The role of refuges in coral reef ecosystems and biological invasions

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Abstract

Refuges play a key role in mediating species interactions, influencing movement patterns and shaping ecological communities. As ecosystems worldwide face increasing pressure from anthropogenic activities, understanding how, and to what extent, refuges contribute to the persistence of biodiversity is crucial for effective conservation management. Using coral reef ecosystems and biological invasions as model systems, this thesis explores whether refuges fulfil their expected roles and how they directly and indirectly influence species behaviour and distribution. First, by reviewing scientific literature on biological invasions, I demonstrate that refuge-mediated processes influence the outcomes of non-native species introductions, revealing common patterns across terrestrial, marine, and freshwater ecosystems. Second, an investigation into depth refuges on coral reefs reveals that mesophotic fish communities have undergone greater compositional changes over time than those in shallower waters, which is inconsistent with the expectations of the deep reef refugia hypothesis. Third, I find no clear evidence that invasive lionfish undergo ontogenetic niche shifts from shallow to deeper waters. This suggests that management efforts at shallow depths will have little impact on deeper populations, which may serve as a refuge from culling efforts. Finally, I show that farming damselfish display different anti-predator behaviours across sites with varying structural complexity. A greater field of view led to more cautious behaviour, while refuge availability had little apparent effect. This suggests that changes in the visual landscape of a reef can shape how fish perceive risk and influence predator-prey dynamics. By examining the role of refuges at multiple ecological levels, from individuals to entire communities, this work provides new insights and suggests future research directions, emphasising the need to acknowledge and integrate refuges into conservation strategies.

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Author’s declaration

This thesis is my own original work and has not been submitted in part or in full for the award of a higher degree elsewhere. All inputs from co-authors and collaborators have been acknowledged throughout.

- James S. Boon, October 2024

Statement of contribution of others

This thesis includes collaborations with my supervisors Richard Field, Sally Keith and Dan Exton. Each data chapter in this thesis reflects collaborations with several other co-authors. I collected the majority of the data presented, but I acknowledge that **Chapter 2** includes some data gathered in 2014 and 2015 by my collaborators. Additionally, in **Chapter 4**, a portion of the field data was collected by a co-author. All collaborator contributions are acknowledged, and their contributions outlined on the title page of the relevant chapter. I conceptualised the research questions and experimental design of all projects, analysed data, and synthesised into manuscripts for publication. My collaborators provided guidance on study design, and field and editorial support. This PhD was funded through the Envision Doctoral Training Programme (DTP) by Natural Environment Research Council (NERC). Additional funding support was provided by Operation Wallacea, the Murray Foundation (UK Registered Charity No. 1162333) and the NERC National Environmental Isotope Facility (grant no. 2542.1022).

General Introduction

0.1 The ecological refuge

Refuges play a fundamental role in shaping ecological communities. Defined as areas of the environment that offer individuals or populations buffering or shelter from one or more stressors, refuges provide this protection over timescales from seconds to several decades (Bongaerts & Smith, 2019; Keppel et al., 2012). This enables individuals or populations to survive and recolonise nearby areas once stressors subside (Bongaerts & Smith, 2019; Keppel et al., 2012). Refuges can be either static, like rock crevices that consistently offer protection, or dynamic, shifting location over time as environmental conditions or species interactions change (Pavey et al., 2017; Reside et al., 2019). It is important to note that this concept differs from ‘refugia’ (singular ‘refugium’), which refers to places where species can persist and adapt to changing abiotic conditions over much longer evolutionary timescales (Ashcroft, 2010; Keppel et al., 2012; Morelli et al., 2016). However, the distinction between refuges and refugia is not always clear, as some areas can function as both, depending on the timescale considered (Bongaerts & Smith, 2019). In the short term, an area may act as a refuge by providing temporary protection from immediate stressors such as predation, extreme weather events, or seasonal environmental fluctuations (Bongaerts & Smith, 2019; Keppel et al., 2012). Over longer, multi-generational timescales, if the same area continues to offer stable conditions that support population persistence and adaptation, it may also serve as refugia (Bongaerts & Smith, 2019; Keppel et al., 2012).

By protecting organisms against stressors, refuges play a crucial role in mediating species interactions (Berryman & Hawkins, 2006), influencing movement patterns (Shaw, 2016), and safeguarding species, communities, and ecological functions that are threatened by anthropogenic activities (Selwood & Zimmer, 2020). Thus, in this era of rapid environmental change, understanding the role of refuges in affecting species interactions and the persistence of ecological communities is increasingly important.

0.1.1 Role of refuges in species dynamics

The concept of the ecological refuge was first proposed in the early 20th century, initially used to describe areas that offer prey protection from predators (Elton, 1939; Gause, 1934). Structurally complex habitats, like branching corals or trees, offer prey crevices and hiding spots that enhance their chances of survival (Hixon & Beets, 1993; Sih, 1987). For predators, these environments increase the time and energy needed to locate prey, lowering their capture rates (Berryman & Hawkins, 2006). These counterbalancing effects help stabilise predator-prey dynamics by regulating population cycles, preventing drops in prey numbers, and reducing the risk of predator population crashes (Chen et al., 2009; Sih, 1987). For example, coral reefs with moderate levels of refuge availability often support the highest predator and prey abundance, but when refuge availability is too high or too low, prey become less accessible, leading to decreased predator growth rates and population sizes (Rogers et al., 2014, 2018). Thus, shifts in structural features and the availability of refuges could disrupt predator-prey dynamics, triggering cascading effects on community structure and ecosystem integrity (Rogers et al., 2018).

Refuges can also moderate competitive interactions. When two populations compete for the same resource, they will either adapt by utilising different resources (niche differentiation), or the weaker competitor will be outcompeted, potentially resulting in its extinction or a shift to a different niche (competitive exclusion; Brown et al., 2013). For competitive exclusion not to occur, sufficient niche space and environmental heterogeneity must exist (Broekhuis et al., 2013). A well-known example is found in the Serengeti, where cheetahs (*Acinonyx jubatus*), as subordinate predators to hyenas (*Crocuta crocuta*) and lions (*Panthera leo*), seek refuge in areas with lower prey densities, which dominant competitors tend to avoid due to limited resources (Durant, 1998). In this scenario, cheetahs use spatial avoidance in a heterogeneous landscape to limit competitive interactions with their more dominant rivals (Durant, 1998).

Movement and migration patterns are often closely tied to the availability of refuges. In some cases, species undergo ‘refuge migrations’, where they leave the habitat they feed and breed in to seek temporary refuge from extreme shifts in climate or biotic interactions (Gnanadesikan et al., 2017; Shaw, 2016). For instance, Bogong moths (*Agrotis infusa*) in Australia feed and reproduce along the coastline, but migrate to mountain caves during the dry and hot summer to survive in cooler conditions (Common, 1954). Similarly, refuges are an important mediator of ontogenetic migrations, where organisms in their early life stages depend on safer areas to avoid predators and withstand environmental pressures (Nakazawa, 2015). The larvae of many reef fish species settle in shallow-water habitats, like seagrasses and mangroves, where predation risk and competition is lower (Lecchini & Galzin, 2005; Mellin et al., 2007; Shima et al., 2012). As they grow, predation risk decreases and resources requirements increase, triggering a movement to more exposed but bountiful habitats, such as the forereef (Dahlgren & Eggleston, 2000).

When refuges are considered a limiting ecological resource, the relationship between refuge availability and species diversity is not necessarily linear (Berryman & Hawkins, 2006). Population models suggest biodiversity peaks at intermediate levels of refuge availability (Hochberg & Hawkins, 1992). When refuges are scarce, increased predation or competition can remove species less adapted to these greater pressures, while too many refuges can suppress predators or competitors, allowing a few dominant species to proliferate (Hawkins et al., 1993). In reality, refuges are not the only limiting resource in the environment and by promoting the coexistence and persistence of species, more refuges typically increases species richness (Berryman & Hawkins, 2006; Caley & St John, 1996; Garrick, 2011; Mohd et al., 2023). For instance, increasing the number of predation and thermal refuges in hedgerow habitats is positively correlated with insect and mammalian species richness (Lecq et al., 2017), and more crevices on reefs can increase fish species richness (Caley & St John, 1996). However, most studies exploring the relationship between refuges and diversity tend to focus on taxonomic diversity, while functional diversity, which is the variation in species traits that affect ecosystem function, remains largely underexplored (Cadotte et al., 2011; Loiseau et al., 2023)

0.1.2 The need to study refuges in a fast-changing world

As ecosystems around the world come under growing pressure from human activities, refuges are increasingly recognised as vital ecological features for effective conservation (Cowan et al., 2021; Selwood & Zimmer, 2020). Areas with lower levels of human disturbance are often prioritised for ecological restoration, the establishment of protected areas, and species reintroduction programs (Braidwood et al., 2018; Keppel et al., 2012; Reside et al., 2019). On a more localised scale, artificial refuges, such as bird shelters, are commonly constructed to replace natural refuges lost to habitat destruction or alteration (Cowan et al., 2021; Watchorn et al., 2022, 2024). As refuges become increasingly important in conservation, it is important to better understand whether they truly serve their intended function and how species and populations of conservation concern utilise them.

0.2 Biological invasions

The impact of non-native species is one of the major global threats facing biodiversity (Pyšek et al., 2020; Roy et al., 2023; Seebens et al., 2017). Non-native species are organisms that have been introduced to regions outside of their natural range because of human interference (Jeschke et al., 2014). This broad definition encompasses ‘invasive’ species, which are non-native organisms that form self-sustaining populations, spread extensively from their point of introduction, and are often associated with negative ecological or economically impacts (Blackburn et al., 2014). Since the beginning of the 20th century, the occurrence of non-native species has increased globally, with more than 13,000 plant species alone being introduced to areas outside their natural habitats (van Kleunen et al., 2015). This rise is primarily driven by the expansion of global transport and trade (Chapman et al., 2017). While non-native species can offer some socio-economic benefits, such as contributing to food, recreation, and fuel resources (Sax et al., 2022, 2023), they can negatively affect native ecosystems across all ecological levels (Blackburn et al., 2014). Non-native species can reduce genetic diversity in their new locations through hybridisation with native species, especially when hybrids have low survival rates or are sterile (Huxel, 1999; Kovach et al., 2015; Mooney & Cleland, 2001). They can also trigger shifts in the behaviour (Ruland & Jeschke, 2020) and movement patterns of native species (Stodola et al., 2013), and alter predation (Doherty et al., 2016) and competition dynamics (Orrock et al., 2010). These combined effects can lead to the loss of biodiversity (Vilà et al., 2011), ecosystem functions and the provision of ecosystem services (Linders et al., 2020; Pejchar & Mooney, 2009; Walsh et al., 2016).

Ecological features that influence species interactions are likely key factors in determining the outcomes of a biological invasion. Despite the high costs associated with managing non-native species, many management strategies prove ineffective or require significant financial and human resources to merely suppress non-native populations temporarily (DiTomaso et al., 2017; McMillan et al., 2023; Zavaleta et al., 2001). Thus, recognising the role of refuges in biological invasions could not only deepen our understanding of non-native species ecology, but also lead to more efficient and sustainable management efforts (**Chapter 1**).

0.3 Coral reef ecosystems

Tropical coral reefs are among the most biodiverse ecosystems on the planet, providing crucial ecosystem services including food, income, and coastal protection (Moberg & Folke, 1999; Woodhead et al., 2019). Although they cover less than 0.01% of the ocean’s surface, they host up to one-third of all marine species (Bellwood & Hughes, 2001; Plaisance et al., 2011). This diversity stems from the structures, habitats, and food sources provided by scleractinian (hard) and non-scleractinian (soft) corals, as well as from sponges and algae (Darling et al., 2017; Graham & Nash, 2013). Over six million people rely on reefs for fishing, which supplies vital protein, micronutrients and financial income (Cinner, 2014; Hicks et al., 2019; Woodhead et al., 2019). The main global threat to reefs is climate change, as rising temperatures increase the likelihood marine heatwaves, which causes mass bleaching events (Hughes et al., 2017, 2018; Spalding & Brown, 2015). This process, where corals expel their photosynthetic symbionts, can result in coral death if warming periods occur over long enough periods (Brown, 1997; Hoegh-Guldberg, 1999; Lesser, 1997). This can lead to shifts in benthic composition, reduce the reef's structural complexity, limit feeding opportunities, and decrease fish diversity (Bellwood et al., 2006; Graham et al., 2007; Pratchett et al., 2011).

Ocean warming, combined with regional stressors like overfishing, pollution, and invasive species, further threatens reef biodiversity and the communities that depend on them (Ban et al., 2014; Ellis et al., 2019; França et al., 2020; Muthukrishnan & Fong, 2014).

0.3.1 Depth as a refuge – mesophotic coral ecosystems

Mesophotic coral ecosystems (MCEs) are typically considered as extensions of shallow-water coral reefs (< 30 m depth) and are located at depths of approximately 30 to 150 m (Hinderstein et al., 2010; Lesser et al., 2009). These ecosystems are largely home to light-dependent communities, such as zooxanthellate corals, algae, and sponges (Kahng et al., 2010). MCEs are often divided into upper (30 – 60 m) and lower zones (60 – 150 m), with the upper zone sharing many species with shallow reefs, while the lower zone hosts distinct communities with more specialised adaptations to low light (Lesser et al., 2019; Semmler et al., 2017). MCEs are thought to cover as much, if not more, area globally than shallow-water counterparts, but are far less studied (Rocha et al., 2018). Detailed studies only began in the latter half of the 20th century due to advancements in SCUBA and submersible technologies, allowing researchers to access these greater depths (Kahng et al., 2014). Consequently, the role MCEs play in the ecology of reef species, and the threats facing these deeper ecosystems, remain poorly understood (Turner et al., 2017).

MCEs have been identified as possible refuges for shallow-water communities. Glynn (1996) was among the first to report that ocean warming events affected shallow reefs more severely than those at moderate depths. Hughes & Tanner (2000) later suggested that deeper reefs could provide refuges for corals with broad depth distributions, a concept subsequently expanded to include fish and sponge species (Lesser et al., 2009). This idea was formally developed by Bongaerts et al. (2010), as the deep reef refugia hypothesis. This hypothesis puts forward that (1) major disturbances affecting shallow-water reefs are less intense on deeper reefs, and (2) deeper reefs can act as a source of recruits for shallower areas, aiding in their recovery post-disturbance (Bongaerts et al., 2010). Under the theoretical framework of the deep reef refugia hypothesis, both mesophotic refuges and refugia are considered (Bongaerts & Smith, 2019). As such, mesophotic reefs may function as both, depending on the timescale considered. In the short term, MCEs can provide refuge, offering protection particular disturbance episodes, such as a singular ocean warming event (Bongaerts & Smith, 2019). Over longer, multi-generational timescales, MCEs may also serve as refugia, providing stable conditions that support species persistence and adaptation over multiple and reoccurring disturbance events, thereby sustaining populations through longer-term climate shifts (Bongaerts & Smith, 2019).

Previous studies have primarily tested the deep reef refugia hypothesis by examining whether shallow and deep reefs share common species, using these similarities to suggest refuge potential (e.g. Laverick et al., 2018 and Semmler et al., 2017). However, the growing number of reports highlighting stressors like marine heatwaves, tropical storms, destructive fishing practices, and invasive species affecting mesophotic reefs raises doubts about whether these deeper habitats can truly serve as refuges for fish communities (Andradi-Brown et al., 2017a; Diaz et al., 2023a; McWhorter et al., 2024; Rocha et al., 2018; Soares et al., 2019; Venegas et al., 2019). A key limitation in assessing the deep reef refugia hypothesis is the lack of long-term data across the reef depth gradient, which makes it challenging to determine whether MCEs provide more stable habitats and support less variable communities compared to shallower depths over time (**Chapter 2**).

0.3.2 Caribbean reefs as a model system

This thesis uses Caribbean coral reefs as the primary study system (**Figure 0.1**). In recent decades, reefs in this region have experienced a 'regime shift' due to cumulative stressors, including the mass mortality of the key herbivore *Diadema antillarum* (Lessios, 1988), increased sedimentation from runoff (Rogers & Ramos-Scharrón, 2022), invasive species (Côté & Smith, 2018), and more frequent thermal stress and storms driven by climate change (Bruno et al., 2009; Hughes, 1994; Mumby, 2009). Once dominated by large branching corals like *Acropora palmata* and *A. cervicornis*, Caribbean reefs are now primarily composed of octocorals, non-scleractinian fire corals (*Millepora spp*.), sponges, and algae (Contreras-Silva et al., 2020; Gardner et al., 2003). As a result, fish communities are now dominated by herbivorous and omnivorous species, with high densities of territorial damselfish, wrasse, and parrotfish (Alvarez-Filip et al., 2015; Andradi-Brown et al., 2016; Newman et al., 2006). In comparison, MCEs in the Caribbean are mainly comprised of planktivorous and piscivorous fish species, with certain species like parrotfish, snappers, and threatened Caribbean reef sharks (*Carcharhinus perezii*) often more abundant at greater depth than in shallower waters (Andradi-Brown et al., 2016).

The loss of hard corals and their structural complexity has led to what is often referred to as the ‘flattening’ of Caribbean coral reefs (Alvarez-Filip et al., 2009; Alvarez-Filip et al., 2011). This decline likely disrupts predator-prey dynamics, as reef structures provide prey with refuge (Camp et al., 2013; Warfe & Barmuta, 2004). However, most studies assessing the impact of this loss on predator-prey interactions focus solely on rugosity, a measure of surface roughness, as the primary metric of complexity (Luckhurst & Luckhurst, 1978; González-Rivero *et al.*, 2017). It is often assumed that higher rugosity means more refuges and is the main factor influencing risk perception (Nunes et al., 2015; Quadros et al., 2019). Theory suggests however, that other aspects of structural complexity can influence prey behaviour, but they have yet to be explored in the context of coral reefs (**Chapter 4**). For instance, an individual's field of view (i.e., extent of observable area from a given position), which can be shaped by the topography of their environment, is also thought to affect when individuals begin to assess predation risk (Ndaimani et al., 2013; Stein et al., 2022).

0.3.3 Invasive lionfish

Invasive lionfish (*Pterois volitans* and *P. miles*) have rapidly spread throughout both shallow and mesophotic reefs in the Caribbean (Schofield, 2009; Whitfield et al., 2002). Originally from the Indian and Pacific Oceans, lionfish were first introduced to the western Atlantic near southern Florida in the mid-1980s, likely from aquarium releases (Whitfield et al., 2002). In just 30 years, they rapidly spread throughout the Caribbean Sea, driven by a lack of natural predators in their new range and their high reproductive capacity (Côté & Smith, 2018; Eddy et al., 2019). Lionfish have colonised most marine and estuarine habitats in the Caribbean, from sea grass and mangrove forests to deep sea habitats of more than 300 m depth (Côté et al., 2013;

Goodbody-Gringley et al., 2019; Gress et al., 2017). As gape-limited opportunistic predators, they consume a wide variety of prey, including fish, crustaceans, and echinoderms (Acero et al., 2019; Albins & Hixon, 2013; Morris & Whitfield, 2009; Peake et al., 2018). Their rapid geographic spread and broad diet has led to declines in native reef fish biomass and diversity, as well as shifts in benthic community structure of reefs (Albins, 2015; Ballew et al., 2016; Green et al., 2012a; Lesser & Slattery, 2011).

In the invaded range of lionfish, the current management strategy primarily relies on opportunistic culling by recreational SCUBA divers using hand spears (Andradi-Brown, 2019). Though this approach can be effective in the short term and in small areas, it requires ongoing removal efforts and substantial resources (Davis, 2018; Davis et al., 2021; Johnston & Purkis, 2015). Moreover, recreational divers tend to stay above 30 m depth, meaning that deeper lionfish are regularly missed (Andradi-Brown, 2019; Andradi-Brown et al., 2017b; Malpica-Cruz et al., 2019). These deeper lionfish are reported to be larger in body size than those at shallower depths (Andradi-Brown et al., 2017a). This pattern has been observed in lionfish populations in Honduras, the Gulf of Mexico, Bahamas and Costa Rica (Andradi-Brown et al., 2017a). One hypothesis for this is that it is driven by ontogenetic niche shifts, where lionfish move from shallow to deeper habitats as they grow (Andradi-Brown, 2019; Andradi-Brown et al., 2017b; Malpica-Cruz et al., 2019). MCEs may therefore serve as a refuge for the largest, most reproductively capable lionfish (**Chapter 3**).

0.4 Methods in studying refuges on coral reefs

Recent technological advancements have improved the ability to explore reef refuges. In the past, studying MCEs was restricted by the logistical challenges of surveying beyond recreational diving depths (Kahng et al., 2014). However, advances in technical diving and remotely operated vehicles (ROVs) have made it possible to explore greater depths and gather foundational data on fish communities at various depths in locations around the world (Lesser et al., 2019). Moreover, traditional methods for assessing reef structural complexity, such as the ‘chain-and-tape’ rugosity technique, have been improved by digital photogrammetry (Aston et al., 2022; Ferrari et al., 2016; Urbina-Barreto et al., 2021). This method provides detailed, three-dimensional data on reef habitats, enhancing our ability to explore ecologically relevant aspects of structural complexity (González-Rivero et al., 2017).

Figure 0.1 Shallow-water reefs (top) and mesophotic coral ecosystems (bottom) in the Caribbean. Photos from Utila, Honduras.

0.5 Thesis overview

The aims and scope of this thesis changed over the course of my PhD. Initially, I set out to develop a novel approach for studying invasive lionfish using a small ROV that could survey MCEs and capture lionfish. My goal was to use demographic models to examine how lionfish populations change with depth and to develop optimal culling strategies. However, in April 2022 it became clear that the ROV was unsuitable for our needs. Consequently, my project aim had to be changed.

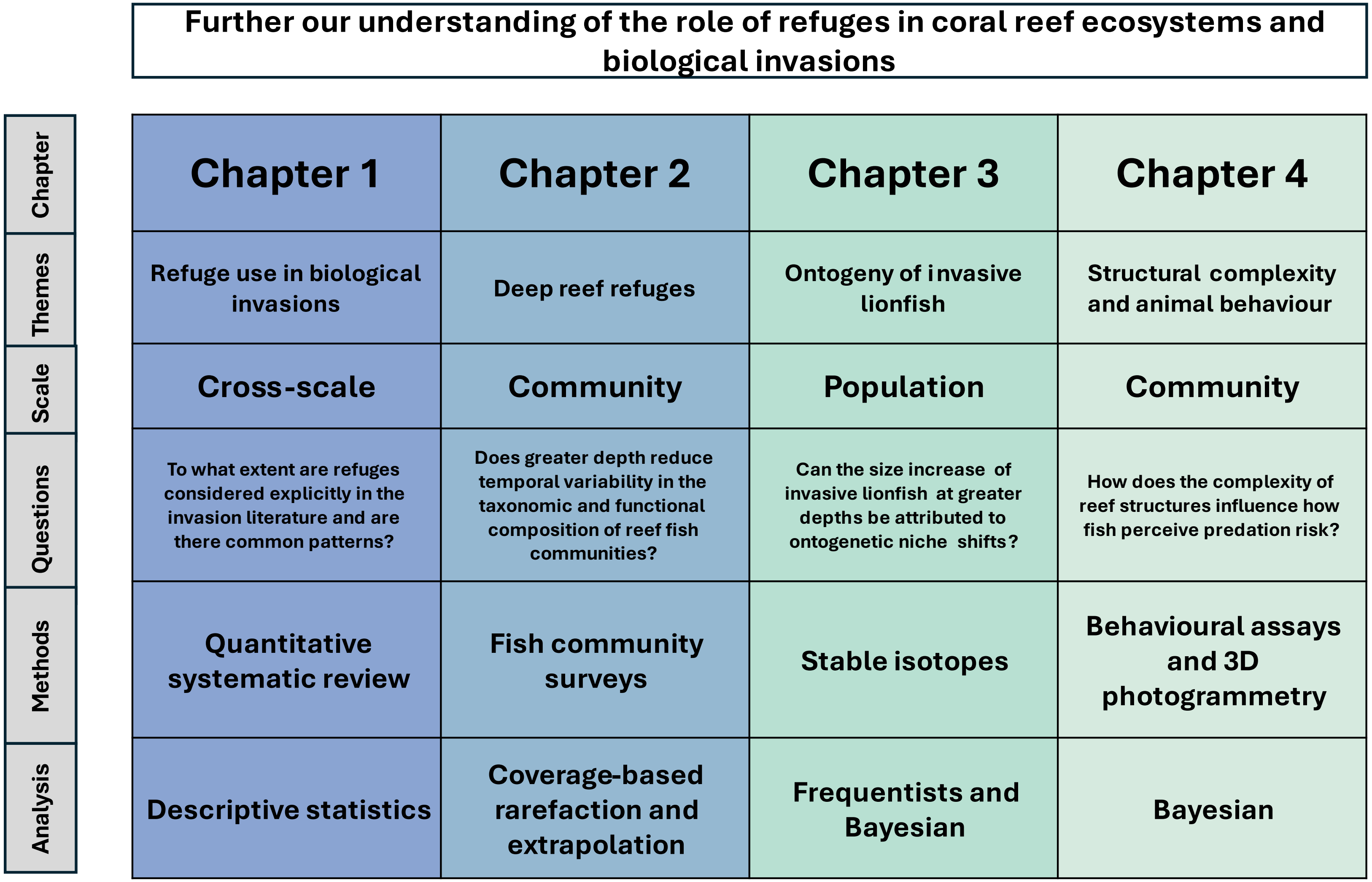
The aim of this thesis is to further our understanding of the role of refuges in coral reef ecosystems and biological invasions (**Figure 0.1**). My thesis improves our knowledge by examining whether refuges fulfil their expected roles and exploring the direct and indirect ways they influence species behaviour and distribution.

This thesis explores the following research questions:

1. To what extent are refuges considered explicitly in the invasion literature and are there common patterns? (**Chapter 1**)
2. Does greater depth reduce the temporal variability in the composition of reef fish communities? (**Chapter 2**)
3. Can the size increase of invasive lionfish with greater depth be attributed to ontogenetic niche shifts? (**Chapter 3**)
4. How do different features of structural complexity influence perceived predation risk of reef fish? (**Chapter 4**)

I address my thesis questions using fish on coral reefs as the primary study system. My thesis combines a synthesis of existing knowledge, *in-situ* field observations, statistical analysis and laboratory-based techniques (**Figure 0.2**). I address the first question in **Chapter 1** of this thesis, where I conducted systematic review of the current knowledge base from scientific publications on refuges in biological invasions to synthesise their role, detect general ecological patterns, and identify research gaps. I then address, in **Chapter 2**, whether greater depth provides a refuge for the broader reef community by exploring the temporal variation in the taxonomic and functional composition of reef fish communities across shallow and deeper reefs. In **Chapter 3**, I focus on one example of refuge use in biological invasions and coral reefs where I explore whether invasive lionfish in deeper habitats represent an extension of their ontogenetic niche shifts using stable isotope analysis. Finally, in **Chapter 4**, I use *in-situ* experiments and 3D photogrammetry to assess how the perceived predation risk of reef fish is influenced by their surrounding structural environment.

The four data chapters (**Chapters 1–4**) of this thesis have been prepared for publication. **Chapter 1** has already been published in *Global Ecology and Biogeography*, while **Chapter 2** is currently under review at *Coral Reefs*. **Chapter 3** will be prepared for submission at a later date, and **Chapter 4** is currently under review at *Behavioural Ecology*.



Further our understanding of the role of refuges in coral reef ecosystems and biological invasions

Chapter	Chapter 1	Chapter 2	Chapter 3	Chapter 4
Themes	Refuge use in biological invasions	Deep reef refuges	Ontogeny of invasive lionfish	Structural complexity and animal behaviour
Scale	Cross-scale	Community	Population	Community
Questions	To what extent are refuges considered explicitly in the invasion literature and are there common patterns?	Does greater depth reduce temporal variability in the taxonomic and functional composition of reef fish communities?	Can the size increase of invasive lionfish at greater depths be attributed to ontogenetic niche shifts?	How does the complexity of reef structures influence how fish perceive predation risk?
Methods	Quantitative systematic review	Fish community surveys	Stable isotopes	Behavioural assays and 3D photogrammetry
Analysis	Descriptive statistics	Coverage-based rarefaction and extrapolation	Frequentists and Bayesian	Bayesian

Figure 0.2 Thesis overview outlining research theme, ecological scale, specific research questions, methodological approach and statistical techniques used.

Chapter 1: The role of refuges in biological invasions: a systematic review

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Author contributions

All authors contributed to conceptualisation of the research; J.S.B performed the research and wrote the first manuscript draft; all authors edited the manuscript.

[Note – text in square brackets indicates where the chapter differs from the published version due to requests from thesis examiners.]

Abstract

Aim: Ecological refuges buffer organisms against stressors and mediate a range of species interactions. However, their role in the context of biological invasions has yet to be synthesised, despite the increasing prevalence and impact of non-native species. To address this, I conducted a systematic review aiming to determine the extent to which refuges are considered explicitly in the invasion literature and to synthesise their function.

Location: Global.

Time period: Present day.

Major taxa studied: All.

Methods: My search of the literature was conducted using the SCOPUS and Web of Science databases and followed the preferred reporting items for systematic reviews and meta-analyses (PRISMA) protocol. I obtained 315 records of refuge use in biological invasions from 300 studies. From each record, I extracted information relating to the experimental design, species characteristics and refuge type, where available.

Results: Refuges and refuge-mediated processes are widely reported in the invasion literature. Native species commonly use refuges to avoid non-native predation and competition, with spatial complexity and habitat heterogeneity key factors in facilitating their coexistence. Records show that artificial structures safeguard non-natives in their introduced range. However, there were key differences in the use of such structures in marine and terrestrial environments. Moreover, the enhanced structural complexity created by non-native plants and bivalves is often reported to act as a predation refuge for other species.

Main conclusions: The ubiquity of refuge-based processes suggests that refuges can play an important role in affecting the persistence, spread and impacts of non-native species, either through previously described mechanisms (i.e. refuge-mediated apparent competition and the persistent pressure scenario) or through a mechanism I describe (i.e. when non-native species use existing refuges), or both.

1.1 Introduction

Ecological refuges have seen growing attention over recent decades due to their ability to mediate a range of ecological processes and species interactions (Berryman & Hawkins, 2006). Refuges are habitat features that provide individuals or populations buffering or protection against environmental, biotic or anthropogenic stressors (Bongaerts & Smith, 2019; Keppel et al., 2012; Pavey et al., 2017). Structures created by habitat-forming species (e.g. plants and corals), areas inaccessible to predators or competitors due to physiological tolerances, geological features, and protected areas are often reported to act as refuges for a broad range of taxa (Berryman & Hawkins, 2006; Gallardo et al., 2017; Selwood & Zimmer, 2020). Among the leading global stressors of biodiversity are biological invasions, which are increasing in frequency and cost (Seebens et al., 2017). Refuges may play a key role in the persistence and spread of non-native species, and in mediating their interactions with native species. Despite the clear importance of the topic, I am not aware of any attempts to review and synthesise the current literature on refuges in invasion biology.

Refuges facilitate the coexistence and persistence of species across a range of contexts. The concept of an ecological refuge has been around since the first half of the 20th century, originally in reference to areas that provide prey with shelter from predation (Elton, 1939; Gause, 1934). Refuges generally have a stabilising effect on predator–prey interactions and allow the coexistence of species by reducing predator effectiveness and lowering extinction risk (Chen et al., 2009; Sih, 1987). Prey refuges are particularly key during vulnerable early life stages, when predation risk is often high (Grof-Tisza et al., 2015). Refuges also mediate competitive interactions, whereby a species with poor competitive abilities can persist in areas where competition is reduced (Durant, 1998). Subordinate competitors may find sanctuary by changing spatial or temporal resource use to reduce niche overlap (Broekhuis et al., 2013; Durant, 1998). Furthermore, the dispersal and migration patterns of organisms can be linked to refuges. For instance, summer steelheads (rainbow trout, *Oncorhynchus mykiss*) move between cool-water areas, migrating upstream during periods of high water temperatures (Hess et al., 2016). Although generally considered to have a positive impact on their inhabitants, the limited resources and sub-optimal conditions often found within refuges can reduce activity, growth and fecundity levels (Orrock et al., 2013). However, refuges with high carrying capacities can result in altered trophic pathways, displaced consumer pressure or predator extinction (Křivan, 1998).

More recently, the identification of refuges in conservation science has seen growing interest, owing to their role in the persistence of species under threat from anthropogenic disturbances (Cowan et al., 2021; Selwood & Zimmer, 2020). Areas less impacted by human stressors are often judged to be priority sites for restoration initiatives, the placement of protected areas and species translocations or re-introductions (Braidwood et al., 2018; Michalak et al., 2018; Selwood & Zimmer, 2020). Furthermore, the creation of artificial refuges is increasingly used as a substitute for natural refuges lost due to habitat alteration or destruction (Chester & Robson, 2013; Cowan et al., 2021).

In the context of biological invasions, refuges against non-native threats can promote the persistence of native species. Environmental conditions beyond the tolerances of non-natives can restrict their growth, competitive ability and distribution, which in turn can provide natives with areas of sanctuary (Kestrup & Ricciardi, 2009; MacDougall et al., 2006; Melbourne et al., 2007). These areas can occur in patches where non-natives are totally excluded, or they can occur along environmental gradients with reduced non-native abundance compared to the broader environment (Astorg et al., 2021). For instance, areas of greater water movement inhibit the establishment of the introduced macrophyte *Utricularia inflata*, thus safeguarding native macrophytes that are otherwise outcompeted for space in sheltered sites (Urban & Titus, 2010). Similarly, conductivity gradients can provide native prey with refuge from introduced round goby (*Neogobius melanostomus*), while the impacts of introduced Nile perch (*Lates niloticus*) diminish along hypoxia gradients (Astorg et al., 2021; Chrétien & Chapman, 2016).

Refuges also influence the persistence and spread of non-native species in their introduced range. The success of a non-native species is often limited by its physiological limits and the climatic regime of the novel location, meaning areas that remain within their physiological thresholds can be crucial for the persistence of non-native populations (Kelley & Cooke, 2014). For example, in freshwater non-native fishes, warm-water effluent flows facilitate the persistence of species invading from warmer climates during cooler temperatures (Nico et al., 2012; Peterson et al., 2005). Invaders can also find refuge in structures created by native habitat-forming species, such as the tub-like shells created by *Galeolaria caespitosa*, which buffer the non-native porcelain crab (*Petrolisthes elongatus*) from stressful abiotic conditions in intertidal rocky shores (Gribben et al., 2020; Uyà et al., 2020; Wright et al., 2016). Knowledge of non-native refuges can also inform management. For example, artificial refuge traps that resemble invasive crayfish burrows can be used in conjunction with hand removal or more effective, but less species-specific, baited minnow traps, to improve culling efficiency (Curti et al., 2021; de Palma-Dow et al., 2020; Green et al., 2018).

Recent work has demonstrated that non-native species can create refuges for other taxa in their introduced range (Holzer & Lawler, 2015; Rodriguez, 2006; Wright et al., 2014). Non-native plants often lack coevolved natural enemies (i.e. enemy release hypothesis), meaning they can survive, grow and spread with less resistance than natives (Keane & Crawley, 2002; Mattos & Orrock, 2010; Oduor et al., 2018). This proliferation can enhance spatial complexity and create novel refuges (Dutra et al., 2011; Pearson, 2009; Vilà et al., 2011). Non-native shrubs that construct thick understories can elicit shifts in the abundance and behaviour of native taxa, particularly low-trophic-level consumers (Dutra et al., 2011; Guiden & Orrock, 2017, 2019; Stewart et al., 2021; Watling et al., 2011; Watling & Orrock, 2010). The Amur honeysuckle (*Lonicera maackii*), which is non-native in the eastern United States, is used as a predation refuge for small mammals and birds and alters levels of seed predation on native plants (Mattos & Orrock, 2010; Schmidt & Whelan, 1999). These novel shelters can also benefit the non-native that creates them. For example, refuge-mediated apparent competition is an established process by which a non-native plant provides a superior refuge than its neighbour and displaces consumer pressure onto native plants, facilitating non-native persistence and spread (Orrock et al., 2010a; Orrock et al., 2010b).

Cases of refuge use and refuge-mediated processes in the invasion literature are currently dispersed and lack synthesis. To address this, I conducted a systematic review aiming to determine the extent to which refuges are considered explicitly in the invasion literature and synthesise their role. In uniting this research under a common theme, we can detect general ecological patterns, identify research gaps and potentially guide future conservation. Specifically, I systematically searched the peer-reviewed literature for studies reporting refuges that: (1) reduce the impact of non-native species on native species; (2) are used by non-native species in their introduced range; or (3) are provided by non-natives.

1.2 Methods

1.2.1 Definitions

In this study, I define a 'refuge' as a habitat feature that provides individuals or populations buffering or shelter against single or multiple stressors (Bongaerts & Smith, 2019; Keppel et al., 2012). They provide this protection over periods ranging from seconds to decades, allowing either individuals or populations to persist and recolonise adjacent areas when stressors are alleviated (Keppel et al., 2012). Refuges can occur in fixed locations that consistently safeguard organisms (e.g. rock crevices), or they can be dynamic, in that their location may shift depending on local abiotic conditions or species associations (Dickman et al., 2011; Magoulick & Kobza, 2003; Orrock et al., 2010a; Pavey et al., 2017; Reside et al., 2019). This characterisation contrasts with 'refugia', a term used to describe locations where species can persist and adapt to changing climates and abiotic conditions over substantially longer evolutionary timescales (Keppel et al., 2012).

I use the term 'non-native' to define species that have been introduced to regions outside of their natural range because of human interference (Jeschke et al., 2014). This broad definition includes but is not limited to 'invasive' species, which are defined as non-native species that form self-sustaining populations and spread significant distances from their initial point of introduction (Blackburn et al., 2011). In policy, 'invasive' species are often associated with negative socio-economic or environmental impacts. Here, however, the term 'non-native' is used irrespective of establishment status, geographic extent or perceived impacts.

1.2.2 Study selection

To find the relevant literature, I first created a Boolean search string using the package litsearchr (Grames et al., 2019) in R v. 4.2.3 (R Core Team, 2023). This uses a Rapid Automatic Keyword Extraction (RAKE) algorithm to select common words from the titles, abstracts and keywords of studies of interest (Grames et al., 2019). However, I initially found the search string too narrow in scope, so I included terms to broaden the search (i.e. included synonyms of the word ‘refuge’) and make the results more pertinent to the review. This included the terms ‘refugia’ and ‘refugium’ because these are often used interchangeably with ‘refuge’ in the literature, despite formal distinctions. Additionally, expert reviewers suggested I include search terms used in the literature that infer but do not explicitly use the word “refuge.” The following search string was deemed suitable: (“refuge” OR “refuges” OR “refugium” OR “refugia” OR “shelter” OR “habitat structure” OR “non-consumptive effects” OR “risk-sensitive foraging” OR “anti-predator behavio*” OR “flight initiation”) AND (“non-native” OR “invasive” OR “exotic” OR “introduced species” OR “invasion” OR “alien” OR “non-indigenous”).

A search of the literature was conducted using the SCOPUS and Web of Science databases on 6 December 2022, applying my pre-defined search string. The search was limited by document type (only peer-reviewed publications) and by language (only studies with an English version), but not by study date or country. Study inclusion criteria were that (1) at least one species of non-native animal, plant, alga or fungus was investigated and (2) a refuge was reported. Papers related to ‘refugia’ (as defined in this study) were not included in the analysis – only those that were defined as ‘refugia’ in the study in question but would be identified as a ‘refuge’ in this study. I did not include studies that (1) investigated non-native bacteria, viruses or pathogens; (2) assessed shelter competition between non-natives and natives; or (3) demonstrated facilitation but did not show that refuge use was the underlying mechanism. Although reviews and meta-analyses were not included in the formal review, I did search their reference lists for additional studies.

I followed the preferred reporting items for systematic reviews and meta-analyses (PRISMA) protocol when appraising studies (Moher et al., 2015). The SCOPUS search identified 3375 studies, and the Web of Science search identified 3116 studies. Following the removal of 2499 duplicates, I was left with 3992 studies to screen. Studies were first filtered by title and abstract to assess general applicability to my aims. This removed 3398 studies. The full texts of the remaining 594 studies were then retrieved and screened in full. Of these, 270 papers met my criteria. From scoping the reference lists of review articles identified by my search string, I then added a further 14 studies. Based on expert advice from peer reviewers, I added a further 16 studies. Therefore, my review contains information from 300 peer-reviewed studies (see PRISMA flow diagram, **Figure 1.1**, and Table **S1.1** for full list of studies included in review). Fifteen studies recorded two separate instances of refuge use, meaning both were included in the analysis. I use the individual record of refuge use as the unit of observation, so in total I found 315 records.

1.2.3 Analysis

From each of the 315 records, I extracted information relating to the study design, native species characteristics, non-native species characteristics and refuge type, where available (see **Table 1.1** for full list). Three records were theoretical works on refuge-mediated apparent competition, meaning I could not ascribe a specific disturbance or a mechanism to them. Similarly, two records did not provide a specific description of the disturbance or habitat. To illustrate connections between taxa, habitats, disturbances, refuges and mechanisms, I created tripartite network diagrams using the R package ‘igraph’ (Csárdi, 2019).

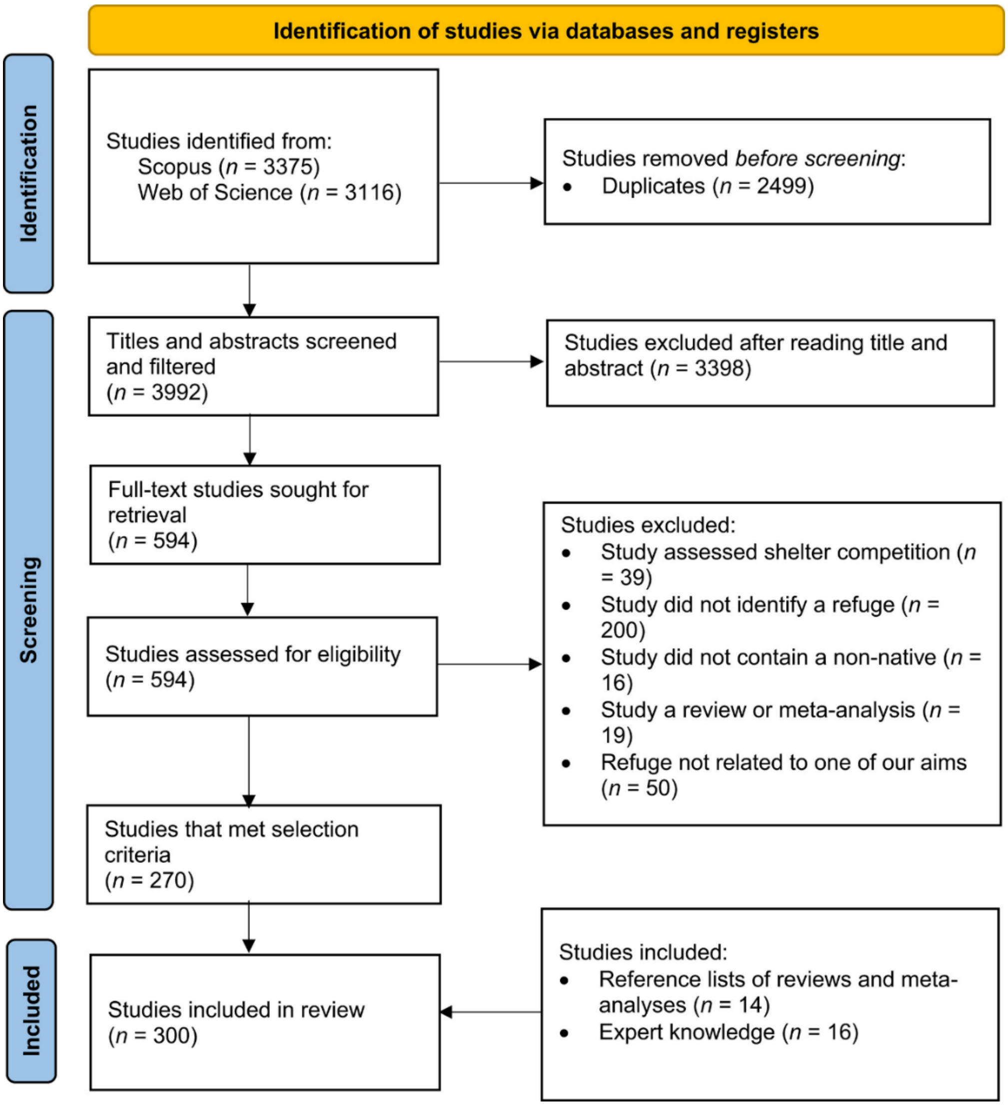

Figure 1.1 Preferred reporting items for systematic reviews and meta-analyses (PRISMA) flow chart showing the screening and appraisal procedure, resulting in the studies retained in the review.

Table 1.1 Data collected from the records included in the review.

Study background	**Reference**	Harvard reference
	Study design	Whether an observational or experimental study
	Region of study	The country or broad region of study
	Latitude & Longitude	Estimate of location. If more than one location was mentioned, then an approximate mid-point was used. If an ex-situ study, the location of the institution was recorded
	System	Terrestrial, freshwater, brackish or marine
	Habitat	Habitat description
Native species information	**Native type**	Classified as plant, fungus, alga or animal
	Native taxon	Animals were classified as amphibian, bird, fish, invertebrate, mammal or reptile. Plants were classified as macrophyte, tree, herb, shrub, grass, cactus or forb. Algae were classified as seaweed or diatom. If more than one, I recorded "several."
	Native family	Family of native taxon. If more than one, I recorded "several."
	Native species	Species of native taxon. If more than one, I recorded "several."
	Native trophic level	Classified as autotroph, detritivore, herbivore, omnivore or carnivore. If more than one, I recorded "several."
Non-native species information	**Non-native type**	Same classification as native taxa
	Non-native taxon	Same classification as native taxa
	Non-native family	Same classification as native taxa
	Non-native species	Same classification as native taxa
	Non-native trophic level	Same classification as native taxa
Refuge information	**Refuge**	A description of the refuge
	Broad disturbance	Biotic, environmental or anthropogenic
	Specific disturbance	A specific description of the disturbance
	Mechanism	How the refuge provides protection against disturbance

1.3 Results

In total, I found 315 records of refuge use in biological invasions (see **Table S1.1** for full dataset). Records were found across all continents (**Figure 1.2a**) except Antarctica. Most records were from the USA (n = 130, 41%), followed by Australia (n = 19, 6%) and Canada (n = 18, 6%), while records from Asia (n = 14, 4%) and Africa (n = 16, 5%) were poorly represented. Refuge use was mainly reported via observational methods (n = 178, 57%) compared to experimental (n = 137, 43%). Freshwater (n = 131, 42%) and terrestrial (n = 107, 34%) systems were highly represented, while fewer records were found in marine (n = 47, 15%) and brackish (n = 30, 10%) environments. Rivers (n = 66, 21%) and lakes (n = 42, 13%) received the most attention of all the habitats (**Figure 1.2b**), while records from desert (n = 4), shrubland (n = 5) and sand dune (n = 1) habitats were rare. Since the early 1980s, research on refuge use in the context of biological invasions has risen considerably (**Figure 1.2c**).

1.3.1 Refuges that reduce the impact of non-native species on native species

Of the records included in my review, 125 reported the use of refuges by native species in response to non-natives. Most were from invaded freshwater (n = 74, 59%) systems, particularly riverine (n = 39, 31%) habitats, while records from marine systems were less common (n = 9, 7%). Native families that were commonly assessed were Gammaridae (n = 11, 9%), Salmonidae (n = 9, 7%) and Unionidae (n = 7, 6%). The most common non-native families that threatened natives in the dataset were Salmonidae (n = 20, 16%), Gammaridae (n = 9, 7%) and Dreissenidae (n = 7, 6%). Common native refuges included structures created by native plants (n = 20, 16%), headwater streams (n = 11, 9%), substrata (n = 7, 6%) and areas with high-velocity water flow (n = 6, 5%; **Figure 1.3a**).

The tripartite network analysis, based on the 125 records, identified two key findings (**Figure 1.3b**). Firstly, predation by non-natives (n = 59, 47%) and competition with non-natives (n = 61, 49%) were the main threats posed to natives. Secondly, the mechanism by which native species found refuge tended to differ according to threat. When competition was the main threat, greater environmental stress tolerance typically allowed natives to find refuge (n = 42), while areas of enhanced structural complexity were rarely reported (n = 4). In response to non-native predation, greater environmental stress tolerance (n = 23) and areas of enhanced structural complexity (n = 21) allowed natives to find refuge.

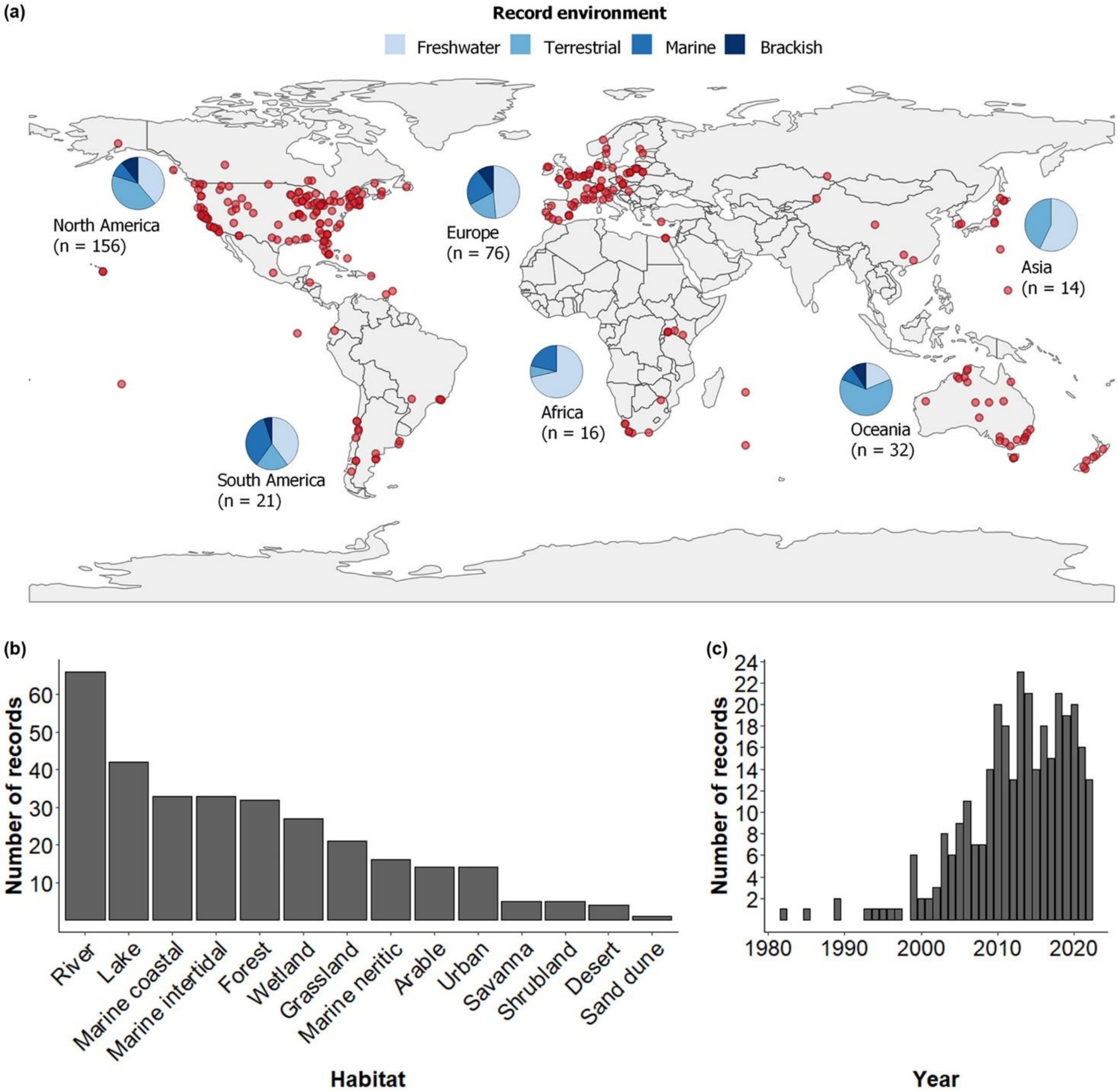

Figure 1.2 Summary of records included in the review. **(a)** Spatial distribution of the records. Red dots represent record location and pie charts represent the proportion of records from freshwater, terrestrial, marine, estuarine or all environments. **(b)** Representation of habitats. **(c)** Year of record publication.

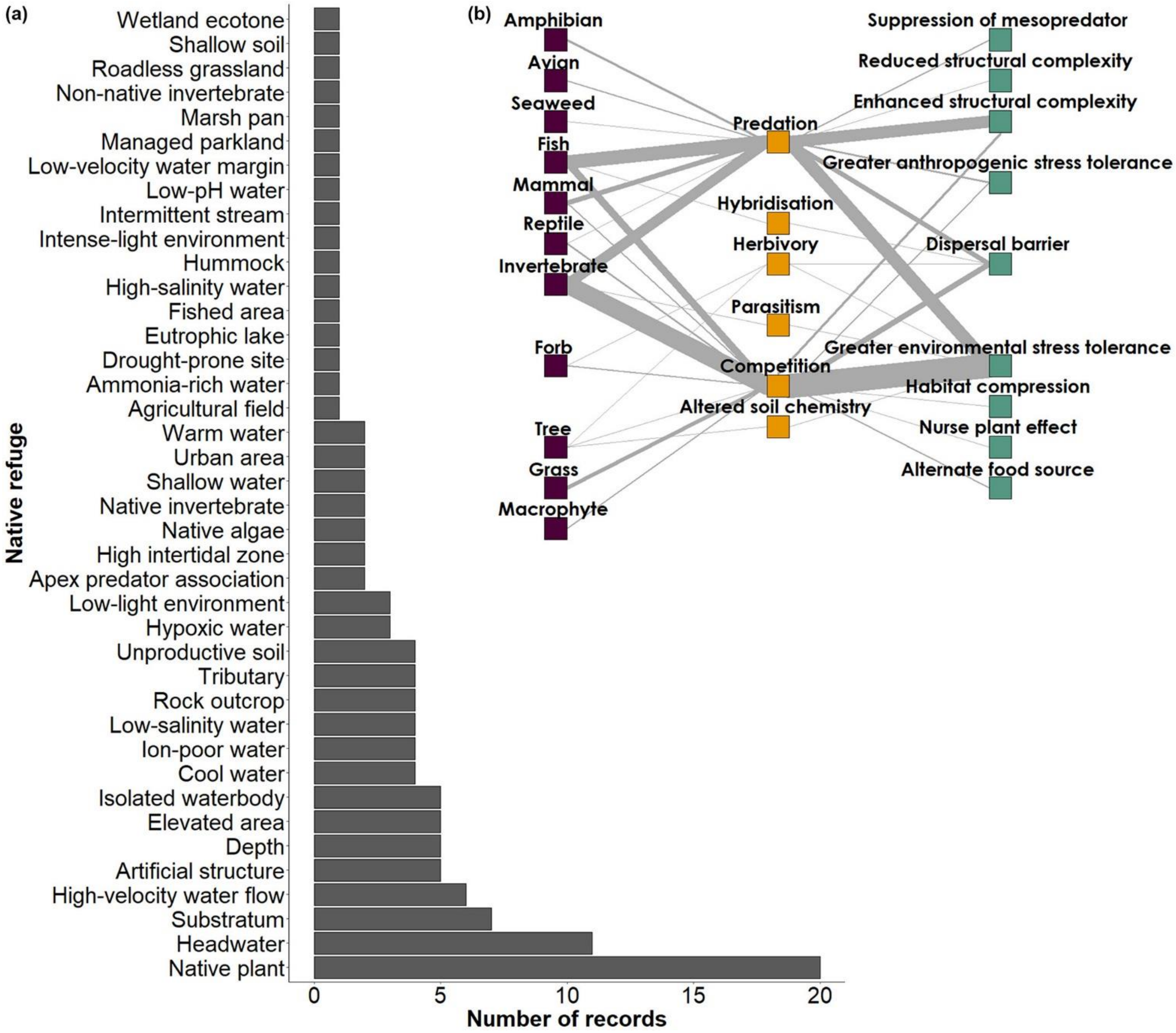

Figure 1.3 Records that reported refuges that buffer native species from non-natives. **(a)** Representation of native refuges, **(b)** Links between native taxa (dark purple), the threat posed by non-native species (yellow) and the process by which the native species sought refuge (teal). The widths of the connecting lines illustrate the numbers of records.

1.3.2 Use of refuges by non-native species in their introduced range

Of the 98 records that reported the use of refuges by non-native species in their introduced ranges, artificial structures were the most frequently reported refuge type (n = 27, 28%; **Figure 1.4a**). These primarily buffered non-natives from environmental stressors such as low temperatures (n = 6), desiccation (n = 4), high-velocity water flow (n = 4) and winter conditions (n = 4), although refuge from predation (n = 7) was also often reported. Native plants (n = 10, 10%), substrata (n = 9) and warm water zones (n = 7) were also commonly reported to act as refuges. Notably, I found several examples of non-natives finding refuge in structures created by other introduced species, particularly non-native plants (n = 4) and invertebrates (n = 2). Refuges from anthropogenic stressors were rarely assessed (n = 4) with few records of refuges from non-native management (n = 3) and anthropogenic disturbance (n = 1).

Refuges primarily buffered non-natives from thermal extremes and predation, although this varied across taxa (**Figure 1.4b**). Non-native invertebrates (n = 57, 58%) were the most studied taxa in this context, particularly in river (n = 19) and marine intertidal habitats (n = 13). Invertebrates sought refuge from predation (n = 21), low temperatures (n = 10) and winter conditions (n = 11). Similarly, non-native fish and mammals sought refuge from the same stressors. On the other hand, introduced amphibians primarily sought refuge from desiccation (n = 4), high temperatures and areas of high-velocity water flows. Interestingly, few records reported the use of refuges by non-native plants (n = 5) or algae (n = 2) in their introduced ranges.

1.3.2 The provision of refuge by non-native species

Ninety-two records reported the provision of refuges by non-native species. Examples were found across terrestrial (n = 39, 42%), freshwater (n = 24, 26%), marine (n = 18, 20%) and brackish (n = 11, 12%) environments. Non-native plants were commonly reported to provide refuge (n = 57), particularly those from the Poaceae (n = 18) and Caprifoliaceae (n = 8) families. Introduced invertebrates (n = 20) also provided refuges, although these records were largely restricted to bivalves in the families Ostreidae (n = 8) and Dreissenidae (n = 7). No records reported the provision of a refuge from a non-native mammal, fish, amphibian or reptile. Non-natives mainly provided refuges from predation (n = 60; **Figure 1.5a**), although various other stressors were identified, such as herbivory, desiccation, anthropogenic disturbances and parasitism. Refuges were primarily created through the enhancement of structural complexity (n = 70; **Figure 1.5b**). In fact, enhancement of spatial complexity accounted for 97% of records of non-natives providing predation refuges.

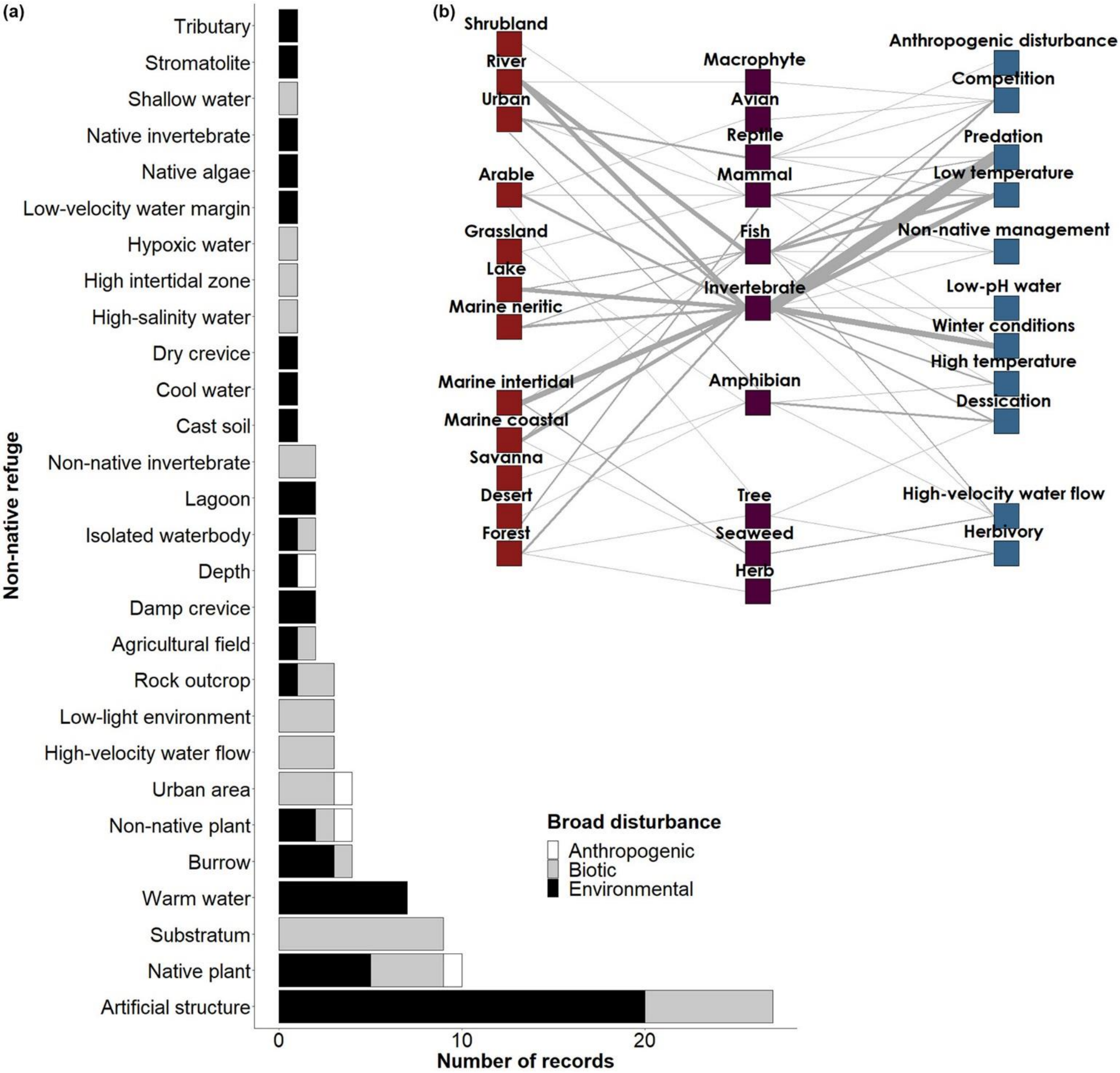

Figure 1.4 Records that reported refuge use by non-natives in their introduced range. **(a)** Representation of non-native refuges split between the broad disturbance types they buffered, and **(b)** links among habitat (red), non-native taxa (dark purple) and the specific disturbance that refuges buffered (blue). The widths of connecting lines illustrate the numbers of records.

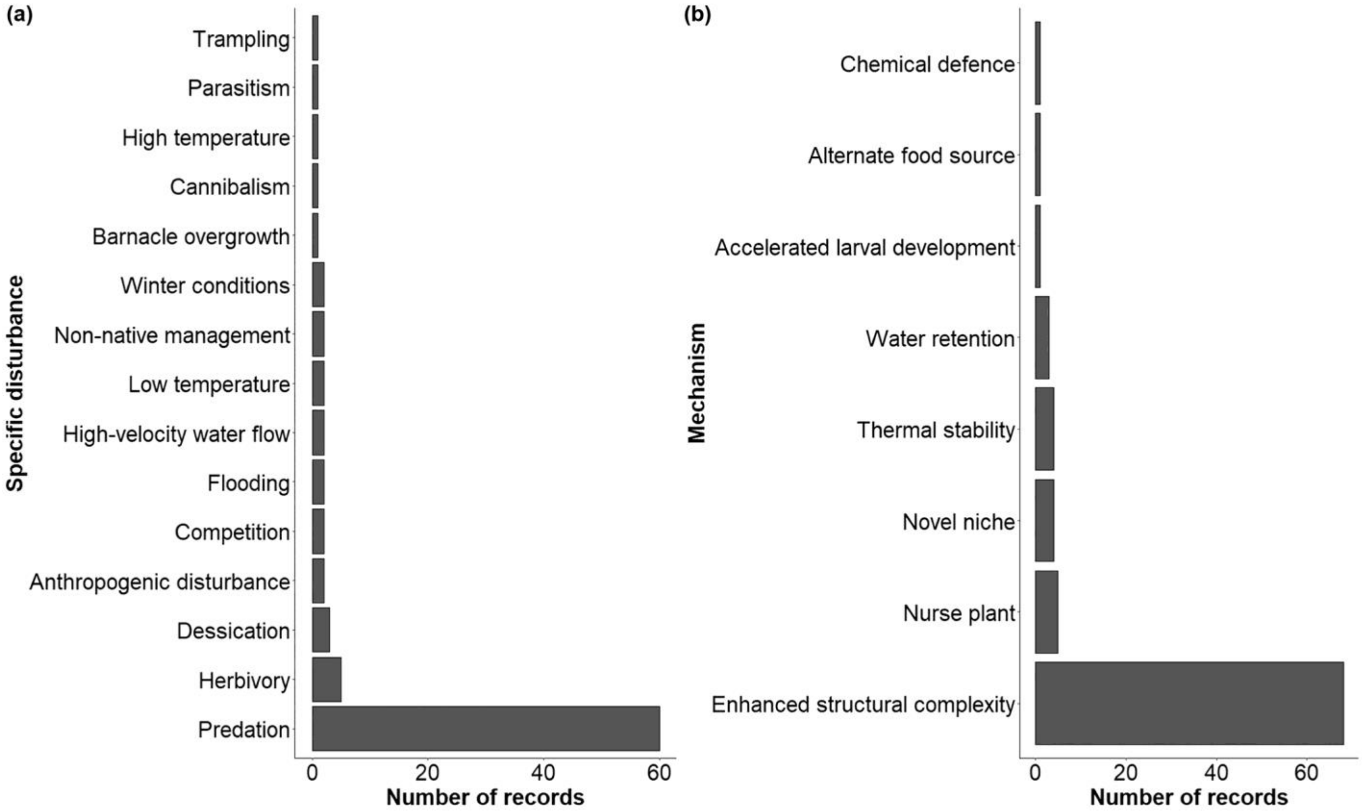

Figure 1.5 Refuges provided by non-natives. **(a)** Representation of the disturbance against which non-natives were recorded to provide protection. **(b)** The mechanism of refuge provision.

1.4 Discussion

As biological invasions are considered a global threat to biodiversity, ecological features that consistently influence the interactions between native and non-native species require attention. Here, I have synthesised research on refuge use in biological invasions, considering refuges for natives, non-natives and those created by non-natives. I present a large number of records that, together, highlight the significance and ubiquity of refuge-mediated processes in the invasion biology literature (**Figure 1.2**). I reveal geographic biases towards North America and Europe, although examples are found globally, and habitat bias towards freshwater systems. Refuges are more frequently reported for rivers and lakes than other habitats, although I demonstrate that refuges are key elements in invaded habitats ranging from marine neritic zones to forests, to urban settlements. The refuge concept has been applied to biological invasions for several decades, although research effort has increased substantially since the start of the 21st century, suggesting growing recognition of its significance.

1.4.1 Refuges for natives

In areas of enhanced structural complexity, natives are often able to find refuge from non-native predation and competition by means of greater tolerance of environmental extremes (**Figure 1.3**). Structurally complex environments increase the foraging time of predators and decrease their encounter rate with prey, thereby increasing prey survival (Gotceitas & Colgan, 1989; Sih, 1987). This increases the potential for predator and prey species to coexist, which is reflected in the high number of records that highlight the importance of vegetation in safeguarding natives from non-native predation. For instance, densely vegetated areas were found to be the most important factor facilitating the coexistence of non-native trout (Salmonidae) and native prey species (Hartman et al., 2013).

Structurally complex environments also provide more niche space, which can mediate competitive interactions (Holbrook & Schmitt, 2002). When two species are in competition for a shared resource, they will either be driven to use different resources (niche differentiation), or the subordinate competitor will be displaced, leading to their extinction or shift to a new niche (competitive exclusion). For competitive exclusion to be avoided via niche differentiation, there must be adequate habitat complexity and heterogeneity (Brown et al., 2013), which can be provided by refuges. We must also consider that the impacts of non-natives often diminish as abiotic conditions move closer to their physiological limits, meaning communities in harsher environments can have greater biotic resistance, and thus exist as refuge communities (Environmental Matching Hypothesis; Ricciardi et al., 2013; Iacarella et al., 2015). I found many records that showed empirical support for these ideas, as natives found refuge from non-native interactions in more complex habitats and through greater environmental stress tolerances, notably in areas of extreme water velocity, temperature, salinity and ion concentrations. This review, therefore, offers strong empirical support for the already-recognised importance of habitat heterogeneity and structural complexity in mitigating non-native threats

(Astorg et al., 2021; Gea-Izquierdo et al., 2007; Hollandsworth et al., 2011; Ricciardi et al., 2013; Vander Zanden et al., 2017).

Determining the viability of refuge populations over generational timescales could be a key future research direction. Refuges incur costs for their inhabitants, as it can be inefficient to persist in refuges for long periods of time due to greater levels of competition, reduced resources and sub-optimal abiotic conditions (Orrock et al., 2013; Persson, 1993). Moreover, if totally constrained to refuge habitats, native populations may become isolated, resulting in reduced genetic diversity and lower population-level resistance to other stressors (Keller & Waller, 2002).

1.4.2 Refuges for non-natives

Records revealed that non-native species frequently use artificial structures as refuges against abiotic and biotic stressors (**Figure 1.4**). Artificial structures are considered focal points for biological invasions due to their proximity to common introduction vectors (e.g. ports and roads), the provision of colonisable structures away from interactions with native species and through the amelioration of abiotic stressors (Dafforn, 2017; Giachetti et al., 2020; Price & Banks, 2018; Twining et al., 2021). However, there were important differences in the use of such structures in marine and terrestrial environments. In aquatic systems, artificial structures were used by non-native species to buffer both abiotic and biotic threats in aquatic systems, whereas in terrestrial systems, they were typically used as shelters from abiotic stressors. For instance, non-native bryozoans and ascidians find sanctuary from benthic and neritic predators on artificial pilings and aquaculture installations, where natural predators are unable to colonise (Dumont et al., 2011a; Dumont et al., 2011b; Giachetti et al., 2020). The seaweeds *Codium fragile ssp. tomentosoides* and *Caulerpa racemosa* find refuge against high-velocity water flows through the enhanced structural complexity of artificial structures (Bulleri & Airoldi, 2005; Vaselli et al., 2008). In contrast, terrestrial non-native lizards, flies, snails and rodents all used artificial habitats as a source of thermal stability against low temperatures and winter conditions (Bergey, 2019; Mitchell et al., 2021; Rossi-Stacconi et al., 2016; Singleton et al., 2007). It is unclear why this contrast exists and whether it is simply an artefact of research bias or reflects important ecological differences, such as the relatively small temperature fluctuations in aquatic habitats compared with terrestrial (Steele, 1985).

In the context of non-native refuges, I found two key research areas that warrant further investigation. Refuges for non-native plants and refuges from anthropogenic stressors were rarely assessed. Only five records identified plants using refuges in their introduced ranges, which is surprising considering plants are some of the most prolific invaders; this could prove a fruitful space for future research (Keller et al., 2011). Furthermore, determining how non-natives find refuge from anthropogenic stressors may become more important in understanding how they sustain their populations under increasing habitat modification and climatic variability.

Notably, I found several records of non-natives that found shelter in structures created by other non-native species. This demonstrates how invasional meltdown (i.e. where non-native species facilitate other non-natives) could occur through the provision of refuge habitats (*sensu* Simberloff & Von Holle, 1999). For example, structures created by introduced Pacific oysters (*Magallana gigas*) may represent refuges for non-native barnacles against native competitors (Firth et al., 2021). Moreover, non-native amphipods utilise introduced zebra mussel (*Dreissena polymorpha*) structures as refuges from native predators more efficiently than native amphipods, possibly due to both non-natives originating from the Ponto-Caspian region (Kobak et al., 2014). The invasional meltdown theory has received conflicting support in the past (see Braga et al., 2018; Jackson, 2015); nevertheless, meltdown due to refuge provision is currently an underexplored concept.

1.4.3 The provision of refuge by non-natives

Many records show that the enhanced structural complexity created by introduced plants can provide novel predation refuges (**Figure 1.5**). Reduced levels of predation around non-natives may lead to the aggregation of herbivores around their structures (Utz et al., 2020; Watling et al., 2011; Watling & Orrock, 2010). This can lead to consumers foraging across larger distances due to the reduced levels of perceived risk (Mattos & Orrock, 2010). For instance, small mammals feed on seeds across wider areas in habitats invaded by buckthorn (*Rhamnus cathartica*) compared to sites where buckthorn is absent (Guiden & Orrock, 2017). As a result, seed predation is less intense but spread over a greater area, resulting in reduced seedling establishment across the broader environment and greater pressure on native plants (Orrock et al., 2008). These refuge-induced shifts in animal behaviour can also influence temporal patterns in behaviour. For example, non-native plants that reduce moonlight penetration at ground level increase the activity of small mammals at night due to reduced predation risk (Guiden & Orrock, 2019; Johnson & De León, 2015). Similarly, introduced plants that keep their leaves for longer into winter months can extend the seasonal activity of small mammals (Bartowitz & Orrock, 2016). These indirect effects of predator refuges created by non-native plants can have unexpected community-wide implications and deserve more attention (Stewart et al., 2021).

The altered dispersal patterns of species associated with non-native plants can influence the abundance and distribution of disease vectors (Allan et al., 2010). The spread of white-tailed deer (*Odocoileus virginianus*), their associated ticks and tick-borne disease, depends on the non-native shrub *Lonicera maackii*, which the deer use for shelter when bedding (Allan et al., 2010). Similarly, the understorey created by introduced Japanese barberry (*Berberis thunbergia*) provides black-legged ticks (*Ixodes scapularis*) protection against desiccation, resulting in higher tick abundance and higher prevalence of *Borrelia burgdorferi*, a primary cause of Lyme disease in humans (Williams & Ward, 2010).

Non-native bivalves can create similar shifts in habitat complexity and benthic community structure of plants. Mussels and oysters form dense aggregations of living and dead shells, which can alter hydrological processes and create sheltered microhabitats for benthic species, often increasing the abundance of benthic invertebrates (Beekey et al., 2004; Karatayev et al., 2002; Nicholls et al., 2011; Stewart et al., 1998). However, non-native bivalves can also lead to the homogenisation of benthic communities, reducing variability in species composition across substrates and habitat types (Burlakova et al., 2012). Moreover, these novel refuges can lead to increased predator abundance, increased deposition rates, altered nutrient flows, disrupted parasite–host interactions and changes in trophic interactions (Botts et al., 1996; Eschweiler & Christensen, 2011; Goedknegt et al., 2020; Lohner et al., 2007; Ward & Ricciardi, 2007). This emphasises that although certain taxa may directly benefit from non-native structures, the indirect effects on the wider ecological community and human health can be complex and potentially harmful. Therefore, any effort to assess the impact of non-native species, especially those that create complex structures, should include potential refuge-mediated effects.

1.4.4 Refuge-mediated processes in biological invasions

In reviewing the literature, I highlight three refuge-mediated processes that influence the establishment, spread and impact of non-natives (**Figure 1.6**). Dumont et al. (2011a) proposed the "persistent pressure scenario," which demonstrates how non-natives use refuges to become established in new environments. When species are initially introduced to new areas, their population levels are low and may be constrained to refuges due to high levels of resistance in the wider community (Dumont et al., 2011b). Propagules are constantly released into the broader habitat by refuge inhabitants, but fail. However, when there is a flux in resources or a disturbance event that weakens this resistance, propagules from the refuge can then successfully establish in the wider habitat, and spread. For instance, the exclusion of native fish and invertebrate predators in rocky-bottom habitats resulted in the establishment of the non-native ascidian *Ciona intestinalis* by recruits from populations on nearby artificial structures, acting as predation refuges for the non-native (Dumont et al., 2011a). Similarly, the proliferation of the non-native green alga *Codium fragile* in Northern Chile after the 1997–1998 El Niño event was probably due to recruits from adjacent aquaculture structures, and because native kelp abundance dropped (Neill et al., 2006).

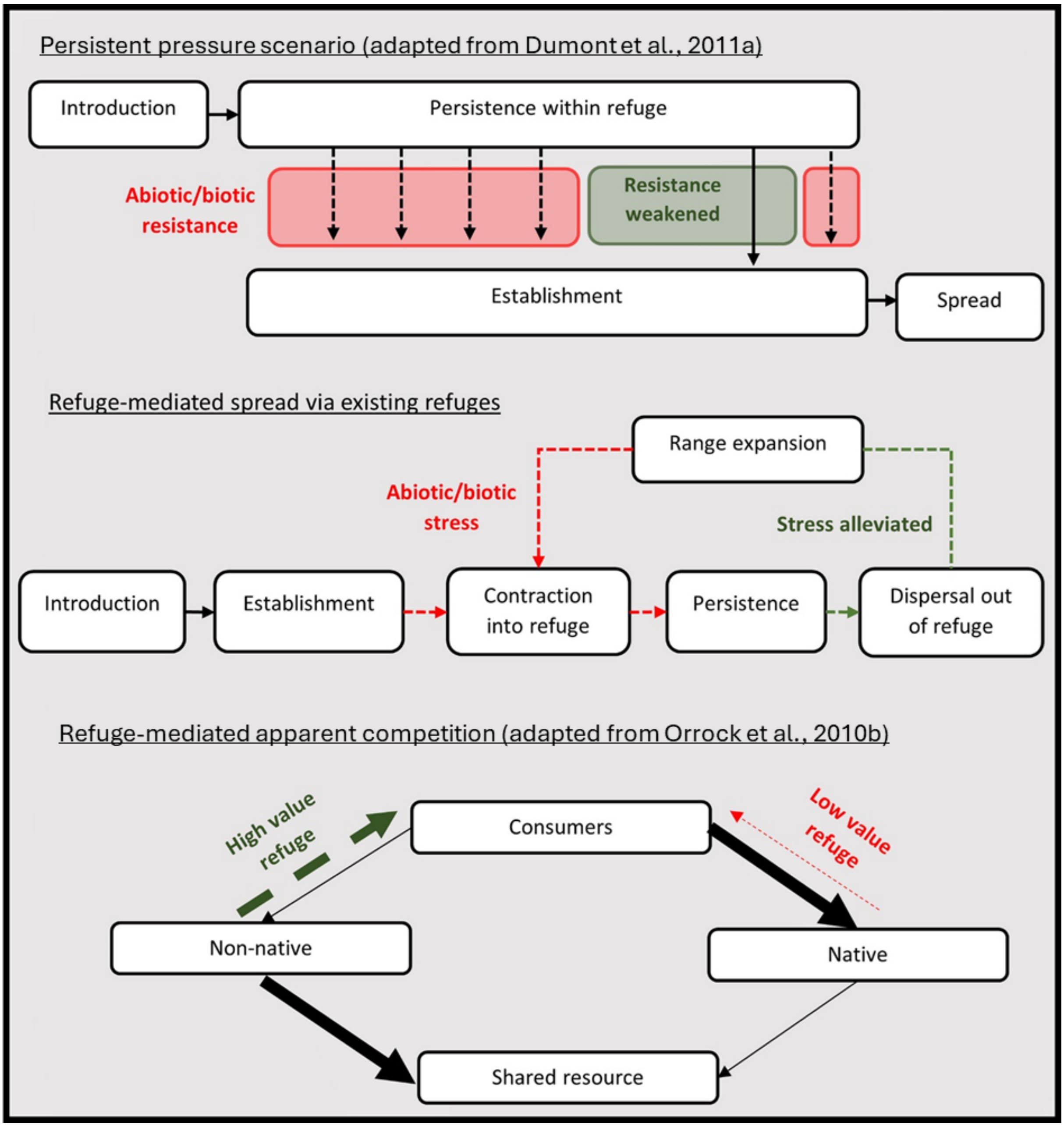

Figure 1.6 Models demonstrating how refuges influence the establishment, spread and impact of non-native species. Dumont et al. (2011a) proposed the persistent pressure scenario (top) to illustrate how non-natives can persist within refuges after their initial introductions and are then able to establish into the broader environment when resistance is alleviated. I propose a model of refuge-mediated spread via existing refuges (middle) to demonstrate how non-native populations may move through novel environments despite recurring stressors. Orrock et al. (2010b) proposed refuge-mediated apparent competition (bottom) to demonstrate how non-natives plants that provide a superior shelter for a shared consumer can displace pressure onto native plants (arrow size shows magnitude of interaction).

Next, I present a model for non-native spread via existing refuges. To spread through their new environments, non-natives need to overcome geographic barriers, abiotic stress and biotic resistance, with some areas able to safeguard individuals from stressors (Blackburn et al., 2011). During unfavourable conditions (e.g. seasonal thermal regimes), individuals in refuge habitats are more likely to persist and allocate energy to reproduction than individuals in the broader environment. When conditions improve, refuge inhabitants can disperse and spread more effectively than those outside the refuge. If stressors return, the same process occurs but in a new location. These waves of expansion out of and contraction into refuges allow a non-native population to spread despite recurring stressors. In this way, individuals located in refuges have a disproportionately large influence on the spread of the non-native population. Thermally stable habitats and anthropogenic structures are often referred to as invasional 'stepping-stones' as they provide surfaces to settle on and refuge from disturbances (Apte et al., 2000; De Mesel et al., 2015; Miranda et al., 2016; Wasson et al., 2001). Non-native spread via existing refuges is similar to the stepping-stone effect in that individuals use isolated habitat patches to enable their range expansion through successive movements (Saura et al., 2014). However, it differs in that the broader landscape is only temporarily unsuitable for the non-native population and can support that population during favourable conditions. Spread via existing refuges is demonstrated by introduced cane toads (*Rhinella marina*) that gather around artificial water installations to avoid desiccation during harsh Australian summers, and spread to new locations from these water points once cooler temperatures return (Gregg et al., 2019). Similarly, non-native arthropods use compost heaps as thermal refuges to survive Nordic winters and then expand out when temperatures warm (Ødegaard & Tømmerås, 2000).

Refuge-mediated apparent competition is an established concept: a process by which a non-native plant can out-compete a native plant by providing a superior refuge for a shared consumer compared with its neighbour, and so displaces consumer pressure onto native species (Orrock et al., 2010b). For example, small rodents do not consume the non-native grass *Ammophila arenaria* but use the grass stands as a refuge, resulting in greater rodent abundance and increased seed predation on adjacent native plants (Pardini et al., 2017). Importantly, the non-native plant experiences less herbivory than the native, allowing the invader to proliferate and reduce the native's competitive ability. This process may be key in invaded habitats with abundant herbivore populations and high levels of predation pressure, as more refuges will promote herbivore survival (Enge et al., 2013; Orrock et al., 2010b). Records of refuge-mediated apparent competition are found in both marine (Enge et al., 2013) and terrestrial (Dutra et al., 2011; Orrock et al., 2008) environments. In concentrating their feeding around non-native plants, herbivores can create free space for the non-native (Orrock et al., 2010a). This results in a progressing invasion front, allowing the non-native to spread through the habitat because of altered consumer behaviour. Non-native spread via refuge-mediated apparent competition is a viable means of spread for introduced plants and has been described in theoretical works that use spatially implicit and spatially explicit models (Orrock et al., 2010a; Orrock et al., 2010b). Empirical work by Malo et al. (2022) also demonstrated that greater seed predation from rodents around the introduced *Rhododendron ponticum*, which acts as a predation refuge, reduced recruitment of native tree species, and probably facilitated the spread of the non-native, possibly due to reduced competition for light.

This is not an exhaustive list of refuge-mediated processes in biological invasions, but it does highlight that theory already exists for how refuges influence the establishment, spread and impacts of non-native populations. Importantly, it is unlikely that these processes operate in isolation and may occur at the same time or at different stages along a species' invasion timeline.

1.4.5 Management implications

Recognising the significance of refuges in biological invasions has the potential to improve the accuracy of predictive modelling, and the effectiveness of management efforts. Species distribution models (SDMs) are regularly used to forecast the spread and impact of non-native populations. SDMs could be improved by explicitly considering refuge availability, which can influence spread, and offer a missing component to better explain the observed spatial patterns. For instance, Conley et al. (2011) showed that predicting oviposition by cavity-dwelling mosquitos is more accurate when the presence of refuge-providing non-native shrubs is included in the landscape-level analysis. Therefore, any effort to model these animals, or associated disease would be much more effective if it incorporated the refuge provided by introduced shrubs (Allan et al., 2010).

The broad-scale removal of non-native individuals is a common strategy, but often uneconomical because of the high management resource requirements. For invaders that periodically retreat into sanctuaries to survive temporary stress, focusing removal efforts on those areas could have a disproportionately greater impact on the overall population than less intense but year-round removal over a broader area. For example, culling non-native rainbow trout in small tributaries during early winter, where fecund females are concentrated to avoid cool temperatures, could increase management effectiveness (Koizumi et al., 2017). Moreover, models showed that only removing introduced carp during years of low water levels, when they were concentrated in deep pools, reduced their population by an equivalent amount as removing them annually, thus potentially saving time and money (Pearson et al., 2022).

Refuges can also be exploited to increase biotic resistance to biological invasions and assist native species in developing novel strategies to escape non-native stressors. Schlaepfer et al. (2005) proposed that refuges could be used to allow natives to be exposed to non-native threats to a sufficient level that they develop their own behavioural or evolutionary strategies to coexist with invaders, while also ensuring population survival. Once these traits become ubiquitous across the population, then there is no longer the need for intensive removal of the non-native species. It is unlikely that this could be used for non-native predators that have general feeding habitats, but for predators with narrower feeding preferences or prey species with small ranges, this could prove an innovative tool (Schlaepfer et al., 2005). Moreover, increasing carrying capacity and biodiversity of protected areas could elicit similar behavioural responses, and promote biological resistance to further invasion (Gallardo et al., 2017).

It is also important to consider potential non-native refuges from management, particularly in relation to culling efforts (Andradi-Brown et al., 2017b; Latham et al., 2018). Shelters from culling could negate the efficacy of management efforts, as they can allow rapid recovery of non-native populations once management efforts reduce. An example of this is invasive lionfish (*Pterois volitans* and *P. miles*) in the Caribbean. High densities of large lionfish are found below the depth of recreational SCUBA limits (30< metres), making them largely inaccessible to culling that uses SCUBA, thus acting as a refuge from management (Andradi-Brown et al., 2017a). As lionfish eggs are buoyant, these deeper populations potentially drive shallow-water recruitment and undermine management efforts (Andradi-Brown et al., 2017a; Andradi-Brown et al., 2017b).

1.4.6 Future research directions

From this review, I offer three broad avenues of future research to expand our understanding of the role of refuges in biological invasions:

1. What is the magnitude of refuge effects in biological invasions? Future research could assess refuge effects using meta-analytical techniques, such as exploring survival of individuals or viability of populations within and outside of noted refuges. The references used in this review could provide a useful foundation for such work.
2. For how long are refuge populations viable? It is important to consider that refuge use can reduce the fitness of individuals, or it is possible that reported refuges are areas where decline or impacts are delayed compared with adjacent areas. Studies could use population viability models and experimental approaches to determine how long native refuges remain viable sources of shelter from non-native species.
3. Will targeting refuge populations increase the efficacy of management programmes? In principle, prioritising refuges in non-native species management can cut resource costs and increase effectiveness, but this is rarely tested. Future research could assess this potential, utilising spatially structured demographic models and cost–benefit analysis.

[*The literature on refuges in biological invasions reveals geographic and taxonomic biases, particularly the underrepresentation of bird species, despite the extensive research on avian invasions (Clavero et al., 2009). The reasons for this gap are unclear but could stem from the challenges of tracking and monitoring birds, or because refuge use in birds is less clear to detect. This could also result from the search strategy employed, as studies on birds might use terms such as "nest" or "roost" to describe refuge behaviour. The overrepresentation of studies from North America and Europe likely arises from the fact that this review only included studies published in English. While this likely covers a large portion of available research, it inevitably overlooks studies published in other languages. This is especially problematic as the most significant impacts of non-native species are often felt in the Global South and non-English-speaking regions (Shackleton et al., 2019), which may be underrepresented in the existing literature. Future meta-analyses or reviews could therefore benefit from exploring literature in multiple languages.*]

In conclusion, this review offers the first attempt to synthesise the role of refuges in biological invasions. I show that refuges and refuge-mediated processes are widely reported in the invasion literature and play key roles in understanding the outcomes of species introductions. I hope to stimulate future research into quantifying broad-scale refuge effects, the viability of native populations and further appreciation of refuges in non-native management practices. I encourage future researchers to use and expand on my reference database to answer these questions.

Chapter 2: Upper-mesophotic reef fish communities exhibit greater temporal variability compared to those at shallower depths

Currently under review

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Author contributions

J.S.B. conceived the idea with input from S.A.K., D.E. and R.F., and conducted the 2022-2023 data collection. J.S.B. analysed the data with advice from S.A.K., D.E. and R.F., and wrote the first manuscript draft. D.A.A and E.G collected the 2014-2015 data. All co-authors contributed critically to chapter drafts.

Abstract

The deep reef refugia hypothesis suggests that reef fish communities at greater depth will be more stable over time compared to those at shallower depths due to the diminished impact of disturbances. I tested this hypothesis by exploring shifts in taxonomic diversity, functional diversity and the composition of fish communities across shallow (5 – 25 m depth) and upper-mesophotic (40 m depth) coral reefs around Utila, Honduras, over a nine-year period. Specifically, I used coverage-based standardisation of diversity and dissimilarity indices, estimated using Hill-Chao numbers with order $q = 0$ (richness) and $q = 2$ (inverse of the Simpson index). In contrast to what would be expected from the hypothesis, I found greater dissimilarity and turnover of both species and functional groups in the upper-mesophotic over time. I observed clear variations in diversity and dissimilarity indices across different sites, with sites that had shallower maximum depths showing more significant changes over time. These results are not consistent with what would be expected from the deep reef refugia hypothesis and suggest that upper-mesophotic depths may not serve as functional or taxonomic refuges for reef fish, as they do not appear to maintain more stable communities.

2.1 Introduction

Tropical coral reefs are hyper-diverse ecosystems that provide important ecosystem services including food, income, and coastal protection (Moberg & Folke, 1999; Woodhead et al., 2019). However, they have become increasingly impacted by local and global stressors, such as overexploitation, habitat destruction, and climate change (Ban et al., 2014; Hughes et al., 2018; Mora et al., 2011). Most research has assessed the impacts of these stressors on shallow coral reefs (< 30 m depth), leading to growing interest in the potential of deeper zones (> 30 m) to offer refuge to reef communities (Bongaerts et al., 2010; Glynn, 1996; Lesser et al., 2009; Riegl & Piller, 2003). Despite this interest, accessing greater depths is logistically challenging, resulting in a lack of temporal data across the depth gradient, particularly on fish communities. This gap in knowledge limits our understanding of how fish communities change over time at different depths, hindering our ability to determine whether deeper reefs can effectively act as areas of refuge in response to anthropogenic threats.

Mesophotic coral ecosystems (MCEs) are reef communities found at depths of approximately 30 to 150 m, where light starts to diminish (Baldwin et al., 2018; Eyal et al., 2021; Hinderstein et al., 2010; Lesser et al., 2009). As depth increases, benthic communities transition from being dominated by zooxanthellate corals and macro-algae to sponges and heterotrophic soft corals, which are better adapted to low light conditions (Lesser et al., 2018, 2019). These communities are primarily structured by the reduced solar irradiance for photosynthesis associated with increased depth, along with shifts in other biophysical factors such as temperature, wave energy and sedimentation (Diaz et al., 2023b; Laverick et al., 2020; Slattery et al., 2024). As a result of these shifts in abiotic conditions and the benthic community, fish communities transition from a dominance of herbivorous fishes in the shallows to a greater abundance of large-bodied carnivores in the mesophotic zone (Andradi-Brown et al., 2016, 2021; Loiseau et al., 2023; Pinheiro et al., 2016; Semmler et al., 2017). Fish species richness reduces across shallow and mesophotic depths, whereas community dissimilarity and species turnover increase along the depth gradient (Andradi-Brown et al., 2016; Rocha et al., 2018).

Additionally, there is strong evidence of depth specificity, with many coral reef fish species found exclusively in MCEs (Pinheiro et al., 2016; Rocha et al., 2018; Thresher & Colin, 1986). As a result, MCEs are often separated into two zones, the upper-MCE (30 – 60 m) and lower-MCE (60 – 150 m) which represent distinct shifts in community composition (Lesser et al., 2019; Semmler et al., 2017).

The intensity of some disturbances have been reported to decrease with increased depth, leading to the idea that deeper reef communities might serve as refuges for shallow-water fish and invertebrate communities (Assis et al., 2016; Glynn, 1996; Hughes & Tanner, 2000; Lesser et al., 2009). The deep reef refugia hypothesis proposes that: (1) disturbances affecting shallow-water reefs are less severe on deeper reefs, and (2) deeper reefs can provide recruits for shallower areas, aiding recovery post-disturbance (Bongaerts et al., 2010). Research on brooding coral species suggests that lower-MCEs have limited potential as refugia for shallow-water communities due to greater community dissimilarity and reduced population and genetic connectivity, while upper-MCEs show greater promise (Bongaerts et al., 2017; Brazeau et al., 2013; Slattery et al., 2024). Bongaerts and Smith (2019) described this as the ‘disturbance/divergence trade-off’. Furthermore, there are growing reports of stressors like marine heatwaves, tropical storms, destructive fishing, and invasive species affecting mesophotic reefs, which cast doubt on whether these deeper habitats can truly serve as a refuge for fish communities (Andradi-Brown et al., 2017a; Diaz et al., 2023a; McWhorter et al., 2024; Rocha et al., 2018; Soares et al., 2019; Venegas et al., 2019).

Studies examining the deep reef refugia hypothesis in relation to reef fish communities over time are rare, and none have investigated multiple metrics of diversity or dissimilarity. Single metrics offer a clear but limited view, so incorporating functional diversity and different diversity orders can provide a deeper understanding of community dynamics and ecosystem function shifts (Loiseau et al., 2023). Also, recent evidence suggests that fish and benthic species richness and abundance are generally less stable over time than would be expected if the deep reef refugia hypothesis were accurate (Slattery et al., 2018). This instability is particularly evident when communities are threatened by invasive species or storm damage (Abesamis et al., 2018; Lesser & Slattery, 2011). Understandably, logistical challenges make repeated surveys at depth difficult, and there is a pressing need to document the location of unrecorded MCE habitats and undescribed species to improve conservation efforts (Turner et al., 2019). However, if deep reefs exhibit significant temporal variability in fish species diversity and composition, it may suggest their role as consistent refuges is compromised. Furthermore, the deep reef refugia hypothesis has principally focused on the taxonomic diversity of fish species rather than their functional diversity (Loiseau et al., 2023). As such, at mesophotic depths, fish communities may experience changes in species composition over time, but these species might share the same functional traits, offering a functional refuge for key ecosystem processes (Loiseau et al., 2023). Therefore, it is important to consider both the taxonomic and functional aspects of fish communities when evaluating the potential of deep reefs to serve as refuges for shallow-water populations — an area that remains underexplored.

To address these knowledge gaps, I investigated changes in the taxonomic and functional diversity and composition of fish communities across shallow and upper-mesophotic reefs in Utila, Honduras, over nine years. Like many areas of the Caribbean over recent decades, Utila's reefs have been impacted by invasive lionfish, ocean warming, storms and pollution (Bove et al., 2022; Gardner et al., 2003; Mumby, 2009). Drawing on the deep reef refugia hypothesis, I predict that the fish communities at greater depth will experience less change because depth reduces the impact of disturbances, providing a more stable community. I would therefore expect taxonomic and functional diversity to exhibit greater change at shallower depths compared to the upper-mesophotic. Moreover, I expect communities to exhibit less taxonomic and functional dissimilarity over time at greater depths. This research is among the first to explore temporal shifts in the taxonomic and functional composition of reef fish communities across shallow and upper-mesophotic depths, highlighting trends for these seriously understudied ecosystems.

2.2 Methods

2.2.1 Study location

Data were collected at five fringing reef sites surrounding the island of Utila, Honduras (**Figure 2.1**). Located on the southern Mesoamerican Barrier Reef, Utila is one of the three main islands and 53 cays that make up the Bay Islands Marine National Park. Two study sites, The Maze and Raggedy Cay, were situated on the island's exposed northern shore. Reefs on the northern shore are located along a steep reef wall that quickly reaches beyond 100 m depth. The Maze and Raggedy Cay have more extensive shallow reef communities, with large back reefs behind the reef crest and greater wave exposure throughout much of the year compared to the south shore sites (Andradi-Brown et al., 2016). The other three sites — Little Bight, Coral View, and Rocky Point — were located on the sheltered southern shore of the island. Little Bight and Coral View are the shallowest of all the sites; here, the reef slope gradually drops to 40 m where the bottom levels out to a patch reef system in the upper-mesophotic zone. Little Bight and Coral View have lower hard substratum availability at 25m and 40m compared to other sites. Rocky Point on the other hand bottoms out slightly deeper, at 60 m. The reef slope angle on the southern shore sites was similar at 5, 15 and 25m depth bands, but the seabed was flatter at 40m depth (Andradi-Brown et al., 2016). Sites were selected based on the locations of initial surveys conducted in 2014 and 2015 to ensure continuity in data collection and allow for direct comparisons over time. Research permits for the study were issued by the Instituto de Conservación Forestal (ICF), Honduras (Permit number: DE-MP-108-2023).

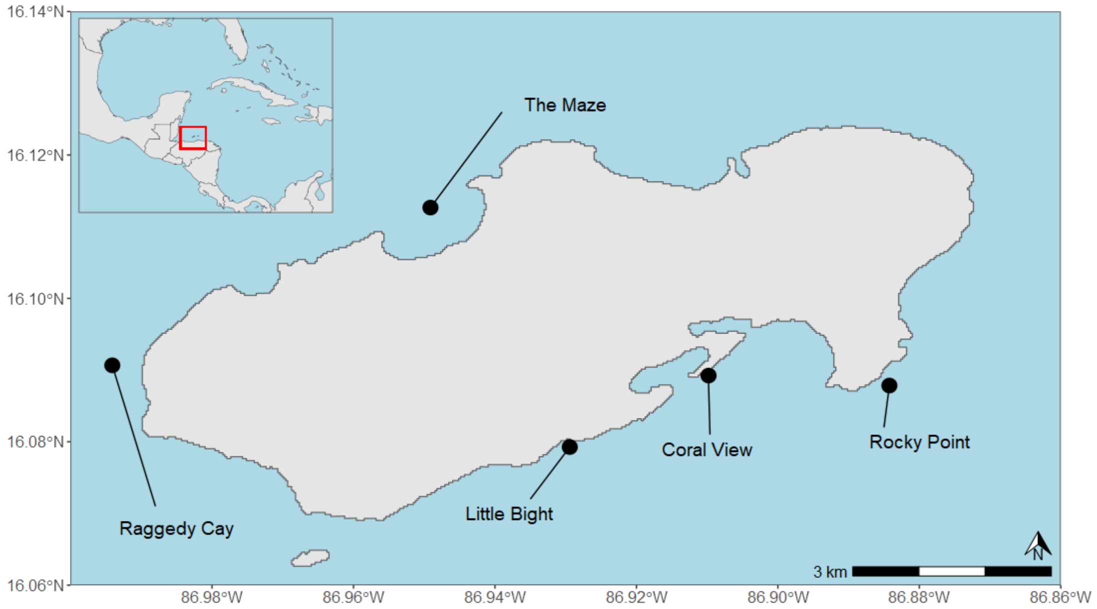

Figure 2.1 Map of study sites around the Island of Utila, Honduras. Inset map shows the location of Utila relative to the Caribbean region.

2.2.2 Fish community surveys

Fish community surveys were conducted at each site at depths of 5 m, 15 m, 25 m, and 40 m in the years 2014, 2015, 2022, and 2023. All surveys were conducted between June and August. Surveys consisted of a calibrated diver-operated stereo-video system (SVS; SeaGIS, Melbourne, Australia) along a 50 m transect that followed the reef contour (Goetze et al., 2019). Transects were spaced with 10 m intervals between replicates. Each transect was surveyed by a team comprising an SVS operator and a second diver responsible for measuring the distance. The cameras, angled approximately 20 degrees downward, were maintained around 0.5 m above the seabed or away from the reef wall during filming. In 2014 and 2015, the SVS setup included two Canon HFS21 high-definition video cameras. This equipment was changed to two GoPro Hero 8 cameras for the 2022 and 2023 surveys. Divers conducting surveys at 40 m used mixed-gas open-circuit SCUBA, while shallower surveys used regular air. In all years, the SVS and camera systems were calibrated using a calibration cube and CAL software (http://www.seagis.com.au/bundle.html). To ensure each transect was distinct, I always swam either left or right of the site buoy along the reef slope, preventing resampling. Due to logistical constraints, no more than three transects could be conducted at a given depth per dive, as time and air limitations restricted survey time. Therefore, transects at each depth were spread across multiple dives, minimising pseudoreplication.

Footage was analysed using EventMeasure software (SeaGIS, Melbourne, Australia), which allowed for the synchronisation of the calibrated SVS footage and measurement of fish total lengths. As the video moved through the transect, fish located outside of 2.5 m to either side or 5 m in front of the cameras were excluded from analysis as they were not within the transect perimeter. All fish visible within these transects were recorded to species-level where possible, using Humann and Deloach (2014), and had their lengths measured. In cases where we could not take measurements (e.g., when the fish was not in a clear line of site of the cameras), the species was recorded, and the average length for that species at the same site, depth, and time was used. If no other individuals of that species were observed under those conditions, the average length for that species across all sites and depths for that year was used. Species abundance data were pooled into two time periods — 2014 and 2015, and 2022 and 2023 — due to uneven sampling efforts across the years. Fewer transects were conducted at depths of 25 m and 40 m due to the increased logistical challenges that comes with deeper diving. Consequently, the number of 50 m long transects conducted at each site, depth and time varied, ranging from 1 to 12, with a median of 8 (**Tables S2.1 & S2.2**). In 2022-2023, due to logistical constraints, only one transect was conducted at 40 m at each of Little Bight and Coral View. Abundance data from all transects at the same depths and sites in each time were pooled together.

I acknowledge that binning depth, a continuous variable, may hide finer-scale patterns and reduce statistical precision. However, I have adopted this approach to ensure consistency with the 2014–2015 data from Andradi-Brown et al. (2016), to facilitate direct comparisons over time. Moreover, while the depth range associated with mesophotic conditions can vary between sites based on local abiotic conditions, classifying 40 m as the upper-mesophotic at our study location is justified by past studies showings distinct ecologically-relevant shifts in benthic composition and fish diversity below 25 m (Andradi-Brown et al., 2016; Laverick et al., 2017).

2.2.3 Taxonomic and functional α-diversity

To estimate and compare taxonomic and functional diversity, sampling units must first be standardised (Chao & Jost, 2012). I used a sample coverage approach, which standardises the diversity estimates in each site, depth and time combination by the proportion of observed diversity with respect to the estimated true diversity (Chao et al., 2021). Diversity estimates were therefore standardised following the non-asymptotic approach recommended by Chao and Jost (2012) and using the iNEXT.3D (Chao et al., 2021) package in R v. 4.2.3 (R Core Team, 2023). Specifically, taxonomic and functional α-diversity were estimated for each site, depth, and time combination. These were estimated using Hill-Chao numbers with order $q = 0$ (richness) which is more sensitive to rare species and $q = 2$ (inverse of the Simpson index) which focuses on abundant species. To limit prediction bias, all estimates for $q = 0$ were calculated to the coverage of double the reference sample size (C_{max}). This is equal to the sample coverage of the time, site and depth zone with the lowest coverage, which is then extrapolated to twice the original number (Chao et al., 2021). In my case, C_{max} was 83.27%. As extrapolation for $q > 0$ results in only small error, diversity estimates for $q = 2$ were extrapolated to 100% sample completeness (Chao et al., 2014).

The estimate3D function in iNEXT.3D was used to determine taxonomic α-diversity ($q = 0$ and $q = 2$). To estimate functional α-diversity ($q = 0$ and $q = 2$), five traits were compiled (2 categorical: diet and position in the water column; 3 continuous: average body length in the dataset, vertical home range, trophic level) for all fish species in the dataset (**Table 2.1**). Information was collected to species level. Based on these functional traits, the multidimensional trait distance (Gower distance) between species was calculated (Gower, 1971) using the mFD package in R (Magneville et al., 2022). To estimate functional α-diversity ($q = 0$ and $q = 2$) at each site, depth and time combination, the estimate3D function was used with the abundance dataset and the Gower functional distance matrix, using the default Fdtype = ‘AUC’ (area under the curve of the tau profile).

For both taxonomic and functional α-diversity, I plotted diversity estimates with 95% confidence intervals (CIs). Statistical significance at 5% can conservatively be inferred where CIs do not overlap (Chao et al., 2014), as per Cumming et al. (2007), Diaz et al (2024), Gorta et al. (2023) and Hacala et al. (2024).

2.2.4 Taxonomic and functional community change across depth over time

To ensure samples were statistically comparable when assessing dissimilarity, I standardised dissimilarity indices via a sample coverage-based approach, using the iNEXT.beta3D package (Chao et al., 2023) in R v. 4.2.3 (R Core Team, 2023). Taxonomic and functional dissimilarity of fish communities were assessed using Sørensen-type measures based on Hill numbers with order q = 0 and q = 2 (Chao et al., 2019). Sørensen-type dissimilarity indices using q = 0 shows the richness-based Sørensen index which assigns all species or functional groups as equally weighted. Sørensen-type dissimilarity q = 2 is equal to the frequency-based Morisita-Horn index and is more sensitive to abundant species or functional groups (Chao et al., 2019). The same traits and Gower functional distance matrix used to explore functional diversity were used to determine functional dissimilarity. Using iNEXT.beta3D, estimates for taxonomic and functional turnover for each site, depth and time combination were all based on C_{max} = 83.27% for q = 0 and a sample coverage of 100% for q = 2 (Chao et al., 2023).

The dissimilarity of communities at the same depth and site between the two time periods was explored using a Sørensen-type non-overlap measurement. This index, based on the calculation by Chiu et al. (2014), evaluates the average proportion of species not shared within an assemblage. This measure of community dissimilarity is most effective when using raw species abundance datasets, as in this study (Chao et al., 2019). I also assessed the extent of taxonomic and functional turnover within communities at the same depth and site over time, using the Sørensen-type turnover index. This measure calculates turnover relative to alpha diversity.

The output from iNEXT.beta3D provided taxonomic and functional Sørensen-type non-overlap and turnover estimates with 95% CIs. Significant differences were inferred where 95% CIs did not overlap (Chao et al., 2023). This conservative approach was used partly to account for multiple testing. To summarise variation in taxonomic and functional dissimilarity of fish communities, I used Non-Metric Multidimensional Scaling (NMDS; Minchin, 1987). I performed NMDS ordination using the "metaMDS" function in the R package vegan (Oksanen et al., 2022). This was done by creating a matrix with Sørensen-type non-overlap estimates for all combinations of site, depth, and time for q = 0 and q = 2.

Table 2.1 Description of traits used to determine functional diversity and dissimilarity.

Trait name	Ecological relevance	Trait levels	References
Diet	Different diet groups provide different reef functions	Herbivore, Planktivore, Carnivore, Invertivore, Omnivore, Piscivore	Froese and Pauly (2024); Humann and Deloach (2014)
Average body size	Correlates with size at maturity, fecundity, growth rate and longevity	Continuous (cm)	Estimate calculated from our dataset
Position in the water column	A measure of their association with the reef matrix	Benthic, Benthopelagic, Pelagic	Froese and Pauly (2024); Humann and Deloach (2014)
Vertical home range (depth range where the species is known to occur)	Relates to breadth of habitat suitability	Continuous (m)	Froese and Pauly (2024)
Trophic level	Relates to predation and competition	Measured 2 to 4.7. Higher values denote higher trophic level	Froese and Pauly (2024)

2.3 Results

2.3.1 Taxonomic and functional α-diversity across depth over time

In total, 33820 individuals were recorded across the two time periods (2014-2015 n = 16906; 2022-2023 n = 16914). This included 29 families, 54 genera and 119 species of reef fish. Notably, in 2014-2015 there were nine instances of invasive lionfish (*Pterois volitans*), all recorded at a depth of 40 m (from 30 transects at 40 m), whereas none were recorded at 40 m (from 11 transects at 40 m) or any other depth in 2022-2023.

Taxonomic species richness (q = 0) exhibited no consistent pattern across depth over time, with high levels of site variation (**Figure 2.2**). In 2014-2015, mean species richness across all sites ranged from 13.5 ± 6.9 (standard deviation (sd)) at 25 m to 14.3 ± 4 .9 at 40 m. In 2022-2023, mean species richness ranged more widely from 11.0 ± 6.0 at 40 m to 18.3 ± 4.3 at 25 m. Generally, there were greater shifts in species richness (q = 0) at shallower depths over time, with Coral View being the only site to experience a significant decrease at 40 m (non-overlapping 95% CIs). Taxonomic Simpsons diversity (q = 2) also exhibited no consistent trends across depth over time (**Figure 2.2**). In 2014-2015, mean Simpsons diversity across all sites ranged from 5.6 ± 2.5 at 40 m to 7.3 ± 2.0 at 5 m, while in 2022-2023, it ranged from 5.9 ± 2.3 at 15 m to 8.6 ± 3.0 at 25 m. There were generally greater shifts in taxonomic Simpsons diversity (q = 2) over time at 5 m compared to the other depths, with all five sites indicating significant shifts.

Functional richness (q = 0) also showed no clear trends across depth over time, with clear site variation (**Figure 2.3**). In 2014-2015 average functional richness across all sites ranged from 4.1 ± 1.1 at 15 m to 4.44 ± 0.4 at 5 m. In 2022-2023, functional richness ranged from 4.6 ± 0.4 at 25 m to 3.55 ± 1.1 at 40 m. Both north shore sites, Raggedy Cay and The Maze, saw significant increases in functional richness at 25 m over time, while 40 m at Coral View saw a significant decrease. There were generally greater shifts in functional Simpsons diversity (q = 2) over time at 5 m compared to the other depths, with all sites indicating significant shifts (**Figure 2.3**).

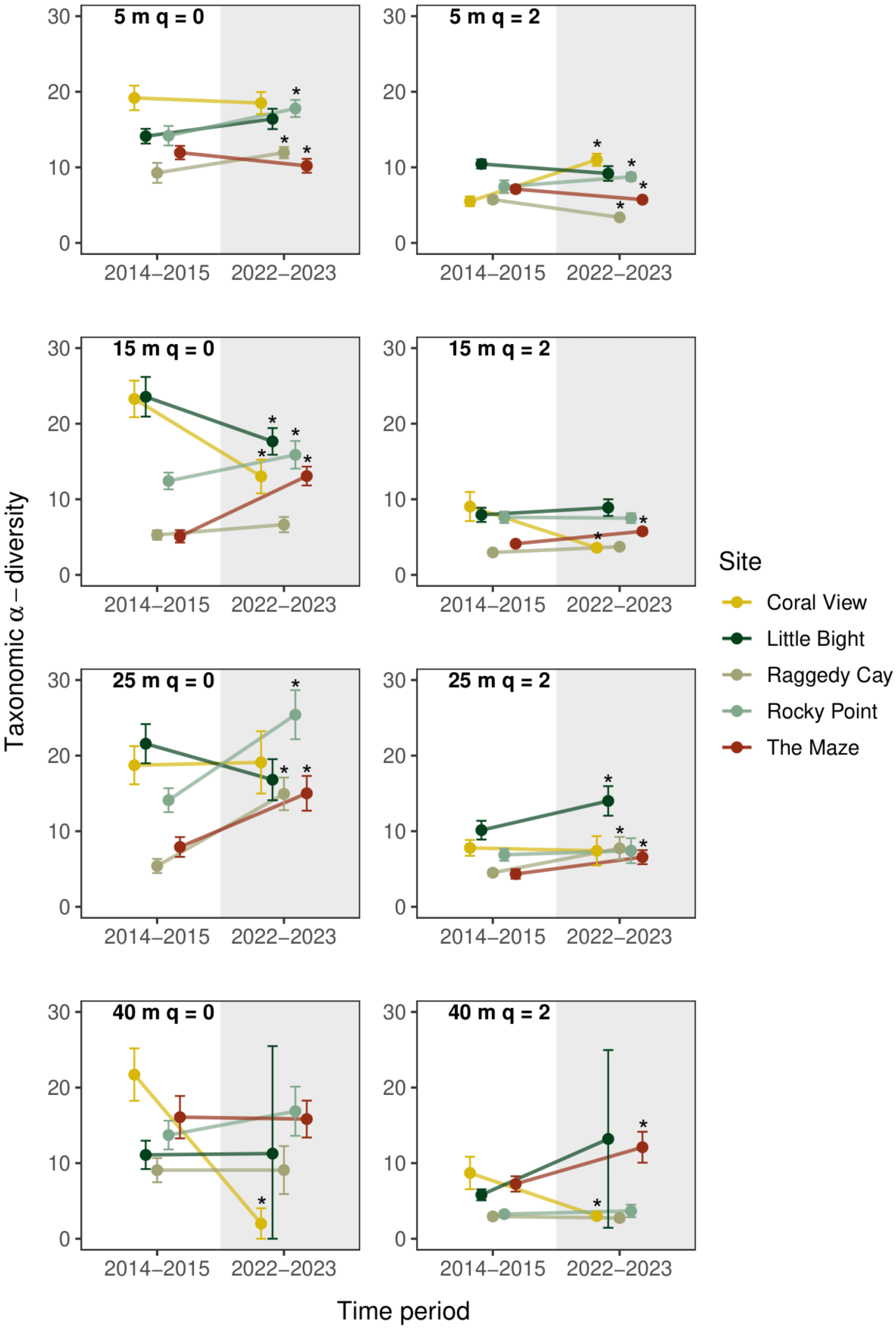

Figure 2.2 Taxonomic α-diversity estimates of Hill numbers q = 0 (species richness) and q = 2 (focus on abundant species) with 95% CIs (error bars) grouped across depth, sites and time. "*" denote significant differences between time periods.

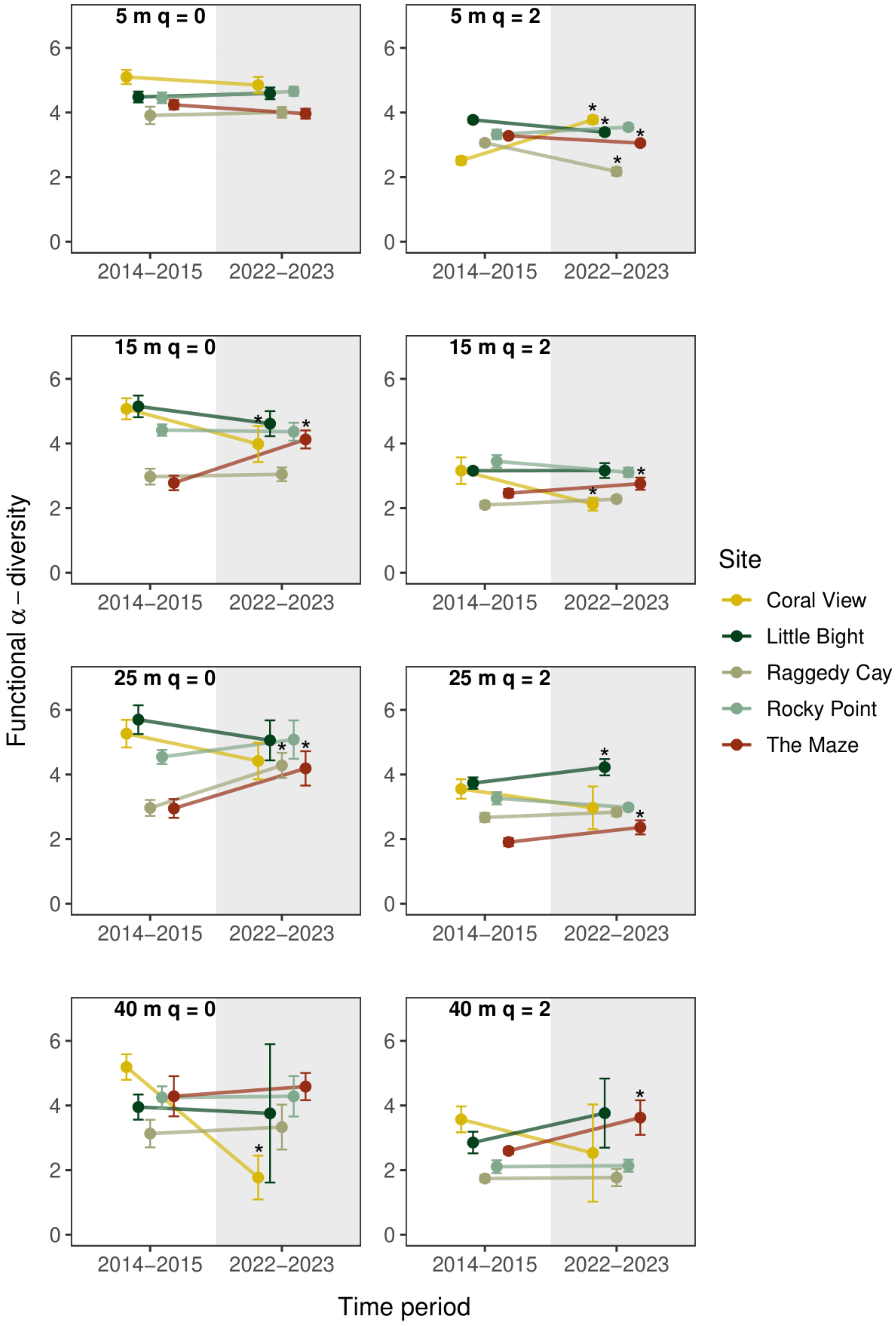

Figure 2.3 Functional α-diversity estimates of Hill numbers q = 0 (functional richness) and q = 2 (focus on abundant functional groups) with 95% CIs (error bars) grouped across depth, sites and time. “*” denote significant differences between time periods.

2.3.2 Taxonomic and functional dissimilarity across depth over time

Fish communities in the upper-mesophotic zone (40 m) exhibited higher levels of taxonomic dissimilarity over time compared to those at shallower depths (**Figures 2.4a-d**). At 40 m, the estimated taxonomic turnover for q = 0 over time was significantly greater than at shallower depths for four of the five sites (indicated by non-overlapping 95% CIs), except for Raggedy Cay (**Figure 2.4a**). In contrast, fish communities at 5 and 15 m experienced consistently low levels of turnover. Taxonomic turnover for q = 2 was also significantly greater at 40 m than at other depths at all sites, except for Raggedy Cay (**Figure 2.4b**). At 40 m, fish communities from Coral View and Little Bight were more taxonomically distinct compared to other sites and depths, sharing fewer rarer (q = 0) and dominant (q = 2) species over time (**Figure 2.4c-d**).

Similarly, fish communities in the upper-mesophotic zone (40 m) generally exhibited higher levels of functional dissimilarity over time compared to those at shallower depths (**Figures 2.5a-d**). Estimated functional turnover for q = 0 over time was significantly greater at 40 m compared to shallower depths for four out of the five sites (non-overlapping 95% CIs; **Figure 2.5a**). No significant difference was found at 40 m for The Maze compared to its shallow depths. Functional temporal turnover focusing on dominant functional groups (q = 2) was greatest at 40 m at all sites (non-overlapping 95% CIs), except for Raggedy Cay, where functional turnover was significantly lower in the upper-mesophotic compared to shallower depths (**Figure 2.5b**). When focusing on rare functional groups (q = 0), all depths at Raggedy Cay became more functional similar to other sites over time (**Figure 2.5c**). Fish communities from Coral View and Little Bight at 40 m were the most functionally dissimilar from other sites and depths across both time periods and became more dissimilar over time (**Figures 2.5c-d**)

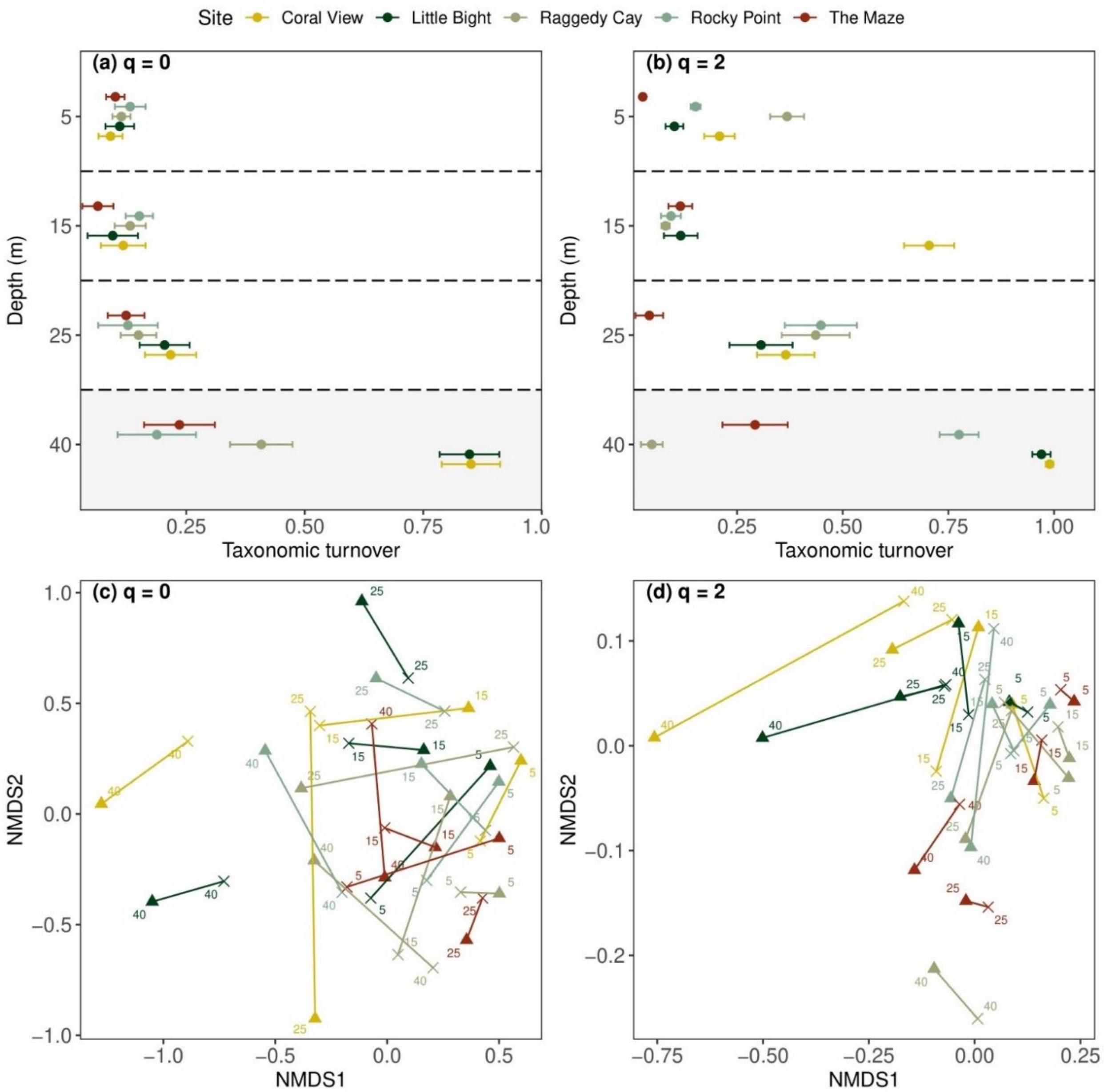

Figure 2.4 Changes in the taxonomic composition of reef fish communities over time. Taxonomic Sorensen-type turnover for each site and depth between the two time periods for **(a)** q = 0 and **(b)** q = 2. Errors bars are 95% CIs. Shaded region signifies upper-mesophotic depth. NMDS ordination based on Sorensen-type non-overlap index of fish communities in 2014-2015 (crosses) and 2022-2023 (triangles), based on taxonomic Sorensen-type non-overlap for **(c)** q = 0 and **(d)** q = 2. Lines connect the same site and depth between the two time periods. The stress value for both NMDS plots was < 0.2.

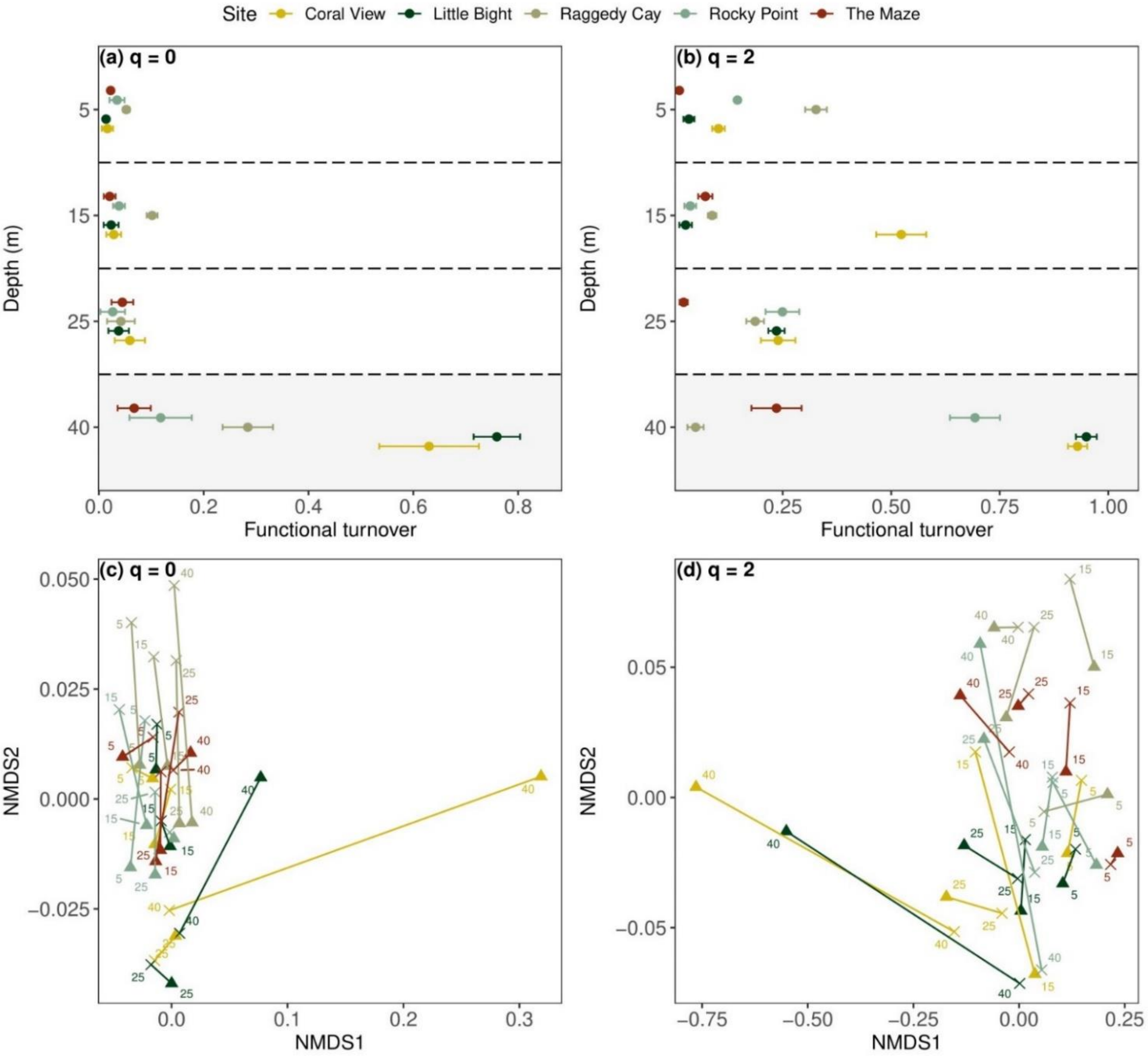

Figure 2.5 Changes in the functional composition of reef fish communities over time. Functional Sorensen-type turnover for each site and depth between the two time periods for **(a)** q = 0 and **(b)** q = 2. Errors bars are 95% CIs. Shaded region signifies upper-mesophotic depth. NMDS ordination based on Sorensen-type non-overlap index of fish communities in 2014-2015 (crosses) and 2022-2023 (triangles), based on functional dissimilarity for **(c)** q = 0 and **(d)** q = 2. Lines connect the same site and depth between the two time periods. The stress value for both NMDS plots was < 0.2.

2.4 Discussion

If the deep reef refugia hypothesis were true, we might expect that reef fish communities at greater depth will experience less temporal variation compared to those at shallower depths due to the diminished impact of disturbances. However, my results indicate that fish communities in the upper-MCE experienced greater levels of taxonomic and functional change over time than those at shallower depths. While there were no consistent trends in the overall number of species or the variety of functional roles they fulfil at different depths over time, turnover and dissimilarity were generally greatest in the upper-mesophotic. I also observed considerable variation in temporal patterns of diversity and dissimilarity between sites around Utila, highlighting the significance of site-specific conditions in stabilising reef communities at depth. Overall, greater functional and taxonomic turnover in upper-MCEs over time suggests that deeper fish communities are not necessarily less variable over time, which may limit the ability of these deeper reefs to act as stable refugia for reef communities.

My findings showed no consistent temporal trends across the depth gradient in taxonomic or functional richness ($q = 0$), or Simpson's diversity ($q = 2$), with high levels of site variability. This variability in diversity estimates highlights the importance of site-specific conditions in shaping community structure (Kahng et al., 2010). For example, Coral View (a shallow site near human settlements, with a maximum depth of 40 m and patchy upper-MCE habitat) experienced significant decreases in species richness, functional richness and evenness over time. The limited availability of hard substrate may contribute to less diverse MCE communities, while closer proximity to human settlements could increase sedimentation or pollution, limiting less tolerant species or traits from inhabiting deeper areas over time (Appeldoorn et al., 2016; Swanborn et al., 2022). In contrast, The Maze on the island's north shore showed an increase in species richness in the upper-mesophotic zone over time. Located further from human settlements and exposed to greater wave energy, this site may be less directly affected by sedimentation or pollution. The increase in diversity at greater depths could be attributed to species migrating from shallower habitats and utilising the steep vertical walls of the site, as suggested by the observed decrease in diversity at 5 m (Hollarsmith et al., 2020). The difference in maximum depth between these sites could also shape these patterns. Coral View's shallow maximum depth of ~40 m limits mesophotic habitat and community complexity, while The Maze, with greater depth and steeper topography, provides more diverse habitats, which could allow for higher diversity and refuge potential (Hollarsmith et al., 2020). Thus, greater depth and geomorphology could drive the increased diversity seen at The Maze. It is important to acknowledge that this study does not account for variations in benthic composition. Since benthic composition is a key factor influencing coral reef fish distributions (Chong-Seng et al., 2012), addressing it will be crucial for future research to identify the factors driving temporal patterns in coral reef fish diversity across depths.

While there were no clear trends in species diversity over time, taxonomic turnover and dissimilarity were consistently higher in the upper-mesophotic zone. Higher turnover for both q = 0 and q = 2 indicates a greater rate of species replacement over time for both rare and abundant species at most sites. This suggests that taxonomic change at these depths is driven by species replacement, with new taxa entering the upper-MCE. One possible explanation is that the upper-mesophotic zone has undergone greater environmental changes compared to shallower depths, allowing new species better suited to the altered conditions to establish themselves while less adaptable species have declined or become locally extinct. Another possibility is that greater environmental changes in shallower reefs have prompted species to migrate to deeper waters. Although taxonomic turnover for rare species (q = 0) remained low at shallower depths, the higher turnover for abundant species (q = 2) suggests that the dominant species are more affected by environmental changes, potentially moving to greater depths over time. This may explain the lack of observed changes in q = 0 turnover at shallower depths. Notably, the higher taxonomic turnover at greater depths across all sites indicates broader environmental changes impacting these communities. In 2020, hurricanes Eta and Iota struck Honduras and the Bay Islands, which may have caused disruption to benthic and fish assemblages in shallow and the upper-mesophotic zone

(Zambrano et al., 2021). Storm damage can significantly impair the capacity of mesophotic habitats to serve as refuges for shallow-water communities, as found by Abesamis et al. (2018). In addition, rising sea surface temperatures have severely impacted Caribbean reefs in the past and upper-mesophotic reefs and have a lower bleaching threshold temperatures compared to shallower reefs (Smith et al., 2016). During our study period, some bleaching of corals did occur in the Bay Islands during the 2016 bleaching event (Muñiz-Castillo et al., 2024), However, given the relatively low hard coral cover at our study sites (Andradi-Brown et al., 2016), any impact of coral bleaching on associated fish communities this warming event may have caused may be limited.

Functional turnover and dissimilarity (q = 0 and q = 2) were also generally higher in the upper-mesophotic compared to shallower depths. This indicates a significant reorganisation in the functions of species within these deeper communities over time. If it were that only taxonomic turnover was increasing without a corresponding rise in functional turnover, it would indicate that while species composition was shifting, the ecological roles and functions within the community remained stable (Loiseau et al., 2023). However, the observed increase in both taxonomic and functional turnover implies that deeper reef fish communities are experiencing changes in both species' composition and the ecological roles they perform (Loiseau et al., 2023). This points to a broader ecological shift, potentially driven by altered benthic conditions. For instance, mesophotic benthic shifts have been observed in reefs off Curaçao and Bonaire, where the upper-mesophotic zone has experienced a marked loss of calcifying organisms and macroalgae, accompanied by a shift toward cyanobacterial mat dominance and increased sponge cover over time (de Bakker et al., 2017). Additionally, the establishment of invasive lionfish on MCEs has altered the functional structure of reef fish communities at depth through predation on herbivores, leading to increased macroalgal abundance (Lesser & Slattery, 2011). Consequently, the functional shifts observed over time imply that deeper reefs may not maintain consistent ecological functions, and at some sites have become more dissimilar to shallower depths, which would limit their ability to serve as effective refuges for the functional diversity of shallow-water communities.

The noticeable absence of invasive lionfish in 2022-2023, compared to several sightings in the upper-mesophotic zone in 2014-2015, suggests low population sizes around Utila. This may be due to the year-round culling efforts around Utila, supported by the numerous dive shops on the island. This is a promising trend, as it provides support that continuous culling effectively reduces lionfish populations (Barbour et al., 2011; Goodbody-Gringley et al., 2023). It is important to note that SVS surveys tend to be biased towards larger, more mobile species, potentially overlooking those residing within the reef structure, such as lionfish, or smaller species, which means I may underestimate the abundance and diversity of species inhabiting the reef matrix (Goetze et al., 2019). Advancements in cost-effective remotely operated vehicles (ROVs), bioacoustics, and eDNA could help address the limitations of solely using classic survey methods such as SVS.

This work adds to the growing consensus that MCEs may not contain more stable communities and provide universal refugia for shallow-water communities (Bongaerts et al., 2017; Diaz, Foster, et al., 2023; Loiseau et al., 2023; Medeiros et al., 2021; Rocha et al., 2018; Slattery et al., 2024; Smith et al., 2016). One reason for this is that depth is not an environmental characteristic on its own; instead, it serves as a proxy for shifts in irradiance, temperature, and wave energy (Diaz et al., 2023a,b; Lesser et al., 2009). Each of these factors can independently impact reef communities, irrespective of depth, and depending on the threat posed. For example, greater turbidity and localised upwellings have been shown to limit coral bleaching in shallow water during extremes in water temperature (Randall et al., 2020; Sully & van Woesik, 2020; van Woesik et al., 2012). Moreover, despite their importance, deep reefs are rarely prioritised in conservation strategies. While addressing climate threats requires large-scale reductions in greenhouse gas emissions, the management of localised threats, such as overfishing and pollution, should also explicitly include MCEs. Efforts to conserve and manage MCEs should therefore focus on the unique communities that inhabit these depths rather than their potential role as refuges for shallow-water species (Rocha et al., 2018).

In conclusion, my findings reveal significant taxonomic and functional turnover in upper-mesophotic reef fish communities which is greater than experienced at shallower depths. This greater variability at depth suggests that deeper fish communities are not necessarily more stable over time, which may mean that these deeper reefs are not the stable refugia the deep reef refugia hypothesis would predict. Instead, the extent to which deeper reefs may serve as refugia appears to be highly site-specific and influenced by local environmental conditions and stressors. These results underscore the need for targeted, site-specific conservation strategies to effectively conserve reef biodiversity in the face of ongoing environmental changes.

Chapter 3: Depth-related changes in resource use across the lifetime of invasive lionfish

Journal submission TBD

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Author contributions

J.S.B. conceived the idea with input from S.A.K., D.E. and R.F., and collected and analysed the data. J.S.B. wrote the first manuscript draft; all authors contributed critically to the writing. G.F assisted with sample preparation. R.A.R.M supervised the isotope analysis and provided guidance on methodological design.

Abstract

Across the western Atlantic, invasive lionfish (*Pterois volitans* and *P. miles*) are reported to be larger in deeper mesophotic coral ecosystems (MCEs: 30 - 150 m) than in shallow waters (< 30 m). One hypothesis for this size increase with depth is that lionfish undergo ontogenetic niche shifts from shallow to mesophotic habitats. However, most evidence supporting the ontogenetic niche shift hypothesis is based on the evidence that lionfish size increases with greater depth, with no studies specifically examining ontogenetic niche shifts throughout individual lifetimes. To address this gap, I conducted stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) on eye lens laminae from 35 lionfish caught between 5 m and 65 m depth at two sites around the island of Utila, Honduras. Natal isotopic niche space of lionfish varied between capture sites and depths, suggesting that individual lionfish do not all exploit the same resources early in life. $\delta^{13}C$ values increased in the later life stages of lionfish, implying shifts in basal carbon sources of prey as lionfish grow, however, depth of capture did not have a direct influence on this relationship. Lionfish caught at greater depths generally had enriched $\delta^{15}N$ signatures, suggesting a dietry shift to higher trophic levels, yet age did not have a consistent impact on this trend. Together, these findings do not support the hypothesis that lionfish move from shallow to deeper habitats as they age. The apparent lack of consistent movement of lionfish acorss shallow and mesophotic reefs suggests that culling efforts in shallow waters will not impact mesophotic populations, allowing depth to serve as a refuge from management.

3.1 Introduction

Ontogenetic niche shifts are an ecological process in which an organism shifts its diet or habitat use during different stages of its development (Nakazawa, 2015; Rudolf, 2020; Werner & Gilliam, 1984). These shifts may be driven by changes in morphology, physiology and behaviour, allowing the organism to exploit different resources or avoid competition and predation at different life stages (Dahlgren & Eggleston, 2000; Kimirei et al., 2013; Mittelbach et al., 1988; Nakazawa, 2015). Tracking habitat and dietary shifts throughout ontogeny is important for species management, as conservation strategies must account for species-habitat relationships during critical life stages, such as natal stages or periods of reproductive activity (D'Amore et al., 2009; Gabler & Siemann, 2012; Galaiduk et al., 2017). This understanding can be particularly useful in the management of non-native species (i.e., species introduced to new regions due to human activity), as identifying habitat shifts during different life stages can help in assessing the impacts of non-natives and in developing effective control strategies.

Native to the Indo-Pacific, invasive lionfish (*Pterois volitans and P. miles*) have spread across the western Atlantic since their initial introduction (Schofield, 2009; Whitfield et al., 2002). The first official sighting of lionfish in the region was in 1985, in the waters off Florida, likely by aquaria releases, and by 2015 they had become established as far south as Brazil and as far north as New York (Ferreira et al., 2015; Schofield, 2009). Lionfish are gape-limited opportunistic predators, meaning they consume a wide variety of prey, including fish, crustaceans, echinoderms and, on occasion, other lionfish (Acero et al., 2019; Albins & Hixon, 2013; Morris & Whitfield, 2009; Peake et al., 2018). Their rapid spread and broad diet has resulted in declines in native reef fish biomass and diversity, as well as shifts in benthic community structure of reefs (Albins, 2015; Ballew et al., 2016; Green et al., 2012a; Lesser & Slattery, 2011).

Evidence suggests that in their invaded range, lionfish are larger in body size in deeper habitats, specifically mesophotic coral ecosystems (MCEs: 30 -150 m depth), than at shallower depths (< 30 m; Andradi-Brown et al., 2017a). This pattern has been observed in lionfish populations in Honduras, the Gulf of Mexico, Bahamas and Costa Rica (Andradi-Brown et al., 2017b). One hypothesis for this size increase with depth is that it is driven by ontogenetic niche shifts from shallow to mesophotic habitats (Andradi-Brown, 2019; Andradi-Brown et al., 2017a; Malpica-Cruz et al., 2019). Herein I refer to this as the 'ontogenetic niche shift hypothesis'. The pelagic eggs of many reef fish species settle in shallow coastal habitats like mangrove forests and back-reefs, where juveniles are better protected from predators. As they grow larger, they move to more exposed, deeper habitats where there is less competition and more resources (Dahlgren & Eggleston, 2000; Gratwicke et al., 2006; Kimirei et al., 2011, 2013; Mellin et al., 2007). Most evidence supporting the ontogenetic niche shift hypothesis is based on the evidence that lionfish size increases with greater depth (Andradi-Brown et al., 2017a). However, no studies have sampled lionfish from shallow and mesophotic environments to specifically examine how their resource use changes with age.

Understanding whether lionfish move to MCEs as they age could help conservation managers to mitigate the impact that lionfish have on reef communities (Côté & Smith, 2018). Current management relies largely on opportunistic culling by recreational SCUBA divers using hand spears and though effective in the short-term, this method requires constant removal of the species (Davis, 2018; Davis et al., 2021; Johnston & Purkis, 2015). Moreover, recreational divers tend to stay above 30 m depth, meaning that deeper lionfish are regularly missed (Andradi-Brown et al., 2017b). Since lionfish eggs are buoyant, deep individuals may contribute to shallow reef recruitment, undermining culling efforts (Andradi-Brown et al., 2017a). As a result, whether lionfish undergo ontogenetic niche shifts has contrasting management implications: if they do shift across depths, targeting shallow individuals could also help reduce population sizes at greater depths. However, if lionfish do not shift across depths, deeper populations may serve as refuges, remaining unaffected by management efforts focused on shallower waters.

One method to assess ontogenetic niche shifts is through the stable isotope analysis of an organism's tissues (Hammerschlag-Peyer et al., 2011; Layman et al., 2012). The stable isotope ratio of carbon ($^{13}C/^{12}C$, reported as $\delta^{13}C$) varies among primary producers with different photosynthetic pathways and generally reflects the broad foraging habitat of an organism (Post, 2002). The nitrogen isotope ratio ($^{15}N/^{14}N$, reported as $\delta^{15}N$) indicates trophic position and increases predictably as an organism moves up trophic levels (Deniro & Epstein, 1981). Recently, stable isotope analysis of vertebrate eye lenses has gained attention due to the ability to record resource use across an individual's life (Bell-Tilcock et al., 2021; Rosinski et al., 2023; Vecchio & Peebles, 2020; Wallace et al., 2014). Eye lenses are spherical and grow in layers (laminae), which, once formed, become metabolically inert (Greiling & Clark, 2012; Wride, 2011). This means that laminae represent unchanged tissue samples from different life stages of an individual (Wallace et al., 2014). Interior laminae are formed early in the organism's life and represent tissue from natal stages, while exterior laminae correspond to tissue produced most recently (Wride, 2011).

Isotopic analyses of eye lens laminae have been conducted in a variety of fish taxa, including lionfish (Harada et al., 2022; Quaeck-Davies et al., 2018; Xu et al., 2019; Young et al., 2022). Using lens laminae, Curtis et al. (2020) revealed invasive lionfish had greater resource overlap with native fish species during the early part of their life compared to later stages. Their study also found clear variation between lionfish individuals, which could be due to patterns of movement across environmental gradients. However, the individuals in their study were caught between 18 and 24 m (Curtis et al., 2020), meaning that potential ontogenetic habitat shifts across depth could not be explored. This depth limitation is likely due to the high logistical and technical requirements of safely collecting individuals at depths beyond 30 m, which requires advanced SCUBA training, more specialised equipment, and comes with greater safety risks.

To investigate whether the size increase in invasive lionfish with greater depth can be attributed to ontogenetic niche shifts, as predicted by the ontogenetic niche shift hypothesis, I analyse the stable isotope compositions of lens laminae from lionfish captured at shallow and mesophotic depths. My core aim is to assess whether lionfish caught from different depths exhibit similar isotopic niche shifts over their lifetime. These shifts would be reflected by changes in the $\delta^{13}C$ and $\delta^{15}N$ signatures across the eye lens laminae. According to the hypothesis, we may expect (1) all the lionfish to reside in similar conditions early in life. If so, the isotope signatures of the interior laminae should be similar for all individuals, regardless of the depth at which they were caught. The hypothesis also predicts that (2) lionfish move to deeper habitats as they grow older. Consequently, I expect the isotopic signatures of lens laminae to consistently shift with increasing lionfish age, with capture depth exerting a stronger influence on isotopic values in later life stages.

3.2 Methods

3.2.1 Study location

Lionfish were collected from two sites around the Island of Utila, Honduras, between June and August 2022 (**Figure 3.1**). Located on the southern Mesoamerican Barrier Reef, Utila is one of the three main islands and 53 cays that make up the Bay Islands Marine National Park. One of the sites, Raggedy Cay, is on the island's exposed northern shore. Reefs on the northern shore are located along a steep reef wall that that quickly reaches beyond 100 m depth. The other site, Black Hills, is located on the more sheltered southern shore and is found on a sea mount, which starts at a depth of 10 m and reaches over 60 m in depth. These sites were selected because they were one of the few locations around Utila where lionfish were able to be consistently found, given their low abundance (see **Chapter 2**). Research permits for the study were issued by the Instituto de Conservación Forestal (ICF), Honduras (Permit number: DE-MP-108-2023).

3.2.2 Lionfish collection and dissection

Lionfish were caught using hand spear, by divers using open-circuit SCUBA, with deeper individuals collected using mixed-gas. Divers swam around each site and caught lionfish opportunistically. The depth of capture was recorded to the nearest 5 m, due to variations in dive computer depth estimates. All specimens were either put on ice and dissected within 6 hours of capture, or frozen at -20 °C and thawed before dissection within 2 weeks of their capture. Genetic analysis indicates that lionfish around Honduras are entirely *P. volitans* (Betancur-R. et al., 2011), so I assumed all individuals caught were *P. volitans*, though I did not confirm this genetically.

Specimens were dissected using the standardised techniques reported by Green et al. (2012b). For each specimen, I recorded total length (length from the tip of the nose to the end of the caudal fin; cm), weight (g), gape width and height (cm), and where possible sex and reproductive status. Female gonads were recorded as follows: immature, early developing, developing, spawning capable and actively spawning. The reproductive status of males was not assessed due to difficulties in reliably distinguishing between immature and spawning-capable individuals. Both eyes were removed from each lionfish by severing the optic nerve and surrounding connecting tissue. Eyes were labelled as left or right and then frozen at -20 °C.

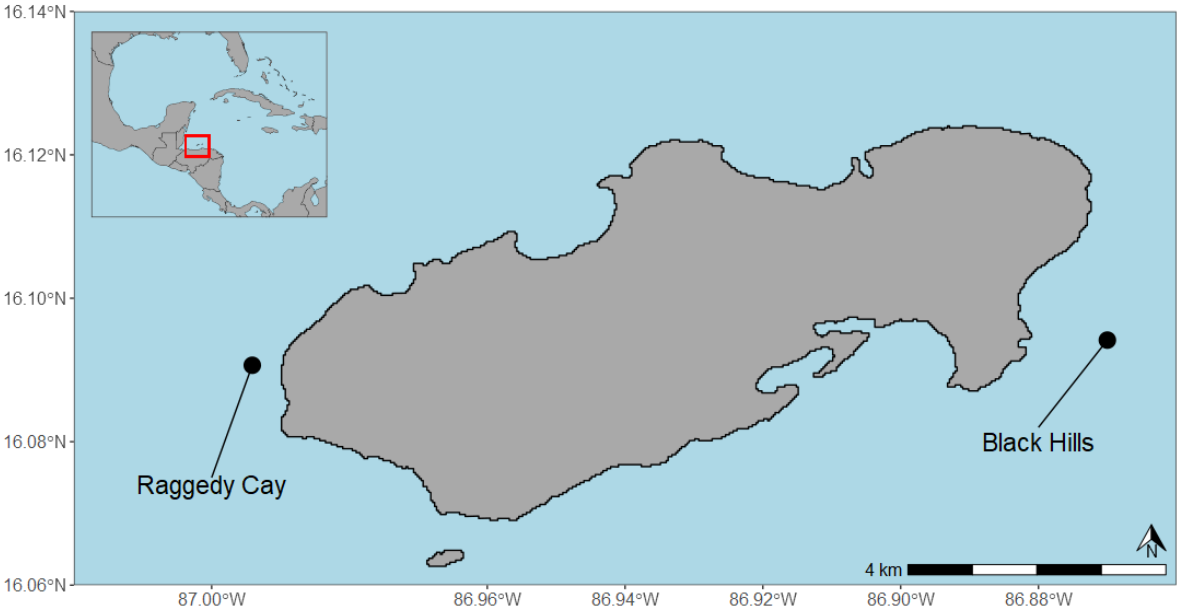

Figure 3.1 Lionfish collection sites around the island of Utila, Honduras.

3.2.3 Eye lens delamination

Before delamination, both eyes from a single specimen were thawed at room temperature for 30 minutes. Once defrosted, the lens was removed from each eye by creating an incision in the cornea. The lenses were rinsed in de-ionised water to remove surrounding eye fluid and tissue. Lens laminae were then sequentially peeled and removed under a dissecting microscope (Microtec Stereo Microscope) using a pair of fine-tipped forceps, following the methods outlined by Wallace et al. (2014). Following the removal of each lamina, the lens diameter was measured at its widest point using an ocular micrometer, rounded to the nearest 0.05 mm. Tools were cleaned in deionised water and dried after each layer was removed. This procedure was repeated until the lens diameter reached 1 mm or less, at which point no further laminae could be removed (i.e., the core of the lens). Lamina samples were left at room temperature for 2-6 hours, until fully dried. Dried laminae were then ground into small pieces. Isotope values do not significantly differ between laminae taken from the left or right eye of the same individual (Wallace et al., 2014), so to obtain enough sample for analysis, I combined laminae from both eyes taken from the same lens diameter. Between 150–900 µg of dried material from each pair of laminae was wrapped in a tin capsule.

3.2.4 Stable isotope analysis

A continuous-flow mass spectrometer (Delta Plus XP; Thermo Scientific, Bremen, Germany) and elemental analyser (vario PYRO cube; Elementar, Langenselbold, Germany) were used to determine the isotope ratios of carbon and nitrogen from each lamina sample. Three internal standards (GEL, ALAGEL & GLYGEL) were used after every 10 samples to maintain instrumental validity. Isotope ratios were denoted as δ values ($\delta^{13}C$/ $\delta^{15}N$) in permil (‰) based on the **Equation 3.1**:

$$\delta^{13}C \text{ or } \delta^{15}N = [(R_{sample}/R_{standard}) - 1] \qquad \textit{(Equation 3.1)}$$

where R_{sample} is the respective ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$, $R_{standard}$ is the international references of Vienna PeeDee Belemnite and atmospheric N^2 for carbon and nitrogen, respectively. All stable isotope analyses were conducted at the National Environmental Isotope Facility (NEIF), based at the Scottish Universities Environmental Research Centre, Glasgow, UK.

3.2.5 Statistical analysis

All data analysis was performed in R v. 4.2.3 (R Core Team, 2023). The non-parametric Wilcoxon rank-sum test was used to explore differences between lionfish body size at the two sites. To explore the relationship between lionfish size and the depth at which they were captured, I ran a Bayesian linear model with body length as the response variable, depth of capture as a fixed effect and the site of capture as a random effect. To explore the relationship between lionfish body size and eye lens diameter, I also ran a linear model with eye lens diameter as the response and body length as the fixed effect. To facilitate interpretation of fixed effects, in both models, continuous fixed effects were standardised prior to analysis so that they had a mean of 0 and a standard deviation of 1.

The isotopic composition of the lens core, representing the natal life stage of each individual lionfish, was analysed using the non-parametric Wilcoxon rank-sum test to assess differences in natal $\delta^{13}C$ and $\delta^{15}N$ between sites and depths. Using SIBER (Stable Isotope Bayesian Ellipses in R; Jackson et al., 2011), $\delta^{13}C$ against $\delta^{15}N$ (‰) ellipses were generated from the lens core isotopic values of each individual lionfish, grouped by their site and depth of capture. Lionfish caught at Raggedy Cay and Black Hills were grouped to account for potential site-specific differences. Due to the minimum sample size required for SIBER analysis, depth of capture was categorised as shallow (<30 m) or MCE (>30 m; Jackson et al., 2011). The standard ellipse areas (SEA) was then estimated, which represent approximately 40% of the data and capture the core isotopic niche, as well as SEAs corrected for small sample sizes (SEAc), and traditional convex hulls for individuals from the same site and depth zone (Layman et al., 2012). Overlap between SEAc ellipses was calculated as the proportion of non-overlapping area between two ellipses, and comparisons were made between shallow and MCE individuals within the same site. Ellipse sizes were compared across different sites and depths using Bayesian estimates of standard ellipse areas (SEAB; Jackson et al., 2011).

Bayesian mixed models were used to explore changes in $\delta^{13}C$ and $\delta^{15}N$ across individual lifetimes. separate models were run for lionfish caught at Raggedy Cay and Black Hills to account for potential site-specific differences. The models for both sites consisted of $\delta^{13}C$ or $\delta^{15}N$ (‰) as the response variable with eye lens diameter and depth as continuous fixed effects. An interaction term was included between the fixed effects to allow us to investigate whether isotopic trajectories over lionfish lifetimes differed between individuals caught at different depths. The predictor variables were log-transformed because previous studies (Curtis et al., 2020), and my own initial exploratory analysis, revealed a non-linear relationship between the lens diameter and isotope values, which appeared logarithmic. Depth was log transformed to ensure the interaction term reflected how changes in the combination of both variables affect the response variable and aid interpretation. For these models, the IDs of individual lionfish were added as a random effect to account for the repeated measurements taken from the same individuals, thereby controlling for individual-specific variations in isotopic values.

All Bayesian models were run with four chains with 2000 iterations (500 warmup) using weakly informative priors (mean of 0 and standard deviation of 5) and fitted with Gaussian error distributions using the R package brm (Bürkner, 2018) implemented in STAN (Stan Development Team, 2023). I assessed model convergence through posterior predictive checks and trace plots. All models had R-hat values of 1.00 and effective sample sizes over 1000, demonstrating models converged well. Following (McElreath, 2016), I interpreted an effect estimate as significant if the 89% credible intervals (CrIs) did not overlap with zero.

3.3 Results

In total, 35 individuals were collected: 14 from Black Hills (shallow: n = 6, MCE: n = 8) and 21 from Raggedy Cay (shallow: n = 10, MCE: n = 11; **Figure S3.2**). Most females were capable of spawning at both shallow (68%) and MCE (79%) depths. Lionfish at Raggedy Cay were significantly larger (26.5 ± 5.9 cm, mean ± SD) than those at Black Hills (22.1 ± 4.3 cm; Wilcoxon rank-sum test, W = 82, P = 0.03). A positive association was observed between lionfish size and the depth of capture (β = 2.18, 89% CrIs = 0.28 to 4.13; **Figure 3.2a**), with larger individuals also displaying greater total eye lens diameters (β = 0.65, 89% CrIs = 0.51 to 0.79; **Figure 3.2b**).

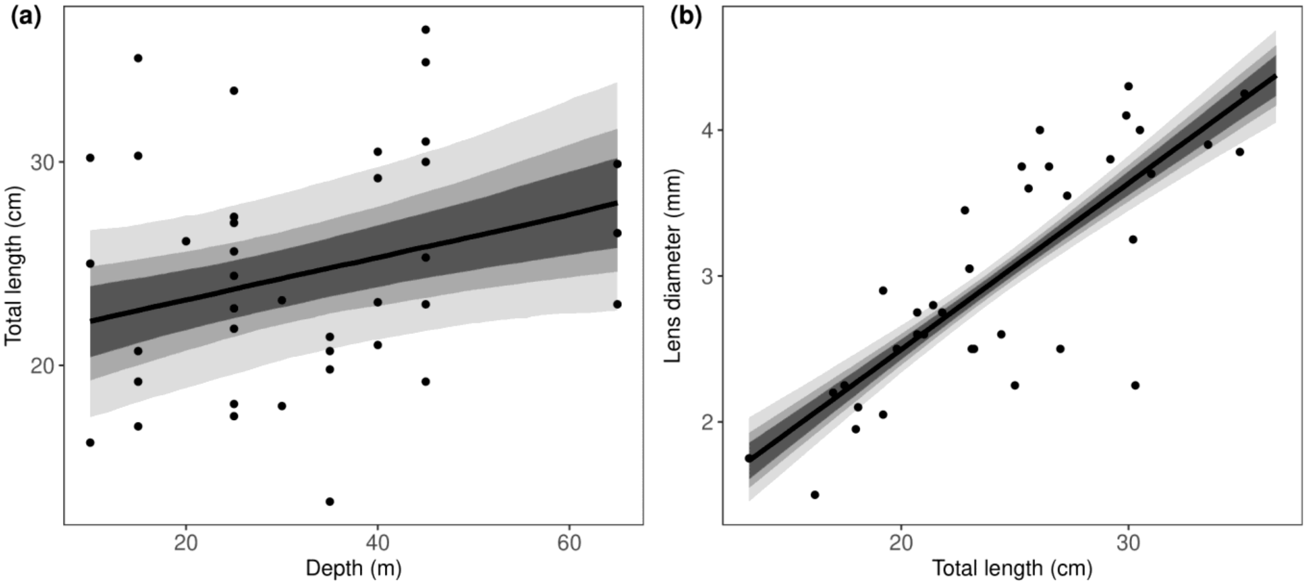

Figure 3.2 (a) Length of lionfish caught across different depths. **(b)** Individual lionfish size and the diameter of their intact eye lens (prior to delamination). The left eye lens was chosen for measurement. Points represent raw data. Trend line represent the expected posterior predictions and shaded areas show 89, 70, and 50% credible intervals (CrIs).

The isotopic niche of lionfish during their natal stage (based on isotopic values from the eye lens core) varied between sites but was not influenced strongly by depth of capture (**Table 3.1**). Natal $\delta^{13}C$ values did not differ significantly between individuals caught at shallow and mesophotic depths within the same site (Wilcoxon rank-sum test, W = 108, P = 0.22), but were overall higher at Black Hills compared to Raggedy Cay (Wilcoxon rank-sum test, W = 67, P = 0.01). Natal $\delta^{15}N$ values did not vary significantly across different sites or depths (Wilcoxon rank-sum test: W = 149, P = 0.87 for sites, and W = 135, P = 0.89 for depths). The within-site overlap of SEAc ellipses for natal tissue from individuals caught from shallow and MCE depths was greater at Raggedy Cay (50.26%) than at Black Hills (19.28%; **Figure 3.3a**). Additionally, the trophic niche width (SEAB) was larger in more than 99% of Bayesian posterior draws at Raggedy Cay compared to Black Hills, regardless of depth (**Figure 3.3b**).

Table 3.1 Natal stable isotope values of lionfish. The convex hull total area (TA), standard ellipse area (SEA) and small sample size corrected SEA (SEAc) of each isotope ellipse grouped by site and depth of capture.

Metric	Black Hills - Shallow	Black Hills - MCE	Raggedy Cay - Shallow	Raggedy Cay - MCE
δ^{13}C‰ (mean ± SD)	-17.20 (± 0.75)	-17.61 (± 0.40)	-16.40 (± 1.13)	-16.65 (± 1.03)
δ^{15}N‰ (mean ± SD)	7.53 (± 0.21)	7.79 (± 0.74)	7.81 (± 0.66)	7.83 (± 0.92)
TA	1.17	0.62	3.97	5.47
SEA	0.73	0.44	2.02	2.80
SEAc	0.85	0.55	2.25	3.19

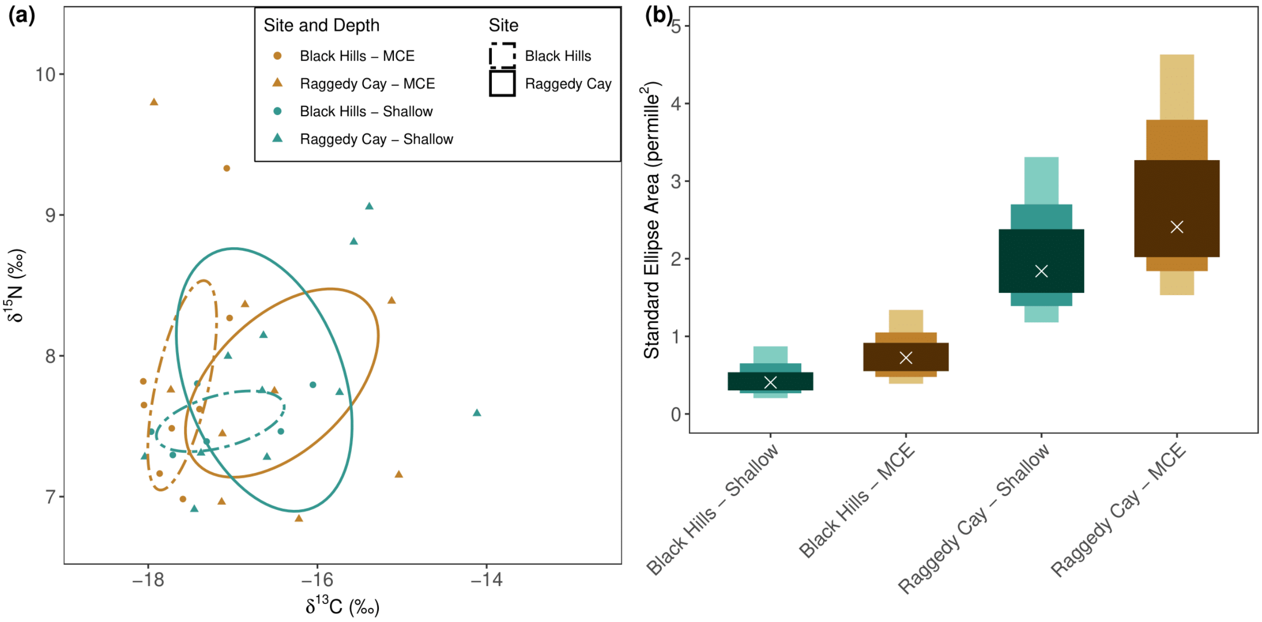

Figure 3.3 Isotopic trophic niche of lionfish at the natal stage (i.e., from the eye lens core). **(a)** Natal isotopic values for individual lionfish (points) and standard ellipse areas corrected for small samples (SEAc) grouped by site and depth of capture. **(b)** Density plot of posterior draws from Bayesian standard ellipse area (SEAB), where the white crosses represent the median standard ellipse areas while the shaded boxed areas show 89, 70, and 50% CrIs.

Both $\delta^{13}C$ and $\delta^{15}N$ varied across the lifetimes of individual lionfish. At both sites, $\delta^{13}C$ values increased with lens diameter (i.e., increasing age). At Raggedy Cay, there was a strong positive association between lens diameter at the point where the lamina was taken and $\delta^{13}C$ values, with laminae taken at larger lens diameters (i.e., later life stages) exhibiting higher $\delta^{13}C$ values (β = 2.51, 89% CrIs: 1.61 to 3.38; **Figure 3.5a**). Depth of capture had no significant effect on $\delta^{13}C$ (CrIs overlapped 0). The interaction between depth of capture and lens diameter was associated with changes in $\delta^{13}C$ values, where laminae taken at larger lens diameters (i.e., later life stages) corresponded to lower $\delta^{13}C$ values at greater depths (β = -0.54, 89% CrIs: -0.80 to -0.27). Similarly, at Black Hills, lamina taken at larger lens diameters showed an increase in $\delta^{13}C$ (β = 1.57, 89% CrIs: 0.26 to 2.89; **Figure 3.5a**), although there was no strong evidence for an interaction between lens diameter and depth.

For lionfish collected at Raggedy Cay, neither lens diameter nor depth of capture had a direct influence on $\delta^{15}N$ values (CrIs overlapped 0; **Figure 3.5b**). There was a positive interaction between lens diameter and depth of capture, with laminae with larger lens diameters (i.e., later life stages) showing increased $\delta^{15}N$ from individuals caught at greater depths (β = 0.22, 89% CrIs: 0.01 to 0.44). In contrast, at Black Hills, depth of capture had a strong positive effect on $\delta^{15}N$ (β = 0.76, 89% CrIs: 0.30 to 1.22), while neither lens diameter nor the interaction between lens diameter and depth of capture had a significant effect (CrIs overlapped 0; **Figure 3.5b**).

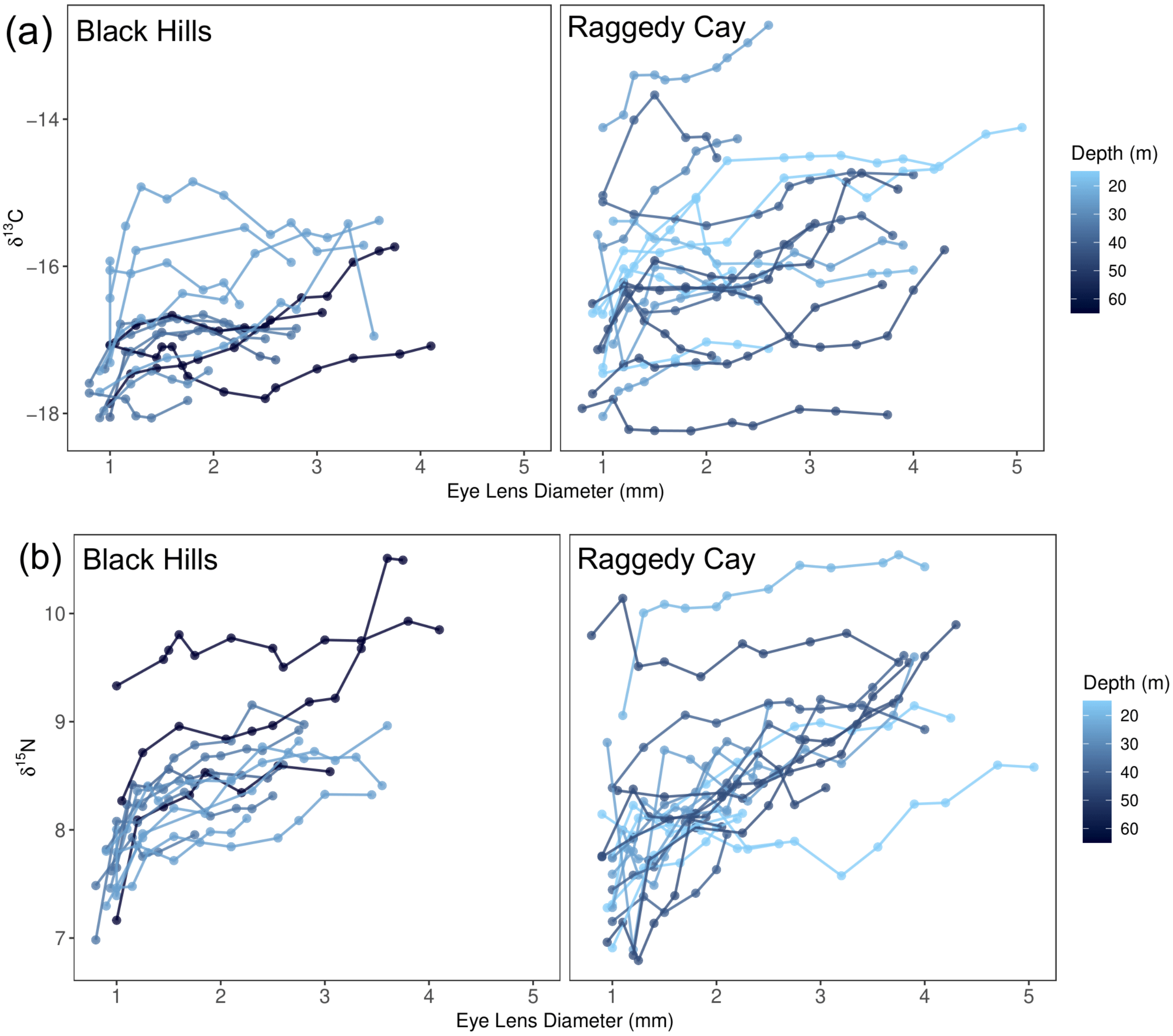

Figure 3.4 Changes in **(a)** $\delta^{13}C$ and **(b)** $\delta^{15}N$ signatures across eye lens laminae of individual lionfish, collected from different sites and depths. Data are plotted relative to the lens diameter where the lamina was taken. Smaller lens diameters correspond to the laminae formed during the early stages of the lionfish's life (younger), while larger diameters represent laminae formed at later life stages (older). Lines connecting data points indicate the chronological progression within the same individual lionfish.

Table 3.2 Results of Bayesian multiple regression analyses examining how capture depth, lens diameter at which the lamina was taken (i.e., age), and their interaction influence δ^{13}C and δ^{15}N. To account for site-level differences, separate models were run for individuals caught at Raggedy Cay and Black Hills. Pseudo-R^2 values were calculated using the *bayes_R2* function from the *brms* package. Effects where the 89% confidence interval (CI) does not include 0 are highlighted in bold.

Raggedy Cay δ^{13}C	**R^2 = 0.88**			
	Estimate	Est.Error	l-89% CI	u-89% CI
Intercept	-16.20	2.07	-19.51	-12.93
Lens diameter (log)	**2.50**	**0.56**	**1.59**	**3.41**
Depth (log)	-0.07	0.61	-1.03	0.91
Lens Diameter (log) * Depth (log)	**-0.53**	**0.17**	**-0.80**	**-0.26**

Black Hills δ^{13}C	**R^2 = 0.76**			
	Estimate	Est.Error	l-89% CI	u-89% CI
Intercept	-14.63	1.78	-17.37	-11.82
Lens diameter (log)	**1.56**	**0.81**	**0.27**	**2.83**
Depth (log)	-0.71	0.50	-1.50	0.06
Lens Diameter (log) * Depth (log)	-0.26	0.22	-0.61	0.10

Raggedy Cay δ^{15}N	**R^2 = 0.83**			
	Estimate	Est.Error	l-89% CI	u-89% CI
Intercept	7.71	1.17	5.83	9.55
Lens diameter (log)	0.11	0.46	-0.64	0.84
Depth (log)	0.04	0.35	-0.51	0.59
Lens Diameter (log) * Depth (log)	**0.22**	**0.14**	**0.01**	**0.44**

Black Hills δ^{15}N	**R^2 = 0.86**			
	Estimate	Est.Error	l-89% CI	u-89% CI
Intercept	5.24	1.07	3.61	6.94
Lens diameter (log)	0.54	0.57	-0.35	1.46
Depth (log)	**0.76**	**0.3**	**0.28**	**1.22**
Lens Diameter (log) * Depth (log)	0.08	0.16	-0.18	0.32

3.4 Discussion

My findings show that early-life feeding habits of lionfish vary both among individuals and between capture sites, suggesting they do not always exploit on the same resources when young. As lionfish aged (indicated by larger lens diameters), their $\delta^{13}C$ values increased, indicating shifts in their prey's basal carbon sources. However, depth of capture did not have a consistent effect on this pattern. Moreover, lionfish caught at greater depths had higher $\delta^{15}N$ values, indicating a shift to higher trophic levels, although age did not consistently influence this trend. Combined, these findings do not support the hypothesis that lionfish move to deeper habitats as they grow. The apparent lack of connectivity between lionfish populations at different depths suggests that culling efforts in shallow waters will not impact mesophotic populations, allowing depth to serve as a refuge from management. Therefore, targeted strategies are needed to reach deeper-dwelling lionfish in this culling refuge and minimise their impact on MCEs.

The natal isotopic niche space of lionfish varied across different capture sites, which does not support the hypothesis that early-life resource use is similar regardless of capture depth. Lionfish caught at Black Hill exhibited low variation in their natal isotopic niche space. Being gape-limited feeders, younger and smaller lionfish are expected to be restricted to a smaller pool of prey species, which likely results in the consumption of prey at similar trophic levels and from similar basal source (Malpica-Cruz et al., 2019; O'Farrell et al., 2014). However, this pattern was not observed in lionfish caught at Raggedy Cay, where there was greater variability and wider niche breadth in their natal isotopic space. This variation was driven by higher $\delta^{13}C$ values, indicating the use of benthic carbon sources, such as algae (Eddy et al., 2020; Stefanoudis et al., 2019). The shallowest depth at Raggedy Cay is approximately 5 m, covering a wide area, whereas the shallowest depth at Black Hill is around 10 m and encompasses a smaller area due to its nature as a seamount. Therefore, the more developed shallow regions at Raggedy Cay provide younger lionfish with access to a broader range of basal carbon sources, both pelagic and benthic, leading to greater niche breadth. In contrast, the reduced shallow cover at Black Hill means lionfish may rely more heavily on only pelagic sources, resulting in narrower niche widths. These differences may also result from variations in terrestrial inputs, which can affect the baseline levels of carbon and nitrogen in coastal marine systems (Kurle & McWhorter, 2017; McMahon et al., 2013). Raggedy Cay, closer to Utila's shoreline, likely receives more nutrient-rich runoff from pollution or natural drainage. In contrast, Black Hills, located ~1 km offshore on a seamount, is more isolated, reducing terrestrial nutrient input and leading to a more restricted trophic niche.

For lionfish caught at both sites, $\delta^{13}C$ values increased with lens diameter (i.e., increasing age), indicating that lionfish experience shifts in basal carbon sources as they grow. This aligns with the previous study by Curtis et al., (2020), which found $\delta^{13}C$ increased logarithmically across eye lens laminae. Similar findings were also obtained from lionfish in the Bahamas, where larger lionfish showed increased $\delta^{13}C$ in their muscle tissue (Malpica-Cruz et al., 2019). However, my results showed that depth of capture had no clear direct effect on $\delta^{13}C$ at either site. Interestingly, at Raggedy Cay, there was evidence of an interaction whereby older lionfish (i.e., laminae taken at larger lens diameters) had lower $\delta^{13}C$ values at greater depths. Considering that this pattern was not observed at Black Hills, this could reflect site-specific movement across depth and highlights the importance of testing theory across multiple sites. Similar patterns have been reported in other taxa, such as teleosts and crustaceans around Bermuda, where $\delta^{13}C$ values decrease with depth as carbon sources transition from benthic to more pelagic or planktonic sources (Eddy et al., 2020; Stefanoudis et al., 2019). This finding for Raggedy Cay could be due to greater prey availability on deeper parts of the reef compared to Black Hills. However, without data on prey abundance across depths at each site, I cannot attribute this finding to that process.

As lionfish aged, there was a clear enrichment of $\delta^{15}N$; however, the influence of capture depth on this relationship was unclear. At Black Hills, capture depth had a strong positive effect on $\delta^{15}N$, suggesting that lionfish at greater depths fed at higher trophic levels. However, there was no significant interaction between age and depth, indicating that the increase in trophic level with depth was not linked to lionfish age. In contrast, at Raggedy Cay, $\delta^{15}N$ enrichment was observed with increasing age and depth, suggesting that as lionfish aged, they moved deeper and consumed higher trophic level species. The consistent nitrogen enrichment across capture depths at both sites likely indicates that lionfish prey on higher trophic level species at greater depths or that the mesophotic zone around Utila is naturally enriched in nitrogen. As depth increases, fish body size and prey trophic level tend to rise (Andradi-Brown et al., 2016), while macroalgal tissue $\delta^{15}N$ has also been found to be higher in mesophotic depths than in shallower waters (Strait et al., 2022). These findings therefore suggest that lionfish alter their diet at greater depths, likely due to a shift towards nitrogen-enriched prey, though no clear trends were observed across lionfish age.

These considerations lead to a key limitation of the study - the lack of contextual information. I was unable to establish baseline isotopic values for prey species across different depths or develop an 'isoscape' (a map of isotope variability) around Utila, both of which help the interpretation of isotopic data (Bowen et al., 2010). In 2022, I collected algae samples from shallow and mesophotic reefs at Raggedy Cay and Black Hills with the aim of building an isoscape. The following year, I planned to gather benthic and pelagic carbon sources to help contextualise these results. However, a 15-month delay in obtaining export permits for the initial set of samples, including the eyes, prevented me from collecting additional samples during the 2023 summer field season. For future work to effectively establish an isotopic baseline for lionfish across the depth gradient, the sampling of key primary producers and prey species at each site should be prioritised. The basal isotopic signatures of shallow and mesophotic food webs should be collected from benthic algae, such as Chlorophyta and Rhodophyta, which can serve as primary carbon sources (Eddy et al., 2020). To account for pelagic contributions, phytoplankton should also be sampled from different depths. Additionally, common lionfish prey species, such as shrimp and gobies (Andradi-Brown, Grey, et al., 2017), should be collected at shallow and mesophotic depths. These combined data would then be suitable to fully interpret shifts in isotopic signatures across eye lens chronologies.

A fundamental assumption of this study is that lionfish caught at specific depths had remained there for extended periods of time, without moving across depths over short periods. Evidence supporting this assumption is mixed. Using acoustic telemetry, Gavriel et al. (2021) reported that some lionfish consistently inhabited the same depth zone, whereas others moved across shallow and mesophotic depths on a daily basis. To address this caveat, future studies could incorporate fine-scale tracking data using telemetry, along with isotopic analysis, to better understand the vertical movement patterns of lionfish. Moreover, there is currently no data on the rate at which lionfish eye lens laminae grow. This information is key for aligning the laminae time series with specific years to examine annual and interannual changes in resource sources, as well as responses to major disturbances like bleaching events or hurricanes.

Since there is no clear evidence that lionfish move to deeper waters as they age, to effectively manage their populations lionfish management efforts (i.e., culling or trapping) should be tailored separately for shallow and mesophotic reefs (Andradi-Brown et al., 2017b). Due to the logistical challenges of removing lionfish from MCEs, culling at greater depths should focus on high-density areas, such as seamounts, for maximum efficiency (Goodbody-Gringley et al., 2023). Moreover, it is possible that the observed trend of increasing lionfish size with depth may be an unintended consequence of culling efforts in shallow waters, where larger individuals are preferentially targeted, reducing overall body size and artificially creating this size pattern (Andradi-Brown et al., 2017b; Frazer et al., 2012). To determine whether this is the cause of size patterns in invasive lionfish, future lionfish surveys could be conducted across different locations with comparable shallow reefs and mesophotic ecosystems, both in areas with and without culling (Andradi-Brown, 2019).

In conclusion, my findings are not consistent with the ontogenetic niche shift hypothesis. This study represents a novel approach in using fish eye lenses to investigate ontogenetic niche shifts across depth, providing new insights. Future studies should prioritise the creation of isoscapes and the use of fine-scale tracking data to explore depth-related movements over both short and long timescales.

Nevertheless, the apparent lack of connectivity between lionfish populations at different depths suggests that culling in shallow waters does not affect mesophotic populations, allowing deeper areas to serve as a refuge from management. Therefore, targeted strategies are needed to control deeper-dwelling lionfish and minimise their impact on MCEs.

Chapter 4: Site-level field of view is associated with altered anti-predator responses in farming damselfish

Currently under review

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Author contributions

J.S.B. conceived the idea with input from S.A.K., D.E. and R.F., and conducted the data collection. J.S.B. conducted the analysis with advice from S.A.K., D.E. and R.F., and wrote the first manuscript draft. J.E.S created the 3D models and assisted with behavioural assays. C.Y developed the code to analyse refuge densities. All co-authors contributed critically to the writing.

Abstract

The three-dimensional (3D) structure of a habitat influences how prey perceive predation risk, yet the effect of habitat features at larger spatial scales remain poorly understood, especially in complex environments like coral reefs. Using 3D reconstructions of three Caribbean reef sites, I characterise site-level metrics such as field of view (extent of observable area), refuge density (density of holes), and rugosity (reef surface roughness). The anti-predator behaviours of damselfish, parrotfish, and wrasse species were then assessed at each site. The damselfish *Stegastes adustus* had shorter flight initiation distances (FID) at Sturch Bank, a site with a significantly greater field of view. Additionally, at Sturch Bank, *S. diencaeus* fled longer distances compared to the other two sites. In contrast, *S. planifrons* fled shorter distances into a refuge at the site with a more restricted field of view. Neither wrasse nor parrotfish species showed variation in escape responses across sites, although body size was positively correlated with both FID and distance fled. Moreover, the lack of significant differences in refuge availability between sites may reflect the ongoing decline in the fine-scale structural complexity of Caribbean coral reefs. Overall, these findings reveal that fish anti-predator behaviours can vary between sites with different levels of structural complexity, though there are different between species even within the same genus. By examining structural features at the site-level, I provide a new perspective on how reef fish behaviours may be influenced by structural complexity.

4.1 Introduction

The three-dimensional (3D) structure of a habitat is a key factor in shaping how species are distributed and behave (MacArthur & MacArthur, 1961; McCoy & Bell, 1991; Warfe & Barmuta, 2004). Habitats with greater structural complexity generally support higher levels of species abundance and diversity due to the increased availability of niches, sheltered areas, and resources (August, 1983; Ghadiri Khanaposhtani et al., 2012; Graham & Nash, 2013b; Gratwicke & Speight, 2005; St. Pierre & Kovalenko, 2014). This complexity is particularly important for predator-prey dynamics, as different features of structural complexity can influence a prey's assessment of predation risk (Camp et al., 2013; Warfe & Barmuta, 2004).

Optimal escape theory states that the escape responses of prey are influenced by a trade-off between the perceived risk of predation and the energetic cost of abandoning foraging or mating to engage in an escape response (Cooper & Frederick, 2007; Ydenberg & Dill, 1986). This decision-making process can be influenced by environmental characteristics, such as the availability of crevices or shelters that provide refuge from predators (Berryman & Hawkins, 2006). When refuges are sparse and far away, an individuals' perceived risk of predation is thought to increase due to the higher energetic costs required to reach safety (Stankowich & Blumstein, 2005). Increased distance to the nearest refuge is associated with heightened risk aversion across various taxa, including birds (Morelli et al., 2022), mammals (Dill & Houtman, 1989), fish (Dill, 1990), and reptiles (Cooper, 2007). Likewise, an individual's field of view (i.e., extent of observable area from a given position), which can be shaped by the topography of their environment, is also thought to affect when individuals begin to assess predation risk (Ndaimani et al., 2013; Stein et al., 2022). A wider field of view allows for earlier predator detection, while a limited field of view delays predator recognition until the threats are much closer (Embar et al., 2011; Gresham et al., 2023; Mols et al., 2022). According to the 'flush early and avoid the rush' hypothesis, animals typically flee shortly after detecting a threat, thereby minimising the costs associated with continued vigilance (Blumstein, 2010). Evidence supporting this hypothesis has been observed in birds and mammals, but it appears to be less applicable to other taxa, such as lizards (Samia et al., 2013).

In reality, perceived risk is often influenced by an interaction amongst these various aspects of structural complexity, further mediated by biological factors. For instance, red deer (*Cervus elaphus*) displayed greater risk aversion in areas with very high and very low fields of view, exhibiting a preference for habitats offering an intermediate level of complexity (Zong et al., 2023). This preference likely comes from a trade-off: while deer require some degree of complexity for concealment to reduce predation risk, they also need open views to detect predators (Zong et al., 2023). Body size can have further confounding effects on this relationship (Chan et al., 2019). According to the asset protection principle, larger individuals, possessing greater energy reserves, can afford to prioritise safety in environments with many refuges, while smaller individuals may need to forage more frequently and accept higher risks due to limited resources (Wahle, 1992). For example, larger sticklebacks (*Gasterosteus aculeatus*) prioritise safety over feeding more so than smaller individuals due to the relatively lower energy costs associated with fleeing, but in areas with fewer refuges, even larger individuals need to compromise safety to fulfil their dietary needs (Krause et al., 2000). Defence strategies, particularly crypsis, can also influence predator avoidance behaviours (Samia et al., 2016). Species that rely on crypsis are more likely to freeze rather than flee (Møller et al., 2019; Samia et al., 2016), and in visually complex environments, this stillness may further reduce detection by predators. This underscores the interactive effects that different structural features and biological factors can have on anti-predator responses of prey, something which is yet to be explored for individuals in highly complex habitats, such as coral reefs.

The architecture of a coral reef is made of a mix of hard and soft corals, sponges, geomorphological features, and the remnants of deceased coral colonies (Graham & Nash, 2013). When quantifying the structural complexity of a reef, studies often combine all these aspects into a single metric known as rugosity, which measures reef surface roughness (Luckhurst & Luckhurst, 1978; González-Rivero *et al.*, 2017). Rugosity is a widely used proxy for habitat complexity; however, it may not fully capture the type of features that influence fish interactions. However, few studies have explored other structural metrics, largely due to the logistical challenges of measuring these on a reef. Fortunately, recent advances in underwater photogrammetric technology have significantly enhanced the speed and scale at which researchers can assess the structural composition of a reef (González-Rivero et al., 2017).

Perceived predation risk in animals is commonly assessed by measuring their Flight Initiation Distance (FID), which is the distance between a stimulus and the prey at the onset of flight (Ydenberg & Dill, 1986). A shorter FID indicates a lower perceived predation risk, whereas a longer FID suggests a higher perceived risk. In reef fish studies, the correlation between FID and habitat structural complexity has predominantly been explored using rugosity as the structural metric, showing a positive correlation in damselfish (Quadros et al., 2019) and some species of wrasse (Labridae) and parrotfish (Nunes et al., 2015). A relatively underused metric in reef fish behaviour studies is distance fled, which measures the extent of the prey's escape path and reflects their assessment of the energy required to reach safety (William & Blumstein, 2015; Ydenberg & Dill, 1986). Distance fled is useful for determining the level of perceived risk an animal faces and how far it needs to travel to escape predation. (Tätte et al., 2018). While this metric has been applied to understand escape investment in birds (Tätte et al., 2018) and lizards (Samia et al., 2016), its use in studying perceived predation risk in reef fish has not yet been explored. Moreover, studies tend to assess complexity at smaller spatial scales rather than at site-level, potentially overlooking broader habitat characteristics that influence escape decisions.

This study aims to determine how the anti-predator responses of reef fish are influenced by different features of habitat complexity. Firstly, I draw on the 'flush early and avoid the rush' hypothesis which suggests that individuals with a greater visual field will flee soon after detecting a predator to minimise the costs associated with continual vigilance. If true, I predict that in sites with a greater field of view, individual fish will (1) exhibit longer FIDs as they can detect predators earlier, and (2) flee shorter distances because the threat of predation will be lower. Furthermore, drawing on optimal escape theory, I expect that individuals with more available refuge options will perceive the cost of fleeing as outweighing the risks of predation. I therefore predict that individuals in environments with more refuges and greater rugosity will (3) have shorter FIDs and (4) flee shorter distances compared to those in less complex environments.

4.2 Methods

4.2.1 Study location

Data were collected at three fringing reef sites surrounding the island of Utila, Honduras (**Figure 4.1**). Located on the southern edge of the Mesoamerican barrier reef, Utila is a popular tourist destination, primarily driven by the SCUBA diving industry. Sites were situated on the island's sheltered southern coastline to facilitate access and were chosen based on *a priori* assumptions of differing structural complexity determined by preliminary visual assessments. All sites were separated by more than 800 m. Data were collected at 5 m depth using open-circuit SCUBA. All three sites are shore reefs with a spur-and-groove system. While community composition was not formally assessed in this study, previous work on Utila indicates that sites along the southern shore have similar fish taxonomic and trophic compositions, with low densities of invasive lionfish and piscivores at 5 m depth (Andradi-Brown et al., 2016; 2017). Research permits for the study were issued by the Instituto de Conservación Forestal (ICF), Honduras (Permit number: DE-MP-108-2023).

4.2.2 Three-dimensional (3D) reef reconstructions

I used structure-from-motion photogrammetry to model the benthic structure at Coral View, Little Bight, and Sturch Bank. The 3D reconstructions were conducted along the reef at each site, extending up to 150 m east or west of the site buoy. At each site, a 50 m transect tape was laid out at a depth of 5 m, with four 0.2 m scale markers placed at regular intervals. A diver swam 1 m above the reef, filming the benthos using three GoPro HERO3 cameras mounted on a straight pole at 0.5 m intervals to ensure effective image overlap. The cameras were angled 45° downward, capturing a 2 m wide area (1 m on either side of the transect tape). To optimise model reconstruction and reduce computational challenges, each 50 m x 2 m survey was divided into two 25 m x 2 m sections. In total, 12 reef transects of 25 m x 2 m were recorded at each site.

Video files from each camera were converted into images by extracting 3 frames per second using Free Video to JPG Converter v5.0.101. These images were then imported to Agisoft Metashape Professional Edition (AgiSoft, 2022) and orthomosaics rendered following the protocol outlined in Young *et al.* (2017). Orthomosaics were then converted into point clouds, scaled and rasterised into digital elevation models (DEMs) in CloudCompare v2.11.3 (CloudCompare, 2022). Resolution was ~ 3 cm per pixel. For each of the three reef sites, 12 reconstructions were performed along a 25 m x 2 m section, resulting in a total of 600 m^2 of reef reconstructed for each site. All videos were recorded, and reconstructions made, between June and August 2022 by J.E.S.

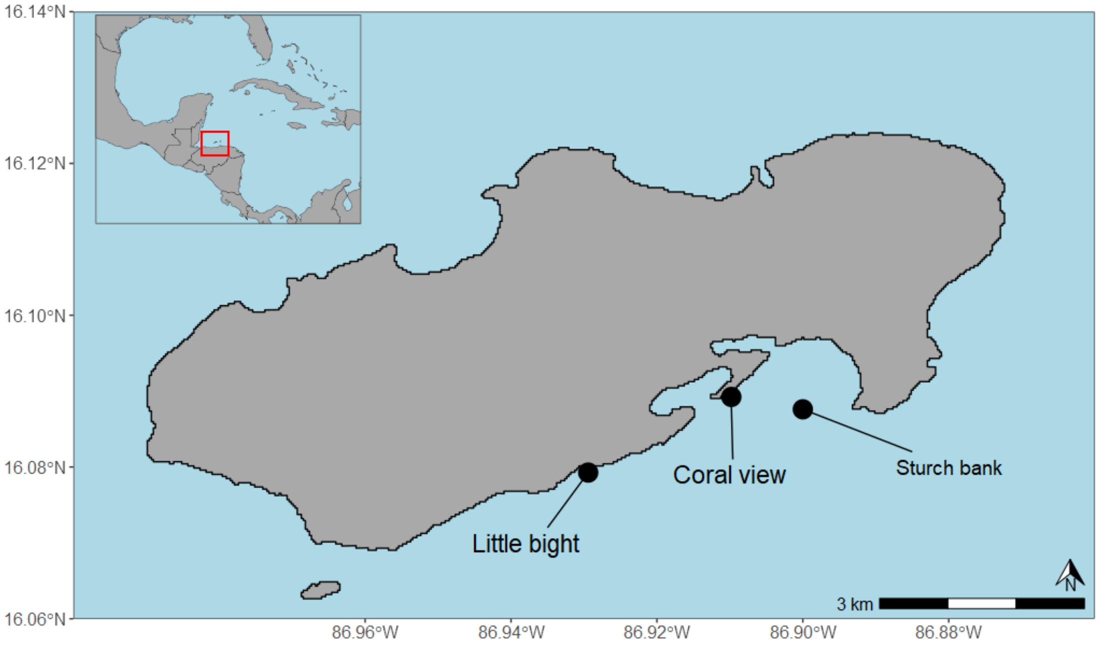


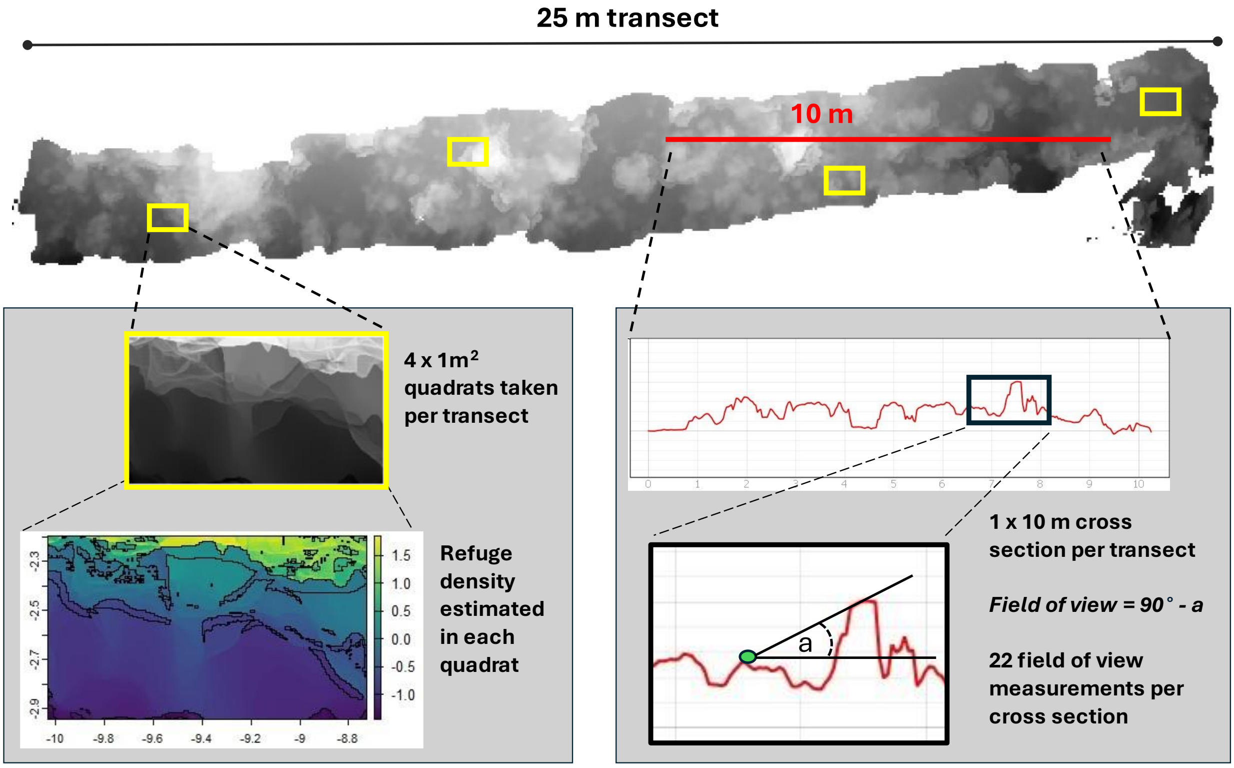
Figure 4.1. Study locations around the island of Utila, Honduras. Inset map shows the location of Utila relative to the Caribbean region.

4.2.3 Features of structural complexity

Field of view was estimated following the protocol outlined by Oakley-Cogan *et al.* (2020). In summary, a 10 m long cross-section was generated for each 25 m segment of the DEM using the Terrain Profile tool in QGIS Desktop v. 3.20.3 (QGIS.org, 2021). These cross-sections were imported and scaled in ImageJ (Schneider et al., 2012). At the start of the cross-section (0 m), a 1.8 m horizontal line was drawn toward the centre of the transect, positioned 2 cm above the substrate surface to represent fish eye height. While I did not measure average eye height in our study, this value was taken from Oakley-Cogan et al. (2020) and is a reasonable approximation from our study taxa. The length of the visual line was selected as 1.8 m based on it being the average starting distance in the anti-predator experiments. An additional 1.8 m line was extended from the start of the horizontal line to the highest topographic point the angled line could reach within the cross-section. The angle formed by the horizontal line and the line to the highest elevation point was subtracted from 90 degrees, which provided the field of view (see **Figure 4.2** for schematic). This process was repeated at 0.5 m intervals along the cross-section, with the horizontal line always aimed towards the centre of the cross section. For the central point, lines were drawn in both directions. In each 10 m cross-section, 22 measurements were recorded and averaged, resulting in 12 values per site (one from each 25 m x 2 m DEM). Higher field of view values correspond to more open lines of site and reflect lower complexity.

To determine the density of refuges (i.e., holes on the reef) at each site, I utilised the 'Hidey Hole' function (see https://github.com/cyesson/HideyHole; Lynch, 2024). From the DEMs of each 25 m x 2 m transect, four 1 m^2 quadrats were chosen randomly and cropped (see **Figure 4.2** for schematic). This approach was chosen to avoid inaccuracies due to edge irregularities in the DEMs and to reduce computational demand. The function analysed each cropped quadrat by examining each pixel's elevation relative to its surrounding neighbourhood to identify depressions. It calculates a local average elevation and flags pixels significantly lower than this average, using a user-defined depth threshold (Dagum et al., 2021). Identified pixels were grouped into contiguous polygons representing potential hidey holes. Here I used a depth threshold of 5 cm, 10 cm and 15 cm, respectively. These hole depths were chosen based on the average length of taxa assessed in this study, with the assumption that any larger holes would not provide a sufficient predation shelter. I estimated total count of 5 cm,10 cm and 15 cm holes per 1 m^2 across sites. Higher hole densities correspond to more potential refuge opportunities.

Planar rugosity was calculated by dividing the geometric surface area of each DEM by the true surface area and then subtracting that value from one (Young et al., 2017). For each site, I obtained 12 rugosity measurements (one from each 25 m x 2 m DEM), where values ranged from zero to one, with higher values correspond to greater structural complexity.



Lynch (2024)

Oakley-Cogan et al. (2020)

Figure 4.2 Schematic illustrating the process for sampling refuge density and field of view at each site. In each 25 m transect reconstruction (12 per site), refuge density was calculated following Lynch (2024), and field of view was determined using the methods from Oakley-Cogan et al. (2020).

4.2.4 Predator-response experiments

Predator-response experiments were conducted from June 26th to July 27th, 2023. The experiments were conducted at the same site as the 3D transects, either east or west of the site buoy, extending up to 150 m in each direction. No experiments were conducted beyond this range, ensuring consistency in location. All experiments were conducted by two observers (J.S.B and J.E.S) following a standardised protocol to ensure consistency in data collection.

Experiments were conducted on a total of 10 species of reef fish across three taxa: wrasse (*Halichoeres garnoti* and *Halichoeres maculipinna*), parrotfish (*Scarus iseri, Scarus taeniopterus, Sparisoma aurofrenatum* and *Sparisoma viride*), and territorial farming damselfish (*Stegastes adustus, Stegastes diencaeus, Stegastes paritus* and *Stegastes planifrons*). These species were chosen because they were common across all study sites and are considered prey species.

Observers swam slowly around each site to identify focal taxa that were either feeding or swimming normally, and in a location that meant they could be approached horizontally. Before approaching, observers noted the species, visually estimated body size (total length in cm), determined the life stage (adult or juvenile), and, when in a monospecific group, counted the number of individuals. To minimise observer effects, both observers used identical measuring devices and practised estimating fish lengths using PVC pipes of various size underwater until they consistently fell within a 1 cm margin of the actual length. Fish length estimates were practised and revalidated every 2–5 days. For this study, a 'group' was defined as all individuals of the same species within a 1 m radius of the focal fish (Nunes et al., 2015). Group size was accounted for because the perception of safety is thought to increase with group size (Ydenberg & Dill, 1986) and may play a role in affecting fish escape decisions (Samia et al., 2019).

An anti-predator response was initiated by moving a 3D printed and painted replica of a black grouper (*Mycteroperca bonaci*; 40 cm total length; **Figure S4.1**) mounted on the end of a 1 m stick (to maintain observer distance) towards the focal subject. This model predator, as opposed to a diver, was used to generate a more realistic anti-predator response. *M. bonaci* was selected as previous fish community surveys around the island have shown *M. bonaci* to be present, though rare, around the island and to predate on a wide variety of fish taxa (Freitas et al., 2017). Due to the size of the model predator, individuals ≥ 25 cm were not included, as it was unlikely individuals of this size would be considered prey.

All anti-predator response experiments began with the observer positioned between 0.7-3 m from the focal individual at depths of ~5 m. The observer dropped a marker on the substrate directly below the point where the nose of the model predator was immediately before starting the experiment. The predator was then pushed horizontally towards the focal fish at a constant speed of an estimated 1 m/s. The escape response was determined to have occurred when the focal individual's swimming speed increased beyond that of the model predator's approach speed (Januchowski-Hartley et al., 2011, 2012).

After the individual's escape, the diver dropped two more markers to indicate the location of both the nose of the predator model and the position of the focal prey individual at the moment escape was initiated (Januchowski-Hartley et al., 2011). The planar distance (cm) between the first and third marker was measured using a measuring tape and represents the starting distance, recorded because starting distance can influence anti-predator responses (Blumstein, 2003). The planar distance (cm) between the second and third markers represents the FID. Escape responses were categorised as either: 'fled into open water', where fish fled but not into a shelter; 'fled into refuge', where the fish entered a hole; 'evade', where the fish manoeuvred side to side or in and out of the reef structure; 'none', where no visible escape response was observed (adapted from Nunes et al., 2015). If the individual fled into open water or a refuge, a fourth marker was then dropped at the approximate location where the fish stopped fleeing (defined as when the focal individual's swimming speed dropped below that of the model predators) or at the shelter it took refuge in. The planar distance between the third and fourth marker represents the distance fled into open water or distance to refuge, depending on the escape response. A shelter was considered occupied if a fish was at least partially inside it immediately after fleeing from the model predator. To avoid resampling the same individuals, each flight experiment was conducted at least 5 m away from the previous FID experiment.

The study did not involve the capture or handling of fishes, only their brief disturbance when initiating an escape response. Procedures were approved by the University of Nottingham Ethics Panel and field permits were issued by the Instituto de Conservacion Forestal, Honduras (permit number: DE-MP-108-2023).

4.2.5 Statistical analysis

Data analysis was performed in R v. 4.2.3 (R Core Team, 2023). A One-Way Analysis of Variance (ANOVA) was used to determine whether there were significant differences in the mean lengths of individuals across different sites. Levene's Test was conducted to assess whether the variances in field of view, rugosity, and refuge density were equal across sites. Since the assumption of equal variances was not required, a Welch's ANOVA was used to analyse the mean values of field of view, rugosity, and refuge density at each site. For post hoc pairwise comparisons between sites, the Games–Howell test, which is appropriate for data with unequal variances, was applied.

If differences in complexity metrics between sites where found, Bayesian mixed-effects models were then used to determine the effects of complexity on antipredator responses using the package brm (Bürkner, 2018) implemented in STAN (*Stan Development Team*, 2023). I structured the model with one of the anti-predator behaviours (FID, distance fled, or distance to refuge) as the response variable and the interaction between species and site as a fixed effect. I acknowledge that using site as a whole creates a spatial disconnect between the exact location of the behavioural experiments and the complexity measurement. However, our goal was to assess how broader-scale complexity at each site influences predator-avoidance behaviours. As body length and group size are known to influence escape decisions, I included these as co-variates in the model. To facilitate interpretation of fixed effects, I standardised continuous covariates prior to analysis so that they had a mean of 0 and a standard deviation of 1. Models included investigator ID (J.S.B or J.E.S) and starting distance as random effects to account for variances in measurements between investigators and the known influence of starting distance on anti-predator responses. Models were run separately for wrasse, damselfish, and parrotfish.

In addition, I investigated the relationship between average field of view and refuge density across transects, examining how these values varied with transect-level rugosity. To model this, I employed a Bayesian linear regression using the brms package. In the model, either field of view or refuge density (10 cm depth holes) was used as the response variable, with rugosity included as a fixed effect.

Models were run with four chains with 3000 iterations (1000 warmup) using weakly informative priors (mean of 0 and standard deviation of 10) and fitted with Gaussian error distributions. I assessed model convergence through posterior predictive checks, trace plots, and ensuring that R-hat values were equal to one. All models had R-hat values of 1.00 and effective sample sizes over 1000, demonstrating models converged well. I interpreted an effect estimate as significant if the 89% credible intervals (CrIs) did not overlap with zero (McElreath, 2016). Post-hoc analyses were conducted using the emmeans package in R to assess the difference in behavioural responses across structural complexity gradients (Lenth, 2024). I report estimates of posterior means and emmeans contrasts, with 89% CrIs.

4.3 Results

4.3.1 Structural complexity metrics across sites

Field of view varied significantly between study sites (Welch's ANOVA, $F_{2,17.6} = 10.99$ $p < 0.01$; **Figure 4.3a**). Sturch Bank had a greater field of view than Little Bight (0.80 ± 0.04 vs. 0.66 ± 0.11, mean ± std. dev) and Coral View (0.70 ± 0.12), with both differences being statistically significant (Games-Howell post hoc, $p < 0.01$ and $p = 0.04$, respectively; Levene's test, $F_{1,22} = 5.79$, $p = 0.03$ and $F_{1,22} = 11.01$, $p < 0.01$). However, no significant difference in field of view was found between Little Bight and Coral View (Games-Howell post hoc, $p = 0.55$; Levene's test, $F_{1,22} = 0.22$, $p = 0.65$).

Rugosity also varied significantly across sites (Welch's ANOVA, $F_{2,19.62} = 7.8$ $p < 0.01$; **Figure 4.3b**). Rugosity at Little Bight was greater than at Coral View (0.62 ± 0.03 vs.

0.53 ± 0.10; Games-Howell post hoc, $p = 0.04$; Levene's, $F_{1,22} = 8.62$, $p < 0.01$) and Sturch Bank (0.57 ± 0.04; Games-Howell post hoc, $p < 0.01$; Levene's, $F_{1,22} = 0.40$, $p = 0.53$). However, no significant difference was found between Sturch Bank and Coral View.

Refuge density showed no clear differences between sites (**Figure 4.3c**). Sturch Bank had the highest density of 10 cm deep refuges (48.04 refuges /m^2 ± 32.50), followed by Little Bight (42.25 refuges /m^2 ± 27.59) and Coral View (37.44 refuges /m^2 ± 27.29), though these differences were not significant, and all showed high levels of variation (Welch's ANOVA, $F_{2,93.47} = 1.49$, $p = 0.23$). Likewise, there were no significant differences in the densities of 5 cm (Welch's ANOVA, $F_{2,93.56} = 0.77$, $p = 0.46$) or 15 cm (Welch's ANOVA, $F_{2,92.92} = 1.54$, $p = 0.22$) refuges. The lack of significant differences in refuge densities meant that refuge density was not modelled against anti-predator behaviours.

There was a weakly negative association between transect rugosity and field of view ($\beta = -0.41$; 89% CrIs = -0.83 to 0.0; **Figure S4.2a**) and no clear association between rugosity and refuge density of 5 cm, 10 cm or 15 cm depth (CrIs overlapped 0; **Figure S4.2b**).

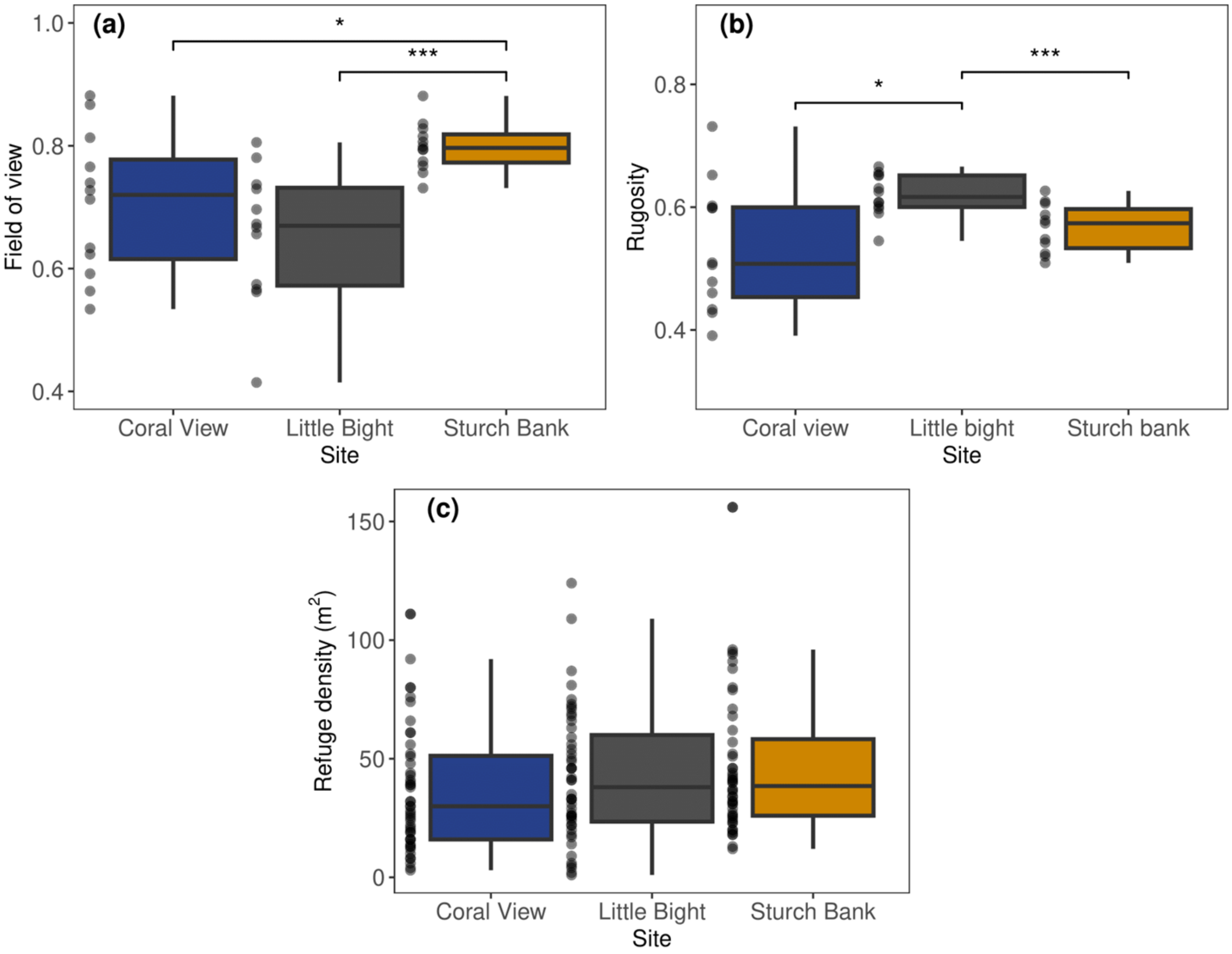


Figure 4.3 Structural complexity metrics across sites. **(a)** Field of view, **(b)** rugosity, and **(c)** 10 cm refuge density. Points represent raw value. Box plots represent medians, interquartile ranges and 1.5× interquartile ranges (Welch's ANOVA statistical significance thresholds: '***' = $p < 0.01$ and '*' = $p < 0.05$).

4.3.2 Anti-predator experiments

A total of 389 individuals were assessed for anti-predator responses across the three sites. Most parrotfish (98.5%) and wrasse (93.9%) tested were juveniles, whereas most damselfish (96.6%) were adults. There were no clear differences in body size within species across sites (One-Way ANOVAs, $p > 0.10$). In response to the model predator, damselfish primarily fled into a refuge (65.1%), whereas parrotfish (80.3%) and wrasse (86.6%) mostly fled into open water. There were no clear differences in these behaviours between sites (see supplementary materials).

The anti-predator responses of damselfish varied across sites and species, whereas those of wrasse and parrotfish remained consistent (CrIs overlapped 0). There was strong evidence that at Sturch Bank, *Stegastes adustus* had shorter flight initiation distances (FID) compared to Coral View and Little Bight (**Figure 4.4**). The FID difference between Coral View and Sturch Bank was 6.46 cm (89% highest posterior density intervals (HPDIs): 0.95 cm to 11.49 cm), equivalent to 79.46% of the species' average size. Similarly, the difference between Sturch Bank and Little Bight was 7.15 cm (89% HPDIs: 0.98 cm to 12.85 cm), representing 97.95% of the species' average size. In contrast, no clear evidence suggested that FID differed between sites for other damselfish species, nor did body length or group size significantly influence FID in any damselfish species (CrIs overlapped 0). Irrespective of site, larger wrasse and parrotfish had larger FIDs (wrasse: $\beta = 1.07$, 89% CrIs = 0.00 to 3.45; parrotfish: $\beta = 3.91$, 89% CrIs = 1.61 to 6.19).

There was strong evidence that *S. diencaeus* fled further into open water at Sturch Bank compared to the other two sites (**Figure 4.5**). At Sturch Bank, *S. diencaeus* fled an estimated 27.43 cm farther than at Little Bight and 21.96 cm farther than at Coral View (89% HPDIs: 13.74 cm to 40.87 cm and 9.23 cm to 33.82 cm, respectively). These distances correspond to 326.16% and 261.12% of the species' average body size. In contrast, there was no clear evidence of differences in open water escape distances across sites for any other species (CrIs overlapped 0). Larger parrotfish, however, consistently fled farther regardless of site or species ($\beta = 8.04$, 89% CrIs: 1.93 to 14.02).

When fleeing into a refuge, there damselfish responses were mixed (**Figure 4.6**). There was strong evidence that *S. diencaeus* fled farther at Sturch Bank than at Little Bight (estimated difference = 9.41 cm, 89% HPDIs: 1.74 cm to 16.81 cm; Figure 4.6), while *S. planifrons* fled shorter distances (estimated difference= -6.64 cm, 89% HPDIs: -13.42 cm to -0.53 cm).

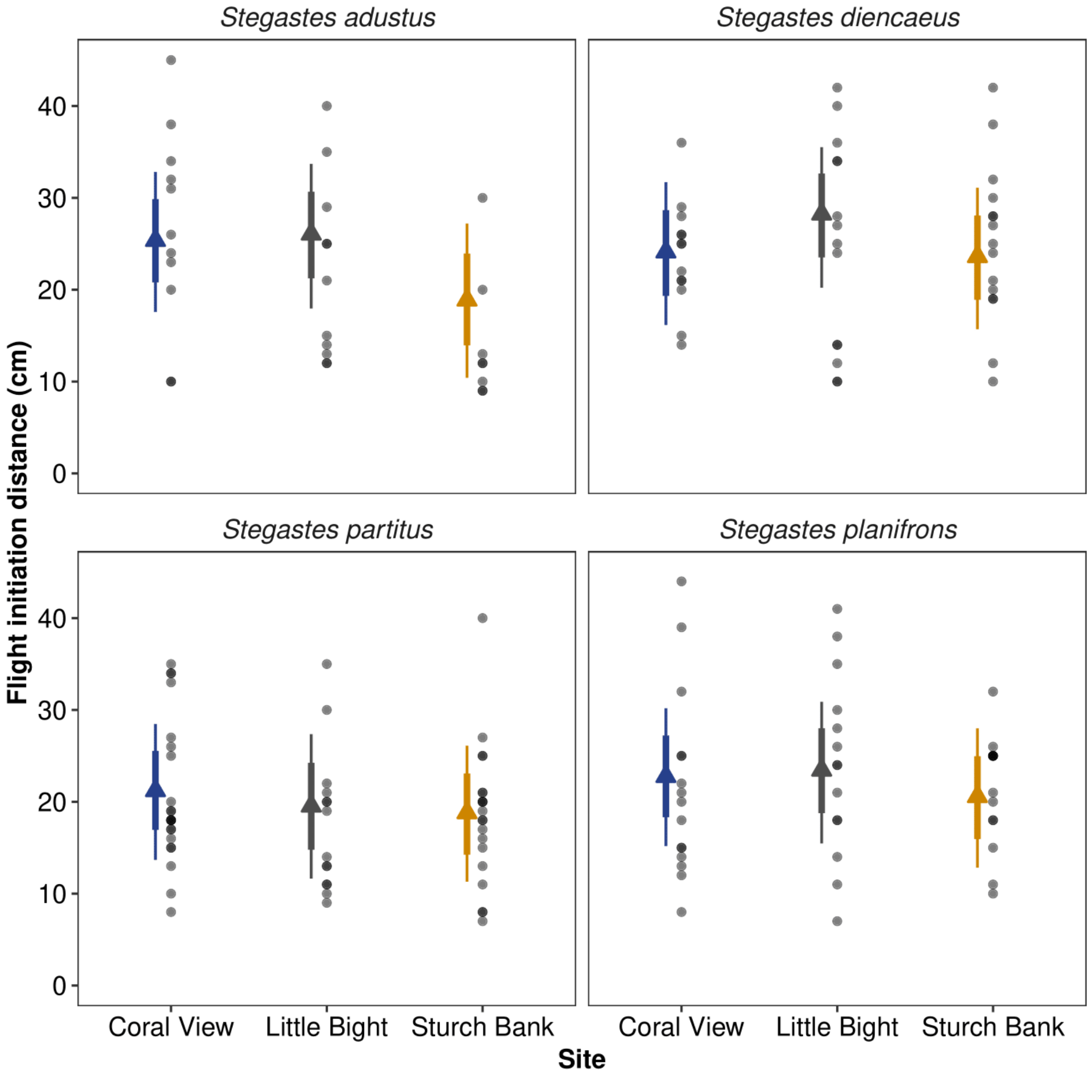


Figure 4.4 Flight initiation distance (FID) of damselfish species at each site. Triangles represent median estimates from Bayesian models using mean values of body length and group size. Lines represent 89 and 70% highest posterior density intervals (HPDIs). Grey points represent raw data.

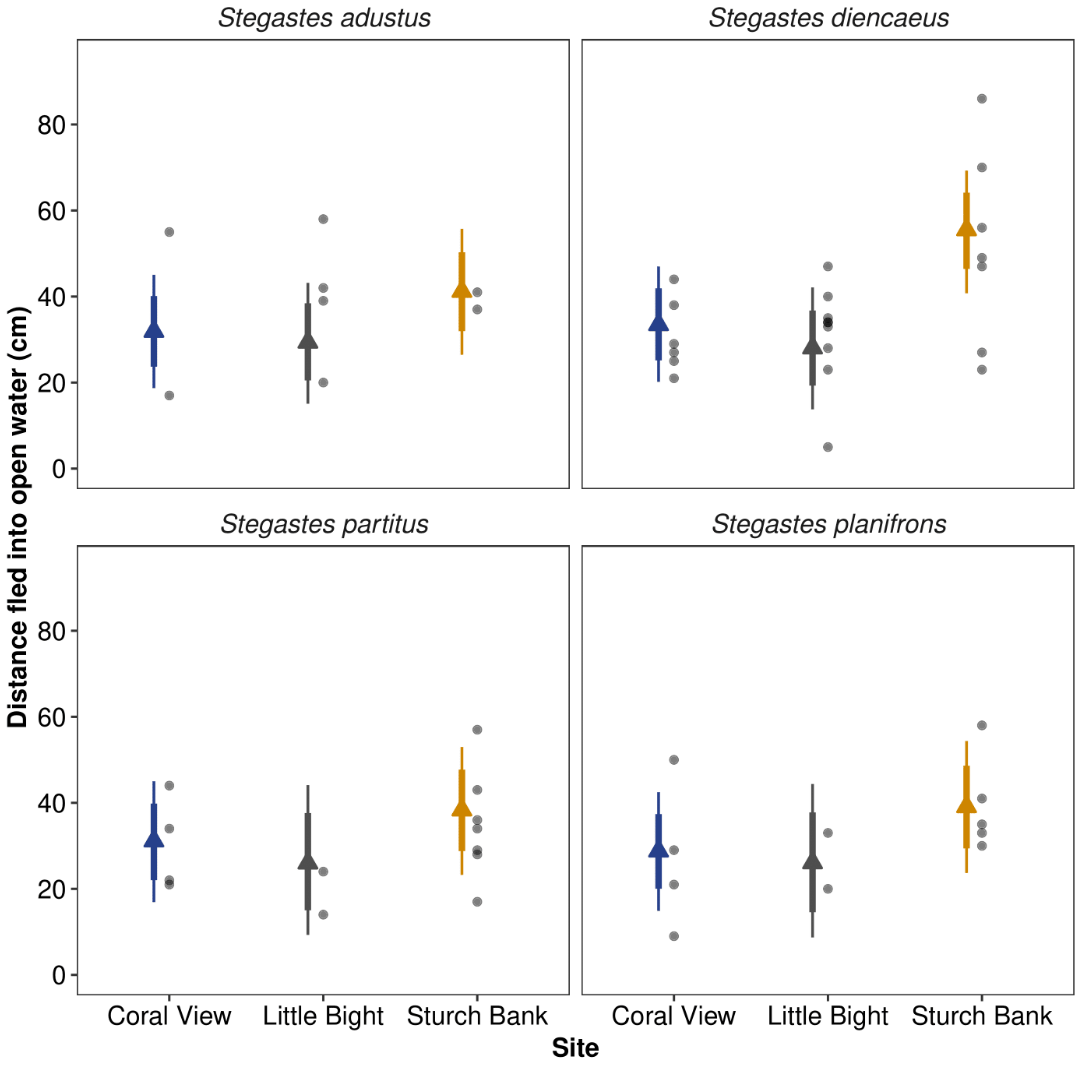


Figure 4.5 Distance fled into open water of damselfish species at each site. Triangles represent median estimates from Bayesian models using mean values of body length and group size. Lines represent 89 and 70% highest posterior density intervals (HPDIs). Grey points represent raw data.

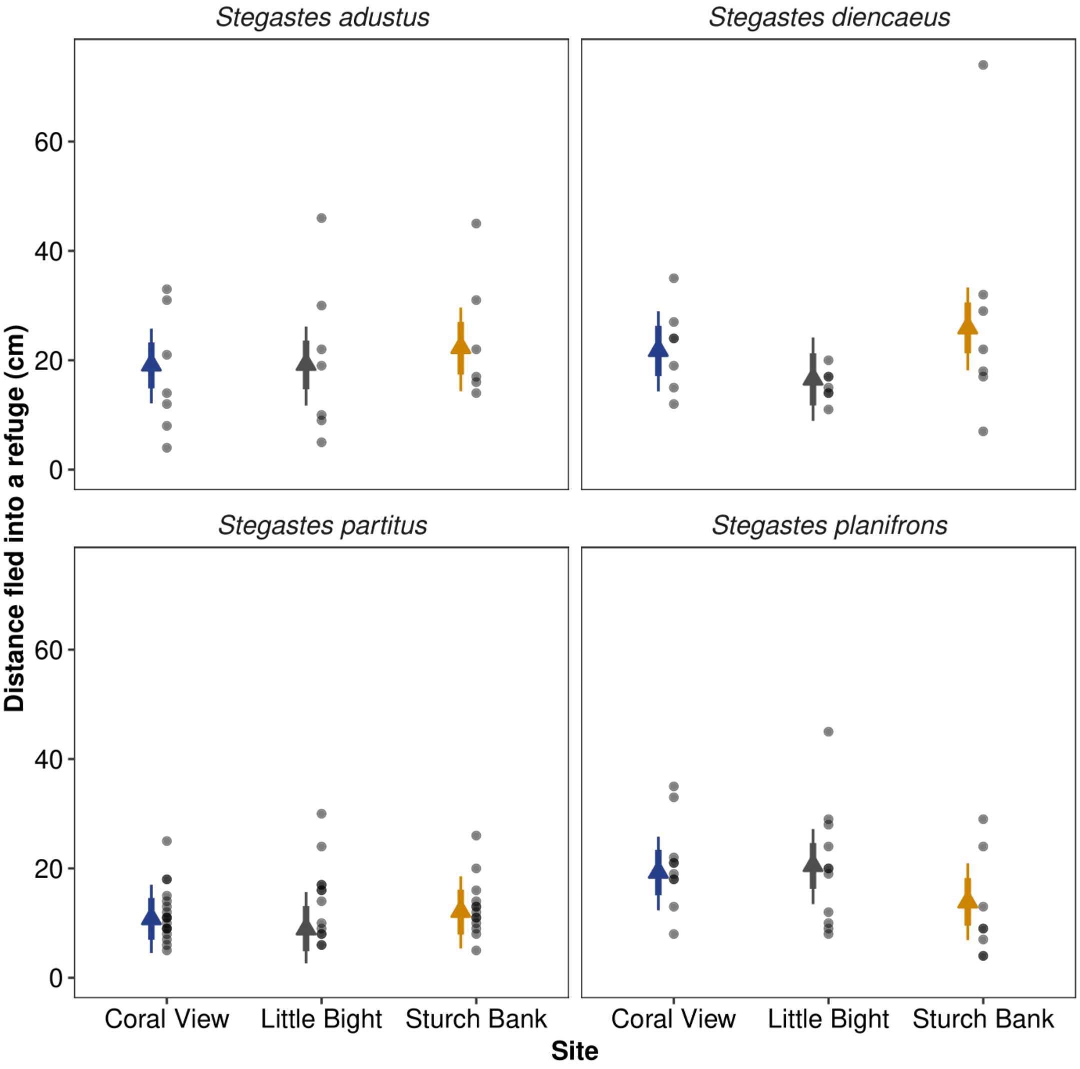


Figure 4.6 Distance fled into a refuge of damselfish species at each site. Triangles represent median estimates from Bayesian models using mean values of body length and group size. Lines represent 89 and 70% highest posterior density intervals (HPDIs). Grey points represent raw data.

4.4 Discussion

These results reveal that territorial damselfish species exhibit varied anti-predator responses between sites with significant differences in field of view and rugosity. *Stegastes adustus* had shorter FIDs at Sturch Bank, a site with significantly greater field of view, a result which does not align with the 'flush early and avoid the rush' hypothesis (Blumstein, 2010). Also, at Sturch Bank, *S. diencaeus* fled longer distances compared to at the other sites, despite showing no significant differences in FID. In contrast, *S. planifrons* fled shorter distances into a refuge at the site with a more restricted field of view. Interestingly, neither wrasse nor parrotfish species showed variation in their escape responses across sites, although body size was positively correlated with both FID and distance fled. Furthermore, the lack of significant differences in refuge availability between sites may reflect the ongoing decline in the fine-scale structural complexity of Caribbean coral reefs (Alvarez-Filip et al., 2009; Alvarez-Filip et al., 2011b). Overall, these findings highlight species-specific differences in anti-predator behaviours between sites of differing complexity, even within the same genus. By looking at structural metrics across entire sites, a scale not previously used to study behaviour, I offer a new perspective on how reef fish respond to habitat complexity.

The territorial farming damselfish *S. adustus* exhibited shorter FIDs at Sturch Bank, where the field of view was significantly greater than at the other two sites. According to the 'flush early and avoid the rush' hypothesis, FIDs should be longer in areas with greater visibility (Blumstein, 2010). However, this finding aligns more closely with what may be predicted by Optimal Escape Theory, as a greater field of view would allow *S. adustus* to detect predators earlier, which would reduce perceived risk and, consequently, reduce FID distance. As a species that invests significant time and energy in maintaining and defending turf algae patches, their primary food source, against competitors, S. *adustus* faces trade-offs between predator avoidance and resource protection (McDougall & Kramer, 2007; Sheppard et al., 2024). Fleeing too soon after detecting a predator could lead to resource loss, so delaying escape may be a cost-effective strategy to minimise this risk (Samia et al., 2013). Moreover, the lack of an body length-FID relationship in damselfish territories might be because these species have their own algal farms and a secure food source, so even smaller individuals do not need to forage more frequently or accept higher risks due to limited resources compared to larger individuals (Wahle, 1992). It remains unclear why only *S. adustus* exhibited differences in FID across sites, while other Stegastes species, which also farm and defend algal territories, did not. Although *S. adustus* are generally larger than the other species, there was no strong evidence that size influenced FID of damselfish. One possible explanation is that *S. adustus* eggs are more concealed compared to those of species like S. diencaeus, whose eggs are naturally more exposed (Little et al., 2013). In areas with greater visibility, they can detect predators earlier and may not need to flee as quickly, allowing them to remain near their eggs longer for protection.

The distance fled by territorial damselfish also differed at Sturch Bank. *S. diencaeus* invested more in their escape and fled further at Sturch Bank, which suggests that the increased field of view may heighten their perception of predation risk in open water. Once escape response is initiated, individuals may perceive a greater risk in open water due to increased visibility to predators, meaning they extend their fleeing distance to avoid exposure and reach a safer location or distance. In contrast, when fleeing into a refuge, *S. planifrons* fled shorter distances Sturch Bank. This could be because the greater field of view allowed *S. planifrons* to detect predators earlier, so begin move closer to their refuge before fully initiating flight. As a result, when they do flee, they are already closer to shelter, reducing the need for a prolonged escape. Lower field of view is strong predictor of *S. planifrons* abundance (González-Rivero et al., 2017) as it provides visual escape from predators. The shorter fleeing distance observed in sites with a greater field of view may reflect the fact that the increased visibility allows *S. planifrons* to detect threats earlier, giving them more time to reach shelter quickly and avoid the need for prolonged escapes.

These findings highlight species-specific differences in anti-predator behaviours between sites of differing complexity, even within the same genus. All damselfish species in this study are territorial and defend their algal patches from intruders. This requires constant vigilance to detect predators early to efficiently manage their energy resources, something that might be species-specific. These species-specific differences in relation to structural complexity could be due a host of biotic considerations not accounted for in the present study. For instance, species that rely more on crypsis may flee from a predator a shorter distance, particularly in environments with a greater field of view where they can detect predators earlier, while species that have less reliance on crypsis may exhibit quicker escape responses. While the damselfish species here do not rely on crypsis, they may differ in other aspects such as swimming or visual ability. Nevertheless, as reef complexity declines in the Caribbean, these results suggest that different species of damselfish may adopt varying anti-predator behaviours. As a result, shifts in the anti-predator behaviours of some species could alter competitive dynamics between damselfish species, potentially changing the 'landscape of fear' they create. This, in turn, could affect the grazing patterns and distribution of herbivores.

Differences in escape responses among Stegastes species appear to be most closely linked to field of view, as the site with the greatest field of view also exhibited the most variation in anti-predator behaviours. This suggests that visibility plays a key role in shaping escape responses. However, rugosity also varied across sites, with Little Bight exhibiting greater rugosity than both Sturch Bank and Coral View. Despite this variation, I found no clear difference in escape responses at Little Bight compared to the other sites. This is in contrast with previous studies that identified an inverse relationship between reef fish FID and rugosity (Burghart et al., 2023; Chan et al., 2019; Quadros et al., 2019). While both rugosity and field of view reflect elevation gradients across the reef, our results indicate that these factors are not strongly correlated. This highlights that relying solely on rugosity as a measure of structural complexity may miss ecologically relevant aspects of structure. Instead, incorporating multiple metrics such as field of view and refuge availability can provide a more comprehensive understanding of how habitat structure influences escape responses and predator-prey dynamics.

The anti-predator responses of wrasse and parrotfish species did not appear to differ between sites of differing complexity. Similar findings were reported by Stamoulis et al. (2019), who suggested that this lack of variation may be due to the roaming, opportunistic feeding strategies of these species. As continuous foragers, wrasse and parrotfish are constantly on the move and less reliant on specific structural features for protection or resource acquisition (Nunes et al., 2015). This mobility may reduce the influence of habitat structure on their escape responses compared to more site-attached species. Additionally, a positive correlation between body size and FID in both wrasse and parrotfish, supporting the asset-protection principle (Clark, 1994). However, this relationship remained consistent across sites, suggesting that the influence of body size on FID is a general trait in these taxa rather than one shaped by localised environmental differences.

Refuge density was similar across all three sites, likely reflecting the long-term decline in the fine-scale structural complexity of Caribbean coral reefs due to repeated bleaching events, disease outbreaks, and extreme weather (Alvarez-Filip et al., 2009; Alvarez-Filip et al., 2011b). The remaining hard structural complexity now stems from slow-growing massive corals like *Montastrea* spp., small weedy corals like *Porites* spp., and the eroded remnants of dead corals (Alvarez-Filip et al., 2011a). These contribute less to the 3D structure compared to the once common major reef-forming corals, *Acropora spp.* and *Orbicella spp.*, which are in decline across the region (Alvarez-Filip et al., 2011a; Perry et al., 2015). The reduced number of refuges impact small fish which rely on them for predator avoidance, while larger fish are less dependent on such complexity, potentially affecting smaller individuals' survival rates and overall fish community structure (Rogers et al., 2014). It is important to note that the lack of significant difference in refuge density among the sites in this study might be due to the large spatial scale of the 3D reconstructions, which may not have had fine enough resolution. This could mask localised variations in refuge density that are relevant to the immediate risk perception and escape behaviours of the study taxa. Additionally, photogrammetry does not accurately represent soft corals that sway in the water, such as gorgonians, which are common in the Caribbean. These soft features may still provide refuges and influence behaviours, but measuring them requires other techniques, such as *in-situ* counts, and could be a valuable area for future research.

It is important to recognise that species-specific associations with structural complexity may operate at different spatial scales (González-Rivero et al., 2017, 2017). In this study, I examined site-level differences, a broader spatial approach that has not been previously explored in relation to behaviours, providing a wider perspective on species' responses to habitat complexity. However, this approach introduced a spatial disconnect between the structural complexity measurements and the precise locations where behavioural observations were conducted. In contrast, previous studies have focused on measuring complexity at the exact sites of anti-predator experiments, offering insight into highly localised responses of reef fish (Nunes et al., 2015a; Quadros et al., 2019). Future research could integrate both approaches, combining fine-scale complexity assessments with broader site-level analyses. This would provide a more comprehensive understanding of how changes in habitat structure and behavioural traits influence predator-prey dynamics over a larger spatial scale, aiming to determine whether these patterns are consistent across all habitats or depend on specific contexts (Keith et al., 2023).

To elicit more natural responses, I used a model grouper predator. While this method is more realistic visually compared to a diver, prey also rely on other sensory cues. Sound, movement and olfaction can also play a critical roles in how fish perceive threats and therefore influence anti-predator responses (Ladich, 2019; McCormick & Manassa, 2008). Diver presence, such as bubbles from SCUBA equipment and diver movement, may contribute to altered behaviours (Branconi et al., 2019; Pereira et al., 2016). While I controlled for these factors as much as possible by approaching individual fish at consistent angles and using a pole-mounted model, there is still potential for unintended influence on escape behaviour. Future research could further refine these methodologies by incorporating multi-sensory predator cues or exploring responses against model predators versus inanimate objects.

Altered habitat structure is being observed across a wide range of habitats in all biomes (Ehbrecht et al., 2021; Ferrari et al., 2016). These changes may include the loss of structural features (Alvarez-Filip et al., 2009; Melis et al., 2019) or increased complexity through ecosystem restoration initiatives in terrestrial and aquatic environments (Chamberlain et al., 2021; Loke et al., 2015; Yanovski & Abelson, 2019). Such changes will inevitably influence species' abundance, distributions and predator-prey interactions. This study highlights the nuanced relationship between structural complexity and anti-predator behaviour of reef fish. While some responses align with theories such as optimal escape theory, others do not. Therefore, when applying these theories, it is important to consider the relevant aspects of complexity and the ecology of individual species. Additionally, broader site-level metrics should be used alongside more localised experiments to gain a better understanding of how changes in structural complexity influence predator-prey dynamics on larger spatial scales.

General conclusion

5.1 Overview

My thesis furthers our understanding of the role of refuges in coral reef ecosystems and biological invasions. By synthesising the literature on refuges in biological invasions, I first demonstrate that refuge-mediated processes are widely reported in shaping interactions between native and non-native species, with similar patterns observed across various biomes. Second, I show that deeper habitats may not universally act as refuges for shallow-water reef fish communities. In fact, at my study site, upper-MCE fish communities exhibited more significant changes over time compared to their shallower counterparts, which is not consistent with predictions of the deep reef refugia hypothesis. Third, I find no clear evidence that invasive lionfish undergo ontogenetic niche shifts across depths, suggesting that culling in shallow waters is unlikely to affect deeper populations. This implies that MCEs may serve as refuges from shallow-water management efforts for controlling this invasive species. Finally, I show that some species of reef fish may adjust their anti-predator behaviour based on site-level structural complexity and that incorporating additional habitat metrics beyond rugosity can offer deeper insights into predator-prey behaviours. Overall, this research provides new insights into the direct and indirect effects of refuges on coral reef communities and biological invasions, emphasising the need to incorporate refuges into future conservation strategies.

When assessing depths refuges on reefs, perhaps the most important point to consider is that depth is not an environmental factor on its own. Rather, it is a proxy for changes in irradiance, temperature, wave energy, and habitat structure (Diaz et al., 2023a; Lesser et al., 2009). Therefore, using depth alone to assess refuge potential will inevitably overlook the factors driving community stability across depth and oversimplify what is in fact a dynamic variable. For instance, **Chapter 2** suggests that mesophotic fish communities at sites with more continuous mesophotic habitats and greater maximum depths may experience less variation over time. More connected habitats enable species to move freely across the depth gradient, accessing resources like shelter and food, which fosters the development of deeper communities with similar taxonomic and functional diversity as shallower reefs, thereby increasing their stability and refuge potential (Abesamis et al., 2018; Slattery et al., 2018). Studivan and Voss (2018) found that *Montastraea cavernosa* had greater refuge potential where continuous hard substrate extended into deeper waters, supporting the deep reef refugia hypothesis by allowing individuals to establish at greater depths, where they could survive disturbances and later repopulate shallower zones. However, in areas with fragmented vertical habitats or limited maximum depth, this connectivity weakens, preventing the establishment of deeper individuals and reducing the refuge potential of greater depths (Serrano et al., 2014). In a similar sense, at Raggedy Cay, where more continuous vertical habitat exists, lionfish appeared to utilise greater depths for feeding (**Chapter 3**). At this site, deeper-dwelling lionfish could be missed during shallow-water culling efforts, suggesting that at this site, increased depth may act as a refuge from management strategies (Andradi-Brown, 2019). At other sites with more fragmented vertical habitats and shallower maximum depths, lionfish may be unable to move to greater depths as they grow, meaning deeper waters will not provide refuge from culling.

A similar concept can be found in terrestrial systems. In mountainous environments, higher elevations are sometimes considered refuges for plants and animals facing stressors in lowland areas, such as deforestation and climatic extremes (Ekberzade et al., 2024; Hardy et al., 2010; Selwood & Zimmer, 2020). However, the capacity of these high-altitude areas to serve as effective refuges depends on the amount of available land at higher elevations and the degree of habitat connectivity between lowland and highland regions, which facilitates species movement (Hardy et al., 2010; Kleijn et al., 2020). This highlights the main limitation in relying solely on one environmental factor, such as altitude or depth, to evaluate an areas refuge potential. Instead, the effectiveness of a refuge is often determined by a complex interaction of multiple factors, including habitat structure, connectivity, resource availability, and the mobility of species (Berryman & Hawkins, 2006; Selwood & Zimmer, 2020).

To mitigate the effects of anthropogenic stressors on ecosystems, prioritising the conservation and management of refuges areas could be an effective strategy (Selwood & Zimmer, 2020). Heterogeneous environments offer a range of abiotic conditions that allow populations or individuals to find refuge from both biotic and abiotic stressors (**Chapters 1** and **4**). Therefore, protected areas should encompass diverse habitats to give species the opportunity to persist and recover, increasing their ability to withstand and adapt to environmental challenges (Chretien & Chapman, 2016). Refuges should not be conserved in isolation but integrated into a broader network of interconnected habitats, enabling species to move, retreat during periods of stress, and expand when conditions improve (Boon et al., 2023; Shaw, 2016). Connectivity between areas is therefore vital, as it supports recolonisation and enhances population viability (Selwood & Zimmer, 2020). Yet, many conservation policies currently treat habitats as isolated units, such as coral reefs or MCEs, rather than as part of an interconnected system (Erdős et al., 2018). While individual habitats have their own intrinsic value, protecting the full environmental mosaic is essential to ensure the survival of species and the maintenance of ecosystem functions in the face of rapid environmental change.

5.2 Future research directions

Continuous benthic habitat spanning shallow and mesophotic reefs may contribute to the stability of coral reef communities (**Chapter 2**). Gaining a deeper understanding of how habitat structure and connectivity across different depths influence community stability, particularly at mesophotic levels, could provide valuable insights into coral reef resilience (Slattery et al., 2024). To achieve this, integrating technologies such as 3D photogrammetry and ROVs to allow large scale mapping at depth alongside fish community surveys could be useful. These methods can help identify areas where deeper reefs offer greater refuge potential, aiding in the strategic planning of marine protected areas. Nevertheless, it is crucial to recognise that mesophotic habitats are not only important as potential refuges but are also unique ecosystems in their own right, deserving focused conservation efforts (Rocha et al., 2018).

Many ecosystems, including coral reefs, have experienced prolonged declines in structural complexity (Alvarez-Filip et al., 2009; Alvarez-Filip, Gill, et al., 2011a). As a result, restoration projects have become increasingly common that aim to restore structural features and promote biodiversity (Boström-Einarsson et al., 2020). In coral reef restoration for example, this is often achieved by adding wire frames or concrete blocks with young corals attached to them, to the benthos (Boström-Einarsson et al., 2020). However, this approach can overlook how the introduced structures influence species distribution and behaviour. Simply increasing complexity without considering species interactions may inadvertently attract pests (Cano et al., 2021) or non-native species (Boon et al., 2023; Bulleri & Airoldi, 2005). Therefore, effective restoration requires understanding which structural features best mediate key species interactions, such as predator-prey (**Chapter 4**) or competitive dynamics. For instance, restoring a reef at a uniform level could create a wide, open field of view, altering predator avoidance behaviours in some, but not all, species (**Chapter 4**). This in turn could affect overall species dynamics and potentially reduce the effectiveness of the restoration effort.

Lastly, the term 'refuge' is used broadly and interpreted in various ways in literature and policy. In this thesis, I used the definition established by Keppel et al. (2012), but I believe there is a need for more precise descriptions when studying and reporting refuges. In the context of depth refuges on reefs, Bongaerts & Smith (2019) developed a framework which distinguished refuges in terms of level of protection and the timescale over which they offer this protection. Like Keppel et al. (2012), Bongaerts & Smith (2019) described a ‘refuge’ as providing short-term shelter from disturbances, and a ‘refugium’ as offering much longer-term protection. They also propose designating certain refuges as ‘resilience areas’, which are places that support communities capable of remaining resilient over the long term, either through resistance to disturbances or rapid recovery. Additionally, they advocate for terms like ‘reseeding potential’, referring to refuge populations that contribute recruits to help restore disturbed areas, and ‘local persistence areas’, which protect species without necessarily aiding population recovery. These concepts and terms are clearly applicable to all environments and ecological contexts, providing a more accurate way to identify and define the specific functions of what we currently refer to broadly as refuges. Providing clearer descriptions and established definitions like these could help guide more effective conservation practices and enhance clarity for policymakers.

5.3 Concluding remarks

In conclusion, my thesis advances our understanding of the role that refuges play in coral reef ecosystems and biological invasions. By examining refuge functions across all ecological levels, from individuals to communities, my thesis highlights how this fundamental ecological feature influences species interactions and promotes community stability. I advocate for more precise descriptions when studying and reporting refuges, as well as for greater recognition of their capacity to improve the effectiveness of conservation initiatives.

References

Aben, J., Pellikka, P., & Travis, J. M. J. (2018). A call for viewshed ecology: Advancing our understanding of the ecology of information through viewshed analysis. *Methods in Ecology and Evolution*, *9*(3), 624–633. https://doi.org/10.1111/2041-210X.12902

Abesamis, R. A., Langlois, T., Birt, M., Thillainath, E., Bucol, A. A., Arceo, H. O., & Russ, G. R. (2018). Benthic habitat and fish assemblage structure from shallow to mesophotic depths in a storm-impacted marine protected area. *Coral Reefs*, *37*(1), 81–97. https://doi.org/10.1007/s00338-017-1635-0

Acero P., A., Bustos-Montes, D., Pabón Quintero, P., Polo-Silva, C. J., & Muñoz, A. S. (2019). Feeding Habits of Pterois volitans: A Real Threat to Caribbean Coral Reef Biodiversity. In C. Makowski & C. W. Finkl (Eds.), *Impacts of Invasive Species on Coastal Environments: Coasts in Crisis* (pp. 269–314). Springer International Publishing. https://doi.org/10.1007/978-3-319-91382-7_8

AgiSoft. (2022). PhotoScan Professional, V 1.8.4. See http://www.agisoft.com/downloads/installer/

Albins, M. A. (2015). Invasive Pacific lionfish Pterois volitans reduce abundance and species richness of native Bahamian coral-reef fishes. *Marine Ecology Progress Series*, *522*, 231–243. https://doi.org/10.3354/meps11159

Albins, M. A., & Hixon, M. A. (2013). Worst case scenario: Potential long-term effects of invasive predatory lionfish (Pterois volitans) on Atlantic and Caribbean coral-reef communities. *Environmental Biology of Fishes*, *96*(10), 1151–1157. https://doi.org/10.1007/s10641-011-9795-1

Allan, B. F., Dutra, H. P., Goessling, L. S., Barnett, K., Chase, J. M., Marquis, R. J., Pang, G., Storch, G. A., Thach, R. E., & Orrock, J. L. (2010). Invasive honeysuckle eradication reduces tick-borne disease risk by altering host dynamics. *Proceedings of the National Academy of Sciences of the United States of America*, 107(43), 18523-18527.

Alvarez-Filip, L., Côté, I. M., Gill, J. A., Watkinson, A. R., & Dulvy, N. K. (2011a). Region-wide temporal and spatial variation in Caribbean reef architecture: Is coral cover the whole story? *Global Change Biology*, *17*(7), 2470–2477. https://doi.org/10.1111/j.1365-2486.2010.02385.x

Alvarez-Filip, L., Dulvy, N. K., Gill, J. A., Côté, I. M., & Watkinson, A. R. (2009). Flattening of Caribbean coral reefs: Region-wide declines in architectural complexity. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1669), 3019–3025. https://doi.org/10.1098/rspb.2009.0339

Alvarez-Filip, L., Gill, J. A., Dulvy, N. K., Perry, A. L., Watkinson, A. R., & Côté, I. M. (2011b). Drivers of region-wide declines in architectural complexity on Caribbean reefs. *Coral Reefs*, *30*(4), 1051–1060. https://doi.org/10.1007/s00338-011-0795-6

Alvarez-Filip, L., Paddack, M. J., Collen, B., Robertson, D. R., & Côté, I. M. (2015). Simplification of Caribbean Reef-Fish Assemblages over Decades of Coral Reef Degradation. *PLOS ONE*, *10*(4), e0126004. https://doi.org/10.1371/journal.pone.0126004

Andradi-Brown, D. A. (2019). Invasive Lionfish (Pterois volitans and P. miles): Distribution, Impact, and Management. In Y. Loya, K. A. Puglise, & T. C. L. Bridge (Eds.), *Mesophotic Coral Ecosystems* (pp. 931–941). Springer International Publishing. https://doi.org/10.1007/978-3-319-92735-0_48

Andradi-Brown, D. A., Beer, A. J. E., Colin, L., Hastuti, Head, C. E. I., Hidayat, N. I., Lindfield, S. J., Mitchell, C. R., Pada, D. N., Piesinger, N. M., Purwanto, & Ahmadia, G. N.

(2021). Highly diverse mesophotic reef fish communities in Raja Ampat, West Papua. *Coral Reefs*, *40*(1), 111–130. https://doi.org/10.1007/s00338-020-02020-7

Andradi-Brown, D. A., Gress, E., Wright, G., Exton, D. A., & Rogers, A. D. (2016). Reef Fish Community Biomass and Trophic Structure Changes across Shallow to Upper-Mesophotic Reefs in the Mesoamerican Barrier Reef, Caribbean. *PLOS ONE*, *11*(6), e0156641. https://doi.org/10.1371/journal.pone.0156641

Andradi-Brown, D. A., Grey, R., Hendrix, A., Hitchner, D., Hunt, C. L., Gress, E., Madej, K., Parry, R. L., Régnier-McKellar, C., Jones, O. P., Arteaga, M., Izaguirre, A. P., Rogers, A. D., & Exton, D. A. (2017a). Depth-dependent effects of culling—Do mesophotic lionfish populations undermine current management? *Royal Society Open Science*, *4*(5), 170027. https://doi.org/10.1098/rsos.170027

Andradi-Brown, D. A., Vermeij, M. J. A., Slattery, M., Lesser, M., Bejarano, I., Appeldoorn, R., Goodbody-Gringley, G., Chequer, A. D., Pitt, J. M., Eddy, C., Smith, S. R., Brokovich, E., Pinheiro, H. T., Jessup, M. E., Shepherd, B., Rocha, L. A., Curtis-Quick, J., Eyal, G., Noyes, T. J., … Exton, D. A. (2017b). Large-scale invasion of western Atlantic mesophotic reefs by lionfish potentially undermines culling-based management. *Biological Invasions*, *19*(3), 939–954. https://doi.org/10.1007/s10530-016-1358-0

Apte, S., Holland, B. S., Godwin, L. S., & Gardner, J. P. (2000). Jumping ship: A stepping stone event mediating transfer of a non-indigenous species via a potentially unsuitable environment. *Biological Invasions*, *2*(1), 75–79

Appeldoorn, R., Ballantine, D., Bejarano, I., Carlo, M., Nemeth, M., Otero, E., Pagan, F., Ruiz, H., Schizas, N., Sherman, C., & Weil, E. (2016). Mesophotic coral ecosystems under anthropogenic stress: A case study at Ponce, Puerto Rico. *Coral Reefs*, *35*(1), 63–75. https://doi.org/10.1007/s00338-015-1360-5

Arnold, S. N., Steneck, R. S., & Mumby, P. J. (2010). Running the gauntlet: Inhibitory effects of algal turfs on the processes of coral recruitment. *Marine Ecology Progress Series*, *414*, 91–105. https://doi.org/10.3354/meps08724

Ashcroft, M. B. (2010). Identifying refugia from climate change. *Journal of Biogeography*, *37*(8), 1407–1413. https://doi.org/10.1111/j.1365-2699.2010.02300.x

Assis, J., Coelho, N. C., Lamy, T., Valero, M., Alberto, F., & Serrão, E. Á. (2016). Deep reefs are climatic refugia for genetic diversity of marine forests. *Journal of Biogeography*, *43*(4), 833–844. https://doi.org/10.1111/jbi.12677

Aston, E. A., Duce, S., Hoey, A. S., & Ferrari, R. (2022). A Protocol for Extracting Structural Metrics From 3D Reconstructions of Corals. *Frontiers in Marine Science*, *9*. https://doi.org/10.3389/fmars.2022.854395

Astorg, L., Sanderson, S., Côté-Gravel, V., Sorbara, F., Windle, M. J., Hendry, A. P., & Derry, A. M. (2021). Different refuge types dampen exotic invasion and enhance diversity at the whole ecosystem scale in a heterogeneous river system. *Biological Invasions*, *23*(2), 443–460

August, P. V. (1983). The Role of Habitat Complexity and Heterogeneity in Structuring Tropical Mammal Communities. *Ecology*, *64*(6), 1495–1507. https://doi.org/10.2307/1937504

Baldwin, C. C., Tornabene, L., & Robertson, D. R. (2018). Below the Mesophotic. *Scientific Reports*, *8*(1), 4920. https://doi.org/10.1038/s41598-018-23067-1

Ballew, N. G., Bacheler, N. M., Kellison, G. T., & Schueller, A. M. (2016). Invasive lionfish reduce native fish abundance on a regional scale. *Scientific Reports*, *6*(1), 32169. https://doi.org/10.1038/srep32169

Ban, S. S., Graham, N. A. J., & Connolly, S. R. (2014). Evidence for multiple stressor interactions and effects on coral reefs. *Global Change Biology*, *20*(3), 681–697. https://doi.org/10.1111/gcb.12453

Barbour, A. B., Allen, M. S., Frazer, T. K., & Sherman, K. D. (2011). Evaluating the Potential Efficacy of Invasive Lionfish (Pterois volitans) Removals. *PLOS ONE*, *6*(5), e19666. https://doi.org/10.1371/journal.pone.0019666

Bartowitz, K. J., & Orrock, J. L. (2016). Invasive exotic shrub (*Rhamnus cathartica*) alters the timing and magnitude of post-dispersal seed predation of native and exotic species. Journal of Vegetation *Science*, *27*(4), 789–799

Beekey, M. A., McCabe, D. J., & Marsden, J. E. (2004). Zebra mussels affect benthic predator foraging success and habitat choice on soft sediments. *Oecologia*, *141*(1), 164–170

Bell-Tilcock, M., Jeffres, C. A., Rypel, A. L., Sommer, T. R., Katz, J. V. E., Whitman, G., & Johnson, R. C. (2021). Advancing diet reconstruction in fish eye lenses. *Methods in Ecology and Evolution*, *12*(3), 449–457. https://doi.org/10.1111/2041-210X.13543

Bellwood, D. R., Hoey, A. S., Ackerman, J. L., & Depczynski, M. (2006). Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. *Global Change Biology*, *12*(9), 1587–1594. https://doi.org/10.1111/j.1365-2486.2006.01204.x

Bellwood, D. R., & Hughes, T. P. (2001). Regional-Scale Assembly Rules and Biodiversity of Coral Reefs. *Science*, *292*(5521), 1532–1535. https://doi.org/10.1126/science.1058635

Bergey, E. A. (2019). Dispersal of a non-native land snail across a residential area is modified by yard management and movement barriers. *Urban Ecosystem*, *22*(2), 325–334

Berryman, A. A., & Hawkins, B. A. (2006). The Refuge as an Integrating Concept in Ecology and Evolution. *Oikos*, *115*(1), 192–196.

Blackburn, T. M., Essl, F., Evans, T., Hulme, P. E., Jeschke, J. M., Kühn, I., Kumschick, S., Marková, Z., Mrugała, A., Nentwig, W., Pergl, J., Pyšek, P., Rabitsch, W., Ricciardi, A., Richardson, D. M., Sendek, A., Vilà, M., Wilson, J. R. U., Winter, M., … Bacher, S. (2014). A Unified Classification of Alien Species Based on the Magnitude of their Environmental Impacts. *PLOS Biology*, *12*(5), e1001850. https://doi.org/10.1371/journal.pbio.1001850

Blackburn, T. M., Pyšek, P., Bacher, S., Carlton, J. T., Duncan, R. P., Jarošík, V., Wilson, J. R., & Richardson, D. M. (2011). A proposed unified framework for biological invasions. *Trends in Ecology & Evolution, 26*(7), 333–339

Blumstein, D. T. (2003). Flight-Initiation Distance in Birds Is Dependent on Intruder Starting Distance. *The Journal of Wildlife Management*, *67*(4), 852–857. https://doi.org/10.2307/3802692

Blumstein, D. T. (2010). Flush early and avoid the rush: A general rule of antipredator behavior? *Behavioral Ecology*, *21*(3), 440–442. https://doi.org/10.1093/beheco/arq030

Bongaerts, P., Ridgway, T., Sampayo, E. M., & Hoegh-Guldberg, O. (2010). Assessing the ‘deep reef refugia’ hypothesis: Focus on Caribbean reefs. *Coral Reefs*, *29*(2), 309–327. https://doi.org/10.1007/s00338-009-0581-x

Bongaerts, P., Riginos, C., Brunner, R., Englebert, N., Smith, S. R., & Hoegh-Guldberg, O. (2017). Deep reefs are not universal refuges: Reseeding potential varies among coral species. *Science Advances*, *3*(2), e1602373. https://doi.org/10.1126/sciadv.1602373

Bongaerts, P., & Smith, T. B. (2019). Beyond the “Deep Reef Refuge” Hypothesis: A Conceptual Framework to Characterize Persistence at Depth. In Y. Loya, K. A. Puglise, & T. C. L. Bridge (Eds.), *Mesophotic Coral Ecosystems* (pp. 881–895). Springer International Publishing. https://doi.org/10.1007/978-3-319-92735-0_45

Boon, J. S., Keith, S. A., Exton, D. A., & Field, R. (2023). The role of refuges in biological invasions: A systematic review. *Global Ecology and Biogeography*, *32*(8), 1244–1271. https://doi.org/10.1111/geb.13701

Boström-Einarsson, L., Babcock, R. C., Bayraktarov, E., Ceccarelli, D., Cook, N., Ferse, S. C. A., Hancock, B., Harrison, P., Hein, M., Shaver, E., Smith, A., Suggett, D., Stewart-Sinclair, P. J., Vardi, T., & McLeod, I. M. (2020). Coral restoration – A systematic review of current methods, successes, failures and future directions. *PLOS ONE*, *15*(1), e0226631. https://doi.org/10.1371/journal.pone.0226631

Botts, P. S., Patterson, B. A., & Schloesser, D. W. (1996). Zebra mussel effects on benthic invertebrates: Physical or biotic? J*ournal of the North American Benthological Society*, *15*(2), 179–184

Bowen, G. J., West, J. B., & Dawson, T. E. (2010). Isoscapes in a Rapidly Changing and Increasingly Interconnected World. In J. B. West, G. J. Bowen, T. E. Dawson, & K. P. Tu (Eds.), *Isoscapes: Understanding movement, pattern, and process on Earth through isotope mapping* (pp. 425–432). Springer Netherlands. https://doi.org/10.1007/978-90-481-3354-3_20

Braga, R. R., Gómez-Aparicio, L., Heger, T., Vitule, J. R. S., & Jeschke, J. M. (2018). Structuring evidence for invasional meltdown: Broad support but with biases and gaps. *Biological Invasions*, *20,* 923–936

Braidwood, D. W., Taggart, M. A., Smith, M., & Andersen, R. (2018). Translocations, conservation, and climate change: Use of restoration sites as protorefuges and protorefugia. *Restoration Ecology*, *26*(1), 20–28. https://doi.org/10.1111/rec.12642

Brazeau, D. A., Lesser, M. P., & Slattery, M. (2013). Genetic Structure in the Coral, Montastraea cavernosa: Assessing Genetic Differentiation among and within Mesophotic Reefs. *PLOS ONE*, *8*(5), e65845. https://doi.org/10.1371/journal.pone.0065845

Branconi, R., Wong, M. Y., & Buston, P. M. (2019). Comparison of efficiency of direct observations by scuba diver and indirect observations via video camera for measuring reef-fish behaviour. *Journal of Fish Biology*, *94*(3), 489-497.

Broekhuis, F., Cozzi, G., Valeix, M., McNutt, J. W., & Macdonald, D. W. (2013). Risk avoidance in sympatric large carnivores: Reactive or predictive? *Journal of Animal Ecology*, *82*(5), 1098–1105

Brown, B. E. (1997). Coral bleaching: Causes and consequences. *Coral Reefs*, *16*(1), S129–S138. https://doi.org/10.1007/s003380050249

Brown, C., Burslem, D. F. R. P., Illian, J. B., Bao, L., Brockelman, W., Cao, M., Chang, L. W., Dattaraja, H. S., Davies, S., Gunatilleke, C. V. S., Gunatilleke, I. a. U. N., Huang, J., Kassim, A. R., LaFrankie, J. V., Lian, J., Lin, L., Ma, K., Mi, X., Nathalang, A., … Law, R. (2013). Multispecies coexistence of trees in tropical forests: Spatial signals of topographic niche differentiation increase with environmental heterogeneity. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1764), 20130502. https://doi.org/10.1098/rspb.2013.0502

Bruno, J. F., Sweatman, H., Precht, W. F., Selig, E. R., & Schutte, V. G. W. (2009). Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. *Ecology*, *90*(6), 1478–1484. https://doi.org/10.1890/08-1781.1

Bulleri, F., & Airoldi, L. (2005). Artificial marine structures facilitate the spread of a non-indigenous green alga, Codium fragile ssp tomentosoides, in the north Adriatic Sea. *JOURNAL OF APPLIED ECOLOGY*, *42*(6), 1063–1072. https://doi.org/10.1111/j.1365-2664.2005.01096.x

Burghart, E., Mar, M., Rivera, S. G., Zepecki, C., & Blumstein, D. T. (2023). How does damselfish risk assessment vary with increased predator and shoal size? *Journal of Experimental Marine Biology and Ecology*, *561*, 151871. https://doi.org/10.1016/j.jembe.2023.151871

Burlakova, L. E., Karatayev, A. Y., & Karatayev, V. A. (2012). Invasive mussels induce community changes by increasing habitat complexity. *Hydrobiologia*, *685*, 121–134

Bürkner, P.-C. (2018). Advanced Bayesian Multilevel Modeling with the R Package brms. *The R Journal*, *10*(1), 395–411.

Cadotte, M. W., Carscadden, K., & Mirotchnick, N. (2011). Beyond species: Functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, *48*(5), 1079–1087. https://doi.org/10.1111/j.1365-2664.2011.02048.x

Caley, M. J., & St John, J. (1996). Refuge Availability Structures Assemblages of Tropical Reef Fishes. *Journal of Animal Ecology*, *65*(4), 414–428. https://doi.org/10.2307/5777

Camp, M. J., Rachlow, J. L., Woods, B. A., Johnson, T. R., & Shipley, L. A. (2013). Examining functional components of cover: The relationship between concealment and visibility in shrub-steppe habitat. *Ecosphere*, *4*(2), art19. https://doi.org/10.1890/ES12-00114.1

Cano, I., Sellares-Blasco, R. I., Lefcheck, J. S., Villalpando, M. F., & Croquer, A. (2021). Effects of herbivory by the urchin *Diadema antillarum* on early restoration success of the coral *Acropora cervicornis* in the central Caribbean. *Journal of Experimental Marine Biology and Ecology*, *539*, 151541. https://doi.org/10.1016/j.jembe.2021.151541

Chamberlain, C. P., Kane, V. R., & Case, M. J. (2021). Accelerating the development of structural complexity: Lidar analysis supports restoration as a tool in coastal Pacific Northwest forests. *Forest Ecology and Management*, *500*, 119641. https://doi.org/10.1016/j.foreco.2021.119641

Chan, Y., Lo, S., Quan, A., & Blumstein, D. T. (2019). Ontogenetic shifts in perceptions of safety along structural complexity gradients in a territorial damselfish. *Current Zoology*, *65*(2), 183–188. https://doi.org/10.1093/cz/zoy091

Chao, A., Chiu, C.-H., Wu, S.-H., Huang, C.-L., & Lin, Y.-C. (2019). Comparing two classes of alpha diversities and their corresponding beta and (dis)similarity measures, with an application to the Formosan sika deer Cervus nippon taiouanus reintroduction programme. *Methods in Ecology and Evolution*, *10*(8), 1286–1297. https://doi.org/10.1111/2041-210X.13233

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., & Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs*, *84*(1), 45–67. https://doi.org/10.1890/13-0133.1

Chao, A., Henderson, P. A., Chiu, C.-H., Moyes, F., Hu, K.-H., Dornelas, M., & Magurran, A. E. (2021). Measuring temporal change in alpha diversity: A framework integrating taxonomic, phylogenetic and functional diversity and the iNEXT.3D standardization. *Methods in Ecology and Evolution*, *12*(10), 1926–1940. https://doi.org/10.1111/2041-210X.13682

Chao, A., & Jost, L. (2012). Coverage-based rarefaction and extrapolation: Standardizing samples by completeness rather than size. *Ecology*, *93*(12), 2533–2547. https://doi.org/10.1890/11-1952.1

Chao, A., Thorn, S., Chiu, C.-H., Moyes, F., Hu, K.-H., Chazdon, R. L., Wu, J., Magnago, L. F. S., Dornelas, M., Zelený, D., Colwell, R. K., & Magurran, A. E. (2023). Rarefaction and extrapolation with beta diversity under a framework of Hill numbers: The iNEXT.beta3D standardization. *Ecological Monographs*, *93*(4), e1588. https://doi.org/10.1002/ecm.1588

Chapman, D., Purse, B. V., Roy, H. E., & Bullock, J. M. (2017). Global trade networks determine the distribution of invasive non-native species. *Global Ecology and Biogeography*, *26*(8), 907–917. https://doi.org/10.1111/geb.12599

Chen, F., Chen, L., & Xie, X. (2009). On a Leslie–Gower predator–prey model incorporating a prey refuge. *Nonlinear Analysis: Real World Applications*, *10*(5), 2905–2908. https://doi.org/10.1016/j.nonrwa.2008.09.009

Chester, E. T., & Robson, B. J. (2013). Anthropogenic refuges for freshwater biodiversity: Their ecological characteristics and management. Bio*logical Conservation, 16*6, 64–75

Chiu, C.-H., Jost, L., & Chao, A. (2014). Phylogenetic beta diversity, similarity, and differentiation measures based on Hill numbers. *Ecological Monographs*, *84*(1), 21–44. https://doi.org/10.1890/12-0960.1

Chretien, E., & Chapman, L. (2016). Habitat heterogeneity facilitates coexistence of native fishes with an introduced predator: The resilience of a fish community 5 decades after the introduction of Nile perch. *BIOLOGICAL INVASIONS*, *18*(12), 3449–3464. https://doi.org/10.1007/s10530-016-1235-x

Cinner, J. (2014). Coral reef livelihoods. *Current Opinion in Environmental Sustainability*, *7*, 65–71. https://doi.org/10.1016/j.cosust.2013.11.025

Clark, C. W. (1994). Antipredator behavior and the asset-protection principle. *Behavioral Ecology*, *5*(2), 159–170. https://doi.org/10.1093/beheco/5.2.159

Clavero, M., Brotons, L., Pons, P. and Sol, D., (2009) Prominent role of invasive species in avian biodiversity loss. *Biological Conservation, 142*(10), pp.2043-2049.

CloudCompare (version 2.11.3) [GPL software]. (2022). Retrieved from http://www.cloudcompare.org/

Common, I. F. B. (1954). A study of the ecology of the adult bogong moth, Agrotis Infusa (Boisd) (Lepidoptera: Noctuidae), with special reference to its behaviour during migration and aestivation. *Australian Journal of Zoology*, *2*(2), 223–263. https://doi.org/10.1071/zo9540223

Conley, A. K., Watling, J. I., & Orrock, J. L. (2011). Invasive plant alters ability to predict disease vector distribution. *Ecological Applications, 21(2)*, 329–334

Contreras-Silva, A. I., Tilstra, A., Migani, V., Thiel, A., Pérez-Cervantes, E., Estrada-Saldívar, N., Elias-Ilosvay, X., Mott, C., Alvarez-Filip, L., & Wild, C. (2020). A meta-analysis to assess long-term spatiotemporal changes of benthic coral and macroalgae cover in the Mexican Caribbean. *Scientific Reports*, *10*(1), 8897. https://doi.org/10.1038/s41598-020-65801-8

Cooper, J., William E., & Blumstein, D. T. (Eds.). (2015). *Escaping From Predators: An Integrative View of Escape Decisions*. Cambridge University Press. https://doi.org/10.1017/CBO9781107447189

Cooper, W. E. (2007). Escape and Its Relationship to Pursuit-Deterrent Signalling in the Curban Curly-Tailed Lizard Leiocephalus carinatus. *Herpetologica*, *63*(2), 144–150.

Cooper, W. E., & Frederick, W. G. (2007). Optimal flight initiation distance. *Journal of Theoretical Biology*, *244*(1), 59–67. https://doi.org/10.1016/j.jtbi.2006.07.011

Côté, I. M., Green, S. J., & Hixon, M. A. (2013). Predatory fish invaders: Insights from Indo-Pacific lionfish in the western Atlantic and Caribbean. *Biological Conservation*, *164*, 50–61. https://doi.org/10.1016/j.biocon.2013.04.014

Côté, I. M., & Smith, N. S. (2018). The lionfish Pterois sp. invasion: Has the worst-case scenario come to pass? *Journal of Fish Biology*, *92*(3), 660–689. https://doi.org/10.1111/jfb.13544

Cowan, M. A., Callan, M. N., Watson, M. J., Watson, D. M., Doherty, T. S., Michael, D. R., Dunlop, J. A., Turner, J. M., Moore, H. A., Watchorn, D. J., & Nimmo, D. G. (2021). *Artificial refuges for wildlife conservation: What is the state of the science?* https://doi.org/10.1111/brv.12776

Csárdi, G. (2019). The comprehensive R archive network. Package “Igraph”. CRAN.

Cumming, G., Fidler, F., & Vaux, D. L. (2007). Error bars in experimental biology. *Journal of Cell Biology*, *177*(1), 7–11. https://doi.org/10.1083/jcb.200611141

Curti, J. N., Fergus, C. E., & de Palma-Dow, A. A. (2021). State of the ART: Using artificial refuge traps to control invasive crayfish in Southern California streams article in freshwater science. *Freshwater Science, 40(3*), 494–507

Curtis, J. S., Albins, M. A., Peebles, E. B., & Stallings, C. D. (2020). Stable isotope analysis of eye lenses from invasive lionfish yields record of resource use. *Marine Ecology Progress Series*, *637*, 181–194. https://doi.org/10.3354/meps13247

Dafforn, K. A. (2017). Eco-engineering and management strategies for marine infrastructure to reduce establishment and dispersal of non-indigenous species. *Management of Biological Invasions, 8(2)*, 153–161

Dagum, L. J., Licuanan, W., Arceo, H., & David, L. (2021). 3D Coral Forms: Structural Complexity Descriptor and Potential Predictor of Fish Abundance. *OCEANS 2021: San Diego – Porto*, 1–6. https://doi.org/10.23919/OCEANS44145.2021.9706023

Dahlgren, C. P., & Eggleston, D. B. (2000). Ecological Processes Underlying Ontogenetic Habitat Shifts in a Coral Reef Fish. *Ecology*, *81*(8), 2227–2240. https://doi.org/10.1890/0012-9658(2000)081[2227:EPUOHS]2.0.CO;2

D’Amore, A., Kirby, E., & McNicholas, M. (2009). Invasive species shifts ontogenetic resource partitioning and microhabitat use of a threatened native amphibian. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *19*(5), 534–541. https://doi.org/10.1002/aqc.1026

Darling, E. S., Graham, N. A. J., Januchowski-Hartley, F. A., Nash, K. L., Pratchett, M. S., & Wilson, S. K. (2017). Relationships between structural complexity, coral traits, and reef fish assemblages. *Coral Reefs*, *36*(2), 561–575. https://doi.org/10.1007/s00338-017-1539-z

Davis, A. C. D. (2018). *Differential effects of native vs. Invasive predators on a common Caribbean reef fish*. https://doi.org/10.1007/s10641-018-0798-z

Davis, A. C. D., Akins, L., Pollock, C., Lundgren, I., Johnston, M. A., Castillo II, B., Reale-Munroe, K., McDonough, V., Moneysmith, S., & Green, S. J. (2021). Multiple drivers of invasive lionfish culling efficiency in marine protected areas. *Conservation Science and Practice*, *3*(11), e541. https://doi.org/10.1111/csp2.541

de Bakker, D. M., van Duyl, F. C., Bak, R. P. M., Nugues, M. M., Nieuwland, G., & Meesters, E. H. (2017). 40 Years of benthic community change on the Caribbean reefs of Curaçao and Bonaire: The rise of slimy cyanobacterial mats. *Coral Reefs*, *36*(2), 355–367. https://doi.org/10.1007/s00338-016-1534-9

De Mesel, I., Kerckhof, F., Norro, A., Rumes, B., & Degraer, S. (2015). Succession and seasonal dynamics of the epifauna community on offshore wind farm foundations and their role as stepping stones for non-indigenous species. *Hydrobiologia, 756*, 37–50 de Palma-Dow, A. A., Curti, J. N., & Emi Fergus, C. (2020). It's a trap! An evaluation of different passive trap types to effectively catch and control the invasive red swamp crayfish (*Procambarus clarkii*) in streams of the Santa Monica Mountains. *Management of Biological Invasions, 11(1)*, 44–62

Deniro, M. J., & Epstein, S. (1981). Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta*, *45*(3), 341–351. https://doi.org/10.1016/0016-7037(81)90244-1

Di Santo, V., O'Boyle, L. A., Saylor, R. K., Dabruzzi, T. F., Covell, M. A., Kaack, K., Scharer, R., Seger, K., Favazza, N., Pomory, C. M., & Bennett, W. A. (2020). Coral loss alters guarding and farming behavior of a Caribbean damselfish. *Marine Biology*, *167*(8), 120. https://doi.org/10.1007/s00227-020-03726-6

Diaz, C., Foster, N. L., Attrill, M. J., Bolton, A., Ganderton, P., Howell, K. L., Robinson, E., & Hosegood, P. (2023a). Mesophotic coral bleaching associated with changes in thermocline depth. *Nature Communications*, *14*(1), 6528. https://doi.org/10.1038/s41467-023-42279-2

Diaz, C., Howell, K. L., Hosegood, P., Bolton, A., & Foster, N. L. (2024). Diverse and ecologically unique mesophotic coral ecosystems in the central Indian Ocean. *Coral Reefs*. https://doi.org/10.1007/s00338-024-02535-3

Diaz, C., Howell, K. L., Robinson, E., Hosegood, P., Bolton, A., Ganderton, P., Arber, P., Attrill, M. J., & Foster, N. L. (2023b). Light and temperature drive the distribution of mesophotic benthic communities in the Central Indian Ocean. *Diversity and Distributions*, *29*(12), 1578–1593. https://doi.org/10.1111/ddi.13777

Dickman, C. R., Greenville, A. C., Tamayo, B., & Wardle, G. M. (2011). Spatial dynamics of small mammals in central Australian desert habitats: The role of drought refugia. *Journal of Mammalogy, 92(6)*, 1193–1209

Dill, L. M. (1990). Distance-to-cover and the escape decisions of an African cichlid fish, Melanochromis chipokae. *Environmental Biology of Fishes*, *27*(2), 147–152. https://doi.org/10.1007/BF00001944

Dill, L. M., & Houtman, R. (1989). The influence of distance to refuge on flight initiation distance in the gray squirrel (Sciurus carolinensis). *Canadian Journal of Zoology*, *67*(1), 233–235. https://doi.org/10.1139/z89-033

DiTomaso, J. M., Van Steenwyk, R. A., Nowierski, R. M., Vollmer, J. L., Lane, E., Chilton, E., Burch, P. L., Cowan, P. E., Zimmerman, K., & Dionigi, C. P. (2017). Enhancing the effectiveness of biological control programs of invasive species through a more comprehensive pest management approach. *Pest Management Science*, *73*(1), 9–13. https://doi.org/10.1002/ps.4347

Doherty, T. S., Glen, A. S., Nimmo, D. G., Ritchie, E. G., & Dickman, C. R. (2016). Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences*, *113*(40), 11261–11265. https://doi.org/10.1073/pnas.1602480113

Dumont, C. P., Gaymer, C. F., & Thiel, M. (2011a). Predation contributes to invasion resistance of benthic communities against the non-indigenous tunicate Ciona intestinalis. Biological Invasions, 13, 2023–2034

Dumont, C. P., Harris, L. G., & Gaymer, C. F. (2011b). Anthropogenic structures as a spatial refuge from predation for the invasive bryozoan Bugula neritina. Marine Ecology Progress Series, 427, 95–103

Durant, S. M. (1998). Competition refuges and coexistence: An example from Serengeti carnivores. *Journal of Animal Ecology*, *67*(3), 370–386. https://doi.org/10.1046/j.1365-2656.1998.00202.x

Dutra, H. P., Barnett, K., Reinhardt, J. R., Marquis, R. J., & Orrock, J. L. (2011). Invasive plant species alters consumer behavior by providing refuge from predation. *Oecologia, 166*, 649–657

Eddy, C., Pitt, J. M., Larkum, J., Altabet, M. A., & Bernal, D. (2020). Stable Isotope Ecology of Invasive Lionfish (Pterois volitans and P. miles) in Bermuda. *Frontiers in Marine Science*, *7*. https://doi.org/10.3389/fmars.2020.00435

Eddy, C., Pitt, J., Oliveira, K., Morris, J. A., Potts, J., & Bernal, D. (2019). The life history characteristics of invasive lionfish (Pterois volitans and P. miles) in Bermuda. *Environmental Biology of Fishes*, *102*(6), 887–900. https://doi.org/10.1007/s10641-019-00877-4

Ehbrecht, M., Seidel, D., Annighöfer, P., Kreft, H., Köhler, M., Zemp, D. C., Puettmann, K., Nilus, R., Babweteera, F., Willim, K., Stiers, M., Soto, D., Boehmer, H. J., Fisichelli, N., Burnett, M., Juday, G., Stephens, S. L., & Ammer, C. (2021). Global patterns and climatic controls of forest structural complexity. *Nature Communications*, *12*(1), 519. https://doi.org/10.1038/s41467-020-20767-z

Ekberzade, B., Yetemen, O., Ezber, Y., Sen, O. L., & Dalfes, H. N. (2024). Latitude or altitude as the future refugium? A case for the future of forests in Asia Minor and its surroundings. *Ecology and Evolution*, *14*(4), e11131. https://doi.org/10.1002/ece3.11131

Ellis, J. I., Jamil, T., Anlauf, H., Coker, D. J., Curdia, J., Hewitt, J., Jones, B. H., Krokos, G., Kürten, B., Hariprasad, D., Roth, F., Carvalho, S., & Hoteit, I. (2019). Multiple stressor effects on coral reef ecosystems. *Global Change Biology*, *25*(12), 4131–4146. https://doi.org/10.1111/gcb.14819

Elton, C. (1939). On the Nature of Cover. *The Journal of Wildlife Management*, *3*(4), 332–338. https://doi.org/10.2307/3796305

Embar, K., Kotler, B. P., & Mukherjee, S. (2011). Risk management in optimal foragers: The effect of sightlines and predator type on patch use, time allocation, and vigilance in gerbils. *Oikos*, *120*(11), 1657–1666. https://doi.org/10.1111/j.1600-0706.2011.19278.x

Enge, S., Nylund, G. M., & Pavia, H. (2013). Native generalist herbivores promote invasion of a chemically defended seaweed via refuge-mediated apparent competition. *Ecology Letters, 16(4)*, 487–492

Erdős, L., Kröel-Dulay, G., Bátori, Z., Kovács, B., Németh, C., Kiss, P. J., & Tölgyesi, C. (2018). Habitat heterogeneity as a key to high conservation value in forest-grassland mosaics. *Biological Conservation*, *226*, 72–80. https://doi.org/10.1016/j.biocon.2018.07.029

Eurich, J. G., McCormick, M. I., & Jones, G. P. (2018). Habitat selection and aggression as determinants of fine-scale partitioning of coral reef zones in a guild of territorial damselfishes. *Marine Ecology Progress Series*, *587*, 201–215. https://doi.org/10.3354/meps12458

Eschweiler, N., & Christensen, H. T. (2011). Trade-off between increased survival and reduced growth for blue mussels living on Pacific oyster reefs. *Journal of Experimental Marine Biology and Ecology, 403*, 90–95

EW Linders, T., Bekele, K., Schaffner, U., Allan, E., Alamirew, T., Choge, S. K., Eckert, S., Haji, J., Muturi, G., Mbaabu, P. R., Shiferaw, H., & Eschen, R. (2020). The impact of invasive species on social-ecological systems: Relating supply and use of selected provisioning ecosystem services. *Ecosystem Services*, *41*, 101055. https://doi.org/10.1016/j.ecoser.2019.101055

Eyal, G., Laverick, J. H., Bongaerts, P., Levy, O., & Pandolfi, J. M. (2021). Mesophotic Coral Ecosystems of the Great Barrier Reef Are Understudied and Underexplored. *Frontiers in Marine Science*, *8*. https://doi.org/10.3389/fmars.2021.622856

Feary, D. A., Cinner, J. E., Graham, N. a. J., & Januchowski-Hartley, F. A. (2011). Effects of Customary Marine Closures on Fish Behavior, Spear-Fishing Success, and Underwater Visual Surveys. *Conservation Biology*, *25*(2), 341–349. https://doi.org/10.1111/j.1523-1739.2010.01613.x

Ferrari, R., Bryson, M., Bridge, T., Hustache, J., Williams, S. B., Byrne, M., & Figueira, W. (2016). Quantifying the response of structural complexity and community composition to environmental change in marine communities. *Global Change Biology*, *22*(5), 1965–1975. https://doi.org/10.1111/gcb.13197

Ferreira, C. E. L., Luiz, O. J., Floeter, S. R., Lucena, M. B., Barbosa, M. C., Rocha, C. R., & Rocha, L. A. (2015). First Record of Invasive Lionfish (Pterois volitans) for the Brazilian Coast. *PLOS ONE*, *10*(4), e0123002. https://doi.org/10.1371/journal.pone.0123002

Firth, L. B., Duff, L., Gribben, P. E., & Knights, A. M. (2021). Do positive interactions between marine invaders increase likelihood of invasion into natural and artificial habitats? *Oikos, 130(3)*, 453–463

França, F. M., Benkwitt, C. E., Peralta, G., Robinson, J. P. W., Graham, N. A. J., Tylianakis, J. M., Berenguer, E., Lees, A. C., Ferreira, J., Louzada, J., & Barlow, J. (2020). Climatic and local stressor interactions threaten tropical forests and coral reefs. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1794), 20190116. https://doi.org/10.1098/rstb.2019.0116

Frazer, T. K., Jacoby, C. A., Edwards, M. A., Barry, S. C., & Manfrino, C. M. (2012). Coping with the Lionfish Invasion: Can Targeted Removals Yield Beneficial Effects? *Reviews in Fisheries Science*, *20*(4), 185–191. https://doi.org/10.1080/10641262.2012.700655

Freitas, M. O., Abilhoa, V., Spach, H. L., Minte-Vera, C. V., Francini-Filho, R. B., Kaufman, L., & Moura, R. L. (2017). Feeding ecology of two sympatric species of large-sized groupers (Perciformes: Epinephelidae) on Southwestern Atlantic coralline reefs. *Neotropical Ichthyology*, *15*, e160047. https://doi.org/10.1590/1982-0224-20160047

Gabler, C. A., & Siemann, E. (2012). Environmental Variability and Ontogenetic Niche Shifts in Exotic Plants May Govern Reinvasion Pressure in Restorations of Invaded Ecosystems. *Restoration Ecology*, *20*(5), 545–550. https://doi.org/10.1111/j.1526-100X.2012.00901.x

Galaiduk, R., Radford, B. T., Saunders, B. J., Newman, S. J., & Harvey, E. S. (2017). Characterizing ontogenetic habitat shifts in marine fishes: Advancing nascent methods for marine spatial management. *Ecological Applications*, *27*(6), 1776–1788. https://doi.org/10.1002/eap.1565

Gallardo, B., Aldridge, D. C., González-Moreno, P., Pergl, J., Pizarro, M., Pyšek, P., Thuiller, W., Yesson, C., & Vilà, M. (2017). Protected areas offer refuge from invasive species spreading under climate change. *Global Change Biology, 23(12)*, 5331–5343

Gardner, T. A., Côté, I. M., Gill, J. A., Grant, A., & Watkinson, A. R. (2003). Long-Term Region-Wide Declines in Caribbean Corals. *Science*, *301*(5635), 958–960. https://doi.org/10.1126/science.1086050

Garrick, R. C. (2011). Montane refuges and topographic complexity generate and maintain invertebrate biodiversity: Recurring themes across space and time. *Journal of Insect Conservation*, *15*(3), 469–478. https://doi.org/10.1007/s10841-010-9349-4

Gause, G. F. (1934). *The Struggle for Existence: A Classic of Mathematical Biology and Ecology*. Williams and Wilkins.

Gavriel, T., Pickholtz, R., & Belmaker, J. (2021). Large Individual-Level Variability in Diel Activity and Depth Use for the Common Lionfish (Pterois miles). *Frontiers in Marine Science*, *8*. https://doi.org/10.3389/fmars.2021.790930

Gea-Izquierdo, G., Gennet, S., & Bartolome, J. W. (2007). Assessing plant-nutrient relationships in highly invaded Californian grasslands using non-normal probability distributions. *Applied Vegetation Science, 10(3)*, 343–350

Ghadiri Khanaposhtani, M., Kaboli, M., Karami, M., & Etemad, V. (2012). Effect of Habitat Complexity on Richness, Abundance and Distributional Pattern of Forest Birds. *Environmental Management*, *50*(2), 296–303. https://doi.org/10.1007/s00267-012-9877-7

Giachetti, C. B., Battini, N., Castro, K. L., & Schwindt, E. (2020). Invasive ascidians: How predators reduce their dominance in artificial structures in cold temperate areas. *Journal of Experimental Marine Biology and Ecology, 533*, 151459

Glynn, P. W. (1996). Coral reef bleaching: Facts, hypotheses and implications. *Global Change Biology*, *2*(6), 495–509. https://doi.org/10.1111/j.1365-2486.1996.tb00063.x

Gnanadesikan, G. E., Pearse, W. D., & Shaw, A. K. (2017). Evolution of mammalian migrations for refuge, breeding, and food. *Ecology and Evolution*, *7*(15), 5891–5900. https://doi.org/10.1002/ece3.3120

Goedknegt, M. A., Buschbaum, C., van der Meer, J., Wegner, K. M., & Thieltges, D. W. (2020). Introduced marine ecosystem engineer indirectly affects parasitism in native mussel hosts. *Biological Invasions, 22(11)*, 3223–3237

Goetze, J. S., Bond, Todd., McLean, D. L., Saunders, B. J., Langlois, T. J., Lindfield, S., Fullwood, Laura. A. F., Driessen, D., Shedrawi, G., & Harvey, E. S. (2019). A field and video analysis guide for diver operated stereo-video. *Methods in Ecology and Evolution*, *10*(7), 1083–1090. https://doi.org/10.1111/2041-210X.13189

González-Rivero, M., Harborne, A. R., Herrera-Reveles, A., Bozec, Y.-M., Rogers, A., Friedman, A., Ganase, A., & Hoegh-Guldberg, O. (2017). Linking fishes to multiple metrics of coral reef structural complexity using three-dimensional technology. *Scientific Reports*, *7*(1), Article 1. https://doi.org/10.1038/s41598-017-14272-5

Goodbody-Gringley, G., Chequer, A., Grincavitch, C., Noyes, T., Dowell, R., Lundberg, A., Corbett, E., & Smith, A. (2023). Impacts of recurrent culling of invasive lionfish on mesophotic reefs in Bermuda. *Coral Reefs*, *42*(2), 443–452. https://doi.org/10.1007/s00338-023-02354-y

Goodbody-Gringley, G., Eddy, C., Pitt, J. M., Chequer, A. D., & Smith, S. R. (2019). Ecological Drivers of Invasive Lionfish (Pterois volitans and Pterois miles) Distribution Across Mesophotic Reefs in Bermuda. *Frontiers in Marine Science*, *6*. https://doi.org/10.3389/fmars.2019.00258

Gorta, S. B. Z., Callaghan, C. T., Samonte, F., Ooi, M. K. J., Mesaglio, T., Laffan, S. W., & Cornwell, W. K. (2023). Multi-taxon biodiversity responses to the 2019–2020 Australian megafires. *Global Change Biology*, *29*(23), 6727–6740. https://doi.org/10.1111/gcb.16955

Gotceitas, V., & Colgan, P. (1989). Predator foraging success and habitat complexity: Quantitative test of the threshold hypothesis. *Oecologia, 80*, 158–166

Gower, J. C. (1971). A General Coefficient of Similarity and Some of Its Properties. *Biometrics*, *27*(4), 857–871. https://doi.org/10.2307/2528823

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

Graham, N. A. J., Wilson, S. K., Jennings, S., Polunin, N. V. C., Robinson, J., Bijoux, J. P., & Daw, T. M. (2007). Lag Effects in the Impacts of Mass Coral Bleaching on Coral Reef Fish, Fisheries, and Ecosystems. *Conservation Biology*, *21*(5), 1291–1300. https://doi.org/10.1111/j.1523-1739.2007.00754.x

Grames, E. M., Stillman, A. N., Tingley, M. W., & Elphick, C. S. (2019). An automated approach to identifying search terms for systematic reviews using keyword co-occurrence networks. *Methods in Ecology and Evolution, 10(10)*, 1645–1654

Gratwicke, B., Petrovic, C., & Speight, M. R. (2006). Fish distribution and ontogenetic habitat preferences in non-estuarine lagoons and adjacent reefs. *Environmental Biology of Fishes*, *76*(2), 191–210. https://doi.org/10.1007/s10641-006-9021-8

Gratwicke, B., & Speight, M. R. (2005). The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *Journal of Fish Biology*, *66*(3), 650–667. https://doi.org/10.1111/j.0022-1112.2005.00629.x

Green, S. J., Akins, J. L., Maljković, A., & Côté, I. M. (2012a). Invasive Lionfish Drive Atlantic Coral Reef Fish Declines. *PLOS ONE*, *7*(3), e32596. https://doi.org/10.1371/journal.pone.0032596

Green, S. J., Akins, J. L., & Morris, J. A. (2012b). *Lionfish dissection: Techniques and applications*. Retrieved 16 August 2024, from https://repository.library.noaa.gov/view/noaa/719

Green, N., Bentley, M., Stebbing, P., Andreou, D., & Britton, R. (2018). Trapping for invasive crayfish: Comparisons of efficacy and selectivity of baited traps versus novel artificial refuge traps. *Knowledge & Management of Aquatic Ecosystems, 419*, 15

Gregg, E. A., Tingley, R., & Phillips, B. L. (2019). The on-ground feasibility of a waterless barrier to stop the spread of invasive cane toads in Western Australia. *Conservation Science and Practice, 1(8)*, 74

Greiling, T. M. S., & Clark, J. I. (2012). Chapter one—New Insights into the Mechanism of Lens Development Using Zebra Fish. In K. W. Jeon (Ed.), *International Review of Cell and Molecular Biology* (Vol. 296, pp. 1–61). Academic Press. https://doi.org/10.1016/B978-0-12-394307-1.00001-1

Gresham, A., Healey, J. R., Eichhorn, M. P., Barton, O., Smith, A. R., & Shannon, G. (2023). Horizontal viewsheds of large herbivores as a function of woodland structure. *Ecology and Evolution*, *13*(11), e10699. https://doi.org/10.1002/ece3.10699

Gress, E., Andradi-Brown, D. A., Woodall, L., Schofield, P. J., Stanley, K., & Rogers, A. D. (2017). Lionfish (Pterois spp.) invade the upper-bathyal zone in the western Atlantic. *PeerJ*, *5*, e3683. https://doi.org/10.7717/peerj.3683

Gribben, P. E., Poore, A. G., Thomsen, M. S., Quesey, P., Weschke, E., & Wright, J. T. (2020). Habitat provided by native species facilitates higher abundances of an invader in its introduced compared to native range. *Scientific Reports, 10(1)*, 6385

Grof-Tisza, P., Holyoak, M., Antell, E., & Karban, R. (2015). Predation and associational refuge drive ontogenetic niche shifts in an arctiid caterpillar. *Ecology, 96(1)*, 80–89

Guiden, P. W., & Orrock, J. L. (2019). Invasive shrubs modify rodent activity timing, revealing a consistent behavioral rule governing diel activity. *Behavioral Ecology, 30(4)*, 1069–1075

Gunn, R. L., Benkwitt, C. E., Graham, N. A. J., Hartley, I. R., Algar, A. C., & Keith, S. A. (2023). Terrestrial invasive species alter marine vertebrate behaviour. *Nature Ecology & Evolution*, *7*(1), 82–91. https://doi.org/10.1038/s41559-022-01931-8

Hacala, A., Salgueiro-Simon, M., Bain, A., Marguerie, D., & Pétillon, J. (2024). Spider and vascular plant assemblages in subarctic peat bogs are complementary ecological indicators of variation in local and landscape factors. *Ecological Indicators*, *158*, 111389. https://doi.org/10.1016/j.ecolind.2023.111389

Hammerschlag-Peyer, C. M., Yeager, L. A., Araújo, M. S., & Layman, C. A. (2011). A Hypothesis-Testing Framework for Studies Investigating Ontogenetic Niche Shifts Using Stable Isotope Ratios. *PLOS ONE*, *6*(11), e27104. https://doi.org/10.1371/journal.pone.0027104

Harada, Y., Ito, S., Ogawa, N. O., Yoshikawa, C., Ishikawa, N. F., Yoneda, M., & Ohkouchi, N. (2022). Compound-Specific Nitrogen Isotope Analysis of Amino Acids in Eye Lenses as a New Tool to Reconstruct the Geographic and Trophic Histories of Fish. *Frontiers in Marine Science*, *8*. https://doi.org/10.3389/fmars.2021.796532

Hardy, P. B., Kinder, P. M., Sparks, T. H., & Dennis, R. L. H. (2010). Elevation and habitats: The potential of sites at different altitudes to provide refuges for phytophagous insects during climatic fluctuations. *Journal of Insect Conservation*, *14*(3), 297–303. https://doi.org/10.1007/s10841-009-9251-0

Hartman, R., Pope, K., & Lawler, S. (2013). Factors mediating co-occurrence of an economically valuable introduced fish and its native frog prey. *Conservation Biology, 28(3)*, 763–772

Hawkins, B. A., Thomas, M. B., & Hochberg, M. E. (1993). Refuge Theory and Biological Control. *Science*, *262*(5138), 1429–1432. https://doi.org/10.1126/science.262.5138.1429

Hess, M. A., Hess, J. E., Matala, A. P., French, R. A., Steele, C. A., Lovtang, J. C., & Narum, S. R. (2016). Migrating adult steelhead utilize a thermal refuge during summer periods with high water temperatures. *ICES Journal of Marine Science, 73(10)*, 2616–2624

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

Hinderstein, L. M., Marr, J. C. A., Martinez, F. A., Dowgiallo, M. J., Puglise, K. A., Pyle, R. L., Zawada, D. G., & Appeldoorn, R. (2010). Theme section on "Mesophotic Coral Ecosystems: Characterization, Ecology, and Management". *Coral Reefs*, *29*(2), 247–251. https://doi.org/10.1007/s00338-010-0614-5

Hixon, M. A., & Beets, J. P. (1993). Predation, Prey Refuges, and the Structure of Coral-Reef Fish Assemblages. *Ecological Monographs*, *63*(1), 77–101. https://doi.org/10.2307/2937124

Hochberg, M. E., & Hawkins, B. A. (1992). Refuges as a Predictor of Parasitoid Diversity. *Science*, *255*(5047), 973–976. https://doi.org/10.1126/science.255.5047.973

Hoegh-Guldberg, O. (1999). Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research*, *50*(8), 839–866. https://doi.org/10.1071/mf99078

Holbrook, S. J., & Schmitt, R. J. (2002). Competition for shelter space causes density-dependent predation mortality in damselfishes. *Ecology, 83(10)*, 2855–2868

Hollandsworth, D., Lowe, R., & Badra, P. (2011). Indigenous unionid clam refugia from zebra mussels in Michigan Inland Lakes. *The American Midland Naturalist, 166(2)*, 369–378

Hollarsmith, J. A., Ramírez-Ortiz, G., Winquist, T., Velasco-Lozano, M., DuBois, K., Reyes-Bonilla, H., Neumann, K. C., & Grosholz, E. D. (2020). Habitats and fish communities at mesophotic depths in the Mexican Pacific. *Journal of Biogeography*, *47*(7), 1552–1563. https://doi.org/10.1111/jbi.13842

Holzer, K. A., & Lawler, S. P. (2015). Introduced reed canary grass attracts and supports a common native amphibian. *The Journal of Wildlife Management, 79(7)*, 1081–1090

Hughes, T. P. (1994). Catastrophes, Phase Shifts, and Large-Scale Degradation of a Caribbean Coral Reef. *Science*, *265*(5178), 1547–1551. https://doi.org/10.1126/science.265.5178.1547

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

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

Hughes, T. P., & Tanner, J. E. (2000). Recruitment Failure, Life Histories, and Long-Term Decline of Caribbean Corals. *Ecology*, *81*(8), 2250–2263. https://doi.org/10.1890/0012-9658(2000)081[2250:RFLHAL]2.0.CO;2

Huxel, G. R. (1999). Rapid displacement of native species by invasive species: Effects of hybridization. *Biological Conservation*, *89*(2), 143–152. https://doi.org/10.1016/S0006-3207(98)00153-0

Iacarella, J. C., Dick, J. T., Alexander, M. E., & Ricciardi, A. (2015). Ecological impacts of invasive alien species along temperature gradients: Testing the role of environmental matching. *Ecological Applications, 25(3)*, 706–716

Jackson, M. C. (2015). Interactions among multiple invasive animals. *Ecology, 96(8)*, 2035–2041

Jackson, A. L., Inger, R., Parnell, A. C., & Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology*, *80*(3), 595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x

Januchowski-Hartley, F. A., Graham, N. A. J., Feary, D. A., Morove, T., & Cinner, J. E. (2011). Fear of Fishers: Human Predation Explains Behavioral Changes in Coral Reef Fishes. *PLoS ONE*, 6(8), e22761. https://doi.org/10.1371/journal.pone.0022761

Januchowski-Hartley, F. A., Nash, K. L., & Lawton, R. J. (2012). Influence of spear guns, dive gear and observers on estimating fish flight initiation distance on coral reefs. *Marine Ecology Progress Series*, *469*, 113–119. https://doi.org/10.3354/meps09971

Jeschke, J. M., Bacher, S., Blackburn, T. M., Dick, J. T. A., Essl, F., Evans, T., Gaertner, M., Hulme, P. E., Kühn, I., Mrugała, A., Pergl, J., Pyšek, P., Rabitsch, W., Ricciardi, A., Richardson, D. M., Sendek, A., Vilà, M., Winter, M., & Kumschick, S. (2014). Defining the Impact of Non-Native Species. *Conservation Biology*, *28*(5), 1188–1194. https://doi.org/10.1111/cobi.12299

Johnston, M. W., & Purkis, S. J. (2015). A coordinated and sustained international strategy is required to turn the tide on the Atlantic lionfish invasion. *Marine Ecology Progress Series*, *533*, 219–235. https://doi.org/10.3354/meps11399

Johnson, M. D., & De León, Y. L. (2015). Effect of an invasive plant and moonlight on rodent foraging behavior in a coastal dune ecosystem. *PLoS ONE, 10(2)*, e0117903

Kahng, S., Copus, J., & Wagner, D. (2014). Recent advances in the ecology of mesophotic coral ecosystems (MCEs). *Current Opinion in Environmental Sustainability*, *7*, 72–81. https://doi.org/10.1016/j.cosust.2013.11.019

Kahng, S. E., Garcia-Sais, J. R., Spalding, H. L., Brokovich, E., Wagner, D., Weil, E., Hinderstein, L., & Toonen, R. J. (2010). Community ecology of mesophotic coral reef ecosystems. *Coral Reefs*, *29*(2), 255–275. https://doi.org/10.1007/s00338-010-0593-6

Karatayev, A. Y., Burlakova, L. E., & Padilla, D. K. (2002). Impacts of zebra mussels on aquatic communities and their role as ecosystem engineers. In E. Leppäkoski, S. Gollasch, & S. Olenin (Eds.), Invasive aquatic species of Europe. Distribution, impacts and management (pp. 433–446). Springer

Kaufman, L. (1977). *The three spot damselfish: effects on benthic biota of caribbean coral reefs*. http://pascal-francis.inist.fr/vibad/index.php?action=getRecordDetail&idt=PASCAL7850221088

Keith, S. A., Drury, J. P., McGill, B. J., & Grether, G. F. (2023). Macrobehaviour: Behavioural variation across space, time, and taxa. *Trends in Ecology & Evolution*, *38*(12), 1177–1188. https://doi.org/10.1016/j.tree.2023.08.007

Keane, R. M., & Crawley, M. J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution, 17(4)*, 164–170

Keller, L. F., & Waller, D. M. (2002). Inbreeding effects in wild populations. *Trends in Ecology & Evolution*, *17(5),* 230–241

Keller, R. P., Geist, J., Jeschke, J. M., & Kühn, I. (2011). Invasive species in Europe: Ecology, status, and policy. *Environmental Sciences Europe, 23*, 1–17

Kelley, A. L., & Cooke, S. (2014). The role thermal physiology plays in species invasion. *Conservation Physiology, 2(1)*, 1–14

Keppel, G., Van Niel, K. P., Wardell-Johnson, G. W., Yates, C. J., Byrne, M., Mucina, L., Schut, A. G. T., Hopper, S. D., & Franklin, S. E. (2012). Refugia: Identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography*, *21*(4), 393–404. https://doi.org/10.1111/j.1466-8238.2011.00686.x

Kestrup, Å. M., & Ricciardi, A. (2009). Environmental heterogeneity limits the local dominance of an invasive freshwater crustacean. *Biological Invasions, 11(9)*, 2095–2105

Kimirei, I. A., Nagelkerken, I., Griffioen, B., Wagner, C., & Mgaya, Y. D. (2011). Ontogenetic habitat use by mangrove/seagrass-associated coral reef fishes shows flexibility in time and space. *Estuarine, Coastal and Shelf Science*, *92*(1), 47–58. https://doi.org/10.1016/j.ecss.2010.12.016

Kimirei, I. A., Nagelkerken, I., Trommelen, M., Blankers, P., van Hoytema, N., Hoeijmakers, D., Huijbers, C. M., Mgaya, Y. D., & Rypel, A. L. (2013). What Drives Ontogenetic Niche Shifts of Fishes in Coral Reef Ecosystems? *Ecosystems*, *16*(5), 783–796. https://doi.org/10.1007/s10021-013-9645-4

Kittinger, J. N., Finkbeiner, E. M., Glazier, E. W., & Crowder, L. B. (2012). Human Dimensions of Coral Reef Social-Ecological Systems. *Ecology and Society*, *17*(4). https://www.jstor.org/stable/26269232

Kleijn, D., Biesmeijer, K. J. C., Klaassen, R. H. G., Oerlemans, N., Raemakers, I., Scheper, J., & Vet, L. E. M. (2020). Chapter Four - Integrating biodiversity conservation in wider landscape management: Necessity, implementation and evaluation. In D. A. Bohan

& A. J. Vanbergen (Eds.), *Advances in Ecological Research* (Vol. 63, pp. 127–159). Academic Press. https://doi.org/10.1016/bs.aecr.2020.08.004

Kobak, J., Jermacz, Ł., & Płąchocki, D. (2014). Effectiveness of zebra mussels to act as shelters from fish predators differs between native and invasive amphipod prey. *Aquatic Ecology, 48*, 397–408

Koizumi, I., Kanazawa, Y., Yamazaki, C., Tanaka, Y., & Takaya, K. (2017). Extreme winter aggregation of invasive rainbow trout in small tributaries: Implications for effective control. *Ichthyological Research, 64*, 197–203

Kovach, R. P., Muhlfeld, C. C., Boyer, M. C., Lowe, W. H., Allendorf, F. W., & Luikart, G. (2015). Dispersal and selection mediate hybridization between a native and invasive species. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1799), 20142454. https://doi.org/10.1098/rspb.2014.2454

Krause, J., Cheng, D., Kirkman, E., & Ruxton, G. (2000). SPECIES-SPECIFIC PATTERNS OF REFUGE USE IN FISH: THE ROLE OF METABOLIC EXPENDITURE AND BODY LENGTH. *Behaviour*, *137*(7–8), 1113–1127. https://doi.org/10.1163/156853900502466

Křivan, V. (1998). Effects of optimal antipredator behavior of prey on predator–prey dynamics: The role of refuges. *Theoretical Population Biology, 53(2)*, 131–142

Kurle, C. M., & McWhorter, J. K. (2017). Spatial and temporal variability within marine isoscapes: Implications for interpreting stable isotope data from marine systems. *Marine Ecology Progress Series*, *568*, 31–45. https://doi.org/10.3354/meps12045

Ladich, F. (2019). Ecology of sound communication in fishes. *Fish and fisheries*, *20*(3), 552-563.

Latham, A. D. M., Cecilia Latham, M., Herries, D., Barron, M., Cruz, J., & Anderson, D. P. (2018). Assessing the efficacy of aerial culling of introduced wild deer in New Zealand with analytical decomposition of predation risk. *Biological Invasions*, *20(1),* 251–266

Laverick, J. H., Piango, S., Andradi-Brown, D. A., Exton, D. A., Bongaerts, P., Bridge, T. C. L., Lesser, M. P., Pyle, R. L., Slattery, M., Wagner, D., & Rogers, A. D. (2018). To what extent do mesophotic coral ecosystems and shallow reefs share species of conservation interest? A systematic review. *Environmental Evidence*, *7*(1), 15. https://doi.org/10.1186/s13750-018-0127-1

Laverick, J. H., Tamir, R., Eyal, G., & Loya, Y. (2020). A generalized light-driven model of community transitions along coral reef depth gradients. *Global Ecology and Biogeography*, *29*(9), 1554–1564. https://doi.org/10.1111/geb.13140

Layman, C. A., Araujo, M. S., Boucek, R., Hammerschlag-Peyer, C. M., Harrison, E., Jud, Z. R., Matich, P., Rosenblatt, A. E., Vaudo, J. J., Yeager, L. A., Post, D. M., & Bearhop, S. (2012). Applying stable isotopes to examine food-web structure: An overview of analytical tools. *Biological Reviews*, *87*(3), 545–562. https://doi.org/10.1111/j.1469-185X.2011.00208.x

Lecchini, D., & Galzin, R. (2005). Spatial repartition and ontogenetic shifts in habitat use by coral reef fishes (Moorea, French Polynesia). *Marine Biology*, *147*(1), 47–58. https://doi.org/10.1007/s00227-004-1543-z

Lecq, S., Loisel, A., Brischoux, F., Mullin, S. J., & Bonnet, X. (2017). Importance of ground refuges for the biodiversity in agricultural hedgerows. *Ecological Indicators*, *72*, 615–626. https://doi.org/10.1016/j.ecolind.2016.08.032

Lenth, R. V. (2024). *emmeans: Estimated Margin2l Means, aka Least-Squares Means* (Version R package version 1.10.3-090006) [Computer software]. https://rvlenth.github.io/emmeans/

Lesser, M. P. (1997). Oxidative stress causes coral bleaching during exposure to elevated temperatures. *Coral Reefs*, *16*(3), 187–192. https://doi.org/10.1007/s003380050073

Lesser, M. P., & Slattery, M. (2011). *Phase shift to algal dominated communities at mesophotic depths associated with lionfish (Pterois volitans) invasion on a Bahamian coral reef*. https://doi.org/10.1007/s10530-011-0005-z

Lesser, M. P., Slattery, M., Laverick, J. H., Macartney, K. J., & Bridge, T. C. (2019). Global community breaks at 60 m on mesophotic coral reefs. *Global Ecology and Biogeography*, *28*(10), 1403–1416. https://doi.org/10.1111/geb.12940

Lesser, M. P., Slattery, M., & Leichter, J. J. (2009). Ecology of mesophotic coral reefs. *Journal of Experimental Marine Biology and Ecology*, *375*(1), 1–8. https://doi.org/10.1016/j.jembe.2009.05.009

Lesser, M. P., Slattery, M., & Mobley, C. D. (2018). Biodiversity and Functional Ecology of Mesophotic Coral Reefs. *Annual Review of Ecology, Evolution, and Systematics*, *49*(Volume 49, 2018), 49–71. https://doi.org/10.1146/annurev-ecolsys-110617-062423

Lessios, H. A. (1988). Mass Mortality of Diadema Antillarum in the Caribbean: What Have We Learned? *Annual Review of Ecology and Systematics*, *19*, 371–393.

Little, K., Draud, M. and Itzkowitz, M., (2013). Interspecific aggression in two highly similar Stegastes damselfish. Ethology Ecology & Evolution, 25(3), pp.227-242.

Lohner, R. N., Sigler, V., Mayer, C. M., & Balogh, C. (2007). A comparison of the benthic bacterial communities within and surrounding Dreissena clusters in lakes. *Microbial Ecology*, *54*, 469–477

Loiseau, N., Villéger, S., Le Bozec, C., Gimenez, M., Kawahara, S. L., & Claverie, T. (2023). Mesophotic reefs are not refugia for neither taxonomic nor functional diversity of reef fishes. *Coral Reefs*, *42*(1), 63–75. https://doi.org/10.1007/s00338-022-02311-1

Loke, L. H. L., Ladle, R. J., Bouma, T. J., & Todd, P. A. (2015). Creating complex habitats for restoration and reconciliation. *Ecological Engineering*, *77*, 307–313. https://doi.org/10.1016/j.ecoleng.2015.01.037

Luckhurst, B. E., & Luckhurst, K. (1978). Analysis of the influence of substrate variables on coral reef fish communities. *Marine Biology*, *49*(4), 317–323. https://doi.org/10.1007/BF00455026

Lynch, J. (2024). *The social-ecological footprint of fisheries on tropical coral reef biodiversity in the Great hoSea Reef, Fiji. Chapter- Neither hole nor there—Introducing a new habitat complexity metric, Hidey Hole.* University College London.

MacArthur, R. H., & MacArthur, J. W. (1961). On Bird Species Diversity. *Ecology*, *42*(3), 594–598. https://doi.org/10.2307/1932254

MacDougall, A. S., Boucher, J., Turkington, R., & Bradfield, G. E. (2006). Patterns of plant invasion along an environmental stress gradient. *Journal of Vegetation Science*, *17(1)*, 47–56

Magneville, C., Loiseau, N., Albouy, C., Casajus, N., Claverie, T., Escalas, A., Leprieur, F., Maire, E., Mouillot, D., & Villéger, S. (2022). mFD: An R package to compute and illustrate the multiple facets of functional diversity. *Ecography*, *2022*(1). https://doi.org/10.1111/ecog.05904

Magoulick, D. D., & Kobza, R. M. (2003). The role of refugia for fishes during drought: A review and synthesis. *Freshwater Biology, 48(7)*, 1186–1198

Malo, A. F., Taylor, A., & Díaz Esteban, M. (2022). Native seed dispersal by rodentsis negatively influenced by an invasive shrub. *Animal Biodiversity and Conservation, 45,* 53–67

Malpica-Cruz, L., Green, S. J., & Côté, I. M. (2019). Temporal and ontogenetic changes in the trophic signature of an invasive marine predator. *Hydrobiologia*, *839*(1), 71–86. https://doi.org/10.1007/s10750-019-03996-2

Mattos, K. J., & Orrock, J. L. (2010). Behavioral consequences of plant invasion: An invasive plant alters rodent antipredator behavior. *Behavioral Ecology, 21(3)*, 556–561

McCormick, M. I., & Manassa, R. (2008). Predation risk assessment by olfactory and visual cues in a coral reef fish. *Coral Reefs*, *27*, 105-113.

McCoy, E. D., & Bell, S. S. (1991). Habitat structure: The evolution and diversification of a complex topic. In S. S. Bell, E. D. McCoy, & H. R. Mushinsky (Eds.), *Habitat Structure: The physical arrangement of objects in space* (pp. 3–27). Springer Netherlands. https://doi.org/10.1007/978-94-011-3076-9_1

McDougall, P. T., & Kramer, D. L. (2007). Short-term behavioral consequences of territory relocation in a Caribbean damselfish, Stegastes diencaeus. *Behavioral Ecology*, *18*(1), 53–61. https://doi.org/10.1093/beheco/arl055

McElreath, R. (2016). *Statistical Rethinking: A Bayesian Course with Examples in R and Stan*. Chapman and Hall/CRC. https://doi.org/10.1201/9781315372495

McMahon, K. W., Hamady, L. L., & Thorrold, S. R. (2013). A review of ecogeochemistry approaches to estimating movements of marine animals. *Limnology and Oceanography*, *58*(2), 697–714. https://doi.org/10.4319/lo.2013.58.2.0697

McMillan, N. A., Fuhlendorf, S. D., Davis, C. A., Hamilton, R. G., Neumann, Landon. K., & Cady, S. M. (2023). A plea for scale, and why it matters for invasive species management, biodiversity and conservation. *Journal of Applied Ecology*, *60*(7), 1468–1480. https://doi.org/10.1111/1365-2664.14411

McWhorter, J. K., Halloran, P. R., Roff, G., & Mumby, P. J. (2024). Climate change impacts on mesophotic regions of the Great Barrier Reef. *Proceedings of the National Academy of Sciences*, *121*(16), e2303336121. https://doi.org/10.1073/pnas.2303336121

Medeiros, A. P. M., Ferreira, B. P., Alvarado, F., Betancur-R, R., Soares, M. O., & Santos, B. A. (2021). Deep reefs are not refugium for shallow-water fish communities in the southwestern Atlantic. *Ecology and Evolution*, *11*(9), 4413–4427. https://doi.org/10.1002/ece3.7336

Melbourne, B. A., Cornell, H. V., Davies, K. F., Dugaw, C. J., Elmendorf, S., Freestone, A. L., Hall, R. J., Harrison, S., Hastings, A., Holland, M., & Holyoak, M. (2007). Invasion in a heterogeneous world: Resistance, coexistence or hostile takeover? *Ecology Letters, 10(1)*, 77–94

Melis, R., Ceccherelli, G., Piazzi, L., & Rustici, M. (2019). Macroalgal forests and sea urchin barrens: Structural complexity loss, fisheries exploitation and catastrophic regime shifts. *Ecological Complexity*, *37*, 32–37. https://doi.org/10.1016/j.ecocom.2018.12.005

Mellin, C., Kulbicki, M., & Ponton, D. (2007). Seasonal and ontogenetic patterns of habitat use in coral reef fish juveniles. *Estuarine, Coastal and Shelf Science*, *75*(4), 481–491. https://doi.org/10.1016/j.ecss.2007.05.026

Michalak, J. L., Lawler, J. J., Roberts, D. R., & Carroll, C. (2018). Distribution and protection of climatic refugia in North America. *Conservation Biology, 32(6)*, 1414–1425

Minchin, P. R. (1987). An evaluation of the relative robustness of techniques for ecological ordination. In I. C. Prentice & E. van der Maarel (Eds.), *Theory and models in* *vegetation science: Proceedings of Symposium, Uppsala, July 8–13, 1985* (pp. 89–107). Springer Netherlands. https://doi.org/10.1007/978-94-009-4061-1_9

Mittelbach, G. G., Osenberg, C. W., & Leibold, M. A. (1988). Trophic Relations and Ontogenetic Niche Shifts in Aquatic Ecosystems. In B. Ebenman & L. Persson (Eds.), *Size-Structured Populations* (pp. 219–235). Springer. https://doi.org/10.1007/978-3-642-74001-5_15

Miranda, N. A., Kupriyanova, E. K., Rishworth, G. M., Peer, N., Bornman, T. G., Bird, M. S., & Perissinotto, R. (2016). An invasive polychaete species found in living marine stromatolites. *Aquatic Invasions, 11(3)*, 257–266

Mitchell, T. S., Folt, B., & Hall, J. M. (2021). Dumpsters and other anthropogenic structures as habitat for invasive African rock agama lizards in Florida. *Biological Invasions, 23(9)*, 2689–2693

Moberg, F., & Folke, C. (1999). Ecological goods and services of coral reef ecosystems. *Ecological Economics*, *29*(2), 215–233. https://doi.org/10.1016/S0921-8009(99)00009-9

Mohd, M. H., Noorani, M. S. M., Kadir, M. F. F. A., & Zakariya, N. (2023). Contrasting effects of prey refuge on biodiversity of species. *International Journal of Nonlinear Sciences and Numerical Simulation*, *24*(2), 811–829. https://doi.org/10.1515/ijnsns-2021-0213

Moher, D., Shamseer, L., Clarke, M., Ghersi, D., Liberati, A., Petticrew, M., Shekelle, P., & Stewart, L. A. (2015). Preferred reporting items for systematic review and meta-analysis protocols (PRISMA-P) 2015 statement. *Systematic Reviews, 4(1)*, 1–9

Møller, A.P., Liang, W. and Samia, D.S., 2019. Flight initiation distance, color and camouflage. Current Zoology, 65(5), pp.535-540.

Mols, B., Lambers, E., Cromsigt, J. P. G. M., Kuijper, D. P. J., & Smit, C. (2022). Recreation and hunting differentially affect deer behaviour and sapling performance. *Oikos*, *2022*(1). https://doi.org/10.1111/oik.08448

Mooney, H. A., & Cleland, E. E. (2001). The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences*, *98*(10), 5446–5451. https://doi.org/10.1073/pnas.091093398

Mora, C., Aburto-Oropeza, O., Bocos, A. A., Ayotte, P. M., Banks, S., Bauman, A. G., Beger, M., Bessudo, S., Booth, D. J., Brokovich, E., Brooks, A., Chabanet, P., Cinner, J. E., Cortés, J., Cruz-Motta, J. J., Magaña, A. C., DeMartini, E. E., Edgar, G. J., Feary, D. A., … Zapata, F. A. (2011). Global Human Footprint on the Linkage between Biodiversity and Ecosystem Functioning in Reef Fishes. *PLOS Biology*, *9*(4), e1000606. https://doi.org/10.1371/journal.pbio.1000606

Morelli, F., Mikula, P., Blumstein, D. T., Díaz, M., Markó, G., Jokimäki, J., Kaisanlahti-Jokimäki, M.-L., Floigl, K., Zeid, F. A., Siretckaia, A., & Benedetti, Y. (2022). Flight initiation distance and refuge in urban birds. *Science of The Total Environment*, *842*, 156939. https://doi.org/10.1016/j.scitotenv.2022.156939

Morelli, T. L., Daly, C., Dobrowski, S. Z., Dulen, D. M., Ebersole, J. L., Jackson, S. T., Lundquist, J. D., Millar, C. I., Maher, S. P., Monahan, W. B., Nydick, K. R., Redmond, K. T., Sawyer, S. C., Stock, S., & Beissinger, S. R. (2016). Managing Climate Change Refugia for Climate Adaptation. *PLOS ONE*, *11*(8), e0159909. https://doi.org/10.1371/journal.pone.0159909

Morris, J., & Whitfield, P. E. (2009). *Biology, ecology, control and management of the invasive Indo-Pacific lionfish: An updated integrated assessment* (Issue 99).

NOAA/National Ocean Service/Center for Coastal Fisheries and Habitat Research. http://hdl.handle.net/1834/20632

Mumby, P. J. (2009). Phase shifts and the stability of macroalgal communities on Caribbean coral reefs. *Coral Reefs*, *28*(3), 761–773. https://doi.org/10.1007/s00338-009-0506-8

Muthukrishnan, R., & Fong, P. (2014). Multiple anthropogenic stressors exert complex, interactive effects on a coral reef community. *Coral Reefs*, *33*(4), 911–921. https://doi.org/10.1007/s00338-014-1199-1

Nakazawa, T. (2015). Ontogenetic niche shifts matter in community ecology: A review and future perspectives. *Population Ecology*, *57*(2), 347–354. https://doi.org/10.1007/s10144-014-0448-z

Ndaimani, H., Murwira, A., & Kativu, S. (2013). Comparing terrain and vegetation-based visibility for explaining sable flight behaviour in a Southern African savanna. *Geocarto International*, *28*(2), 130–143. https://doi.org/10.1080/10106049.2012.677481

Neill, P. E., Alcalde, O., Faugeron, S., Navarrete, S. A., & Correa, J. A. (2006). Invasion of *Codium fragile ssp. tomentosoides* in northern Chile: A new threat for Gracilaria farming. *Aquaculture, 259(1–4)*, 202–210

Newman, M. J. H., Paredes, G. A., Sala, E., & Jackson, J. B. C. (2006). Structure of Caribbean coral reef communities across a large gradient of fish biomass. *Ecology Letters*, *9*(11), 1216–1227. https://doi.org/10.1111/j.1461-0248.2006.00976.x

Nicholls, K. H., Hoyle, J. A., Johannsson, O. E., & Dermott, R. (2011). A biological regime shift in the bay of Quinte ecosystem (Lake Ontario) associated with the establishment of invasive dreissenid mussels. *Journal of Great Lakes Research, 37(2)*, 310–317

Nico, L. G., Butt, P. L., Johnston, G. R., Jelks, H. L., Kail, M., & Walsh, S. J. (2012). Discovery of south American suckermouth armored catfishes (Loricariidae, *Pterygoplichthys spp.*) in the Santa Fe River drainage, Suwannee River basin, USA. *BioInvasions Records, 1(3)*, 179–200

Nunes, J. de A. C. C., Sampaio, C. L. S., & Barros, F. (2015). The influence of structural complexity and reef habitat types on flight initiation distance and escape behaviors in labrid fishes. *Marine Biology*, *162*(3), 493–499. https://doi.org/10.1007/s00227-014-2578-4

Oakley-Cogan, A., Tebbett, S. B., & Bellwood, D. R. (2020). Habitat zonation on coral reefs: Structural complexity, nutritional resources and herbivorous fish distributions. *PLOS ONE*, *15*(6), e0233498. https://doi.org/10.1371/journal.pone.0233498

Ødegaard, F., & Tømmerås, B. Å. (2000). Compost heaps—Refuges and stepping-stones for alien arthropod species in northern Europe. *Diversity and Distributions, 6(1),* 45–59

Oduor, A. M. O., Long, H., Fandohan, A. B., Liu, J., & Yu, X. (2018). An invasive plant provides refuge to native plant species in an intensely grazed ecosystem. *Biological Invasions, 20(10)*, 2745–2751

O'Farrell, S., Bearhop, S., McGill, R. A. R., Dahlgren, C. P., Brumbaugh, D. R., & Mumby, P. J. (2014). Habitat and body size effects on the isotopic niche space of invasive lionfish and endangered Nassau grouper. *Ecosphere*, *5*(10), art123. https://doi.org/10.1890/ES14-00126.1

Orrock, J. L., Baskett, M. L., & Holt, R. D. (2010a). Spatial interplay of plant competition and consumer foraging mediate plant coexistence and drive the invasion ratchet. *Proceedings of the Royal Society B: Biological Sciences, 277(1698)*, 3307–3315

Orrock, J. L., Holt, R. D., & Baskett, M. L. (2010b). *Refuge-mediated apparent competition in plant-consumer interactions*. https://doi.org/10.1111/j.1461-0248.2009.01412.x

Orrock, J. L., Preisser, E. L., Grabowski, J. H., & Trussell, G. C. (2013). The cost of safety: Refuges increase the impact of predation risk in aquatic systems. *Ecology, 94(3)*, 573–579

Orrock, J. L., Witter, M. S., & Reichman, O. J. (2008). Apparent competition with an exotic plant reduces native plant establishment. *Ecology, 89(4)*, 1168–1174

Pardini, E. A., Patten, M. V., & Knight, T. M. (2017). Effects of seed density and proximity to refuge habitat on seed predation rates for a rare and a common Lupinus species. *American Journal of Botany, 104(3)*, 389–398

Humann, P. & Deloach, N. (2014). *Reef Fish Identification: Florida Caribbean Bahamas*. New World Publications Inc.,U.S.

Pavey, C. R., Addison, J., Brandle, R., Dickman, C. R., McDonald, P. J., Moseby, K. E., & Young, L. I. (2017). The role of refuges in the persistence of Australian dryland mammals. Biological Reviews, 2(92), 647–664

Peake, J., Bogdanoff, A. K., Layman, C. A., Castillo, B., Reale-Munroe, K., Chapman, J., Dahl, K., Patterson III, W. F., Eddy, C., Ellis, R. D., Faletti, M., Higgs, N., Johnston, M. A., Muñoz, R. C., Sandel, V., Villasenor-Derbez, J. C., & Morris, J. A. (2018). Feeding ecology of invasive lionfish (Pterois volitans and Pterois miles) in the temperate and tropical western Atlantic. *Biological Invasions*, *20*(9), 2567–2597. https://doi.org/10.1007/s10530-018-1720-5

Pearson, D. E. (2009). Invasive plant architecture alters trophic interactions by changing predator abundance and behavior. *Oecologia, 159(3)*, 549–558

Pearson, J. B., Bellmore, J. R., & Dunham, J. B. (2022). Controlling invasive fish in fluctuating environments: Model analysis of common carp (*Cyprinus carpio*) in a shallow lake. *Ecosphere, 13(5)*, 3985.

Pejchar, L., & Mooney, H. A. (2009). Invasive species, ecosystem services and human well-being. *Trends in Ecology & Evolution*, *24*(9), 497–504. https://doi.org/10.1016/j.tree.2009.03.016

Pereira, P. H. C., Leal, I. C. S., & de Araújo, M. E. (2016). Observer presence may alter the behaviour of reef fishes associated with coral colonies. *Marine Ecology, 37*(4), 760-769.

Perry, C. T., Steneck, R. S., Murphy, G. N., Kench, P. S., Edinger, E. N., Smithers, S. G., & Mumby, P. J. (2015). Regional-scale dominance of non-framework building corals on Caribbean reefs affects carbonate production and future reef growth. *Global Change Biology*, *21*(3), 1153–1164. https://doi.org/10.1111/gcb.12792

Persson, L. (1993). Predator-mediated competition in prey refuges: The importance of habitat dependent prey resources. *Oikos, 68*, 12–22

Peterson, M. S., Slack, W. T., & Woodley, C. M. (2005). The occurrence of non-indigenous Nile tilapia, *Oreochromis niloticus* (linnaeus) in coastal Mississippi, USA: Ties to aquaculture and thermal effluent. *Wetlands, 25(1)*, 112–121

Pinheiro, H. T., Goodbody-Gringley, G., Jessup, M. E., Shepherd, B., Chequer, A. D., & Rocha, L. A. (2016). Upper and lower mesophotic coral reef fish communities evaluated by underwater visual censuses in two Caribbean locations. *Coral Reefs*, *35*(1), 139–151. https://doi.org/10.1007/s00338-015-1381-0

Plaisance, L., Caley, M. J., Brainard, R. E., & Knowlton, N. (2011). The Diversity of Coral Reefs: What Are We Missing? *PLOS ONE*, *6*(10), e25026. https://doi.org/10.1371/journal.pone.0025026

Post, D. M. (2002). Using Stable Isotopes to Estimate Trophic Position: Models, Methods, and Assumptions. *Ecology*, *83*(3), 703–718. https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2

Pratchett, M. S., Hoey, A. S., Wilson, S. K., Messmer, V., & Graham, N. A. J. (2011). Changes in Biodiversity and Functioning of Reef Fish Assemblages following Coral Bleaching and Coral Loss. *Diversity*, *3*(3), Article 3. https://doi.org/10.3390/d3030424

Price, C. J., & Banks, P. B. (2018). Habitat augmentation for introduced urban wildlife: The use of piles of railway sleepers as refuge for introduced black rats *Rattus rattus*. *Australian Zoologist, 39(3)*, 513–519

Pyle, R. L., & Copus, J. M. (2019). Mesophotic Coral Ecosystems: Introduction and Overview. In Y. Loya, K. A. Puglise, & T. C. L. Bridge (Eds.), *Mesophotic Coral Ecosystems* (pp. 3–27). Springer International Publishing. https://doi.org/10.1007/978-3-319-92735-0_1

Pyšek, P., Hulme, P. E., Simberloff, D., Bacher, S., Blackburn, T. M., Carlton, J. T., Dawson, W., Essl, F., Foxcroft, L. C., Genovesi, P., Jeschke, J. M., Kühn, I., Liebhold, A. M., Mandrak, N. E., Meyerson, L. A., Pauchard, A., Pergl, J., Roy, H. E., Seebens, H., … Richardson, D. M. (2020). Scientists' warning on invasive alien species. *Biological Reviews*, *95*(6), 1511–1534. Scopus. https://doi.org/10.1111/brv.12627

QGIS.org (2021) QGIS Geographic Information System. QGIS Association. http://www.qgis.org

Quadros, A. L. S., Barros, F., Blumstein, D. T., Meira, V. H., & Nunes, J. A. C. C. (2019). Structural complexity but not territory sizes influences flight initiation distance in a damselfish. *Marine Biology*, *166*(5), 65. https://doi.org/10.1007/s00227-019-3508-2

Quaeck-Davies, K., Bendall, V. A., MacKenzie, K. M., Hetherington, S., Newton, J., & Trueman, C. N. (2018). Teleost and elasmobranch eye lenses as a target for life-history stable isotope analyses. *PeerJ*, *6*, e4883. https://doi.org/10.7717/peerj.4883

Froese, R & Pauly, D. (2024). FishBase. *World Wide Web Electronic Publication*. www.fishbase.org

Randall, C. J., Toth, L. T., Leichter, J. J., Maté, J. L., & Aronson, R. B. (2020). Upwelling buffers climate change impacts on coral reefs of the eastern tropical Pacific. *Ecology*, *101*(2), e02918. https://doi.org/10.1002/ecy.2918

Randazzo Eisemann, Á., Montero Muñoz, J. L., McField, M., Myton, J., & Arias-González, J. E. (2019). The Effect of Algal-Gardening Damselfish on the Resilience of the Mesoamerican Reef. *Frontiers in Marine Science*, *6*. https://doi.org/10.3389/fmars.2019.00414

R Core Team (2023) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Reside, A. E., Briscoe, N. J., Dickman, C. R., Greenville, A. C., Hradsky, B. A., Kark, S., Kearney, M. R., Kutt, A. S., Nimmo, D. G., Pavey, C. R., Read, J. L., Ritchie, E. G., Roshier, D., Skroblin, A., Stone, Z., West, M., & Fisher, D. O. (2019). *Persistence through tough times: Fixed and shifting refuges in threatened species conservation*. https://doi.org/10.1007/s10531-019-01734-7

Ricciardi, A., Hoopes, M. F., Marchetti, M. P., & Lockwood, J. L. (2013). Progress toward understanding the ecological impacts of nonnative species. *Ecological Monographs, 83(3)*, 263–282

Riegl, B., & Piller, W. E. (2003). Possible refugia for reefs in times of environmental stress. *International Journal of Earth Sciences*, *92*(4), 520–531. https://doi.org/10.1007/s00531-003-0328-9

Rocha, L. A., Pinheiro, H. T., Shepherd, B., Papastamatiou, Y. P., Luiz, O. J., Pyle, R. L., & Bongaerts, P. (2018a). Mesophotic coral ecosystems are threatened and ecologically distinct from shallow water reefs. *Science*, *361*(6399), 281–284. https://doi.org/10.1126/science.aaq1614

Rodriguez, L. F. (2006). Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. *Biological Invasions, 8*, 927–939

Rogers, A., Blanchard, J. L., & Mumby, P. J. (2014). Vulnerability of Coral Reef Fisheries to a Loss of Structural Complexity. *Current Biology*, *24*(9), 1000–1005. https://doi.org/10.1016/j.cub.2014.03.026

Rogers, A., Blanchard, J. L., Newman, S. P., Dryden, C. S., & Mumby, P. J. (2018). High refuge availability on coral reefs increases the vulnerability of reef-associated predators to overexploitation. *Ecology*, *99*(2), 450–463. https://doi.org/10.1002/ecy.2103

Rogers, C. S., & Ramos-Scharrón, C. E. (2022). Assessing Effects of Sediment Delivery to Coral Reefs: A Caribbean Watershed Perspective. *Frontiers in Marine Science*, *8*. https://doi.org/10.3389/fmars.2021.773968

Rosinski, C. L., Glaid, J., Hahn, M., & Fetzer, W. W. (2023). Natal Origin Differentiation Using Eye Lens Stable Isotope Analysis. *North American Journal of Fisheries Management*, *43*(2), 547–555. https://doi.org/10.1002/nafm.10875

Rossi-Stacconi, M. V., Kaur, R., Mazzoni, V., Ometto, L., Grassi, A., Gottardello, A., Rota-Stabelli, O., & Anfora, G. (2016). Multiple lines of evidence for reproductive winter diapause in the invasive pest *Drosophila suzukii*: Useful clues for control strategies. *Journal of Pest Science, 89(3)*, 689–700

Roy, H. E., Pauchard, A., Stoett, P., Renard Truong, T., Bacher, S., Galil, B. S., Hulme, P. E., Ikeda, T., Sankaran, K., McGeoch, M. A., Meyerson, L. A., Nuñez, M. A., Ordonez, A., Rahlao, S. J., Schwindt, E., Seebens, H., Sheppard, A. W., & Vandvik, V. (2023). *IPBES Invasive Alien Species Assessment: Summary for Policymakers*. Zenodo. https://doi.org/10.5281/zenodo.10127924

Rudolf, V. H. W. (2020). A multivariate approach reveals diversity of ontogenetic niche shifts across taxonomic and functional groups. *Freshwater Biology*, *65*(4), 745–756. https://doi.org/10.1111/fwb.13463

Ruland, F., & Jeschke, J. M. (2020). *How biological invasions affect animal behaviour: A global, cross-taxonomic analysis*. https://doi.org/10.1111/1365-2656.13306

Samia, D. S. M., Bessa, E., Blumstein, D. T., Nunes, J. A. C. C., Azzurro, E., Morroni, L., Sbragaglia, V., Januchowski-Hartley, F. A., & Geffroy, B. (2019). A meta-analysis of fish behavioural reaction to underwater human presence. *Fish and Fisheries*, *20*(5), 817–829. https://doi.org/10.1111/faf.12378

Samia, D. S. M., Blumstein, D. T., Stankowich, T., & Cooper Jr., W. E. (2016). Fifty years of chasing lizards: New insights advance optimal escape theory. *Biological Reviews*, *91*(2), 349–366. https://doi.org/10.1111/brv.12173

Samia, D. S. M., Nomura, F., & Blumstein, D. T. (2013). Do animals generally flush early and avoid the rush? A meta-analysis. *Biology Letters*, *9*(2), 20130016. https://doi.org/10.1098/rsbl.2013.0016

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

Sax, D. F., Schlaepfer, M. A., & Olden, J. D. (2022). Valuing the contributions of non-native species to people and nature. *Trends in Ecology & Evolution*, *37*(12), 1058–1066. https://doi.org/10.1016/j.tree.2022.08.005

Sax, D. F., Schlaepfer, M. A., & Olden, J. D. (2023). Identifying key points of disagreement in non-native impacts and valuations. *Trends in Ecology & Evolution*, *38*(6), 501–504. https://doi.org/10.1016/j.tree.2023.03.004

Schlaepfer, M. A., Sherman, P. W., Blossey, B., & Runge, M. C. (2005). Introduced species as evolutionary traps. *Ecology Letters, 8(3)*, 241–246

Schmidt, K. A., & Whelan, C. J. (1999). Effects of exotic Lonicera and Rhamnus on songbird nest predation. *Conservation Biology, 13(6)*, 1502–1506

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, *9*(7), 671–675. https://doi.org/10.1038/nmeth.2089

Schofield, P. J. (2009). Geographic extent and chronology of the invasion of non-native lionfish (Pterois volitans [Linnaeus 1758] and P. miles [Bennett 1828]) in the Western North Atlantic and Caribbean Sea. *Aquatic Invasions*, *4*(3), 473–479.

Schopmeyer, S. A., & Lirman, D. (2015). Occupation Dynamics and Impacts of Damselfish Territoriality on Recovering Populations of the Threatened Staghorn Coral, Acropora cervicornis. *PLOS ONE*, *10*(11), e0141302. https://doi.org/10.1371/journal.pone.0141302

Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., Pagad, S., Pyšek, P., Winter, M., Arianoutsou, M., Bacher, S., Blasius, B., Brundu, G., Capinha, C., Celesti-Grapow, L., Dawson, W., Dullinger, S., Fuentes, N., Jäger, H., … Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, *8*(1), 14435. https://doi.org/10.1038/ncomms14435

Selwood, K. E., & Zimmer, H. C. (2020). *Refuges for biodiversity conservation: A review of the evidence*. https://doi.org/10.1016/j.biocon.2020.108502

Semmler, R. F., Hoot, W. C., & Reaka, M. L. (2017). Are mesophotic coral ecosystems distinct communities and can they serve as refugia for shallow reefs? *Coral Reefs*, *36*(2), 433–444. https://doi.org/10.1007/s00338-016-1530-0

Serrano, X., Baums, I. B., O'Reilly, K., Smith, T. B., Jones, R. J., Shearer, T. L., Nunes, F. L. D., & Baker, A. C. (2014). Geographic differences in vertical connectivity in the Caribbean coral ontastraea cavernosa despite high levels of horizontal connectivity at shallow depths. *Molecular Ecology*, *23*(17), 4226–4240. https://doi.org/10.1111/mec.12861

Shackleton, R.T., Richardson, D.M., Shackleton, C.M., Bennett, B., Crowley, S.L., Dehnen-Schmutz, K., Estévez, R.A., Fischer, A., Kueffer, C., Kull, C.A. and Marchante, E., 2019. Explaining people's perceptions of invasive alien species: A conceptual framework. *Journal of environmental management, 229*, 10-26.

Shaw, A. K. (2016). Drivers of animal migration and implications in changing environments. *Evolutionary Ecology*, *30*(6), 991–1007. https://doi.org/10.1007/s10682-016-9860-5

Sheppard, C. E., Boström-Einarsson, L., Williams, G. J., Exton, D. A., & Keith, S. A. (2024). Variation in farming damselfish behaviour creates a competitive landscape of risk on coral reefs. *Biology Letters*, *20*(5), 20240035. https://doi.org/10.1098/rsbl.2024.0035

Shima, J. S., McNaughtan, D., Geange, S. W., & Wilkinson, S. (2012). Ontogenetic variation in site fidelity and homing behaviour of a temperate reef fish. *Journal of Experimental Marine Biology and Ecology*, *416–417*, 162–167. https://doi.org/10.1016/j.jembe.2012.02.020

Sih, A. (1987). Prey refuges and predator-prey stability. *Theoretical Population Biology*, *31*(1), 1–12. https://doi.org/10.1016/0040-5809(87)90019-0

Simberloff, D., & Von Holle, B. (1999). Positive interactions of nonindigenous species: Invasional meltdown? *Biological Invasions, 1*, 21–32

Singleton, G. R., Tann, C. R., & Krebs, C. J. (2007). Landscape ecology of house mouse outbreaks in South-Eastern Australia. *Journal of Applied Ecology, 44(3)*, 644–652

Slattery, M., Lesser, M. P., Rocha, L. A., Spalding, H. L., & Smith, T. B. (2024). Function and stability of mesophotic coral reefs. *Trends in Ecology & Evolution*, *39*(6), 585–598. https://doi.org/10.1016/j.tree.2024.01.011

Slattery, M., Moore, S., Boye, L., Whitney, S., Woolsey, A., & Woolsey, M. (2018). The Pulley Ridge deep reef is not a stable refugia through time. *Coral Reefs*, *37*(2), 391–396. https://doi.org/10.1007/s00338-018-1664-3

Smith, T. B., Gyory, J., Brandt, M. E., Miller, W. J., Jossart, J., & Nemeth, R. S. (2016). Caribbean mesophotic coral ecosystems are unlikely climate change refugia. *Global Change Biology*, *22*(8), 2756–2765. https://doi.org/10.1111/gcb.13175

Soares, M., Tavares, T., & Carneiro, P. (2019). Mesophotic ecosystems: Distribution, impacts and conservation in the South Atlantic. *DIVERSITY AND DISTRIBUTIONS*, *25*(2), 255–268. https://doi.org/10.1111/ddi.12846

Spalding, M. D., & Brown, B. E. (2015). Warm-water coral reefs and climate change. *Science*, *350*(6262), 769–771. https://doi.org/10.1126/science.aad0349

St. Pierre, J. I., & Kovalenko, K. E. (2014). Effect of habitat complexity attributes on species richness. *Ecosphere*, *5*(2), art22. https://doi.org/10.1890/ES13-00323.1

Stamoulis, K. A., Harvey, E. S., Friedlander, A. M., Williams, I. D., Weng, K. C., Wiggins, C., Wagner, G. W., & Conklin, E. J. (2019). Flight behavior of targeted fishes depends on variables other than fishing. *Ecological Indicators*, *96*, 579–590. https://doi.org/10.1016/j.ecolind.2018.09.006

Stan Development Team (2023) RStan: the R interface to Stan. R package version 2.26.1. See https://mc-stan.org/rstan/articles/rstan.html.

Stankowich, T., & Blumstein, D. T. (2005). Fear in animals: A meta-analysis and review of risk assessment. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1581), 2627–2634. https://doi.org/10.1098/rspb.2005.3251

Steele, J. H. (1985). A comparison of terrestrial and marine ecological systems. *Nature, 313(6001)*, 355–358

Stefanoudis, P. V., Rivers, M., Smith, S. R., Schneider, C. W., Wagner, D., Ford, H., Rogers, A. D., & Woodall, L. C. (2019). Low connectivity between shallow, mesophotic and rariphotic zone benthos. *Royal Society Open Science*, *6*(9), 190958. https://doi.org/10.1098/rsos.190958

Stein, R. M., Lecigne, B., Eitel, J. U. H., Johnson, T. R., McGowan, C., & Rachlow, J. L. (2022). Vegetation and vantage point influence visibility across diverse ecosystems: Implications for animal ecology. *Frontiers in Ecology and Evolution*, *10*. https://doi.org/10.3389/fevo.2022.911051

Stewart, P. S., Hill, R. A., Stephens, P. A., Whittingham, M. J., & Dawson, W. (2021). Impacts of invasive plants on animal behaviour. *Ecology Letters*, *24(4)*, 891–907

Stewart, T. W., Miner, J. G., & Lowe, R. L. (1998). Quantifying mechanisms for zebra mussel effects on benthic macroinvertebrates: Organic matter production and shellgenerated habitat. *Journal of the North American Benthological Society, 17(1)*, 81–94

Stodola, K. W., Linder, E. T., & Cooper, R. J. (2013). Indirect effects of an invasive exotic species on a long-distance migratory songbird. *Biological Invasions*, *15*(9), 1947–1959. https://doi.org/10.1007/s10530-013-0423-1

Strait, N., Williams, T. M., Sherwood, A. R., Kosaki, R. K., Giuseffi, L., Smith, C. M., & Spalding, H. L. (2022). Nitrogen stable isotopes (N) and tissue nitrogen in shallow-water and mesophotic macroalgae differ between the Main Hawaiian Islands and the Northwestern Hawaiian Islands. *Limnology and Oceanography*, *67*(5), 1211–1226. https://doi.org/10.1002/lno.12068

Studivan, M. S., & Voss, J. D. (2018). Population connectivity among shallow and mesophotic Montastraea cavernosa corals in the Gulf of Mexico identifies potential for refugia. *Coral Reefs*, *37*(4), 1183–1196. https://doi.org/10.1007/s00338-018-1733-7

Sully, S., & van Woesik, R. (2020). Turbid reefs moderate coral bleaching under climate-related temperature stress. *Global Change Biology*, *26*(3), 1367–1373. https://doi.org/10.1111/gcb.14948

Swanborn, D. J. B., Stefanoudis, P. V., Huvenne, V. A. I., Pittman, S. J., & Woodall, L. C. (2022). Structure-from-motion photogrammetry demonstrates that fine-scale seascape heterogeneity is essential in shaping mesophotic fish assemblages. *Remote Sensing in Ecology and Conservation*, *8*(6), 904–920. https://doi.org/10.1002/rse2.290

Tätte, K., Møller, A. P., & Mänd, R. (2018). Towards an integrated view of escape decisions in birds: Relation between flight initiation distance and distance fled. *Animal Behaviour*, *136*, 75–86. https://doi.org/10.1016/j.anbehav.2017.12.008

Thresher, R. E., & Colin, P. L. (1986). Trophic structure, diversity and abundance of fishes of the deep reef (30–300m) at Enewetak, Marshall Islands. *Bulletin of Marine Science*, *38*(1), 253–272.

Tobias, J. A., & Pigot, A. L. (2019). Integrating behaviour and ecology into global biodiversity conservation strategies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *374*(1781), 20190012. https://doi.org/10.1098/rstb.2019.0012

Turner, J. A., Andradi-Brown, D. A., Gori, A., Bongaerts, P., Burdett, H. L., Ferrier-Pagès, C., Voolstra, C. R., Weinstein, D. K., Bridge, T. C. L., Costantini, F., Gress, E., Laverick, J., Loya, Y., Goodbody-Gringley, G., Rossi, S., Taylor, M. L., Viladrich, N., Voss, J. D., Williams, J., … Eyal, G. (2019). Key Questions for Research and Conservation of Mesophotic Coral Ecosystems and Temperate Mesophotic Ecosystems. In Y. Loya, K. A. Puglise, & T. C. L. Bridge (Eds.), *Mesophotic Coral Ecosystems* (pp. 989–1003). Springer International Publishing. https://doi.org/10.1007/978-3-319-92735-0_52

Turner, J. A., Babcock, R. C., Hovey, R., & Kendrick, G. A. (2017). Deep thinking: A systematic review of mesophotic coral ecosystems. *ICES Journal of Marine Science*, *74*(9), 2309–2320. https://doi.org/10.1093/icesjms/fsx085

Twining, J. P., Montgomery, W. I., & Tosh, D. G. (2021). Declining invasive grey squirrel populations may persist in refugia as native predator recovery reverses squirrel species replacement. *Journal of Applied Ecology, 58(2)*, 248–260

Urban, R. A., & Titus, J. E. (2010). Exposure provides refuge from a rootless invasive macrophyte. *Aquatic Botany, 92(4)*, 265–272

Urbina-Barreto, I., Chiroleu, F., Pinel, R., Fréchon, L., Mahamadaly, V., Elise, S., Kulbicki, M., Quod, J.-P., Dutrieux, E., Garnier, R., Henrich Bruggemann, J., Penin, L., & Adjeroud, M. (2021). Quantifying the shelter capacity of coral reefs using photogrammetric 3D modeling: From colonies to reefscapes. *Ecological Indicators*, *121*, 107151. https://doi.org/10.1016/j.ecolind.2020.107151

Utz, R., Slater, A., Rosche, H., & Carson, W. (2020). Do dense layers of invasive plants elevate the foraging intensity of small mammals in temperate deciduous forests? A case study from Pennsylvania, USA. *NeoBiota, 56,* 73–88

Uyà, M., Bulleri, F., Wright, J. T., & Gribben, P. E. (2020). Facilitation of an invader by a native habitat-former increases along interacting gradients of environmental stress. *Ecology, 101(4)*, 02961

Vander Zanden, M. J., Hansen, G. J., & Latzka, A. W. (2017). A framework for evaluating heterogeneity and landscape-level impacts of non-native aquatic species. *Ecosystems, 20,* 477–491

van Kleunen, M., Dawson, W., Essl, F., Pergl, J., Winter, M., Weber, E., Kreft, H., Weigelt, P., Kartesz, J., Nishino, M., Antonova, L. A., Barcelona, J. F., Cabezas, F. J., Cárdenas, D., Cárdenas-Toro, J., Castaño, N., Chacón, E., Chatelain, C., Ebel, A. L., … Pyšek, P. (2015). Global exchange and accumulation of non-native plants. *Nature*, *525*(7567), 100–103. https://doi.org/10.1038/nature14910

van Woesik, R., Houk, P., Isechal, A. L., Idechong, J. W., Victor, S., & Golbuu, Y. (2012). Climate-change refugia in the sheltered bays of Palau: Analogs of future reefs. *Ecology and Evolution*, *2*(10), 2474–2484. https://doi.org/10.1002/ece3.363

Vaselli, S., Bulleri, F., & Benedetti-Cecchi, L. (2008). Hard coastal-defence structures as habitats for native and exotic rocky-bottom species. *Marine Environmental Research, 66(4)*, 395–403

Vecchio, J. L., & Peebles, E. B. (2020). Spawning origins and ontogenetic movements for demersal fishes: An approach using eye-lens stable isotopes. *Estuarine, Coastal and Shelf Science*, *246*, 107047. https://doi.org/10.1016/j.ecss.2020.107047

Venegas, R. M., Oliver, T., Liu, G., Heron, S. F., Clark, S. J., Pomeroy, N., Young, C., Eakin, C. M., & Brainard, R. E. (2019). The Rarity of Depth Refugia from Coral Bleaching Heat Stress in the Western and Central Pacific Islands. *Scientific Reports*, *9*(1), 19710. https://doi.org/10.1038/s41598-019-56232-1

Vilà, M., Espinar, J. L., Hejda, M., Hulme, P. E., Jarošík, V., Maron, J. L., Pergl, J., Schaffner, U., Sun, Y., & Pyšek, P. (2011). Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters, 14(7)*, 702–708

Wahle, R. A. (1992). Body-Size Dependent Anti-Predator Mechanisms of the American Lobster. *Oikos*, *65*(1), 52–60. https://doi.org/10.2307/3544887

Wallace, A. A., Hollander, D. J., & Peebles, E. B. (2014). Stable Isotopes in Fish Eye Lenses as Potential Recorders of Trophic and Geographic History. *PLOS ONE*, *9*(10), e108935. https://doi.org/10.1371/journal.pone.0108935

Walsh, J. R., Carpenter, S. R., & Vander Zanden, M. J. (2016). Invasive species triggers a massive loss of ecosystem services through a trophic cascade. *Proceedings of the National Academy of Sciences*, *113*(15), 4081–4085. https://doi.org/10.1073/pnas.1600366113

Ward, J. M., & Ricciardi, A. (2007). Impacts of Dreissena invasions on benthic macroinvertebrate communities: A meta-analysis. *Diversity and Distributions, 13(2)*, 155–165

Warfe, D. M., & Barmuta, L. A. (2004). Habitat structural complexity mediates the foraging success of multiple predator species. *Oecologia*, *141*(1), 171–178. https://doi.org/10.1007/s00442-004-1644-x

Wasson, K., Zabin, C. J., Bedinger, L., Diaz, M. C., & Pearse, J. S. (2001). Biological invasions of estuaries without international shipping: The importance of intraregional transport. *Biological Conservation, 102(2)*, 143–153

Watchorn, D. J., Cowan, M. A., Driscoll, D. A., Nimmo, D. G., Ashman, K. R., Garkaklis, M. J., Wilson, B. A., & Doherty, T. S. (2022). Artificial habitat structures for animal conservation: Design and implementation, risks and opportunities. *Frontiers in Ecology and the Environment*, *20*(5), 301–309. https://doi.org/10.1002/fee.2470

Watchorn, D. J., Dickman, C. R., Greenville, A., Wilson, B. A., Garkaklis, M. J., Driscoll, D. A., Hodgens, P., Hoadley, D., Groffen, H., & Doherty, T. S. (2024). Artificial refuges provide post-fire habitat for small vertebrates. *Biological Conservation*, *291*, 110501. https://doi.org/10.1016/j.biocon.2024.110501

Watling, J. I., Hickman, C. R., & Orrock, J. L. (2011). Invasive shrub alters native forest amphibian communities. *Biological Conservation, 144(11)*, 2597–2601

Watling, J. I., & Orrock, J. L. (2010). Measuring edge contrast using biotic criteria helps define edge effects on the density of an invasive plant. *Landscape Ecology, 25*, 69–78

Werner, E. E., & Gilliam, J. F. (1984). The Ontogenetic Niche and Species Interactions in Size-Structured Populations. *Annual Review of Ecology and Systematics*, *15*, 393–425.

Whitfield, P. E., Gardner, T., Vives, S. P., Gilligan, M. R., Jr, W. R. C., Ray, G. C., & Hare, J. A. (2002). Biological invasion of the Indo-Pacific lionfish Pterois volitans along the Atlantic coast of North America. *Marine Ecology Progress Series*, *235*, 289–297. https://doi.org/10.3354/meps235289

Williams, S. C., & Ward, J. S. (2010). Effects of Japanese barberry (Ranunculales: Berberidaceae) removal and resulting microclimatic changes on *Ixodes scapularis* (Acari: Ixodidae) abundances in Connecticut, USA. E*nvironmental Entomology, 39(6)*, 1911–1921

Woodhead, A. J., Hicks, C. C., Norström, A. V., Williams, G. J., & Graham, N. A. J. (2019). Coral reef ecosystem services in the Anthropocene. *Functional Ecology*, *33*(6), 1023–1034. https://doi.org/10.1111/1365-2435.13331

Wride, M. A. (2011). Lens fibre cell differentiation and organelle loss: Many paths lead to clarity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1568), 1219–1233. https://doi.org/10.1098/rstb.2010.0324

Wright, J. T., Byers, J. E., Devore, J. L., & Sotka, E. E. (2014). Engineering or food? Mechanisms of facilitation by a habitat-forming invasive seaweed. *Ecology, 95(10),* 2699–2706

Wright, J. T., Gribben, P. E., & Latzel, S. (2016). Native ecosystem engineer facilitates recruitment of invasive crab and native invertebrates. *Biological Invasions, 18*, 3163–3173

Xu, W., Chen, X., Liu, B., Chen, Y., Huan, M., Liu, N., & Lin, J. (2019). Inter-individual variation in trophic history of *Dosidicus gigas*, as indicated by stable isotopes in eye lenses. *Aquaculture and Fisheries*, *4*(6), 261–267. https://doi.org/10.1016/j.aaf.2019.05.001

Yanovski, R., & Abelson, A. (2019). Structural complexity enhancement as a potential coral-reef restoration tool. *Ecological Engineering*, *132*, 87–93. https://doi.org/10.1016/j.ecoleng.2019.04.007

Ydenberg, R. C., & Dill, L. M. (1986). The Economics of Fleeing from Predators. In J. S. Rosenblatt, C. Beer, M.-C. Busnel, & P. J. B. Slater (Eds.), *Advances in the Study of Behavior* (Vol. 16, pp. 229–249). Academic Press. https://doi.org/10.1016/S0065-3454(08)60192-8

Young, G. C., Dey, S., Rogers, A. D., & Exton, D. (2017). Cost and time-effective method for multi-scale measures of rugosity, fractal dimension, and vector dispersion from coral reef 3D models. *PLOS ONE*, *12*(4), e0175341. https://doi.org/10.1371/journal.pone.0175341

Young, M. J., Larwood, V., Clause, J. K., Bell-Tilcock, M., Whitman, G., Johnson, R., & Feyrer, F. (2022). Eye lenses reveal ontogenetic trophic and habitat shifts in an imperiled fish, Clear Lake hitch (Lavinia exilicauda chi). *Canadian Journal of Fisheries and Aquatic Sciences*, *79*(1), 21–30. https://doi.org/10.1139/cjfas-2020-0318

Zambrano, L. I., Fuentes-Barahona, I. C., Henriquez-Marquez, K. I., Vasquez-Bonilla, W. O., Sierra, M., Muñoz-Lara, F., Luna, C., Bonilla-Aldana, D. K., & Rodriguez-Morales, A. J. (2021). COVID-19 and Hurricanes: The Impact of Natural Disasters during a Pandemic in Honduras, Central America. *Prehospital and Disaster Medicine*, *36*(2), 246–248. https://doi.org/10.1017/S1049023X21000182

Zavaleta, E. S., Hobbs, R. J., & Mooney, H. A. (2001). Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology & Evolution*, *16*(8), 454–459. https://doi.org/10.1016/S0169-5347(01)02194-2

Zong, X., Wang, T., Skidmore, A. K., & Heurich, M. (2023). LiDAR reveals a preference for intermediate visibility by a forest-dwelling ungulate species. *Journal of Animal Ecology*, *92*(7), 1306–1319. https://doi.org/10.1111/1365-2656.13847

Appendix A: Supplementary material

Chapter 1 Supplementary material

Table S1.1 Full list of studies included in the review. Including data extracted from each study.

Please follow this link and see Supporting Information at the bottom of the page for the full dataset: https://onlinelibrary.wiley.com/doi/full/10.1111/geb.13701

Chapter 2 Supplementary material

Table S2.1 Number of SVS transects at each site and depth in 2014-2015.

	Coral View	**Little Bight**	**Raggedy Cay**	**Rocky Point**	**The Maze**
5 m	10	10	4	4	10
15 m	9	10	4	4	10
25 m	8	8	4	4	8
40 m	7	7	4	4	8

Table S2.2 Number of SVS transects at each site and depth in 2022-2023.

	Coral View	**Little Bight**	**Raggedy Cay**	**Rocky Point**	**The Maze**
5 m	12	12	12	12	12
15 m	2	12	12	12	12
25 m	8	8	8	8	8
40 m	1	1	7	6	7

Chapter 3 Supplementary material

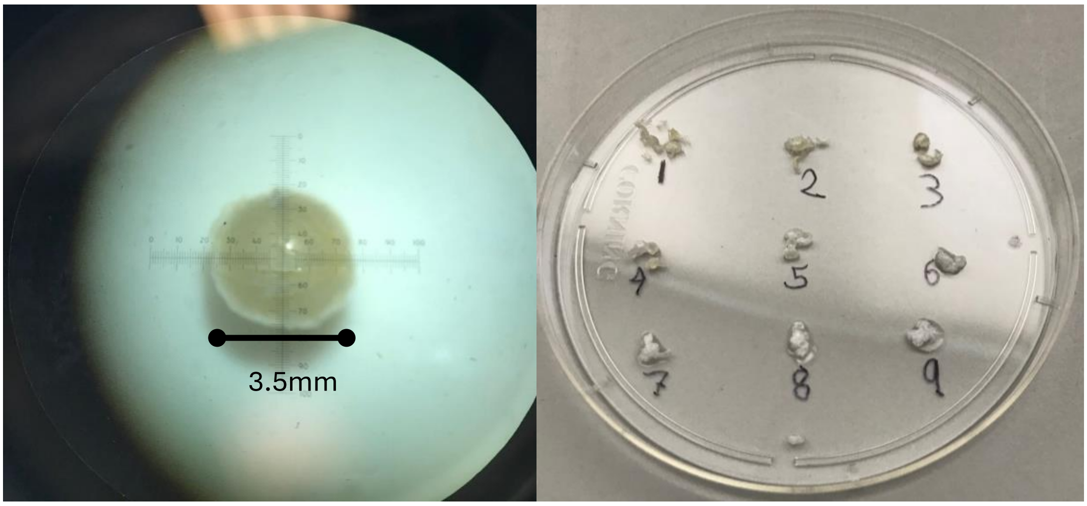


Figure S3.1 Lionfish eye lens before delamination (left) and individual laminae from the lens after delamination (right).

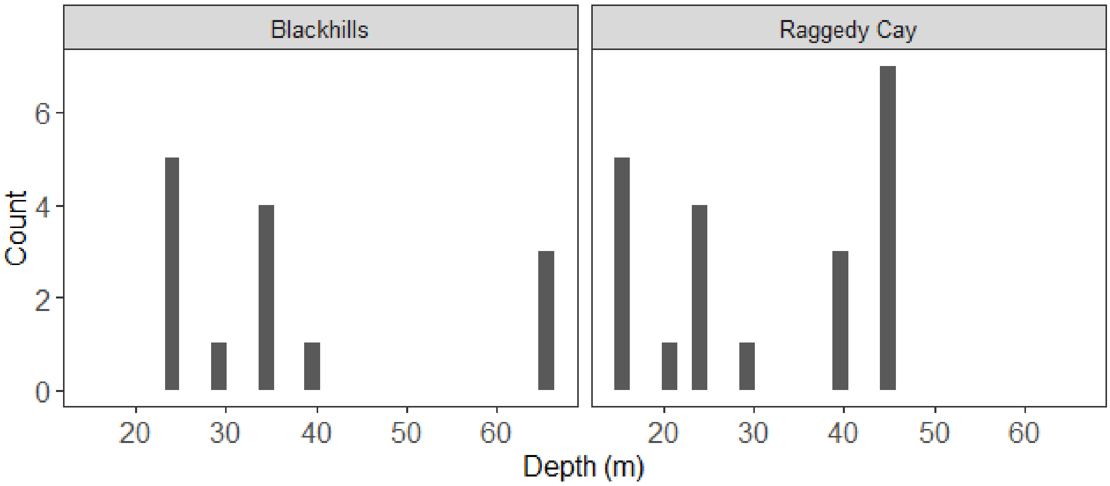


Figure S3.2 Depths at which lionfish were captured at each site.

Chapter 4 Supplementary material

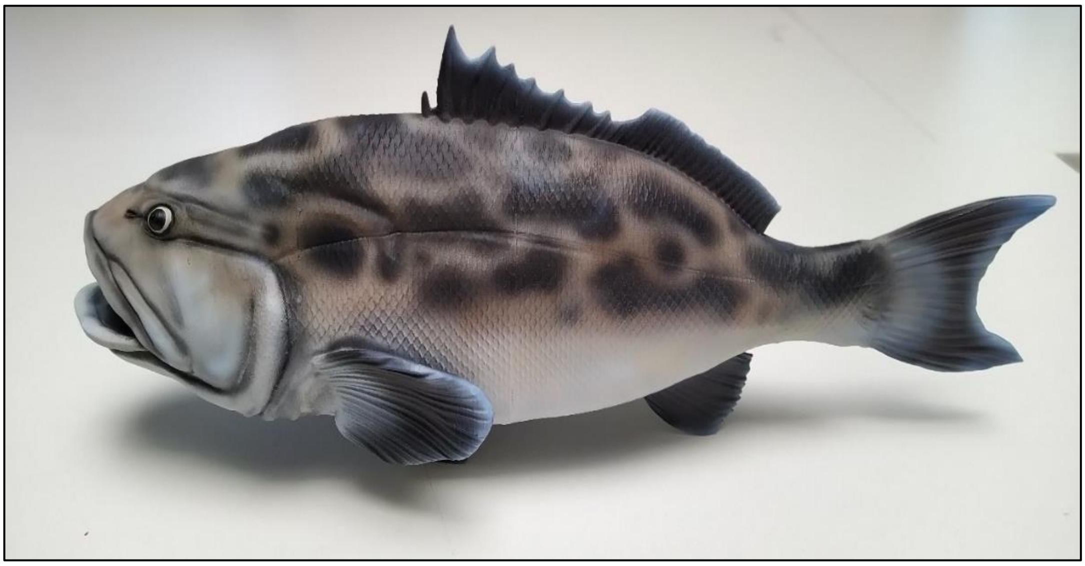


Figure S4.1 Model *Mycteroperca bonaci* used in predator-response experiments. 45 cm total length. Manufactured by 3d-consultancy.com.

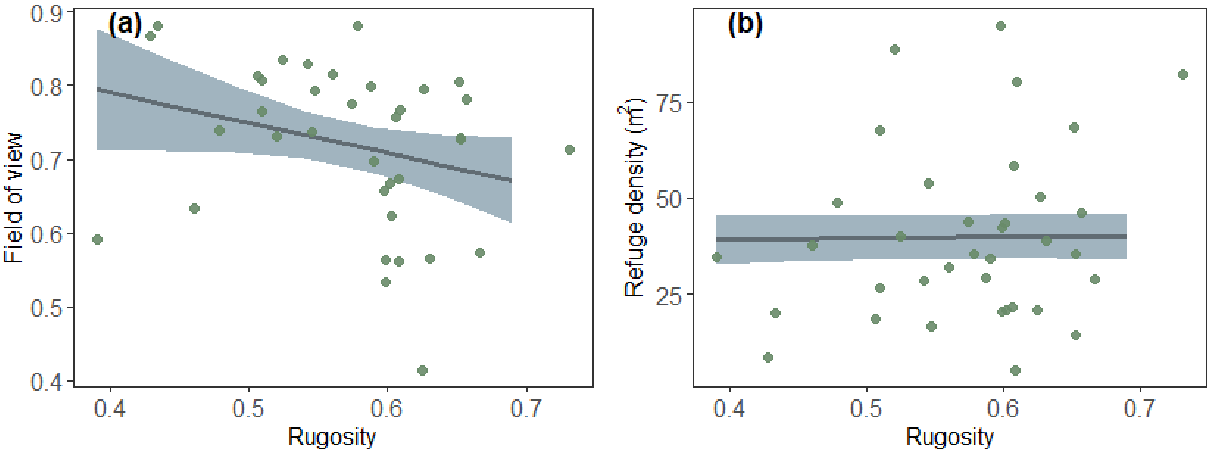


Figure S4.2 The relationship between rugosity and **(a)** field of view and **(b)** 10 cm refuge density (points are raw data, line represents conditional effect, and shading indicates 89% CrIs).

Appendix B: Peer-reviewed papers published over the course of the PhD

[1] **Boon, J. S.**, Keith, S. A., Exton, D. A., & Field, R. (2023). The role of refuges in biological invasions: A systematic review. *Global Ecology and Biogeography*, 32, 1244–1271. https://doi.org/10.1111/geb.13701

Boon, J. S., Vaudin, G., Millward-Hopkins, H., O'Leary, B.C., McClean, C.J. & Stewart, B.D. (2024). Shifts in the size and distribution of marine trophy fishing world records. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 1–13. https://doi.org/10.1002/aqc.4051

Roberts, C., Béné, C., Bennett, N., **Boon, J. S.,** Cheung, W. W. L., Cury, P., Defeo, O., De Jong Cleyndert, G., Froese, R., Gascuel, D., Golden, C. D., Hawkins, J., Hobday, A. J., Jacquet, J., Kemp, P., Lam, M. E., Le Manach, F., Meeuwig, J. J., Micheli, F., Morato, T., Norris, C., Nouvian, C., Pauly, D., Pikitch, E., Amargos, F. P., Saenz-Arroya, A., Sumaila., U. R., Teh, L., Watling, L. & O'Leary, B. C. (2024). Rethinking sustainability of marine fisheries for a fast-changing planet. *Npj Ocean Sustainability*, 3(1), 1–11. https://doi.org/10.1038/s44183-024-00078-2

[1] *Presented in **Chapter 1** of this thesis*