitat in many places (Buelow & Sheaves, 2015; Moreno-Mateos et al, 2012; Murray et al., 2018).

1.1 The Coastal Ecosystem Mosaic

The CEM describes how the interconnections among habitats in a meta-ecosystem enables them to function in union, and support a diverse assemblage of fauna and flora (Berkström et al., 2020; Dubuc et al., 2019; Gamfeldt & Hillebrand, 2008; Loreau, Mouquet & Holt, 2003; Oakley-Cogan et al., 2020). Tropical coastal seascapes are very productive and biodiverse, and the organisms that move within and between habitats are of particular importance in supporting the ecosystem and maintaining resilience in the seascape (Ballantyne et al., 2024; Sheaves et al., 2024). These linkages span large timescales – from daily trophic migrations to ontogenetic migrations which can affect the entire lifespan through spawning migrations, dispersal of gametes and larvae, migration to juvenile or nursery habitats, and migrations to join the adult population (Sheaves, 2009).

Understanding the species associated with these migrations that exceed habitat boundaries provides important information about how these ecosystems function collectively. Different species may use different habitats for several reasons, such as protection from predators, ambush hunting, foraging, and other food web dynamics, or reproduction, and understanding the function of the habitat and how it is utilised by species within the CEM may help us understand the resilience of the seascape (Bradley et al., 2017; Kulbicki et al., 2022). Consequently, trophic migrations by fish modify the food web in the CEM and creates significant trophic coupling through the ecosystem (Buelow & Sheaves, 2015; Gamfeldt & Hillebrand, 2008; Sheaves, 2009). In areas where the tidal regime affects habitat availability, fish must migrate between intertidal and subtidal habitats, which is evidence for the interconnectedness of habitats (Bradley et al., 2017). Where life-histories of species depends on this interconnectedness of habitats, the links among them through space and time are critical. The loss of one of these habitats may therefore affect the entire mosaic: even small changes may have large consequences on the ecosystem (Bradley et al., 2017; Gamfeldt & Hillebrand, 2008; Sheaves, 2009; Kulbicki et al., 2022).

The concept of connectivity is mostly apparent through the movement and migration of organisms between habitats, and as a consequence it shapes population structures and communities through nutrient transfers, pollution filtration, ontogenetic migrations, and can transform the food web of the CEM (Abrantes et al., 2015; Sheaves, 2009; Sheaves, Johnstone & Baker, 2016). However, the interconnectedness of the CEM does not mean that they cannot function exclusively from each other, as Sheaves (2009) argues – mangroves are largely associated with tropical estuaries, but there are estuaries with no mangroves and mangrove forests on remote islands far from an estuary. It can therefore be difficult to establish the importance of each individual habitat in the CEM, and the habitat use and function may differ from system to system. By comparison, Henderson et al. (2022) carried out a study and concluded that the connectivity between surf zones in ocean-exposed beaches and the rest of the seascape, where beaches that were near more structurally complex habitats, exhibited higher species richness and diversity. This is also in line with studies by Schlacher, et al. (2020).

The CEM enables greater feeding opportunities through its interconnectedness, and this also enables higher biodiversity and functional diversity and creates opportunities for niche differentiation to fully utilise the seascape (Gamfeldt et al., 2023; Kanno et al., 2023; Nagelkerken et al., 2008; Sheaves et al., 2016). This niche space may therefore be specific to the habitats available in the CEM, and vary from ecosystem to ecosystem. The niche occupation lays the base for the resilience of the CEM, and the more overlap between niches the higher the resilience to change.

Habitats with more structural complexity and ecosystem engineering species generally have more functional niches and exhibit higher species richness and diversity (Henderson et al., 2022; Huston, 1994; Nagelkerken et al., 2008). The interconnectedness of the CEM also enables resource redundancy, further influencing resilience (Sheaves, 2009). Redundancy describes the substitution of the ecosystem functioning role of one species with another (Kulbicki et al., 2022; Stuthmann, Castellanos-Galindo & Robertson, 2022).

There is increasing support for ecosystem-based management and a shift towards management of systems rather than species per se (Semenuik & Creswell, 2018). The emerging evidence of connectivity emphasises the need for management focused on connected ecosystems, and it is getting increasingly accepted as an important consideration when establishing management efforts (Martin et al., 2015). This recognition of interconnectedness within the seascape, the functionality and utilisation of specific habitats, and the understanding of functional diversity and niche utilisation helps to understand how each habitat functions as a part of wider seascape connectivity (Abrantes et al., 2015). Understanding the function of connectivity and incorporating this into management of the seascape from local to regional and global scales is therefore crucial to facilitate resilience and redundancy of the CEM.

1.2 Utilisation of the mangrove habitat by fish

The mangrove forest is often an important part of the tropical and subtropical seascape. It consists of various types of flora that inhabit the intertidal zone and saline coastal waters in the tropics and subtropics (Kannan, 2014; Semenuik & Cresswell, 2018). Mangroves also facilitates the transfer of nutrients, enables carbon storage by acting as a sink, and provides ecosystem functions and services for both marine and terrestrial species (Buelow & Sheaves, 2015; Nagelkerken, 2008). The role of mangrove forests in ecological subsidies must however be considered in relation to the connectivity of the seascape, and how fish migrations affected by the tidal cycle facilitates this transfer (Buelow & Sheaves, 2015; Walters, Kraus & Mills, 2020).

Mangrove habitats in the CEM have a variety of ecosystem functions and ecological subsidies related to productivity, such as primary production and degradation of biological materials producing detritus, and thus enabling nutrient cycling. This then provides feeding opportunities for benthic and pelagic detritivores which sustains the entire food web through trophic migrations (Faridah-Hanum et al., 2019; Oakley-Cogan et al., 2020; Semenuik & Cresswell, 2018; Van der Stocken et al., 2019; Walters, Kraus & Mills, 2020). The structural complexity of the mangrove habitat provides organisms with an environment enabling refuge or potential for ambush for predators (Oakley-Cogan et al., 2020). Mangrove forests also act to stabilise the coastline by providing a barricade to composite against extreme weather and preventing or mitigating erosion (Aardiansyah & Safe'i, 2020; Kannan, 2014). As it is positioned in the interface between land and marine habitats along the coast, utilisation of the mangrove habitat is influenced by environmental factors such as tides, distances between habitats in the seascape, salinity and temperature gradients, and benthic structure (Jones et al., 2010, Nagelkerken et al., 2008, Reis-Filho et al.,2020). The fish assemblage in the mangrove forest is therefore driven by these conditions, and the innate tolerances of each species. Understanding the differences in physicochemical conditions within the mangrove habitat may therefore facilitate the understanding of the organism assemblage using the forest (Igulu et al., 2014; Stuthmann et al., 2022).

1.2.1 Clear-water Mangroves and Estuarine Mangroves

The mangrove habitat can be divided into clear-water or estuarine forests and can vary substantially in relation to species assemblage and distribution, structural complexity, salinity and temperature fluctuations, tidal fluctuations, turbidity, nutrient availability, and connectivity with surrounding habitats. Estuarine mangroves generally have larger salinity fluctuations due to the terrestrial riverine inflow, and higher turbidity and nutrient content due to the proximity to terrestrial habitats. Estuarine mangroves also have less connectivity with coral reef habitats along the coast, as coral reefs need oligotrophic and clear waters to thrive. Clear-water mangroves surrounding islands often exist in proximity to coral reefs, and have less fluctuating salinity due to terrestrial sources (Wolanski et al., 2001). Clear-water mangroves are thus characterised by their proximity to coral reefs and minimal terrestrial input. Estuarine mangroves are generally adjacent to less structurally complex habitats, such as mud flats or sand habitats, while clear-water mangroves are associated with proximity to coral reefs and seagrass beds – two habitats with high structural complexity and high biodiversity. Studies have also shown that clear-water mangroves often exhibit less biodiversity than estuarine mangroves (Hemingson & Bellwood, 2020).

As one of the determining factors for mangrove growth is a low-energy environment, mangroves are often associated with low-energy benthic habitats such as mud or fine sand. However, clear-water mangrove forests associated with clean, oligotrophic water may also be associated with a more high-energy rock or boulder substratum (Bradley et al., 2019; Department of Environment and Energy, 2017; Wolanski et al., 2001). The environmental conditions of the mangrove forest can therefore vary substantially, and it is important to differentiate between clear-water and estuarine mangroves.

This variety indicates that mangrove forests may be utilised by a wide range of fauna, depending on their intrinsic environmental context (Nagelkerken, 2007). Clear-water and estuarine mangroves may host completely different species assemblages (Honda et al., 2013; Igulu et al., 2014). A study by Bradley et al. (2019) reported considerable difference in utilisation of the mangrove habitat by juvenile fish in clear-water and estuarine forests, with the estuarine mangrove forest being important to fish species such as *Acanthophagus pacificus*, *Acanthophagus australis*, *Lutjanus argentimeculatus*, *Lutjanus russellii*, *Epinephelus coioides* and *Epinephelus malabaricus*. However, the clear-water mangroves were more important for juvenile Carangidae, Lethrinidae, and Lutjanidae associated with coral reefs, with only *Lutjanus fulviflamma* and *Caranx sexfasciatus* showing significant habitat use. These authors argue that this may be because of the rocky substratum associated with the clear-water mangrove habitat where they did their study, and that the juveniles present were associated with the rocky reef rather than the mangrove habitat itself. These authors do, however, also discuss that a rocky substratum may still differ in importance and habitat use depending on if it is in an estuarine or marine context. A study by Robertson & Duke (1987) in Australia also reported that juvenile fish utilise the mangrove habitat and discuss that differences in community structure across seasons and depends on local environmental context, including frequency and duration of tidal inundations in mangrove forests. A study by Barnes et al. (2012) however provided evidence that only a small subset of coral reef fish seemed to utilise the clear-water mangrove habitat in the Indo-Pacific, with no evidence of juvenile habitat utilisation for any of the species, contradicting Bradley et al. (2019) and Robertson & Duke (1987). These authors did however discuss that the clear-water mangroves may be used as foraging grounds for coral reef fish. This hypothesis is also supported by Nagelkerken et al. (2008) and Kulbicki et al. (2022), where these authors discuss how the clear-water mangrove habitat is utilised by detritivores, crustaceavores, and planktivores due to the diverse assemblage of microbial, epifaunal and sessile organisms, which in turn attract larger piscivores, as well as how it provides refuge areas and reproductive sites.

Mangroves are often described as being important to other habitats in the seascape. It is often discussed in context with coral reefs, and how coral reef fishes utilise the mangrove forest (Barnes et al., 2012). However, studies have shown that this perceived relationship between mangroves and coral reefs may vary substantially between ecosystems (Barnes et al., 2012; Bradley et al., 2019; Dubuc et al., 2019;

Hemingson & Bellwood, 2020; Stuthmann, Castellanos-Galindo & Robertson, 2022). Bradley et al. (2017) argue that it may be more beneficial to investigate the fish assemblage and functional diversity first, and then relate it to the environmental context to establish habitat boundaries, rather than defining a habitat boundary determined by an anthropocentric perception of environmental conditions. This may thus give a broader understanding of the habitat use by fish of the seascape (Stuthmann et al., 2022).

1.2.2 The Tidal Regime of the Mangrove Habitat

An important aspect of the mangrove forest within the CEM is the effect of the tidal regime on the habitat availability, connectivity and flow of nutrients (Buelow & Sheaves, 2015). The mangrove habitat must therefore be defined along a tidal spectrum, as this largely influences the physical environment of the habitat (Semenuik & Creswell, 2018). The tidal signal may make the mangrove forest range from ideal to unsuitable for many organisms over a small or large temporal scale. This signifies that connectivity is an important factor for such a habitat – the marine species utilising the mangrove habitat during high tide must utilise another habitat during low tide. This fluctuating availability of the mangrove habitat adds to the complexity with interconnected, complex trophic food webs and transfer of functionality (Dubuc et al., 2019; Kimirei et al., 2013; Nagelkerken, 2007; Olds et al., 2013; Sheaves, 2005, 2009). The utilisation of the mangrove forest is therefore restricted by the tidal cycle, and adjacent habitats must fill the functional role of the mangrove habitat as it is unavailable (Manson et al., 2005).

The dynamics of the tidal regime generates other environmental factors such as decreased salinity and temperature through freshwater flow from land and rainfall during low tide, and increased salinity and temperature through evaporation (Semenuik & Cresswell, 2018). Depending on the strength of the tidal signal, and the sediment, the flow of water may also affect turbidity in the water column. Differences in tolerances of the species utilising the mangrove habitat may therefore create unique niches depending on the tidal signal where species utilise the habitat within their tolerance spectrum. This may result in fish communities being structured around specific salinity and temperature tolerances which vary throughout the day – thus it can be argued that the value of a habitat that is temporally inaccessible is dynamic rather than static (Bradley et al., 2019).

The temporal inaccessibility of the mangrove habitat, and thus the forced connectivity with surrounding habitats, does however increase the risk of predation as fish requiring access to the mangrove forest during high tide must migrate across different habitats (Sheaves, 2005). The risk and energy loss associated with this movement may exceed the benefits of using the mangrove habitat as a potential foraging ground, and dependency on the mangrove forest by fish may be lower in areas with larger tidal fluctuations (Igulu et al., 2014; Kimirei et al., 2013; Sheaves, 2005). This inaccessibility does, however, give the invertebrate fauna tolerant of exposure to low tide refuge and time to recover, which enables the mangrove habitat to potentially be an important feeding area. The benefit of staying in the mangrove forest during the low tide for refuge, must however be calculated against the risk of getting stuck as the tide goes out. As coral reefs generally have a higher number of predators, the risk of utilising the coral reef as refuge habitat may be outweighed by the benefit of the structural complexity only when other options are not available (Sheaves, 2005).

The response to the tidal fluctuations and variations in environmental context is species-specific, and the advantage and utilisation of the mangrove habitat must be put in context with these factors (Dubuc et al., 2019; Sheaves, 2005). A study by Laegdsgaard and Johnson (2001) revealed that prey fish such as *Atherinomorus vaigiensis* and *Gerres subfasciatus* conduct tidal migrations in Indo-Pacific mangrove forests for feeding and refuge. The presence of prey fish may then in turn attract predators. On the other hand, in areas where the tidal regime allows the mangrove habitat to be continuously inundated, the utilisation of different habitats may be of less importance and connectivity through daily migrations may have less of an effect on the CEM. Instead, there might be a stronger seasonal effect through ontogenetic migrations. Research by Nagelkerken et al. (2001) has, however, indicated that dial migrations for foraging and reproduction occur even in continuously inundated mangrove habitats.

Sheaves (2005) discusses four hypotheses investigating the probability of fauna to migrate into the mangrove habitat; firstly, there are few feeding areas that fill the same role as the mangrove habitat. Secondly, there are many feeding areas that fill the same role, but the risk of migrating to the mangrove habitat is low. Thirdly, there are many feeding areas that fill the same role, and the risk of migrating is high. And lastly, the mangrove habitat is used for refuge and the risk of migrating is high. If the risk of migrating was low, there would be no need to seek refuge. It can therefore be reasoned that foraging migrations seem to be of higher importance than refuge migrations, unless there is no other continuously available suitable refuge. These are cost-benefits analyses that must be considered when the value and utilisation of a habitat in the seascape is established. These theories were established based on turbid estuaries, but the theories themselves can apply to any interconnected ecosystem.

The Caribbean generally has smaller daily tidal variations compared to the Indo-Pacific region, and the mangrove habitat there is continuously available to fish (Igulu et al., 2014). Hemingson & Bellwood (2020) discussed how the tidal signal had implications for connectivity, diversity, and abundance, and how the Indo-Pacific through the large tidal variation seemed to have less fish dependent on solely the mangrove habitat for nursery or recruitment functions. Instead, macroalgal and seagrass beds may fulfill more of a nursery or juvenile function, as these habitats are subtidal, and more continuously available; and this is further corroborated by Igulu et al. (2014). As there are few studies focusing solely on the nursery function and connectivity between mangroves and coral reefs, especially for non-estuarine or clear-water mangroves as seagrass beds usually are a large part of the seascape, the nursery role of the mangrove habitat is yet to be determined – especially in the Indo-Pacific region (Hemingson & Bellwood, 2020; Nagelkerken, 2007).

1.2.3 The Nursery Habitat Theory

A nursery habitat is defined as a habitat utilised by juveniles of a species conducting ontogenetic, or life-history, migrations, where the number of recruits to the adult populations are predominantly from this nursery ground (Dahlgren et al., 2006). A habitat can therefore harbour a great number of juveniles, but depending on the survival rate and recruitment success of individuals in that habitat and those nearby, it may not serve as a nursery habitat but rather what is described as a 'juvenile habitat' – a habitat that juveniles have been proven to utilise. It is therefore complicated and time-consuming to fully establish a habitat as a 'nursery habitat'. One would need to establish empirical evidence of the recruitment and survival rate of the adult population, and for the ontogenetic migrations to and from that specific habitat and other habitats utilised by the juveniles (Gillanders et al., 2003). A nursery habitat is therefore also species-specific. This definition also fails to account for the size of the 'nursery area' – as the densities of juveniles per unit area may be low but still have a large contribution to adult populations due to the size of the habitat (Nagelkerken et al., 2008; Nagelkerken et al., 2015).

The mangrove habitat has long been viewed as an important nursery habitat based on research from the Caribbean, but the paradigm that all mangrove forests act as nursery habitats has had implications for management efforts even though it is not fully understood (Kimirei et al., 2013). This paradigm is based on two arguments; firstly, there have been recordings of large numbers of juveniles present in mangrove forests, and in some cases more than in other nearby coastal habitats. Secondly, there is some evidence of increased stocks in fisheries adjacent to mangrove habitats (Barnes et al., 2012; Buelow & Sheaves, 2015). However, neither of these hypotheses have been tested empirically to support or confirm the nursery habitat theory.

A study by Manson et al. (2005) found an increase in catch per unit effort in fisheries along the Queensland coast when there was a mangrove habitat adjacent. The factors that had the largest influence on this increase where forest area and perimeter, and the species researched were banana prawns, mud crabs and barramundi. These authors did however discuss how many of the characteristics associated with the mangrove habitat may be shared with the estuarine ecosystem as a whole, such as nutrient rich waters and high turbidity, and the species studied may therefore be less dependent on the mangrove habitat and rather correlated with more general environmental factors of the area. A study by Bradley et al. (2019) found evidence of different habitat use by juveniles in estuarine and marine conditions, which indicates that the theory presented by Manson et al. (2005) might be accurate – the juvenile fauna present are more associated with the general environmental conditions of the seascape rather than the mangrove habitat. Bradley et al. (2019) also found evidence of juveniles migrating between habitats to utilise the different benefits associated with each habitat, and therefore argues that the entire seascape may have more of a nursery function rather than each habitat. This raises the question if there are other benefits of the mangrove habitat that may explain the larger abundance of juveniles present in the forest.

A study by Igulu et al. (2014) indicated higher use of mangroves and seagrasses as nursery, or juvenile, habitats in the Caribbean than in the Indo-Pacific, and this study was based on observed densities. In the Indo-Pacific, seagrasses and coral reefs seem to be of greater importance as nursery or juvenile habitats than mangroves. A study by Kimirei et al. (2013) found that replenishment of adult reef populations by juveniles from mangrove forests were significant in both Caribbean and Indo-Pacific seascapes, but that the interactions between different habitats in the seascape operate as one nursery ecosystem rather than juveniles being dependent on solely one habitat. This view is further corroborated by Nagelkerken et al. (2015) and Sheaves, Johnstone & Baker (2016).

Consequently, the literature regarding connectivity in the seascape, and the nursery habitat hypothesis, is often contradictory. Differences in research methodology, environmental context (marine or estuarine, Caribbean or Indo-Pacific ecosystems, tidal regime, etc.), the disregard for connectivity of the seascape and adjacent habitats, and the investigation of just juveniles without taking the adult population into account, all contribute to this lack of consistent conclusions (Bradley et al, 2019; Gillanders et al., 2003; Kimirei et al., 2013; Sheaves et al., 2014a). To understand the nursey habitat theory and how juveniles are migrating through the seascape before joining adult populations, we must therefore first understand the connectivity and the nature of those migrations, and how juvenile fish use each habitat within the CEM. As it is quite challenging to track juvenile migrations between habitats, and as these migrations are species-specific, there is yet to be fully empirical evidence of the mangrove forest being utilised as a nursery habitat for coral reef fish species (Barnes et al., 2012; Hemingson & Bellwood, 2020). Most studies have assumed migration between habitats by studying the distribution of adults compared to juveniles in different habitats, however this does not account for factors that may influence this such as different growth rates or mortality (Buelow & Sheaves, 2015; Kimirei et al., 2013). For instance, coral reefs have a higher presence of predators which may affect the population of juveniles to sub-adults by increased mortality rates (Gillanders et al., 2003). It is therefore argued that the mangrove habitat may be of more importance for foraging and refuge, and that is what creates its value as a nursery habitat (Buelow & Sheaves, 2015). This may, however, be inferring the importance of the mangrove habitat as a juvenile or nursery habitat, because the function of increased recruitment from a different habitat remains the same. Without empirical evidence of migrations and mortality rates, one cannot assume the nursery habitat theory to be true. The ontogenetic migrations of fish in the mangrove habitat, the nursery function and the connectivity of the seascape is therefore still poorly understood.

1.2.4 Functional Diversity and Trophic Migrations

The diversity of the fauna present, their functional groups, and size structure can help explain the structure and utilisation of different habitats in the seascape. Studies have shown that the diversity of specific consumer species may facilitate our understanding of the length of the food chain, and the dynamics on the food webs. It is therefore important to understand the functional diversity and redundancy of the different components of the CEM, as this can explain predator-prey dynamics, and indicate if a habitat is used for foraging in line with the ecosystem subsidy theory (Duffy et al., 2007; Gamfeldt & Hillebrand, 2008; Polis et al., 1997).

Functional redundancy describes the overlap of functions between species and individuals in an ecosystem, and is thus a measure of the stability and resilience of an ecosystem. Functional redundancy will, however, only correspond to the chosen traits of the analysis, and thus may not fully encompass the variations and resolutions in the niche space (Dick, 2023). In a complex ecosystem there will be many smaller niches as the community present will be more effective at using the available resources. A functional niche must be described in relation to the function filled, but how small a resolution is feasible? With species loss some functions will inevitably be lost, but the loss of competition within that niche may allow less specialised species to fill the missing function. Does diversity equal stability (da Silva et al., 2019; Gamfeldt & Hillebrand., 2008)? Species filling the same functional role might react differently to stressors, and thus create functional resilience (Paganelli, et al., 2012). Functional diversity is therefore an important metric to consider alongside taxonomic richness when identifying areas for protection or conservation (Mammola, et al., 2021; Sheaves, Johnstone & Baker, 2016; Stuthmann, et al., 2022; Walsh, et al., 2022).

Connectivity therefore has implications beyond the migrations and movements of organisms – it affects the trophic levels and functionality of the entire seascape. Nutrient subsidies, which describe how nutrients are transferred across ecosystem boundaries, are, for instance, a consequence of connectivity (Polis et al., 1997; Sheaves, 2009). Studies by Sheaves & Monoly (2000) and Sheaves et al. (2014b) investigated how the groupers *Epinephelus coioides* and *Epinephelus malabaricus,* the snapper *Lutjanus argentimaculatus*, and the breams *Acanthopagrus australis* and *Acanthopagrus pacificus* feed on sesarmid crabs in the mangrove habitat, and thus create trophic links to offshore habitats as they migrate. This feeding behaviour also shortens the food chain from primary producers to top consumers. This is further corroborated by Abrantes et al. (2015), who argue that coastal environments are highly productive and create a nutrient transport to offshore waters by trophic migrations. The inter-habitat migrations in the CEM may cause an ecological bottleneck, as the controlling factor of habitat utilisation may be exaggerated. For instance, for organisms that feed or seek refuge in temporally inaccessible habitats such as the intertidal Indo-Pacific mangrove forest, the existence of subtidal habitats where they can seek refuge during low tide may affect the abundance more than the spatial extent of the mangrove forest itself (Sheaves, 2005). A study by Kitchingman et al. (2023) did however find that fish mostly utilise the fringe of the mangrove forest, which may create a gradient of resource availability throughout the habitat.

A study by Abrantes & Sheaves (2010) also showed that the rainfall during the wet season in tropical Australia affected the input of organic matter in the estuarine coastal environment, which in turn boosts the detritus-based trophic levels. This in turn increases the primary production through nutrient availability, which creates food for planktivores and herbivores, and thus support the foraging of piscivores. This indicates the importance of temporal aspects such as seasonality when investigating the faunal assemblage within a habitat or ecosystem.

The flow of nutrients throughout the seascape is an important consideration when evaluating the productivity of an ecosystem. A study by Sheaves, Johnstone & Baker (2016) investigated how estuarine mangroves are utilised by different trophic groups, to understand the flow of nutrients and trophic levels present. These authors found that there was an uneven distribution of functional groups throughout the estuary, and thus an uneven or unequal productivity level in the seascape. Hemingson & Bellwood (2020) conducted a study comparing the multihabitat use in the Caribbean and Indo-Pacific, and found that even though the fish composition differed, there was evidence for multihabitat use in both realms. These authors sorted the fish into two groups – one that had life-history related ontogenetic migrations, and one that had daily foraging or refuge migrations. The results provide evidence of ontogenetic migrations in the Caribbean, but not in the Indo-Pacific.

The understanding of food webs and trophic migrations is therefore important to understand the value, productivity, and habitat use in the seascape. These food webs underpin the functioning and productivity of ecosystems and population dynamics. The understanding of the complex interactions is of great importance for management efforts, as important trophic links may be modified by defining boundaries of protected areas that do not represent the actual habitat use by organisms in the seascape. Within each habitat there is a food chain that is interconnected with the food web of the entire ecosystem, and the pathways between these food chains to the general food web differ depending on the habitat, environmental context, and faunal assemblage. As well as spatial factors, there are however, also temporal factors such as cohort age, and seasonality aspects (nutrient availability, temperature, rainfall, storms) that affect these interactions (Abrantes et al., 2015; Bradley et al., 2017; Nagelkerken et al., 2008; Sheaves, 2005).

1.2.5 Research from the Caribbean and the Indo-Pacific

As discussed in previous sections, there are many factors that influence the habitat use, functionality, and faunal assemblage in the CEM. As most studies on the role of the mangrove habitat in the Indo-Pacific region have been conducted in estuaries, there is a lack of research on clear-water mangroves in this region. In the Caribbean, however, most research has been conducted on clear-water mangroves, but due to the large differences in environmental context between the Caribbean and the Indo-Pacific the results from these studies may not be applicable to Indo-Pacific clear-water mangrove systems (Dubuc et al., 2019; Nagelkerken, 2007). Due to the tidal signal, the different fauna assemblages and their biogeographic history, the two different regions may be as different as a terrestrial forest found in Sweden compared to one found in Aotearoa New Zealand. In the Caribbean, the Pleistocene reduced the extent of shallow-water habitats, and fish that adapted to this change and utilised different habitats, such as mangroves, during this time period had a higher survival rate and thus could reoccupy the coral reefs when the sea level was higher, and the coral reefs could re-establish. In the Indo-Pacific, the sea level fluctuations during this time period had less effect on the coral reef habitat as it was already widespread, and had less land barriers, and thus fish could evolve to be more adapted to, and dependent on, a single habitat such as the coral reef. This indicates that fish in the Caribbean might have a higher dependency on the entire CEM, than fish in the Indo-Pacific (Cowman & Bellwood, 2013; Hemingson & Bellwood, 2020; Ludt & Rocha, 2015). Connectivity between habitats has therefore, both historically and today, played a big part in shaping fish assemblages, ecosystem services and functions, and food webs, especially since the regions have been separated for 20 million years (Barnes et al., 2012; Buelow & Sheaves, 2015).

1.3 Current Understanding of the Habitat Use of the Tropical Indo-Pacific Seascape

So, how do you study connectivity and functionality in such a complex ecosystem as the CEM? Each bioregion differs substantially from each other, with few studies including the differences in environmental context between clear-water and estuarine mangroves and how the tidal regime affects the habitat use (Barnes et al., 2012; Dubuc et al., 2019; Hemingson & Bellwood, 2020). What we know about habitat use in the tropical Indo-Pacific seascape today is therefore relatively little compared to the Caribbean. As many results from different studies contradict it can be difficult to distinguish what is relevant and what is not, and the shortcomings in connectivity research in the CEM results in that little to no consistent methodology has been established (Bryan-Brown et al., 2017; Gardner et al., 2024). Firstly, we must question the assumption that clear-water and estuarine mangrove forests are equal, and that research from either area is conclusive. Environmental context may affect the fish assemblages more than habitat type, and one must be careful when analysing scientific papers to ensure that the author has understood the differences between bioregions and environmental context (Bradley et al., 2019). Secondly, the tidal signal in the Caribbean and Indo-Pacific has large implications on the availability of habitats in the seascape. Mangrove habitats in the Caribbean and Indo-Pacific cannot be utilised in the same way, when one is only available for half of the time that the other one is. This must therefore be considered when studying the connectivity and diversity of the seascape (Hemingson & Bellwood, 2020; Sheaves et al., 2024). Thirdly, the evolutionary history of these two bioregions may have created a larger dependency on multihabitat use in the Caribbean during the Pleistocene than in the Indo-Pacific (Cowman & Bellwood, 2013; Hemingson & Bellwood, 2020; Ludt & Rocha, 2015). The reason there is less evidence of connectivity in the Indo-Pacific may therefore simply be because there is more single-habitat coral reef dependent fish, and thus a smaller proportion of fish are dependent on multihabitat utilisation than in the Caribbean. This may however be because evolutionary history prevented species with single-habitat coral reef dependency to evolve in the Caribbean, and this does not make multihabitat use for some species in the Indo-Pacific less important.

To fully understand the complexity, ecosystem functioning, services, and ecological subsidies of the CEM one must therefore first understand the value of each habitat within its environmental context, and how it is utilised through ecological or evolutionary connectivity by fish on several spatial and temporal scales. Without the understanding of each piece by itself, one cannot lay the puzzle to see the entire picture that is the CEM.

The aims of this thesis were to investigate the spatial distribution and habitat use of fish in clear-water mangroves in the Indo-Pacific seascape. Through investigating community composition and taxonomic diversity as well as functional diversity this study aims to understand how a temporally inaccessible intertidal habitat is used by fish, and how it contributes to ecosystem subsidies in the CEM meta-ecosystem. The first aim was to understand the community composition and juvenile habitat use within the clear-water mangrove forest, and how this related to microhabitats and environmental context, such as tidal regime, depth, substrate type and seasonal variability, with the purpose to understand how the juvenile and nursery habitat paradigm fit within Indo-Pacific ecosystems, and how the environmental context influences the habitat use of this temporally inaccessible habitat. The second aim was to investigate the functional diversity and redundancy within the clear-water mangrove forest, and how this relates to foraging and refugia theories. The purpose was to investigate the habitat use by fish based on functional trait diversity to infer utilisation patterns based on an environmental context, such as higher structurally complex environments being related to higher diversity.

2 Taxonomic Diversity and Juvenile Habitat Use in an Indo-Pacific Clear-water Mangrove Habitat: how Environmental Conditions affect Community Composition

2.1 Introduction

The coastal ecosystem mosaic (CEM) is home to a diverse range of marine ecosystems, with mangrove forests being an important part of the seascape. They act as transition zones between land and sea, and are critical habitats where marine, coastal and terrestrial species interact. They provide shelter, breeding grounds and feeding areas for a wide variety of organisms, making them integral to maintaining the health and productivity of adjacent ecosystems, including coral reefs and seagrass beds. Despite their ecological importance, mangrove forests globally are under threat from various anthropogenic pressures, including coastal development, erosion, pollution and climate change (Buelow & Sheaves, 2015). The loss of mangroves not only disrupts the ecosystems they support, but also influences the livelihoods of communities that rely on the for fisheries, coastal protection and other ecosystem services.

Mangrove forest can generally be divided into two types; estuarine and clear-water mangroves. Estuarine mangroves are typically found in areas where rivers meet the sea, making them influenced by freshwater and terrestrial inputs. In contrast, clear-water mangroves are less affected by terrestrial runoff, as they are found in more oligotrophic waters often surrounding islands, and are more closely connected to marine ecosystems such as coral reefs and seagrass beds (Dorenbosch et al., 2005; Mumby, 2006). The clear-water mangroves form a key component of the metacommunity in the seascape, facilitating the movement and interactions between species across different habitats (Buelow & Sheaves, 2015). This interconnectedness allows for the transport of resources and nutrients across habitat boundaries, and supports a range of ecological functions that help maintain ecological balance (Gamfeldt & Hillebrand, 2008). This connectivity between habitats is there for important for the functioning and resilience of the ecosystem. In a dynamic system like the Indo-Pacific seascape, where large tidal fluctuations make the clear-water mangrove habitat range from ideal to unsuitable, the interactions between species and habitats are crucial for maintaining biodiversity. Fish move between mangroves, coral reefs and seagrass beds for foraging, refugia and reproduction (Baker & Sheaves, 2009; Sheaves, 2005). This movement enhances biodiversity and supports complex community structures within these ecosystems. The clear-water mangroves in the Indo-

Pacific, therefore, play a significant role in the larger marine ecosystem, not just as isolated habitats but as critical links in the broader seascape (Buelow & Sheaves, 2015).

The taxonomic diversity within clear-water mangroves is influenced by factors such as habitat characteristics, seasonal changes and environmental context which all play an important role in shaping the species composition and community structure of these mangrove forests (Dubuc et al., 2019). However, studying mangrove ecosystems, particularly in terms of taxonomic diversity and community composition, poses several challenges. These ecosystems are complex, with many overlapping biotic and abiotic factors influencing their function. Furthermore, the physical inaccessibility of some clear-water mangrove areas, combined with their dynamic environmental conditions, makes it difficult to conduct comprehensive studies. As a result, much of the research on Australian mangroves have focused on estuarine systems (Barnes et al., 2012).

In many cases, findings from research conducted in Caribbean clear-water mangroves have also been applied to Australian mangrove systems without sufficient empirical evidence to support such comparisons. This has led to paradigms such as the nursery habitat theory, which was established in clear-water mangroves in the Caribbean, to be assumed to be true for all mangrove systems without proper empirical studies conducted in the Indo-Pacific (Hemingson & Bellwood, 2020; Nagelkerken et al., 2008; Kimirei et al, 2013). According to the nursery theory, certain habitats, like mangroves, contribute disproportionately to the recruitment of juvenile fish to adult populations. This means that the loss of such habitats would have a significant impact on adult fish populations. While the nursery theory has been well studied in Caribbean mangroves, similar efforts have not been definitively established in Australian mangroves (Hemingson & Bellwood, 2020; Kimirei et al., 2013; Nagelkerken et al., 2008). The clear-water mangroves in Australia differ from their Caribbean counterparts in several ways. One of the most significant differences is that Australian clear-water mangroves are only inundated for part of the day due to the larger tidal signal in the Indo-Pacific region. This limited inundation time may affect the availability of mangroves as a habitat for juvenile fish, challenging the assumptions made by the nursery habitat theory (Manson et al., 2005; Sheaves, 2005). Tidal cycles create fluctuating conditions that connect mangroves with broader habitats in vastly different ways. This highlights the critical role of connectivity, as marine species that utilise mangroves at high tide must find alternative habitats at low tide, adding complexity to their interactions within the ecosystem. These fluctuations impact not only habitat availability but also the structure of trophic food webs and functional dynamics, as species adapt to their changing environment (Dubuc et al., 2019; Kimirei et al., 2013). This complexity underscores the importance of adjacent habitats, which must compensate for the temporary inaccessibility of mangroves due to the tides moving in and out (Manson et al., 2005). Tidal fluctuations also drive predation risks and energy expenditure as fish must migrate between habitats for foraging and refuge, particularly in areas with significant tidal variation, where reliance on mangroves may be lower (Igulu et al., 2014; Sheaves, 2005). Tidal fluctuations play a significant role in determining when and how marine species can access mangroves for foraging and refuge (Sheaves et al., 2024). At high tide, fish species enter mangrove habitats to feed or seek protection from predators. However, as the tide recedes, these organisms are forced to migrate to other habitats, such as seagrass beds or coral reefs. This alternating access means that mangrove habitat use is dynamic, depending on tidal rhythms, and adjacent habitats must fill functional roles when mangroves are inaccessible (Buelow & Sheaves, 2015; Dubuc et al., 2019). The foraging area model also argues that the ability of predators to successfully reduce the number of preys is determined by access to shelter (Walters & Martell, 2004). Thus, the structurally complex mangrove habitat may be used as shelter by prey species and juveniles or subadults of predator species which have less competitive power in the adult habitat, such as the coral reef. The complexity of these interactions underscores the importance of connectivity between mangroves and other habitats in maintaining the balance of the coastal ecosystem. Many species take advantage of the high nutrient availability in mangroves, but their feeding windows are limited by the tidal cycle. Species like *Atherinomorus vaigiensis* and *Gerres subfasciatus* conduct tidal migrations into mangroves for feeding, and in turn, these fish attract larger predators, illustrating how foraging dynamics are intricately tied to tidal movements (Laegdsgaard & Johnson, 2001). The rich detritus-based food chain in mangroves supports not only herbivores and detritivores but also higher trophic level species, creating a complex web of foraging interactions that vary with the tides (Abrantes et al., 2015). However, the risk of predation during these tidal migrations may limit the extent to which species rely on mangroves for foraging.

Refugia theory suggests that mangroves offer essential shelter from predators, particularly for juvenile fish and invertebrates. The structural complexity of mangrove roots provides protection, potentially making it an ideal refuge during high tide. However, as the tide recedes, species must leave and move to other habitats, increasing their vulnerability to predators (Sheaves, 2005). The benefit of remaining in the mangroves during low tide is balanced by the risk of becoming trapped and exposed to predators as water levels drop. Additionally, invertebrates that can tolerate exposure during low tide benefit from a reprieve from predators and have time to recover, reinforcing the importance of mangroves as both a feeding ground and a refuge (Igulu et al., 2014). The role of clear-water mangroves in supporting fish populations and maintaining connectivity within the seascape is therefore likely more complex than previously thought. It is therefore essential to conduct more research on these systems to establish their ecological importance before further degradation occurs.

This research seeks to provide a deeper understanding of how these ecosystems function and the contribution to ecological subsidies through migration within the coastal seascape. Understanding the biodiversity and environmental conditions shaping community composition of clear-water mangroves in the Indo-Pacific is crucial for developing effective management strategies. Given the threats posed by coastal development and climate change, it is imperative that we enhance our understanding of these habitats and their role within the interconnected CEM to ensure their protection. The research focusing on clear-water mangroves in the Indo-Pacific, and their role within the CEM, represent a relatively new field in mangrove habitat research. The aim of this study is to establish the importance and habitat use of clear-water mangrove forests for fish populations in the Indo-Pacific ecosystem by investigating how environmental and temporal factors, such as tidal regime and substrate, affects fish community structures and juvenile habitat use.

2.2 Methodology

2.2.1 Study site

The study was carried out at Orpheus Island, which is part of the Palm Island group in Great Barrier Reef World Heritage Area approximately 110 km north of Townsville in North Queensland, Australia. Orpheus Island is approximately 12 km long, with the waters surrounding the island protected under the Great Barrier Reef Marine Park and Great Barrier Coast Marine Park (Queensland Government, 2021). Data were collected from six sites on the western, leeward side of the island. Sites 4-6 are in a Marine National Park (Green) zone, while Sites 1-3 are in a Conservation Park (Yellow) zone (Figure 2.1). A Marine National Park (Green) zone is an area where extractive activities are forbidden, but boating, swimming, snorkelling and sailing is allowed. In a Conservation Park (Yellow) zone limited extractive use such as personal fishing is allowed (Great Barrier Reef Marine Park Authority, 2017).

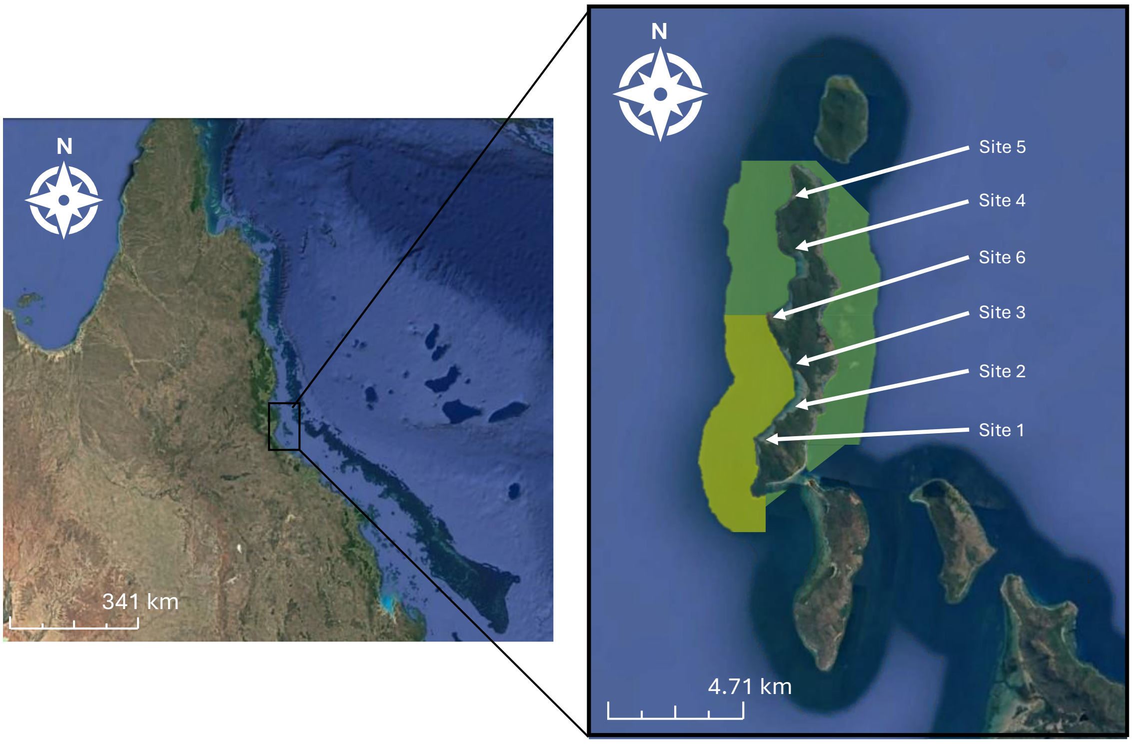

Figure 2.1

Orpheus Island with Green and Yellow zones according to the Great Barrier Reef Marine Park Authority zoning plan (2017), part of the Palm Island group on the North Queensland coast (18°36’57.85” S, 146°29’49.92” E). The arrows indicate the location of the sites where data were collected (Google Earth, 2023).

The mangrove forests at Orpheus Island are clear-water mangroves, immediately adjacent in the seascape to coral reefs, with minimal terrestrial freshwater input. The mangrove sites had either benthic substrate consisting predominantly of sand (Sites 1 and 2), or rocks/boulders (Sites 3,4 & 5). Site 6 had a mixture of sand and rock. The mangrove forests mainly consist of the species *Avicennia marina* and *Rhizophora stylosa* (Figure 2.2**Error! Reference source not found.**).

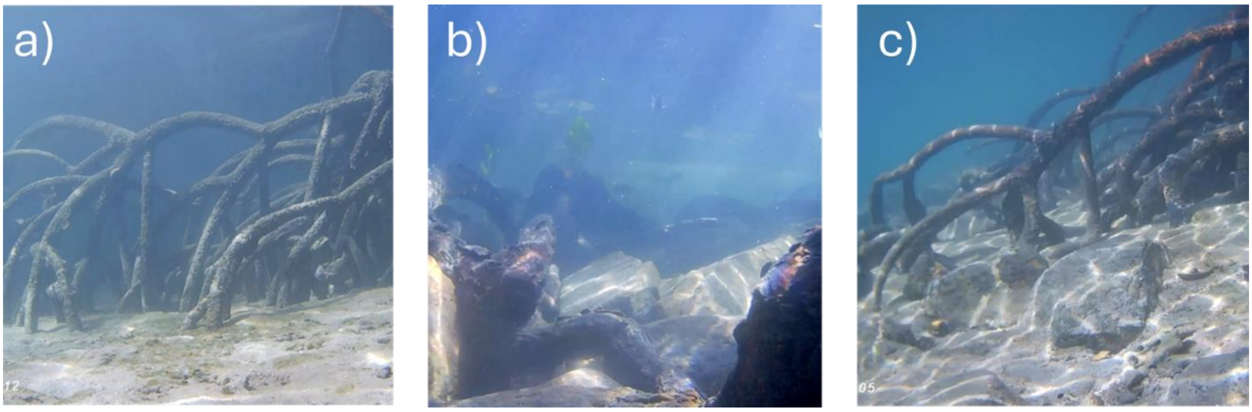

Figure 2.2

Photographs illustrating the three substrate types observed in the study: (a) sand substrate dominated by fine sediments, (b) rock substrate characterized by large, stable rock surfaces, and (c) mixed substrate combining elements of sand and rock.

The tides at Orpheus Island are semi-diurnal (Parnell, 1986), and the mangrove forests are inundated for approximately 65 % of the day estimated from the depth loggers. The rock mangroves were generally higher above the water line and thus inundated for a shorter period of time. The maximum water depth recorded for the duration of this study was approximately 3 meters at Site 1 (Figure 2.3) (see Appendix A, Figure A.1).

Figure 2.3

The mangrove fringe at site 1 during a) low and b) high tide. The footage is from the same video recording, but 100 minutes apart.

2.2.2 Data Collection

Data was collected throughout the year to record seasonality during five field trips in July, September, and December 2022, and March and August 2023. The July 2022 trip was a pilot study to identify suitable camera sites, tidal heights when water reached the forest, and travel times between sites.

On the remaining four field trips remote underwater cameras (GoPro HERO3 Silver Edition HD3.02.03.00 or Adventure Kings Action Camera 1080P Full HD) were placed at the edge of the western edge of the forest (camera 1), and approximately 50 to 60 meters further along the edge of the forest (camera 2). The cameras were placed facing parallel along the forest edge, so it could be determined whether fish observed on the cameras were swimming in, out, or along the forest edge. The cameras were placed at either rising tide, right before water hits the forest, or on the falling tide. The cameras were left recording for a minimum of 2 hours, whereby the battery had been depleted. The cameras were placed as close to the benthos as possible while still capturing most of the water column profile. Visibility varied throughout the study, ranging from a few centimetres to several meters as observed on the videos. Generally, the visibility was poorer with lower water depth (beginning of rising tide recordings or end of falling tide). Video observations were conducted when the visibility was good enough to see the mangrove structure in the video. Each field trip consisted of four days of field work, with each day representing a replicate per field trip. In total, 180 hours and 25 minutes of video recordings were collected and analysed.

As the mangrove habitats are only inundated for a period during the day, high frequency water level data loggers (HoboWare, HOBO U20L) were installed at the two sites on the south (Site 1) and north (Site 5) end of the island. The water level data loggers were placed in December 2022 and retrieved in August 2023. Water depth (kPa) and temperature (°C) were measured every 20 minutes for the deployment duration to capture the tidal regime with as high resolution possible within the limits of the battery life of the data loggers.

2.2.3 Data Analysis

Data from the unbaited Remote Underwater Videos (RUV) were logged in a central database, with date, tidal regime (rising or falling), substrate structure, fish species and approximate size (cm) recorded. The size of the fish was approximated using the mangrove roots as a reference, as these facilitate in estimating size with in-picture depth and dimension in the video. This approach was determined to be the most appropriate as introducing foreign objects to estimate size could potentially disturb the fish (Figure 2.4).

Figure 2.4

Screenshot from a remote underwater video (RUV) recorded at Site 5, depicting the mangrove root structure and a size measurement reference (circled) used for scaling and standardizing observations.

Fish were identified to the lowest possible taxonomic level using a combination of body shape, size, colouration and patterns, and behaviour. All *Abudefduf* spp. were pooled together, as juveniles were difficult to identify. If all juveniles were counted as *Abudefduf* spp. while all adults were sorted into exact species there would be skewness in the abundance counts and size estimates of all *Abudefduf* species. The fish observations were cross-referenced with at least three different sources and reviewed by independent experts as necessary (Froese & Pauly, 2023; Randall et al., 1996; Stuart-Smith et al., 2015). To account for the same individual swimming in front of the camera (repeat counting), a methodology was adapted based on Dubuc et al. (2019), where if a fish of the same species and approximate size (unless without doubt a different individual e.g. female/male form) was seen within 5 minutes of the previous sighting, it was assumed to be the same individual and was not counted.

The time of day the fish were seen was then calculated based on the date and time of the camera deployment, and when in the video the fish was observed. This was then correlated with the data loggers to estimate the exact kPa at the time of the sighting. Water depth at the sites without a depth logger were estimated by finding the measured kPa at Site 1 logger when Sites 2, 3, 4 and 6 first became inundated. The pressure was then estimated to be the 'zero' point, and the kPa was estimated based on the difference between the 'zero' and the kPa of the time the fish was seen. Depth was then calculated for all kPa values by using the formula:

$$mH_2O = kPa \times 0.101972$$

The depth was sorted into six levels (<30 cm, 30-50 cm, 50-70 cm, 70-90 cm, 90-110 cm, 110-190 cm) to account for variability in these calculations affecting the exact water depth. The water depth was verified by randomly choosing a fish observation and estimating how well the calculated depth equated the observed depth, and the calculations were deemed accurate enough for the purposes of this study.

The benthic structure of each site was categorised as either predominantly sand, mixed, or predominantly rock/boulders. The wet season was estimated to start in October 2022 and continued until April 2023, and the dry season was therefore estimated to be from April 2023 to when the cameras were collected in August 2023, as according to the Australian Bureau of Meteorology (2023).

The differences in community composition based on environmental factors were tested with a two-way multivariate analysis of variance based on 999 permutations (PERMANOVA) using Bray-Curtis similarity. The environmental variables selected for the analysis were: (1) tidal flow (two levels: rising and falling), (2) water depth (six levels: <30 cm, 30-50 cm, 50-70 cm, 70-90 cm, 90-110 cm and >110 cm), (3) season (two levels: wet and dry), and (4) substrate (three levels: rock, sand and mixed). The depth values were sorted into bins as to keep the highest resolution with the lowest margin for error. The interaction between tidal regime and depth, and season and substrate, was included in the experimental design. A biomass matrix of the species was created based on these environmental variables, and this was then transformed to a distance matrix. A post-hoc analysis using multilevel pairwise comparison was then conducted for the significant environmental variables. Species diversity was estimated with the Shannon Diversity index, which is a measure of biodiversity that considers both abundance and evenness of the species present in the community, and the Simpson Diversity index, which measures the probability that two individuals randomly selected from a sample will belong to the same species (Arias-Gonzales et al., 2012; Schleuter et al., 2010; Villeger, Mason & Mouillot, 2008). The difference in Shannon and Simpson diversity was tested using a Kruskal-Wallis test.

In studies by Dorenbosch, et al. (2005) and Nagelkerken & van der Velde (2002) in clear-water mangroves, fish were considered juvenile if they had a size ratio below ⅓ of their maximum size (Froese & Pauly, 2023). These authors tested this against the age of maturity of species where it was available and found this approximation to be accurate. They also counted individuals less than ½ of their maximum size as small adults. Therefore, fish were considered juvenile in this study if they were less than ⅓ of their maximum size and therefore have not reached their size of maturity, and small adults if they are less than ½ of their maximum size. The differences in presences of juveniles were tested using the same experimental design as differences in community composition based on taxonomy, with the environmental variables: (1) season (two levels: wet and dry), (2) substrate, (three levels: rock, sand and mixed), and (3) site (six levels: 1, 2, 3, 4, 5 and 6). The proportion of juveniles in the community was calculated by dividing the number of juveniles by the total count of fish. This was then tested against sites, seasons and substrates using a linear mixed-effects model. The normality of residuals was tested using Shapiro-Wilks, and the homoscedasticity by plotting the residuals against the fitted values. Sites were a random intercept, while seasons and substrates were fixed factors. The relationship between size-ratio and predators were tested by estimating all species with a trophic level above 3.5 as predators (Dodds & Whiles, 2010). These were then sorted into four categories: (1) juveniles (< 0.3 of maximum size), (2) small adults (> 0.3 of maximum size and < 0.5 of maximum size), (3) under maximum size (< 0.5 of maximum size), and (4) adults (> 0.5 of maximum size). A generalized linear model with a binomial family and logit link function was applied to examine the relationship between being a predator (TRUE/FALSE) and the likelihood of the fish being categorized as under maximum size (TRUE/FALSE) in the dataset. The logit link function was used to transform the predicted probabilities to the log-odds scale, which allowed estimation of the effect of the predator variable on the likelihood of the individual fish being less than half of the recorded maximum size. The model was checked for overdispersion using the overdispersion function, and the test result (*1.000363*) suggested that there was no significant overdispersion in the data, indicating that the binomial distribution was appropriate for this analysis. A Spearman correlation test was also done to test the non-linear relationship between trophic level and size.

A Generalized Additive Model (GAM) was employed to examine the relationship between fish size, size ratio, trophic level, and the probability of fish occurring in the "in" versus "edge" microhabitat. The response was binary (In = TRUE/FALSE), so a binomial family with a logit link was used. To handle the wide range of the variables, fish size and size ratio were log-transformed to stabilize model fitting. Smooth terms were included for both size and trophic level using moderate basis dimensions to balance flexibility and interpretability. The interactions between trophic level, fish size and size ratio were also tested using a tensor product smooth. The model was estimated via Restricted Maximum Likelihood (REML) to ensure stable smoothing parameter estimation. Model fit was assessed through residual diagnostics, deviance explained, adjusted R^2, and the Area Under the Curve (AUC) of the resulting predictions. Basis dimensions (k-values) were chosen based on diagnostic checks (including k-index tests) to ensure that the model captured necessary non-linearities without overfitting or convergence issues. The analyses were performed using the ‘vegan’ package, the ‘mgcv’ package and the ‘lme4’ package in RStudio (Bates et al., 2015; Oksanen et al., 2022; Wood, 2023). This research aimed to establish the taxonomic and functional diversity present in clear-water mangroves in the Indo-Pacific, however, as only one island was investigated the patterns found in this study should be compared with other clear-water mangroves in the Indo-Pacific to establish how these findings relate to local variations and habitat use patterns.

2.3 Results

2.3.1 Community Composition

In total, 5,513 individuals belonging to 70 species in 28 families were observed from the mangrove edge. The most abundant fish, with 1,686 individuals observed, was the small schooling species *Fibramia lateralis*. The most abundant non-schooling fish, with over 300 individuals observed, were *Gerres spp.* (n = 548), *Abudefduf spp.* (n = 461) and *Siganus lineatus* (n = 398). The most dominant families in terms of species richness were *Labridae* (n = 9) and *Serranidae* (n = 7). Of the total number of species recorded, 55.7 % had a tolerance for brackish or freshwater, while over 90 % of the species were reef-associated according to FishBase (Froese & Pauly, 2023) (Figure 2.5) (see Appendix A, Table A.1). The highest Shannon diversity (H) and Simpson diversity (D) was found at site 6, in rock substrate and during the dry season (Table 2.1). However, the Kruskal-Wallis test did not find significant differences in Shannon (H) or Simpson (D) diversity between sites, substrates or seasons.

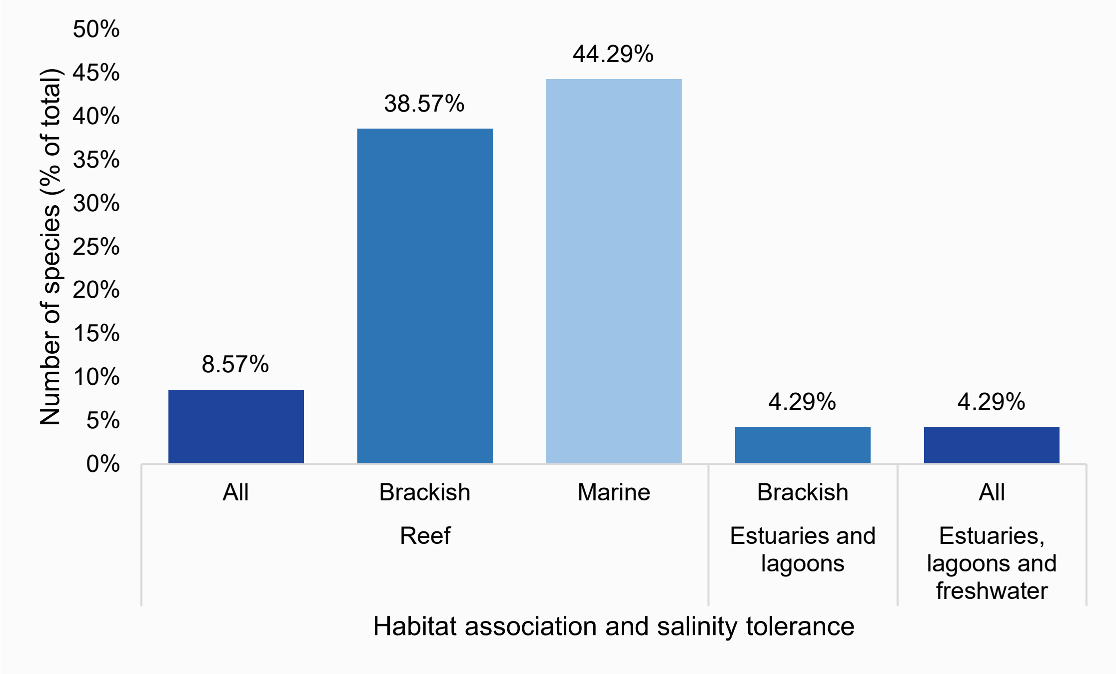

Figure 2.5.

Percentage composition of fish species categorized by habitat association and salinity tolerance. The y-axis represents the proportion of the total fish community (%), while the x-axis represents habitat association and salinity tolerance. Within each habitat category, species are classified by their salinity preference, illustrating the relative distribution of fish communities across different environmental conditions.

Table 2.1

Comparison of Shannon and Simpson diversity indices across six sampling sites (Sites 1–6), three substrate types (rock, mixed, sand), and two seasons (dry, wet). The table displays how each index varies with location, habitat characteristics, and seasonal changes, providing an overview of diversity patterns among the sampled communities.

SITE	SITE 1	SITE 2	SITE 3	SITE 4	SITE 5	SITE 6
SHANNON	2.000	*1.556*	2.544	2.289	2.718	**2.900**
SIMPSON	0.821	*0.600*	0.891	0.824	0.896	**0.926**
SUBSTRATE	ROCK	MIXED	SAND			
SHANNON	**2.900**	2.785	*1.806*			
SIMPSON	**0.926**	0.892	0.*696*			
SEASON	DRY	WET				
SHANNON	**2.811**	*2.519*				
SIMPSON	**0.902**	*0.821*				

Note. The Shannon Diversity Index considers both species abundance and evenness, whereas the Simpson Diversity Index quantifies the probability that two individuals randomly selected from a sample belong to the same species. Bold values represent the highest diversity per trait group, while italicized values indicate the lowest diversity.

The PERMANOVA analysis of species community composition revealed a strong influence when considering both season and substrate, as well as the interaction between season and substrate in the model (Table 2.2). The post-hoc multilevel pairwise comparison indicated a high significant difference between all substrate types. The post-hoc multilevel pairwise comparison also indicated that the difference between seasons is significant (Table 2.3).

Table 2.2

PERMANOVA results examining the effects of substrate, season, and their interaction on species community composition. Reported are the Pseudo-F values, the proportion of the total variance explained (R^2), and corresponding p-values for each factor

PERMANOVA	**Pseudo-F**	**R^2**	**p-value**
SUBSTRATE	6.8885	9.45 %	0.001
SEASON	2.7398	3.76 %	0.001
INTERACTION	3.9923	5.47 %	0.001

Note. All p-values are significant at α = 0.05, indicating that substrate, season, and their interaction each have a significant influence on species community composition.

Table 2.3

Post-hoc PERMANOVA pairwise comparisons examining differences in species community composition among substrate types (sand, rock, mixed) and between seasons (dry, wet). Displayed are Pseudo-F values, the proportion of total variance explained (R^2), and corresponding p-values for each comparison.

Post-hoc multilevel pairwise	**Pseudo-F**	**R^2**	**p-value**
SAND & ROCK	7.0781	14.72 %	0.001
SAND & MIXED	5.5114	12.11 %	0.001
ROCK & MIXED	2.2932	5.55 %	0.001
DRY & WET	2.3924	3.78 %	0.05

Note. All substrate comparisons are highly significant ($p < 0.001$), and the difference between dry and wet seasons is also significant ($p < 0.05$) at $\alpha = 0.05$.

The relatively low R^2 values suggest that the effect of seasons and substrates, though present, is not the sole factor driving the observed variations. In the PERMANOVA analysis, the residual variance (unexplained by the model) was high, with a Sum of Squares of 15.428, accounting for 65.83% of the total variance. This indicates that a significant portion of the variation in community composition was not explained by the factors included in the model. In the pairwise comparison between both substrates and seasons, while a significant effect was observed, the residuals still accounted for a large proportion of the variance (Table 2.4). The significant effect does however allow for the community composition to be sorted into two metacommunities, one based on substrate, and the other based on season. A linear model was then applied to test differences in biomass across sites, seasons and substrates, with season and substrate as fixed effects and site as a random effect. The intercept was significant, with an estimate of 2631.46, meaning that the baseline is approximately 2631.46. Site had no effect, and substrate had only a small and non-significant effect on biomass. However, the wet season had a negative and significant effect ($\beta = -1335.57$, $t = -3.312$, $p < 0.001$), suggesting that biomass is lower during the wet season compared to the dry season. A PERMANOVA based on presence-absence did although indicate that there was still a significant difference in species community between seasons, when biomass was not considered (*pseudo-F* = 2.4817, $R^2 = 3.17\%$, $p = 0.02$).

Table 2.4

Post-hoc residuals from pairwise PERMANOVA comparisons among substrates (sand, rock, mixed) and between seasons (dry, wet). Displayed are the sum of squares (SS) of the residuals and the proportion of variance (R^2) unexplained by the model for each comparison.

Post-hoc multilevel pairwise residuals	**SUM OF SQUARES**	**R^2**
SAND & ROCK	13.2799	85.28 %
SAND & MIXED	13.4547	87.89 %
ROCK & MIXED	13.4918	94.45 %
DRY & WET	22.5459	96.22 %

Note. High R^2 values in the residuals indicate that a substantial portion of the variation remains unexplained by the factors of substrate and season, even though the pairwise comparisons revealed statistically significant effects.

2.3.2 Juvenile Habitat Use of Clear-water Mangrove Forests

The PERMANOVA analysis of juvenile community composition revealed significant influences of substrate and site, but not season (Table 2.5). Substrate explained approximately 32 % of the variance in juvenile community composition, however the post-hoc multilevel pairwise comparison indicated no significant difference between sand, mixed and rock.

Table 2.5

PERMANOVA results for juvenile community composition across different substrates (sand, mixed, rock) and sites. Reported are the Pseudo-F values, the percentage of total variance explained (R²), and the associated p-values for each significant factor tested.

PERMANOVA	**Pseudo-F**	**R^2**	**p-value**
SUBSTRATE	4.2330	32.625 %	0.047
SITE	5.0654	19.52 %	0.041

Note. Although substrate and site each have a significant influence on juvenile community structure, subsequent pairwise comparisons revealed no significant differences among the three substrate types, suggesting that other unmeasured variables or high within-substrate variability may partly explain the observed patterns.

Based on the linear mixed model, neither the type of substrate nor the season significantly influenced the proportion of juveniles compared to adults. This indicates that, within the scope of this study, juvenile fish proportions remain relatively consistent across different substrate types and seasonal conditions. However, due to the restricted sample size, there may be a limited ability to detect significant effects. When looking at the proportion of juveniles, 57% of all individuals counted were juveniles in the sand substrate, while 35% and 22% were juveniles in rock or mixed substrate respectively. For the wet season 50% of all individuals counted were juveniles, while for the dry season 37% were juveniles. In total, 29 species had juveniles present in the mangrove forest. Of these, 18 species were more commonly observed as juveniles than adults, with *Caranx fulvoguttatus*, *Epinephelus fuscoguttaus*, *Platax orbicularis* and *Lutjanus argentimaculatus* being only present in the forest as juveniles (100%).

Approximately 70.2% of all individuals and 78.1% of all predators (trophic level above 3.5) found were less than half of their maximum size in the mangroves. 29.8% of all predators and 23.3% of all individuals were small adults, and 48.3% of all predators and 46.4% of all individuals were juveniles. The linear regression model of for size and trophic level indicated that the average size of non-predatory fish was about 15.56cm ($\beta = 15.5628, p < 0.001$), and that predatory fish tend to be smaller by about 2.90 cm on average compared to non-predatory fish ($\beta = -2.8959, p < 0.001$). The negative coefficient indicates that predatory species, on average, are smaller than non-predatory species. The coefficient for predator was positive (*0.774*), and the corresponding p-value (*<2e-16*) indicated that the effect of predators on being under maximum size was statistically significant. This suggests that being a predator increases the odds of a fish being under its maximum size. The Spearman correlation indicated a significant negative coefficient between size and trophic level, suggesting a tendency for fish at higher trophic levels to be smaller ($\rho = -0.34738$ $p < 0.001$).

Generalized Additive Models (GAMs) were then used to examine how fish body size and trophic level influenced their likelihood of being observed inside the mangrove forest versus along its edge. The first model, testing size and trophic level, explained approximately 16 % of the variance (*adjusted* $R^2 = 0.16$) and had a moderate predictive performance ($AUC \approx 0.756$). Smooth terms for both size and trophic level were significant ($p < 0.001$), indicating non-linear effects on the probability of being inside the forest. The smooth for size (Figure 2.6) suggested a complex relationship: medium-sized individuals showed a slightly lower probability of being inside the mangrove relative to either very small or very large fish. In particular, as fish length approached larger values, the partial effect on the log-odds of being inside the forest increased, indicating that larger individuals were more likely to be found inside the forest. However, in the upper range of log size (i.e., for the largest individuals), there was an increase in variability, indicated by wider confidence intervals and a more pronounced rise in the curve. This likely reflects a combination of fewer data points and greater natural variability among the largest fish, making the model's estimates in that size range less certain. However, despite this uncertainty, the overall trend still suggests that larger fish are more likely to be inside the mangrove forest.

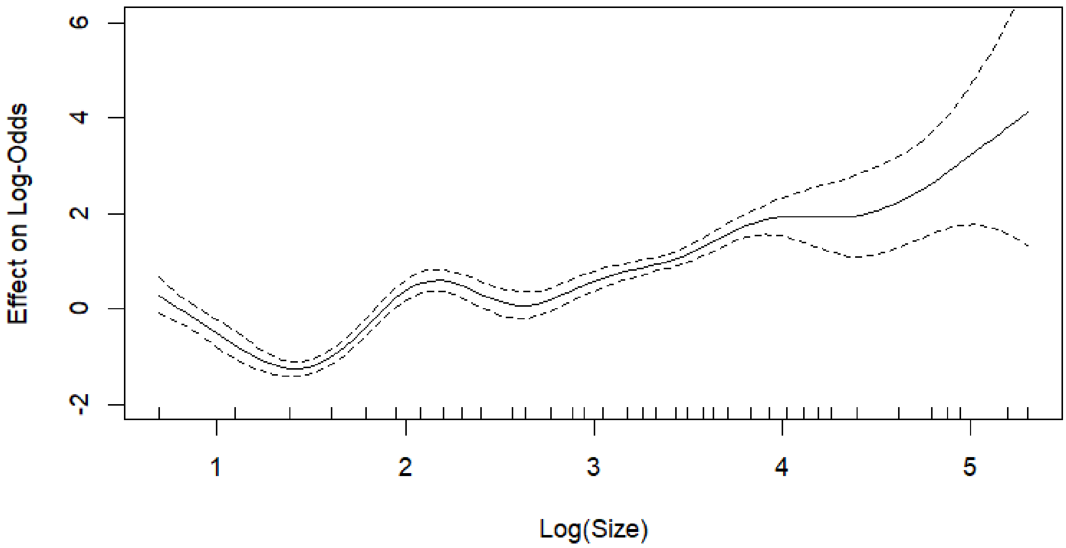

Figure 2.6

Partial effect of log size on the log-odds of being inside the mangrove forest, estimated by the GAM. The solid line represents the fitted smooth, and the dashed lines show the approximate 95% confidence intervals. Notably, the curve and its confidence intervals widen at higher values of log size, reflecting greater variability and fewer data points among the largest individuals.

The effect of trophic level (Figure 2.7) was subtler. Although significant, the partial effect curve remained close to zero with a slight decline at higher trophic levels, suggesting that more predatory species may be more likely to occur at the edge.

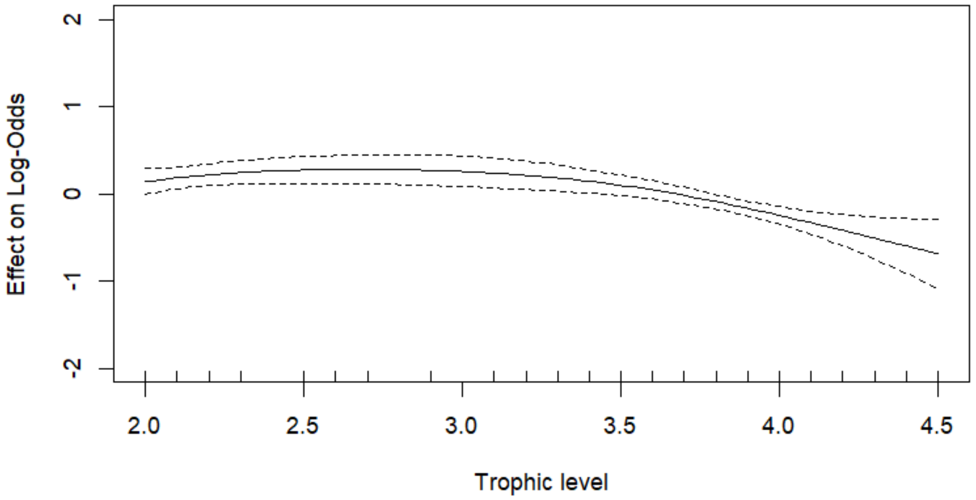

Figure 2.7

Partial effect of trophic level on the log-odds of being inside the mangrove forest, estimated by the GAM. The solid line represents the fitted smooth, and the dashed lines show the approximate 95% confidence intervals.

The model also revealed a significant interaction between log size and trophic level in predicting the likelihood of an individual being observed in the forest interior versus the edge (*tensor product smooth: edf = 36.5, Chi-sq = 754.8, p < 2e-16*). The model explained 18.7% of the variance (*adjusted $R^2 = 0.187$*) with good overall fit (*AUC ≈ 0.76*). Smaller sizes were consistently associated with a high probability of being inside the forest regardless of their trophic level. However, larger sizes indicated more complex patterns, with the probability of being in the forest decreasing as trophic level increased. This indicates that larger predators generally have a higher probability of being along the edge of the mangrove forest. At higher trophic levels, the probability of being inside the forest decreases for all sizes, but with the effect being most pronounced for larger individuals. However, although there was a significant interaction, size seem to drive the probability of being inside the forest or on the edge more than trophic level (see Appendix A, **Error! Reference source not found.**).

In the second GAM, both log size ratio and trophic level smooths were highly significant (*$p < 0.001$*). The deviance explained (*13.6%*) and AUC (*≈ 0.744*) indicated a similar level of model performance. Early life stages (low size ratios around 0.1) were less likely to be found inside the forest, while a clear pattern was not found for most life stages (effect around 0) (Figure 2.8). As individuals approached larger size ratios, the likelihood of occurring inside the mangrove again increased slightly, but with more uncertainty in the model due to smaller sample size and more variation.

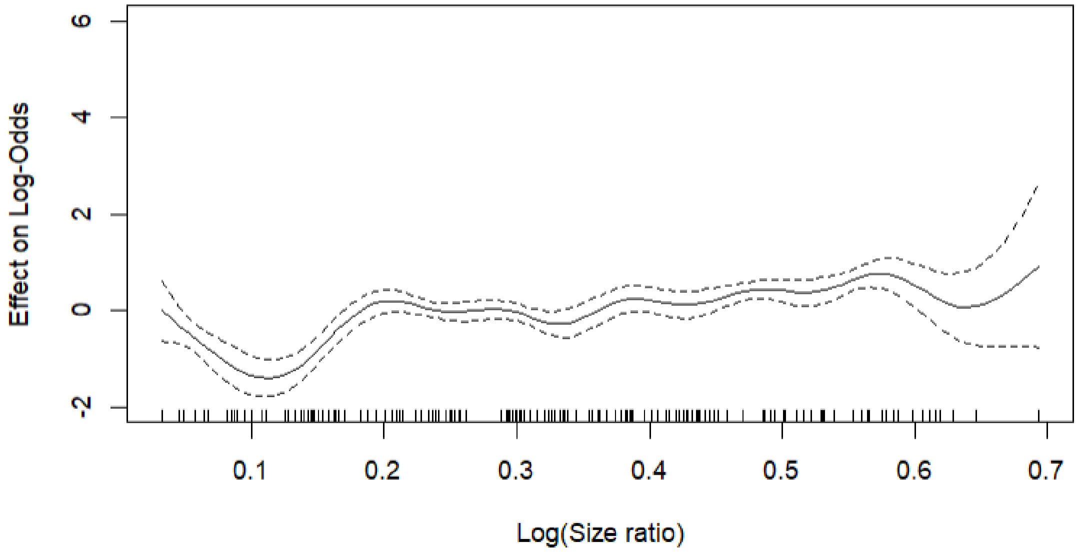

Figure 2.8

Partial effect of log size ratio on the log-odds of being inside the mangrove forest, estimated by the GAM. The solid line represents the fitted smooth, and the dashed lines show the approximate 95% confidence intervals. Notably, the curve and its confidence intervals widen at higher values of log size ratios, reflecting greater variability and fewer data points among the oldest individuals.

The trophic level smooth (Figure 2.9) was more complex than in the first model, showing multiple fluctuations rather than a near-flat line. This pattern indicates variation among different trophic levels. Lower trophic levels (< 2.5) were associated with being inside the forest, along with trophic groups between 3.5 and 4. However, at trophic level 4 there was a pronounced likelihood to be associated with the edge of the forest.

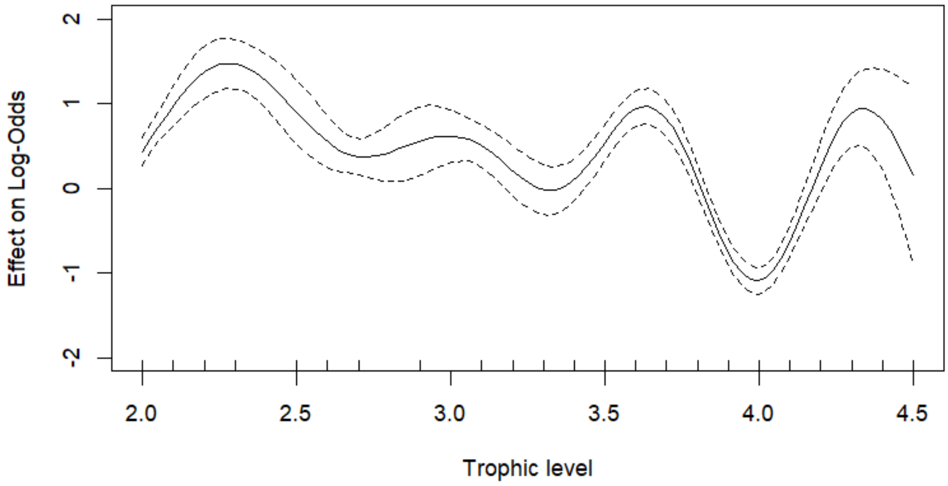

Figure 2.9

Partial effect of trophic level on the log-odds of being inside the mangrove forest, estimated by the GAM. The solid line represents the fitted smooth, and the dashed lines show the approximate 95% confidence intervals.

The GAM incorporating the interaction between log size ratio and trophic level explained around 20 % of the variance (*adjusted* $R^2 = 0.199$). The tensor product smooth for the interaction was also significant (*edf = 72.5, Chi-sq = 840.8,* $p < 2e\text{-}16$) and had a good model fit (*AUC* ≈ 0.76). The model indicates that smaller size ratios (younger or less mature individuals) were associated with being inside the forest, and as the size ratio increased the likelihood of being inside the forest decreased. However, this relationship exhibited oscillations, which suggests variability in the habitat use patterns for different age stages. Lower trophic levels were also generally associated with being inside the forest, while at higher trophic levels this probability decreased across all size ratios.

2.4 Discussion and Conclusion

2.4.1 Environmental Variation and Taxonomic Community Patterns

Clear-water mangroves must contribute to connectivity in the seascape by the fact that they are only partly inundated; the fish community utilising the mangrove forest must be somewhere else when there is no water. The surrounding habitats to the mangrove forest may therefore explain why substrate is a significantly influential factor on fish community composition, as different substrate types are associated with different environmental conditions (water velocity, current patterns, etc.). Barnes et al. (2012) also found similar patterns on Orpheus Island in 2002. The impact of substrate appears to be more pronounced at the community level as species biomass did not significantly differ between substrates, but community composition did. Substrate type thus influence the types and proportions of species present rather than the abundance of individual species. Site 6, rock substrate and the dry season also had the highest Shannon and Simpson diversity, suggesting a richer and more evenly distributed community, and a lower probability of randomly selecting two individuals of the same species.

As the microtidal regime forces individuals to migrate in and out of the habitat, the benefits of utilising the clear-water mangroves in the Indo-Pacific must outweigh the cost. The reason there are many smaller individuals recorded within the mangrove forests in this study may indicate that it is used by juveniles and small adults which have less competitive power in habitats where the adults and larger predators are present. This observation is supported by the Generalized Additive Model (GAM) results, where smaller absolute sizes (log-transformed) and lower size ratios (indicating earlier life stages) were significantly more likely to occur inside the forest. The foraging area model argues that the ability of predators to successfully reduce the number of preys is determined by access to shelter (Walters & Martell, 2004). Moreover, the GAM analyses revealed notable differences in habitat use across size ratios and trophic levels. Whereas trophic level appeared relatively flat when modelled with absolute size, modelling size ratio uncovered a more complex, wave-like relationship. At lower size ratios, trophic level had a comparatively minor effect on habitat choice, suggesting that young fish, regardless of their position in the food web, are inclined to seek shelter inside the forest. However, at higher size ratios, the partial effect of trophic level increased, and larger-bodied predators (trophic levels above 3.5) were more frequently associated with edge use rather than forest interior. As most individuals found in the forest were less than half of their maximum size (70.2% and 78.1% for predators), it appears that the clear-water mangrove habitat in the Indo-Pacific may serve as refugia for potential prey species, where the risk of predation in coral reefs or other adjacent habitats is likely higher.

This risk of predation must then outweigh the risk of migrating into the mangrove forest. This correlation between connectivity and predation may therefore have an important effect on community composition, which is corroborated by Sheaves (2005) and Sheaves (2009). Those studies also argue that if the major driver for entering the forest is food, the individual would follow the incoming tide as the food source will be most abundant, however, if the major drive is refugia, the fish may stay as long as the tide permits. A study by Dubuc et al. (2019) also indicated that community composition varied significantly across the tidal cycle. However, these patterns were not observed in this study, as tidal regime and depth had no significant effect on community composition. It is possibly the combination of food acquisition and refugia that is the benefit of the mangrove habitat, and according to Sheaves (2005), this could be why there is no clear differences in community composition depending on tidal regime or depth. This may also explain the patterns of in-forest versus edge-utilisation, as larger predators unable to hunt within the forest, or more than a few meters into the forest, thereby scout the edges while waiting for prey fish in the forest to leave. Larger predatory fish in this study were shown to swim along the edge more than into the forest. These results also indicated that younger fish prefer being inside the mangrove forest habitat, and that it may be important for both refugia and foraging.

At lower size ratios, trophic level had a smaller effect than for higher size ratios, where higher trophic levels were increasingly associated with edge use. This is further discussed by Baker & Sheaves (2009), where those authors found that smaller piscivores had a significant effect on the mortality rate of recruiting fish in juvenile habitats.

Thus, the mangrove forest interior can benefit smaller or younger predators, although they have a higher probability to utilise the edge of the forest as they age. The 3D partial effect surface (see Appendix A, **Error! Reference source not found.**) indicates that the interior mangrove forest may serve as a refuge for early life stages of predator species, possibly helping them avoid competition and reducing predation risk from larger predators. As they grow, their habitat preferences appear to shift, with higher trophic-level fish at larger size ratios being increasingly associated with the mangrove edge. This may be explained by greater predatory capability with larger size ratios, and less need for cover, as well as in limitations in navigating dense root structures. These findings reinforce the importance of ontogeny in habitat use: while the forest interior is favoured by smaller fish and younger predators for refugia and foraging, larger fish—particularly those at higher trophic levels—tend to occupy the mangrove fringe as they mature.

Ecology is often studied in two different aspects: (1) community which considers the biotic interactions within an ecosystem, and (2) ecosystem which is a more holistic explanation to energy flows (Gamfeldt & Hillebrand, 2008). Biodiversity thus exists in a complex interaction between the living and non-living parts of an ecosystem. A study by Martin et al. (2015) found *Siganus fuscescens* to exhibit feeding behaviour in the mangrove forest, and this had a significant impact on fish assemblages on reefs adjacent to the mangrove forest. That study also found that protected areas may facilitate nutrient transfer and flow out of mangrove forest and to the rest of the seascape by protection of commercially important species. A study by Barnes et al. (2012) found that *Halichoeres miniatus*, *Lethrinus harak*, *Lutjanus fulviflamma* and *Siganus lineatus* had a higher presence in mangrove forests than in adjacent coral reefs, and these species also had high presence in the mangrove forests in this study. Barnes et al. (2012) also reported that *Abudefduf bengalensis*, *Abudefduf sexfasciatus*, *Scarus rivulatus*, *Siganus lineatus* and *Lutjanus fulviflamma* had statistically different mean sizes between mangrove and reef habitats, with *Scarus rivulatus* generally being larger in mangrove habitats, while the other species were smaller. However, in that study the authors only found a 20 % overlap of species between clear-water mangroves and coral reefs. This indicates that the species utilising the clear-water mangrove habitat when it is inundated may come from different habitats in the seascape. In another study, Stuthmann et al (2022) claims that most mangrove species in the Eastern Indo-Pacific compared to the Caribbean are estuarine, as only 7 out of 25 species (28 %) in that study were reef-associated, but this is contradicted by Dubuc et al (2019), reporting that most species associated with clear-water mangroves in New Caledonia to be reef-associated and marine. In a separate study in New Caledonia, Kulbicki et al. (2022) investigated the taxonomic overlap of fish communities in the seascape and noticed that mangroves had the lowest number of species, and that there was a low overlap of species between coral reefs and nearby mangroves forests. However, the mangroves examined were mostly estuarine, with a small sub-sample being clear-water mangrove forests. In this study, 64 out of 70 species (~91 %) had a recognised reef-association. This is in line with the hypothesis that external factors, such as inundation period and proximity to surrounding habitats, influences the clear-water mangrove fauna, and that environmental context, predator-prey dynamics and competition may be the strongest predictors of community composition here (Lugendo et al., 2007). As the tides move in and out, there has to be connectivity with surrounding habitats for a species to be able to migrate in and out of the mangrove forests, and a study by Honda et al. (2013) argues that the lower species diversity reported in clear-water mangroves compared to estuarine mangroves may be because of this proximity to more complex habitats. A study by Bradley et al. (2024) found that proximity to reefs and tidal regimes may be of the biggest importance in explaining community composition and functionality in Indo-pacific mangrove systems. The rock substrate mangroves in this study are a result of high energy environments. As can be seen in **Error! Reference source not found.**, the rock substrate mangroves are facing south or south-east which renders them more exposed. The rock mangroves were also generally higher above the water line and thus inundated for a shorter period of time compared to the sand mangroves. The sand mangroves were characterised by a reef flat followed by algae mats and a low sloping sand flat leading up to the mangrove forest. The mangrove rock substrate had a steeper drop off to deeper water and a coral reef in closer proximity to the forest, and was without algae mats and sand flats. These differences in adjacent habitats may therefore be an important determinant in the significant effect on community composition (Lugendo et al., 2007). The tidal regime and depth did not have significant effect on community composition. In Bradley et al.'s (2024) study they found that lower tidal ranges and proximity to a coral reef had a significant effect on juvenile reef specialist fish, while species richness of adult reef fish were determined by substrate type. Although this study found no effect of tidal ranges on juvenile habitat use and presence, substrate did have a significant effect. As proximity to coral reef was not tested conclusions about its effect cannot be drawn, but this may be connected with substrate and high energy environments which have been shown to affect the community composition. As argued by Mumby (2006), to understand the connectivity between different habitats in the seascape, one must first understand the community and dynamics within in each interconnected habitat, and the cost and benefit of migration.

2.4.2 Juvenile Utilisation and the Paradigm of the Nursery Habitat

The paradigm that mangrove forests are important nursery habitats stems from research in the Caribbean, where the continuously inundated forests and evolutionary history of fish leading to less dependence on coral reef habitats, have indicated that juveniles may utilise mangrove forests before migrating out to the reef as adults (Bellwood et al., 2017; Manson et al., 2005; Nagelkerken, 2007; Sheaves et al., 2014a). This theory does not hold in the Indo-Pacific clear-water mangroves, as the tidal signal would force juveniles to migrate in and out of the habitat, and thus utilise other habitats during low tide, which at most would make the clear-water mangroves a juvenile habitat for only a few hours each day. For a habitat to be truly a nursery habitat, the net contribution through ontogenetic migrations from that juvenile habitat to the adult habitat must be larger than the contribution from any other juvenile habitat (Gillanders et al., 2003; Nagelkerken, 2007). The study by Manson et al (2005) did however indicate that the estuarine mangrove forest may be an important juvenile habitat for certain commercially important species, although the relationships may possibly be explained by the proximity to an estuary rather than the mangrove habitat itself, as it only accounts for correlation – not causation. A study by Nagelkerken (2007) indicated that the combination of mangroves and seagrass beds may contribute to the adult population on adjacent coral reefs, but that the dependence is not obligate and thus the reef species will suffice without the connectivity to these habitats. Both these studies mentioned here align with Naglekerken’s (2007) theory about mangrove forests acting as sinks for juveniles and subadults, rather than as juvenile or nursery habitats. However, although the relationship between estuarine mangroves and reef fish in the Indo-Pacific show low connection between coral reefs and mangroves, mainly because of the lack of coral reefs adjacent to estuarine mangroves, the non-estuarine clear-water mangroves of the Indo-Pacific may play a bigger role in sustaining populations in the seascape. This is further corroborated by Bradley et al. (2019), where the authors argue that estuarine or marine context is of greater importance to juvenile fish than the habitat itself. Many juvenile species may utilise a larger range of different habitats in the seascape, and microhabitats within the mangrove forest, in order to optimise foraging and refugia resources to meet their needs.

Results from the size ratio GAM reinforce the idea that juveniles and sub-adults, regardless of trophic level, are more likely to be found inside the mangrove forest. At lower size ratios, individuals may take advantage of the structural complexity for both foraging and refugia, while larger, higher-trophic-level fish increasingly occupy the edge. This pattern aligns with the hypothesis that younger fish—often less competitive or more susceptible to predation—benefit from the complex root systems. Consequently, Indo-Pacific clear-water mangroves with large tidal fluctuations may serve as foraging grounds and refugia for fish at earlier life stages, before they transition to the adult habitat.

2.4.3 Conclusion

In conclusion, local environmental conditions and the internal microhabitats of the mangrove forest appear to be the most influential factors shaping fish assemblages and community structure in Indo-Pacific clear-water mangroves. Although the forest provides benefits in terms of foraging and refuge – particularly for juveniles and smaller fish – these advantages must be weighed against the risks of migrating in and out with the tide. The findings of this study suggest that these factors, combined with predator-prey dynamics and intraspecific competition, helps to explain the sometimes-contrasting results observed across mangrove forests worldwide. By considering variables such as size ratio (indicative of life stage) and trophic level, as well as physical habitat features like substrate type and seasonal aspects, we can better understand how different fish species make use of clear-water mangrove forests in the Indo-pacific. This study emphasizes that local environmental context, including substrate composition and seasonal changes, can substantially affect how fish communities utilise and benefit from clear-water mangrove habitats throughout their life history.

3 Functional Diversity of Fish in the Indo-Pacific Clear-water Mangrove Habitat: Habitat Use Patterns and Functional Redundancy

3.1 Introduction

3.1.1 Functional Diversity

In marine ecosystems, the unique features and behaviours of organisms, termed functional traits, are fundamental to ecosystem dynamics. These traits encompass a range of ecological roles, from feeding habits to morphological adaptations (Bellwood et al., 2003; Schleuter, et al., 2010; van der Linden, et al., 2012).

Ecosystem functioning depends on both biodiversity and functional diversity, and is influenced by both environmental context and species distribution (Cadotte et al., 2011; van der Linden et al., 2012). While individual species play crucial roles, the collective diversity of an ecosystem is key to its overall health and productivity. Thus, in studying how species interact with their environment, functional trait analysis aids in understanding the variety of roles different organisms play in their habitats. This approach allows for a deeper understanding of why species live where they do and how they contribute to their environment's health. The understanding of functional diversity is therefore key to protecting and managing natural habitats effectively. It goes beyond taxonomic diversity to consider the role that species play in the ecosystem dynamics (Chao, et al., 2014; Duffy, et al., 2007; Galindo-Uribe, et al., 2022; Magneville, et al., 2022; Stuart-Smith, et al., 2013). It therefore also accounts for redundancy – species that fill the same ecological niche. Functional redundancy is an important measure of the stability of an ecosystem (Cadotte et al., 2011; Delfan, et al., 2021; Gamfeldt & Hillebrand., 2008).

Functional diversity is assessed through various parameters to capture the complexity and multidimensional nature of ecological systems. The three most used functional indices are richness, evenness, and divergence (D'Allesandro et al., 2020; Mammola, et al., 2021; Mason, et al., 2013; Mouchet, et al., 2010; Schleuter, et al., 2010; van der Linden et al., 2012). Functional richness represents the volume of traits space occupied by a community, functional evenness represents how species are distributed in this trait space and accounts for abundances, biomass or species counts, and functional divergence measures how much of the community is associated with the variances and clustering at the edges of the trait space and also accounts for abundances, biomass or species counts. Functional richness therefore encompasses how the trait space of a subset community differs from the metacommunity and how much niche space is occupied (Leibold, et al., 2004). Functional evenness describes the distribution of species within this trait space, the skewness of data and can indicate resource utilisation and productivity. Functional divergence aims to describe resource differentiation and how traits are spread across the trait space (Lin et al., 2021; Mason et al., 2013; Schleuter et al., 2010). Greater differences in the utilisation of resources have been shown to increase the functionality of the ecosystem, and how divergence can be related to competition and resilience (Cadotte et al., 2011).

Diversity can be calculated using two levels of organisation: α-diversity, or β-diversity. For functional diversity, α-diversity describes the functional space within (species, communities, regions etc.), while β-diversity describes the functional space spatiotemporal differences between (species, communities, regions etc.) (Mammola, et al., 2021; Villeger, et al., 2012). β-diversity measures nestedness or turnover, with nestedness investigating if the community traits present is a subset of communities with greater richness. Turnover on the other hand measures environmental filtering, which describes how the existence of certain trait in the environment is controlled by physical factors of the environment (water velocity, salinity, temperature etc.), by indicating unique traits within communities that are not present at communities with greater richness (Walsh, et al., 2022). Taxonomic and functional diversity combined may therefore explain the species habitat use within the ecosystem. For instance, high taxonomic β-diversity but low functional β-diversity may indicate that even though there are differences in species composition between the communities in a population, the functional processes are largely the same (Villeger, et al., 2012).

The functional traits chosen for analysis must therefore reflect the ecological functions that are being investigated (Anderson et al., 2022; Chiu et al., 2014; D'Allesandro, et al., 2020; Galindo-Uribe, et al., 2022; Leps, et al., 2006; Magneville et al., 2022). Functional traits can be morphological or physiological traits which represent utilisation of habitats or trophic structure (e.g. body size, mouth gape, salinity tolerance), trophic traits (e.g. diet), reproductive and ontogenetic traits (e.g. spawning mode, egg size, larval stage duration), or behavioural traits (e.g. schooling behaviour, position in water column). Careful consideration of the research question, the ecological relevance of the traits, as well as how many traits to include and how they are correlated is therefore crucial to accurately represent the ecological functionality (Cadotte et al., 2011; da Silva et al., 2019; Kulbicki et al., 2022; Leps et al., 2006; Paganelli et al., 2012; Schleuter et al., 2010). How traits vary in response to different environmental conditions is also an important question to consider in functional diversity and community dynamics (Dray et al., 2007). For instance, the size of a predator indicates the prey size consumed, but may restrict manoeuvrability, especially in a structurally complex habitats such as the mangrove forest (Scharf, et al., 2000). In clear-water mangrove forests, including salinity tolerance may affect the distribution of data as there is no or a relatively small salinity gradient affecting fauna. This may be an explanatory term for estuarine communities, but may create bias by reducing the functional divergence in a community where it is not relevant. Correlation between traits may also create bias by doubling the effect of one function. Therefore, exclusion of one of the correlated traits, weighing the trait differently, or calculating an ecologically relevant ratio may be used instead. It is therefore more ecologically relevant to investigate the functional differences in traits relating to specific functions, e.g. functional diversity of trophic traits within a community. This better explains the actual habitat use, rather than a general functional diversity index (Leps, et al., 2006). For instance, a ratio between maximum size and average size may be used as an explanatory term to describe the age structure of a community. This could be ecologically relevant in mangrove habitats, as many studies indicate their function as juvenile or nursery habitats (Stuthmann, et al, 2022).

To fully understand the relationship between species and functional diversity, the environmental conditions influencing the community composition must however be considered. Environmental gradients may affect the trait distribution, and thus taxonomic and functional diversity (Cadotte, et al., 2011; Mouchet, et al., 2010). How communities are compared and what reflects the ecosystem boundaries must be established to interpret the biological relevance and the energy flows of the ecosystem (Anderson, et al., 2022). The functional traits can thus also be utilised to describe the environmental conditions of an ecosystem, and how the processes and functions shape the community composition through environmental filtering (Walsh, et al., 2022).

3.1.2 The Indo-Pacific Clear-water Mangroves

Mangrove forests are located in the intertidal zone and are part of the interface between land and sea in the Australian coastal ecosystem mosaic (CEM). Most mangrove forests in Australia exist in estuaries, where the freshwater flow has a more significant impact on community composition. In contrast, most mangroves in the Caribbean are clear-water mangroves, situated on islands or in environments where the terrestrial inputs are less influential than marine inputs. These habitats are however often compared in literature without making the distinction between type of mangrove forest, and clear-water mangroves in the Indo-Pacific remain relatively understudied (Barnes et al., 2012). Clear-water mangroves in the Indo-Pacific are also often affected by larger tidal fluctuations than in the Caribbean, and are thus only inundated for part of the day (Dubuc et al., 2019; Stuthmann et al., 2022). They are however still utilised by species in the seascape, and this translates to connectivity in the seascape (Barnes et al., 2012). To understand the energy flow of a temporally inaccessible habitat to the CEM, one must investigate the taxonomic and functional diversity present in the Indo-Pacific clear-water mangroves, to infer ecosystem processes and functions related, especially as research on clear-water mangroves in the Indo-Pacific is relatively new (Abrantes et al., 2015; Dubuc et al., 2019).

The aims of this study are to: (1) identify changes in functional diversity in clear-water mangroves with varying environmental conditions, and (2) investigate how functional traits are related to environmental filtering and resilience within the seascape. This study thus aims to identify changes in functional diversity in clear-water mangroves with varying environmental conditions to examine how environmental filtering affect a migrating community. It also aims to investigate how species habitat use differs between clear-water mangroves with different environmental conditions in the coastal seascape in Queensland, Australia. The goal of this research is thus to understand how the temporarily accessible clear-water mangrove forests in Australia is utilised by fish in the seascape by using functional traits and behavioural patterns to infer habitat use for foraging and refugia.

3.2 Methodology

Sampling was undertaken along six sites on the western, leeward side of Orpheus Island, which is part of the Palm Island group in the Great Barrier Reef World Heritage Area (Queensland Government, 2021) (Figure 3.1). The mangrove forests at Orpheus Island are clear-water mangroves, near habitats in the seascape such as coral reefs, and with minimal terrestrial freshwater input. The mangrove sites had either benthic substrate consisting predominantly of sand (Site 1 and 2), or rock/boulder (Site 3,4,5). Site 6 had a mixture of sand and rock, and was therefore analysed as ‘mixed’. The mangrove forests mainly consist of the species *Avicennia marina* and *Rhizophora stylosa*. The tides at Orpheus Island are semi-diurnal (Parnell, 1986), and the mangrove forests are inundated for approximately 65 % of the day estimated from the depth loggers. The maximum water depth recorded for the duration of this study was approximately 3 meters at Site 1.

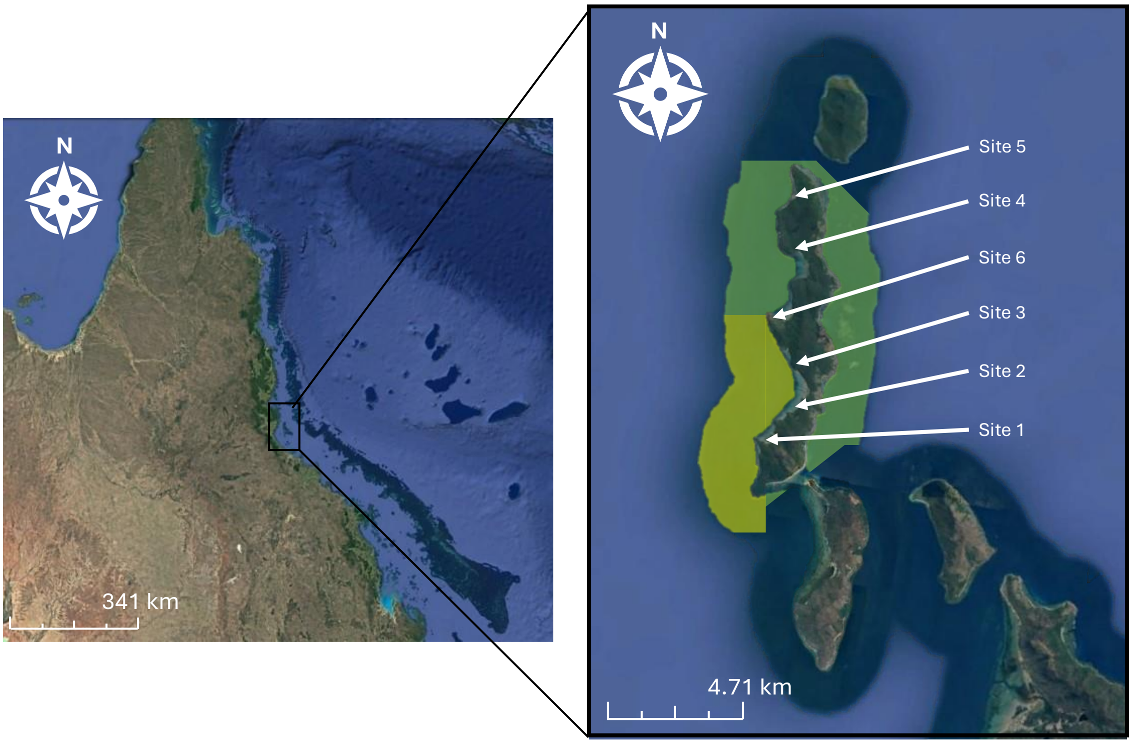

Figure 3.1.

Orpheus Island with Green and Yellow zones according to the Great Barrier Reef Marine Park Authority zoning plan (2017), part of the Palm Island group on the North Queensland coast (18°36’57.85” S, 146°29’49.92” E). The arrows indicate the location of the sites where data were collected (Google Earth, 2023).

3.2.1 Data Collection

Five field trips in July, September and December 2022, and March and August 2023 were completed. Each field trip consisted of four days of field work, with each day representing a replicate per field trip. In total 180 hours and 25 minutes of video recordings were analysed.

A pilot study was conducted on the field trip in July to determine where to place the unbaited remote underwater cameras, estimate at what tidal heigh the habitat was workable and how to optimise camera placement, and estimate how long it takes to travel between sites. On the following field trips remote underwater cameras (GoPro HERO3 Silver Edition HD3.02.03.00 or Adventure Kings Action Camera 1080P Full HD) were deployed along the western edge of the forest, as well as approximately 50 meters further along the edge towards the middle of the forest. Camera placement was conducted so the field-of-view was alongside the forest edge, where it could be determined whether fish were swimming in to, out of, or along the edge of the mangrove forest. Camera deployment was conducted with the rising tide as the water hits the forest edge, or at high tide as it starts to fall. They were placed as to allow the greatest field-of-view of the water column, while being as close to the bottom as possible. The visibility varied with the tidal regime, with lower water levels generally being associated with less visibility. The cameras recorded for approximately 2 hours.

Water level data loggers (HoboWare, HOBO U20L) were placed at two of the six sites, to record the patterns in inundation in the mangrove forest. The water level data loggers were placed at Site 1 and Site 5 in December 2022 and retrieved in August 2023. Water depth (kPa) and temperature (°C) were measured every 20 minutes for the deployment duration.

3.2.2 Data Analysis

Date, tidal regime (rising or falling), substrate type (sand, rock or mixed), fish species and approximate size (cm) were recorded in a central database. Fauna was identified to the lowest taxonomic level by considering their body shape, size, colouration, patterns and behaviour. All species of Abudefduf were counted as one species (*Abudefduf spp.*) given the high presence of juveniles which were difficult to identify to species level. Therefore, even when adults were identified they were counted as *Abudefduf spp*. to reduce skewness in the data due to the differences in size estimates and abundance counts between juveniles and adults. All fish identified were cross-referenced with existing literature and reviewed by independent experts when deemed necessary (Froese & Pauly, 2023; Randall et al., 1996; Stuart-Smith et al., 2015). To prevent repeat counting of the same individual, a fish of the same species and approximate size swimming in front of the camera within 5 minutes of the previous observation, was assumed to be the same individual and therefore not counted. This methodology was adapted from Dubuc et al. (2019). The approximate size of individual fish was estimated using the mangrove roots structure as this allows size comparisons at different distances to the camera. This was determined to be the best course of action, as introducing foreign objects for size estimation may disturb the fauna and thus affect the data collection.

The time of the day the fish were observed was calculated based on when the camera was deployed, and this was correlated with the data loggers to estimate kPa and thus water depth at the time of the observation. The depth was estimated by assuming that the lowest pressure equalled the atmospheric pressure, and this was subtracted from the kPa at the time of the observation and then translated to depth by the formula:

$$\mathrm{mH2O} = \mathrm{kPa}\ \times 0.101972$$

For the sites where a depth logger was not present, the depth was estimated by the difference in kPa from the time the site was inundated in relation to the data from one of the loggers, and the time of the observation. Depth was sorted into six levels (<30 cm, 30-50 cm, 50-70 cm, 70-90 cm, 90-110 cm, 110-190 cm) to account for the variability and error in these calculations affecting the exact water depth, while keeping the highest resolution. This was then verified by randomly selecting a fish observation and estimate the match between the calculated depth intervals and the observed depth.

Data were sorted into two seasons, wet and dry, where the wet season was deemed to have started in October 2022 to April 2023. The dry season was from May 2023 until cameras were collected in August 2023. This was estimated according to the Australian Bureau of Meteorology (2023). Benthic structure was sorted into three categories: predominantly sand (1, or 100 % affiliation with sand substrate), mixed (0.5, of 50 % affiliation with sand and 50 % affiliation with rock/boulder substrate), or predominantly rock/boulders (0, or 0 % affiliation with sand substrate).

A functional diversity analysis was conducted using the ‘mFD’ package in RStudio (Magneville et al., 2022). The traits were sorted into two different categories for the tests: all traits and trophic traits. The traits chosen for the analysis of all traits were: (1) trophic level from Fishbase; (2) position in the water column based on where fish were most frequently observed (Surface, Mid, Bottom), as an ordered factor; (3) average size of species based on observations sorted into categories using an exponential curve of $y=x^{(1.2)}$; (4) schooling behaviour from FishBase as a fuzzy trait for species that exhibit more than one type of schooling (Solitary, Groups (pairs or small groups), Large schools); (5) How often the fish was observed swimming in or out of the forest, contrary to along the edge of the forest, measured as a factor with three levels representing the strength of the affiliation of the fish with the mangroves (Low, Medium, High); (6) mouth form (terminal, subterminal, inferior) estimated from Fishbase and FAO Species Identification Sheet (1983); (7) eye diameter ratio relative to standard length (SL); and (8) horizontal mouth gape ratio, estimated by measuring from the tip of the lip to where the premaxilla and dentary meet, again relative to SL. The traits chosen for the trophic traits were: (1) trophic level from FishBase; (2) position in the water column; (3) average size; (4) mouth form; (5) eye diameter; and (6) mouth gape (Table 3.1). Eye diameter and mouth gape were estimated using ImageJ, where the eye diameter and mouth gape were measured and divided by the SL of the fish in pixels. This was then multiplied with the size of each fish counted from the RUVs, to calculate the eye diameter and mouth gape size of each individual. Five specimens were measured using ImageJ to get body size ratios, when five individuals could not be found in the videos, external footage from iNaturalist was used (iNaturalist. Available from https://www.inaturalist.org. Accessed 9 December 2022). The number of specimens were chosen according to Walsh et al. (2022).

Table 3.1.

Biological trait categories, definitions, and levels used in the functional diversity analyses for both the all-traits and trophic-traits groups.

TRAITS	TYPE OF VARIABLE	LEVELS	CATEGORY
TROPHIC LEVEL	Factor, ordered	2-2.5 2.5-3 3-3.5 3.5-4 4-4.5 4.5-5	All Trophic (Anderson et al., 2022; Henderson et al., 2020; Henderson et al., 2022; Stuart-Smith et al., 2013)
POSITION IN WATER COLUMN	Factor, ordered	Bottom Mid Surface	All Trophic (Henderson et al., 2020, Stuthmann et al., 2022)
AVERAGE SIZE (CM)	Factor, ordered	0-5 5-7 7-10 10-16 16-28 28-54 54-122 122-320	All Trophic (da Silva et al., 2019; Henderson et al., 2020; Stuthmann et al., 2022; Walsh et al., 2022)
SCHOOLING BEHAVIOUR	Fuzzy	Solitary Pairs/Groups Schooling	All (Anderson et al., 2022)
AFFILIATION WITH IN-FOREST VS. EDGE UTILISATION	Factor, ordered	Low Medium High	All (Sheaves, Johnston & Baker, 2016)
MOUTH FORM	Factor, ordered	Terminal Subterminal Inferior	All (Bellwood & Goatley, 2009; Henderson et al., 2022) Trophic (da Silva et al., 2019)
EYE DIAMETER (SL RATIO)	Factor, ordered	0.00772-0.0288 (0.7 %-3 %) 0.0288-0.0498 (3 %-5 %) 0.0498-0.0707 (5 %-7 %) 0.0707-0.0917 (7 % - 9 %) 0.0917-0.113 (9 %-11 %)	All (Bellwood & Goatley, 2009; Henderson et al., 2022) Trophic (Bellwood & Goatley, 2009; da Silva et al., 2019; Henderson et al., 2020; Walsh et al., 2022)
MOUTH GAPE (SL RATIO)	Factor, ordered	0.0317-0.0541 (3 %-5.5 %) 0.0541-0.0763 (5.5 %-7.5 %) 0.0763-0.0985 (7.5 %-10 %) 0.0985-0.121 (10 %-12 %) 0.121-0.143 (12 %-14 %)	All (Bellwood & Goatley, 2009) Trophic (Bellwood & Goatley, 2009; da Silva et al., 2019; Walsh et al., 2022)

Note. All morphological measurements are given as ratios relative to the Standard Length (SL) of each fish species. Citations next to the trait categories refer to key studies that have defined these classifications for functional trait analysis.

All factor variables were ordered, as this can be translated into a continuous scale appropriate for analysis. The continuous functional trait variables were tested for correlation, with ‘maximum size’ and ‘average size from video’ highly correlated (*0.81*), and it was then decided to use the ‘Average size from video’ for the analysis. A distribution matrix was generated based on species biomass per site, season and substrate.

The ‘mFD’ package in RStudio was used to calculate all α and β functional indices (Magneville et al., 2022). First, functional trait-based distances were calculated for all trait groups and communities (site, season, and substrate) using Gower distance and equal weights for traits. Then the multidimensional functional spaces were calculated by performing a PCoA with the trait-based distances. The quality of each functional space was estimated, and the number of PC axes were chosen for each trait group. The functional α diversity indices functional richness, functional evenness and functional divergence were then calculated. Functional richness is the proportion of functional space, or the volume inside the convex-hull describing the functional space. Functional evenness is the regularity of distribution in the functional space, and functional divergence is the proportion of extreme functional traits present close to the edge of the convex-hull functional space. Functional β diversity was then calculated on an occurrence, or presence-absence, distance matrix using the Jaccard index (Magneville et al., 2022).

To evaluate the distribution of species in a functional trait space, a 3D Kernel Density Estimation (KDE) was employed. This analysis was based on the first three principal axes derived from the multidimensional functional diversity (mFD) analysis. These axes represented the most significant dimensions of trait variation among the species in the study. The KDE requires an estimation of a bandwidth matrix, which determines the smoothness of the resulting density estimates. The bandwidth matrix was estimated using Hpi, which implements a plug-in selector method to optimise the matrix for multivariate data. The KDE output provides density estimates over a grid of points in the functional space. These grid points represent a structured three-dimensional array, where the density value at each point indicates the likelihood of species occurrence in that region of the trait space. The 3D KDE heatmap allowed for the identification of regions in the functional space with high species density, corresponding to common trait combinations. On the other hand, regions with low density revealed species that are functionally unique, potentially indicating outliers. These outliers were further examined to understand their ecological significance and potential role in the community. The 3D KDE was performed using the RStudio packages ‘ks’ and ‘plotly’ (Duong et al., 2024; Sievert et al., 2024). Based on the results from the 3D KDE heatmap, the ‘outlier’ species were excluded from analysis and the functional diversity analysis using the ‘mFD’ package was re-run to test how the exclusion of the species at the edge of the trait space affected the functional trait space. To test which traits were driving the differences between axes, species were grouped based on their median values of traits to create a ‘high’ and ‘low’ group, then tested using the Wilcoxon Rank-Sum test to compare the distribution between these groups. The p-values from these tests determine whether the traits significantly differ between groups, indicating which traits drive separation along the PC axes.

Functional redundancy was calculated based on a report by Dick (2023), as well as the code supplied in the supporting information by Dick (2023). In that report, Dick (2023) describes functional redundancy as the extent to which multiple species fulfill similar functional roles. This estimate uses the Gini-Simpson index (D) which represents the probability of selecting two species at random and which accounts for species richness and abundances, and a generalized form of the Gini-Simpson index referred to as Q which extends it by integrating the functional dissimilarity between species. Functional redundancy can thus be calculated according to de Bello et al. (2007) or Ricotta et al. (2016). According to de Bello et al. (2007), absolute functional redundancy can be defined as the absolute differences between the Gini-Simpson index D and Q, and quantifies how much functional diversity is ‘redundant’ in the community. According to Ricotta et al. (2016), functional redundancy is defined as the relative difference between D and Q, and normalized by D. It expresses redundancy as a proportion of the community’s total functional diversity. Functional redundancy was calculated using both de Bello et al. (2007) and Ricotta et al. (2016).

A fourth corner and RLQ analysis was performed to test how the traits varied with environmental filters using the ‘ade4’ package in RStudio (Dray & Dufour, 2007). For the co-inertia RLQ analysis, a correspondence analysis was performed on the distance data, a PCoA analysis on the trait data, and a Hill-Smith function that allows for both quantitative and categorical variables was used on the environmental data. Trait weights were established using equal weights for all traits, and ⅓ for the three fuzzy-coded traits. The RLQ analysis was then performed and compared to the separate analyses performed on the species, trait and environmental data. A multivariate test was done to test the significance of the traits-environment relationships using the total inertia, or correspondence between rows and columns, of the RLQ analysis. Then, the links between the RLQ axes and the traits and environmental variables were tested directly. The fourth corner analysis was then conducted to test the statistical significance of the inertia, using 49999 permutations for model 2, model 4 and model 6. model 6 is a combination of model 2, which permutates the rows of the species-environment table and thus test if there is a relationship between species traits and environmental variables when the species distribution is random across sites, and model 4, which permutates the traits table and thus test if the observed trait-environment association are more than what would be expected by random distribution of traits among species. Model 6 thus permutates within columns of the species-environment table and test if species with certain traits are more likely to occur in certain environmental conditions, regardless of the overall site characteristics. The analysis was done using False Discovery Rate (FDR) p-value adjustment to reduce the risk of false-positive results. Finally, a random forest analysis was conducted to investigate the relative importance of environmental variables, such as substrate type, season, depth, and species identity, in predicting fish size, fish size ratio and trophic level. The analyses were performed using the ‘ranger’ package in Rstudio (Wright & Ziegler, 2017), fitting a regression model with the chosen trait as the response variable and the environmental variables as predictors. The model was built using 500 trees and a randomly selected subset of two predictors (mtry = 2) at each split. Variable importance was calculated using the impurity measure, which reflects the decrease in node impurity contributed by each variable. The model was trained on a dataset with 4,576 observations, and out-of-bag (OOB) error estimation was used to evaluate model performance, resulting in mean squared errors (MSE) and R^2 values indicative to a strong predictive ability. Partial dependence plots were generated to interpret the relationships between predictors and the response variable, providing insights into how substrate, depth, season, and species influence the chosen traits. Additionally, Shapley additive explanations (SHAP) were employed to assess the contributions of individual predictors for specific observations, further clarifying the importance and influence of the environmental variables in the model. The RLQ and fourth-corner was used to identify broad linear patterns and complementary gradients in traits and environments, while the Random Forest models explore the non-linearities, thresholds, and complex interactions of the significant traits that may be hard to interpret form the RLQ and Fourth-corner analyses. This research aimed to establish the taxonomic and functional diversity present in clear-water mangroves in the Indo-Pacific, however, as only one island was investigated the patterns found in this study should be compared with other clear-water mangroves in the Indo-Pacific to establish how these findings relate to local variations and habitat use patterns.

3.3 Results

A total of 5,513 individuals belonging to 70 species in 28 families counted from the mangrove videos were sorted into communities based on sites, seasons and substrates. The functional indices richness, evenness and divergence were calculated for all functional trait groups and all communities. For the 6-dimensional functional space for all functional traits the 1st axis explains 31.9 % and the 2nd axis explain 16.48 %. For the 5-dimensional space for the trophic traits the 1st axis explains 30.42 % and the 2nd axis explain 17.15 % of the variation.

3.3.1 Diversity across Sites

The functional richness observed varied from values around or below 0.1 to above 0.4 for both trait groups, indicating that the sites differed in the functional traits present both when all traits and the trophic traits were considered (Table 3.2). The functional divergence was relatively consistent across all sites and trait groups. Site 2 consistently had the highest functional richness, and relatively high functional divergence, indicating that it fills a large proportion of the trait space, but that many of the species driving this exist at the edge of the trait space. Site 3, on the other hand, had lower richness and divergence, but higher evenness indicating that this community is more balanced although less functional space is occupied. Site 1, when all traits were considered, had both low richness and evenness, but high divergence indicating that the community is imbalanced, fills a small proportion of the trait space, and is driven by species at the edge of the trait space. For trophic traits Site 1 had higher evenness, indicating that the trophic community is more balanced, but it still exhibited low richness and high divergence (Table 3.2).

Table 3.2.

This table combines data on the site-based (a) species richness and (b) alpha (α) functional indices (functional richness, evenness, divergence) calculated for both the entire trait set (ALL) and the subset of trophic traits (TROPHIC).

SITE	SPECIES RICHNESS (a)
1	21
2	37
3	25
4	28
5	40
6	42

TRAIT GROUP	SITE	FUNCTIONAL RICHNESS	FUNCTIONAL EVENNESS	FUNCTIONAL DIVERGENCE (b)
ALL	1	0.1029	*0.2555*	**0.9370**
	2	**0.4354**	0.5073	0.9048
	3	*0.0822*	**0.5393**	*0.7650*
	4	0.0961	0.4569	0.8292
	5	0.1577	0.3994	0.8480
	6	0.2405	0.4723	0.8881
TROPHIC	1	0.0685	0.4190	**0.9017**
	2	**0.4242**	0.3967	0.8842
	3	*0.0470*	0.4216	*0.7410*
	4	0.1124	*0.3692*	0.8160
	5	0.3100	0.3952	0.8013
	6	0.3099	**0.4391**	0.8703

Note. (a) species richness per site, n = 70, total number of species. Species richness indicates the total number of species per site. (b) Functional indices represent the distribution of species' traits: richness (trait range), evenness (distribution uniformity), and divergence (deviation from the community trait centre). Bold values indicate the highest, and italicized values the lowest, within each trait group.

The highest β-functional diversity, measured as Jaccard dissimilarity, occurred between Sites 2 and 4 for the all-trait group, and between Sites 2 and 3 for the trophic trait group (Table 3.3). In both cases, most of the observed dissimilarity was attributed to Jaccard turnover (i.e., species replacement) rather than nestedness (i.e., one site's community being a subset of the other). These results indicate that the functional trait differences among these sites mostly comes from having distinct sets of species or functional traits, rather than one of the sites having a subset of the species or traits present at the other one.

Table 3.3.

Jaccard beta (β) functional indices (dissimilarity, turnover, and nestedness) for each pairwise comparison among six sites, calculated for the two trait groups ("All" and "Trophic").

TRAIT GROUP	SITE X1	SITE X2	JACCARD DISSIMILARITY	JACCARD TURNOVER	JACCARD NESTEDNESS
ALL trophic level position in the water column average size schooling behaviour swimming in or out of the forest mouth form eye diameter ratio horizontal mouth gape ratio	1	2	0.7430	0.3750	0.3680
	1	3	0.6520	0.5434	0.1086
	1	4	0.6795	0.5774	0.1021
	1	5	0.5789	0.5483	0.0306
	1	6	0.5007	0.1502	0.3505
	2	3	0.8054	0.3257	0.4797
	2	4	**0.8641**	0.5733	0.2908
	2	5	0.7318	0.4098	0.3221
	2	6	0.5766	0.3812	0.1954
	3	4	0.5803	0.5762	0.0041
	3	5	0.6014	0.4217	0.1797
	3	6	0.6817	0.2639	0.4178
	4	5	0.5935	0.4007	0.1928
	4	6	0.6746	0.2288	0.4458
	5	6	*0.4888*	0.2157	0.2731
TROPHIC trophic level position in the water column average size mouth form eye diameter ratio horizontal mouth gape ratio	1	2	0.8609	0.2164	0.6444
	1	3	0.7111	0.6198	0.0912
	1	4	0.7590	0.6550	0.1040
	1	5	0.8442	0.4063	0.4379
	1	6	0.7863	0.0532	0.7331
	2	3	**0.9240**	0.4515	0.4725
	2	4	0.8839	0.6699	0.2140
	2	5	0.6836	0.6021	0.0814
	2	6	0.5656	0.4408	0.1249
	3	4	0.6194	0.1215	0.4979
	3	5	0.8501	0.0189	0.8313
	3	6	0.8606	0.1324	0.7282
	4	5	0.7307	0.3374	0.3934
	4	6	0.7334	0.3463	0.3871
	5	6	*0.5162*	0.5160	0.0002

Note. Jaccard dissimilarity ranges from 0 to 1, with higher values indicating greater differences in trait composition between sites. Site X1 and X2 refers to the sites being compared. Turnover quantifies dissimilarity driven by species or trait replacement, whereas nestedness captures dissimilarity resulting from one site being a subset of another. Bold values represent the highest Jaccard dissimilarity for each trait group, and italicized values represent the lowest.

These differences between sites are visualised in the multidimensional spaces of Figure 3.2. The differences in functional richness between Sites 2 and 4 are mostly driven by Jaccard turnover, as can be seen in the different shapes of the functional space. The differences are mostly driven by the species *Pseudomugil signifier*, *Fibramia lateralis*, *Urogymnus granulatus* and *Pastinachus sephen* which are present at the edges of the trait space at Site 2. These species drive the higher functional richness found at Site 2 by existing at the edge of the trait space, and thus creating 'empty space' between species. As functional richness is a convex hull volume, these species disproportionately drive the functional richness found at Site 2. At site 4, most species are centred and there are less species at the edge of the trait space driving the differences.

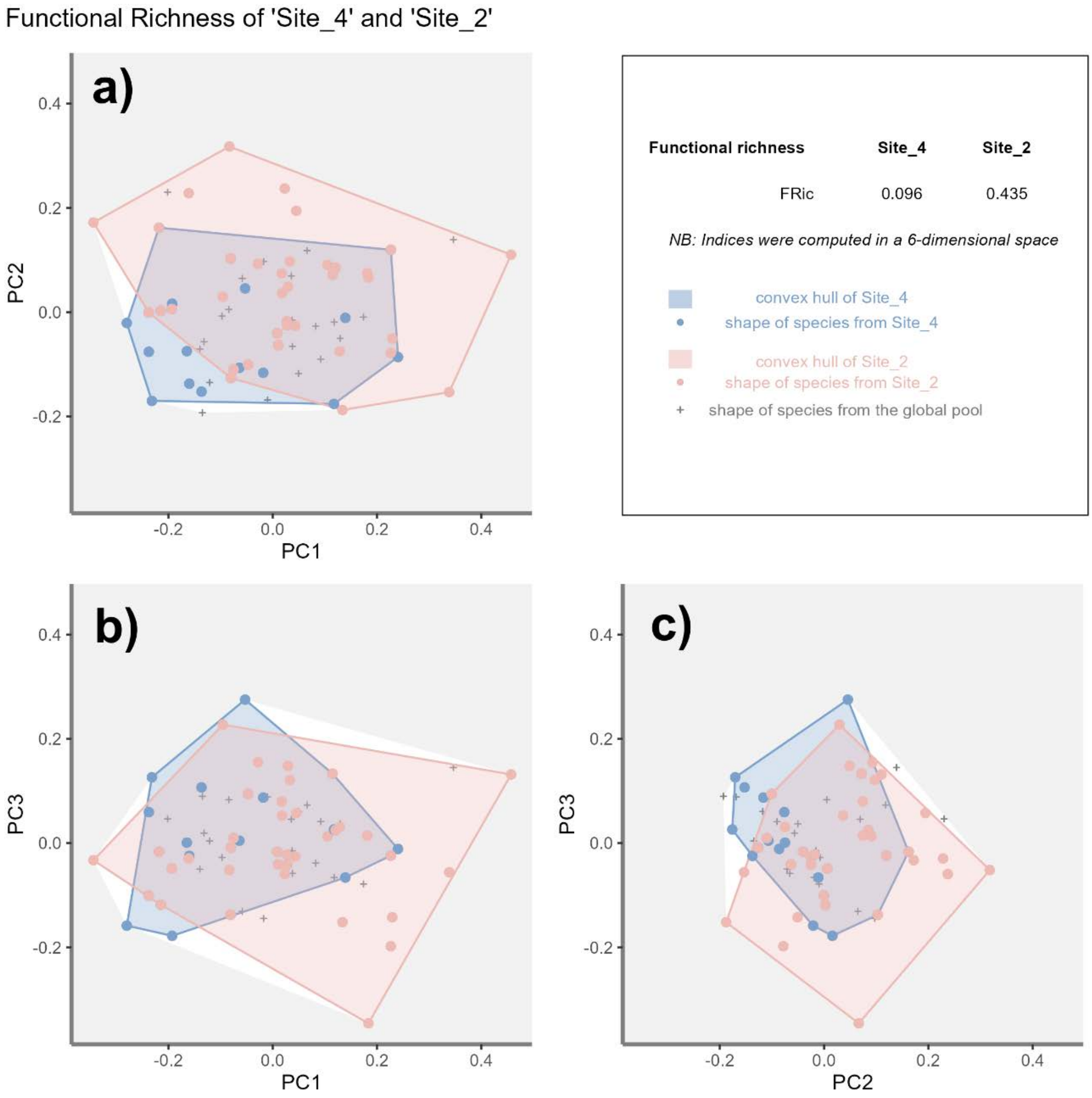

Figure 3.2.

Multidimensional visualization of functional richness for all traits for site 2 (pink) and 4 *(blue) across the first three principal component (PC) axes: (a) PC1 and PC2, (b) PC1 and PC3, (c) PC2 and PC3. Each dot represents a fish species, and the polygons outline the convex hull for each site. Site 2 exhibits a larger polygon because species at the edges of the trait space expand the functional trait space. In contrast, Site 4 has fewer edge species, resulting in a smaller polygon.*

For the trophic traits there are similar patterns, and the drivers of the differences in trophic traits between Sites 2 and 3 are from the species *Gerres spp.*, *Fibramia lateralis*, *Pseudomugil signifier*, *Pateobatis fai*, *Aetobatus ocellatus*, *Negaprion acutidens*, *Pastinachus sephen* and *Urogymnus granulatus* (Figure 3.3).

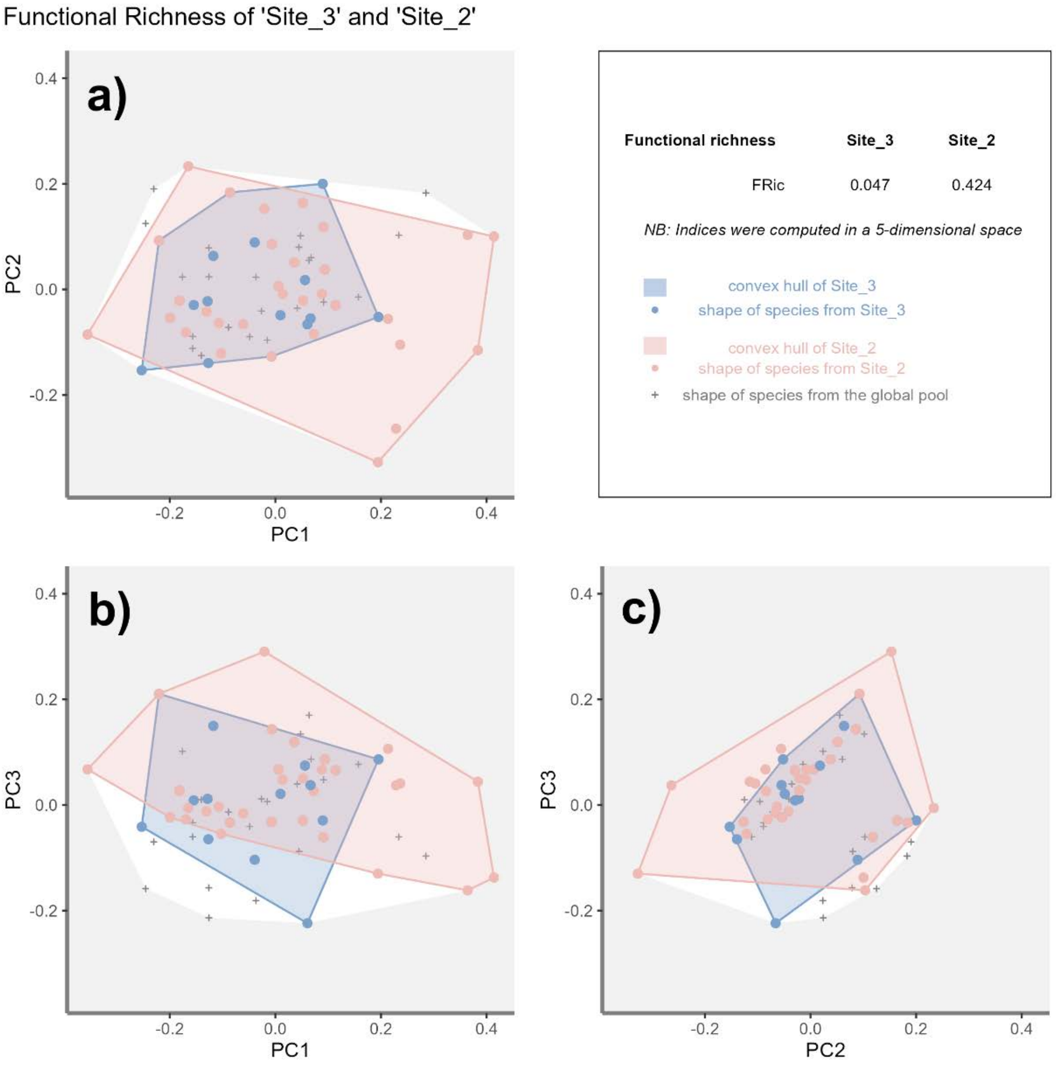

Figure 3.3.

Multidimensional visualization of functional richness for the trophic traits for site 2 (pink) and 3 (blue) across the first three principal component (PC) axes: (a) PC1 and PC2, (b) PC1 and PC3, (c) PC2 and PC3. Each dot represents a fish species, and the polygons *outline the convex hull for each site. Site 2 again exhibits a larger functional trait space driven by species at the edge of the polygon.*

3.3.2 Diversity across Substrates

For the communities based on substrates, the patterns that emerged when comparing the sites become clearer. Sand substrate had higher richness and divergence, but lower evenness, once again indicating that a large proportion of the trait space is filled, but mostly driven by species at the edge of the trait space and a less balanced community. The rock substrate, on the other hand, had a relatively balanced community although less of the trait space was filled even though it had the highest species richness (Table 3.4).

Table 3.4.

This table combines data on the substrate-based (a) species richness and (b) alpha (α) functional indices (functional richness, evenness, divergence) calculated for both the entire trait set (ALL) and the subset of trophic traits (TROPHIC).

SUBSTRATE	**SPECIES RICHNESS** (a)
ROCK	51
MIXED	42
SAND	45

TRAIT GROUP	**SUBSTRATE**	**FUNCTIONAL RICHNESS**	**FUNCTIONAL EVENNESS**	**FUNCTIONAL DIVERGENCE** (b)
ALL	Rock	0.3257	**0.7080**	*0.7804*
	Mixed	*0.2406*	0.6575	0.8065
	Sand	**0.6065**	*0.6532*	**0.8605**
TROPHIC	Rock	0.4226	**0.6568**	0.7929
	Mixed	*0.3099*	0.6566	*0.7918*
	Sand	**0.5114**	*0.5947*	**0.8171**

Note. (a) species richness, n = 70, total number of species. Species richness indicates the total number of species per substrate. (b) Functional indices represent the distribution of species' traits: richness (trait range), evenness (distribution uniformity), and divergence (deviation from the community trait centre). Bold values indicate the highest, and italicized values the lowest, within each trait group.

The highest β-functional diversity in the form of Jaccard dissimilarity was found between rock and sand substrate for both trait groups. For both trait groups, turnover, or the proportion of dissimilarity due to species or traits replacement, was the highest. Especially for the trophic trait group, where most of the dissimilarity comes from Jaccard turnover (Table 3.5).

Table 3.5.

Jaccard beta (β) functional indices (dissimilarity, turnover, and nestedness) for each pairwise comparison among the three substrates, calculated for both trait groups (“All” and “Trophic”).

TRAIT GROUP	SUBSTRATE X1	SUBSTRATE X2	JACCARD DISSIMILARITY	JACCARD TURNOVER	JACCARD NESTEDNESS
ALL	Rock	Mixed	*0.4538*	0.3253	0.1285
	Rock	Sand	**0.5926**	0.3786	0.2140
	Mixed	Sand	0.5661	0.1108	0.4554
TROPHIC	Rock	Mixed	*0.5064*	0.3591	0.1473
	Rock	Sand	**0.6446**	0.5920	0.0526
	Mixed	Sand	0.5568	0.3137	0.2431

Note. Jaccard Dissimilarity reflects differences in species composition between substrates, Jaccard Turnover indicates dissimilarity due to species replacement, and Jaccard Nestedness shows dissimilarity from one substrate having a subset of the traits present at another substrate. Bold values represent the highest Jaccard dissimilarity per trait group, and italicized values represent the lowest. Data are calculated across three substrates (Sand, Rock, Mixed) and two trait groups ("All" and "Trophic").

The species at the edge of the trait space in the sand substrate become apparent in all figures in Figure 3.4. The sand substrate has almost double the functional richness of the rock substrate (Table 3.4 & Figure 3.5), but much of these differences are explained by the species at the edge of the trait space for both trait groups; *Pseudomugil signifier*, *Fibramia lateralis*, *Urogymnus granulatus*, *Pastinachus sephen* and *Aetobatus ocellatus*. There is also a split in the community apparent between axes PC2 and PC3 for the trophic traits.

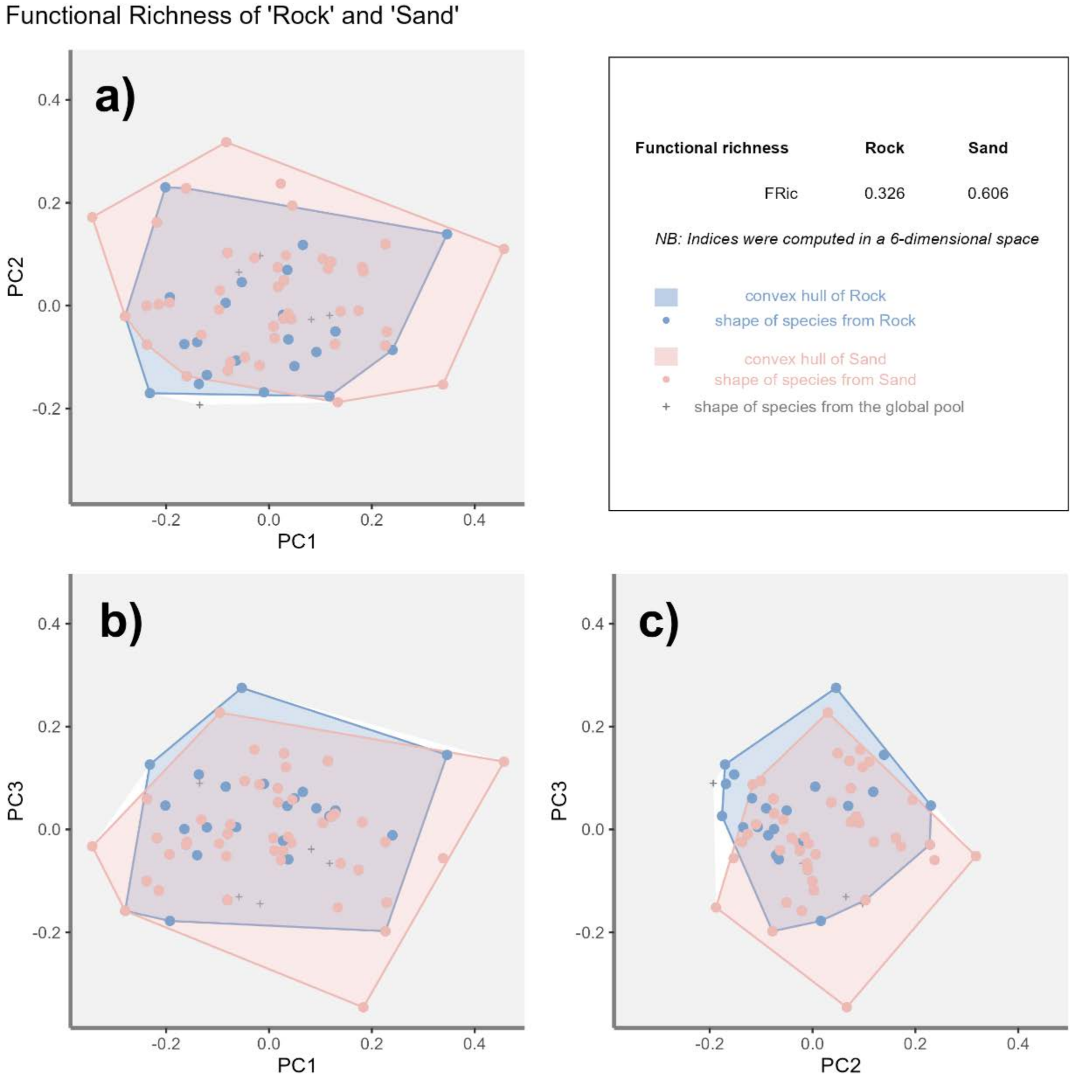

Figure 3.4.

Multidimensional visualization of functional richness for all traits for sand substrate (pink) and rock substrate (blue) across the first three principal component (PC) axes: (a) PC1 and PC2, (b) PC1 and PC3, (c) PC2 and PC3. Each dot represents a fish *species, and the polygons outline the convex hull for each substrate. Sand substrate exhibits a larger functional trait space driven by species at the edge of the polygon.*

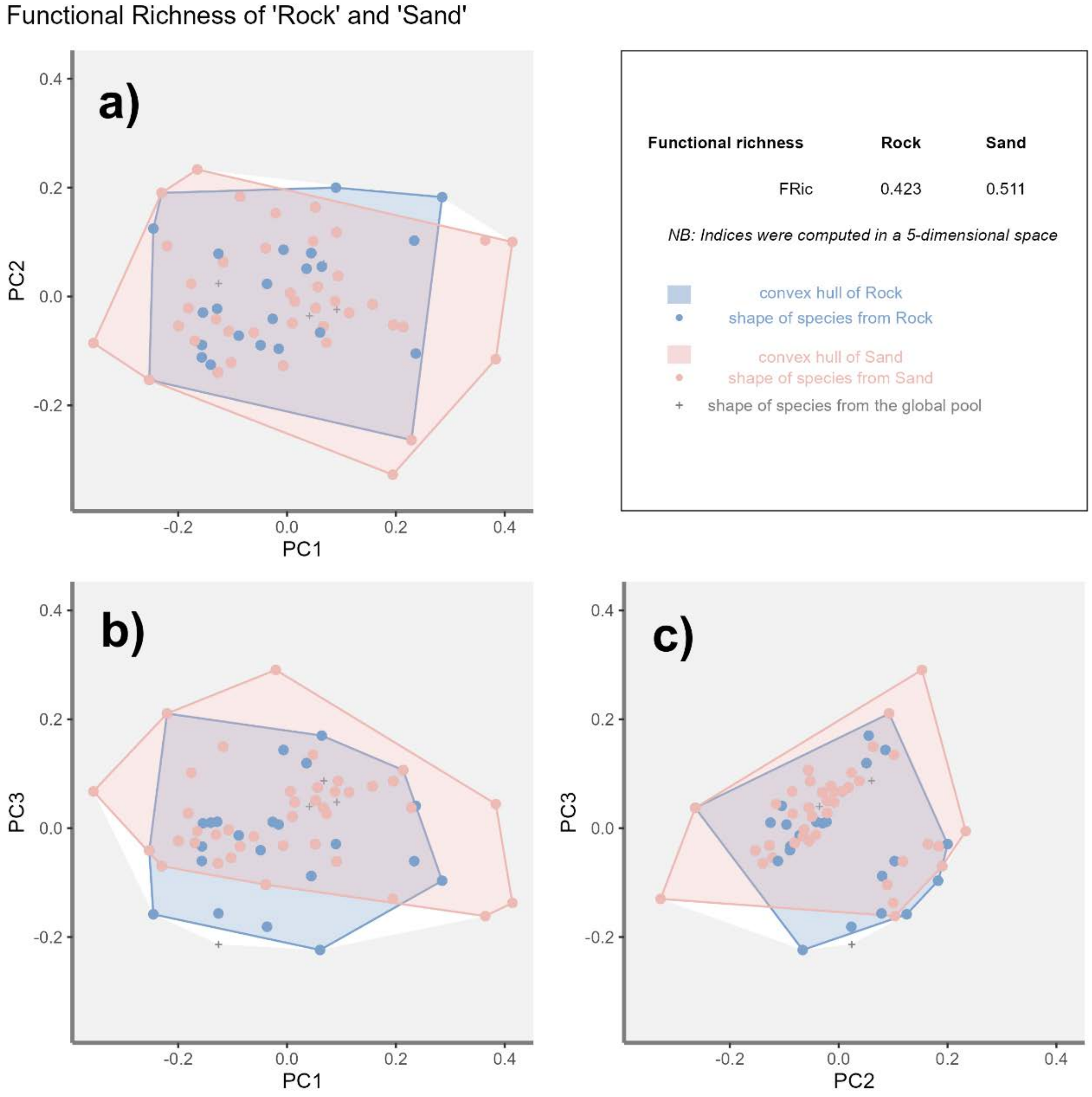

Figure 3.5.

Multidimensional visualization of functional richness for the trophic traits for sand substrate (pink) and rock substrate (blue) across the first three principal component (PC) axes: (a) PC1 and PC2, (b) PC1 and PC3, (c) PC2 and PC3. Each dot represents a fish species, and the polygons outline the convex hull for each substrate. Sand substrate exhibits a larger functional trait space driven by species at the edge of the polygon.

3.3.3 Diversity across Seasons

The differences in functional diversity were smaller between seasons, with the dry season having slightly higher functional richness and evenness for both trait groups, indicating that a similarly sized functional space is filled across the seasons although the species composition differs (Table 3.6).

Table 3.6.

This table combines data on the season-based (a) species richness and (b) alpha (α) functional indices (functional richness, evenness, divergence) calculated for both the entire trait set (ALL) and the subset of trophic traits (TROPHIC).

SEASON	**SPECIES RICHNESS** (a)
WET	55
DRY	62

TRAIT GROUP	**SEASON**	**FUNCTIONAL RICHNESS**	**FUNCTIONAL EVENNESS**	**FUNCTIONAL DIVERGENCE** (b)
ALL	Dry	**0.6562**	**0.6595**	**0.8345**
	Wet	*0.6203*	*0.6298*	*0.8315*
TROPHIC	Dry	**0.6877**	**0.7010**	*0.7991*
	Wet	*0.5935*	*0.5992*	**0.8202**

Note. (a) Species richness, n = 70, total number of species. Species richness indicates the total number of species per season. (b) Functional indices represent the distribution of species' traits: richness (trait range), evenness (distribution uniformity), and divergence (deviation from the community trait centre). Bold values indicate the highest, and italicized values the lowest, within each trait group.

The β-functional diversity in the form of Jaccard dissimilarity between seasons indicated that most of the differences could be explained by turnover, and thus a different set of traits present across seasons. This indicates that although the functional space is similar throughout the year, different species and sets of traits fill these functions (Table 3.7).

Table 3.7.

Jaccard beta (β) functional indices (dissimilarity, turnover, and nestedness) for each pairwise comparison among the two seasons, calculated for both trait groups (“All” and “Trophic”).

TRAIT GROUP	SEASON X1	SEASON X2	JACCARD DISSIMILARITY	JACCARD TURNOVER	JACCARD NESTEDNESS
ALL	Dry	Wet	0.4296	0.3439	0.0856
TROPHIC	Dry	Wet	0.5082	0.4476	0.0605

Note. Jaccard Dissimilarity reflects differences in species composition between seasons, Jaccard Turnover indicates dissimilarity due to species replacement, and Jaccard Nestedness shows dissimilarity from one season having a subset of the traits present at another season. Data are calculated across two seasons (Dry, Wet) and two trait groups ("All" and "Trophic").

3.3.4 Drivers of the Functional Diversity

The KDE analysis revealed that the differences in functional diversity were largely driven by species present at the edge of the trait space; *Urogymnus granulatus, Taenuria lymma, Pateobatis fai* and *Aetobatus ocellatus* for the all-trait group, and *Pseudomugil signifier*, *Fibramia lateralis*, *Negaprion acutidens*, *Aetobatus ocellatus*, *Pastinachus sephen*, *Taenuria lymma* and *Urogymnus granulatus* for the trophic trait group. These findings are in line with the observed patterns from the multidimensional space for functional richness (Figure 3.2, Figure 3.3, Figure 3.4 & Figure 3.5), but more detailed as the KDE analysis allows for clearer understanding of how species are related in the trait space. The presence of these species belonging to the Batoidea and the smaller, more estuarine associated, species driving the functional richness thus seem to be part of the explanation of the different functional spaces observed. The specific species driving the differences for each trait group were therefore excluded, to test how the functional diversity was affected.

A majority of the excluded species were present in the sand substrate, as is further indicated by the lower species richness after the exclusion. The exclusion of these species also reduced the total trait space available, and the rock substrate thus filled a larger proportion of it. However, for the trophic traits, the functional richness of the sand substrate became drastically lower, and the rock substrate now exhibited the highest richness, evenness and divergence (Table 3.8). The Jaccard dissimilarity after exclusion also indicated that a larger proportion of the dissimilarity was explained by nestedness rather than turnover, indicating that when these species at the edge of the trait space were excluded, the dissimilarity between substrates are driven by one of the communities being a subset of the other (Table 3.9).

Table 3.8.

This table combines data on the substrate-based (a) species richness and (b) alpha (α) functional indices (functional richness, evenness, divergence) calculated for both the entire trait set (ALL) and the subset of trophic traits (TROPHIC), after exclusion of the species at the edge of the trait space.

TRAIT GROUP	**SUBSTRATE**	**SPECIES RICHNESS** (a)
ALL	Rock	50
	Mixed	41
	Sand	42
TROPHIC	Rock	48
	Mixed	39
	Sand	39

TRAIT GROUP	**SUBSTRATE**	**FUNCTIONAL RICHNESS**	**FUNCTIONAL EVENNESS**	**FUNCTIONAL DIVERGENCE** (b)
ALL	Rock	0.4142	**0.7131**	*0.7944*
	Mixed	*0.2961*	0.6600	0.8249
	Sand	**0.6095**	*0.6519*	**0.8824**
TROPHIC	Rock	**0.7024**	**0.7069**	**0.8381**
	Mixed	0.5347	0.6923	0.8373
	Sand	*0.5247*	*0.6607*	*0.8091*

Note. (a) Species richness, n = 66 for the all-trait group, and n = 63 for the trophic trait group. Species richness indicates the total number of species per substrate. (b) Functional indices represent the distribution of species' traits: richness (trait range), evenness (distribution uniformity), and divergence (deviation from the community trait centre). Bold values indicate the highest, and italicized values the lowest, within each trait group.

Table 3.9.

Jaccard beta (β) functional indices (dissimilarity, turnover, and nestedness) for each pairwise comparison among the two seasons, calculated for both trait groups ("All" and "Trophic"), after exclusion of the species at the edge of the trait space.

TRAIT GROUP	**SUBSTRATE X1**	**SUBSTRATE X2**	**JACCARD DISSIMILARITY**	**JACCARD TURNOVER**	**JACCARD NESTEDNESS**
ALL	Rock	Mixed	*0.4476*	0.2736	0.1740
	Rock	Sand	**0.5107**	0.3906	0.1201
	Mixed	Sand	0.4941	0.1233	0.3709
TROPHIC	Rock	Mixed	*0.3546*	0.0655	0.2891
	Rock	Sand	**0.5098**	0.2136	0.2963
	Mixed	Sand	0.4062	0.3340	0.0722

Note. Jaccard Dissimilarity reflects differences in species composition between substrates, Jaccard Turnover indicates dissimilarity due to species replacement, and Jaccard Nestedness shows dissimilarity from one site having a subset of the traits present at another site. Bold values represent the highest Jaccard dissimilarity per trait group, and italicized values represent the lowest. Data are calculated across three substrates (Sand, Rock, Mixed) and two trait groups ("All" and "Trophic").

The KDE analysis combined with the significant traits of each PC axis highlighted the key drivers of variation across species (See Appendix B, Figure B.4 & Figure B.5). For all traits, PC1 was driven by body size, trophic level, and social behaviour. Larger, solitary predators such as *Aetobatus ocellatus, Negaprion acutidens,* and *Pastinachus sephen* clustered together due to their higher trophic levels, contrasting with smaller, schooling species like *Pseudomugil signifier*, which feed at lower trophic levels. This axis illustrates how predatory strategies and schooling behaviour define species roles, with apex predators dominating one end and smaller prey-focused species at the other. PC2 was driven by differences in water column position and social behaviour. Mid-water and surface-dwelling species like *Fibramia lateralis* were contrasted with benthic species such as *Urogymnus granulatus* and *Taenuria lymma*. This axis captures the gradient between open-water species and benthic specialists, as well as the distinction between solitary species and those forming small groups, reflecting the influence of social behaviour and habitat preference on ecological roles. PC3 incorporated body size along with the traits defining PC2, further differentiating species based on the interaction between size, habitat preference, and social behaviour. Larger species with specific habitat preferences, such as *Pateobatis fai*, were distinguished from smaller species, emphasizing how size shapes functional niches and ecological interactions.

In the analysis of trophic traits, PC1 separated species based on their roles in the food web and morphological features, such as eye diameter and mouth gape. Larger predators like *Aetobatus ocellatus* and *Negaprion acutidens* exhibited adaptations for predatory behaviour that distinguished them from smaller species like *Pseudomugil signifier*. This axis demonstrates the importance of morphological adaptations in defining trophic roles, with larger predators positioned at the top of the food web and smaller species at lower trophic levels. PC2 reflected differences in water column position and feeding adaptations, separating species like *Fibramia lateralis*, which possesses traits for visual hunting of small prey, from benthic species such as *Urogymnus granulatus* and *Taenuria lymma*, which exhibit seabed-feeding specializations. PC3 combined body size with traits defining PC2, providing a nuanced view of how size interacts with habitat and feeding specializations. Larger benthic species, such as *Pateobatis fai*, were contrasted with smaller mid-water species, indicating that this axis represents specialized ecological niches where size, habitat preference, and feeding behaviour converge. These results highlight the importance of functional traits in shaping species' ecological roles and defining their niches within the ecosystem.

3.3.5 Functional Traits and Environmental Context

The functional redundancy calculated from Dick (2023) indicated similar values across all substrates for both de Bello and Ricotta redundancy. For sites there was a larger spread, with Site 1 having the lowest redundancy and Site 6 the highest (Table 3.10 & Table 3.11).

Table 3.10.

Absolute (de Bello) and relative (Ricotta) functional redundancy metrics for six sites (1 through 6) and three substrate types (sand, rock, mixed). The values are adapted from Dick (2023) to illustrate how redundancy varies within different habitats and among sites.

	de Bello	Ricotta	General
SITE 1	*0.606*	*0.377*	1.003
SITE 2	1.167	0.536	1.01
SITE 3	0.622	0.383	*1.003*
SITE 4	0.848	0.458	1.005
SITE 5	1.179	0.539	1.009
SITE 6	**1.426**	**0.585**	**1.012**
SAND	2.334	0.693	**1.032**
ROCK	**2.336**	**0.695**	1.03
MIXED	*2.286*	*0.689*	*1.027*

Note. Absolute and relative redundancy values are calculated using de Bello et al. (2007) and Ricotta et al. (2016) metrics based on Dick (2023). These redundancy measures reflect functional redundancy across sites and substrates. Bold values represent the highest value per trait group, and italicized values represent the lowest. Calculations follow a generalized Hill numbers framework, providing a flexible approach to comparing functional redundancy across communities.

Table 3.11.

Absolute (de Bello) and relative (Ricotta) functional redundancy metrics for six sites (1 through 6) and three substrate types (sand, rock, mixed). The values are adapted from Dick (2023) to illustrate how redundancy varies within different habitats and among sites after excluding species at the edge of the trait space.

	de Bello	Ricotta	General
Site 1	*0.578*	*0.365*	1.003
Site 2	1.098	0.521	1.01
Site 3	0.622	0.383	*1.003*
Site 4	0.848	0.458	1.005
Site 5	1.161	0.535	1.009
Site 6	**1.384**	**0.578**	**1.012**
Sand	*2.189*	*0.680*	**1.032**
Rock	**2.299**	**0.691**	1.03
Mixed	2.206	0.682	*1.027*

Note. Absolute and relative redundancy values are calculated using de Bello et al. (2007) and Ricotta et al. (2016) metrics based on Dick (2023). These redundancy measures reflect functional redundancy across sites and substrates. Bold values represent the highest value per trait group, and italicized values represent the lowest. Calculations follow a generalized Hill numbers framework, providing a flexible approach to comparing functional redundancy across communities.

For the RLQ analysis, the 1st axis explained 90.27 % of the inertia or covariance. The Monte-Carlo permutation test with 9999 repetitions of Model 6 to assess the significance of the RLQ axes through the fourth-corner analysis indicated that Model 2 had a significant p-value ($p < 0.001$), suggesting that the relationships observed are unlikely to be due to random chance, while Model 4 was non-significant for both trait groups. Model 2 explains the relationship between species traits and environmental variables when the species distribution is random across sites and a significant relationship indicates associations between species traits and environmental variables.

The RLQ and Fourth-corner analyses revealed several significant associations between environmental factors and fish traits. Substrate type was associated with multiple traits, including trophic level, size ratio, average size, and mouth gape, indicating the importance of substrate in shaping functional characteristics. Depth influenced traits like eye diameter and mouth gape, suggesting adaptive responses to environmental gradients. Significant relationships, as reflected in the adjusted p-values, highlight the role of these environmental factors in structuring functional traits in fish assemblages (Table 3.12). Substrate and depth therefore had the largest influence on species traits. According to model 2, environmental factors thus influence which fish traits are more common, but environmental context alone doesn’t determine which fish species are present based on their traits.

Table 3.12.

Results of the combined RLQ and Fourth-corner analysis examining the influence of environmental variables on species traits. Test stat. represents the test statistic. Obs. the observed test statistic. Std.obs represents the standardized version of the observed test statistic, and p.adj the adjusted p-value obtained from a Monte-Carlo permutation test under Model 2, which evaluates associations between the environmental variables and species traits.

ENVIRONMENTAL VARIABLE	TRAIT	TEST STAT.	OBS.	STD. OBS	ADJUSTED p-VALUE
Substrate	**Trophic level**	Chi2	1597.76	0.1198	0.00010
Substrate	**Size ratio**	Chi2	1243.08	0.5169	0.00010
Substrate	**Size**	Chi2	1320.77	7.1730	0.00010
Substrate	**Mouth gape**	Chi2	2145.13	1.1619	0.00010
Depth	**Eye diameter**	Chi2	1456.96	2.4989	0.04174
Substrate	**Eye diameter**	Chi2	2290.18	8.6788	0.00010
Depth	**Mouth gape**	Chi2	1797.87	2.8472	0.02498

Note. Where p.adj (FDR) < 0.05, the trait's distribution is considered significantly linked to the specified environmental factor, based on the RLQ and Fourth-corner analyses. Std.obs quantifies how extreme the observed value is relative to the distribution of the test statistic under the null hypothesis (i.e., no association). A positive std.obs indicates that the observed association is stronger (or in the positive direction) than what would be expected by chance, and a negative that the observed association is weaker (or in the negative direction) than what would be expected by chance.

The Random Forest regression model for predicting fish size explained a substantial portion of the variance, with an out-of-bag (OOB) R^2 of 0.841, indicating that 84.1% of the variation in fish size was accounted for by the model. The OOB mean squared error (MSE) was 32.70. Among the predictors, species identity was the most influential variable, followed by depth, substrate type, and season. Partial dependence plots revealed that sand substrates were associated with smaller fish sizes, while rock and mixed substrates were linked to larger sizes. Depth exhibited a non-linear relationship with fish size, with intermediate depths associated with the largest individuals (Figure 3.6). Additionally, fish size tended to be slightly smaller during the wet season compared to the dry season, but not significantly.

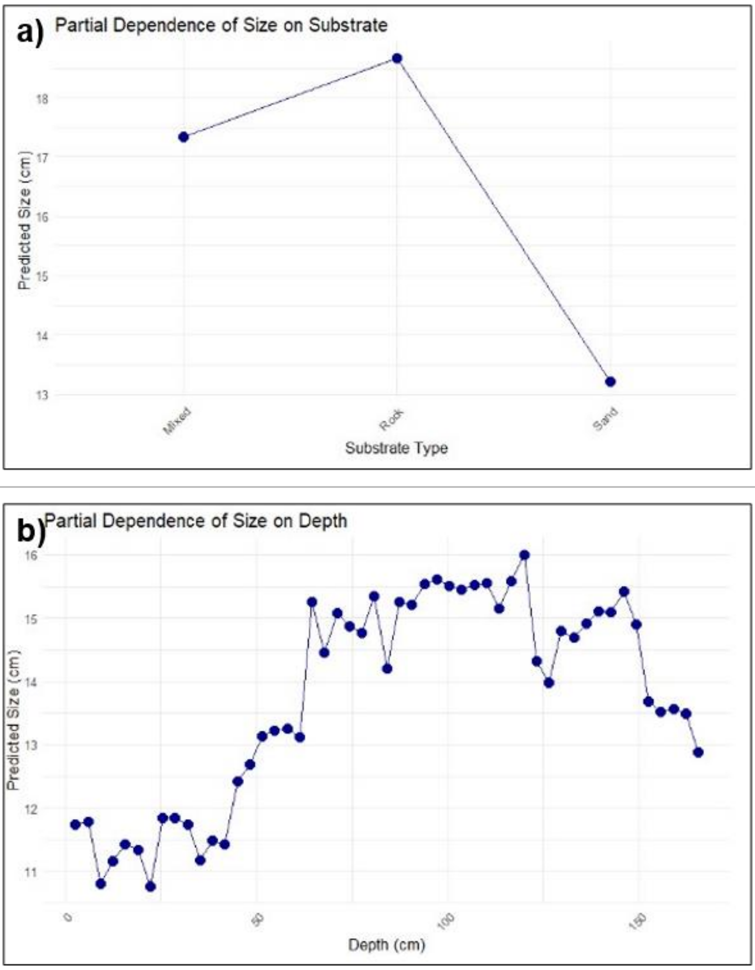

Figure 3.6

Partial dependence plots showing the predicted relationships between environmental variables and fish size from the Random Forest regression model. a) Fish size as influenced by substrate type, where sand substrates are associated with the smallest predicted sizes, and rock substrates are associated with the largest predicted sizes. b) Fish size as influenced by depth, illustrating a non-linear relationship where *intermediate and deeper depths are associated with larger predicted sizes, while shallower depths correspond to smaller predicted sizes (< 50 cm). These plots highlight the importance of environmental gradients in shaping fish size distributions.*

The Random Forest regression model for size ratio also performed well, with an OOB R^2 of 0.864, explaining 86.4% of the variation. The OOB MSE was 0.0053. Similar to size, species identity was the most important predictor, followed by depth, substrate type, and season. Partial dependence plots showed that sand substrates were associated with lower size ratios, while rock substrates were linked to higher size ratios. Depth again showed a non-linear pattern, with size ratios peaking at intermediate depths (Figure 3.7). Seasonal differences were modest but suggested slightly lower size ratios during the wet season.

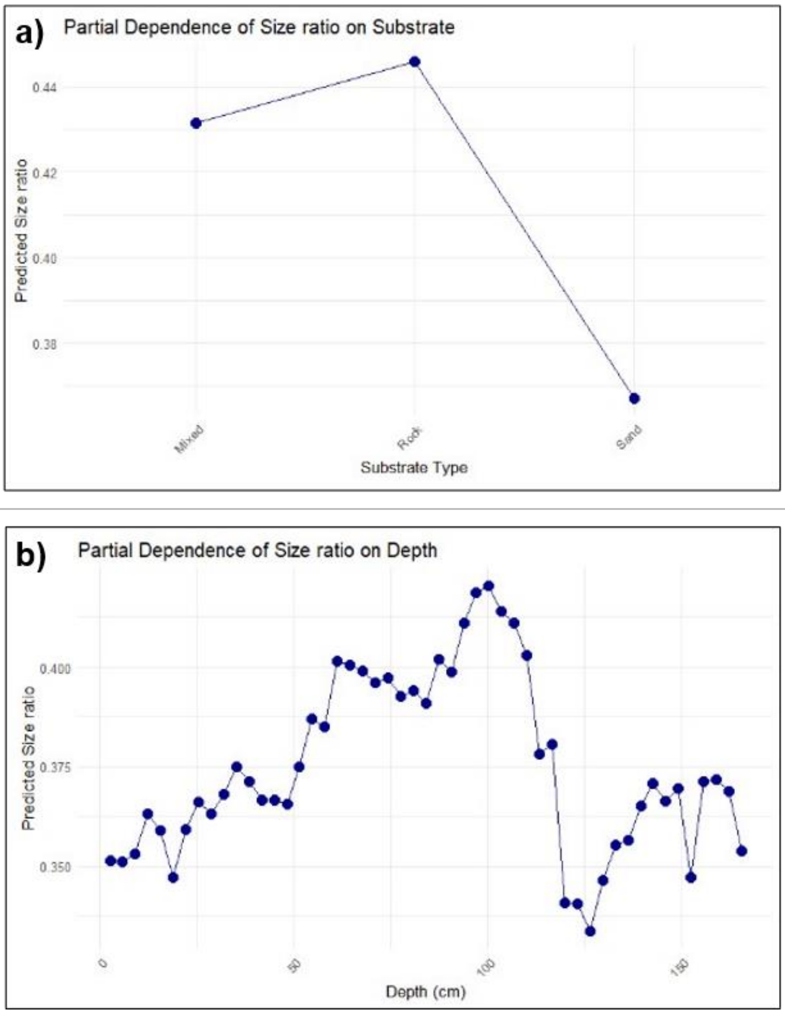

Figure 3.7

Partial dependence plots showing the predicted relationships between environmental variables and fish size ratio from the Random Forest regression model. a) Size ratio as influenced by substrate type, with sand substrates associated with the smallest *predicted size ratios and rock substrates associated with the largest size ratios. b) Size ratio as influenced by depth, illustrating a non-linear relationship where intermediate depths (~50–100 cm) exhibit higher predicted size ratios, while shallower and deeper depths correspond to lower size ratios. These plots emphasize the role of environmental factors in influencing size ratios within fish assemblages.*

The Random Forest regression model for trophic level also indicated a good predictive performance, with an OOB R^2 of 0.979, explaining 97.9% of the variance. The OOB MSE was 0.0130, the lowest among the three models. Species identity was again the most critical predictor, followed by depth, substrate type, and season. Partial dependence plots indicated that rock and mixed substrates were associated with higher trophic levels, while sand substrates were linked to lower trophic levels. Depth had a positive relationship with trophic level, with deeper habitats favoring species at higher trophic positions (Figure 3.8). Season had the least impact but indicated slightly higher trophic levels during the wet season.

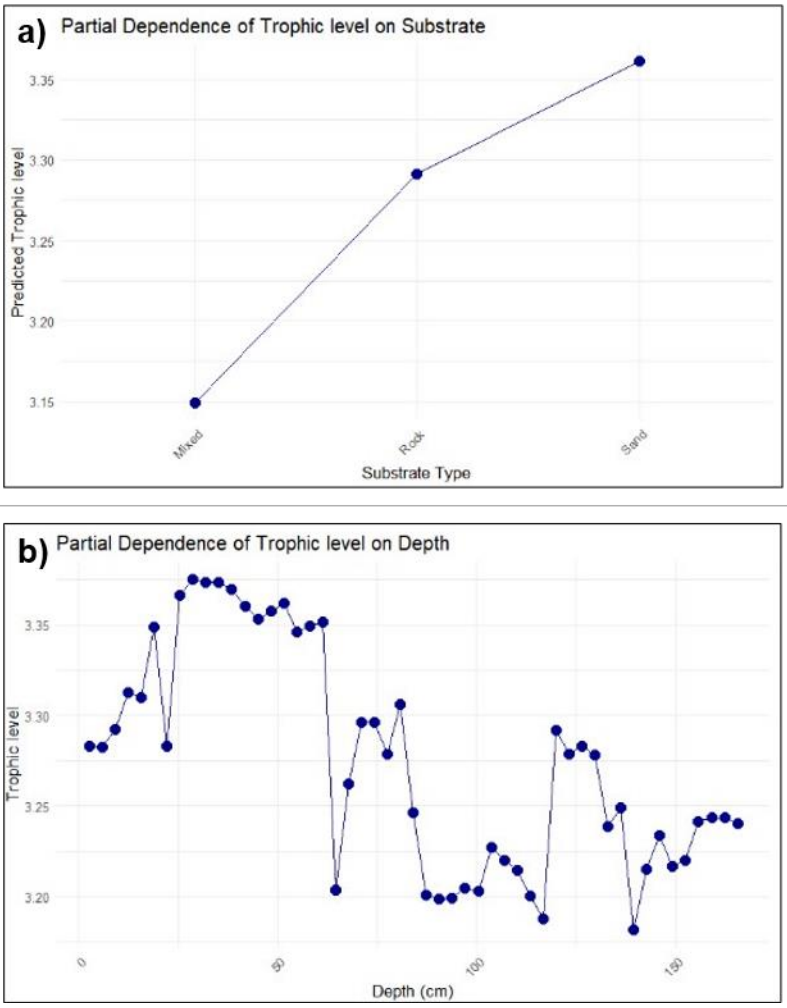

Figure 3.8

Partial dependence plots showing the predicted relationships between environmental variables and fish trophic level from the Random Forest regression model. a) Trophic level as influenced by substrate type, with mixed substrates associated with the lowest predicted trophic levels and sand substrates associated with the highest. b) Trophic level as influenced by depth, illustrating a non-linear relationship where intermediate depths (~50–100 cm) exhibit higher predicted trophic levels, while shallower and deeper depths correspond to lower levels. These plots highlight the role of substrate and depth in shaping trophic dynamics within fish assemblages.

Across all models, species identity was the strongest predictor of size, size ratio, and trophic level. For the environmental variables, depth and substrate had the most influence on functional traits distribution. Sand substrates were generally associated with smaller sizes, lower size ratios, and lower trophic levels, whereas rock and mixed substrates were linked to larger sizes, higher size ratios, and higher trophic levels. Depth had a consistent non-linear effect, with intermediate depths associated with larger sizes and higher size ratios, and deeper habitats favoring species with higher trophic levels. Seasonal effects, although weaker, showed slightly lower sizes and size ratios during the wet season but negligible effects on trophic level. These results highlight the interplay between species-specific traits and environmental gradients in structuring ecological patterns. It also indicates that the presence of juveniles is species-specific, and certain species have a higher juvenile presence in the forest. Species such as *Gerres erythourus*, *Abudefduf spp.*, *Lethrinus nebulosus*, *Taenuria lymma*, *Terapon jarbua*, *Turrum fulvoguttatum* and *Urogymnys granulatus* were generally smaller in relation to their maximum size, while *Pseduomugil signifier* and *Scarus rivulatus* were larger (Figure 3.9Error! Bookmark not defined.).

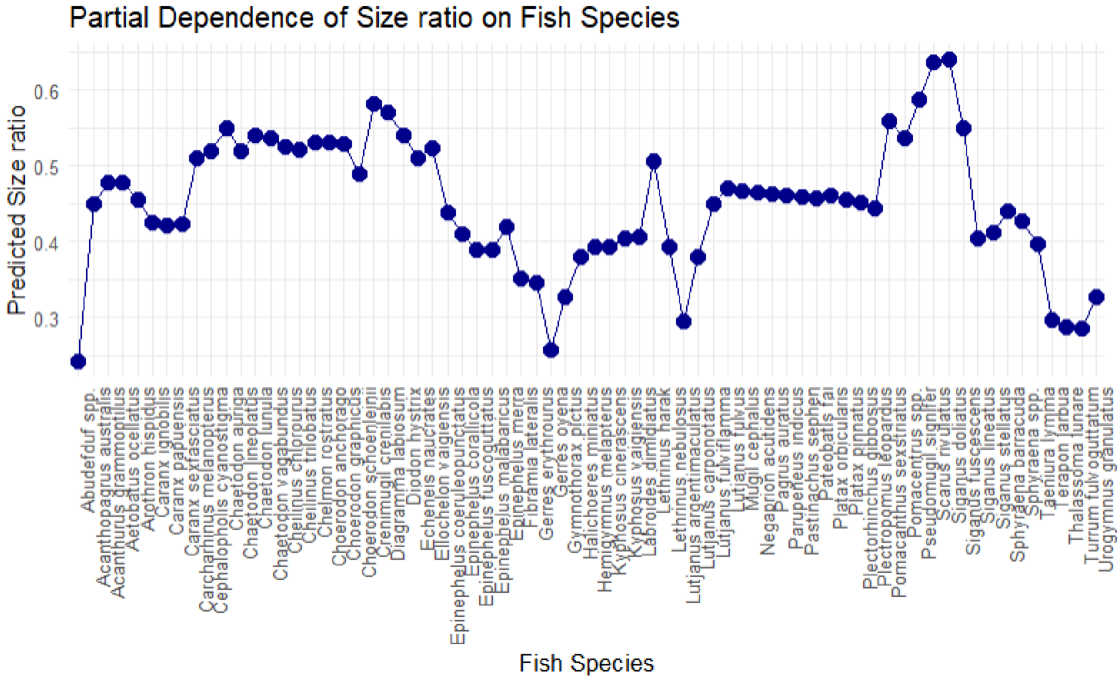

Figure 3.9*Error! Bookmark not defined.*

Partial dependence plot showing the predicted relationships fish species identity and fish size ratio from the Random Forest regression model, indicating the age proxy structure of species within the clear-water mangrove forests.

These findings highlight the influence of environmental gradients, particularly substrate type and depth, on the functional traits of fish assemblages. These associations suggest micro-habitat driven functional specialization. These results provide a foundation for exploring the ecological implications of trait-environment relationships in shaping community dynamics and ecosystem functioning.

3.4 Discussion and Conclusion

Clear-water mangrove forests, particularly in Indo-Pacific ecosystems, are critical habitats that support a rich diversity of marine species and play an essential role in maintaining ecosystem processes (Nagelkerken et al., 2008; Unsworth et al., 2008). Functional diversity is key to ecosystem resilience, as it enhances the ability of ecosystems to recover from disturbances through functional redundancy, where multiple species can perform similar roles (Mouillot et al., 2014; Villeger et al., 2010). In mangrove-associated fish communities, this diversity supports critical functions such as nutrient cycling and habitat structuring, contributing to the overall stability and productivity of these ecosystems (Duke et al., 2007; Mumby et al., 2004). Research has demonstrated that functional diversity within these ecosystems is a key driver of resilience, as it enables ecosystems to buffer against biodiversity loss and maintain critical functions in the face of environmental change (Mouillot et al., 2011).

3.4 1 Differences in Functional Trait Diversity in Clear-Water Mangrove Habitats

High functional diversity is often associated with ecosystems that are more resilient to disturbances due to the presence of multiple species possibly fulfilling similar roles, a concept known as functional redundancy (Villeger et al., 2012). The high functional richness observed at Site 2 indicates a wide variety of ecological roles being fulfilled within this habitat. As Site 2 also had high levels of both absolute (de Bello) and relative (Ricotta) functional redundancy according to Dick (2023), this is in line with these findings. The high functional divergence observed across all sites, with only Site 3 being below 0.8, suggests that certain species occupy extreme niches within the trait space, which could indicate specialised roles in the ecosystem. This is critical for maintaining ecosystem functionality, as specialised species can perform unique functions that generalists cannot, contributing to the overall resilience and stability of the ecosystem (Mouchet et al., 2010; Cadotte et al., 2011). The exclusion of the species at the edge of the trait space reflects this, as the absolute and relative redundancy reduces in the sites and substrates where the Batoidea are mostly present. The contrast between sand and rock substrates in this study is in line with findings from Sheaves, Johnston & Baker (2016), who noted that substrate heterogeneity often leads to greater ecological complexity and diversity. Magneville et al. (2022) also found that substrate type can significantly influence species composition and functional diversity, and what this study highlights is how these indices must be interpreted. High functional richness and divergence, but low evenness, may indicate that the functional trait space occupied seems large, but is mostly driven by species being present at the edge of the trait space (Schleuter et al., 2010). High functional evenness has been shown to be associated with stable and homogenous habitats (Lin et al., 2021). The temporal variability in the environmental conditions related to the Indo-Pacific clear-water mangrove forests, as well as the fact that they are only inundated for part of the day, may thus explain the lower values of functional evenness found in this study. Low functional evenness, on the other hand, can reflect environmental filtering with most individuals fitting into a niche reflecting the environment, which may be the case in this study (Mammola et al., 2021). However, the low evenness suggests that these diverse and divergent traits are not evenly distributed across species. Some species significantly contribute to the community's functional traits, while others contribute less, leading to potential vulnerability in ecosystem functioning if key species are lost. This might reflect a skewed distribution where few species capitalise on the available resources, perhaps due to specialized feeding adaptations or behaviours that provide significant competitive or survival advantages (Gomes et al., 2023). However, as Walsh et al. (2022) argues, temporally variable and high-stress environments in general restrict the functional trait diversity. Less functional richness can therefore indicate higher stress environments, as all the forests are temporally unavailable. However, in very challenging environments, different species or individuals might end up developing similar traits because those traits are the best ways to survive. This results in multiple organisms having the same or similar functions or roles in the ecosystem, which in turn increases resilience. In addition, seasonal variations in functional diversity further highlight the dynamic nature of these systems. The dry season exhibited higher functional richness and evenness, potentially due to more stable environmental conditions such as reduced freshwater influx and consistent salinity levels (Sheaves, Johnstone & Baker, 2016). In contrast, the wet season showed a slight decrease in functional diversity. This seasonal variation could thus be attributed to changes in resource availability, water temperature, and habitat accessibility, which are known to drive shifts in species composition and functional roles (Duffy et al., 2007). The study’s findings are consistent with those of Dubuc et al. (2019), who documented similar seasonal shifts in clear-water mangrove-associated fish communities, linking them to the broader seascape connectivity and environmental conditions.

Simply looking at the functional diversity values may thus not explain the drivers of this diversity, and how the species are distributed in the trait space. The functional space in the sand substrate was, for instance, largely driven by the presence of Batodiea and the smaller, estuarine-associated species, which filled unique trophic niches not found in rock or mixed substrate. The exclusion of these species had an effect on the trait space and distribution of traits, indicating that these groups of species contribute to high functional richness and divergence, and thus unique ecological functions. These differentiations in feeding strategies and habitat preferences highlights the ecological differentiation and adaptation to specific environmental niches within the clear-water mangroves (Jacobsen & Bennett, 2013; Rutledge, 2022). These species, particularly the rays (Batoidea), perform crucial roles in shaping the functional trait space due to their unique ecological functions (Jacobsen & Bennett, 2013; Kanno et al., 2023; Rutledge, 2022). Rays, with their large body size, benthic feeding habits, and higher trophic levels, explain the differences in functional richness and divergence. Their presence at the edges of the trait space, suggests that they occupy specialized niches that are not easily replaced by other species. Excluding rays and estuarine species from the functional diversity analysis provided insights into how these groups influence the overall trait space and ecological dynamics. The removal of rays led to a more homogenized trait space, particularly over the sand substrates, where functional richness and divergence decreased. This suggests that rays add complexity to the mangrove ecosystem by occupying unique functional niches that are not easily replaced by other species (Davy et al., 2015; Kanno et al., 2023). Their exclusion results in a loss of functional diversity, which could have implications for ecosystem resilience and stability, particularly in the face of environmental change (Cadotte et al., 2011). The changes observed in the trait space following the exclusion of these species emphasises the importance of considering both species presence and their functional roles in understanding ecosystem dynamics. These findings emphasise the need to protect and conserve species that contribute significantly to functional diversity, as their loss could lead to a reduction in ecosystem resilience and functionality (Mouchet et al., 2010). Moreover, the turnover between different substrates, particularly between rock and sand, suggests that species composition and functional traits are closely linked to the physical environment. This means that the main source of dissimilarity comes from different species or traits being present. Some of the dissimilarity can however still be explained by nestedness, which indicates that the observed differences partly can be explained by one of the areas having a subset of the traits present at the other. This supports the concept of environmental filtering, where the abiotic environment shapes the community by selecting species with traits suited to specific conditions (Walsh et al., 2022).

3.4.2 Species and Traits Driving Diversity

The RLQ and Fourth-corner analyses revealed significant relationships between environmental variables and species traits, particularly substrate type and depth. Substrate was significantly associated with trophic level, size ratio, average size, mouth gape, and eye diameter, while depth influenced mouth gape and eye diameter. These findings suggest that substrate and depth play critical roles in shaping functional traits, such as feeding adaptations and visual characteristics. However, the significance of only model 2 indicated that while environmental factors select for certain traits, these traits do not necessarily dictate which species dominate a community.

The Random Forest models provided additional insights into these relationships, emphasizing the non-linear interactions between traits and environmental variables. Partial dependence plots indicated that sand substrates were associated with smaller fish sizes, while rock and mixed substrates supported larger individuals. Depth exhibited a non-linear relationship, with intermediate and deeper depths (>50 cm) favouring the largest fish sizes. The analysis also revealed that sand substrates were linked to smaller size ratios, while rock substrates were associated with larger ratios. This pattern may stem from the differing structural complexities of these habitats, which influence resource availability and interspecific interactions, as suggested by Walsh et al. (2022), who found that substrate complexity plays a crucial role in shaping fish functional traits. The observed size ratios tended to increase up to 100 cm depth and then decline, highlighting the potential interplay between habitat features and ontogenetic shifts in resource use.

For trophic level, sand substrates were associated with lower values, while rock and mixed substrates supported higher trophic levels. This could be indicative of the prey availability and migration pathways associated with the environmental conditions these substrates reflect, as noted in studies emphasizing the connectivity between mangroves and adjacent habitats. For example, Mumby et al. (2004) demonstrated that mangroves enhance coral reef fish biomass by serving as critical feeding and juvenile grounds, which may explain the higher trophic levels observed in rock substrates closer to such ecotones. These predators may therefore use the mangroves to avoid competition on the reef (Sheaves, 2005). Depth also influenced trophic levels, with a non-linear relationship showing peaks at shallower depths and dips around 100 cm. Overall, the results align with the understanding that functional diversity is shaped by a combination of habitat complexity, resource availability, and environmental gradients. This is consistent with theoretical frameworks such as the Resource Partitioning Hypothesis (Sheaves et al., 2016), which emphasize the importance of spatial and temporal heterogeneity in shaping ecological communities

A study by Walsh et al. (2022) found that complexity in depth and substrate may affect fish occupation in microhabitats, and may help explain the patterns found in this study. Walsh et al. (2022) also identified a significant relationship between water velocity and fish assemblage structure, which may help explain the observed differences between clear-water mangroves with sand or rock substrate. Rock substrate sites, being more exposed to wind and water movement, may host species better suited to high-energy environments, while the lower water velocities associated with sand substrate reflect calmer, low-energy habitats. However, while both Sites 1 and 2 share similar environmental conditions in terms of substrate, tidal signal, inundation period, proximity to reef, and geographical location – the functional indices differed between the two. This suggests that even small environmental or ecological variations, such as slight differences in water velocity, prey availability, or habitat structure, can have significant impacts on community structure and function. While substrate and depth are key drivers of functional traits, species-specific characteristics and non-linear interactions also play a significant role, emphasizing the complexity of trait-environment relationships in these ecosystems.

4. General Discussion and Conclusions

This research regarding taxonomic and functional diversity, and thus ecological role of species, within the clear-water mangrove forests of Orpheus Island, Australia, investigated the spatial and temporal patterns affecting fish community structure and juvenile habitat use. This study contributes to a deeper understanding of the biodiversity and functional diversity within clear-water mangroves, which are less influenced by terrestrial input and more closely linked to coral reefs and other marine habitats that estuarine mangroves. The research fills a significant gap in the existing literature, particularly given the emphasis on estuarine mangroves in prior studies. The project also provides insights into how functional diversity and species composition are shaped by environmental variables such as substrate type, tidal regime, and water depth, and this research thus offers a comprehensive view of how clear-water mangroves function within the larger CEM in the Indo-Pacific. By addressing both taxonomic and functional diversity, this research contributes to a deeper understanding of the ecological processes that sustain these habitats and offers valuable insights for their conservation.

4.1 Fish Habitat Use of the Clear-water Mangrove Habitat in the Indo-Pacific

4.1.1 Habitat Use by Fish Species and Environmental Drivers

The differences in community based on environmental conditions was highlighted in Chapter 2, where the community could be sorted based on the spatial and temporal factors related to substrate type and season. These differences were shown to not be due to differences in biomass, and the metacommunity could thus be sorted into localised communities based on these environmental factors. As different substrates give indication of the conditions related to the area, substrate is a useful indication of whether the fish prefer a high-energy or low-energy environment. Thus, the patterns seen here may be influenced by the conditions that create the substrate type. These differences in substrate will also create differences in the microhabitats available within the forest, and thus the functional niches that can be utilised. Chapter 2 found higher Shannon and Simpson diversity at site 6 and in clear-water mangrove forests with rock substrate, and the findings from Chapter 3 indicated that these communities also had the higher absolute (de Bello) and relative (Ricotta) redundancy. Chapter 3 also indicated that site 2 and sand substrate had the highest functional richness and redundancy. The lower levels of functional evenness in both these communities indicate that the drivers of the functional richness are at the edge of the trait space, and this therefore drives the higher richness compared to the other sites. At closer investigation using the KDE analysis, it was revealed that the species driving these differences between sand and rock substrate mainly belong to the Batoidea (rays) and the smaller, estuarine-associated species *Fibramia lateralis* and *Pseudomugil signifier*. The exclusion of these species revealed that they filled unique niches related to feeding behaviour associated traits within the sand substrate clear-water mangroves, and were important drivers of the functional diversity observed. At the exclusion of these, sand substrate for trophic traits had almost half the functional richness of the rock substrate, indicating that the sand substrate's diversity was mostly driven by extreme and unique niches related to feeding behaviour associated traits in the sand while the rock substrate community was more balanced. This also explains the higher Shannon and Simpson diversity, as well as functional redundancy from Dick (2023). It is however important to note that this study focuses solely on the data collected and does not account for the presence of other fish species that may utilise the habitat. The influence of additional species on habitat dynamics and juvenile fish proportions was not considered due to the limitations of the available data. Future research should aim to include and examine the roles of other species to provide a more comprehensive understanding of the ecosystem.

The tidal flow and depth did not have a significant effect on community composition according to Chapter 2, however, this may be related to a combination of foraging and refugia. Sheaves (2005) argues that a fish using a temporally inaccessible habitat for foraging will swim in with the incoming tide to have first access to important food sources, while a fish utilising the habitat for refugia will stay as long as the water level allows to avoid predation. As there were no such patterns found in this report, the clear-water mangrove forest may be important both for refugia and foraging purposes, or neither. However, the RLQ and fourth-corner analysis in Chapter 3 found that depth was linked to substrate type, with sand substrate being more associated with shallower water, and rock substrate with deeper water at the time of utilisation by fish. This may be as the rock substrate in itself is more complex and inundated later, thus providing less refugia and foraging area at lower tides. The sand substrate associated mangroves however had more structurally complex root structures within the forests. The sand slope leading up to the sand mangroves may instead facilitate migration in lower water levels, but was also observed to be further from the coral reef. This may thus leave larger predators at risk of getting stuck in the outgoing tide, but may also place prey at risk of predation with longer migration. However, the migration into these forests may be less dangerous as the larger piscivores cannot swim in as shallow water – the sand slope leading up to the mangrove forest may thus offer protection rather than increased risk from marine predators (Sheaves, 2005). The Random Forest analysis on the significant associations between environmental variables and traits revealed non-linear patterns, indicating different habitat use patterns depending on substrate and depth. Sand substrate was generally associated with smaller average sizes, lower size ratios (age-proxy), and higher trophic levels. It is in line with the refugia and foraging hypotheses, where younger, smaller fish can seek shelter and have access to important food sources such as invertebrates and small prey fish, where they may also escape from larger, predatory fish. The clear-water mangroves' sand substrate may therefore offer enhanced shelter due to higher structural complexity and increased prey availability, particularly in the form of invertebrates and small fish, which are essential food sources for these juveniles. The sand substrate then being associated with juveniles and sub-adults of higher trophic level and predatory fish (trophic level above 3.5), has also previously been discussed by Baker & Sheaves (2009). These authors argued that smaller and/or younger piscivores feed in shallow-water juvenile habitats, such as the mangrove forest. Although the study was done on estuarine mangroves, this study indicates that this hypothesis may be applicable to other systems such as the seascape with clear-water mangroves as well.

Chapter 2 indicated that larger sizes are generally found inside the forest as opposed to on the edge, but that trophic level was less of a predictor as to whether an individual could be found inside the forest or on the edge. What must be noted however is that this study does not investigate how far into the forest that the individuals swim. What may drive this affinity for larger fish to be present inside the forest is the Mangrove whipray (*Urogymnus granulatus*), often observed to be feeding within the forest. As these rays are generally larger than the fish observed not belonging to the elasmobranchs observed in this study (*mean size of U.granulatus: 57.00 cm, mean size of others: 14.04 cm*), this may explain why larger sizes are associated with presence inside the forest. The oscillations and complex interactions between size ratio and trophic level for the GAM model does however indicate species specific utilisation patterns at different life stages. Both predictors influenced the affinity to be inside the forest, and at lower size ratios, trophic level had a relatively minor effect, whereas at higher size ratios, higher trophic levels were increasingly associated with edge use (see Appendix A, **Error! Reference source not found.** & **Error! Reference source not found.**). Notably, the model identified a region where younger individuals at higher trophic levels still exhibited a positive partial effect on the log-odds of being “in.” This suggests that young predators may utilize the interior of the mangrove forest. As the log size ratio increases—indicating more mature or larger individuals at higher trophic levels—the effect gradually shifts toward more “edge” use. Overall, the model highlights that size ratio plays a role in shaping microhabitat choice for both prey and predator species.

When trophic level was analysed alongside size, the partial effect of trophic level on habitat use remained relatively small, suggesting little variation in the influence of trophic level. However, when size ratio was used instead of size, the shape of the trophic level curve became noticeably more complex and oscillating. This indicates that when fish size is normalized by species-specific maximum length—a proxy for ontogenetic stage—trophic level exerts a more intricate, stage-dependent influence on habitat use. In other words, certain trophic groups appear more likely to inhabit the mangrove interior at particular life stages, while others may shift their distribution toward the edge as they mature. Thus, incorporating size ratio rather than size revealed a more nuanced, non-linear relationship between trophic level and habitat use that were not apparent under the simpler, absolute size measure.

4.1.2 Juvenile Habitat use

Chapter 2 revealed that 70.2 % of all fish, and 78.1 % of all predatory fish recorded (trophic level above 3.5) were present in the clear-water mangrove forest as small adults or juveniles (less than 0.5 of their maximum size). Approximately ~ 50 % of all individuals recorded were juveniles, defined as less than 0.3 of the maximum size (Dorenbosch et al., 2005; Nagelkerken & van der Velde, 2002). Chapter 2 also found that predatory fish tended to be smaller in comparison to their maximum size than non-predatory fish, and that higher trophic levels also tended to be smaller in comparison to their maximum size. This is in line with the findings of Baker & Sheaves (2009), who found that smaller piscivores dominate shallow-water habitats. These authors argue that the reduced competitive pressure compared to associated adult habitats, along with potential for ambush predatory behaviour and refugia from larger predators, provides the younger fish with an ideal environment. This may explain the higher number of young and small fish in the higher trophic levels found in this study. Baker & Sheaves (2009) also found that juveniles and smaller individuals belonging to Sillaginids, Ambassids, Sparids and Carangids have an unproportionate effect on new recruit mortality. In this study Carangidae, Lutjanidae and Lethranidae were commonly observed in the clear-water mangroves as juveniles or small adults. In the videos, predatory behaviour was observed on the small, schooling species belonging to Atherinidae and Apogonidae on several occasions – especially by juveniles of Carangidae and Lutjanidae. A study by Bradley et al. (2019) found similar juvenile utilisation patterns in clear-water mangroves, with them being of importance to juvenile Carangiade, Lethrinidae and Lutjanidae, with *Lutjanus fulviflamma* and *Caranx* *sexfasciatus* having significant habitat use. In their paper they argue that the rock substrate of the mangroves explains these patterns – however in this study most juveniles were present in the sand substrate mangroves. This may indicate that clear-water mangroves may be of importance to juveniles and sub-adults regardless of substrate, or because of other extrinsic environmental or biological factors driving these patterns. For instance, the habitat use may rather be driven by accessibility and proximity to a coral reef or other adult habitat, and the clear-water mangrove habitat is likely used for foraging and refugia rather than as a true juvenile or nursery habitat. The proximity to other habitats in the seascape is an important factor to consider, as the tidal regime of Indo-Pacific clear-water mangroves enforces connectivity with other habitats as they are temporarily inaccessible due to being exposed (Igulu et al., 2014; Kimirei et al., 2013; Sheaves, 2005). The rock substrate is also inundated for a shorter period of time, which may make the cost of migrating for refugia higher and instead provide better opportunities for foraging. What must be noted is however that the presence of juveniles is tested on individuals, while the functional trait analysis is done on species level.

4.2 Management Implications

This study has aimed to lay the foundation for the habitat use of the clear-water mangrove habitat in the Indo-Pacific by fish, by conducting a thorough analysis of the taxonomic and functional trait diversity present in these habitats. It has created a foundation for further research, where the differentiation between clear-water and estuarine mangroves can be established more thoroughly. It has also investigated how a clear-water mangrove system in the Indo-Pacific is utilised in relation to its environmental context, without the bias of studies from the Caribbean shaping the research question. It is important to consider both taxonomic and functional diversity in conservation planning. While taxonomic diversity provides a measure of species richness, functional diversity offers deeper insights into ecosystem processes and resilience. Incorporating functional diversity metrics into conservation strategies can lead to more effective and sustainable outcomes, particularly in complex and dynamic ecosystems like the Indo-Pacific CEM.

The clear-water mangroves in the Indo-Pacific have only started being studied in the recent years, and as of yet there is little to no differentiation between estuarine and clear-water mangrove habitats in management planning (Suman, 2019). As this study has shown, clear-water mangroves may be of great importance for juvenile and young adult reef fish, and play an important role in recruitment control, and foraging and refugia for fish. It also provides many microhabitats and niches for a wide variety of species depending on the environmental context. The access is driven by the tidal flow, and even though it is only temporally accessible it fills an important role for species in the Indo-Pacific seascape (Table 4. 1).

Table 4. 1

Management implications for the conservation of clear-water mangroves in the Indo-Pacific, focusing on ecological functions, habitat restoration, and sustainable practices.

MANAGEMENT ASPECT	IMPLICATIONS
CONSERVATION EFFORTS	Differentiate between clear-water and estuarine mangrove habitats in management planning to ensure targeted conservation efforts.
TAXONOMIC AND FUNCTIONAL DIVERSITY	Incorporate both taxonomic (species richness) and functional diversity metrics into conservation strategies for clear-water mangroves.
JUVENILE FISH HABITAT	Protect clear-water mangroves as critical habitats for juvenile and young adult reef fish, emphasizing their roles in recruitment, foraging, and refuge.
MICROHABITATS AND NICHES	Preserve the variety of microhabitats within clear-water mangroves to support diverse species and ecological functions.
TIDAL ACCESSIBILITY	Recognize and accommodate the temporal accessibility of mangroves driven by tidal patterns in management plans.
FUNCTIONAL NICHES	Maintain ecological functions provided by species occupying unique functional niches, as they are unique within the community.
ENVIRONMENTAL VARIABILITY	Utilize data on species composition and functional traits across different substrates and environmental conditions to guide habitat restoration and protected area design.
FUTURE RESEARCH	Promote further research into clear-water mangroves to establish patterns in taxonomic and functional diversity, and understand variations across microhabitats and environmental conditions.
EDUCATION AND AWARENESS	Increase stakeholder awareness about the ecological importance of clear-water mangroves to encourage sustainable practices and community support for conservation initiatives

Note. The table highlights key management priorities derived from the study findings, emphasizing the integration of functional and taxonomic diversity metrics, protection of critical habitats, and the importance of stakeholder awareness in achieving sustainable conservation outcomes.

The findings of this study provide insights that can inform mangrove management strategies by emphasising the importance of preserving not just the species but rather the ecological functions they perform, by highlighting the interaction between taxonomic and functional diversity within clear-water mangrove ecosystems. The presence of functional niches at the edge of the trait space, non-replaceable by other species in the community, indicate that the ecological function of clear-water mangroves and the microhabitats within are sensitive to changes. The focus in this study on the variability of species composition and functional traits across different substrates and other environmental conditions provides valuable data that can guide habitat restoration efforts and the design of protected areas. Effective management should consider these findings to maintain the ecological balance of mangrove forests, ensuring that they continue to provide essential services such as supporting fisheries, protecting shorelines, and mitigating the impacts of climate change (Mouchet et al., 2010; Stuthmann et al., 2022). As the clear-water mangroves of the Indo-Pacific are rarely properly investigated, and most research is contradictory, this study aims to lay a broad foundation for the patterns in taxonomic and functional diversity that can be found in this habitat, as well as how it varies with microhabitats and environmental conditions. To establish proper management and conservation approaches, one must first understand the habitat, and the community utilising it, one is trying to protect.

4.3 Thesis Limitations and Future Directives for Research

This research aimed to establish the taxonomic and functional diversity present in clear-water mangroves in the Indo-Pacific, however, as only one island was investigated the patterns found in this study should be compared with other clear-water mangroves in the Indo-Pacific to establish how these findings relate to local variations and habitat use patterns. As the models for taxonomic variation in this study did not fully capture the variation observed, more studies should be conducted incorporating more environmental variables and possible connections to other habitats in the seascape. Connectivity can be inferred by the fact that fish are present in the forest while there is water, and not present when there is not, however, to fully establish connectivity patterns in the Indo-Pacific seascape one must investigate all habitats related to this migration. This study provides a one-sided estimation of connectivity with other habitats, inferred by the habitat association of the species present, as well as their habitat use patterns within the forest. It therefore cannot draw any conclusions about connectivity patterns with other habitats in the seascape, but rather how it is utilised by the fish present in it. The functional diversity in this study was also estimated on species level based on averages from FishBase and data collected on the underwater video cameras, and may thus not fully represent the intra-specific variations in the community.

The reliance on underwater video recordings, though effective for gathering non-invasive data, may have limitations in accurately identifying smaller or cryptic species, potentially leading to an underestimation of species richness or the presence of rare species. Another limitation is the potential bias introduced by the selection of functional traits used in the analysis. While the chosen traits were relevant for understanding the ecological roles of species within the clear-water mangrove ecosystems, other important traits that influence species interactions and ecosystem processes may have been overlooked.

To build on the findings on this study, future research should prioritise inclusion of more clear-water mangrove habitats in different geographical locations. This broader approach would enable a more comprehensive understanding of the variability and local variations in taxonomic and functional diversity across different environmental contexts. Comparative studies could explore how local factors such as water quality, sediment composition, connectivity with other habitats, water movement and human impacts influence species composition and ecological functions in clear-water mangrove systems. Incorporating a wider range of environmental variables into the models used to assess taxonomic and functional variation will provide a more accurate and holistic picture of the factors driving biodiversity patterns in these ecosystems. By linking these variables to the broader seascape, researchers can unravel the complex web of connectivity that exists between clear-water mangroves and adjacent habitats, such as coral reefs, seagrass beds, and open water environments.

Furthermore, to address the limitations identified in this study, future research should employ functional diversity on the individual fish level to capture the full spectrum of biodiversity within clear-water mangroves (Fontana, Petchey & Pomati, 2016). Additionally, expanding the range of functional traits considered in the analysis would provide a more nuanced understanding of how different species contribute to ecosystem processes. This could include traits related to reproduction, dispersal, or physiological tolerances, which are critical for understanding how species adapt to changing environmental conditions. Furthermore, investigating connectivity patterns more comprehensively across the entire seascape, rather than inferring them solely from the presence or absence of species in the clear-water mangroves, will offer a more detailed understanding of how these ecosystems function as part of a larger interconnected network. Such research would not only deepen our understanding of clear-water mangroves but also provide the necessary data to inform more targeted and effective management practices aimed at preserving these vital ecosystems in the face of ongoing environmental change.

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Table A.1

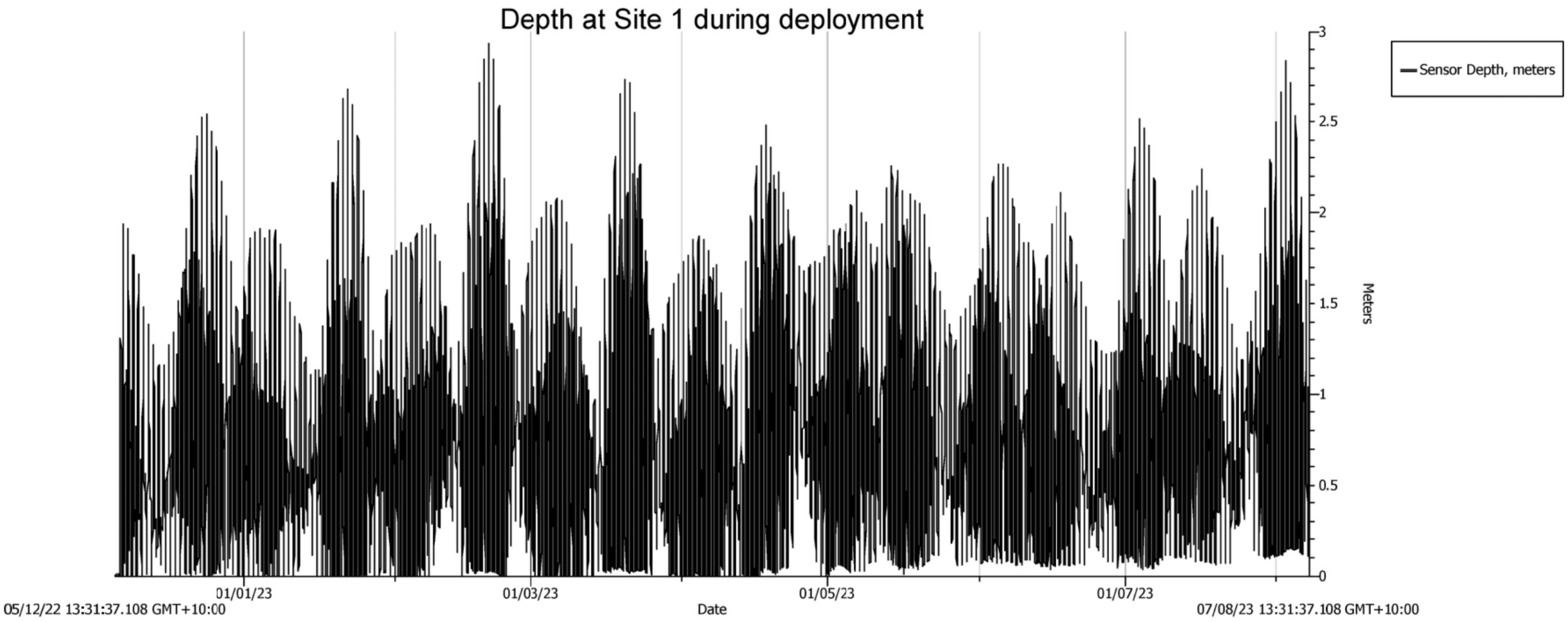
Species within each habitat association and salinity tolerance. The table categorizes fish species and their salinity tolerance (marine, brackish, or all) and their primary habitat association (reef, estuaries, lagoons, or freshwater).

SPECIES	SALINITY TOLERANCE	HABITAT ASSOCIATION
Abudefduf spp.	Marine	Reef
Acanthopagrus australis	Brackish	Estuaries and lagoons
Acanthurus grammoptilus	Marine	Reef
Aetobatus ocellatus	Brackish	Estuaries and lagoons
Arothron hispidus	Brackish	Reef
Caranx ignobilis	Brackish	Reef
Caranx papuensis	Brackish	Reef
Caranx sexfasciatus	All	Reef
Carcharhinus melanopterus	Brackish	Reef
Cephalopholis cyanostigma	Marine	Reef
Chaetodon auriga	Marine	Reef
Chaetodon lineolatus	Marine	Reef
Chaetodon lunula	Marine	Reef
Chaetodon vagabundus	Marine	Reef
Cheilinus chlorourus	Marine	Reef
Cheilinus trilobatus	Brackish	Reef
Chelmon rostratus	Brackish	Reef
Choerodon anchorago	Brackish	Reef
Choerodon graphicus	Marine	Reef
Choerodon schoenleinii	Marine	Reef
Crenimugil crenilabis	Brackish	Reef
Diagramma labiosum	Brackish	Estuaries and lagoons
Diodon hystrix	Marine	Reef
Echeneis naucrates	Brackish	Reef
Ellochelon vaigiensis	All	Reef
Epinephelus coeruleopunctatus	Marine	Reef
Epinephelus corallicola	Brackish	Reef
Epinephelus fuscoguttatus	Marine	Reef
Epinephelus malabaricus	Brackish	Reef
Epinephelus merra	Marine	Reef
Fibramia lateralis	All	Reef
Gerres erythrourus	Brackish	Reef

Gerres spp.	Brackish	Reef
Gymnothorax pictus	Brackish	Reef
Halichoeres miniatus	Marine	Reef
Hemigymnus melapterus	Marine	Reef
Kyphosus cinerascens	Marine	Reef
Kyphosus vaigiensis	Marine	Reef
Labroides dimidiatus	Marine	Reef
Lethrinus harak	Brackish	Reef
Lethrinus nebulosus	Brackish	Reef
Lutjanus argentimaculatus	All	Reef
Lutjanus carponotatus	Marine	Reef
Lutjanus fulviflamma	Brackish	Reef
Lutjanus fulvus	All	Reef
Mugil cephalus	All	Estuaries, lagoons and freshwater
Negaprion acutidens	Brackish	Reef
Pagrus auratus	Brackish	Reef
Parupeneus indicus	Brackish	Reef
Pastinachus sephen	Brackish	Reef
Pateobatis fai	Marine	Reef
Platax orbicularis	Brackish	Reef
Platax pinnatus	Marine	Reef
Plectorhinchus gibbosus	All	Reef
Plectropomus leopardus	Marine	Reef
Pomacanthus sexstriatus	Marine	Reef
Pomacentrus spp.	Marine	Reef
Pseudomugil signifer	All	Estuaries, lagoons and freshwater
Scarus rivulatus	Marine	Reef
Siganus doliatus	Marine	Reef
Siganus fuscescens	Brackish	Reef
Siganus lineatus	Brackish	Reef
Siganus stellatus	Marine	Reef
Sphyraena barracuda	Brackish	Reef
Sphyraena spp.	Brackish	Reef
Taeniura lymma	Marine	Reef
Terapon jarbua	All	Estuaries, lagoons and freshwater
Thalassoma lunare	Marine	Reef
Turrum fulvoguttatum	Marine	Reef

Urogymnus granulatus	Brackish	Reef

Note. A majority of the species (55.7%, n = 39) exhibited tolerance for brackish or freshwater conditions, while over 90% (n = 64) were primarily associated with reef habitats. This highlights the dominance of reef-associated species and their varying salinity tolerances in the studied habitats.



Depth at Site 1 during deployment

Figure A.1

Tidal fluctuations at Orpheus Island, recorded by a depth logger deployed at Site 1. The figure illustrates changes in sensor-recorded depth over time, highlighting the tidal regime and periodicity during the deployment period. The barometric pressure was estimated to be 100.7 for the Barometric Compensation Assistant in HOBOware Pro to estimate depth from recorded kPa values.

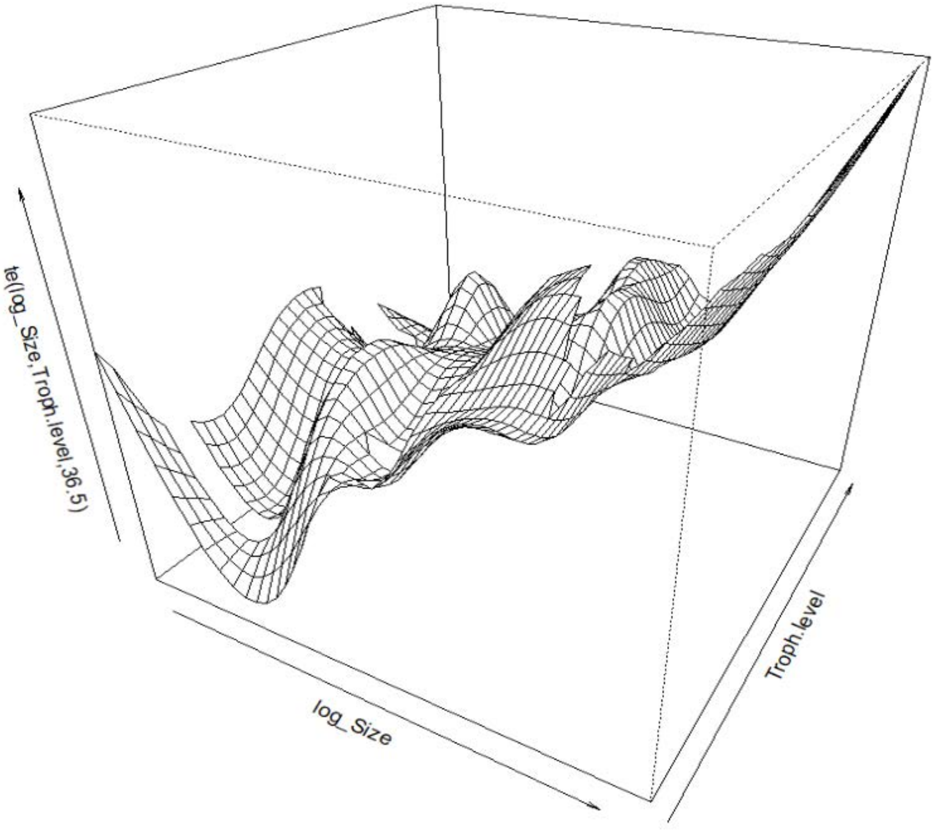


Figure A.2

The predicted probabilities of a fish being present inside the mangrove forest versus on the edge based on the interaction between log-transformed size and trophic level in the size model. The x-axis represents the log-transformed size (log_Size), and the y-axis represents trophic level. The z-axis represents the smooth interaction term, which reflects the predicted probability of being observed in the forest interior based on the interaction of size and trophic level. The surface illustrates a generally upward trend for larger sizes, indicating a decreasing likelihood of being in the forest interior for larger individuals. Trophic level shows a slight downward trend at higher levels, particularly for smaller individuals, suggesting larger high trophic-level fish are more likely to *remain at the edge. The surface is relatively smooth with minor undulations, indicating some interaction effects but primarily driven by size rather than trophic level.*

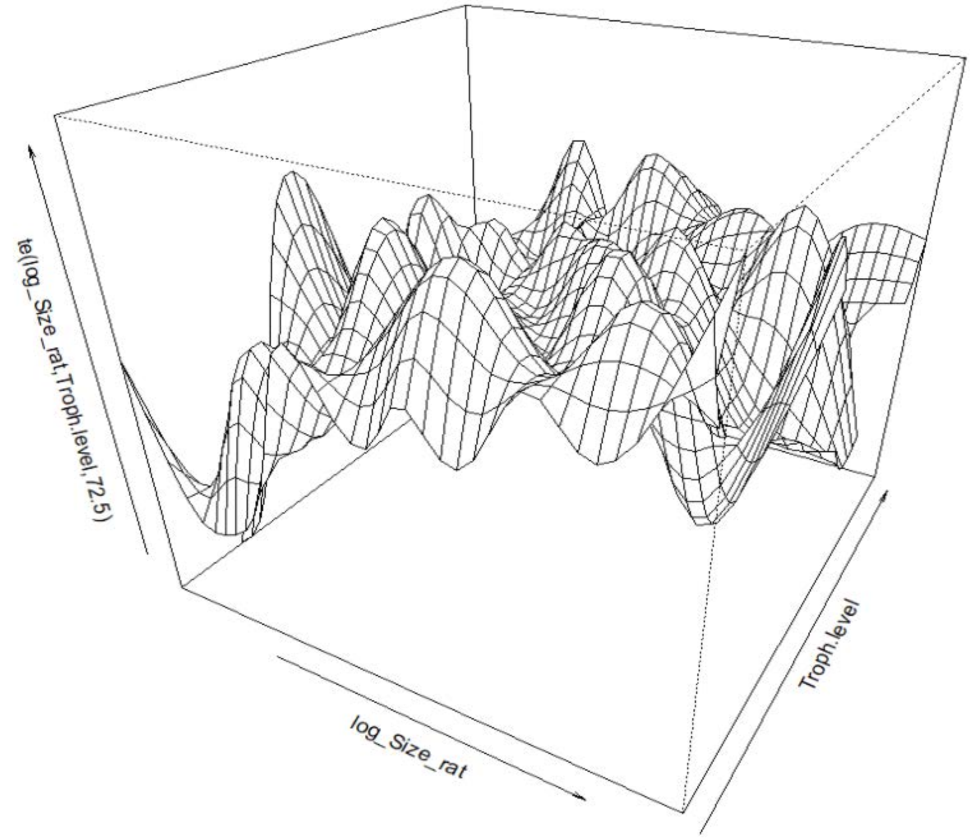


Figure A.3

The predicted probabilities of a fish being present inside the mangrove forest versus on the edge based on the interaction between log-transformed size ratio and trophic level. The x-axis represents the log-transformed size ratio, a measure of an individual's relative size compared to its species' maximum size, and the y-axis represents trophic level. The z-axis reflects the smooth interaction term, showing the predicted probability of being in the forest interior based on the interaction of size ratio and trophic level. The surface displays greater oscillations compared to the size model, indicating more variability and non-linear interactions between size ratio and trophic level. Smaller size ratios are associated with a higher probability of being inside the forest, particularly at lower trophic levels. At higher size ratios, the probability of being inside the forest decreases for most trophic levels, but some localized peaks suggest specific combinations of size ratio and trophic level are associated with greater interior use. The *undulating surface at higher trophic levels highlights the complex interplay between these two variables.*

Relation between traits and PCoA axes

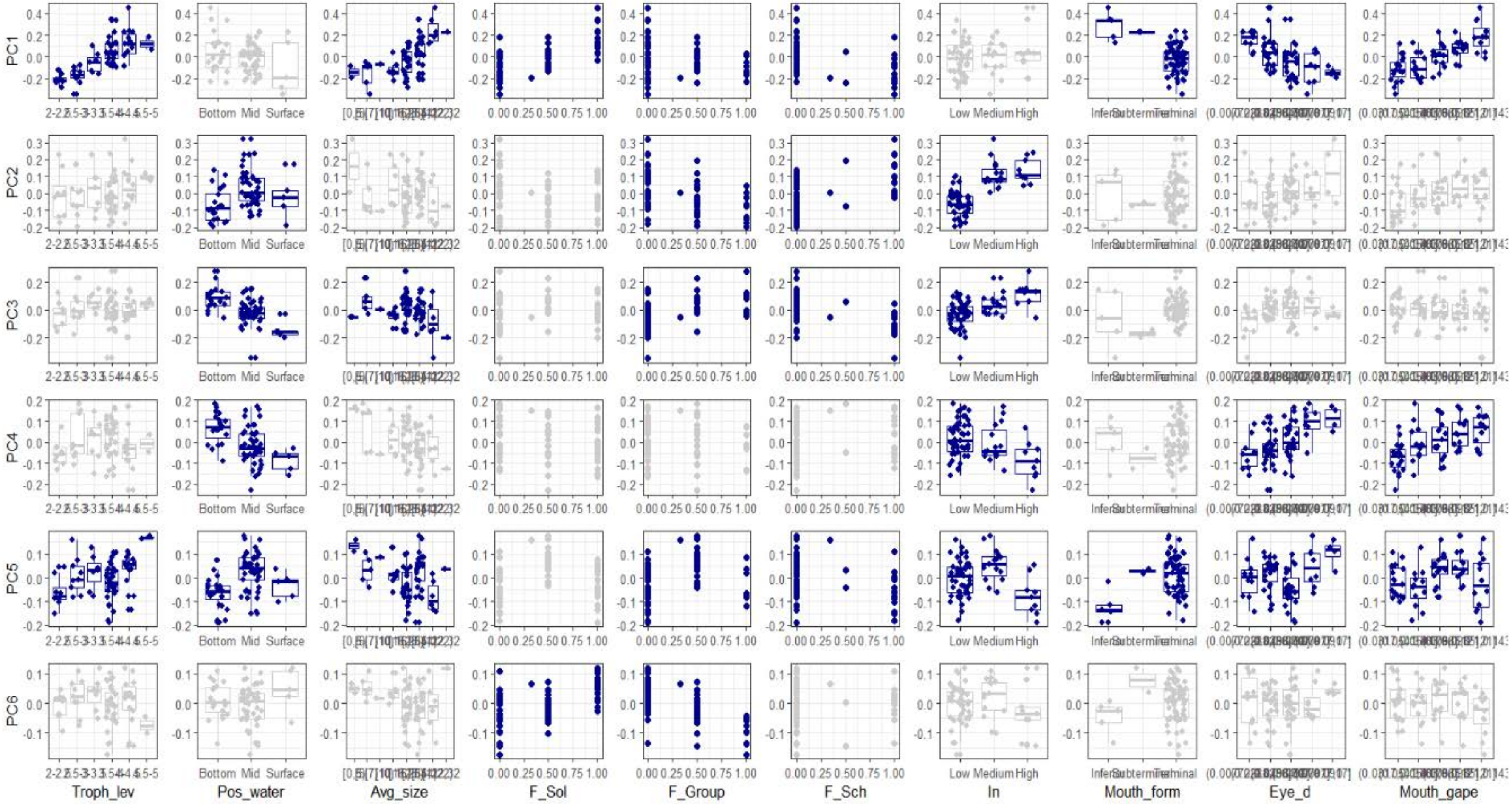


Figure B.4

Relationships between functional traits and principal coordinates analysis (PCoA) axes based on the all-traits dataset. Each panel represents the distribution of individual functional traits across six principal coordinate axes (PC1–PC6). The scatterplots and boxplots illustrate how traits such as trophic level, position in the water column, size, schooling behaviour, and morphological features (e.g., eye diameter, mouth gape) are associated with each axis. Traits are plotted against their respective PCoA scores to visualize their contributions to functional trait space. The blue plots indicate which traits are significant drivers of each principal coordinate axis.

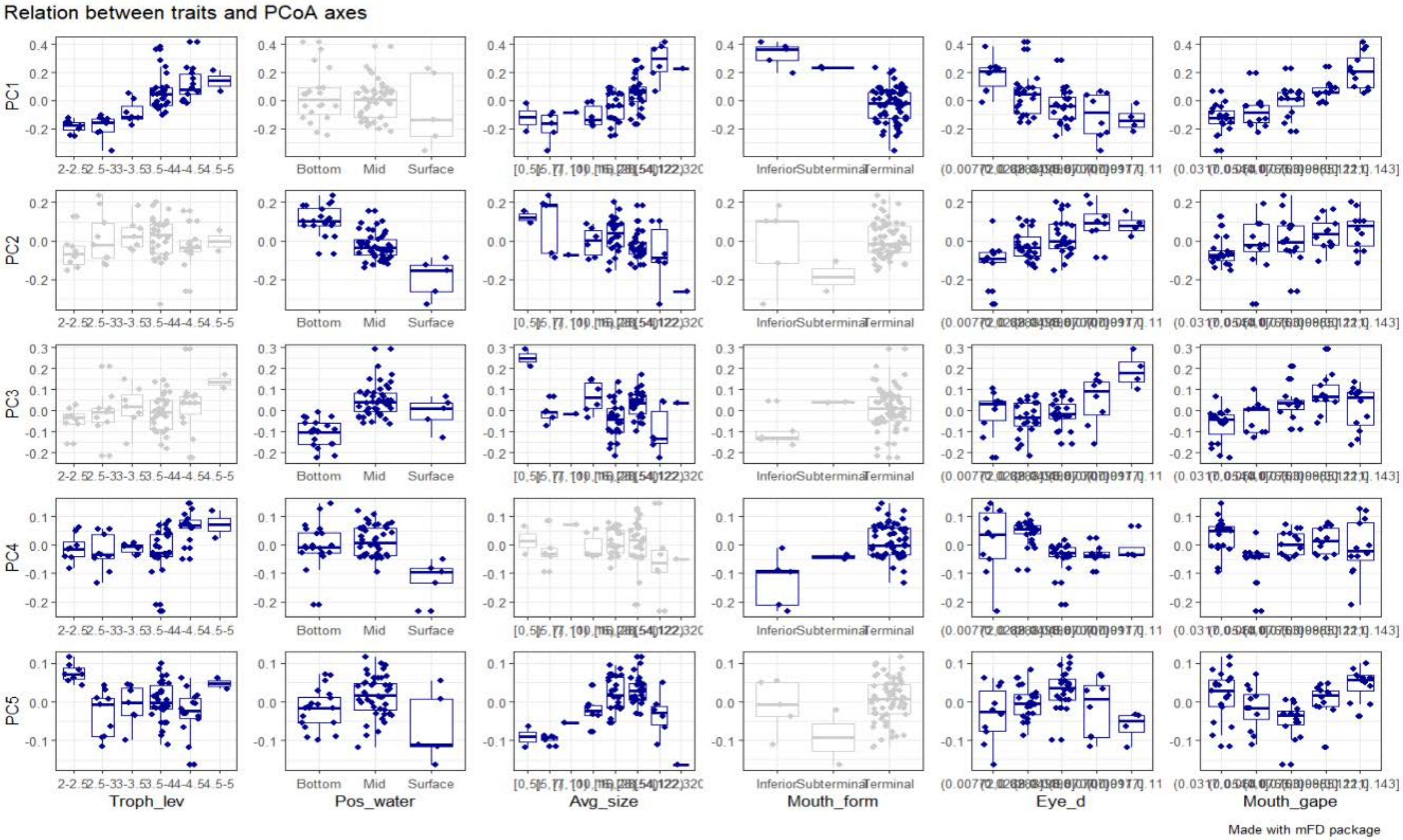

Relation between traits and PCoA axes
PC1
PC2
PC3
PC4
PC5
0.4
0.2
0.0
-0.2
0.3
0.1
-0.1
2-2.5
2.5-3
3-3.5
3.5-4
4-4.5
4.5-5
Bottom
Mid
Surface
Inferior
Subterminal
Terminal
Troph_lev
Pos_water
Avg_size
Mouth_form
Eye_d
Mouth_gape
Made with mFD package

Figure B.5

Relationships between functional traits and principal coordinates analysis (PCoA) axes based on the trophic trait dataset. Each panel represents the distribution of individual functional traits across five principal coordinate axes (PC1–PC5). The scatterplots and boxplots illustrate how traits such as trophic level, position in the water column, size, and morphological features (e.g., eye diameter, mouth gape) are associated with each axis. Traits are plotted against their respective PCoA scores to visualize their contributions to functional trait space. The blue plots indicate which traits are significant drivers of each principal coordinate axis