The cross-scale role of reef fish behaviour in mediating space use and behavioural cascades on coral reefs

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Catherine Elizabeth Sheppard: The cross-scale role of reef fish behaviour in mediating space use and behavioural cascades on coral reefs

Abstract

Interspecific interactions play a fundamental role in shaping ecological communities. Whilst the non-consumptive effects of predation on animal behaviour and interspecific interactions are widely studied, the role of aggressive interactions between competitors in behavioural cascades is largely unknown. Using coral reef fish as a model system, I address this significant knowledge gap and improve our understanding of how competitive interactions may drive behavioural cascades across multiple ecological levels and taxa. Firstly, I take a macroecological approach to demonstrate strong links between coral reef benthic state and herbivorous fish functional group co-occurrence and their functional group diversity. Secondly, I demonstrate that between-individual variation in aggressive behaviour by farming damselfish creates a competitive landscape of risk on coral reefs. Thirdly, I identify that competitive risk avoidance between reef fish drives behavioural cascades in other taxa, reducing cleaning rates and client diversity at Pederson's cleaner shrimp *Ancylomenes pedersoni* stations. Finally, I demonstrate that intraspecific aggression between territorial farming damselfish can be predicted by familiarity and differences in body size. The results presented in this thesis improve our knowledge of both the driving mechanisms and ultimate consequences of competition to community dynamics and ecosystem function. Furthermore, by drawing links across ecological scales, from between-individual behavioural variation to the macroecology of co-occurrence patterns, my thesis highlights the multiple pathways through which co-occurrence and competition may drive behaviourally mediated cascades throughout ecosystems.

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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.

- Catherine E. Sheppard, June 2024

Statement of contribution of others

This thesis includes collaborations with my supervisors Sally Keith, Gareth Williams and Dan Exton, as well as co-author Lisa Boström-Einarsson. I conceptualised the research questions and experimental design of my project, collected and analysed data, and synthesised into manuscripts for publication. My collaborators provided guidance, and field and editorial support. Author contributions for each data chapter are provided on its title page. This PhD was funded through the Envision Doctoral Training Programme (DTP) by Natural Environment Research Council (NERC). Additional funding support was provided by my project collaborator, Operation Wallacea.

General Introduction

0.1 The role of interspecific interactions

Interspecific interactions play a fundamental role in shaping ecological communities. Pairwise interactions between species rarely occur in isolation and instead form large complex networks of interactions that affect each other (Wootton, 2002; Koprivnikar and Penalva, 2015; Sheehy *et al.,* 2018). One mechanism driving these cascading effects is interaction modifications, where the direct interaction between two species is affected by the density of another species (Wootton, 1993). Previously known as higher order interactions, interaction modifications were introduced to better predict the effects of interactions in multi-species systems (Neill, 1974). Much of our understanding of these indirect effects comes from studies of predator-prey relationships, where the density and avoidance of predation risk shapes prey behaviour, driving behaviourally mediated cascades throughout ecosystems (Abrams, 1984). A well-known example is that of the reintroduction of grey wolves *Canis lupus* to Yellowstone National Park. Increased predation risk by wolves not only drove changes to the space use of elk *Cervus elaphus*, but indirectly led to increased abundance of beavers *Caster canadensis* and taller aspen trees *Populus tremuloides* (Ripple and Beschta, 2012). Predator avoidance has also been shown to modify interactions between competing prey species (Sheehy *et al.,* 2018) and parasitism (Doherty and Ruehle, 2020). However, interaction modifications and behavioural cascades can also be driven by interspecific competition.

0.1.1 Introduction to interspecific competition

Alongside predation, interspecific competition is a fundamental determinant of ecological community structure. Most theory on interspecific competition focuses on exploitative competition, which refers to the indirect negative effects on one population resulting from the depletion of shared resources by a closely related species (Amarasekare, 2002). In contrast, interference competition is the direct negative interaction between species arising from territoriality, overgrowth, chemical competition and other encounters (Schoener, 1983). Both exploitative and interference competition can alter the abundance of sympatric species and drive ecological niche partitioning. In extreme cases, in a situation where one species is competitively superior or more aggressive, interference competition can even lead to the demise of whole species through competitive exclusion (Amarasekare, 2002). Despite its widespread prevalence in nature, interference competition has received less attention in ecological theory than exploitative competition (Amarasekare, 2002).

0.1.2 Interspecific territoriality and aggression

One of the most empirically researched forms of interference competition is interspecific aggression in the form of territoriality (Peiman and Robinson, 2010). Territoriality is the active interference between competing individuals through the defence of an exclusive area. Aggressive interference is defined as “intimidating or violent interactions between individuals of different species, including threats, displays, and territoriality, but not including predator–prey interactions” (Grether *et al.,* 2017). Aggressive interference therefore encompasses not only physical aggression but displays associated with such. Historically, the importance of aggressive interspecific territoriality has been doubted (Myrberg and Thresher, 1974), with it being proposed that interspecific territoriality was simply a misidentification of interspecific intruders as intraspecific (Murray, 1971; 1976). Some have even suggested that there is no advantage to interspecific aggression, as no territory holder can afford to defend against all intruders (Lorenz, 1963). However, decades of research have provided evidence to the contrary, hypothesising that interspecific territoriality is an adaptive response to overlapping resources or reproductive interference between species and carries significant benefits (Maher and Lott, 2000; Blowes *et al.,* 2013; Cowen *et al.,* 2020; Drury *et al.,* 2020). We now know that territoriality and aggressive interference between species is pervasive and carries significant implications to species distributions and species coexistence (Murray, 1971; Grether *et al.,* 2013; 2017; Bonin *et al.,* 2015). By shaping population distributions and community composition, interspecific interactions play a critical role in determining biodiversity.

0.1.3 Biodiversity-ecosystem function relationships

Biodiversity loss is driving global changes to ecosystem function (Hooper *et al.,* 2012). Species diversity in terms of richness (number of species), evenness (relative abundances of species) and composition (mixture of species present), as well as interactions between species, can affect key functions and processes by maintaining the fluxes of energy and material within an ecosystem (Brandl *et al.,* 2019). Identifying the mechanisms driving biodiversity-ecosystem function relationships is necessary in order to predict how biodiversity loss may impact ecosystem function and how these effects could be exploited to improve management (Duffy, 2003; Connolly *et al.,* 2013; Benkwitt *et al.,* 2020). However, our understanding and ability to predict changes to ecosystem function is limited by our knowledge of the mechanisms through which biodiversity is maintained. Interspecific interactions and species coexistence are two of the fundamental mechanisms that maintain diversity and subsequently impact ecosystem function (Chesson, 2000a; Tilman, 2000). We can explore how interspecific interactions and species coexistence influences biodiversity-ecosystem function relationships through diversity-interactions models (**Chapter 1**).

Diversity-interactions models quantify ecosystem function as the product of individual species identity (identity effects) and diversity effects (Kirwan *et al.,* 2009), modelled as the proportional abundances of different species within a community. Diversity effects are observed as the excess performance by a mixture of species than that expected from the performance of component species identities alone (Kirwan *et al.,* 2009). Diversity effects can result from interspecific interactions and can be synergistic (e.g. niche partitioning and facilitation) or antagonistic (e.g. competition) (Kirwan *et al.,* 2009). These interactions are not necessarily direct biological interactions, and diversity effects can instead arise simply through species co-occurrence, where the presence of two or more species in different relative abundances influences ecosystem function (Connolly *et al.,* 2013).

0.1.4 Species distributions and behavioural cascades

As well as large-scale patterns of species coexistence, interspecific competition can shape local community structure and the spatial distribution of populations (Durant, 2000; Ferry *et al.,* 2016; Swanson *et al.,* 2016). Interference competition, through which aggressive interactions among competitors prevent access to a shared resource, is the main mechanism driving differences in patterns of resource use between species (Ritchie and Johnson, 2009; Swanson *et al.,* 2016; Eurich *et al.,* 2018a). Territoriality and aggressive interference typically result in the more dominant or aggressive species monopolising resources which triggers active avoidance and limits access by competitive subordinates (Swanson *et al.,* 2016; Eurich *et al.,* 2018a; Sheppard *et al.,* 2024; **Chapter 2**). This partitioning of resources ultimately shapes the spatial distribution of populations of interspecific competitors. Spatial avoidance by subordinate or less aggressive competitors is a mechanism through which to minimise the cost of interference competition (Swanson *et al.,* 2016). The ecological consequences of spatial avoidance are well established in predator-prey systems (Laundré *et al.,* 2001; Madin *et al.,* 2010a; Ripple and Beschta, 2012) and typically comprise of the behavioural response of prey species to an increased perceived risk of predation (Gaynor *et al.,* 2019). It is reasonable to expect similar processes between competitors in response to increased risk of aggressive encounters. One way we can explore competition-driven spatial distribution is through the "landscape of risk" framework (**Chapter 2**).

The landscape of risk is a derivative of the "landscape of fear", which was introduced to understand how predation risk shaped the spatial distribution and behaviour of elk and bison *Bison bison* upon reintroduction of wolves to Yellowstone National Park (Laundré *et al.,* 2001). The landscape of fear is defined as the spatial variation in prey perception of predation risk (Gaynor *et al.,* 2019) and constitutes a three-dimensional landscape whose "hills" and "valleys" represent differing levels of risk (Laundré *et al.,* 2001; 2010). Since its introduction, the landscape of fear has been become a central concept to the study of predator-prey interactions (Gaynor *et al.,* 2019) in both terrestrial (Ripple and Beschta, 2012; Dupuch *et al.,* 2014) and marine environments (Madin *et al.,* 2011).

More recently, the landscape of risk framework, defined as the spatiotemporal pattern of risk (Norum *et al.,* 2015), has been employed to study other interspecific interactions such as parasite avoidance, coined the landscape of disgust (Weinstein *et al.,* 2018; Doherty and Ruehle, 2020). Individuals are subject to multiple sources of risk (predation, parasites, competition). Expanding the landscape of risk framework provides a useful tool to understand how risks other than predation shape species distribution and drive behavioural cascades. For example, competition-driven landscapes of risk may represent spatial variation in the risk of aggressive encounters and provide a framework on which to understand and predict the distribution and behaviour of foragers under direct interference competition (**Chapter 2**).

Landscapes of risk can further be used to understand and predict cascading effects throughout interaction networks. For example, when both predation and parasite risk were present, Northern leopard tadpoles *Lithobates pipiens* preferentially foraged under the threat of parasitism (Koprivnikar and Penalva, 2015), putting them at greater risk of infection. One group of interspecific interactions that may be affected by competitive risk avoidance is mutualistic cleaning interactions (**Chapter 3**). Patterns of cleaning interactions vary both spatially (Bansemer *et al.,* 2002; Romain *et al.,* 2020) and temporally (Titus *et al.,* 2015). Though many factors have been identified to explain broad-scale patterns in cleaning interactions, including conditions of the physical environment (Marcogliese, 2002; Artim and Sikkel, 2013), parasitic load (Grutter, 1995) and client body size (Arnal *et al.,* 2000), the drivers of more localised variation are less understood. By modelling behavioural cascades through landscapes of risk, we can explore whether risk avoidance drives spatial variation in cleaning interactions (e.g. Arnal and Côté, 1998), thereby offering another mechanism through which risk affects parasitic infection.

0.1.5 The importance of trait variation in interspecific competition

The landscape of risk framework typically focuses on behaviour at the population or species level and relies on patterns of distribution and density to create spatial variation in risk (Gaynor *et al.,* 2019). However, behavioural variation between individuals can have profound effects on interspecific interactions and community dynamics (Bolnick *et al.,* 2011; Milles *et al.,* 2020; Nicastro *et al.,* 2020). In some instances, the ecological impacts of intraspecific trait variation can match or even exceed those of variation between species (Start and Gilbert, 2019; Nicastro *et al.,* 2020). Evolutionary biologists regularly consider trait variation between individuals, as this forms the basis for evolution and adaptation. However, community ecologists have historically overlooked the impact of between-individual variation, concentrating on differences between species and modelling interspecific interactions based on population means (Bolnick *et al.,* 2011). Reviews have encouraged that this knowledge gap be addressed, arguing the importance of considering intraspecific trait variation when studying community structure and dynamics (Bolnick *et al.,* 2011). Interest in how between-individual variation influences ecological dynamics has since increased, both in theoretical and empirical research (Start and Gilbert, 2017; 2019; Milles *et al.,* 2020; Nicastro *et al.,* 2020).

Many territorial species hold contiguous territories (Kitchen, 1974; Itzkowitz, 1978; Adams, 1998; Potts *et al.,* 2013), creating a mosaic of aggressively defended territories across a landscape, which means there is little spatial pattern in their distribution. However, between-individual variation in territorial aggression is common (Hyman *et al.,* 2004; Eriksson *et al.,* 2010; Chaloupka *et al.,* 2022). Therefore, it stands to reason that variation in territorial behaviours, and the spatial nature of territoriality, may result in spatial variation in the degree of aggressive interactions across landscapes (**Chapter 2**).

0.1.6 Thinking across scales

One key area that remains elusive is how behaviour mediates ecological dynamics across scales. Behavioural traits can be measured in common units across biological scales, from individual to communities, making them a useful tool for multi-level studies on the ecological impacts of trait variation. This bears particular importance where predator- or competitor-mediated cascades cause disruption to community composition and ecosystem processes (Sih *et al.,* 2012; Start and Gilbert, 2017; 2019). For example, between-population trait variation in predatory dragonflies *Epitheca canis* had a greater impact on prey composition, trophic cascades and ecosystem function than within-population variation (Start and Gilbert, 2019). We may also expect similar consequences to community composition driven by between-individual variation in aggressive behaviour or competitive ability within competing species. Incorporating trait variation across scales will provide critical insight into the impacts of risk avoidance on population spatial distribution (**Chapter 2**), community composition and dynamics (**Chapter 3**), and ecosystem dynamics (**Chapter 1**) in natural systems.

0.2 Determinants of aggression in interspecific territoriality

Though the benefits of territoriality are clear, in terms of priority access to resources, the associated aggressive behaviours carry costs, including increased energy expenditure (Start and Gilbert, 2017) and risk of injury (Clutton-Brock and Huchard, 2013). Hence, territoriality is expected to evolve when the benefits of holding a territory outweigh the costs of its defence, and when resources are limited (Ord, 2021). The benefits and costs of territorial defence are likely to vary between different competitors (Peiman and Robinson, 2010) and may be understood in terms of the level of threat posed. Potential threat may be determined by multiple factors, including resource overlap and uncertainty.

0.2.1 Resource overlap hypothesis

Territoriality and associated aggressive interactions occur when there is strong competition for a limited resource which, when considering interspecific competition, is driven by resource overlap. The resource overlap hypothesis predicts that interspecific aggression will be heightened when the degree of resource overlap between competitors and the value of the shared resource are higher (Peiman and Robinson, 2010). For example, herbivorous jewel damselfish *Plectroglyphidodon lacrymatus* were more aggressive towards other herbivores, with presumed greater degree of dietary overlap (Paola *et al.,* 2012). However, a limitation of the resource overlap hypothesis is that not all adaptive interspecific aggression may be the result of a shared resource. One such example is the aggressive defence of nest sites against interspecific species that predate on eggs or infants (e.g. Garcia and Arroyo, 2002; Goiran and Shine, 2015).

0.2.2 Offspring-defence hypothesis

The offspring-defence hypothesis predicts that female territoriality in the absence of dietary drivers is associated with the defence of vulnerable young from infanticide by members of the same species (Wolff and Peterson, 1998). I argue that this hypothesis can be extended to any individual, male or female, that holds a territory with the purpose of egg-laying or rearing infants, and that aggressive defence will be directed towards any species that threatens their offspring, such as egg predators. Species of farming damselfishes *Stegastes* spp. that hold multipurpose territories are often observed aggressively chasing juvenile bluehead wrasse *Thalassoma bifasciatum* (**Chapters 2-3**); a common egg predator (Froese and Pauly, 2023). Following this extended offspring-defence hypothesis, interspecific territoriality will be predicted in species whose territories serve a reproductive purpose.

0.2.3 Uncertainty hypothesis

Aggressive interactions between different species likely carry a greater degree of uncertainty as to the outcome than between individuals of the same species (Peiman and Robinson, 2010). This is because individuals are thought to be better able to predict the outcome of interactions with intraspecific competitors compared with interspecific species due to the coevolution of signals and displays (Parker, 1974). The uncertainty hypothesis makes three main predictions: 1) that signalling will be more common between intraspecific competitors, 2) that interspecific aggression will be more varied, and 3) that individuals will be less willing to approach interspecific competitors than intraspecific (Peiman and Robinson, 2010). Empirical evidence in support of the uncertainty hypothesis is mixed. Field observations of jewel damselfish showed little difference in the level of aggression directed towards intraspecific compared with interspecific intruders, yet threat displays were more common in intraspecific interactions (Paola *et al.,* 2012). However, behavioural manipulations in the field found that lacertid lizards *Podarcis melisellensis* and *Dalmatolacerta oxycephala* were more aggressive towards interspecific rather than intraspecific competitors, even though dietary overlap was low (Lailvaux *et al.,* 2012). Furthermore, uncertainty in the outcome of interspecific interactions may be mediated by competitor recognition. By recognising competitors, individuals can adjust their response to competitors based on the level of threat they pose, minimising the costs of engaging in aggressive interactions (Arnott and Elwood, 2009).

0.2.4 Intraspecific competition

Territory defence requires energy (Marler *et al.,* 1995; Neat *et al.,* 1998). Therefore, territory holders must balance the energetic requirements of aggressive behaviour between different competitors to minimise these costs. It has been suggested that interspecific aggression and territoriality may be driven based on the relative densities between intra- and interspecific competitors (Mikami and Kawata, 2004). Heightened intraspecific competition, as a result of increased relative density, may promote species coexistence as territory holders prioritise energy spent on territory defence against intraspecific competitors rather than individuals of other species. However, focusing on densities alone does not consider the relative cost of intrusion between intra- and interspecific competitors. For example, if the relative costs of intrusion by interspecific competitors are low (i.e. low resource overlap) then interspecific aggression may not be favoured, even when the relative density of interspecific competitors is high. Equally, species that have significant overlap in resource use may favour interspecific aggression at lower relative densities. It is important to consider the interplay between intra- and interspecific competition, and any mechanisms that alter the relative threat posed by both. One such mechanism that may reduce the costs of territory defence against intraspecific competitors is familiarity (**Chapter 4**).

Game theory proposes that through fighting, animals gain information on the resource holding potential (RHP) of their opponents and can better assess the likelihood of winning or losing ("fight-to-learn": Parker and Rubenstein, 1981; Getty, 1989; Arnott and Elwood, 2009). Increased familiarity between individuals inevitably leads to greater knowledge of their opponents RHP, meaning that the potential outcome of subsequent aggressive encounters is more predictable. As such, the familiarity hypothesis predicts that known individuals will elicit a weaker aggressive response than strangers, as frequent past encounters result in reduced conflict in subsequent interactions (Ydenberg *et al.,* 1988; Temeles, 1994). By recognising and adjusting aggressive responses towards known individuals that are encountered more often than strangers (**Chapter 4**), individuals can minimise the energetic costs of territory defence against intraspecific competitors. Thus, familiarity between intraspecific competitors could indirectly drive competition between species as more energy is available for interspecific territory defence.

0.3 The importance of competition in managing human impact

Anthropogenic environmental disturbances are changing animal behaviour and spatial distributions across the globe (Wilson *et al.,* 2020). Animal behaviour underpins many ecological processes, including primary productivity, intra- and interspecific competition, predation and parasitism (Sih *et al.,* 2010; Koprivnikar and Penalva, 2015; Start and Gilbert, 2017). As such, the ever-expanding impact of humans has the potential to drive behavioural cascades throughout ecosystems with large-scale consequences. Human-induced environmental change is impacting community and ecosystem dynamics by altering interspecific interactions and driving behaviourally mediated cascades (Wilson *et al.,* 2020). For example, by changing the dynamics between a single pair of species, through removal of a predator (Madin *et al.,* 2010b; 2016) or competitor (Bolnick *et al.,* 2010), human impact can cascade to influence other parts of the interaction network. In turn, these interaction modifications can shape ecosystem processes and functions. Deepening our understanding of competition-driven interaction modifications across ecological scales is critical in order to better predict and manage human impact.

0.4 Coral reef ecosystems

Coral reefs are one of the most diverse and productive ecosystems on the planet, supporting a third of all marine species and providing critical services to millions of people (Plaisance *et al.,* 2011; Hughes *et al.,* 2017). Scleractinian corals (hard corals) form the foundation of coral reefs, building structurally complex habitats and providing essential shelter and dietary resources to a wide variety of taxa (Graham and Nash, 2013). However, human-induced environmental disturbances are driving rapid coral reef decline (Hughes *et al.,* 2017). Globally, rising temperatures are increasing the frequency of mass coral reef bleaching events, where corals expel their symbiotic zooxanthellae, placing them at risk of starvation (Sully *et al.,* 2022; Vessaz *et al.,* 2022). When prolonged, these bleaching events can result in large-scale coral mortality and loss of structural complexity, reducing reef fish diversity and driving population declines (Wilson *et al.,* 2006). These changes to reef fish community composition alter the dynamics of interspecific interactions between reef inhabitants. Locally, selective fishing of larger herbivorous fish is shifting the composition of herbivore communities and reducing herbivore biomass by over 50% in areas accessible to fishing (Edwards *et al.,* 2014). Herbivory is a key process on coral reefs and herbivores exert a huge influence on the physical structure of coral reefs by removing algae and supporting coral accretion (Green and Bellwood, 2009). Maintaining herbivore biomass is fundamental in supporting healthy ecosystem function and reducing the risk of phase shifts to algal-dominated states on tropical coral reefs (Adam *et al.,* 2015; Graham *et al.,* 2015). However, preserving functional diversity is also important.

Herbivores can be broken down into functional groups based on their feeding behaviour (Green and Bellwood, 2009; Edwards *et al.,* 2014; Bellwood *et al.,* 2019; Tebbett *et al.,* 2022). Croppers (also referred to as grazers) graze on epilithic turf algae and can limit macroalgal growth. Scrapers and excavators also feed on turf algae but remove some of the reef substratum by scraping the reef surface. The extent to which they excavate the substratum characterises these two groups (Bellwood and Choat, 1990; Green and Bellwood, 2009). Finally, browsers consume macroalgae and play a role in reducing overshading of coral. Maintaining functional diversity of herbivorous fish can further support algal control through feeding complementarity (Burkepile and Hay, 2008). However, competition and agonistic interactions between herbivorous species may have detrimental effects on coral reef benthic state.

0.4.1 Territoriality and aggression in coral reef fish

Interspecific competition between reef fish is prevalent and can shape the spatial distribution of species at both macro and local scales (Bonin *et al.,* 2015; Fontoura *et al.,* 2020). Competition between pairs of fish species is often highly asymmetrical (Bonin *et al.,* 2015). These asymmetries often occur through interference competition, where one species is more aggressive and/or territorial, and can result in the exclusion of subordinate or less aggressive species from an area (Amarasekare, 2002). By shaping community composition and species spatial distributions, interference competition between herbivores will undoubtedly influence herbivory on coral reefs and subsequently impact the risk of phase-shifts to algal-dominated states.

Aggressive behaviour and territoriality are common among reef fish, and many species exhibit highly stable site-attachment (Ceccarelli *et al.,* 2001; Blowes *et al.,* 2017; Manning and McCoy, 2023). One such group of species are the territorial farming damselfishes, whose unusual turf-farming behaviour has such a dramatic effect on coral reefs that they are widely recognised as keystone species (Hixon and Brostoff, 1983, Ceccarelli *et al.,* 2005a). Though categorised as croppers, the farming behaviour of damselfishes often distinguishes them as a separate herbivorous functional group (Ceccarelli *et al.,* 2005b). Some of the most aggressive species are within the genus *Stegastes* (Ceccarelli *et al.,* 2001), which hold small individual but contiguous territories that they defend from both intra- and interspecific intruders (Itzkowitz, 1978; Ceccarelli *et al.,* 2001). Aggressive interactions with farming damselfishes are expected to influence the distribution and foraging behaviour of other reef inhabitants, however evidence of this is varied. Experimental removal of farming damselfishes which allowed other herbivores access to previously defended areas of reef found both subsequent increased herbivory rates (Mahoney, 1981), and no effect to benthic composition (Ceccarelli *et al.,* 2001). High abundance of farming damselfishes may also decrease rates of coral predation (Tiddy *et al.,* 2023) and juvenile parrotfish recruitment (Tolimieri, 1998). The presence of farming damselfishes has even been found to alter the composition of cleaning clientele by cleaner gobies *Elacatinus* spp. (Arnal and Côté, 1998). Although general patterns of the impacts of aggressive damselfish are uncertain, these species have clear cascading consequences to coral reef communities.

0.5 Thesis overview

In this thesis, I aim to improve our understanding of how interspecific competition may drive behavioural cascades throughout ecosystems (Figure 0.1), with a focus on competitive risk avoidance. My thesis will improve our knowledge of both the driving mechanisms and ultimate consequences of interspecific competition to community dynamics. Furthermore, I draw links across ecological scales, from between-individual behavioural variation to the macroecology of co-occurrence patterns, offering insight into how behavioural cascades can transverse throughout ecological systems (Figure 0.1).

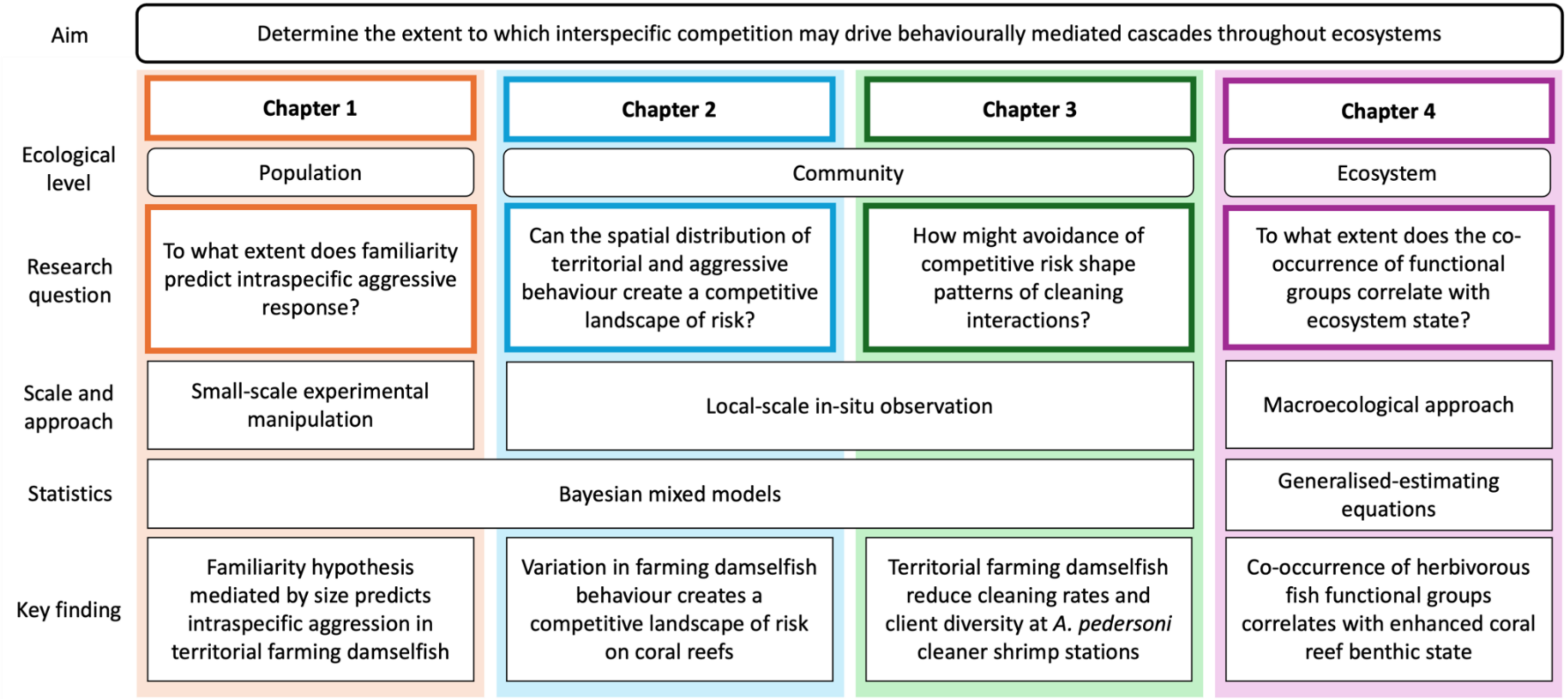
This thesis will address the following research questions:

1. To what extent does the co-occurrence of functional groups correlate with ecosystem state?

2. Can the spatial distribution of territorial and aggressive behaviour create a competitive landscape of risk, and to what extent does this shape competitor distribution?
3. How might avoidance of competitive risk shape patterns of cleaning interactions?
4. To what extent does familiarity predict intraspecific aggressive response?

I use coral reef fish as a model system to answer my research questions, with a focus on aggressive interactions with territorial farming damselfish of the genus *Stegastes*. Throughout my thesis, I combine empirical field observations with novel techniques and manipulative experiments. I expand upon current theory on interspecific interactions to direct my research and form hypotheses. Firstly, I apply diversity-interactions models that use statistical interactions to reveal how the co-occurrence of herbivorous functional groups affects measures of coral reef benthic state. I use an extensive dataset of 16541 transects from 601 sites in 12 countries across the western Atlantic, taking a macroecological approach to study biodiversity-ecosystem function relationships (**Chapter 1**). Secondly, I expand upon the landscape of risk framework to explore how interspecific territoriality can shape a competitive landscape of risk in subordinate or less aggressive species. I use detailed spatial and behavioural data to investigate whether farming damselfishes shape the spatial distribution of other reef fish (**Chapter 2**). Following our findings, I begin to explore how spatial avoidance of competitors may drive behavioural cascades in other interspecific interactions, namely mutualistic cleaning interactions. Specifically, I examine the patterns of cleaning interactions with Pederson’s cleaner shrimp *Ancylomenes pedersoni* between cleaning stations located inside and outside of farming damselfish territories (**Chapter 3**). Finally, I explore whether familiarity affects intraspecific aggression in farming damselfishes by presenting territory holders with both neighbouring individuals and non-neighbours and recording their subsequent aggressive response (**Chapter 4**).

Each of the four data chapters (**Chapters 1-4**) within my thesis were written for publication. **Chapter 1** and **Chapter 2** have been published in *Global Ecology and Biogeography* and *Biology Letters* respectively. **Chapter 4** has been submitted to *Behavioural Ecology*. I am currently working in collaboration with Dr Rachel Gunn, University of Tübingen, to extend my results from **Chapter 3** with datasets of cleaning interactions with cleaner gobies. This collaborative manuscript is being prepared for submission and will explore how territorial farming damselfishes shape patterns of cleaning interactions with Pederson’s cleaner shrimp and cleaner gobies.



Aim	Determine the extent to which interspecific competition may drive behaviourally mediated cascades throughout ecosystems			
	Chapter 1	**Chapter 2**	**Chapter 3**	**Chapter 4**
Ecological level	Population	Community		Ecosystem
Research question	To what extent does familiarity predict intraspecific aggressive response?	Can the spatial distribution of territorial and aggressive behaviour create a competitive landscape of risk?	How might avoidance of competitive risk shape patterns of cleaning interactions?	To what extent does the co-occurrence of functional groups correlate with ecosystem state?
Scale and approach	Small-scale experimental manipulation	Local-scale in-situ observation		Macroecological approach
Statistics	Bayesian mixed models			Generalised-estimating equations
Key finding	Familiarity hypothesis mediated by size predicts intraspecific aggression in territorial farming damselfish	Variation in farming damselfish behaviour creates a competitive landscape of risk on coral reefs	Territorial farming damselfish reduce cleaning rates and client diversity at *A. pedersoni* cleaner shrimp stations	Co-occurrence of herbivorous fish functional groups correlates with enhanced coral reef benthic state

Figure 0.1 Thesis overview outlining research aim and questions, ecological and spatial scale, approach, statistical methods and key findings.

Chapter 1: Co-occurrence of herbivorous fish functional groups correlates with enhanced coral reef benthic state

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Author Contribution

All authors contributed to conceptualisation of the research. CES led the methodology design, data analysis with support from all authors. CES wrote the first manuscript draft; all authors edited the manuscript.

Abstract

Aim: Biodiversity loss is impacting essential ecosystem functions and services across the globe. More recently, our interest in the benefits of biodiversity on ecosystem function has shifted focus from measurements of species richness to functional diversity and composition. However, the additional importance of other community characteristics, such as species evenness and co-occurrence, for diversity-driven ecosystem function is less known. We used herbivorous coral reef fish as a model system to investigate how co-occurrence of different functional groups, rather than purely functional diversity, within an assemblage may affect coral reef benthic state.

Location: Western Atlantic

Time period: 2007 – 2017

Major taxa studied: Herbivorous reef fish

Methods: We analysed benthic and fish assemblage data from 601 sites across 12 countries in the Western Atlantic. Using Diversity-Interactions models, we investigated how the composition and relative abundances of reef fish functional groups correlated with benthic cover and estimates of coral calcification rates. We used statistical interactions to explore the importance of herbivorous fish functional group co-occurrence for coral reef benthic state.

Results: We found that co-occurrence of herbivorous fish functional groups, as well as functional diversity, was correlated with reduced algal cover and increased coral accretion. Moreover, pairwise statistical interactions between functional groups were significantly correlated with improved coral reef benthic state.

Main conclusions: Our results support the idea that functional group co-occurrence, as well as functional diversity, within herbivorous fish offers additional benefits to coral reef benthic state. We identify farming damselfish and excavating parrotfish as potential key determinants of coral reef benthic state, and highlight that co-occurrence of cropping and scraping herbivores may promote coral accretion. Our findings support the argument that protecting herbivore abundance without regard to the species and functional groups present is not enough to preserve coral reef health, and that fine-scale community composition must be considered.

1.1 Introduction

Biodiversity loss is driving changes to ecosystem function across biomes (Hooper *et al.,* 2012). Ecosystem function, defined as the fluxes of energy and material within an ecosystem (Bellwood *et al.,* 2019), can be mediated by the identity and composition of species present, and their interactions with their environment (Brandl *et al.,* 2019). Historically, the positive effects of biodiversity on ecosystem function focussed on measures of species richness, likely due to the prominent interest in and irreversibility of species loss (Chapin *et al.,* 2000; Kirwan *et al.,* 2007; Hooper *et al.,* 2012). However, more recently, interest in diversity-driven ecosystem function has shifted towards functional diversity and the composition of functional traits (Cheal *et al.,* 2010; Mouillot *et al.,* 2011; Finn *et al.,* 2013; Stuart-Smith *et al.,* 2013; Bellwood *et al.,* 2019; Grange *et al.,* 2021). When fewer species are present, increased functional diversity improves a community's ability to extract resources from its environment and maintain ecosystem function (Cadotte *et al.,* 2011). Equally, niche partitioning between species allows for better utilisation of an ecosystem's limited resources and increases the probability of positive co-occurrence effects on ecosystem function (Duffy *et al.,* 2017).

Coral reefs are highly diverse, productive ecosystems and provide numerous ecosystem services that benefit human well-being, including food provisioning and cultural importance (MEA, 2005; Woodhead *et al.,* 2019). Like many tropical systems, anthropogenic impacts, such as overfishing, pollution and climate change, are increasingly altering species composition and fundamentally changing ecological processes on coral reefs (Mora *et al.,* 2011; Hughes *et al.,* 2017; Williams and Graham, 2019). Functional diversity within herbivorous reef fish is widely recognised to support healthy coral reef function. Herbivorous fish play a crucial role in maintaining the physical structure and continued accretion of coral reefs (Green and Bellwood, 2009). By removing algal biomass, herbivores support reef-building benthic organisms and help prevent regime shifts to fleshy macroalgal dominated systems (Graham *et al.,* 2015). High functional diversity within the herbivore guild can increase measurements indicative of enhanced reef function, such as total fish biomass (Duffy *et al.,* 2016), standing biomass (Mora *et al.,* 2011) and herbivory rate (Lefcheck *et al.,* 2019).

Complementary feeding behaviours between herbivorous reef fish can also lower the abundance of certain algae and increase hard coral cover (Burkepile and Hay, 2008).

Understandably, there is much emphasis on broadly protecting herbivory in order to conserve the functions and services of coral reefs (Adam *et al.,* 2015). However, high functional diversity within herbivorous reef fish (Green and Bellwood, 2009) means that such broad approaches to managing herbivores as a whole fail to appreciate the importance of their fine-scale community composition. Furthermore, little is known of how functional group evenness and co-occurrence within the herbivore guild influences coral reef state and resilience (Brandl *et al.,* 2019). It is plausible that co-occurrence of different herbivore species, or functional groups, provides additional benefits to coral reef function than their single identities alone. Consequently, any attempt to predict ecosystem function based solely on species richness and community composition may be inaccurate.

We can explore the potential effects of individual versus combinations of herbivores using Diversity-Interactions models. These models quantify the effects of species identity and diversity on ecosystem function, separating the contributions of different species and their statistical interactions (Kirwan *et al.,* 2009). “Interactions” are not necessarily direct biological interactions, and may simply imply that the presence of various species in different relative abundances significantly impacts ecosystem function (Connolly *et al.,* 2013). As such, interaction effects may be understood as the additional effects arising through species co-occurrence. Even so, this approach aids the understanding of how interspecific interactions may affect ecosystem function and allows us to develop more explicit hypotheses for future exploration.

Previous work using Diversity-Interactions models to investigate diversity-driven coral reef function found that species diversity enhanced herbivory rates on coral reefs, yet no additional effect of herbivore species co-occurrence was identified (Lefcheck *et al.,* 2019). However, these analytical approaches were limited to an “average interaction” term rather than separate pairwise interactions (Lefcheck *et al.,* 2019). This modelling approach is analogous to the “evenness model” (Kirwan *et al.,* 2009), which assumes that the strength of any statistical interaction between species is the same for all pairwise combinations. By modelling each pairwise statistical interaction separately, we can explore and identify the pairwise co-occurrences between herbivorous fish functional groups with the greatest potential effects.

Here, we investigate the influence of community composition and co-occurrence of herbivorous fish functional groups using measurements of coral reef benthic state as a proxy for reef function. To achieve this aim, we apply Diversity-Interactions models (Kirwan *et al.,* 2009) to a large-scale dataset spanning 10 years, located across 12 countries in the western Atlantic. Specifically, we use benthic cover and estimates of dynamic processes, hereafter referred to collectively as “benthic metrics”, and relative abundances of reef fish functional groups. Using these results, we discuss the potential importance of functional group co-occurrence within herbivorous reef fish communities to coral reef benthic state.

1.2 Methods

1.2.1 AGRRA dataset description

In total, our analysis used data from 942 surveys across 601 sites. We analysed benthic and fish abundance data from 16541 transects collected as part of the Atlantic and Gulf Rapid Reef Assessment (AGRRA; Marks, 2018) between 2007 and 2017, bolstered with past estimations of coral calcification rates (González-Barrios and Álvarez-Filip, 2018). The AGRRA dataset consists of a comprehensive set of measurements that quantify multiple components of coral reef ecosystem state and covers a large geographic extent (latitude: 12.0° – 27.3°, longitude: -96.1° – -61.5°; 12 countries, 601 sites) across the western Atlantic (see Appendix A, Figure S1.1).

AGRRA surveys benthic and fish communities with a focus on ecologically or commercially important reef fish species, alongside measurements of coral reef benthic condition (Marks, 2018). Fish species were recorded along belt transects (30 m x 2 m) and their body size estimated as one of six size categories (0-5 cm; 6-10 cm; 11-20 cm; 21-30 cm; 31-40 cm; > 40 cm). From these size estimates, biomass was calculated using standardised length-to-weight relationships from FishBase (fishbase.org; Froese and Pauly, 2023). Belt transects (10 m x 1 m) were also used to capture coral colonies ≥ 4 cm in maximum length, which were identified where possible to the species level (occasionally genera; 2.01 % of observations included in our analysis) and their maximum length and width recorded. Depth was measured at the start and end of each fish transect and an average calculated.

Benthic composition was recorded using 10 m long point intercept transects (PIT) where substrate type was noted every 0.1 m (totalling 100 points). Coral recruits ≤ 2 cm in maximum length within a 25 cm x 25 cm square quadrat placed at 2 m intervals along these transects were also recorded, as well as the number of adult and juvenile *Diadema antillarum* (historically important herbivorous urchins on western Atlantic reefs; Bodmer *et al.,* 2015). For each site, geographic coordinates, ecoregion and geographical subregion were available. Sites included in our analysis were spread across 47 subregions and five ecoregions (Appendix A, Figure S1.1).

1.2.2 Calculation of herbivore functional group abundances

Our data included 99 fish taxa. Herbivorous fish are commonly assigned to four main functional groups based on their feeding behaviour: croppers (e.g. surgeonfish: Acanthuridae), browsers (e.g. chubs: Kyphosidae), scrapers and excavators (e.g. parrotfish: Labridae) (Green and Bellwood, 2009; Edwards *et al.,* 2014; Bellwood *et al.,* 2019; Tebbett *et al.,* 2022). Additionally, the unusual farming behaviour displayed by territorial damselfish often distinguishes these species as a separate functional group (Ceccarelli *et al.,* 2005b). Territorial farming damselfish are known to affect species occurrence and subsequent changes to coral reef benthic structure (Ceccarelli *et al.,* 2001; Ceccarelli, 2007). As our main aim is to explore the effects of herbivore co-occurrence on coral reef benthic state, we reason that the distinct behaviours and ecological consequences of this group of herbivores necessitates their inclusion in our analysis as a separate functional group. It must be noted that recent work by Tebbett *et al.* (2022) examining the functional roles of surgeonfishes classified *Acanthurus chirurgus* and *A. tractus* as sediment suckers rather than croppers. However, sediment suckers are functionally very similar to croppers in relation to their role in algal removal in the Atlantic and were, therefore, grouped alongside *A. coeruleus* as croppers in our study.

Following these common classifications, we grouped herbivorous fish species into five functional groups (croppers, browsers, farmers, scrapers and excavators) based on the literature (Green and Bellwood, 2009; Choat *et al.,* 2012; Adam *et al.,* 2018; Appendix A, Table S1.1). Parrotfish of the genera *Scarus* and *Sparisoma* that were not identified in Adam *et al.* (2018) were assigned functional groups guided by the closest related species (for further details, see Appendix A, Table S1.1: Bellwood and Choat 1990; Bernardi *et al.,* 2000; Choat *et al.,* 2012). Species from the parrotfish genus *Cryptotomus* did not appear in Adam *et al.* (2018) and were assigned functional groups using dietary data available from Fishbase (Froese and Pauly, 2023; Appendix A, Table S1.1).

Proportional abundances of each herbivorous functional group, as well as total herbivorous fish biomass, were calculated per transect. We focus on proportional abundance rather than proportional biomass as, in this context, the number of individual fish per functional group is more useful for investigating the importance of co-occurrence. We believe this is justified as it is presence and behaviour of individuals that shape activities at the population level which, in turn, have consequences to community structure and interspecific interactions. Although herbivore biomass is an important determinant of coral reef benthic state (Williams *et al.,* 2019; Williams and Polunin, 2001), when divided into functional groups, proportional biomass can be dramatically skewed by just a few large-bodied individuals, particularly excavating parrotfish (e.g. *Sparisoma viride*; Adam *et al.,* 2018) (per survey; mean number of excavators: 1.80; mean proportional biomass of excavators: 0.24). As such, it seemed more appropriate to use proportional abundance as a measure of community structure to remove this size bias. Total herbivore biomass was, however, included in our analysis as a separate explanatory variable.

1.2.3 Calculation of benthic metrics

We calculated multiple metrics associated with coral reef benthic state using methods adapted from Lester *et al.* (2020). Our benthic metrics were chosen to reflect the core coral reef processes laid out by Brandl *et al.* (2019) and focus on measurements relating to algal and coral communities (full summary in Appendix A, Table S1.2). These metrics help to identify the most dominant benthic organism (algae or coral) and rate of coral reef accretion and expansion, offering an indication of coral reef health and function.

Our data included 63 coral taxa. Coral species were classified into four trait-based groups as per Darling *et al.* (2012); competitive, weedy, stress-tolerant and generalist. Coral species not identified in Darling *et al.* (2012) and those not recorded at the species-level were classified based on genus and known traits (Madin *et al.,* 2016; Appendix A, Table S1.3). Grouping corals in this way allows us to explore the correlation between herbivore and coral community compositions. This is important as different trait-based groups of coral vary in their contribution to coral reef accretion and function (Green *et al.,* 2008; Darling *et al.,* 2012; González-Barrios and Álvarez-Filip, 2018; González-Barrios *et al.,* 2021). Coral species richness (total number of coral species) and coral cover (m^2) were computed per transect, as well as the cover of each separate trait-based coral group (m^2). Total calcification rates (kg $CaCO_3$ m^{-2} $year^{-1}$) per transect were calculated by applying mean species-specific calcification rates (González-Barrios and Álvarez-Filip, 2018) to coral cover estimates. Where corals were not recorded at the species-level, we applied the average calcification rate across all species in the genus (González-Barrios and Álvarez-Filip, 2018). Coral taxa with no calcification estimates available were removed from our analysis (<0.0002 percent area). We used PIT counts to estimate percentage cover of fleshy and calcareous macroalgae, turf algae and crustose coralline algae (CCA). Adult and juvenile *Diadema* counts were summed across each PIT to calculate total *Diadema* population.

Fish transects (number of transects per survey: n = 10) and corresponding coral transects (n = 2) and benthic PITs (n = 6) were grouped into whole surveys to collate data of fish abundance and benthic cover (Note: some sites were surveyed multiple times; n = 194; range: 2 – 5 times). Occasionally, fish transects within the same survey were not all conducted on the same day due to forces beyond the control of the surveyors such as interruption by weather events (2.1% of surveys included had fish transects over multiple days). We considered all transects taken within 14 days of each other as the same survey, which is a reasonable assumption as shifts in coral, fish and algal assemblages, particularly after a disturbance (Airoldi, 1998; Wilson *et al.,* 2006), typically take much longer. Average benthic metrics and proportional abundances of herbivorous fish functional groups were calculated for each survey, alongside average depth (range: 1.0 – 24.6 m), total *Diadema* population (individuals/10 m^2) and total herbivore biomass (g/60m^2). Preliminary analysis which included *Diadema* abundance as an explanatory variable revealed that their abundance was significantly correlated with metrics of coral reef benthic state. We therefore excluded all surveys where *Diadema* populations were not counted to have *Diadema* abundance in all further analysis. One survey with a *Diadema* abundance greater than 25 standard deviations above the average from across all surveys was also removed from our analysis as this was concluded to be highly unlikely and therefore an error (observed: 168 individuals/10 m^2, mean: 1.3 individuals/10 m^2).

1.2.4 Data analysis

To test the extent to which pairwise statistical interactions between herbivorous fish functional group abundances correlated with metrics of coral reef benthic state, and whether functional groups varied in their correlation with benthic composition, we applied the Diversity-Interactions modelling framework, as presented by Kirwan *et al.* (2009). The Diversity-Interactions modelling framework offers a suite of linear regression models designed to test biologically meaningful hypotheses about how species and functional group interactions may contribute to ecosystem function (Kirwan *et al.,* 2009). We fit three separate Diversity-Interactions models: null model, species identity model, and full pairwise interactions model (Figure 1.1). Briefly, the null model assumes no effect of species identity or interactions on ecosystem function. The identity model considers only the effects of species identity on ecosystem function, whereas the pairwise interactions model includes the effects of both species identity and interactions separately.

The null model (Model 1; Figure 1.1) reflects an ecosystem in which a change in species diversity or relative abundances has no effect on ecosystem function, and is as follows:

$$y = \beta + \alpha M + \varepsilon \qquad \textbf{Equation 1.1}$$

where α represents the effect of changing species abundance (M) and β is the level of ecosystem function at average M.

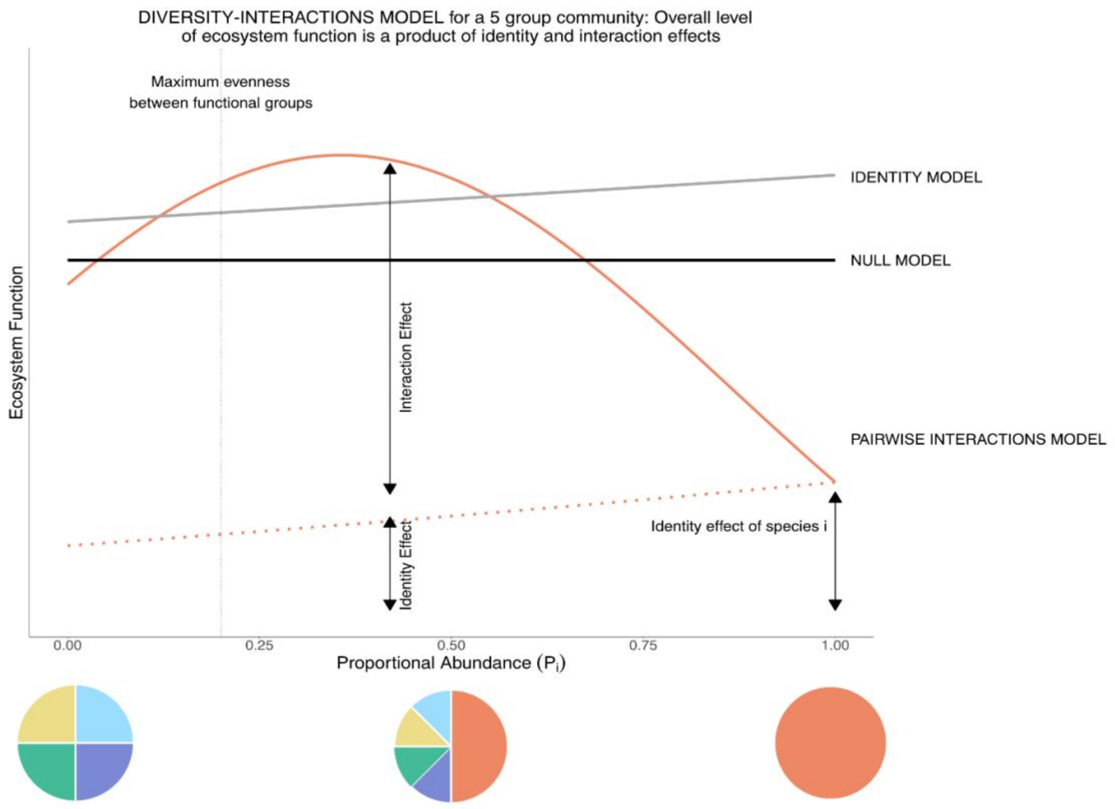

Figure 1.1 Illustration of the Diversity-Interactions modelling approach of an ecosystem function (y) in a community of five functional groups. For the pairwise interactions model (Model 3), overall ecosystem function is a product of identity and interaction effects. Coloured pie charts illustrate the changing proportional abundance of five functional groups.

The species identity model (Model 2; Figure 1.1) assumes that species differ in their individual effects on ecosystem function, but that interactions between species do not affect ecosystem function. In this instance, the level of ecosystem function of a community can be calculated using the proportional abundance (*P*) of each individual species and the level of ecosystem function when they are the sole species present (*P* = 1). Their individual performance (ecosystem function when *P* = 1) is as follows:

$$y = \sum_{i=1}^{s} \beta_i P_i + \alpha M + \varepsilon \qquad \textbf{Equation 1.2}$$

where β_i represents the estimated effect of changing the proportional abundance of species *i* (P_i) on the level of ecosystem function (its identity effect). We can test whether individual species’ identity effects are significantly different by conducting an *F* test (or equivalent) between Models 1 and 2.

When species interact to affect ecosystem function, the performance of a community formed of different species can be significantly different from that estimated using separate identity effects alone. These interactions can have a positive (synergistic) or negative (antagonistic) effect. This full pairwise interactions model (Model 3; Figure 1.1) is as follows:

$$y = \sum_{i=1}^{s} \beta_i P_i + \alpha M + \sum_{\substack{i,j=1 \\ i<j}}^{s} \delta_{ij} P_i P_j + \varepsilon \qquad \textbf{Equation 1.3}$$

where δ_{ij} measures the effect of changing relative abundances between species *i* and *j* on ecosystem function. In this model, the relative abundances of the two species, *i* and *j*, determines how strongly their interaction correlates with ecosystem function. The sum of all pairwise interaction terms form the net interaction effect, defined as:

$$\sum_{\substack{i,j=1 \\ i<j}}^{s} \delta_{ij} P_i P_j \qquad \textbf{Equation 1.4}$$

We can test whether pairwise interactions between species have a significant effect on ecosystem function by conducting an *F* test (or equivalent) between models 2 and 3 (Kirwan *et al.,* 2009). When net interaction effects play a significant role in driving ecosystem function, domination by one functional group will reduce interaction effects and subsequently cause ecosystem function to be compromised.

All analyses were conducted in RStudio V. 1.4.1717 (RStudio Team, 2021) using the tidyverse (Wickham *et al.,* 2019) and geepack packages (Halekoh *et al.,* 2006). We fit benthic metrics (dependent variable) against proportional abundances of herbivorous fish functional groups (independent variable) using generalised estimating equations (GEE: geeglm function in the geepack package; Halekoh *et al.,* 2006). This approach allowed us to control for any spatial correlation between sites within the same subregion (Appendix A, Table S1.4) by including an exchangeable correlational structure within subregions which provided an estimate of correlation (α). GEE are a common approach to analysing correlated non-normal data (Zuur *et al.,* 2009) and can be understood as analogous to generalised mixed models (GLM), in which subregion would be included as a random effect. To resolve the issue of multicollinearity between proportional independent variables that sum to one (i.e. one variable can be predicted from the others), the intercept was removed from Models 2 and 3.

As some study sites were surveyed multiple times (n = 194; range: 2 – 5 times), we used a bootstrapping approach to prevent pseudoreplication. For all sites surveyed multiple times, we selected one survey at random and joined these to all single-surveyed sites (n = 407) to form a temporary dataset of 601 independent surveys which we then used to fit our three GEE models. Within each iteration, we tested GEE models against each other, as described above, using an analysis of the "Wald statistic" (analogous to *F* test), and extracted all test statistics and model coefficients. We repeated this whole process 1000 times with replacement. All benthic metrics were lower-bound at zero and algal percentage cover was upper-bound at 100. Benthic metrics relating to coral (coral richness, calcification rate, coral cover and recruitment) were, therefore, modelled using a Poisson distribution and algal cover was modelled using a binomial distribution (transformed to a 0 to 1 scale). Total herbivore biomass, depth, year and *Diadema* abundance were included in all GEE models as additional fixed effects. Note that not all surveys had data for all benthic and coral metrics; however, we modelled all benthic metrics separately, and did not include surveys that were missing the benthic metric being analysed.

Visual model validation was conducted following methods outlined by Zuur *et al.* (2009). We plotted all explanatory variables against the appropriate residuals, Pearson residuals (Poisson distributed variables) or deviance residuals (binomial distributed variables), to check that no patterns were observed (See online code). Unlike GLM, GEEs are not based on the maximum likelihood theory and therefore statistics derived under this theory, such as Akaike's information criterion, may not be applied to GEE. The quasi-likelihood information criterion (QIC) (Pan, 2001) was introduced as an alternative method of model selection in a GEE setting, however these methods are commonly disputed and can give rise to errors (Wang *et al.,* 2015). Model choice and correlation structure can therefore be guided by the data (Wang *et al.,* 2015). As the premise of our study is based around the statistical tests between models, use of the QIC here was deemed inappropriate. Mean and standard deviation of all model summary statistics and statistical tests between models can be found in Table 1.1 and Appendix A: Table S1.5.

Mean coefficients from the full pairwise interaction models (Model 3) were used to predict benthic metrics on hypothetical reefs along a scale of varying herbivorous fish community composition. Each functional group was set along a scale of proportional abundance from 0 to 1, with all other functional groups kept equal to each other. For example, when the proportional abundance of functional group *i* was 0.5, all other functional group proportional abundances were 0.125 (see Figure 1.1). As a community of five distinct groups, maximum evenness between functional groups was reached when the proportional abundances (*P*) of all functional groups was 0.2. For calculations of predicted values, we set total herbivore biomass, depth, year and *Diadema* abundance across all surveys to the mean.

1.3 Results

1.3.1 Functional group co-occurrence

Coral richness, total coral cover and calcification rate were predicted to be higher on reefs where herbivorous fish functional groups had the same relative abundance (P = 0.2; maximum evenness) compared with when a single functional group was present (P_i = 1) (Figure 1.2). The model also predicted moderate levels of fleshy and calcareous macroalgal, turf algal and CCA cover under these circumstances (Figure 1.2; see Table 1.2 for percentages and predicted maximums of all benthic metrics).

Statistical interactions between the proportional abundances of herbivore functional groups were significantly correlated with improved coral reef benthic state (Table 1.1; Test 2). In addition, when separated into functional group identity (identity effects) and functional group co-occurrence (interaction effects) (see Figure 1.1), predicted benthic metrics were largely made up of the contribution of functional group co-occurrence (Figure 1.3). Due to the nature of proportional abundances, it is difficult to interpret the size of the interaction effects, as increasing the proportion of one functional group inevitably changes the proportion of others. Therefore, we focus on the direction of correlation between functional group co-occurrence and benthic state, whether it is positive (synergistic) or negative (antagonistic).

Table 1.1 Comparison of Diversity-Interactions models using analysis of the Wald statistic (analogous to *F* test). Test 1 (Model 1: Null model vs Model 2: Identity model) tests whether herbivore functional groups differ significantly in their association with coral reef benthic state. Test 2 (Model 2: Identity model vs Model 3: Full pairwise interactions model) tests whether interactions between herbivore functional groups are significantly associated with coral reef benthic state. Values represent the mean ± standard deviation of 1000 bootstrapped iterations. Percentage refers to the percentage of bootstrapped iterations with *p*-values ≤ 0.05. Significant results are shown in bold and indicate that functional groups differ in their association with benthic state (Test 1) and that interactions between functional groups are associated with benthic state (Test 2).

	Test 1: Model 1 vs Model 2			**Test 2: Model 2 vs Model 3**		
	Wald	*p*	%	Wald	*p*	%
Coral Richness	24.94 ± 4.10	**0.00 ± 0.00**	**100**	45.38 ± 9.59	**0.00 ± 0.00**	**100**
Total Coral Cover	64.25 ± 15.76	**0.00 ± 0.00**	**100**	69.89 ± 21.15	**0.00 ± 0.00**	**100**
Coral Calcification Rate	39.25 ± 7.88	**0.00 ± 0.00**	**100**	52.16 ± 13.48	**0.00 ± 0.00**	**100**
Coral Recruitment	43.66 ± 11.81	**0.00 ± 0.00**	**100**	11.50 ± 5.84	0.43 ± 0.29	11.4
Competitive Coral Cover	3.71 ± 1.05	0.46 ± 0.14	0	27.46 ± 9.25	**0.03 ± 0.07**	**85.3**
Weedy Coral Cover	54.60 ± 15.56	**0.00 ± 0.00**	**100**	25.94 ± 10.75	**0.05 ± 0.09**	**73.9**
Stress-tolerant Coral Cover	36.43 ± 5.39	**0.00 ± 0.00**	**100**	82.01 ± 34.61	**0.00 ± 0.00**	**100**
Generalist Coral Cover	51.39 ± 9.88	**0.00 ± 0.00**	**100**	65.75 ± 15.63	**0.00 ± 0.00**	**100**
Fleshy Macroalgal Cover	42.63 ± 7.47	**0.00 ± 0.00**	**100**	18.85 ± 5.92	0.10 ± 0.13	48.3
Calcareous Macroalgal Cover	6.09 ± 1.78	0.23 ± 0.13	4.1	22.23 ± 5.03	**0.03 ± 0.04**	**78.8**
Turf Algal Cover	17.88 ± 5.20	**0.01 ± 0.01**	**99.3**	25.26 ± 5.6.	**0.02 ± 0.03**	**92**
CCA Cover	11.80 ± 2.50	**0.03 ± 0.03**	**83.6**	36.06 ± 14.11	**0.01 ± 0.04**	**91.1**

Table 1.2 Predicted maximums, percentages and break downs of metrics of coral reef benthic state.

Response	Predicted maximum	Predicted response at maximum functional group evenness ($P = 0.2$)	% of predicted maximum at $P = 0.2$	% of predicted response composed of interaction effects at $P = 0.2$
Coral Richness	11.15	10.09	90.47	61.85
Total Coral Cover	6.46	4.69	72.56	99.44
Coral Calcification Rate	4.17	3.45	82.68	99.77
Coral Recruitment	2.68	1.75	65.28	31.03
Fleshy Macroalgal Cover	38.49	21.97	57.09	71.94
Calcareous Macroalgal Cover	14.83	6.43	43.39	42.09
Turf Algal Cover	99.87	19.13	19.16	65.62
CCA Cover	24.80	10.37	41.82	10.12

Not all pairwise statistical interactions between herbivore functional groups were significantly correlated with coral-related benthic metrics (coral richness, calcification rate, total coral cover), however those that were showed a positive correlation (13 out of 40; Appendix A, Table S1.5). The majority of these significant correlations involved excavators (9 out of 13; Appendix A, Table S1.5). Other significant pairwise statistical interactions between croppers and scrapers were correlated with increased coral richness, coral cover, and coral calcification rate, and browsers and scrapers were correlated with increased coral richness.

Net interaction effects (the sum of all pairwise interaction effects; Equation 4) were consistently positively correlated with fleshy macroalgal cover, coral richness, total coral cover and coral calcification rate (Figure 1.3). Net interaction effects were positively correlated with coral recruitment except in communities dominated by farmers ($P_{farmers} > 0.67$), where correlation was negative (Figure 1.3). Net interaction effects were positively correlated with calcareous macroalgal cover except when communities were dominated by croppers ($P_{croppers} > 0.57$), where correlation was negative. Similarly, net interaction effects were positively correlated with CCA cover, however, when browsers were more abundant ($P_{browsers} > 0.26$), or where croppers were rare ($P_{croppers} < 0.14$), the correlation between net interaction effects and CCA cover was negative.

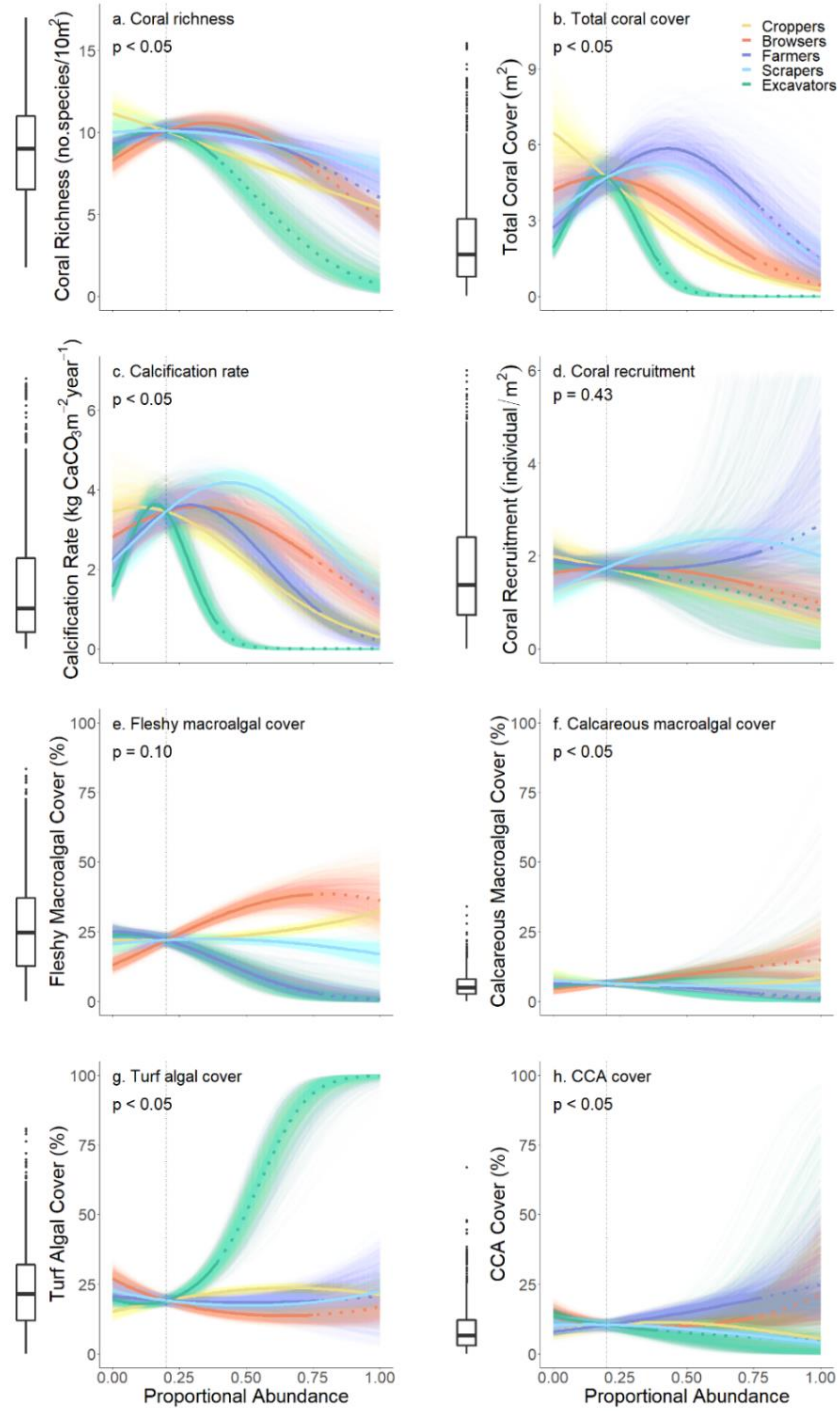

Figure 1.2 Predicted coral reef benthic state using results from 1000 iterations of bootstrapped pairwise interaction models (Model 3). Thicker lines represent mean predicted values. Dotted segments represent predictions extrapolated from empirical data (i.e. no survey in our analysis had proportional abundance of excavators > 0.39). Vertical dotted lines represent maximum evenness between functional groups ($P = 0.2$). *p*-values represent analysis of Wald statistic between Models 2 and 3, which tests the significance of statistical interactions between functional groups (Table 1.1; Test 2). Note: coral recruitment y-axis has been limited for ease of viewing. Boxplots represent the spread of raw data by survey and have been limited to correspond with predicted values (see Appendix A, Figure S1.4 for full boxplots).

In some cases, pairwise statistical interactions between herbivorous fish functional groups were significantly correlated with algal metrics: excavators and scrapers, and excavators and browsers with reduced turf algal cover (Appendix A, Table S1.5); croppers and scrapers with increased CCA cover. No singular pairwise functional group statistical interaction was significantly correlated with calcareous macroalgal cover (Appendix A, Table S1.5), even though the correlation with the net interaction effect was significant (Table 1.1; Test 2).

Not all pairwise statistical interactions between herbivore functional groups were significantly correlated with coral-related benthic metrics (coral richness, calcification rate, total coral cover), however those that were showed a positive correlation (13 out of 40; Appendix A, Table S1.5). The majority of these significant correlations involved excavators (9 out of 13; Appendix A, Table S1.5). Other significant pairwise statistical interactions between croppers and scrapers were correlated with increased coral richness, coral cover, and coral calcification rate, and browsers and scrapers were correlated with increased coral richness.

1.3.2 Comparison of functional group identity effects

The correlation between herbivore functional groups and benthic metrics (their identity effects) were significantly different from each other, with the exception of calcareous macroalgal cover and competitive coral cover (Table 1.1, Test 1). Across our study sites, the cover of calcareous macroalgae and competitive corals was low (mean: 5.78% and 0.40 m^2, respectively) reducing the likelihood that relationships would be detectable in the data.

Reefs dominated by one herbivore functional group ($P > 0.2$) were predicted to have lower levels of all coral-related benthic metrics (richness, recruitment, cover and calcification rate), with the exception of farmer- or scraper-dominated reefs, which were predicted to have higher coral recruitment (Figure 1.2). In particular, coral richness, total coral cover and calcification rate were predicted to be substantially lower on reefs dominated by excavators. Higher coral calcification rate was predicted on reefs where scrapers were relatively abundant (up to a point; $P_{farmers} = 0.31$ and $P_{scrapers} = 0.44$; Figure 1.2), whereas coral richness was predicted to be higher when

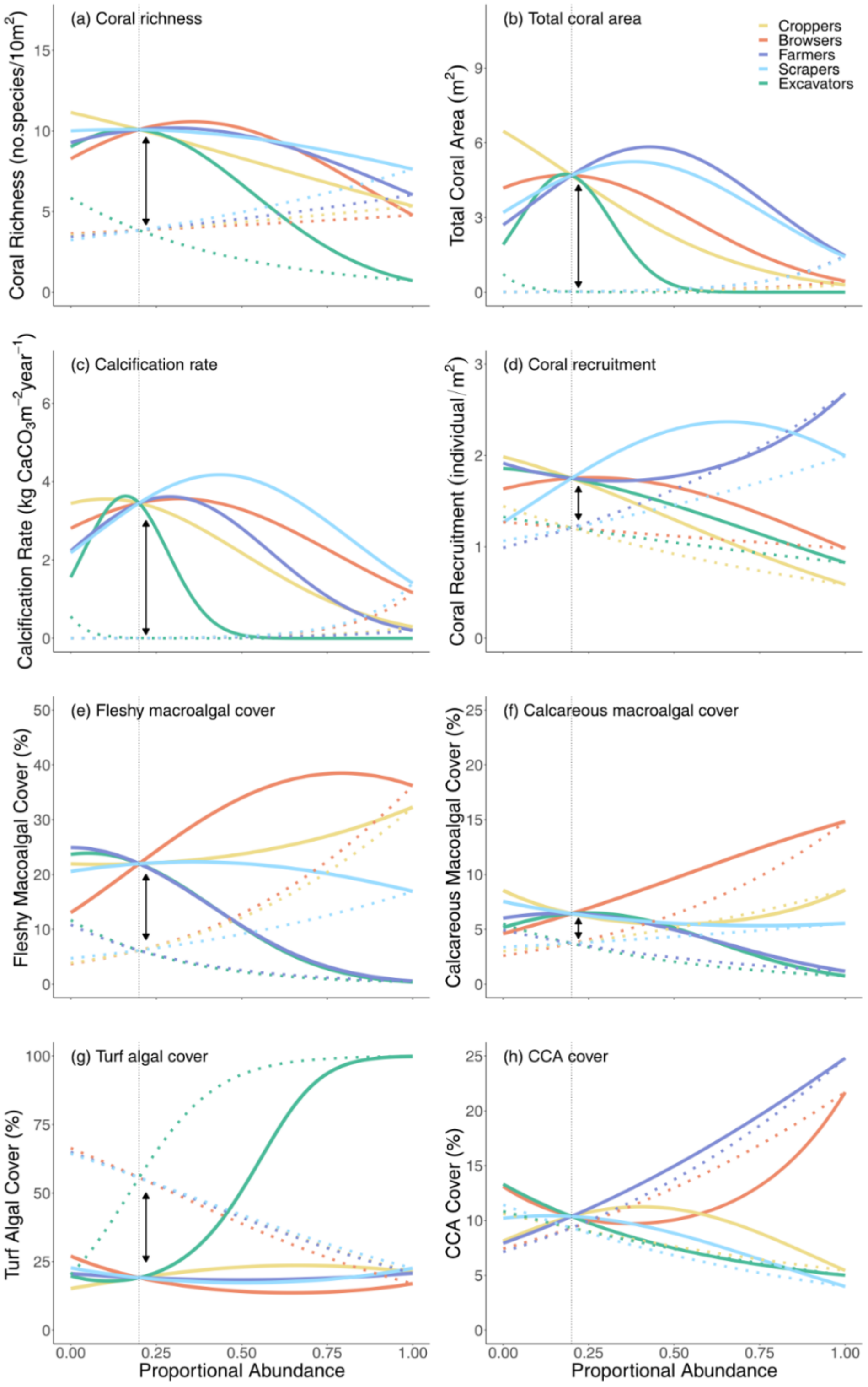

Figure 1.3 Mean predicted metrics of coral reef benthic state using results from pairwise interactions models (Model 3), separated into net identity (dotted lines) and net interaction effects (black arrows). Vertical dotted lines represent maximum evenness between functional groups (*P* = 0.2).

browsers were more abundant (up to a point; $P_{browsers} = 0.36$). Coral recruitment rate was predicted to be higher on reefs dominated by farmers or scrapers (Figure 1.2). Overall, metrics of coral reef benthic state were lower on reefs where one functional group were less abundant ($P < 0.1$) or absent (Figure 1.2).

Extremely high turf algal cover ($P_{excavators} = 0.5$; Turf cover = 51%) and low macroalgal cover were predicted on reefs dominated by excavators (Figure 1.2). In contrast, reefs dominated by browsers had higher macroalgal cover and lower turf algal cover (Figure 1.2). Lower macroalgal cover and higher CCA cover were predicted on reefs where farmers were more common. Lower CCA cover was predicted on reefs dominated by scrapers and excavators (Figure 1.2). The correlation between CCA cover, and both croppers and browsers, was less clear and nonlinear.

Total coral cover was predicted to be higher on reefs where farmers and scrapers were relatively abundant (Figure 1.2). However, this correlation was inconsistent when observing coral cover of trait-based groups separately. Weedy coral cover was predicted to be higher when farmers were relatively abundant (Appendix A, Figure S1.2), whereas stress-tolerant coral cover was predicted to be greater with increasing abundance of browsers (Appendix A, Figure S1.2). Competitive coral cover was predicted to be higher when functional groups had the same relative abundance in a community ($P = 0.2$; Appendix A, Figure S1.2) and with increasing abundance of browsers. Generalist coral cover was predicted to be substantially greater on reefs with increasing abundance of scrapers (Appendix A, Figure S1.2).

1.4 Discussion

Using data collected across 12 countries within the western Atlantic, we found strong correlations between herbivorous fish functional diversity and improved coral reef benthic state. These correlations were mostly driven by the co-occurrence of fish functional group proportional abundances.

Statistical interactions between functional groups were significantly correlated with reduced turf algal cover and increased calcareous macroalgal and CCA cover, as well as increased coral cover and coral calcification rate (Table 1.1; Test 2). However, no such correlation was found with coral recruitment. Calcareous macroalgae (e.g. *Halimeda* spp.) and CCA play an important role in reef-building by binding sediment and contributing to calcium carbonate production, assisting the growth of coral reefs (Birrell *et al.,* 2008). In contrast, when relieved from grazing pressure, turf algae can form dense mats which smother coral, leading to mortality and a decline in coral reef accretion (Birrell *et al.,* 2008). Our findings support previous consensus that co-occurrence of herbivorous fish functional groups could be an important mediator of reef function by controlling turf algal cover (Burkepile and Hay, 2008; Green and Bellwood, 2009; Adam *et al.,* 2015; Duffy *et al.,* 2016; Holbrook *et al.,* 2016; Lefcheck *et al.,* 2019). As such, co-occurrence of functional groups may promote reef accretion indirectly by mediating competition with algae, rather than through a direct benefit to coral recruitment and settlement.

Fleshy macroalgal cover was not significantly correlated with statistical interactions between functional group proportional abundances. This finding is reasonable to expect given that, of the five functional groups investigated, only browsers (e.g. chubs; Kyphosidae; Green and Bellwood, 2009) directly affect fleshy macroalgae through consumption (Green and Bellwood, 2009). However, correlations between different functional groups and fleshy macroalgal cover did significantly differ. Herbivorous fish functional groups vary widely in their preferred diet and feeding behaviours (Green and Bellwood, 2009; Kelly *et al.,* 2016). Therefore, it can be expected that the composition of algal assemblages will affect the community composition of herbivorous fish through a bottom-up effect. For example, as browsing herbivores are the only functional group that rely on macroalgae as a dietary resource (Green and Bellwood, 2009), we would expect their proportional abundance to be higher on reefs with greater macroalgal cover, as we observed (Figure 1.2).

The general assumption is that herbivore abundance and diversity benefits coral reefs by controlling the abundance of algae (Adam *et al.,* 2015; Holbrook *et al.,* 2016). With increased functional diversity and niche partitioning, a community is better able to fully utilise the limited resources from its environment, helping to maintain ecosystem function (Cadotte *et al.,* 2011). Although we must acknowledge bottom-up effects of algal assemblages on herbivore community composition, it seems reasonable to expect that co-occurrence of herbivore functional groups improves algal control on coral reefs by increasing the dietary breadth and resource utilisation of herbivorous fish as a whole. Here, we demonstrate significant correlation between herbivorous fish functional group co-occurrence, reduced algal cover and increased coral accretion. Our results support the expectation that functional diversity within the herbivore guild enhances coral reef benthic state, and suggests that co-occurrence of functional groups could have an important positive effect on wider coral reef function. This would infer that the identity and abundances of herbivorous fish functional groups alone are not enough to accurately predict coral reef benthic state. Both the identity model (Model 2) and full pairwise interaction model (Model 3) made similar predictions of coral reef benthic state when all functional groups had similar relative abundance (Figures 1.2 and S1.3). However, when the proportional abundance of one functional group increased, predictions between models were no longer comparable. This inconsistency supports the idea that detailing patterns of herbivorous reef fish co-occurrence may allow us to predict coral reef benthic state more accurately.

1.4.1 Co-occurrence of croppers and scrapers correlated with increased coral reef accretion

By modelling each pairwise interaction separately, the full pairwise interactions model (Model 3) can be used to identify functional group pairings that are most correlated with coral reef benthic state. Statistical interactions between scrapers and croppers were correlated with a moderate increase in CCA cover and coral-related measures (coral richness, coral cover and calcification rate). Scraping herbivores, such as smaller parrotfish species (e.g. *Scarus vetula*; Labridae; Adam *et al.,* 2018), are widely recognised to facilitate the settlement and growth of CCA and corals by limiting the establishment and growth of macro- and turf algae (Hoey and Bellwood, 2008; Green and Bellwood, 2009). Croppers (e.g. surgeonfish *Acanthurus coeruleus*; Acanthuridae; Green and Bellwood, 2009) and browsers also play an important role in controlling algal abundance by consuming algae, which competes with CCA and coral recruits for space and shades adult corals (Green and Bellwood, 2009; Smith *et al.,* 2010; Barott *et al.,* 2012). Our results suggest that, in addition to their individual benefits to coral reef benthic state, the co-occurrence of scrapers and croppers may further support CCA growth and indirectly benefit coral diversity and growth. As such, we would predict reefs higher in proportional abundance of both scrapers and croppers to demonstrate a more favourable benthic state, in which algal cover is well-maintained and corals are the dominant benthic organism.

1.4.2 Evidence in support of excavating and farming herbivores as key determinants of coral reef benthic state

Herbivorous fish functional groups varied significantly to each other in their correlation with coral reef benthic state (Table 1.1; Test 1). It is well established that herbivore functional groups perform alternative roles within coral reef communities (Ceccarelli *et al.,* 2005b; Burkepile and Hay, 2010; Edwards *et al.,* 2014), yet few studies have quantified and compared these effects. Here, we quantify the correlation between herbivore functional groups and benthic cover, from which we can begin to infer which groups may have the greatest impact on aspects of coral reef benthic state.

We found that coral reef benthic state was particularly strongly correlated with the abundance of excavating herbivores. Coral cover and calcification rates were predicted to be higher on reefs that had a proportional abundance of excavators within a narrow window ($P_{excavators} > 0.1$ and < 0.2; Figure 1.2). Large excavating herbivores, such as larger-bodied parrotfish (e.g. *Scarus coelestinus*; Adam *et al.,* 2018), play a key role in bioerosion on coral reefs, clearing space for the settlement of CCA and corals by removing both dead and live corals through their intense feeding behaviours (Bellwood and Choat, 1990; McCauley *et al.,* 2014; Adam *et al.,* 2018). The direction (positive or negative) and strength of the effects of large parrotfish on coral reefs is based partly on their abundance (McCauley *et al.,* 2014). The intermediate disturbance hypothesis suggests that diversity and ecosystem function is maximised when ecological disturbance is present at an intermediate level (Connell, 1978). We would therefore expect excavating herbivores to be of maximum benefit to coral richness and coral cover when at intermediate proportional abundance (observed here and in previous studies; Figure 1.2).

Turf algae, on the other hand, which can outcompete corals for space (Birrell *et al.,* 2008; Barott *et al.,* 2012), thrive on reefs that are subject to frequent disturbance and are often the first species to colonise a disturbed area (McManus and Polsenberg, 2004; Done *et al.,* 2007; Gove *et al.,* 2015). With increasing abundance of excavators, we would expect the greater ecological disturbance caused by their feeding behaviours to result in expanding turf algal cover (as observed here; Figure 1.2), leading to an overgrowth of corals and reduction of coral reef state. In accordance with the intermediate disturbance hypothesis, we found that higher coral richness and coral cover was predicted on reefs that held an intermediate proportional abundance of excavating herbivores (Figure 1.2). In addition, turf algal cover was predicted to expand rapidly on reefs with increasing proportional abundance of excavators. However, it is worth noting that this rapid expansion of turf algal cover stems from proportional abundances of excavators beyond what we observed in our empirical data. Our findings support the notion that excavating herbivores are key determinants of coral reef benthic state (Bellwood and Choat, 1990; McCauley *et al.,* 2014; Adam *et al.,* 2018), but that their benefits may not be universal and instead depend on their abundance (McCauley *et al.,* 2014).

All statistical interactions between the proportional abundance of excavators and other functional groups were significantly correlated with increased coral cover and coral calcification rate. Additionally, statistical interactions between browsers and excavators, and scrapers and excavators were significantly correlated with reduced turf algal cover. As the proportional abundance of excavators increases, we would expect these pairwise interaction effects to become stronger (up to a point; $P_{\text{excavators}} = 0.6$) and would anticipate an associated decline in turf algal cover and increase in coral cover. However, turf algal cover was predicted to increase sharply on reefs with a proportional abundance of excavators above maximum functional group evenness ($P > 0.2$), whilst coral cover and calcification rate were predicted to decline. Although our results suggest that co-occurrence of excavators and other functional groups is correlated with improved turf algal control, and subsequent increase in coral growth, functional group co-occurrence may not be enough to buffer the negative impacts of disturbance by high-level excavating feeding behaviours.

Coral reefs relatively abundant in farming damselfishes ($P_{farmers} > 0.2$) were predicted to have lower macroalgal cover and higher CCA cover, whilst turf algal cover remained reasonably unchanged (Figure 1.2). Concurrently, total coral cover and coral recruitment were predicted to rise (up to a point). Upon closer inspection of coral cover, we found that increasing abundance of farming damselfishes was correlated with a disproportionate expansion of non-framework, weedy species of coral (e.g. *Porites astreoides*; Green *et al.,* 2008; Darling *et al.,* 2012) (Appendix A, Figure S1.2). Weedy coral species have relatively low calcification rates compared with other trait-based groups (e.g. weedy: *Porites astreoides*: 5.78 kg CaCO3m^{-2}year^{-1}; competitive: *Acropora cervicornis*: 19.28 kg CaCO3m^{-2}year^{-1}; González-Barrios and Álvarez-Filip, 2018), which may explain why calcification rate was not predicted to increase alongside coral cover with increasing abundance of farmers (Figure 1.2).

The relationship between farming damselfishes and coral reef health remains unclear (Green and Bellwood, 2009). Territories of farming damselfishes may provide refuge for CCA and coral recruits, as their aggressive territorial behaviour drives away corallivores and excavating herbivores (Sammarco, 1983; Bellwood and Choat, 1990). On the other hand, farming damselfishes can indirectly harm coral communities by cultivating turf algae, leading to a reduction of available space for recruits and mortality of adult corals (Sammarco and Williams, 1982). Farming damselfishes require areas of hard substratum on which to grow their turf algal farms (Ceccarelli *et al.,* 2001; 2005b) and their abundance is often strongly associated with live coral cover (Wilson *et al.,* 2008; Pratchett *et al.,* 2012; Komyakova *et al.,* 2019). Given this reliance, we would expect a positive correlation between proportional abundance of farmers and greater coral cover, as our results show. However, as the abundance of farming damselfish continued to rise ($P_{farmers} > 0.5$; Figure 1.2), predicted coral cover and coral calcification rate declined despite an increase in CCA cover and coral recruitment (Figure 1.2). These findings support the idea that territorial farming damselfishes may benefit coral by protecting coral recruits when at an intermediate abundance, yet negatively impact reef accretion when populations grow. These negative impacts of rising proportional abundance of farmers may be due to their intensive farming behaviour (Hata and Kato, 2004) or simply through lack of functional diversity within the herbivore guild as a whole. Further investigation is required to fully disentangle the relationship between farming damselfishes, benthic state and coral health and identify a possible threshold between the benefits and costs of territorial behaviour on coral reef ecosystem state.

1.4.3 Practical implications – the impact of selective fishing

Selective fishing of predators and larger herbivorous species is shifting the composition of herbivorous fish communities, causing a disproportionate reduction of certain functional groups and reducing herbivore diversity (Edwards *et al.,* 2014; Heenan *et al.,* 2016). Large excavating parrotfish are particularly vulnerable to high fishing pressure and are declining across the Caribbean (Adam *et al.,* 2015; Shantz *et al.,* 2020). Despite their intense feeding behaviours, these species play an important role in continued coral accretion by clearing space for the settlement of CCA and corals (Bellwood and Choat, 1990; McCauley *et al.,* 2014; Adam *et al.,* 2018; Figure 1.2), and their decline may come at significant cost to coral reef function (Green and Bellwood, 2009). On the other hand, small farming damselfishes are subject to a low fishing pressure and are becoming increasingly abundant worldwide (Edwards *et al.,* 2014; Vermeij *et al.,* 2015). Although our results give support for the potential benefits of farming damselfishes on coral recruitment (Figure 1.2), their aggressive territorial defence indirectly promotes algal growth by excluding other reef herbivores, leading to both recruit and adult coral mortality (Sammarco and Williams, 1982). Our analysis also predicted an expansion of weedy coral cover on reefs with rising populations of farmers, suggesting that farming damselfishes may influence coral composition by disproportionately promoting the growth of non-framework, weedy coral species. The abundance of weedy coral species is increasing across the Caribbean and is thought to be contributing to the reduction in coral reef function (Green *et al.,* 2008; Alvarez-Filip *et al.,* 2011; González-Barrios and Álvarez-Filip, 2018). The proliferation of damselfish populations as a result of selective fishing of predators and larger herbivores could explain this shift towards weedy coral species and subsequent decline in coral reef function.

1.5 Conclusion

Our results demonstrate a positive correlation between functional diversity of herbivorous reef fish and increasing coral richness, total coral cover and reef calcification rate (Table 1.1; Test 2). Furthermore, by modelling pairwise statistical interactions, we found that functional group co-occurrence positively correlates with improved coral reef benthic state. Using these results, we explored the potential role that herbivore functional diversity and functional group co-occurrence may play in determining the dominant benthic organisms on tropical coral reefs. We highlight excavating and farming herbivorous fish as potential key determinants of coral reef benthic state, predicting that their benefits may be greatest when at intermediate abundances. Using Diversity-Interactions models, we highlight the importance of managing for a diverse herbivorous fish assemblage and co-occurrence of functional groups to promote coral reef persistence.

Chapter 2: Variation in farming damselfish behaviour creates a competitive landscape of risk on coral reefs

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Author Contribution

CES conceptualised the idea, collected and analysed data, and led the writing of the chapter. SAK and LBE supported data analysis. All co-authors contributed critically to chapter drafts.

Abstract

Interspecific interactions are fundamental drivers of animal space use. Yet whilst non-consumptive effects of predation risk on prey space use are well-known, the risk of aggressive interactions on space use of competitors is largely unknown. We apply the landscape of risk framework to competition-driven space use for the first time, with the hypothesis that less aggressive competitors may alter their behaviour to avoid areas of high competitor density. Specifically, we test how aggressive risk from territorial algal-farming damselfishes can shape the spatial distribution of herbivore fish competitors. We found that only the most aggressive damselfishes had fewer competitors in their surrounding area, demonstrating that individual level behavioural variation can shape spatial distributions. In contradiction to the landscape of risk framework, abundances of farming damselfishes and other reef fish were positively associated. Our results suggest that reef fish do not simply avoid areas of high damselfish abundance, but that spatial variation in aggressive behaviour, rather than of individuals, created a competitive landscape of risk. We emphasise the importance of individual-level behaviour in identifying patterns of space use and propose expanding the landscape of risk framework to non-predatory interactions to explore cascading behavioural responses to aggressive risk.

2.1 Introduction

Human-induced environmental change is altering the behaviour and spatial distribution of animals worldwide (Wilson *et al.,* 2020). These behavioural shifts can cascade through ecosystems to affect species persistence, ecosystem services and resilience under climate change (Wilson *et al.,* 2020). The abiotic drivers of behavioural and spatial patterns are well-known, however biotic factors also play a role. Non-consumptive effects of predators on the spatial distribution of prey are well established and encompass the behavioural responses of prey to predation risk (Bleicher, 2017; Gaynor *et al.,* 2019). Interspecific competition is also a fundamental driver of spatial distribution in ecological communities (Bonin *et al.,* 2015). Yet how the perceived risk of encountering aggressive competitors shapes spatial distribution in less aggressive species is unknown. We can explore competition-driven space use through the "landscape of risk" framework (Norum *et al.,* 2015).

The landscape of risk typically represents spatiotemporal patterns of predation risk (Norum *et al.,* 2015). However, similarly, the risk of encountering aggressive competitors may shape space use in less aggressive species. Competitors may avoid aggressive interactions by changing their behaviour, such as avoiding areas of high competitor density, helping them to navigate their environment at a lower risk of encountering aggressive competitors. Expanding the landscape of risk framework to competitive interactions provides a useful tool to explore these spatial and behavioural cascades.

Coral reef fish communities present an excellent system to study competition-driven space use in response to aggressive risk. Many species demonstrate clear site-attachment and aggressive and territorial behaviour (Ceccarelli *et al.,* 2001; Blowes *et al.,* 2017; Manning and McCoy, 2023). One such group of fish that are thought to influence the spatial distribution of reef inhabitants are the territorial farming damselfishes. Aggressive behaviour by farming damselfishes is expected to drive away herbivores and suppress herbivory inside damselfish territories, increasing turf algal cover as a result (Ceccarelli *et al.,* 2001). However, evidence of this effect is mixed. Experimental removal of farming damselfishes, giving access to roving herbivores, have found both subsequent reductions in algal biomass (Mahoney, 1981) and no effect on benthic communities within territories (Ceccarelli *et al.,* 2005a). Feeding by surgeonfish has even been found to decrease upon removal of farming damselfishes (Eurich *et al.,* 2018a). In addition to their potential effects on herbivory, farming damselfish abundance can influence coral predation rates (Tiddy *et al.,* 2023) and juvenile parrotfish recruitment (Tolimieri, 1998). The aggressive behaviour of farming damselfishes has clear cascading effects on reef fish behaviour. One way to better understand their impact is to look at how they shape the space use of reef fish.

Based on the landscape of risk framework, we expect a negative association between the abundances of farming damselfish and other reef fish, as fish avoid areas of coral reef with greater aggressive risk. We explore how interspecific competition and aggressive risk by farming damselfishes may shape the spatial distribution of the wider reef fish community on coral reefs. Specifically, we examine the spatial distribution and variation in aggressive behaviour by farming damselfishes, which we term the competitive landscape of risk, alongside the spatial distribution of other reef fish.

2.2 Material and methods

2.2.1 Field methodology

Data were collected between 13 July and 1 August 2022 at Coral View reef, Utila, Honduras (N 16.08823274, W -86.91094506), across two belt transects 25 m long x 2 m wide (separated by > 10 m; 100 m^2 total) at approximately 5 m depth (Figure 2.1). The territories of all adult damselfishes of the species *Stegastes diencaeus* (n = 26) and *S. planifrons* (n = 22), hereafter *Stegastes* spp., within the belt transects were tagged with identification numbers. *Stegastes diencaeus* and *S. planifrons* were the most abundant damselfish species in the area and exhibit similar aggressive territorial behaviours (per. obs.). Although territories are used for both cultivation of turf and egg protection, no evidence of eggs or nesting behaviour was observed.

2.2.2 Territory mapping

We mapped the territories of *Stegastes* spp. within our belt transects using methods similar to Robles *et al.* (2018). We attached a GoPro HERO camera to a stand 1.5 m above the focal territory such that the camera had a field of view of 1.5 m x 2 m, with a visible 30 cm scale. Focal individuals were recorded for 15 min, discarding the first 5 min as an acclimation period (Robles *et al.,* 2018). Territory recordings were taken after behavioural videos to avoid disruption caused by placing a frame over a territory. To estimate territory size, 21 screengrabs taken approximately every 30 s across a 10 min period were imported into ImageJ (Schneider *et al.,* 2012). We recorded the position of the focal individual as a point on each screengrab and calculated the minimum convex polygon around all points (Figure S2.1). In *S. diencaeus*, territory size

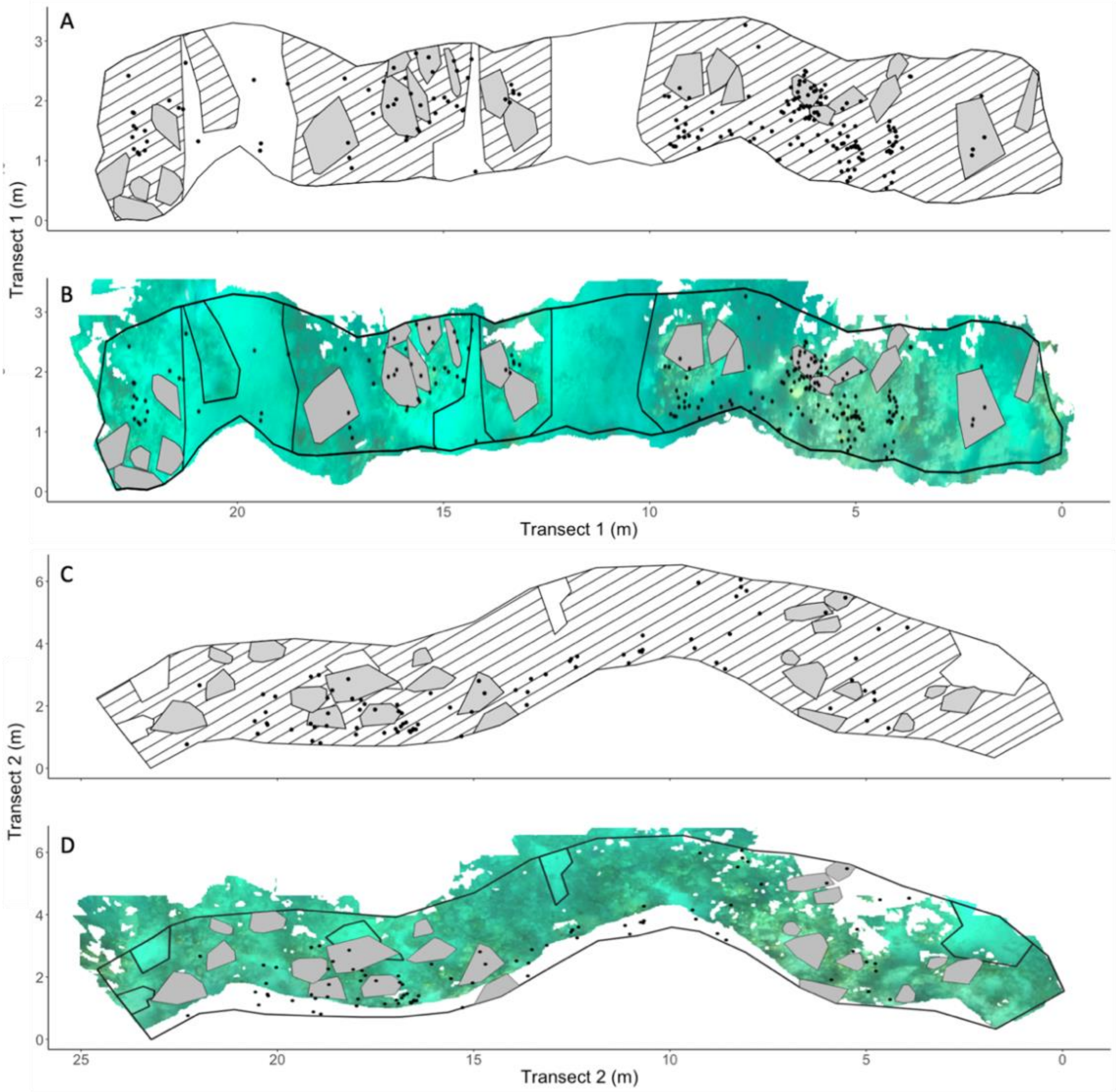

Figure 2.1 Transect maps (A & B: Transect 1, C & D: Transect 2). Hashed boxes represent hard substrate, grey areas show individual *Stegastes* spp. territories, points show location of non-*Stegastes* reef fish. Subplots B and D show underlying orthomosaics. Note belt transects were 2 m wide and 25 m long, however as surveys followed the reef line, figure axes represent absolute position.

may correlate with body size when a broad size range is observed (McDougall and Kramer, 2007; unpublished observations), however effects may not be seen over a smaller range (McDougall and Kramer, 2007). Individuals must be caught to accurately measure *Stegastes* body size (e.g. Itzkowitz *et al.,* 1995; McDougall and Kramer, 2007), which may disrupt territorial behaviour and was therefore judged unnecessary for this study.

2.2.3 Behavioural observations

To explore the landscape of risk around farming damselfish territories, we recorded the aggressive response of focal *Stegastes* spp. in terms of chases of reef fish that moved through their territory, known as intruders. This measure of aggression is widely used in studies of territorial farming damselfishes (Robles *et al.,* 2018; Fontoura *et al.,* 2020; Gunn *et al.,* 2023). Each focal individual was recorded once for 30 min using GoPro HERO cameras between 07:00 and 15:00, discarding the first 5 min as an acclimation period from diver/snorkeller presence (Nanninga *et al.,* 2017). Cameras were placed 1 – 2 m from the focal individual's territory such that the focal individual and intruders could be observed. Previous studies recorded mean territory sizes of 1.08 and 2.83 m^2 for *S. planifrons* and sister species *S. adustus* respectively (Dromard *et al.,* 2018). Therefore, the order in which focal individuals were recorded was strategically randomised such that individuals recorded at the same time were at least 3 m from each other to assure independence. Analysis of behavioural videos was undertaken in BORIS software V. 8.6.2 (Friard and Gamba, 2016). We recorded chase behaviours associated with aggressive response, defined as accelerated swimming movements of the focal individual towards intruders. Intruders that did not elicit an aggressive response were also noted. These were identified as any non-*Stegastes* fish that entered the focal individual's territory, which was visually estimated before analysis (Figure S2.2). Intruders were identified to the family level.

2.2.4 Reef and fish surveys

Reef fish were surveyed on SCUBA following a standardised protocol (Appendix A, Chapter 2 Supplementary material) using a diver-operated stereo-video system (SVS), allowing for accurate measurement of fish position (Goetze *et al.,* 2019). Belt transects were surveyed five times, with each survey spaced at least 3 hours apart to reduce the likelihood of repeat samples of roving individuals. Coordinates of two reference points for each fish along the transect were also recorded. These included strategically placed golf balls and visual landmarks along the reef, such as distinct corals and rock formations.

We used structure-from-motion underwater photogrammetry to construct orthomosaics of belt transects (Young *et al.,* 2017; Agisoft, 2022), on which to map *Stegastes* spp. territories and non-*Stegastes* reef fish locations (Appendix A, Chapter 2 Supplementary material). Orthomosaics were imported into QGIS Desktop V. 3.28.2 (QGIS Geographic Information System, 2022), on which reference points corresponding to the same reference points in the SVS data were plotted as a multipoint shapefile layer. X and Y coordinates of reference points were then extracted and used for coordinate transformation (Appendix A, Chapter 2 Supplementary material).

2.2.5 Statistical analysis

Data manipulation and statistical analyses were conducted in QGIS and RStudio V. 12.1.402 (RStudio team, 2024). In QGIS, we plotted the minimum convex polygons of 45 focal *Stegastes* spp. alongside 285 reef fish on our orthomosaics (Figure 2.1). 1 m and 0.5 m buffers were drawn around focal *Stegastes* spp. territories and the number of non-*Stegastes* fish within the territories and buffer combined were counted. These buffers were chosen based on mean territory size (*S. diencaeus:* 0.55 ± 0.25 m^2; *S. planifrons*: 0.29 ± 0.13 m^2) and that farming damselfish chases are typically shorter (< 0.5 m). The number of *Stegastes* spp. whose territories overlapped with the buffers was counted to calculate abundance of *Stegastes* spp. within buffers. Due to the prolific abundance of *Stegastes* spp. at our study site, it was not possible to draw buffers containing hard substrate but no *Stegastes* spp.

We calculated aggression metrics for each focal *Stegastes* spp. based on the proportion of non-*Stegastes* intruders that were chased, placing individual-level aggression on a scale of 0 to 1. Individual aggressive response towards heterospecific intruders differed between species (*S. diencaeus*: mean ± sd = 0.63 ± 0.28; *S.*

planifrons: 0.41 ± 0.15). However, as our study focused on the effect of individual-level behaviour across *Stegastes* spp., and both species exhibited wide within-species variation in aggressive response (*S. diencaeus*: range = 0.10 – 1.00; *S. planifrons*: 0.19 – 0.76), species was not included in further analysis. Aggression metrics were calculated for all non-*Stegastes* intruders, and herbivorous and non-herbivorous non-*Stegastes* species separately. All fish were categorised as herbivorous or non-herbivorous according to Fishbase (Froese and Pauly, 2023). To check for temporal variation in aggressive response, Spearman's rank tests were conducted between individual-level aggression and time of recording. No correlation between the two variables was found ($r_s = 0.08$, $p = 0.60$), therefore time of recording was not included in further analysis.

Using the brms package (Bürkner, 2017) implemented in STAN (RStan, 2023), we ran Bayesian models with a negative binomial distribution to model counts of non-*Stegastes* fish against individual-level aggression and *Stegastes* spp. abundance. Bayesian models ran for 5000 iterations, with a warm-up of 1000 iterations over four chains. Weakly informative priors were used and transect ID included as a grouping factor to account for spatial dependence. As the territory and buffer area differed between focal *Stegastes* spp., the area within which fish were counted was included as an offset. Using offsets as opposed to densities is advantageous as fitted values and confidence intervals are always positive yet heterogeneity in survey area is accounted for (Zuur *et al.,* 2009). This also accounted for survey area differences resulting from buffers being truncated when they extended beyond the transect window. As transects were 2 m wide, this was unavoidable, and most buffers were affected. Counts of herbivores and non-herbivores were modelled separately to explore whether *Stegastes* spp. affect the spatial distribution of dietary groups differently. Bayesian models were visually validated for fit and convergence using graphical posterior predictive checks, trace and density plots and Gelman-Ruban convergence diagnostic (R-hat) (Gelman and Rubin, 1992). To reduce the number of divergent transitions to below 20 for all models, the adapt delta control parameter was increased to 0.95. All models had R-hat values of 1.00 and effective sample sizes over 1000 signifying good model convergence. We checked for highly influential data points using leave-one-out cross validation (LOO). Pareto-k values above 0.7 are considered highly influential (Vehtari *et al.,* 2017).

2.3 Results

The number of non-*Stegastes* fish within 1 m and 0.5 m buffers increased with increasing *Stegastes* spp. abundance (1 m: β = 0.28, 95% CI = 0.04 to 0.53; 0.5 m: β = 0.47, 95% CI = 0.06 to 0.90; Figure 2.2). When split by dietary group, the number of non-*Stegastes* non-herbivorous fish within 1 m and 0.5 m buffers increased with increasing abundance of *Stegastes* spp. (1 m: β = 0.35, 95% CI = 0.08 to 0.63; 0.5 m: β = 0.55, 95% CI = 0.09 to 1.03; Figure S2.3). The association between the number of non-*Stegastes* herbivorous fish within 1 m and 0.5 m buffers and *Stegastes* spp. abundance was weakly positive (1 m: β = 0.14, 95% CI = -0.14 to 0.42; 0.5 m: β = 0.22, 95% CI = -0.24 to 0.69; Figure S2.4).

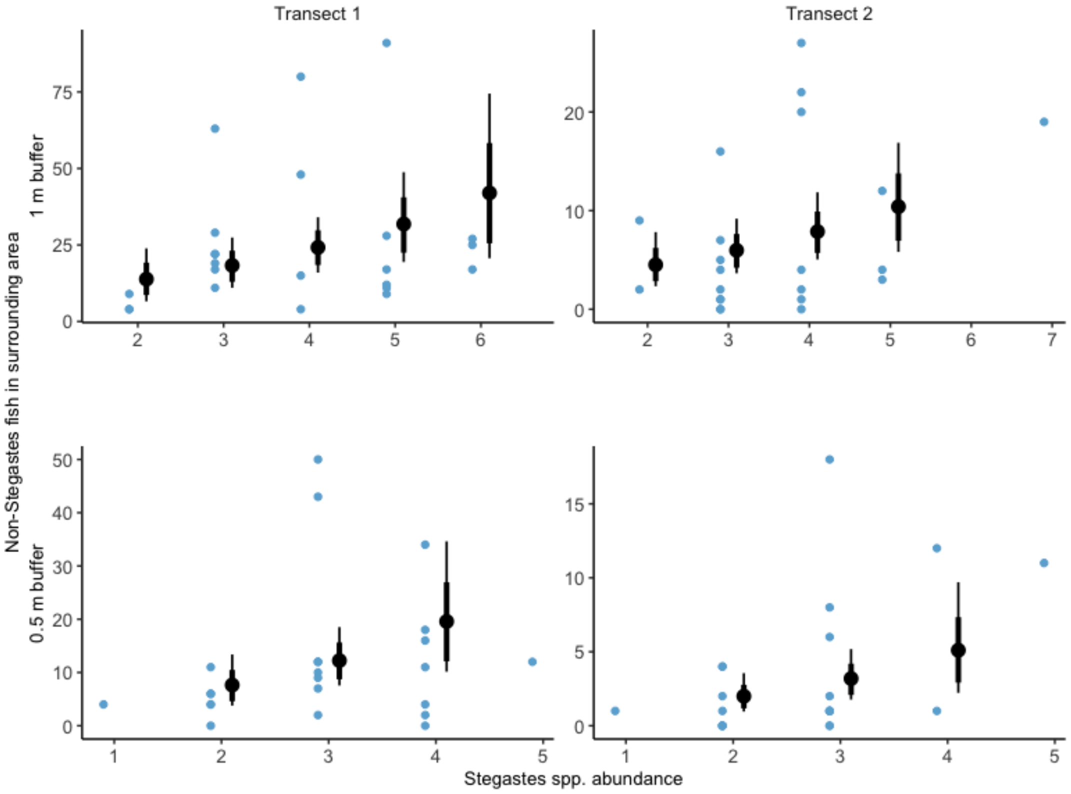

Figure 2.2 The number of non-*Stegastes* fish within *Stegastes* spp. territories and surrounding area (1 m and 0.5 m buffer) increases with increasing abundance of *Stegastes* spp. Each column shows data from a different transect, the identities of which were included as grouping factors. Blue points represent raw data. Black points and interval lines represent the expected posterior predictions and confidence intervals (80 and 95%) from Bayesian models using mean values of *Stegastes* spp. aggression and measurement area.

More aggressive *Stegastes* spp. had fewer non-*Stegastes* fish within a 1 m and 0.5 m buffer around their territory (1 m: β = -1.41, 95% CI = -2.50 to -0.33; 0.5 m: β = -0.77, 95% CI = -2.07 to 0.57; Figure 2.3). More aggressive *Stegastes* spp. had fewer non-*Stegastes* non-herbivorous fish within a 1 m buffer (1 m: β = -1.55, 95% CI = -2.80 to -0.34; 0.5 m: β = -0.57, 95% CI = -2.03 to 0.87; Figure S2.5). There was little association between individual-level aggression and number of non-*Stegastes* herbivorous fish within a 1 m and 0.5 m buffer (1 m: β = -0.23, 95% CI = -1.14 to 0.73; 0.5 m: β = -0.31, 95% CI = -1.61 to 1.00; Figure S2.6). Both *S. diencaeus* and *S. planifrons* demonstrated wide variation in individual aggressive response towards heterospecific intruders (range: 0.10 – 1.00 and 0.19 – 0.76 respectively). No influential points were found in any model (Pareto k value > 0.7).

2.4 Discussion

We applied the landscape of risk framework to demonstrate that between-individual variation in aggressive behaviour by territorial *Stegastes* spp. may shape the spatial distribution of coral reef fish. More aggressive *Stegastes* spp. had fewer fishes near to their territories than less aggressive individuals, suggesting that fish may avoid areas of reef occupied by more aggressive individuals. This could be a learned behaviour from previous encounters or recognition of stronger threat signals given by more aggressive individuals. In contradiction to the landscape of risk framework (Laundré *et al.,* 2010), the abundances of *Stegastes* spp. and other fishes were positively correlated. This may result from clustering of reef fish around live coral and hard substrate (see Figure 2.1). Our results suggest that reef fish do not simply avoid areas of high *Stegastes* spp. abundance but may avoid areas defended by more aggressive individuals.

Between-individual behavioural variation can have profound effects on interspecific interactions and community dynamics (Bolnick *et al.,* 2011; Milles *et al.,* 2020; Nicastro *et al.,* 2020). Yet landscapes of risk typically focus on behaviour at the population or species level, relying instead on spatial variation created by patterns in distribution or density (Gaynor *et al.,* 2019). *Stegastes* spp. are prolific in the Caribbean (McDougall and Kramer, 2007; Dromard *et al.,* 2018) and occupy large areas of coral reefs, meaning there is little spatial pattern in their distribution beyond being reliant on hard

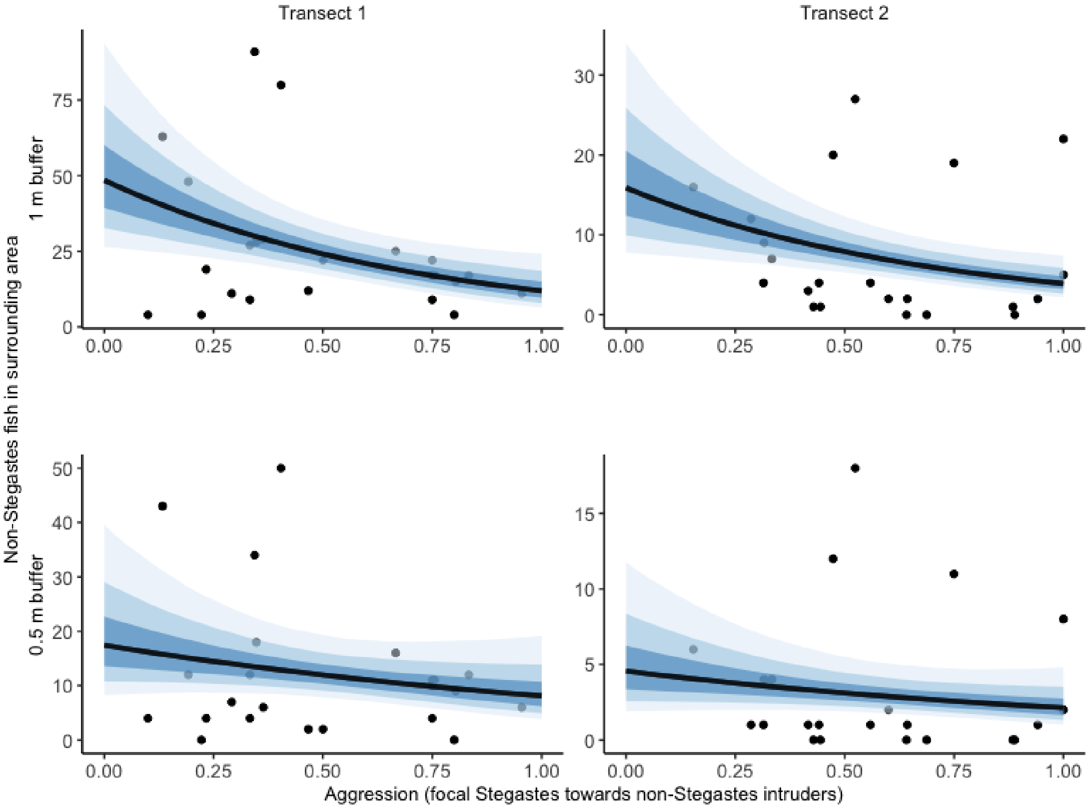

Figure 2.3 The number of non-*Stegastes* fish within focal *Stegastes* spp. territories and surrounding area (1 m and 0.5 m buffer) declines with increasing individual-level aggression of focal *Stegastes* spp. towards intruders (1 m: β = 0.28, 95% CI = 0.04 to 0.53; 0.5 m: β = 0.47, 95% CI = 0.06 to 0.90). Columns show data from two transects, the identities of which were included as grouping factors. Points represent raw data. Trend line and shaded areas represent the expected posterior predictions and confidence intervals (50, 80 and 95%) from Bayesian models using mean values of *Stegastes* spp. abundance and measurement area. Aggression measured as the proportion of intruders into the focal territory that were chased.

substratum (see Figure 2.1). However, both *S. diencaeus* and *S. planifrons* demonstrated wide variation between individuals in aggressive response to heterospecific intruders, creating spatial variation in aggressive competitive risk, which we term a competitive landscape of risk. We identified that between-individual variation in *Stegastes* spp. aggressive response may play a role in shaping fish distribution across reefs, adding to the growing pool of evidence of the ecological importance of individual-level behaviour (Bolnick *et al.,* 2011). We demonstrate that incorporating between-individual behavioural variation may greatly improve our understanding of spatial patterns in response to risk (French *et al.,* 2022).

It is generally assumed that heterospecific aggression is greater with increased resource overlap (Peiman and Robinson, 2010). It is therefore reasonable to expect that the response to aggressive risk be influenced by the degree of resource overlap. However, *Stegastes* spp. aggression showed little association with the abundance of non-*Stegastes* herbivores. Instead, there was a weakly positive association between the abundances of *Stegastes* spp. and herbivores. Our results support previous findings that aggressive interactions with farming damselfishes may not affect herbivore abundance and subsequent herbivory rates (Ceccarelli *et al.,* 2005a; Eurich *et al.,* 2018a). Instead, herbivores may be attracted to resources within damselfish territories and the surrounding area. The farming behaviours of damselfish modify algal composition within their territories, increasing epiphyte load and cover of palatable turf algae (Ceccarelli *et al.,* 2005b), which may attract herbivores despite the increased aggressive risk. This unexpected relationship between herbivore and *Stegastes* spp. abundance further demonstrates the complexities in the spatial distribution of herbivores.

Contrastingly, more aggressive *Stegastes* spp. had less non-herbivorous fishes in the area surrounding their territory. This finding suggests that non-herbivorous fishes responded more strongly to aggressive behaviour by farming damselfishes than herbivores, contrary to expectation. This finding is unlikely due to non-herbivores reacting more strongly to aggressive risk, and instead likely the result of herbivores being attracted to *Stegastes* spp. territories. However, damselfish abundance has previously been found to influence the behaviour of non-herbivores, such as reduced coral predation (Tiddy *et al.,* 2023). Therefore, the effects of aggressive risk by farming damselfishes on the spatial distribution of non-herbivorous fishes cannot be overlooked.

Aggressive risk by territorial farming damselfishes has the potential to shape fish distribution across vast areas of coral reef. Farming damselfishes are widely considered key drivers of coral reef benthic composition (Hixon and Brostoff, 1983, 1996; Ceccarelli *et al.,* 2001; Hixon, 2015). Therefore, changes to spatial distribution and community composition of reef fish driven by aggressive risk may have cascading consequences to coral reef health (Sheppard *et al.,* 2023). Just as predation risk drives prey space use and subsequent effects on ecosystem health, aggressive risk between competitors may shape spatial variation in multiple critical functions of coral reefs by altering the spatial distribution of fishes (for a review of core coral reef functions, see Brandl *et al.,* 2019).

Competition-driven habitat selection between pairs of species has been well-studied (Dickman, 1986; Dupuch *et al.,* 2014; Ferry *et al.,* 2016; Eurich *et al.,* 2018b) and demonstrates a general trend of more aggressive species forcing subordinate competitors into less profitable habitats. However, few attempts have been made to model this interaction spatially (However see Ferry *et al.,* 2016). We applied the landscape of risk framework to demonstrate that aggressive interactions between competitors may shape their spatial distribution. Furthermore, we show that between-individual behavioural variation may play a role in forming landscapes of risk, and that population means may not be enough to identify these driving forces. The landscape of risk framework is most applied to interactions between predator and prey (although see Doherty and Ruehle, 2020; Daversa *et al.,* 2021). However, competition is also a key ecological driving force. Extending the landscape of risk framework to non-predatory interspecific interactions provides opportunity to explore how behavioural responses to aggressive risk can cascade throughout communities.

Pairwise interactions represent a small part of a much larger complex network of interactions that shape one another (Sheehy *et al.,* 2018), including competitive interactions and predation. For example, shared predators reduce competitive exclusion between prey species (Sheehy *et al.,* 2018), and aggressive competitors can reduce clientele richness in cleaning interactions (Dunkley *et al.,* 2023). Although the impacts of competitive interactions on predation risk have been documented (Dupuch *et al.,* 2014), there has been no attempt to model the spatial variation of predation and competition risk simultaneously. Incorporating multiple layers into landscapes of risk, representing various trophic levels, taxonomic groups and interspecific relationships, will deepen our understanding of behavioural cascades through these complex interaction webs.

Chapter 3: Territorial farming damselfishes drive interaction modifications and reduce cleaning rates and client diversity at *A. pedersoni* cleaner shrimp stations

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In preparation for submission

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Author Contribution

CES conceived the ideas, collected and analysed data, and led the writing of the chapter. DAE helped conceive the ideas and provided field support. SAK and LBE supported data analysis. All co-authors contributed critically to chapter drafts.

Abstract

Species interactions link to form large, complex networks that indirectly shape one another. One mechanism behind such behavioural cascades are interaction modifications, where the presence and density of one species affects the pairwise interaction between two other species. Much of our understanding of such indirect effects comes from predator-prey systems, where the avoidance of predation risk drives behavioural cascades throughout ecosystems. Interspecific competition is also fundamental in shaping interaction networks, yet little is known of how avoidance of aggressive competitors may drive equivalent interaction modifications. We explored how close proximity to aggressive territorial farming damselfishes may indirectly shape mutualistic cleaning interactions with Pederson’s cleaner shrimp. We found that cleaning stations situated within farming damselfish territories were visited less frequently and had reduced clientele diversity compared with stations outside of territories. Our results offer evidence that risk avoidance of aggressive competitors may have cascading consequences to cleaning interactions on coral reefs, and we propose that exploring behavioural cascades driven by competitive risk avoidance may offer important insight into how interaction networks are shaped.

3.1 Introduction

Interactions between species are fundamental drivers in ecology, yet rarely do pairwise interactions stand alone. Instead, species interactions link to form complex interaction networks with cascading consequences that indirectly shape one another (Wootton, 1993; Koprivnikar and Penalva, 2015; Sheehy *et al.,* 2018). One mechanism driving these indirect effects is interaction modifications (also known as higher order interactions), where the density of one species affects the direct interaction between two other species (Wootton, 1993). Much of our understanding of these indirect effects centres around predator-prey interactions. By influencing the behaviour and spatial distribution of prey species, predation risk and predator avoidance can modify interspecific competition between prey species (Sheehy *et al.,* 2018) and parasitism (Koprivnikar and Penalva, 2015). However, interspecific competition is itself a key ecological driving force that can indirectly modify other interspecific interactions. Similarly to predation risk, the risk of encountering aggressive competitors can shape the distribution of subordinate or less aggressive species (Sheppard *et al.,* 2024), which may drive comparable behavioural cascades throughout interaction networks. One group of interactions that may be modified by competitive risk avoidance is mutualistic cleaning interactions.

On tropical coral reefs, cleaning interactions involve a wide variety of taxa and form an integral part of the wider reef interaction network (Quimbayo *et al.,* 2018). Cleaner species, typically small fishes (gobies, wrasse) and shrimp, remove ectoparasites and damaged tissue from larger clients. Clients are most commonly reef fish, however marine reptiles (Buck *et al.*, 2018; Weinstein *et al.,* 2018), elasmobranchs (Dewar *et al.,* 2008) and cephalopods (Johnson and Chase, 1982) have also been observed visiting cleaning stations. Removal of parasites is important for the health of individual clients, as parasitic load is associated with higher stress levels (Bshary *et al.,* 2007; Allan *et al.,* 2020), behavioural change (Allan *et al.,* 2020) and even increased mortality (Hayes *et al.,* 2011). On the other hand, dedicated cleaners, defined as species with a committed cleaning lifestyle, are thought to derive all their nutrients from clients (Vaughan *et al.,* 2017). As such, cleaning interactions carry implications for dynamics at higher ecological scales. For example, the presence of cleaners has been shown to increase fish diversity on coral reefs (Côté, 2000; Bshary, 2003; Grutter *et al.,* 2003; Waldie *et al.,* 2011).

Patterns of cleaning behaviour on coral reefs vary widely, both between client species and between individual cleaning stations (e.g. Arnal and Côté, 1998; Arnal *et al.,* 2000; Titus *et al.,* 2015; Romain *et al.,* 2020). For example, temporal variation is observed between different cleaner species in the time of day during which they preferentially clean (Titus *et al.,* 2015). The frequency and duration of cleaning interactions also varies between client species, with benthic feeders often observed having longer cleaning durations (Marcogliese, 2002). Drivers of such variation are diverse and include abiotic and biotic factors, such as levels of sedimentation and coral cover (Marcogliese, 2002; Artim and Sikkel, 2013), parasitic load (Grutter, 1995) and client body size (Arnal *et al.,* 2000). Whilst these variables may explain broad-scale patterns of cleaning behaviour, the drivers of more localised variation in cleaning interactions between stations are less understood. One mechanism behind such variation may be interaction modifications mediated by the presence, or avoidance, of predators or aggressive competitors.

The majority of research focused on cleaner-client interactions have focused on cleaner fishes; however cleaner shrimp, which make up around one fifth of all marine cleaner species (Vaughan *et al.,* 2017), are relatively understudied limiting our understanding (Quimbayo *et al.,* 2018). The most common cleaner shrimp on Caribbean coral reefs is Pederson's cleaner shrimp *Ancylomenes pedersoni*; a dedicated cleaner. *A. pedersoni* inhabit sea anemones, most commonly the corkscrew anemone *Bartholomea annulata* (Briones-Fourzán *et al.,* 2012; Mascaró *et al.,* 2012), and can be found living singularly or in small groups (Titus *et al.,* 2015). The host anemone of *A. pedersoni* acts as a visual cue for clients seeking cleaners (Huebner and Chadwick, 2012a). Numerous studies describe the client pool of *A. pedersoni*, but few have sought to explain the variation observed in cleaning behaviour between *A. pedersoni* cleaning stations. Studies have indicated that local conditions, such as coral cover and turbidity, may drive variation in cleaning rates and behaviour between geographically close but ecologically distinct sites (Romain *et al.,* 2020). One untested factor that could affect cleaning rates and clientele composition of *A. pedersoni* is the presence of territorial farming damselfishes.

Territorial farming damselfishes are a herbivorous group of highly aggressive reef fish that can influence the spatial distribution and behaviour of other reef inhabitants (Arnal and Côté, 1998; Tolimieri, 1998; Eurich *et al.,* 2018; Sheppard *et al.,* 2024). Some of the most aggressive species are within the genus *Stegastes*, who hold small individual territories (*S. diencaeus*: 0.55 ± 0.25 m^2; *S. planifrons*: 0.29 ± 0.13 m^2; Sheppard *et al.,* 2024) that they aggressively defend from intruders (Ceccarelli *et al.,* 2001). Species of *Stegastes* are particularly prolific in the Caribbean, occupying vast areas of coral reef. Moreover, territorial farming damselfishes are increasing in abundance worldwide (Edwards *et al.,* 2014). By shaping the spatial distribution of reef fish (Sheppard *et al.,* 2024), aggressive behaviour by territorial farming damselfishes may indirectly modify the patterns of cleaning interactions on coral reefs. Indeed, residing near to farming damselfishes led to reduced cleaning rates and altered clientele composition at cleaner goby *Elacatinus* spp. stations (Arnal and Côté, 1998), however this relationship has not been explored across taxa. Considering the wider implications of cleaning interactions on reef fish diversity, this is important to understand as it may have far-reaching consequences to ecological processes at the ecosystem level.

Here, we explore whether territorial farming damselfishes drive interaction modifications that affect the scope and effectiveness of cleaning interactions on coral reefs. Specifically, we compare how the presence of damselfishes modifies the clientele composition, cleaning rates, and clean durations at *A. pedersoni* cleaning stations located outside and inside of *Stegastes* spp. territories. Past studies have found that reef fish spatially avoid aggressive *Stegastes* spp. (Arnal and Côté, 1998; Tolimieri, 1998; Sheppard *et al.,* 2024), therefore we predict that cleaning stations inside territories will have lower cleaning rates. The resource overlap hypothesis suggests that interspecific aggression will be greatest between species that have a large degree of dietary overlap (Peiman and Robinson, 2010). We therefore predict that cleaning stations within *Stegastes* spp. territories will have a modified clientele composition. More specifically, we expect that cleaning stations within territories will be visited by fewer herbivores, which overlap with *Stegastes* spp. in dietary sources, and more piscivorous fishes, which *Stegastes* spp. are less likely to aggressively defend against. We also compare cleaning durations of different dietary groups with those of *Stegastes* spp. territory holders in order to explore whether cleaning interactions with territory holders themselves mitigates some of the costs of residing within their territory.

3.2 Material and methods

3.2.1 Field methodology

All data were collected between 25 June and 29 July 2023 at Coral View reef, Utila, Honduras (N 16.088233, W -86.910945), by teams of snorkellers and SCUBA divers. A total of 23 *A. pedersoni* cleaning stations were located opportunistically between 2.1 and 13.7 m depth and marked with biodegradable flagging tape. Approximate locations of cleaning stations were noted using underwater landmarks and the number of *A. pedersoni* on each cleaning station were counted. Cleaning stations were observed *in situ* to determine whether they were located inside a *Stegastes* spp. territory, which are visually apparent based on the foraging and farming behaviour of territory holders and their aggressive chases of other reef fish in defence of that territory. Out of 23 *A. pedersoni* cleaning stations, 13 were located inside a *Stegastes* spp. territory.

3.2.2 Cleaning observations

Tagged cleaning stations were recorded using GoPro video cameras (HERO 7|8 black) until battery power was lost (approx. 70 min per recording). Cameras were placed within 1 m of the cleaning stations so that cleaning interactions could be observed clearly. As cleaning rates at *A. pedersoni* stations in Utila are low (approximately 1 clean hour^{-1}; Romain *et al.*, 2020), cleaning stations were revisited and recorded multiple times (1 – 3 times; 1 hour 6 min – 4 hour 5 min total footage duration) making it more likely that variation between stations would be detected. In total, 64 hours of footage were recorded across 23 cleaning stations. Videos were recorded between 07:00 and 16:00. Time of day has previously been shown not to affect cleaning interactions on the same reefs in Honduras (Titus *et al.,* 2015).

Analysis of cleaning interactions was undertaken using BORIS software V. 8.6.2 (Friard and Gamba, 2016). We recorded the start and end of each cleaning interaction, defined as any instance where at least one *A. pedersoni* individual was on the body of a client fish (Titus *et al.,* 2015). The number of cleaning interactions, duration of each clean, and cumulative cleaning time were recorded, and client fish identified to species level. Client fishes were classified into four dietary groups using data available from Fishbase; herbivore, omnivore, piscivore, and benthic invertebrate feeder (Froese and Pauly, 2023).

3.2.3 Statistical analysis

All data manipulation and statistical analysis was conducted in RStudio V. 12.1.402 (RStudio team, 2024). To account for differences in recording time between *A. pedersoni* cleaning stations, cleaning rates (cleans hour^{-1}) and cumulative cleaning time (seconds hour^{-1}) were calculated, as well as mean duration of a single clean (seconds).

We conducted Bayesian analysis using the brms package (Bürkner, 2017) implemented in STAN (RStan, 2023). We modelled cleaning rates (cleans hour^{-1}), mean cleaning duration (seconds) and cumulative cleaning duration (seconds hour^{-1}) with Bayesian hurdle-gamma regression models against damselfish presence. To investigate whether the cleaning duration of *Stegastes* spp. territory holders differed from other dietary groups, we modelled all cleaning interactions with a log-normal distribution against dietary group. Cleaning station ID was included as a grouping factor and an adapt delta control of 0.95 was used to limit divergent transitions to below 10 (Bürkner, 2017). All models included the number of cleaner shrimps as an additional explanatory variable. Previous work on *A. pedersoni* cleaning stations on Utila detected no effect of anemone size on cleaning rate (Romain *et al.,* 2020). Therefore, it was considered reasonable to exclude anemone size from analysis. All models were run with weakly informative priors (Hadfield, 2010) for 5000 iterations, with a warm-up of 1000 iterations, over four chains. Model fit and convergence were visually checked using graphical posterior predictive checks, trace and density plots and Gelman-Ruban convergence diagnostic (R-hat) (Gelman and Rubin, 1992). All models had an R-hat value of 1.00, indicating good convergence.

Table 3.1 Fish species observed visiting *A. pedersoni* cleaning stations outside *Stegastes* spp. territories, inside *Stegastes* spp. territories, or both outside and inside *Stegastes* spp. territories. Dietary group given in brackets: H – Herbivore, O – Omnivore, P – Piscivore, B – Benthic invertebrate feeder (Froese and Pauly, 2023).

Stations outside *Stegastes* spp. territories	**Stations outside and inside *Stegastes* spp. territories**	**Stations inside *Stegastes* spp. territories**
Canthigaster rostrata (B)	*Epinephelus cruentatus* (P)	*Haemulon sciurus* (B)
Haemulon plumieri (B)	*Sparisoma viride* (H)	*Stegastes diencaeus* (H)
Halichoeres garnoti (O)		
Scarus croicensis (H)		
Scarus taeniopterus (H)		
Stegastes partitus (H)		
Thalassoma bifasciatum (O)		

3.3 Results

The composition and species richness of clientele of *A. pedersoni* varied between cleaning stations located inside and outside of *Stegastes* spp. territories (Table 3.1). We observed 11 client species overall, with seven species only visiting *A. pedersoni* cleaning stations outside of *Stegastes* spp. territories. Other than *Stegastes diencaeus* territory holders, one species, Bluestriped grunt *Haemulon sciurus*, was observed only at cleaning stations inside *Stegastes* spp. territories. Of the 10 stations outside *Stegastes* spp. territories, three received no clients (i.e. cleaning rate of 0 hour^{-1}). Whereas, of the 13 stations inside *Stegastes* spp. territories, three were observed to only clean territory holders and eight received no clients at all.

A. pedersoni cleaning stations within *Stegastes* spp. territories received fewer clients than stations outside of *Stegastes* spp. territories (Outside *Stegastes* spp. territories: mean ± sd = 1.14 ± 1.26 cleans hour^{-1}; Inside *Stegastes* spp. territories: 0.50 ± 0.81; Figure 3.1). The predicted probability of receiving no clients (i.e. cleaning rate of 0 hour^{-1}) at *A. pedersoni* cleaning stations within *Stegastes* spp. territories was 44% higher than at cleaning stations outside of *Stegastes* spp. territories (Outside territories: estimated marginal mean (EMM) probability = 0.19, 95% highest posterior density interval (HPDI) = 0.01 to 0.44; Inside territories: EMM probability = 0.63, HPDI = 0.38 to 0.86). When looking at non-territory holder cleans only, the predicted probability of receiving no clients was 67% higher at cleaning stations within *Stegastes* spp. territories than outside (Outside territories: EMM = 0.17, 95% HPDI = 0.01 to 0.41; Inside territories: EMM = 0.86, HPDI = 0.66 to 0.99).

Discounting stations that did not receive any clients, both cumulative cleaning time (Outside: EMM = 24.7 s hour^{-1}, HPDI = 9.7 to 54.4 s hour^{-1}; Inside: EMM = 44.8 s hour^{-1}, HPDI = 10.6 to 127.4 s hour^{-1}; Figure 3.2c) and mean duration of cleaning interactions (Outside: EMM = 23.5 s, HPDI = 9.7 to 49.8 s; Inside: EMM = 36.8 s, HPDI = 10.5 to 105.9 s; Figure 3.2d) did not differ between *A. pedersoni* stations inside and outside *Stegastes* spp. territories. Number of shrimps had no association with cleaning rate (EMM = -0.03, HPDI = -0.35 to 0.31; Figure 3.3a), cumulative cleaning time (EMM = -0.09, HPDI = -0.56 to 0.44; Figure 3.3b), or mean duration of cleaning interactions (EMM = 0.03, HPDI = -0.44 to 0.51; Figure 3.3c).

The duration of cleaning interactions differed between dietary groups (Figure 3.4). Cleaning interactions with piscivores were the longest (EMM = 132.2, HPDI = 16.1 to 420.1), followed by benthic invertebrate feeders (EMM = 42.3, HPDI = 13.1 to 88.3), and omnivores (EMM = 28.1, HPDI = 5.2 to 76.8). Cleaning interactions with herbivores were the shortest (EMM = 13.1, HPDI = 6.4 to 22.5). Cleaning interactions with territory holders was comparable to other herbivores (EMM = 12.6, HPDI = 4.5 to 29.0). Number of shrimps had no association with cleaning duration of different dietary groups (EMM = -0.14, HPDI = -0.43 to 0.16).

3.4 Discussion

Farming damselfishes are widely recognised to affect the behaviour and space use of reef fish (Foster, 1985; Tolimieri, 1998; Tiddy *et al.,* 2023; Sheppard *et al.,* 2024). Here, we conduct one of the first studies exploring the indirect effects of farming damselfishes on interspecific interactions across phyla, namely the invertebrate *A. pedersoni* cleaner shrimp. In line with our predictions, we found that *A. pedersoni* at cleaning stations inside *Stegastes* spp. territories had reduced cleaning rates and lower

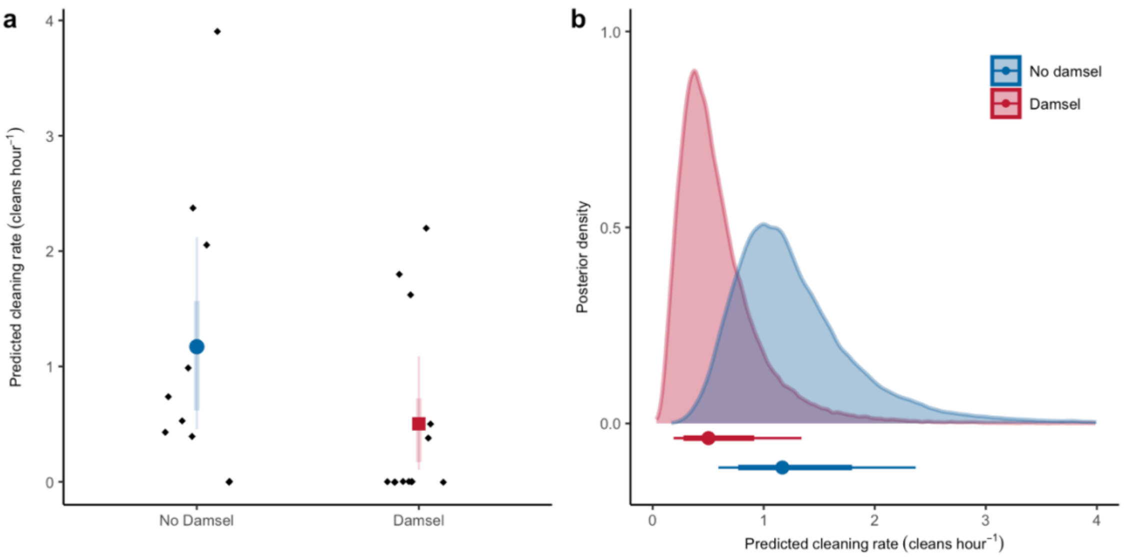

Figure 3.1 Cleaning rate (cleans hour^{-1}) was lower at *A. pedersoni* cleaning stations inside *Stegastes* spp. territories than outside *Stegastes* spp. territories. Points and trend intervals represent the median expected posterior predictions and confidence intervals (70 and 90%) from Bayesian hurdle-gamma models. Black points represent raw data. a) Predicted cleans per hour. b) Expected posterior predictions presented for cleans per hour. Note x-axis limited to 4 cleans hour^{-1} for ease of viewing.

client diversity showing that vertebrate behaviour can impact the behaviour of invertebrates. Most notably, cleaning stations inside *Stegastes* spp. territories had a substantially increased probability of receiving no clients. In line with previous studies (Romain *et al.,* 2020), cleaning rate and duration were not affected by number of *A. pedersoni* at each station.

Variation in cleaning interactions can be driven by many factors, including parasite load, client body size, and client identity (Grutter, 1994; 1995; Arnal *et al.,* 2000; Luque and Poulin, 2008; Carrassón *et al.,* 2019). However, the drivers of such variation on a local scale are poorly understood (however see Arnal and Côté, 1998; Romain *et al.,* 2020). Cleaning rates in *A. pedersoni* vary widely between geographically close cleaning stations, even on the same reef (observed range 0 – 3.34 hour^{-1}) (also see Romain *et al.,* 2020). In accordance with past studies on *Elacatinus* spp. cleaner gobies (Arnal and Côté, 1998), we found that the presence of *Stegastes* spp. was associated with substantial reduction in the use of *A. pedersoni* cleaning stations. Specifically, we found that cleaning stations inside *Stegastes* spp. territories had a much greater probability of receiving no cleans. Moreover, only two *A. pedersoni* stations inside *Stegastes* spp. territories were observed cleaning a fish other than the territory holder.

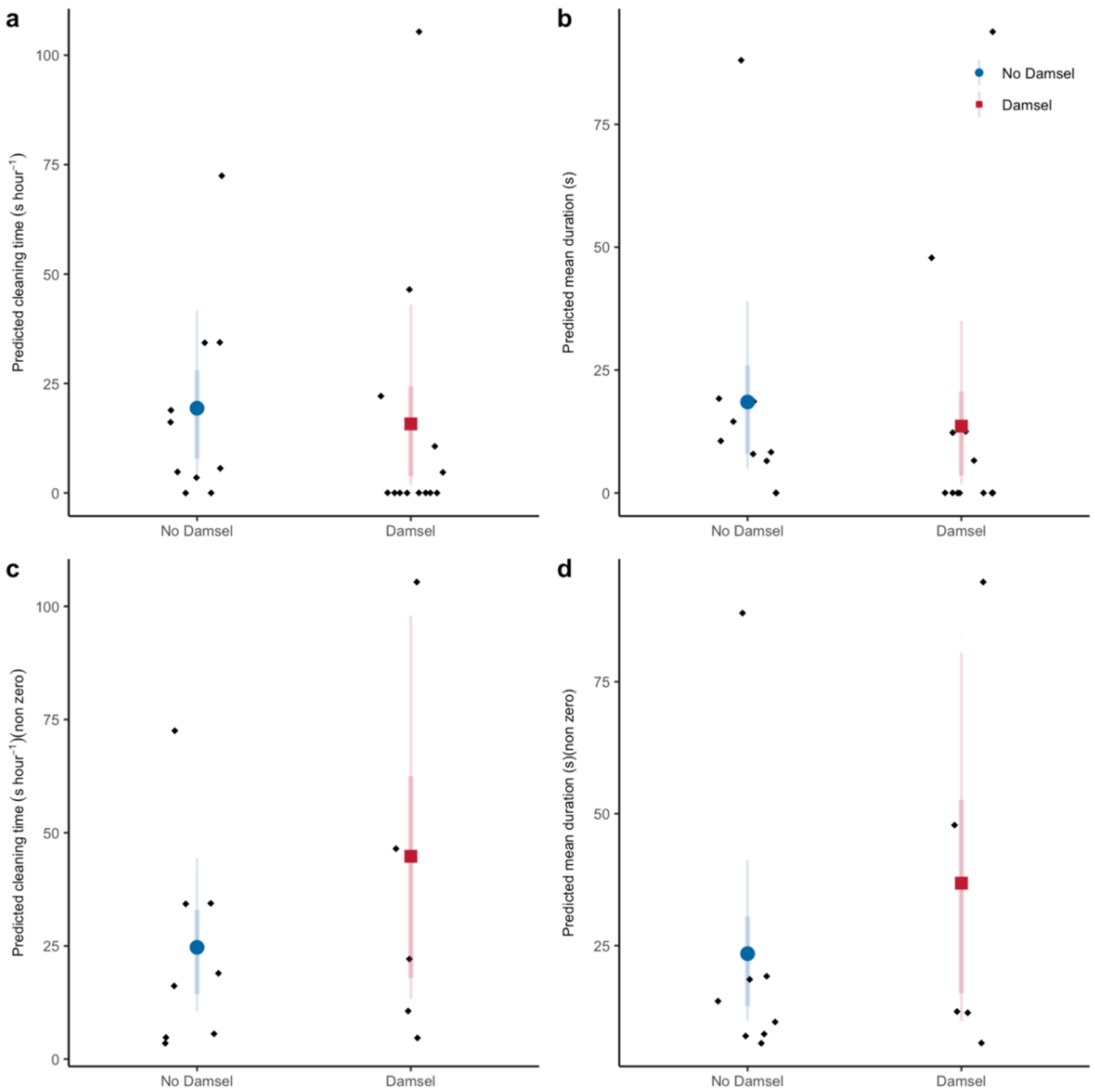

Figure 3.2 Cumulative cleaning time (seconds hour^{-1}) and mean cleaning duration (seconds) at *A. pedersoni* cleaning stations inside *Stegastes* spp. territories and outside *Stegastes* spp. territories. Points and trend intervals represent the median expected posterior predictions and confidence intervals (70 and 90%) from Bayesian hurdle-gamma models. a) Predicted cumulative cleaning time (seconds hour^{-1}) and b) Predicted mean clean duration (seconds). c) Predicted cumulative cleaning time (seconds hour^{-1}) from non-zero part of model and d) Predicted mean clean duration (seconds) from non-zero part of model.

Aggressive competitive interactions with farming damselfishes have been shown to shape the spatial distribution and behaviour of reef fish (Arnal and Côté, 1998; Tolimieri, 1998; Eurich *et al.,* 2018b; Sheppard *et al.,* 2024). By driving spatial avoidance of interspecific aggression in client species, farming damselfishes may prompt interaction modifications that cascade to negatively impact cleaning interactions with *A. pedersoni*. Avoidance of aggressive competitors therefore may offer a mechanism mediating variation in cleaning interactions on local scales.

A wide variety of reef fish are known to frequent cleaning stations (Arnal and Côté, 1998; Huebner and Chadwick, 2012b; Romain *et al.,* 2020). However, there is commonly a mismatch between the potential and realised clientele of cleaner species (Grutter and Poulin, 1998; Arnal *et al.,* 2000; Dunkley *et al.,* 2019; Romain *et al.,* 2020). For example, species of the families Serranidae (groupers) and Lutjanidae (snappers) were overrepresented relative to their local abundance in the clientele of *A. pedersoni* in Utila (Romain *et al.,* 2020). One explanation offered for this variation is the difference in parasitic load between dietary groups (Grutter, 1994; Luque and Poulin, 2008; Carrassón *et al.,* 2019). Differences in parasitic abundance and diversity can be affected by the trophic level and feeding environment of the host, such that higher loads are observed in benthic-demersal species or those occupying higher trophic levels (Luque and Poulin, 2008). This may explain why certain families frequent cleaning stations more often but does not explain variation in clientele composition between *A. pedersoni* cleaning stations. We observed differences in the clientele composition of *A. pedersoni* between cleaning stations outside and inside *Stegastes* spp. territories. Species of the family Labridae (wrasse) were only observed at stations outside of *Stegastes* spp. territories, as were more species of herbivorous Scaridae (parrotfish). Though Labridae are classified as omnivorous and do not overlap with *Stegastes* spp. in dietary resources, juveniles are known egg predators (Froese and Pauly, 2023). *Stegastes* spp. territories are multi-purpose and are a space for males to care for and protect eggs. We may therefore expect heightened aggression towards Labridae as *Stegastes* spp. defend their eggs (offspring-defence hypothesis; Wolff and Peterson, 1998), which may explain the absence of these species at cleaning stations inside territories. Our findings provide evidence that the presence of *Stegastes* spp. alters the composition of *A. pedersoni* clients, which may in turn reduce the quantity and diversity of nutrients for *A. pedersoni*.

Although *Stegastes* spp. were found to affect cleaning rates and client diversity, their presence showed no effect on cleaning duration by *A. pedersoni*. However, we found that individual clean durations varied substantially between dietary groups. Trophic level and feeding environment can affect parasitic load (Grutter, 1994; Luque and Poulin, 2008; Carrassón *et al.,* 2019) and therefore the duration of cleaning interactions. In accordance with previous findings (Huebner and Chadwick, 2012b; Titus *et al.,* 2015; Romain *et al.,* 2020), we observed that piscivorous Serranidae, a higher-trophic family, had much longer cleans than lower-level herbivorous Scaridae. Benthic invertebrate feeders had the second highest clean durations. These species are thought to be subjected to higher parasitic load as they forage in the benthos where the majority of parasitic exchange occurs (Marcogliese, 2002). Our results add to evidence that dietary group influences the duration of cleaning interactions with *A. pedersoni* (Titus *et al.,* 2015).

Given the lowered cleaning rates in the presence of farming damselfishes, our results lend the question of why *A. pedersoni* would settle inside *Stegastes* spp. territories. Visitations to cleaning stations by territory holders themselves may offer one explanation. Fishes of the family Pomacentridae, including *Stegastes* spp., are some of the most common clients of *A. pedersoni* (Titus *et al.,* 2015; Romain *et al.,* 2020). Indeed, at three cleaning stations located inside *Stegastes* spp. territories, we observed cleaning interactions only between *A. pedersoni* and the territory holder. Farming damselfishes are highly site-attached (Ceccarelli *et al.,* 2005b; McDougall and Kramer, 2007), whereas other common clients of *A. pedersoni* have much larger home ranges (e.g. *Sparisoma viride* and *Scarus iseri*; 200 – 300 m^2; Manning and McCoy, 2023) and may be less likely to repeatedly seek the same cleaning station. The costs associated with residing inside *Stegastes* spp. territories may therefore be outweighed by the benefits of having one faithful client. Indeed, *S. diencaeus* with cleaner gobies *Elacatinus* spp. inside their territories spend significantly more time being cleaned than individuals visiting cleaning stations outside of their territories (Cheney and Côté, 2001).

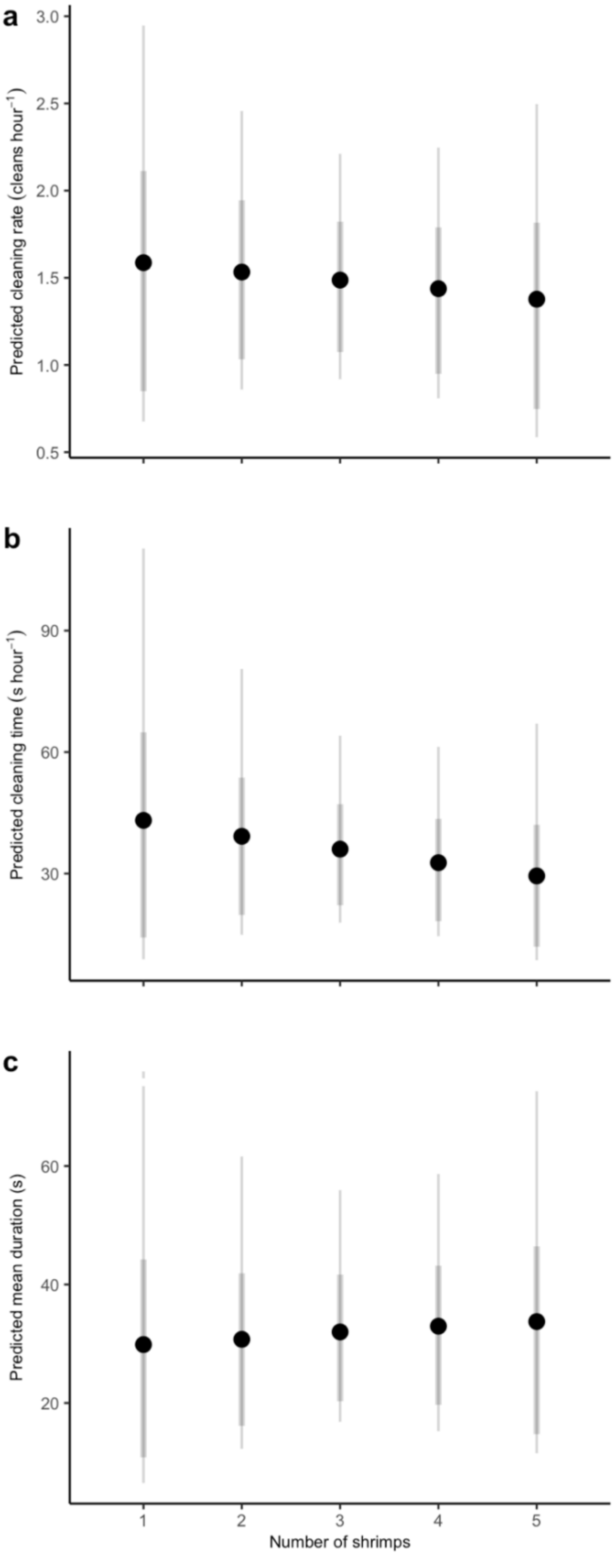

Figure 3.3 The number of shrimp at *A. pedersoni* cleaning stations had no association with a) cleaning rate (cleans hour^{-1}), b) cumulative (seconds hour^{-1}) and c) mean clean duration (seconds). Points and trend intervals represent the median expected posterior predictions and confidence intervals (70 and 90%) from Bayesian hurdle-gamma models.

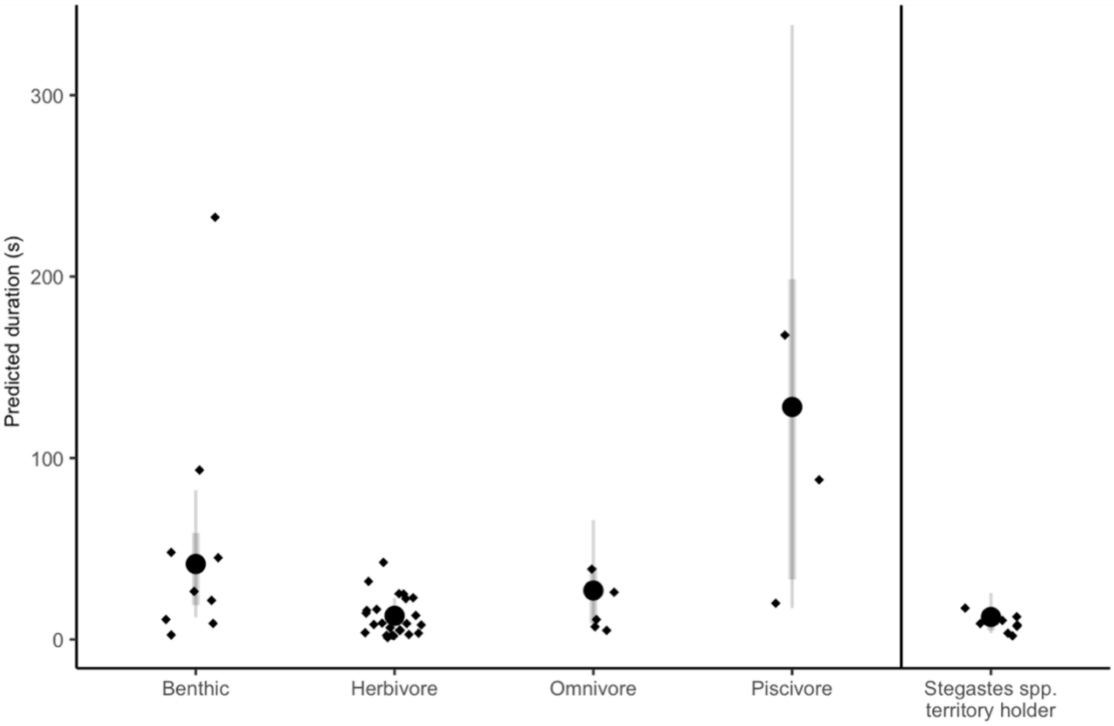

Figure 3.4 Predicted cleaning duration for different dietary groups and *Stegastes* spp. territory holders at *A. pedersoni* cleaning stations. Points and trend intervals represent the median expected posterior predictions and confidence intervals (70 and 90%) from Bayesian log normal models. Black points represent raw data.

Another benefit of residing inside *Stegastes* spp. territories may be protection from predators, though this explanation is less likely. Predation of cleaner shrimp by clients is rare (Côté, 2000). Moreover, cleaner shrimp have been shown to alter their behaviour towards predatory versus non-predatory clients (Caves *et al.,* 2019), demonstrating their own ability to avoid predation. We observed predators of shrimp (e.g. *Haemulon flavolineatum* and *H. sciurus*) visiting cleaning stations both outside and inside *Stegastes* spp. territories and observed relatively few chases of predators of shrimp by territory holders (Lutjanidae and Haemulidae; 4 out of 119 chases).

The primary benefit of cleaning interactions to clients is parasite removal. Increased parasitic load carries numerous negative impacts to reef fish, both physiological (Bshary *et al.,* 2007; Grutter *et al.,* 2011; Allan *et al.,* 2020) and behavioural (Allan *et al.,* 2020), and can even increase mortality (Hayes *et al.,* 2011). By removing parasites, *A. pedersoni*, which have been found to remove 100% of parasitic isopods in laboratory trials (Bunkley-Williams and Williams, 1998), can help to relieve these negative effects. At the community level, cleaner species have been shown to drive local diversity of reef fish (Côté, 2000; Bshary, 2003; Grutter *et al.,* 2003; Waldie *et al.,* 2011). Our findings suggest that farming damselfishes may indirectly affect both individual reef fish health and wider community dynamics by reducing the rate of cleaning interactions.

Although we have only just begun to resolve the impacts of residing inside farming damselfish territories for cleaner shrimp, our study is one of the first attempts to investigate the cascading effects of farming damselfishes on interspecific interactions with taxa other than fish. We show that farming damselfishes may result in interaction modifications that reduce cleaning interactions and client diversity and argue how this may have indirect consequences at both the individual and community level. Further studies are needed to clarify this relationship and find explanations for why cleaner species may settle in damselfish territories despite reduced clientele richness and cleaning rates of species other than territory holders. Examining the role of repeat visitations to the same cleaning station may offer an interesting avenue of exploration, as well as whether cleaning stations inside damselfish territories show reduced tenancy length. Given the proliferation of territorial damselfishes in the Caribbean, and across the globe (Edwards *et al.,* 2014), cleaner species such as *A. pedersoni* may have no alternative but to reside inside damselfish territories, accentuating the importance of our findings. In addition, because of the low cleaning rates at *A. pedersoni* cleaning stations, we must find ways to increase sample size (e.g. video cameras with longer recording capabilities).

Although marine cleaning interactions are widely explored, it has been argued that research must shift focus towards broader behavioural and ecological contexts to better understand the driving mechanisms and implications of variation in cleaning interactions (Caves, 2021). Our findings indicate that avoidance of aggressive competitors, driving interaction modifications, may offer one such mechanism. We propose that exploring behavioural cascades driven by risk avoidance of predators or competitors may prove an interesting and important research avenue for cleaning interactions.

Chapter 4: Familiarity hypothesis mediated by body size predicts intraspecific aggression in territorial farming damselfishes

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Submitted to *Behavioural Ecology*

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Author Contribution

CES conceived the ideas, collected and analysed data, and led the writing of the chapter. SAK and LBE supported data analysis. All co-authors contributed critically to chapter drafts.

Abstract

Aggressive territoriality can have significant benefits for resource acquisition yet is a costly behaviour. Selection should therefore favour mechanisms that allow an individual to modify their behaviour to maintain and defend their territory whilst minimising costs. One such mechanism between intraspecific territorial competitors is neighbour-stranger discrimination. The familiarity hypothesis suggests that territory holders will respond less aggressively to neighbours they recognise than to strangers they do not recognise. Conversely, in systems where neighbours pose a greater threat to territory loss than strangers, the threat-level hypothesis predicts that neighbours will elicit a greater aggressive response. We tested these opposing hypotheses in territorial farming damselfishes using a common bottle presentation experiment design to initiate aggressive responses by territory holders to neighbouring and non-neighbour individuals. Neighbours that were smaller in body size than the territory holder elicited the greatest aggressive response, whereas larger neighbours elicited the weakest. The aggressive response elicited by non-neighbours did not vary greatly with body size difference between the stimulus fish and territory holder. We demonstrate that aggressive response in territorial farming damselfishes is influenced by both familiarity and potential threat determined by body size. These findings add to the growing pool of evidence that an understanding of multiple factors is needed to identify the drivers of neighbour-stranger discrimination.

4.1 Introduction

Territoriality is widespread across the animal kingdom yet carries significant cost in the form of aggression. Aggressive behaviour for the purpose of territory defence increases energy expenditure (Marler *et al.,* 1995; Neat *et al.,* 1998) and the risk of injury (Clutton-Brock and Huchard, 2013). Thus, territory holders are expected to modify their behaviour in such a way that reduces these costs while still upholding their territory and minimising resource loss by intrusion. One such mechanism between intraspecific competitors is neighbour-stranger discrimination, where territory holders recognise and react differently towards neighbouring individuals than strangers (Ydenberg *et al.,* 1988; Temeles, 1994).

There are two alternative hypotheses that aim to explain neighbour-stranger discrimination. The first, the familiarity hypothesis, predicts that frequent past encounters with the same individual will result in reduced conflict and aggression in subsequent encounters (Ydenberg *et al.,* 1988; Temeles, 1994). It is proposed that when animals fight, they gain information on the fighting ability, termed resource holding potential (RHP), of their opponent and can make a better assessment of their chances of winning or losing (Parker and Rubenstein, 1981; Getty, 1989; Arnott and Elwood, 2009). Neighbours have less to learn about each other and have better knowledge of the potential outcome of subsequent aggressive encounters, resulting in fewer or reduced escalation of fights (Getty, 1989).

Alternatively, the threat-level hypothesis emphasises the importance of potential threat in determining aggressive response. When neighbours and strangers differ in their potential threat, the aggressive response of territory holders should be strongest towards the greatest threat (Temeles, 1994). Strangers may be perceived as roving individuals seeking a territory of their own (Wilson, 1975), and therefore present a greater threat to territory loss than neighbours who already hold a territory of their own. This may be more pronounced in species that hold multi-purpose, breeding territories (Temeles, 1994; Werba *et al.,* 2022), as territory holders stand to lose fitness as well as resources. In such systems where strangers present a greater threat than neighbours, the familiarity hypothesis and threat-level hypothesis predict the same outcome; that strangers elicit a stronger aggressive response than neighbours. However, in some territorial species, neighbours may pose a greater threat to territory or resource loss than strangers and, as such, are predicted to elicit a stronger aggressive response (e.g. Temeles, 1990; Müller and Manser, 2007; Newey *et al.,* 2010; Munguía-Steyer *et al.,* 2016). This is expected when intense competition continues after territory boundaries are established and neighbours are continually trying to expand their territory (Müller and Manser, 2007; Munguía-Steyer *et al.,* 2016).

Neighbour-stranger discrimination is observed in a variety of taxa, including birds (Temeles, 1990), mammals (Müller and Manser, 2007), insects (Munguía-Steyer *et al.,* 2016) and fish (Sogawa and Kohda, 2018). However, the mechanisms behind such discrimination have been inferred from studies limited in taxonomic breadth, with a disproportionate investment in birds, particularly breeding males (Werba *et al.,* 2022). This imbalance limits our understanding of the generality of trends in neighbour-stranger discrimination across taxa (Werba *et al.,* 2022). Marine species in particular have received very little attention, likely because of the challenges of underwater research. Moreover, the few studies testing the effect of familiarity on aggression in marine species have primarily worked in laboratory settings (e.g. Tricarico *et al.,* 2011; Silveira *et al.,* 2020). Though laboratory testing allows for greater manipulation and control and provides important insight into the drivers of such discrimination, investigating neighbour-stranger discrimination in the field, with the trade-off of smaller sample sizes, is critical to understanding how this phenomenon impacts processes in complex ecological systems.

Territorial farming damselfishes present an ideal model system to explore the alternative hypotheses to neighbour-stranger discrimination in the field. Individual farming damselfish hold small contiguous territories, which both sexes aggressively defend from intra- and interspecific intruders. Encounters between neighbouring damselfishes along shared boundaries are frequent. Species of the genus *Stegastes* are some of the most aggressive (Ceccarelli *et al.,* 2001) and hold multipurpose territories used for cultivating turf algae and, in the case of males, a space to care for and protect eggs. These species are highly site-attached (Itzkowitz *et al.,* 1995; McDougall and Kramer, 2007), taking occasional short forays (< 7 m; *Stegastes planifrons*; Itzkowitz,

1978) outside of their territories. In *Stegastes diencaeus*, studies have found no evidence of nonterritorial roving individuals and infrequent relocation of territories by adults (McDougall and Kramer, 2007) suggesting that individuals hold the same territory for long periods of time. This lack of relocation provides the opportunity for familiarity to build up between neighbours.

We tested whether the familiarity hypothesis or threat-level hypothesis provides the most plausible explanation for patterns of aggression in the territorial farming damselfish species *Stegastes diencaeus*. In farming damselfish, the familiarity hypothesis predicts that neighbours should elicit a weaker aggressive response by territory holders than non-neighbours (strangers). However, given the high frequency of encounters with neighbours and limited natural territory relocation in this species (McDougall and Kramer, 2007), we expect that neighbours will pose a greater potential threat to territory loss than non-neighbours. As such, the threat-level hypothesis predicts that territory holders should react more aggressively to neighbours than non-neighbours. We tested these opposing hypotheses by presenting captured *S. diencaeus* neighbours and non-neighbours to territory holders and measuring subsequent aggressive response and time spent within close proximity of the stimulus.

4.2 Materials and Methods

4.2.1 Field Methodology

We conducted our study between 01 June and 14 July 2023 at Coral View reef, Utila, Honduras (N 16.088233, W -86.910945). Eighteen focal *S. diencaeus* were chosen opportunistically (depth range 4.9 – 11.1 m), with the criteria of having at least one intraspecific neighbour with adjoining territory. Territories were marked with biodegradable flagging tape, which is a reliable method of identification (Snekser *et al.,* 2009; Weimann *et al.,* 2018) because this species is highly site-attached (McDougall and Kramer, 2007). Previous work recorded a mean territory size of 0.55 m^2 for *S. diencaeus* at this site (Sheppard *et al.,* 2024) (maximum 1.19 m^2; unpublished data). Therefore, focal *S. diencaeus* were located at least 5 m away from each other to maximise independence of the samples. No evidence of eggs or nesting behaviour was observed in any of the fish used in this experiment.

4.2.2 Bottle presentations

The aggressive response of *S. diencaeus* to intraspecific neighbours and non-neighbours was tested using a common presentation experiment which presents stimulus fish to focal individuals in clear bottles (originally developed by Myrberg and Thresher 1974; Figure 4.1). We used 3 L clear plastic cylinders (14 x 24 cm) in which stimulus fish could swim freely, modified with mesh lids and perforated bottoms to allow waterflow. Using barrier nets and spray bottles filled with a mix of ethanol and clove oil (3:1) (Whiteman and Côté, 2002), teams of SCUBA divers captured two neighbouring *S. diencaeus*, one from each of two focal individuals. Both captured *S. diencaeus* were used as stimulus fish for two focal individuals, offering a neighbour and non-neighbour stimulus, to reduce the number of animals required. Upon capture, stimulus fish within bottles were placed in their own territory, covered, and left to recover for at least 30 min. This also allowed any residual clove oil in the area to dissipate.

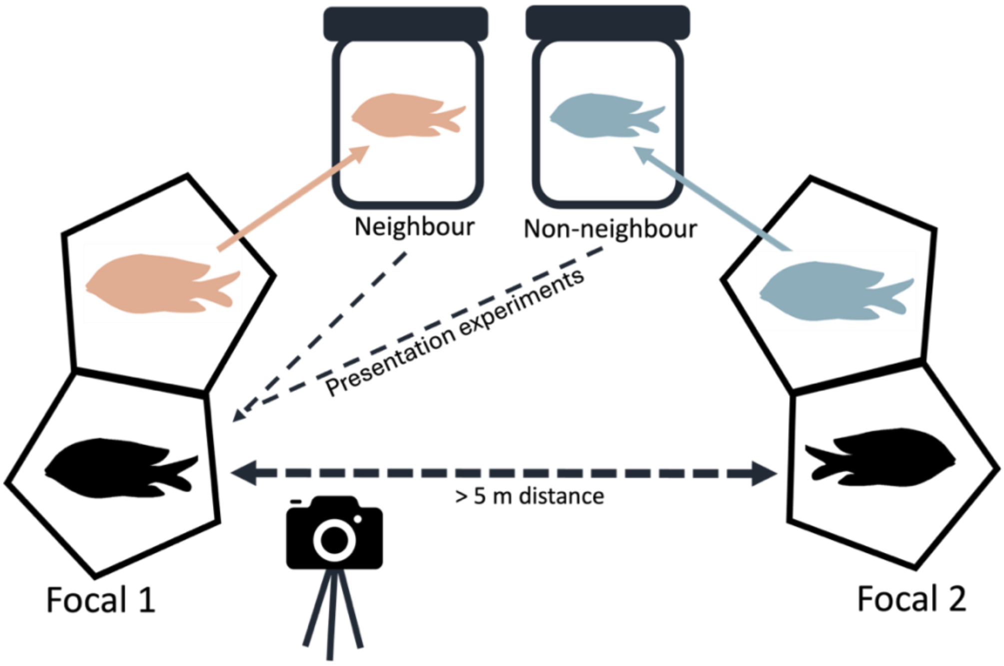

Figure 4.1 Bottle-presentation study design in respect to focal individual 1. Hexagons represent *S. diencaeus* territories. Black fish represent focal *S. diencaeus*, whilst orange and blue fish represent neighbouring *S. diencaeus*. Neighbouring *S. diencaeus* of two focal individuals (> 5 m apart), representing a neighbour and non-neighbour, were captured and contained in 3 L clear plastic bottles. After a period of acclimatisation, stimulus fish within their bottles were placed successively into the centre of the territory of the focal *S. diencaeus* and the aggressive response was video recorded for 3 minutes. The stimulus fish were presented to both focal individuals before being returned to their own territory.

After the recovery period, stimulus fish within their bottles were placed successively into the centre of the territory of the focal *S. diencaeus* for 3 minutes, with the resultant behaviour recorded using a GoPro HERO camera (HERO Black 7|8|9) placed approximately 1 m away. Stimulus fish were presented from a different direction than their own territory. During presentations, SCUBA divers retreated to at least 2 m so as not to influence behaviour passively. A subset of nine focal *S. diencaeus* were also presented with an empty bottle for 3 min to act as a control. The order in which stimulus fish and controls were presented was randomised and focal *S. diencaeus* were allowed to return to normal behaviour between presentations, confirmed by resumption of foraging or farming. Upon completion of the experiment, stimulus fish were returned and released back into their territories. During presentations to one focal *S. diencaeus,* a grouper, a known predator of damselfishes, intruded into the immediate area. This focal individual was removed from further analysis to exclude any effects of predator presence on aggressive behaviour. Our final dataset contained paired presentation experiments to 17 focal *S. diencaeus.*

4.2.3 Ethical note

This study approved by the Animal Welfare and Ethical Review Body (AWERB), considering the three R’s principle: replacement, reduction, and refinement. Each captured fish was presented to two focal individuals, reducing the number of animals needed for the experiment. Using a mix of clove oil and ethanol prior to capture reduced the stress caused by this process. After capture, individuals in their containers were placed back into their own territories and covered in a small tarp to allow them to destress and for the effects of the clove oil to wear off. The fish used in this study were contained for no more than 180 minutes and were released in the same area from which they were caught. Contained fish were presented for 3 minutes to two focal individuals, equating to 6 minutes in total per animal. These time limits minimised the duration with which they were subject to aggressive displays and reduced distress to the animals. During presentations, the behaviour of both captured and focal individuals was continually monitored for signs of unnaturally high stress (e.g. swimming rapidly in circles, or withdrawing into a corner and remaining still). The health status of the captured fish was checked after capture and release. Data were collected under permit number DE-MP-108-2023 issued by the Honduran government’s Instituto de Conservación Forestal (ICF).

4.2.4 Statistical analysis

Behavioural videos were analysed using the BORIS software V. 8.6.2 (Friard and Gamba, 2016). We recorded the total number of bites and rams directed towards the stimulus over the 3 min presentations, as well as the time spent (seconds) within close proximity (< 15 cm) of the bottle. As it was difficult to discern when contact with the bottle was made, the number of bites and rams were summed to give a total count of aggressive displays. An important aspect to consider in studies of aggressive response is body size differences between individuals, as this can determine asymmetries in RHP (Arnott and Elwood, 2009). The standard lengths of focal and stimulus *S. diencaeus* were measured using ImageJ software (Schneider *et al.,* 2012). Screengrabs were taken from behavioural footage such that the fish were positioned parallel to the bottle, allowing the bottle to be used for scale. Due to the restricted accuracy of this method, body size differences between stimulus and focal fish were recorded binomially as smaller or larger (with respect to focal).

All data manipulation and statistical analysis was conducted in RStudio V. 12.1.402 (RStudio team, 2024). We ran Bayesian models using the brms package (Bürkner, 2017) implemented in STAN (RStan, 2023). We fitted total counts of aggressive displays and time spent within close proximity of the stimulus fish against the type of stimulus (neighbour/non-neighbour) and body size difference (smaller/larger), with a negative binomial and gaussian distribution, respectively. The interaction effect between type of stimulus fish and body size difference was also included. Focal damselfish ID was included as a grouping factor to account for individual variation in aggression. Weakly informative priors were used for both Bayesian models (Hadfield, 2010). Models were run for 5000 iterations, with a warm-up of 1000 iterations over four chains. The adapt delta control parameter was increased to 0.95 to avoid any divergent transitions (Bürkner, 2017). Model fit and convergence were visually validated using graphical posterior predictive checks, trace and density plots and Gelman-Ruban convergence diagnostic (R-hat) (Gelman and Rubin, 1992). Both models had an R-hat value of 1.00, signifying that the models had converged well.

4.3 Results

The total count of aggressive displays was influenced by the interaction effect between the type of stimulus fish and body size difference (Figures 4.2 and S4.1). Smaller neighbours elicited the greatest aggressive response (estimated marginal mean (EMM) = 10.2, 95% highest posterior density interval (HPDI) = 1.7 to 25.6), whereas larger neighbours elicited the weakest aggressive response (EMM = 3.9, HPDI = 0.5 to 12.2). The total count of aggressive displays directed towards non-neighbours did not vary greatly with body size difference, however smaller non-neighbours elicited a marginally greater response than larger non-neighbours (smaller non-neighbours: EMM = 7.0, HPDI = 1.2 to 19.3; larger non-neighbours: EMM = 5.3, HPDI = 0.8 to 13.9). The distributions of expected posterior predictions of aggressive response to larger fish demonstrated a sharp rise and fall at values of weaker aggression. In contrast, the distributions of expected posterior predictions of response to smaller fish, particularly smaller neighbours, demonstrated much wider variation in aggression.

Time spent (seconds) within close proximity (< 15 cm) of the stimulus was also influenced by the interaction effect between the type of stimulus fish and body size difference (Figure 4.3 and S4.2). The time spent within close proximity of neighbours did not vary with body size difference (smaller neighbours: EMM = 97.0, HPDI = 65.9 to 125.1; larger neighbours: EMM = 94.4, HPDI = 63.9 to 124.5). Territory holders spent similar time within close proximity of smaller non-neighbours as they did neighbours (EMM = 92.6, HPDI = 63.4 to 123.8). However, territory holders spent less time within close proximity of larger non-neighbours (EMM = 81.7, HPDI = 49.8 to 112.3). The expected posterior predictions of time spent in close proximity to all fish demonstrated a fairly symmetrical distribution (Figure 4.3).

Only one focal *S. diencaeus* was observed to aggressively ram the empty control bottle once, no other aggressive response was elicited by the empty control bottles. Focal *S. diencaeus* spent very little time in close proximity to empty control bottles (Figure S4.2). This demonstrates the lack of response to empty bottles, and that aggressive responses were elicited by stimulus fish.

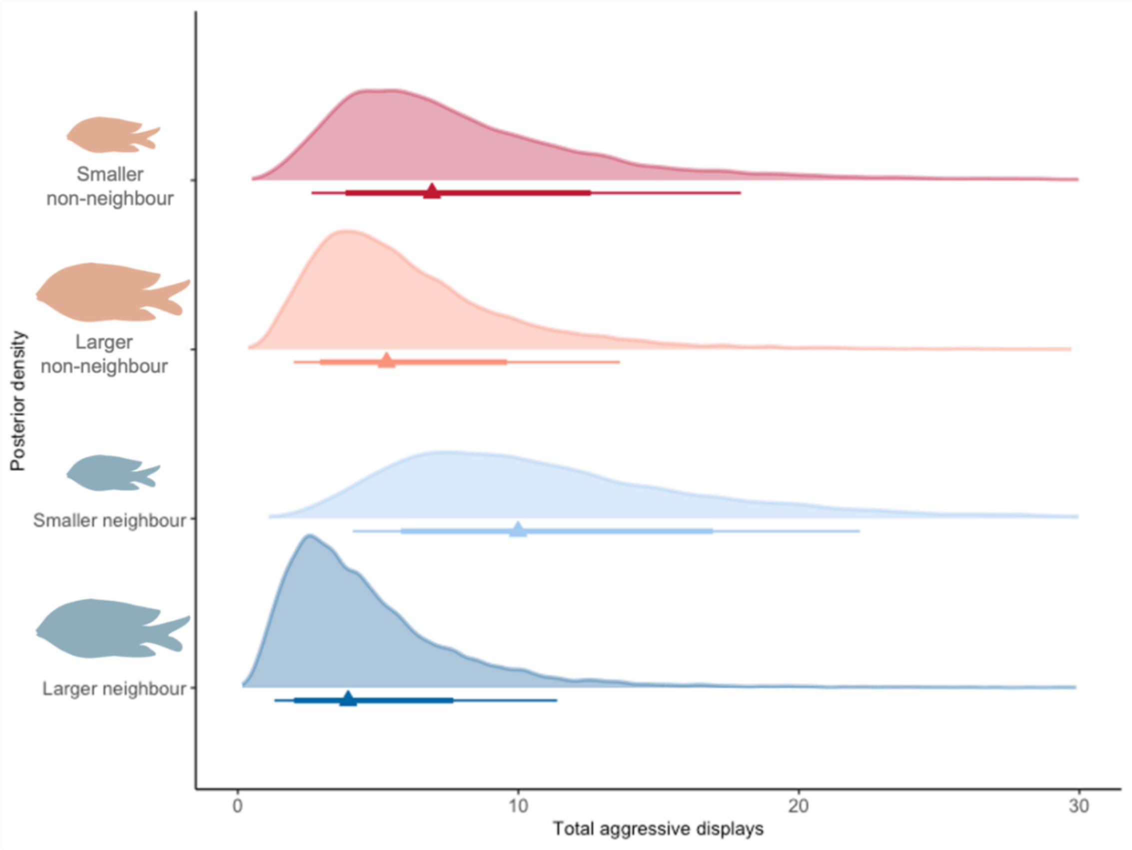

Figure 4.2 Total aggressive displays directed towards intraspecific stimulus fish by *S. diencaeus* territory holders is influenced by both familiarity and body size difference between territory holder and stimulus fish. Expected posterior predictions presented for *S. diencaeus* neighbours and non-neighbours. Point intervals represent median estimates and lines represent 90 and 70% highest posterior density intervals (HPDIs). Note x-axis limited to 30 for ease of viewing.

4.4 Discussion

The aggressive response elicited by intraspecific neighbours and non-neighbours in *S. diencaeus* territory holders was dependant on both familiarity and body size difference between the territory holder and stimulus fish. This finding suggests that the familiarity hypothesis may offer a plausible explanation for aggression of *S. diencaeus* territory holders, but the exact response is mediated by body size differences. When neighbours pose a greater threat to territory loss than non-neighbours, as we argue is likely in territorial farming damselfish, the familiarity and threat-level hypotheses make opposing predictions for the level of aggressive response elicited by neighbours and non- neighbours (Temeles, 1994).

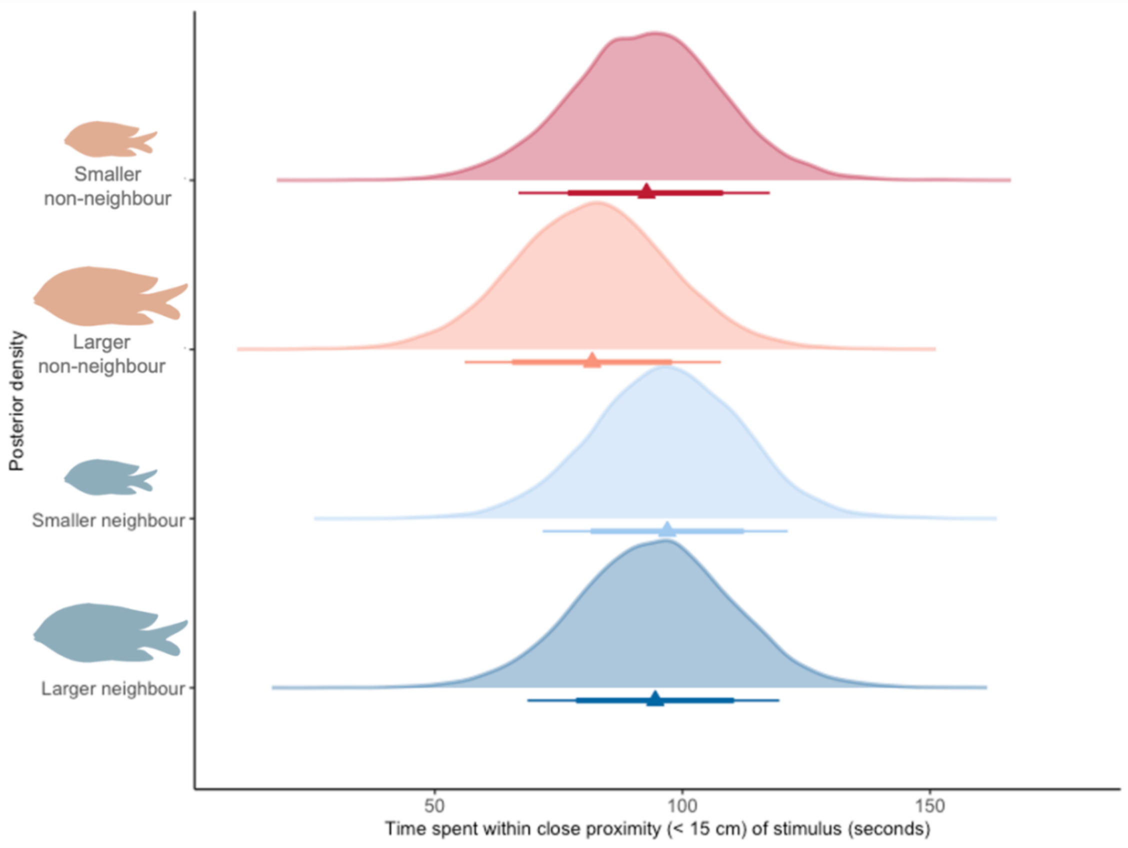

Figure 4.3 Time spent within close proximity (< 15 cm) of intraspecific stimulus fish (seconds) by *S. diencaeus* territory holders is influenced by both familiarity and body size difference between territory holder and stimulus fish. Expected posterior predictions presented for *S. diencaeus* neighbours and non-neighbours. Point intervals represent median estimates and lines represent 90 and 70% highest posterior density intervals (HPDIs).

The familiarity hypothesis proposes that familiarity between neighbouring individuals based on past encounters reduces aggressiveness of responses in subsequent interactions (Ydenberg *et al.,* 1988). However, we found that in *S. diencaeus*, neighbours elicited a weaker aggressive response than non-neighbours only when they were larger in body size than the territory holder. One key aspect that the familiarity hypothesis overlooks is that familiarity does not always confer potential threat (Temeles, 1994). The threat-level hypothesis reasons that aggressive response should be strongest when directed towards the greatest threat (Temeles, 1994). In territorial species, neighbours may pose a greater threat to territory loss than non-neighbours and, in such circumstance, are predicted to elicit a greater aggressive response than non-neighbours (e.g. Müller and Manser, 2007; Newey *et al.,* 2010; Munguía-Steyer *et al.,* 2016). However, this assumes that all neighbours pose the same level of threat. We found that the aggressive response elicited by neighbouring *S. diencaeus* depended on the body size difference between them and the territory holder. One explanation for this may be that the body size of a neighbour influences their potential threat and subsequent aggressive response. For example, size-determined hierarchies affect aggression and the potential threat between neighbours (Hemelrijk, 2000; Hobson, 2020; Tibbetts *et al.,* 2022).

Dominance hierarchies are widespread in group-living and aggregating species and are commonly established based on previous wins and losses during competitive encounters between neighbouring individuals (Tibbetts *et al.,* 2022). Winners and losers are largely determined by asymmetries in RHP, such that individuals with greater RHP are more likely to win fights and become dominants (Parker, 1974). Body size is often a key factor in determining an individual's RHP, therefore dominance rank is often strongly correlated with body size (Favre *et al.,* 2008; Clutton-Brock, 2017; Wright *et al.,* 2019). While having a high-ranking dominance position can be beneficial for access to quality resources (Harwood *et al.,* 2003; Pimentel *et al.,* 2022), aggressive behaviour involved in dominance interactions carries costs in terms of energy expenditure (Marler *et al.,* 1995; Neat *et al.,* 1998) and injury risk (Clutton-Brock and Huchard, 2013). Selection should therefore favour strategies that allow individuals to maintain or attain their position within dominance hierarchies whilst reducing cost to themselves. Typically, subordinates stand to gain more if they rise through the ranks and are therefore more likely to test dominant individuals (Cant and Johnstone, 2000), posing a greater threat to those above them. As such, it is expected that dominant individuals direct aggression to subordinates directly below them in the hierarchy (Dehnen *et al.,* 2022). Moreover, dominance hierarchies depend on past encounters, so it is unlikely that any such relationships exist between non-neighbours.

The application of these ideas to territorial farming damselfishes, such as *Stegastes*, has not been widely explored. Although farming damselfishes are described as solitary species, individual territories are often contiguous, forming intraspecific aggregations (Itzkowitz, 1978; Robertson and Lassig, 1980; McDougall and Kramer, 2007). Though dominance hierarchies are typically present in group-living species, it has been argued that in territorial species, individuals with neighbouring territories may form dominant-subordinate relationships (rather than hierarchies) based on previous encounters

(Rubenstein, 1981; Fernö, 1987). In *Stegastes partitus*, a territorial damselfish, dominance relationships have been found to be size-based (Sadovy, 1985). Following the expectation that dominant individuals direct greater aggression towards subordinates (Dehnen *et al.,* 2022), we would expect territory holders to direct stronger aggressive responses towards neighbours that are smaller than themselves compared with those that are larger. We found that neighbouring *S. diencaeus* that were smaller than focal territory holders, and therefore likely subordinate, elicited a stronger aggressive response than larger neighbours. This finding offers evidence of dominance relationships between neighbouring *S. diencaeus*. On the other hand, the aggressive response directed towards stranger *S. diencaeus* by territory holders was not associated with body size difference, supporting a lack of dominance relationships between unfamiliar *S. diencaeus*.

An alternative perspective on the determinants of aggressive behaviour is to focus on the costs of aggressive encounters rather than the potential threat posed by an opponent. Costs of aggressive encounters are higher when the asymmetry in RHP between opponents is lower (i.e. opponents are more closely matched) (Arnott and Elwood, 2009) and, intuitively, for individuals with lower RHP, such as those of smaller body size. Therefore, the escalation of fights and the strength of aggressive response relies on an individual’s assessment of their own RHP and that of their opponent (Arnott and Elwood, 2009). Previous encounters with neighbours offer territory holders more information regarding their opponents RHP (fight to learn; Getty, 1989), allowing for more accurate mutual assessment of the costs of subsequent interactions (Taylor and Elwood, 2003; Arnott and Elwood, 2009). In contrast, when faced with unfamiliar individuals, territory holders have less information on their opponent (Taylor and Elwood, 2003; Arnott and Elwood, 2009) and consequently, the costs are less predictable.

Applying cost assessment theory, we might expect a weaker aggressive response 1) between unfamiliar individuals and 2) towards opponents with a larger RHP than the territory holder, as we observed in *S. diencaeus*. Given the uncertainty and potential for greater costs, we may also expect territory holders to behave more cautiously towards opponents that are unfamiliar or with greater RHP. Indeed, we found that time spent within close proximity (< 15 cm) of stimulus fish was influenced by both familiarity and body size difference, with territory holders spending substantially less time within close proximity to larger non-neighbours. Assessment of the cost of an aggressive encounter may therefore mediate the familiarity hypothesis and provide an explanation to our findings.

Our findings rely on measuring aggressive response as the number of aggressive displays, in terms of bites and rams, directed by the territory holder to the stimulus fish. These behaviours are highly detectable to a human observer. However, damselfishes are known to communicate through a wide array of signals and displays which are more difficult to observe. For example, the presence and absence of UV patterns affects aggression between intraspecific *Pomacentrus amboinensis* (Siebeck, 2004), and colouration patterns are integral to individual recognition in *Amphiprion hicinctus* (Fricke, 1973) and *Stegastes planifrons* (Thresher, 1979). The function of these cryptic communications is largely unknown (however see Fricke, 1973; Siebeck, 2004) but there is potential for these signals to aid the assessment of a competitor's RHP. Experiments to investigate the role of more cryptic signals in the communication of fighting ability and subsequent impact on aggressive territorial behaviour could add significant insight into these behaviours.

Aggressive behaviour associated with territoriality carries costs (Marler *et al.,* 1995; Neat *et al.,* 1998; Clutton-Brock and Huchard, 2013). As such, natural selection should favour any mechanism or strategy that allows a territory holder to minimise these costs whilst upholding their territory and preventing resource loss from intrusion (Arnott and Elwood, 2009). We demonstrate that both familiarity and threat level, interpreted with the added information provided by body size, predicts the level of aggressive response by *S. diencaeus* territory holders. Studies on neighbour-stranger discrimination are common (see Werba *et al.,* 2022). However, our findings add to the growing pool of evidence that argue the need to include additional factors (e.g. dominance or body size: Tierney *et al.,* 2013; Wright *et al.,* 2019: density: Morales *et al.,* 2014) when investigating the drivers of variation in territorial aggression between neighbours and non-neighbours. In doing so, we will be able to better predict not only individual behavioural responses but also how these responses scale up to influence population and community dynamics.

General Discussion

5.1 Overview

My thesis has added to our understanding of how competitive interactions can mediate spatial distribution and behavioural cascades throughout multiple ecological scales and taxa. Firstly, taking a macroecological approach, I found evidence of the importance of herbivorous fish functional group co-occurrence, in addition to functional group diversity, to coral reef benthic state. Secondly, I demonstrated that between-individual variation in aggressive territorial response by farming damselfishes to intruders may create a competitive landscape of risk within fish communities on coral reefs. Thirdly, I identified that close proximity to territorial farming damselfishes may reduce cleaning rates and client diversity at Pederson's cleaner shrimp *Ancylomenes pedersoni* stations, driving behavioural cascades in other taxa. Finally, I found that intraspecific aggression between farming damselfish could be predicted by familiarity and body size difference. My thesis showcases competitive risk avoidance as a mechanism through which competition may shape the spatial distribution and space use of animals. By recognising this pathway, we can begin to understand and predict the cascading consequences of competition throughout ecological levels, from individuals to ecosystems (Figure 5.1).

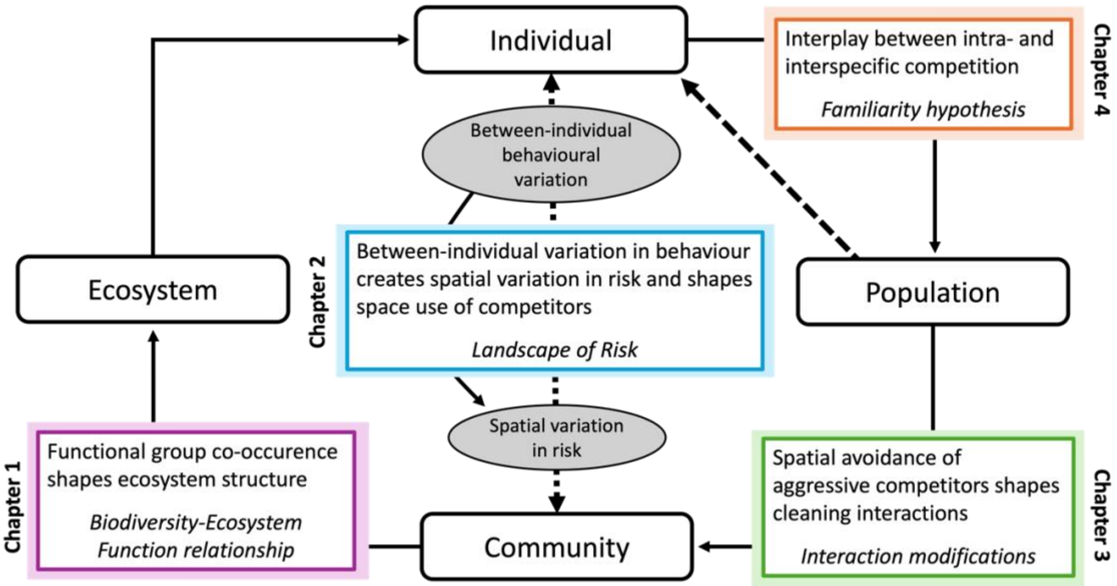

Figure 5.1 Competitive interactions may mediate spatial distribution and behavioural cascades throughout multiple ecological scales

5.2 Competition mediates spatial distribution and space use

In **Chapters 2-3**, I applied the landscape of risk framework to explore how competitive risk avoidance may drive behavioural cascades throughout coral reef communities. **Chapter 2** strongly indicated that avoidance of aggressive territorial farming damselfishes shapes the spatial distribution of reef fish, creating a competitive landscape of risk on coral reefs. These findings were reflected in **Chapter 3**, which found reduced cleaning rates and client diversity at *A. pedersoni* cleaning stations located within farming damselfish territories. Risk avoidance, which can be defined as the behavioural response to a known threat, is a behavioural strategy enabling an individual to navigate their environment at a reduced risk (Gaynor *et al.,* 2019). Historically, the landscape of risk framework has been used to explore how spatiotemporal patterns of predation risk drives patterns of space use in prey species (reviewed in Bleicher, 2017; Gaynor *et al.,* 2019), as well as the cascading impacts to communities and ecosystems (Ripple and Beschta, 2004, 2012; Start and Gilbert, 2017). More recently, this framework has been expanded to explore alternative non-lethal risks, such as by parasites (known as the landscape of disgust) (Weinstein *et al.,* 2018; Doherty and Ruehle, 2020). **Chapters 2-3** provide evidence that risk avoidance of aggressive competitors is fundamental in shaping the spatial distribution and space use of coral reef fish. Furthermore, I demonstrate that the landscape of risk framework offers a useful tool in developing our understanding of how competition mediates behavioural cascades.

5.3 Ecological impacts of interspecific competition

5.3.1 Cross-scale effects of cleaning interaction modifications

In **Chapter 3**, cleaning rates were much lower at *A. pedersoni* stations located within farming damselfish territories, which strongly suggests that risk avoidance of aggressive competitors drives interaction modifications in marine cleaning mutualisms. Interaction modifications have been observed as a result of predation risk avoidance, such as promoting coexistence between competing prey species (Sheehy *et al.,* 2018), or increasing the risk of parasitism (Doherty and Ruehle, 2020). These top-down effects of predators are widely regarded as an important determinant of community and ecosystem structure (Duffy, 2003; Baum and Worm, 2009; Ripple and Beschta, 2012). By driving the spatial distribution and space use in competitive subordinates (**Chapters 2-3**), we can expect competitive risk avoidance to carry similar indirect effects.

Cleaning mutualisms represent a central node in marine interaction networks (Quimbayo *et al.,* 2018) and are critical for the health of individual fish, and the wider community and ecosystem (Grutter *et al.,* 2003; Bshary *et al.,* 2007; Caves, 2021). By modifying cleaning interactions (**Chapter 3**), risk avoidance of farming damselfishes has the potential to drive significant indirect effects throughout all ecological levels. As discussed in **Chapter 3**, avoiding cleaning stations near to farming damselfishes carries clear negative impacts to the health of clients and cleaners at the individual and population level. At the community level, competitive risk avoidance of farming damselfishes may reduce fine scale diversity of clients and shape local community composition near to cleaning stations (**Chapter 3**). Finally, marine cleaning mutualisms are known to increase the wider diversity of coral reef communities (Côté, 2000; Bshary, 2003; Grutter *et al.,* 2003; Waldie *et al.,* 2011), which in turn can mediate ecosystem function and benthic state (**Chapter 1**).

5.3.2 Community composition mediates local ecosystem function

Biodiversity is a known driver of coral reef function (Brandl *et al.,* 2019; Benkwitt *et al.,* 2020). In accordance with previous findings (Burkepile and Hay, 2008), **Chapter 1** provides evidence that reef fish community composition is a key determinant of coral reef benthic state (Sheppard *et al.,* 2023). Therefore, not only are cleaning interactions critical for individual- and population-level health (Côté, 2000; Bshary *et al.,* 2007; Caves, 2021), but upholding cleaning mutualisms may also play an important role in maintaining reef health by mediating local biodiversity and community composition (**Chapters 1 & 3**). Territorial farming damselfish populations are increasing worldwide (Burkepile and Hay, 2008), leading to vast areas of coral reefs being aggressively defended. If cleaning interactions continue to be impacted with increasing damselfish abundance, we may see associated changes to community composition and a reduction in fish diversity across whole reefs, with consequences at the ecosystem level. By considering multiple ecological scales, my thesis therefore provides evidence of the potential cross-scale impacts of interaction modifications mediated by competitive risk avoidance (**Chapters 1-3**).

5.3.3 The interplay between intra- and interspecific competition

Whilst **Chapters 2-3** focus on the effects of interspecific competition, intraspecific competition and the interplay with interspecific competition cannot be ignored. It is widely regarded that in order for two species to coexist, intraspecific competition must be greater than interspecific competition (Chesson, 2000b). If one species increases in abundance, intraspecific competition must hinder population growth thereby stabilising coexistence (Barabás *et al.,* 2016). On way in which we can consider this relationship is in energetic terms. Aggressive behaviours associated with interference competition require energy (Marler *et al.,* 1995; Neat *et al.,* 1998), and individuals must balance these energetic requirements between different types of competitors (intra- vs interspecific). Stronger intraspecific competition, driven by greater dietary overlap (Peiman and Robinson, 2010) or increased relative density (Mikami and Kawata, 2004), may force individuals to prioritise energy spent on aggressive behaviours directed towards intraspecifics rather than individuals of other species, thereby indirectly promoting coexistence. However, there are mechanisms that reduce intraspecific competition, such as competitor recognition and familiarity.

In **Chapter 4**, I observed that familiarity, mediated by difference in body size, could predict intraspecific aggressive behaviour in territorial farming damselfishes. The familiarity hypothesis predicts that past encounters between neighbouring individuals reduces aggression in subsequent interactions (Ydenberg *et al.,* 1988; Temeles, 1994). As a result, familiarity allows territorial individuals to adjust their aggressive response towards neighbours (**Chapter 4**) that inevitably come into contact with each other more frequently than non-neighbours. Thus, familiarity may reduce the energetic cost of intraspecific competition, which could indirectly promote greater interspecific competition as more energy is available. By altering the relative strength of intra- vs interspecific competition, familiarity between intraspecific competitors may have the potential to disrupt coexistence on a local scale. Although more work is required to empirically explore these energetic trade-offs, **Chapter 4** supports familiarity as a determinant of intraspecific aggression and the importance of considering the strength of intraspecific competition in studies of competition between species. However, reducing species coexistence to such a simple comparison ignores indirect effects that influence the competitive dynamics between species (Barabás *et al.,* 2016).

5.3.4 The role of disruptive processes in destabilising coexistence

Both competition and predation, and the interactions between them (Sih *et al.,* 1985), are fundamental drivers shaping marine and terrestrial ecological communities (Duffy, 2002; Estes *et al.,* 2011; Sheppard *et al.,* 2024) (**Chapters 2-3**). Predators exert critical top-down effects which can mediate competition and coexistence amongst prey, particularly when a disproportionate pressure is applied on the competitive dominant (Chesson, 2000b). The intermediate disturbance hypothesis proposes that coexistence is maintained under intermediate disturbance regimes (Shea *et al.,* 2004). We may therefore expect that, in natural systems, intermediate levels of predator abundance promote species coexistence. However, disruption to predation pressure may alter competitive dynamics and destabilise coexistence patterns between species. Predator removal is one the most disruptive environmental impacts by humans worldwide (Estes *et al.,* 2011). In marine systems, overfishing of predatory species has contributed to a disproportional increase in the abundance of territorial farming damselfishes (Edwards *et al.,* 2014; Heenan *et al.,* 2016). By removing predators from coral reefs, continued human impact may have the potential to disrupt the stable coexistence between farming damselfishes and other reef fish.

5.4 Future research

5.4.1 Cascading landscapes

In **Chapter 2**, I show that the landscape of risk framework, developed for predator-prey systems, serves as an excellent research tool to explore how competitive risk may shape population and community dynamics. However, risk of enemies (predators, parasites and competitors) is not the only driver shaping animal spatial distribution and interaction networks. For example, cleaning stations are said to provide a “safe haven” for their clients due to reduced aggression and predation events (Cheney *et al.,* 2008). Given the clear spatial nature of cleaner species, which are often highly site-attached (Romain *et al.,* 2020; Côté and Brandl, 2021), and the effects of spatial risk avoidance on cleaning interactions (**Chapter 3**), one might envisage how the landscape of risk could be expanded to “safe” interspecific interactions. Gaynor *et al.* (2019) presented the landscape of risk as just one of multiple distinct landscapes representing the physical landscape, predation risk, prey perception and response. Drawing on this idea, I propose an expanded framework that brings together various types of interspecific relationships in order to better understand how behavioural changes cascade throughout interaction networks (Figure 5.2).

5.4.2 The macroecology of individual behaviour

Community ecology has historically neglected individual-level behaviour (Violle *et al.,* 2012). Indeed, the landscape of risk framework typically focuses on predator abundance and population-level averages of behaviour, predicting that prey species will avoid areas of high predator abundance (Bleicher, 2017; Gaynor *et al.,* 2019). Comparably, competitive subordinates would be expected to avoid areas of high abundance of dominant or more aggressive species. However, **Chapter 2** demonstrated that the abundance of aggressive farming damselfishes and other reef fish were positively correlated. Instead, individual-level behaviour of farming damselfish was found to mediate the spatial distribution of competitive subordinates, creating a competitive landscape of risk on coral reefs (**Chapter 2**). Whilst population averages are valuable measurements for exploring broader scale behavioural cascades, theoretical and empirical work has stressed the importance of individual-level behaviour in community ecology (Bolnick *et al.,* 2011; Cantor *et al.,* 2021). **Chapter 2** provides evidence supporting the importance of between-individual behavioural variation in mediating risk avoidance. I argue that incorporating individual-level behaviour into the landscape of risk framework may prove an important research avenue in understanding behavioural cascades mediated by risk.

The recent surge in interest in how individual-level behaviour shapes communities is also gaining notice in studies of species coexistence (Hart *et al.,* 2016). Models based on the Lotka-Volterra model of species coexistence argue that variation in aggressive behaviour or competitive ability between intraspecific individuals would reduce competitive imbalances between species, thereby promoting species coexistence (Begon and Wall, 1987). As such, individual-level behavioural variation may alter spatial patterns of competitors, excluding competitive subordinates from areas defended by highly aggressive individuals (as observed in **Chapter 2**), but indirectly promoting coexistence in regions occupied by less aggressive individuals. However, views on whether intraspecific variation promotes species coexistence are mixed. Some theoretical work suggests that intraspecific variation in competitive ability supports species coexistence only within intermediate competitor densities (Lichstein *et al.,* 2007). Once the abundance of the competitive dominant rises to reach a threshold, intraspecific variation no longer has a supportive effect. This aligns with the intermediate disturbance hypothesis (Shea *et al.,* 2004). On the other hand, drawing from classical niche theory (Roughgarden, 1972), intraspecific variation may destabilise coexistence by reinforcing competitive imbalances between species via non-linear averaging (whereby the relationship between individual-level traits and population growth are non-linear) (Hart *et al.,* 2016). In other words, the gains made by highly competitive individuals outweighs the loss by individuals with a lower competitive ability (Hart *et al.,* 2016). These alternative hypotheses highlight that quantifying the strength of intraspecific variation is not sufficient when comparing intra- vs interspecific competition and the impact to species coexistence. Instead, we must also uncover the relationship between competitive ability, population growth and the potential feedback between them.

Macrobehaviour is an emerging field which brings together behavioural ecology and macroecology to better understand the broader scale impacts of behavioural variation (Keith *et al.,* 2023). Though behaviour is fundamental in structuring ecological systems beyond the level of the population, broad-scale patterns of behavioural variation and their role in mediating ecosystems are understudied (Keith *et al.,* 2023; Marske *et al.,* 2023). The importance of addressing this knowledge gap is even greater when we consider that individual behaviour is often the first thing to respond to environmental disturbance (Sih, 2013; Wong and Candolin, 2015). To develop our understanding of how individual-level behaviour mediates ecological processes, we must first address the issues of accessibility, time and standardisation. Measuring individual behaviour is undeniably time consuming, and accessing individual-level data across space, time and taxa will require huge collaborative effort. Additionally, to generalise trends across taxa, ecological levels and spatial scales, measurements of individual behaviours must be standardised. Fortunately, behavioural traits are easily measured in common units across ecological levels and taxa (Sih *et al.,* 2012; Start and Gilbert, 2017; 2019) and, with proper protocols and transparency in research methods, can be used to scale-up the effects of individual behaviour.

5.5 Conclusion

In conclusion, my thesis has distinguished competitive risk avoidance as a key ecological driver of spatial distribution and space use patterns in coral reef fish. By considering all ecological levels, from individual to ecosystem, my thesis conceptualises how aggressive territoriality may mediate behavioural cascades and ecological processes at higher scales. Furthermore, I advocate that incorporating individual behaviour in macroecological studies should be a fundamental goal to improve our understanding of and ability to predict behavioural cascades throughout ecosystems.

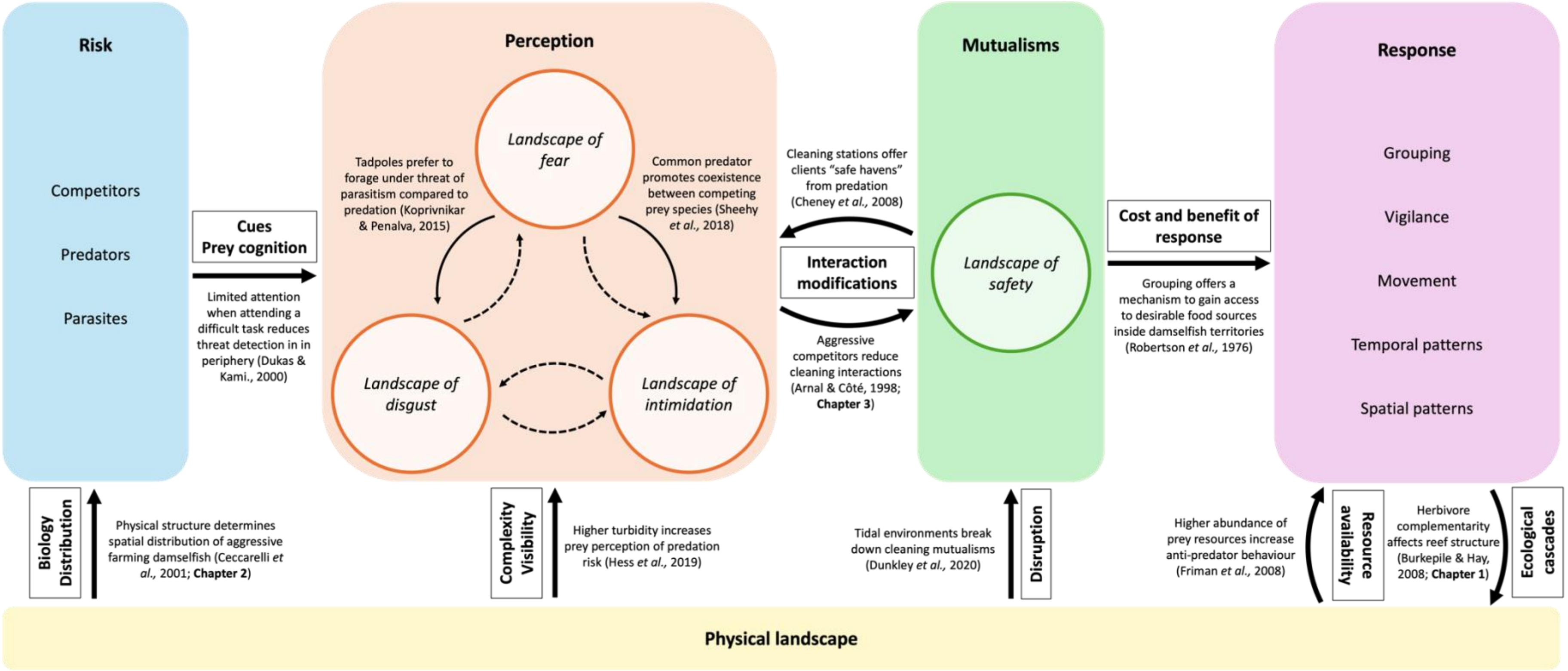

Figure 5.2 Cascading landscapes: An expanded framework bringing together various types of interspecific interactions for understanding the ecological drivers and consequences of behavioural cascades throughout interaction networks and ecosystems (building upon that proposed by Gaynor *et al.,* 2017). Coloured boxes represent physical landscape, distribution of risk, risk perception, mutualistic ("safe") interactions, and behavioural response. Connections offer mechanisms through which one landscape affects another, with examples from the literature.

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Appendix A: Supplementary material

Chapter 1 Supplementary material

Table S1.1 Classification of fish species into herbivore functional groups: croppers, browsers, farmers, scrapers and excavators.

Functional Group	Family	Species	Reference
Cropper	Surgeonfish (Acanthuridae); Parrotfish (Labridae)	*Acanthurus chirurgus; A coeruleus; A tractus; Scarus coeruleus*	Green and Bellwood, 2009; Adam *et al.,* 2018
Browser	Chubs (Kyphosidae); Parrotfish (Labridae)	*Sparisoma atomarium*; Sp radians* (Sp chrysopterum); Cryptotomus roseus; Sp aurofrenatum; Sp chrysopterum; Sp rubripinne; Kyphosidae (not identified to species level)*	Bellwood and Choat 1990; Bernardi *et al.,* 2000; Green and Bellwood 2009; Adam *et al.,* 2018; Froese and Pauly, 2023
Farmer	Territorial Damselfish (Pomacentridae)	*Microspathodon chrysurus; Stegastes planifrons*	Green and Bellwood 2009
Scraper	Parrotfish (Labridae)	*S taeniopterus; S vetula; S iseri* (S vetula)*	Green and Bellwood 2009; Choat *et al.*, 2012; Adam *et al.,* 2018
Excavator	Parrotfish (Labridae)	*S coelestinus; S guacamaia; Sp viride*	Green and Bellwood 2009; Adam *et al.,* 2018

* Parrotfish of the genera *Scarus* and *Sparisoma* that were not identified in Adam *et al.* (2018) were grouped guided by their closest related species, given in parenthesis.

Table S1.2 Metrics of coral reef benthic state

Benthic Metric	**Description**
Coral species richness	The number of coral species encountered on each survey/site
Total coral cover	Total cover (m^2) of all coral colonies ≥ 4 cm across a standardized transect ($10m^2$)
Competitive/weedy/stress-tolerant/generalist coral cover	Total cover (m^2) of all coral colonies ≥ 4 cm classified as competitive/weedy/stress-tolerant/generalist, according to Darling et al. (2012), across a standardized transect ($10m^2$)
Coral calcification rate	Total calcification rate (kg $CaCO_3$ m^2 $year^1$) per transect, calculated using mean species-specific calcification rates (González-Barrios and Álvarez-Filip, 2018) and coral area estimates
Coral recruitment density	Count of all hard coral colonies less than 2cm in diameter (individuals/m^2)
Fleshy/Calcareous macroalgal/Turf algal/CCA cover	Percentage algal cover estimated from benthic point counts

Table S1.3 Trait-based groupings of coral species not identified in Darling *et al.* (2012). Classification was made based on genus, phylogeny and known traits (coraltraits.org).

Species	**Coral Group**
Orbicella faveolata	Generalist
Orbicella franksi	Generalist
Orbicella sp.	Generalist
Cladocora arbuscula	Stress-tolerant
Dichocoenia stellaris	Stress-tolerant
Dichocoenia stokesii	Stress-tolerant
Oculina diffusa	Stress-tolerant
Oculina varicosa	Stress-tolerant
Oculina sp.	Stress-tolerant
Orbicella annularis	Stress-tolerant
Pseudodiploria clivosa	Stress-tolerant
Pseudodiploria strigosa	Stress-tolerant
Pseudodiploria sp.	Stress-tolerant
Solenastrea bournoni	Stress-tolerant
Solenastrea hyades	Stress-tolerant
Solenastrea sp.	Stress-tolerant
Helioseris cucullata	Weedy
Mussa angulosa	Weedy
Scolymia cubensis	Weedy
Scolymia lacera	Weedy
Scolymia wellsi	Weedy
Scolymia sp.	Weedy

Table S1.4 Spatial correlation between sites within the same subregion (α). Values represent the mean ± standard deviation of 1000 bootstrapped iterations. Percentage refers to the percentage of bootstrapped iterations with *p*-values ≤ 0.05. Significant results shown in bold.

Metric	**Model 1**				**Model 2**				**Model 3**			
	Alpha	SE	*p*	%	Alpha	SE	*p*	%	Alpha	SE	*p*	%
Coral Richness	0.14 ± 0.01	0.07 ± 0.00	0.06 ± 0.01	27	0.12 ± 0.01	0.07 ± 0.00	0.08 ± 0.02	0	0.10 ± 0.01	0.07 ± 0.01	0.17 ± 0.03	0
Total Coral Cover	0.08 ± 0.01	0.05 ± 0.01	0.10 ± 0.05	18.6	0.08 ± 0.01	0.06 ± 0.00	0.19 ± 0.04	0	0.08 ± 0.01	0.05 ± 0.00	0.11 ± 0.04	3.2
Coral Calcification Rate	0.03 ± 0.01	0.04 ± 0.01	0.45 ± 0.09	0	0.03 ± 0.01	0.04 ± 0.01	0.48 ± 0.10	0	0.05 ± 0.01	0.04 ± 0.01	0.27 ± 0.10	0.3
Coral Recruitment	0.13 ± 0.01	0.06 ± 0.00	**0.02 ± 0.01**	**94.7**	0.09 ± 0.01	0.05 ± 0.01	0.07 ± 0.03	30.7	0.09 ± 0.01	0.06 ± 0.01	0.11 ± 0.04	8.9
Competitive Coral Cover	0.03 ± 0.00	0.05 ± 0.01	0.53 ± 0.08	0	0.03 ± 0.00	0.06 ± 0.01	0.64 ± 0.08	0	0.01 ± 0.01	0.75 ± 2.09	0.89 ± 0.09	0
Weedy Coral Cover	0.15 ± 0.02	0.05 ± 0.01	**0.01 ± 0.02**	**92**	0.18 ± 0.02	0.07 ± 0.01	**0.02 ± 0.02**	**82.7**	0.17 ± 0.02	0.06 ± 0.01	**0.01 ± 0.03**	**95.5**
Stress-tolerant Coral Cover	0.04 ± 0.01	0.03 ± 0.00	0.15 ± 0.05	0.5	0.03 ± 0.01	0.03 ± 0.00	0.29 ± 0.07	0	0.03 ± 0.01	0.03 ± 0.00	0.29 ± 0.10	0
Generalist Coral Cover	0.00 ± 0.01	0.01 ± 0.00	0.67 ± 0.21	0	0.00 ± 0.01	0.02 ± 0.00	0.75 ± 0.18	0	0.02 ± 0.01	0.07 ± 0.07	0.72 ± 0.12	0
Fleshy Macroalgal Cover	0.47 ± 0.01	0.27 ± 0.01	0.08 ± 0.01	0	0.39 ± 0.01	0.22 ± 0.01	0.07 ± 0.01	0.8	0.43 ± 0.02	0.24 ± 0.01	0.07 ± 0.01	2.1
Calcareous Macroalgal Cover	0.13 ± 0.01	0.06 ± 0.00	**0.04 ± 0.02**	**63.3**	0.13 ± 0.01	0.07 ± 0.01	0.07 ± 0.02	24.5	0.14 ± 0.01	0.08 ± 0.01	0.07 ± 0.02	20.3
Turf Algal Cover	0.30 ± 0.02	0.10 ± 0.01	**0.00 ± 0.00**	**100**	0.32 ± 0.02	0.11 ± 0.01	**0.01 ± 0.00**	**100**	0.34 ± 0.02	0.14 ± 0.01	**0.02 ± 0.01**	**99.2**
CCA Cover	0.21 ± 0.02	0.10 ± 0.01	0.05 ± 0.02	53.5	0.23 ± 0.02	0.13 ± 0.01	0.07 ± 0.03	27.6	0.25 ± 0.02	0.15 ± 0.01	0.11 ± 0.03	2

Table S1.5 Coefficients for all three Diversity-Interactions models for all metrics of coral reef benthic state. Note: values are raw and therefore log-transformed. Values represent the mean ± standard deviation of bootstrapped iterations. Percentage refers to the percentage of bootstrapped iterations with *p*-values ≤ 0.05. Significant results shown in bold.

Please find at https://onlinelibrary.wiley.com/doi/full/10.1111/geb.13638

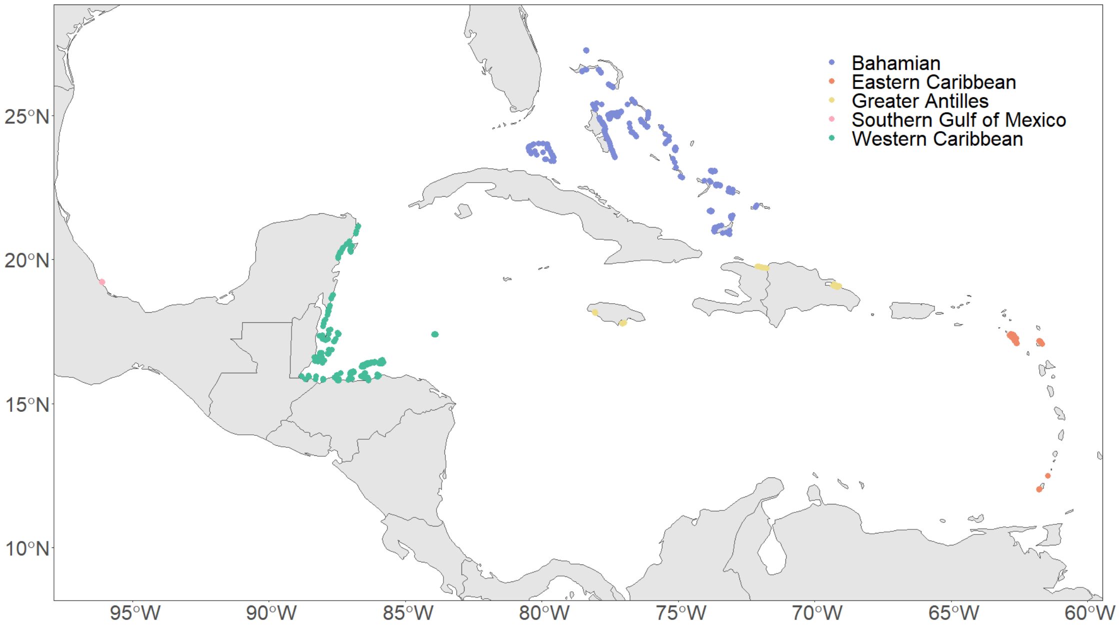

Figure S1.1 Map of Atlantic and Gulf Rapid Reef Assessment (AGRRA) survey sites included in our analysis. Colour groups depict five ecoregions.

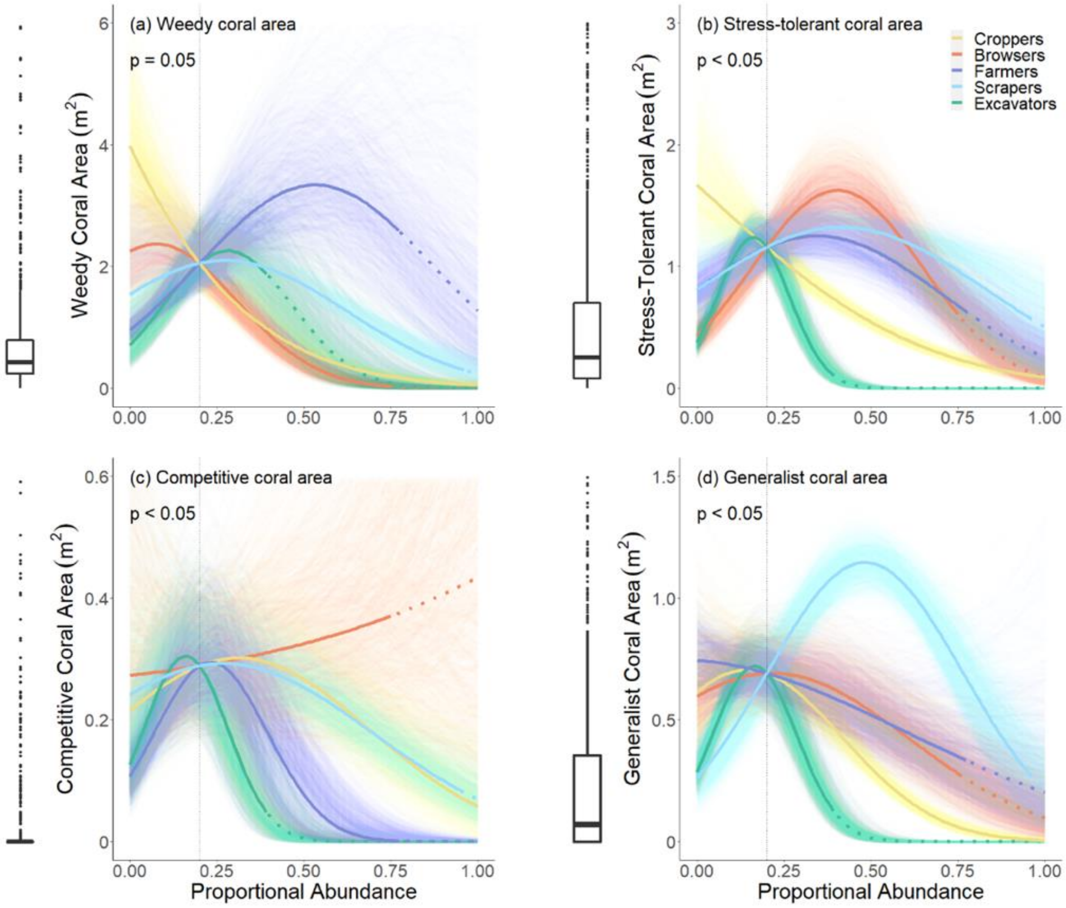

Figure S1.2 Predicted metrics of coral cover separated into trait-based groups, using results from 1000 iterations of bootstrapped pairwise interaction models. Thicker lines represent mean predicted coral cover. Dotted segments represent predictions that are extrapolated from empirical data. Vertical dotted lines represent maximum evenness between functional groups ($P = 0.2$). p-values correspond to analysis of Wald statistic between the identity model (Model 2) and pairwise interaction model (Model 3) (Table 1.1; Test 2). Boxplots represent the spread of raw metrics of coral cover by survey and have also been limited to correspond with predicted values for ease of viewing (see Figure S1.4 for full boxplots).

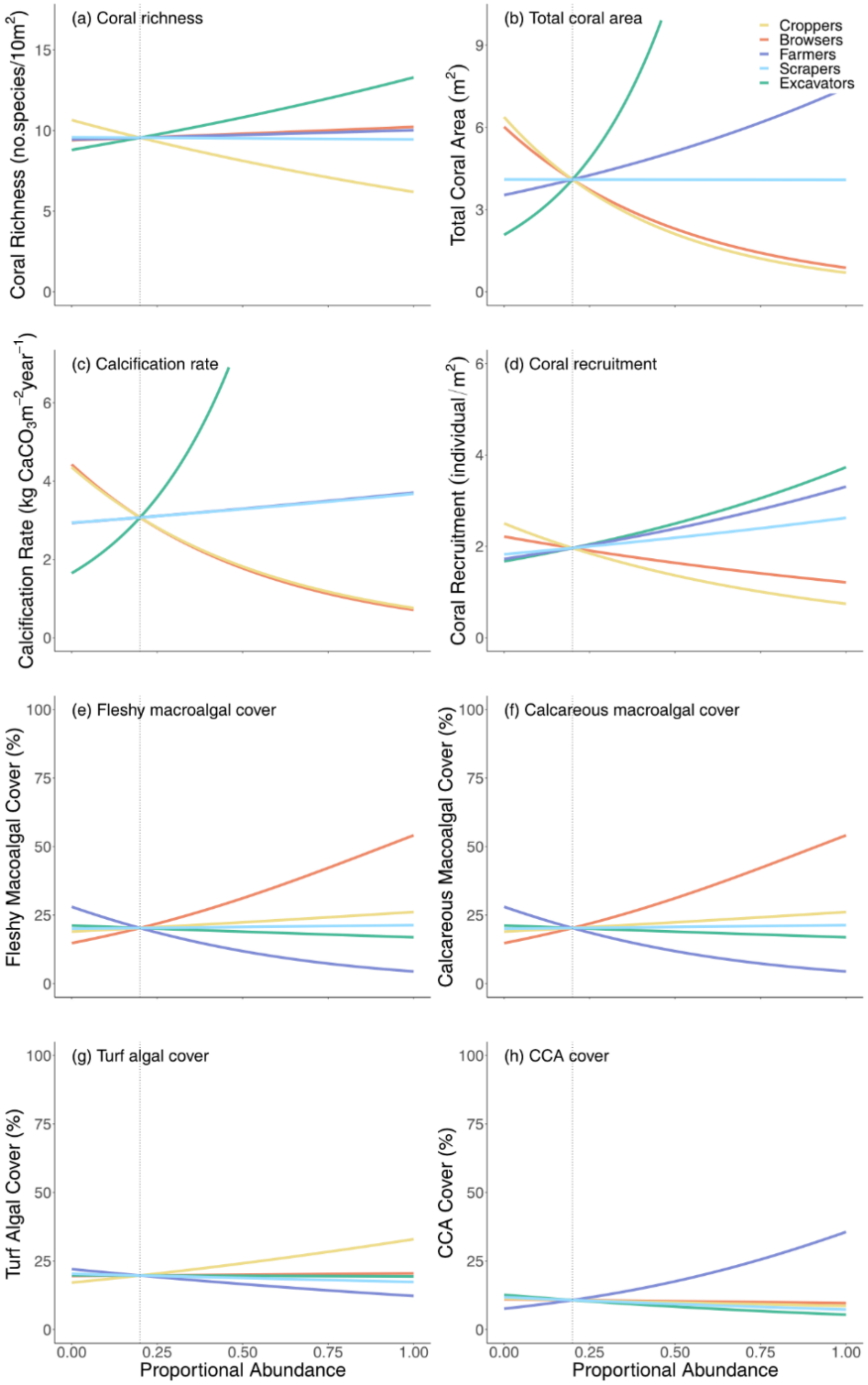

Figure S1.3 Mean predicted metrics of coral reef benthic state using results from identity model (Model 2). Vertical dotted lines represent maximum evenness between functional groups (*P* = 0.2). Note: y-axes have been limited to correspond with Figure 1.2 for ease of comparison.

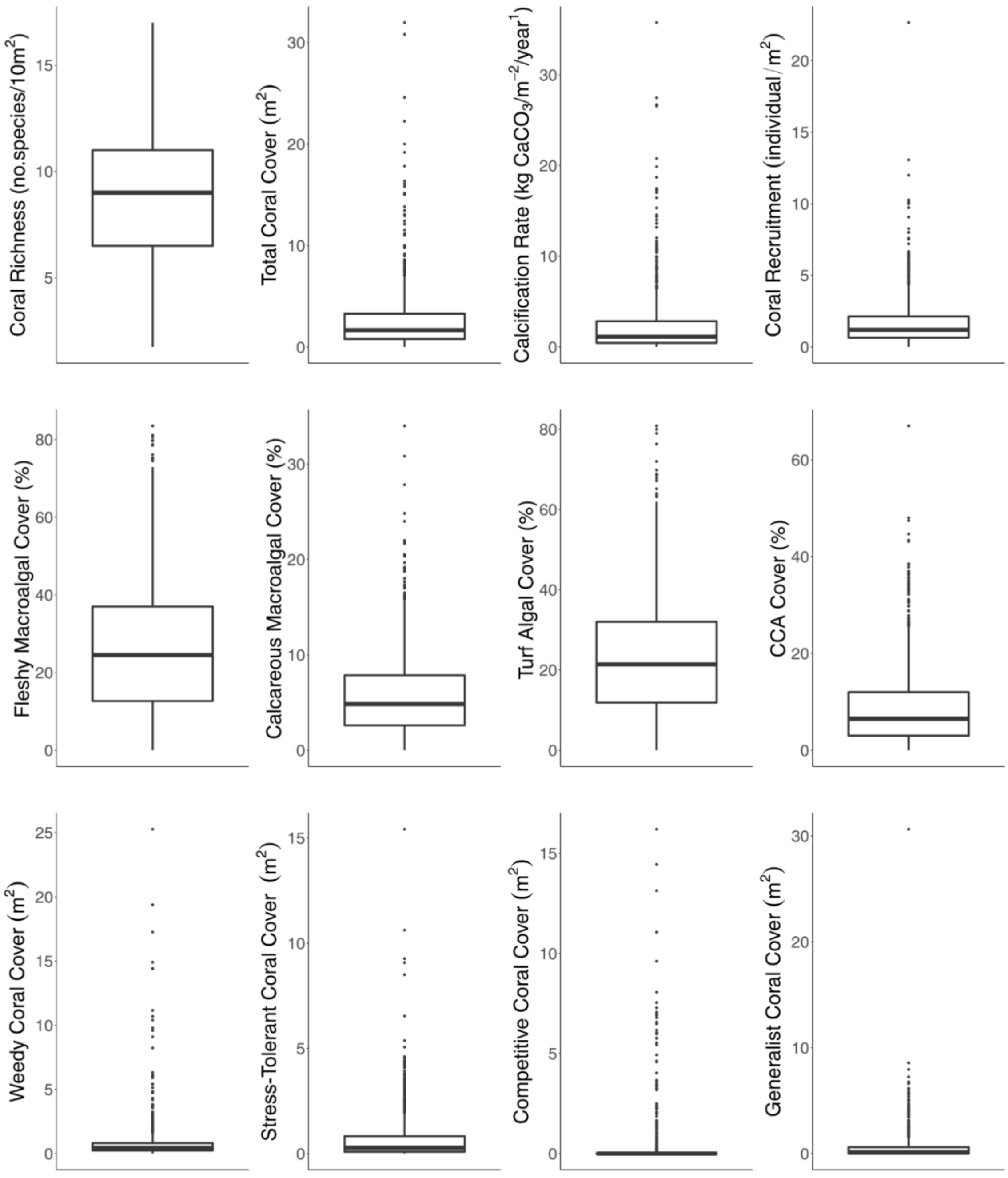

Figure S1.2 Full boxplots of raw measurements of coral reef benthos by survey in our analysis.

Chapter 2 Supplementary material

1. Reef fish surveys

Surveys were conducted by teams of SCUBA divers following a standardised protocol. SVS operators swam at a consistent depth (approx. 5 m) at a speed of around 10 m/min following the reef line. SVS comprised of two GoPro HERO4 cameras in SeaGIS housings, mounted horizontally on a frame 0.8 m apart and pointing inwardly such that the cameras' fields of view overlapped. EventMeasure V. 5.51 plus CAL (calibration software; www.seagis.com.au) were used for georeferencing the observed reef fishes.

2. Structure-from-motion orthomosaic construction

Video scans of transects were taken from a top-down perspective using three GoPro HERO8 cameras attached to a single mount, held approximately 1 m above the substrate. Scale bars of 0.25 m were placed at intervals along the transects beforehand. Videos were converted to still frames at a rate of 3 frames per second using Free Video to JPG Converter v5.0.101. These images were imported into Agisoft Metashape V. 1.8.4 (Agisoft, 2022) and orthomosaics were constructed.

3. Coordinate transformation

SVS coordinates of non-*Stegastes* fishes were transformed to match the coordinate system of the orthomosaics using corresponding reference points with the following equations:

$$p = (x3 - x1)(x2 - x1) + (y3 - y1)(y2 - y1)$$

$$q = -(x3 - x1)(y2 - y1) + (y3 - y1)(x2 - x1)$$

$$x3b = x1b + \frac{p(x2b - x1b) - q(y2b - y1b)}{(x2 - x1)^2 + (y2 - y1)^2}$$

$$y3b = y1b + \frac{p(y2b - y1b) + q(x2b - x1b)}{(x2 - x1)^2 + (y2 - y1)^2}$$

where (x1, y1) and (x2, y2) are the SVS coordinates of spatial reference points and (x3, y3) are the SVS coordinates of fish locations. Coordinates (x1b, y1b) and (x2b, y2b) are the orthomosaic coordinates of spatial reference points and (x3b, y3b) are the transformed fish locations for plotting on orthomosaics. Any fish located outside of the transect windows were discounted. The resulting dataset contained 285 fish with transformed x and y coordinates.

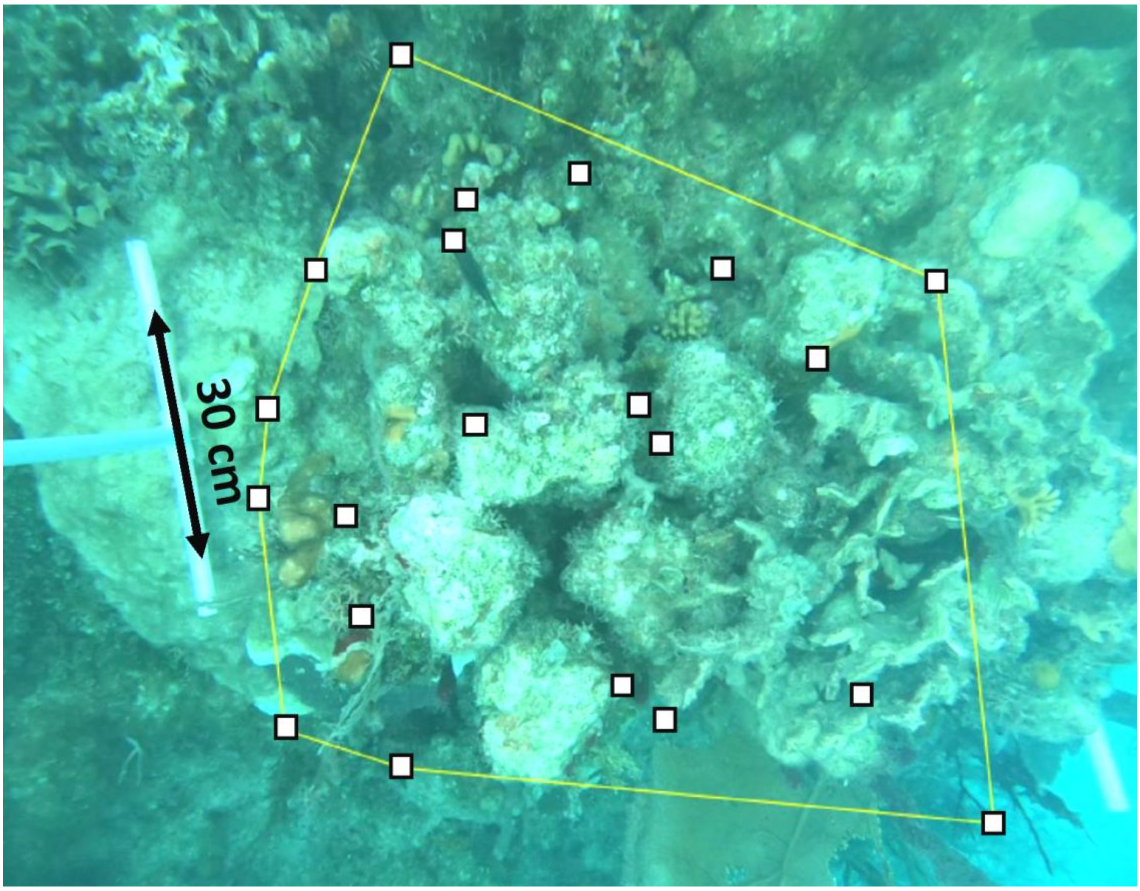

Figure S2.1 Diagram of territory mapping method showing location of focal individual from 21 screengrabs, minimum convex hull and 30 cm scale bar.

Figure S2.2 Visual estimation of individual territory in behavioural videos, and chase behaviour of intruding *Acanthurus coeruleus* (bottom right).

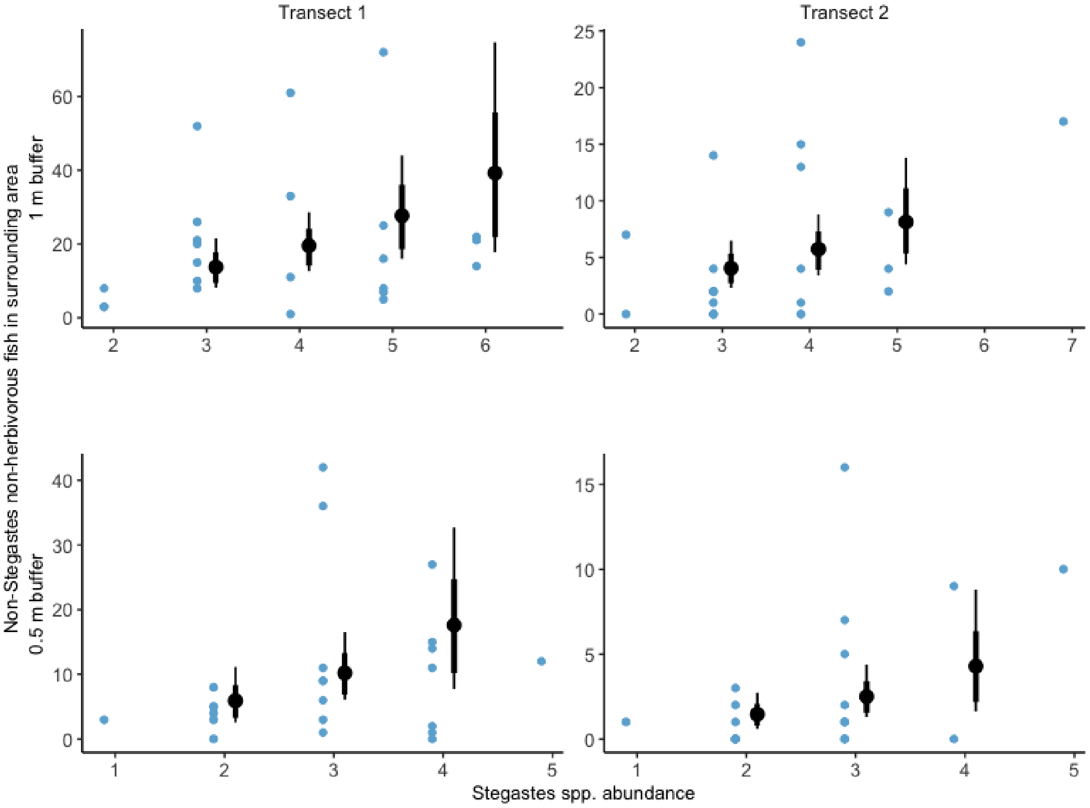

Figure S2.3 The number of non-*Stegastes* non-herbivorous fish within *Stegastes* spp. territories and surrounding area (1 m and 0.5 m buffer) increases with increasing abundance of *Stegastes* spp. Each column shows data from a different transect, the identities of which were included as grouping factors. Blue points represent raw data. Black points and interval lines represent the expected posterior predictions and confidence intervals (80 and 95%) from Bayesian models using mean values of *Stegastes* spp. aggression and measurement area.

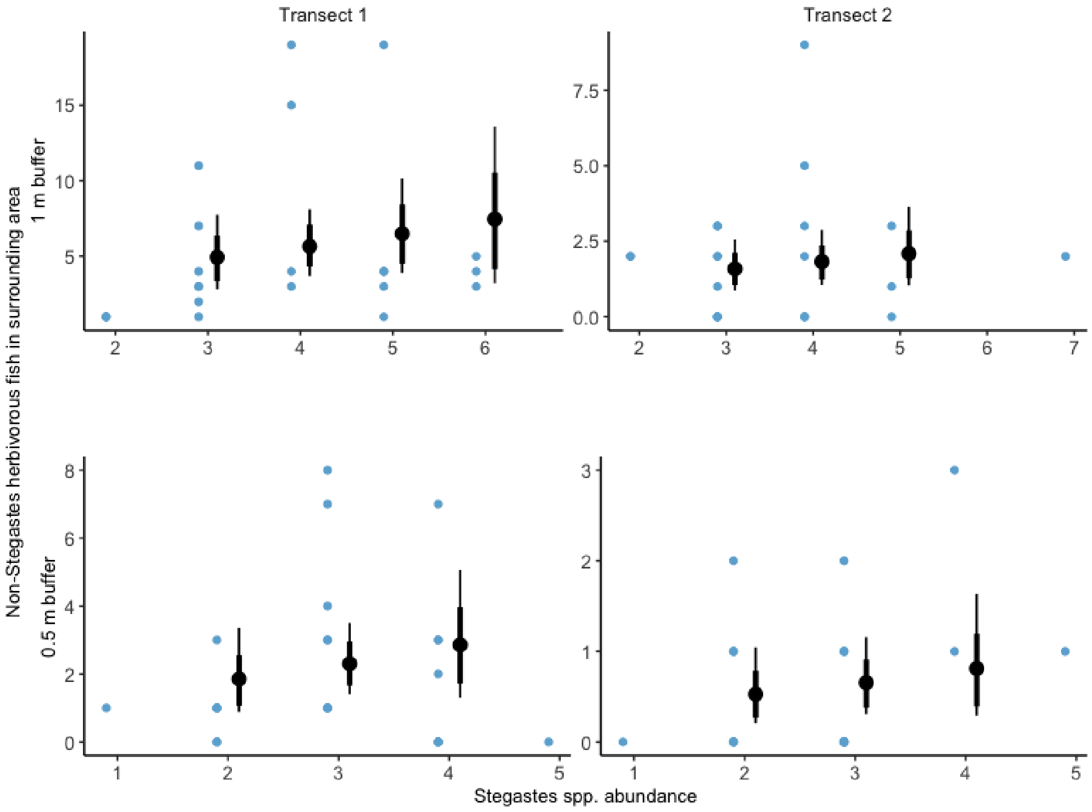

Figure S2.4 The abundances of *Stegastes* spp and non-*Stegastes* herbivorous fish within territories and surrounding area (1 m and 0.5 m buffer) show a weakly positive association. Each column shows data from a different transect, the identities of which were included as grouping factors. Blue points represent raw data. Black points and interval lines represent the expected posterior predictions and confidence intervals (80 and 95%) from Bayesian models using mean values of *Stegastes* spp. aggression and measurement area.

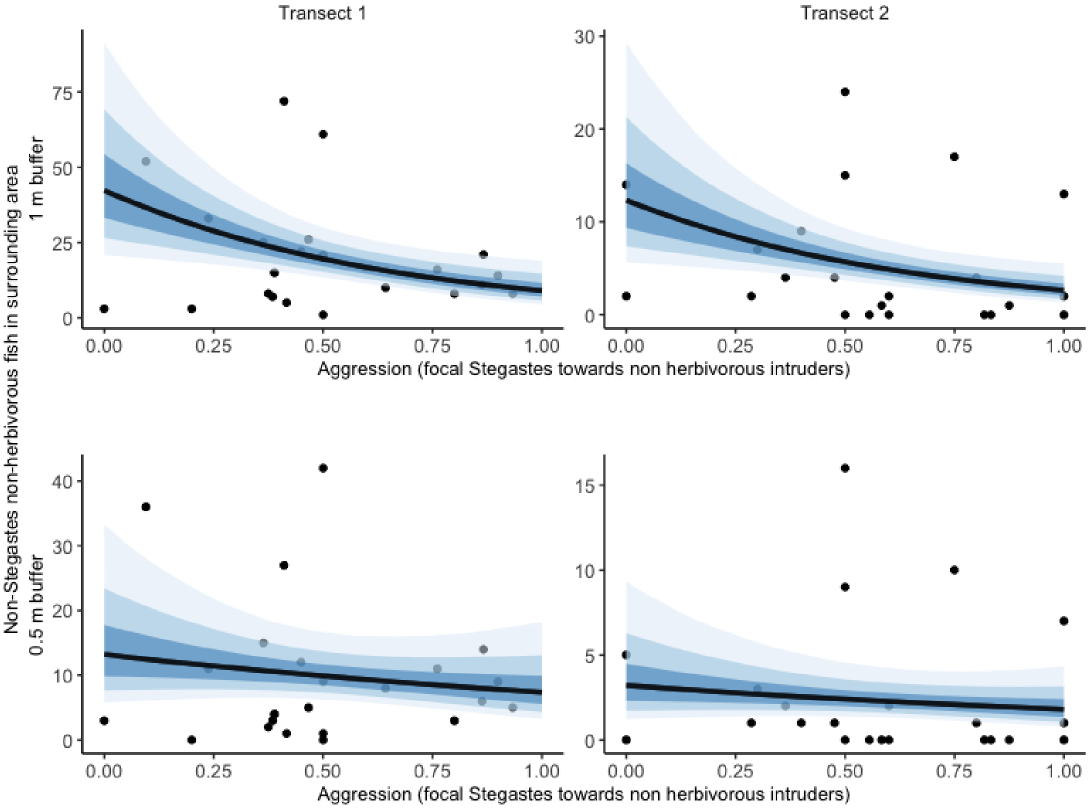

Figure S2.5 The number of non-*Stegastes* non-herbivorous fish within focal *Stegastes* spp. territories and surrounding area (1 m and 0.5 m buffer) declines with increasing individual-level aggression of focal *Stegastes* spp. towards intruders. Columns represent different transects, the identities of which were included as grouping factors. Points represent raw data. Trend line and shaded areas represent the expected posterior predictions and confidence intervals (50, 80 and 95%) from Bayesian models using mean values of *Stegastes* spp. abundance and measurement area. Aggression measured as the proportion of intruders into the focal territory that were attacked/chased.

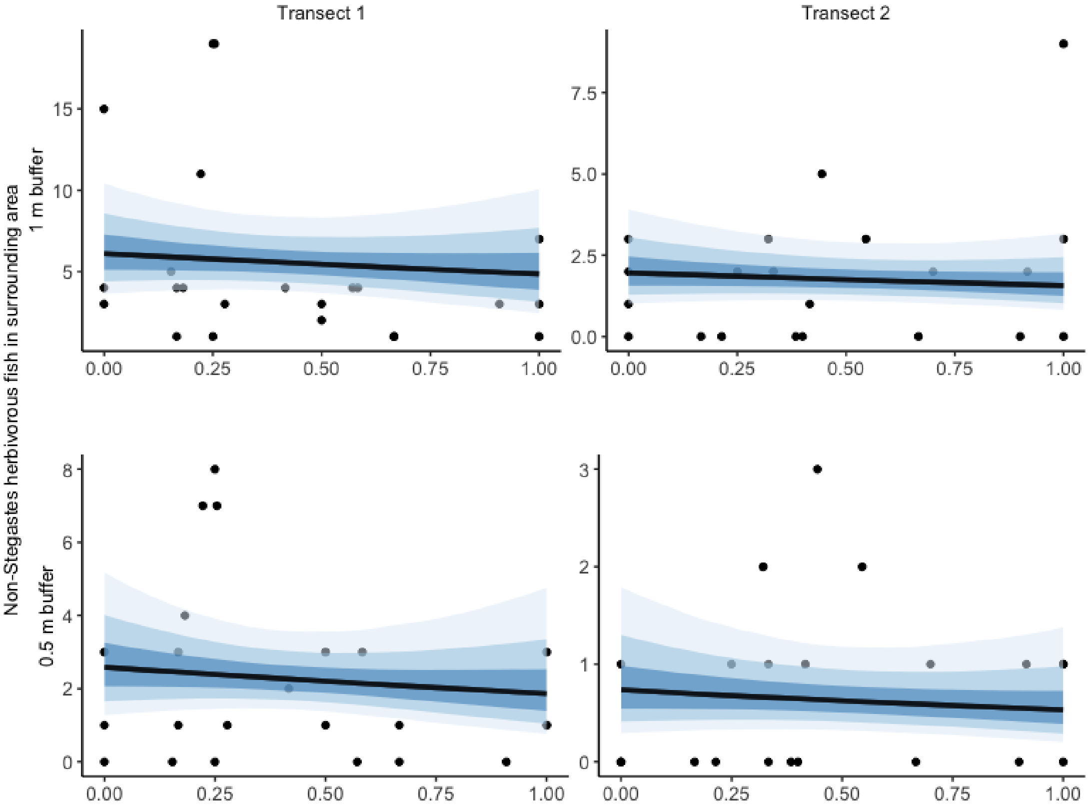

Figure S2.6 The number of non-*Stegastes* herbivorous fish within focal *Stegastes* spp. territories and surrounding area (1 m and 0.5 m buffer) show little association with individual-level aggression of focal *Stegastes* spp. towards intruders. Columns represent different transects, the identities of which were included as grouping factors. Points represent raw data. Trend line and shaded areas represent the expected posterior predictions and confidence intervals (50, 80 and 95%) from Bayesian models using mean values of *Stegastes* spp. abundance and measurement area. Aggression measured as the proportion of intruders into the focal territory that were attacked/chased.

Chapter 4 Supplementary material

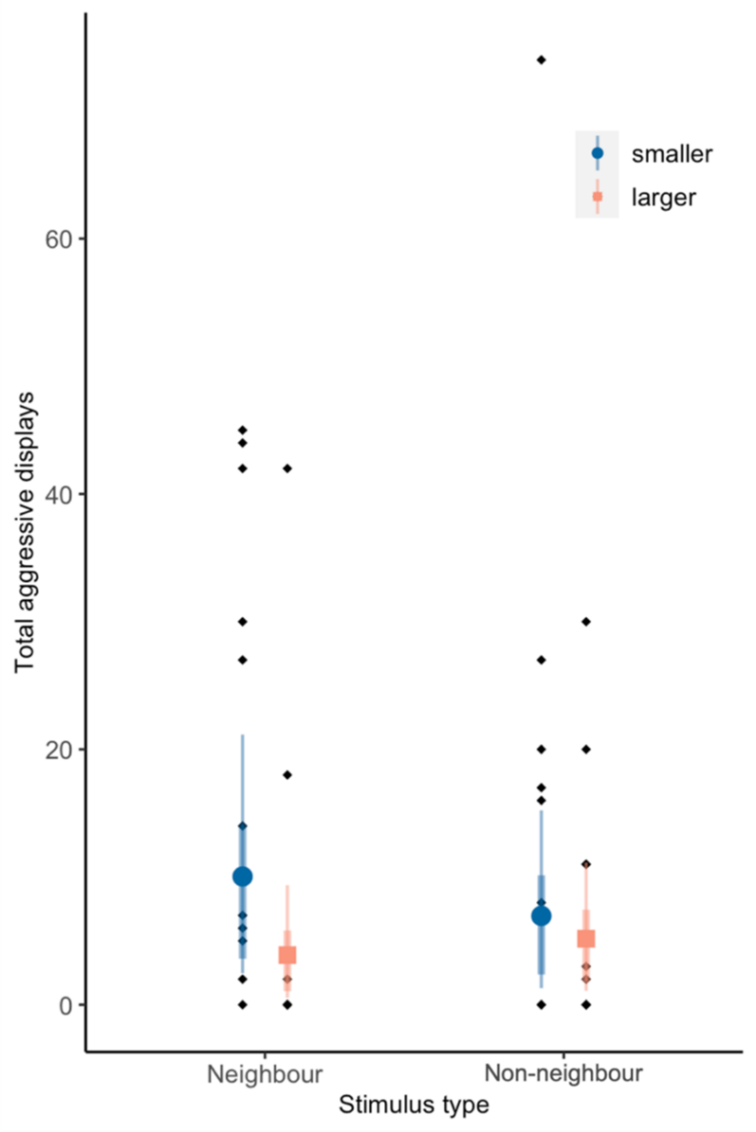

Figure S4.1 Total aggressive displays directed towards intraspecific stimulus fish by *S. diencaeus* territory holders is influenced by both familiarity and body size difference between territory holder and stimulus fish. Expected posterior predictions presented for *S. diencaeus* neighbours and non-neighbours. Point intervals represent median estimates and lines represent 90 and 70% highest posterior density intervals (HPDIs). Black points represent raw data.

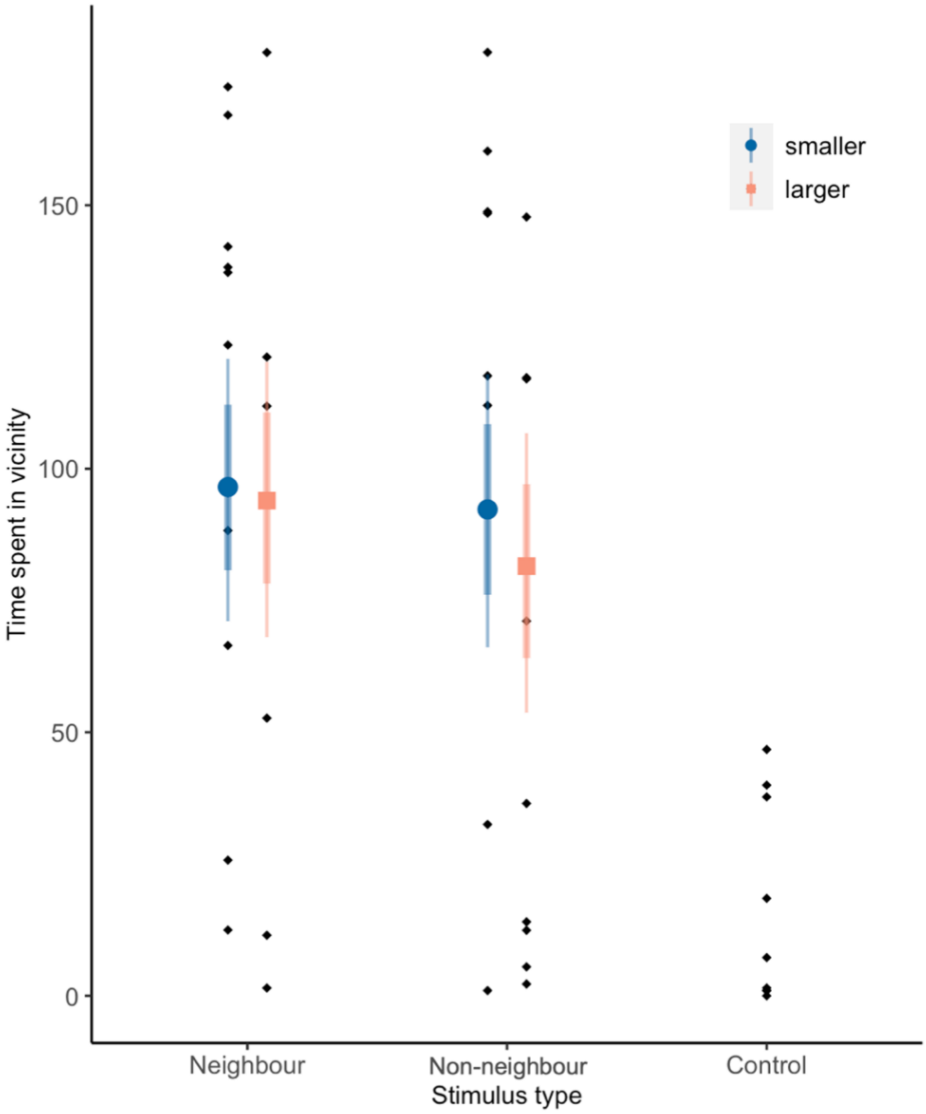

Figure S4.2 Time spent within close proximity (< 15 cm) of intraspecific stimulus fish (seconds) by *S. diencaeus* territory holders is influenced by both familiarity and body size difference between territory holder and stimulus fish. Expected posterior predictions presented for *S. diencaeus* neighbours and non-neighbours. Point intervals represent median estimates and lines represent 90 and 70% highest posterior density intervals (HPDIs). Black points represent raw data.

Appendix B: Publications arising from thesis to date

Sheppard, C.E., Williams, G.J., Exton, D.A., & Keith, S.A. (2023). Co-occurrence of herbivorous fish functional groups correlates with enhanced coral reef benthic state. *Global Ecology and Biogeography*, 32: 435–449. https://doi.org/10.1111/geb.13638

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: 20240035. https://doi.org/10.1098/rsbl.2024.0035