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CATARINA**

Centro de Ciências Biológicas  
Departamento de Ecologia e Zoologia  
Programa de Pós-Graduação em Ecologia



**JUAN PABLO QUIMBAYO AGREDA**

**DETERMINANTS OF FISH ASSEMBLAGES IN OCEANIC  
ISLANDS**

**FATORES DETERMINANTES DAS ASSEMBLEIAS DE PEIXES  
EM ILAS OCEÂNICAS**

**Florianópolis/SC**

**Julho 2017**

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Tese apresentada ao Programa de Pós-Graduação em Ecologia, da Universidade Federal de Santa Catarina, como parte dos requisitos para a obtenção do título de Doutor em Ecologia.

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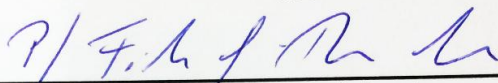
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**"Fatores determinantes das assembleias de peixes recifais em ilhas oceânicas"**

Por

**Juan Pablo Quimbayo Agreda**

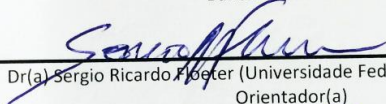
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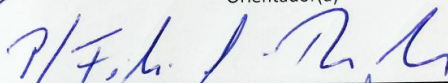
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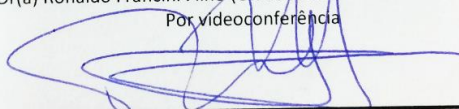
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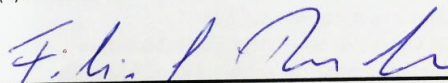
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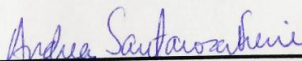
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*“Is it not too much to say that when we have mastered the difficulties presented by the peculiarities of island life we shall find it comparatively easy to deal with the more complex and less clearly defined problems of continental distribution”*

Alfred Russel Wallace

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## RESUMO

Recifes são ecossistemas altamente complexos influenciados por processos que interagem em diferentes escalas espaciais determinando a estruturação e manutenção das comunidades. Estes processos ocorrem em escalas locais e regionais. Os processos locais especificamente, são mediados pelas relações entre as espécies e seu entorno, enquanto os processos regionais como a dispersão das espécies e sua importância para o incremento da diversidade. Muitos dos esforços realizados para entender estes processos, têm sido centrados apenas na riqueza de espécies, enquanto outros componentes da diversidade tais como a densidade de indivíduos, a diversidade funcional, a biomassa e as interações entre as espécies permanecem pouco explorados. Esta falta de conhecimento é ainda maior quando comparamos ambientes terrestres e marinhos, pois estes apresentam um impedimento adicional imposto pelo meio aquático, o que dificulta fazer inferências nesses ambientes. Esta tese teve como objetivo avaliar a influência de processos locais e regionais sobre diferentes componentes da diversidade (riqueza de espécies, diversidade funcional, densidade, biomassa) e as interações entre espécies (interações de limpeza). Para tal, esta tese foi dividida em três capítulos nos quais são explorados diferentes processos locais e regionais. No capítulo 1 “*Unusual reef fish biomass and functional richness at Malpelo, a remote island in the Tropical Eastern Pacific*” foi explorado como os fatores locais determinam a riqueza de espécies, riqueza funcional, densidade de indivíduos e biomassa de peixes em uma ilha oceânica no Pacífico Oriental Tropical. No capítulo 2 “*Determinants of fish assemblages in tropical oceanic islands*” foram explorados como fatores biogeográficos, energéticos e antropogênicos explicam a variação dos componentes de diversidade observados em 18 ilhas oceânicas de cinco províncias biogeográficas marinhas. Finalmente no capítulo 3 “*Dedicated cleaners structure marine mutualistic networks*” foi avaliado como os atributos das espécies podem influenciar o nível de aninhamento das redes de interações de limpeza e suas implicações nas comunidades recifais. Na escala local (ilha oceânica – capítulo 1), fatores como a exposição, a profundidade e a distância do

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Palavras-chave: Variação espacial, ilhas oceânicas, interações de limpeza, componentes de diversidade.



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## INTRODUÇÃO GERAL

Compreender o significado dos processos ecológicos que operam em diferentes escalas é um tema central na ecologia, pois os padrões naturais observados frequentemente variam e são limitados por processos temporais que ocorrem em escalas locais e regionais (Mittelbach & Schemske, 2015). Dada essa variação, ecólogos e biogeógrafos tem desenvolvido diferentes hipóteses ecológicas e evolutivas abordando os principais processos responsáveis pela geração e manutenção da diversidade biológica como especiação, colonização, imigração e extinção (Ricklefs, 1987; Hortal *et al.*, 2012). Algumas destas hipóteses exploram aspectos abióticos (área, isolamento, profundidade, temperatura, produtividade primária) ou biológicos (competição, mutualismo, predação, parasitismo) em escalas locais, que afetam a persistência das populações dentro de seus habitats (Hillebrand & Blenckner, 2002) e regionais que determinam os mecanismos que influenciam as regras de montagem das comunidades. Estas hipóteses frequentemente predizem que as comunidades são montadas por eventos determinísticos (competição) e sua composição de espécies está relacionada com fatores locais e ambientais. Por exemplo, a riqueza de espécies aumenta com área disponível enquanto é inversamente proporcional ao nível de isolamento (MacArthur & Wilson, 1967).

Por outro lado, a cooperação entre espécies através de relações mutualísticas ajudam a minimizar o efeito da competição favorecendo, assim a coexistência de espécies dentro das comunidades (Bastolla *et al.*, 2009). Hipóteses que abordam escalas regionais, como as teorias biogeográficas ou de metapopulações estão centradas no papel do movimento das espécies entre os diferentes habitats e as barreiras que podem limitar a colonização e dispersão (Hillebrand & Blenckner, 2002). Estas hipóteses, ao contrário das abordadas em escalas locais, predizem que as comunidades são montadas por eventos estocásticos associados principalmente à colonização e extinções locais. Por

exemplo, o surgimento do Istmo do Panamá que separou as espécies marinhas do Caribe e Pacífico, provocando a extinção de várias espécies de corais no Pacífico, mas ao mesmo tempo favoreceu um alta taxa de endemismo regional de peixes no Pacífico (Floeter *et al.*, 2008); além disso favoreceu a dispersão de mamíferos e plantas provenientes da América Central e/ou América do Sul, os quais usaram esta formação de terra como uma ponte entre as massas continentais (Leigh *et al.*, 2014).

Em muitos sistemas terrestres e marinhos é evidente que processos que ocorrem em escalas regionais e locais regulam a composição e diversidade de espécies (Hillebrand & Blenckner, 2002; Witman *et al.*, 2004). No entanto, a pergunta sobre a contribuição relativa dos processos locais e regionais que geram a variação geográfica na estrutura das comunidades ainda permanece pobremente compreendida (Mittelbach & Schemske, 2015). Um dos caminhos para estimar a importância de cada processo tem é examinar a forma da relação entre a riqueza local e regional (Loreau, 2000). Por exemplo, se interações locais como a predação ou competição, limitam o número de espécies que poderiam coexistir em um ambiente e dessa forma a riqueza regional alcança uma assíntota (Figura I-1). Alternativamente, se a colonização e dispersão entre os ambientes é alta espera-se uma relação exponencial entre ambas as riquezas (Loreau, 2000). Outro caminho para examinar a contribuição de cada processo é examinar o efeito que variáveis abióticas e bióticas têm sobre a estrutura das comunidades. Por exemplo, na escala local (recife) a riqueza de peixes pode ser determinada pela profundidade e a complexidade estrutural (Quimbayo *et al.*, 2017), enquanto na escala regional esta riqueza é principalmente determinada por área recifal disponível e *pool* regional de espécies (fator derivado dos processos de dispersão, especiação e extinção; Parravicini *et al.*, 2013).

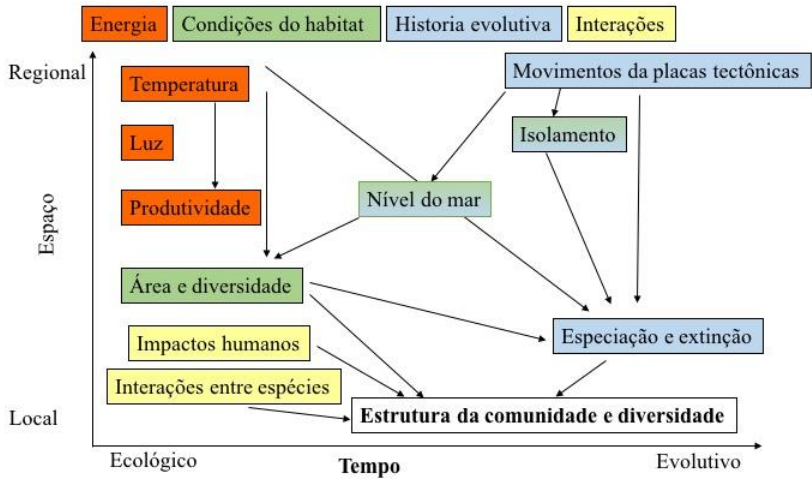


Figura I- 1. Processos que podem influenciar a organização das espécies em diferentes escalas espaciais e temporais.

Apesar dos esforços para determinar a contribuição dos processos locais e regionais que intervêm na estruturação e manutenção das comunidades, nosso conhecimento está enviesado, pois a riqueza de espécies tem dominado nossa visão sobre estes processos, enquanto outros componentes da diversidade, tais como a diversidade funcional e biomassa continuam pouco explorados (Stuart-Smith *et al.*, 2013). Estes componentes podem representar a unificação de várias teorias ecológicas e evolutivas, que permitem a quantificação do espaço ocupado por uma espécie (hipervolume) dado seus atributos morfológicos, comportamentais e filogenéticos (Blonder *et al.*, 2014; Violle *et al.*, 2014). Estes atributos representam tanto os diferentes processos de especiação (evolução de características específicas) e as interações entre as espécies e seu entorno (Lobato *et al.*, 2014). Por exemplo, algumas linhagens de peixes recifais desenvolveram uma boca com mandíbula protrátil que permite reduzir a distância entre eles e suas presas favorecendo assim as interações de limpeza (Floeter *et al.*, 2017). Por outro lado, estes componentes de diversidade também podem ajudar

no desenvolvimento de estratégias de conservação e manejo dos recursos, pois altos valores de biomassa de peixes, por exemplo, são usados como indicadores do estado de saúde das comunidades marinhas (Cinner *et al.*, 2016). Outros exemplos sobre a importância destes componentes de diversidade para a compreensão dos processos locais e regionais determinam que lugares com alta diversidade funcional de peixes recifais apresentam uma maior capacidade de recuperação frente a mudanças climáticas ou induzidas pelo homem (D'agata *et al.*, 2016) e que ambientes com altos valores de biomassa como ilhas oceânicas apresentam cadeias tróficas invertidas típicas de ambientes marinhos prístinos (Trebilco *et al.*, 2013).

As ilhas apesar de representarem só uma pequena fração da superfície da terra, tem cativado a atenção de cientistas desde a época de Charles Darwin e Alfred Wallace, pois estes ambientes são considerados laboratórios naturais que representam o balanço entre os processos locais e regionais (Whittaker & Fernández-Palacios, 2007; Vermeij, 2008). Este balanço é o resultado da interação entre as condições físicas destes ambientes (ex. nível isolamento, área disponível, o tipo de formato, elevação, a idade e/ou origem) e atributos das espécies (ex. tamanho corporal, capacidade de dispersão, dieta e/ou tipo de reprodução; Gillespie, 2007). Algumas das primeiras observações feitas por Darwin e Wallace apontaram que a riqueza de espécies pode variar entre ilhas de um mesmo arquipélago e o continente, sugerindo então que existe um balanço entre os processos locais e regionais que influenciam estas comunidades e que cada ilha é uma unidade independente. Estas observações foram cruciais para o desenvolvimento de teorias robustas sobre os padrões de biodiversidade observados hoje como a Teoria de Biogeografia Ilhas (MacArthur & Wilson, 1967).

Apesar da relevância das ilhas para o desenvolvimento de novas teorias e suas condições ambientais únicas – alto endemismo, riqueza variável e condições físicas – estes ambientes são altamente vulneráveis

frente a mudanças bióticas, climáticas ou induzidas pelo homem (Sadler, 1996). Atualmente, 70% das extinções de espécies de aves conhecidas aconteceram nestes ambientes (Triantis *et al.*, 2010), devido principalmente à baixa capacidade de adaptação das espécies frente a mudanças, à baixa variabilidade genética – efeito fundador – e aos baixos números populacionais. Embora esta cifra seja alarmante, nosso conhecimento sobre os processos que ocorrem em ilhas principalmente no ambientes marinhos é escasso, pois menos 5% dos estudos nestes sistemas consideram grupos marinhos (Hendriks, 2006). Esta baixa porcentagem é de certa forma esperada pois organismos terrestres são estudados há muito mais tempo e muito mais facilmente que organismos marinhos (Ferreira *et al.*, 2017). Além disso as dificuldades logísticas impostas pelo meio aquático são maiores, dado que ambientes terrestres não estão sujeitos às mesmas restrições que os ambientes marinhos (Dawson, 2015). Por exemplo, espécies terrestres em ilhas costeiras estão rodeadas por água, o que limita sua distribuição, enquanto espécies marinhas não estão sujeitas a esta barreira física, pois apresentam uma fase larval que permite-lhes usar este meio para dispersão (Ferreira *et al.*, 2017).

Atualmente 21 tipos de ilhas têm sido reconhecidas tanto nos ambientes terrestres quanto marinhos (Dawson, 2015), sendo as ilhas oceânicas as menos estudadas devido a seu alto nível de isolamento. No entanto, os poucos estudos feitos até hoje sugerem que este fator favorece a manutenção da biodiversidade, pois ilhas altamente isoladas permanecem intactas ou pouco alteradas pelas ações antrópicas, sendo os últimos ambientes marinhos prístinos (Sandin *et al.*, 2008a,b). Dada estas características é fundamental incluir estes ambientes em estudos evolutivos e ecológicos, pois estes irão contribuir no avanço de novas teorias e modelos que ajudem a explicar a contribuição que de processos locais e regionais têm sobre as comunidades.

Peixes recifais são considerados um dos grupos de vertebrados mais diversos do planeta, com mais de 6 mil espécies distribuídas ao longo de ambientes tropicais e subtropicais (Kulbicki *et al.*, 2013). Esta alta diversidade taxonômica é acompanhada tanto por uma alta diversidade funcional, a qual determina a dinâmica e manutenção dos ambientes recifais (Mouillot *et al.*, 2014), assim como a variedade de interações observadas – predação, competição, mutualismo. Além disso, muitos serviços ambientais são prestados por este grupo às sociedades humanas, pois são umas das principais fontes de proteína animal provenientes de ambientes recifais (FAO, 2014). Apesar destas características e de sua importância nos ambientes marinhos, algumas de suas populações estão sendo levadas ao colapso ou extinção local devido à constante necessidade de recursos e crescimento exponencial das populações humanas (Mora *et al.*, 2011). Alguns exemplos recentes de extinções funcionais no Brasil: 1) diminuição drástica do Budião-Azul em Arraial do Cabo, RJ (Bender *et al.*, 2014) e 2) perda histórica do tubarão de Galápagos (*Carcharhinus galapagensis*) no Arquipélago de São Pedro e São Paulo (Luiz & Edwards, 2011). O acúmulo destas perdas podem comprometer a manutenção da diversidade e os processos locais e regionais, já que ao retirar espécies do sistema as mesmas não poderão interagir com outras espécies gerando um efeito cascata, logo outros níveis dentro da comunidade serão comprometidos (Johansson *et al.*, 2013). Um exemplo deste problema foi observado no Caribe, nos anos 80, onde 70% das espécies de peixes herbívoros foram removidos pelo pesca, o que favoreceu o crescimento de algas – fortes competidores dos corais – alterando a estrutura do ambiente, passando de um recife dominado por corais para um recife dominado por algas (Mumby *et al.*, 2006).

Diante da importância de avaliar e comparar a estrutura de peixes recifais em lugares isolados e lugares costeiros, esta tese teve como objetivo explorar vários processos locais que incluem as relações entre espécies e seu entorno e processos regionais que incluem barreiras



físicas, fisiológicas e efeitos antropogênicos. Especificamente, neste estudo foi explorado como fatores locais (exposição e profundidade) influenciam a riqueza de espécies, densidade, biomassa e riqueza funcional de peixes recifais em uma ilha oceânica (Capítulo 1). Como fatores biogeográficos (área, isolamento, distancia ao recife mais próximo), energéticos (temperatura superficial do mar e produtividade primária) e antropogênicos (densidade humana, distância do continente, e nível de proteção ambiental) influenciam a riqueza de espécies, a diversidade funcional, densidade e biomassa de peixes em ilhas oceânicas localizadas em cinco diferentes províncias marinhas (Capítulo 2). Como as interações de limpeza são estruturadas em recifes tropicais (ilhas e lugares costeiros), especificamente como os atributos dessas espécies determinam como ocorre essa interação (Capítulo 3).

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## CAPÍTULO 1

### **Unusual reef fish biomass and functional richness at Malpelo, a remote island in the Tropical Eastern Pacific**

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Quimbayo J.P., Mendes T.C., Kulbicki M., Floeter S.R., Zapata F.A. (2017). Unusual reef fish biomass and functional richness at Malpelo a remote island in the Tropical Eastern Pacific. *Environmental Biology of Fishes* 100:149-162.

**Unusual reef fish biomass and functional richness at Malpelo, a remote island in the Tropical Eastern Pacific**

Running page head: Reef fish assemblage at Malpelo Island

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**Key words:** *Marine protected area, endemism, biomass, reef fish, Malpelo Island, Colombia.*

## **Abstract**

Fish assemblages can vary across temporal and spatial scales due to changes in habitat structure and the influence of local factors such as wave exposure, depth and anthropogenic influence. This study presents a description of species richness, functional richness, density and biomass of fish assemblages of Malpelo Island, a Marine Protected Area located in the Tropical Eastern Pacific (TEP) region and considered a World Heritage site. Underwater visual censuses ( $n = 103$ ) from two years and a local checklist were used to characterize the reef fish assemblage of Malpelo Island. Our results show a numerical dominance, during both sampling years, by the planktivore species *Chromis atrilobata* and *Apogon atradorsatus*, which are regional TEP endemic species. Among the most striking results found were the high biomass values ( $706.2 \text{ g/m}^2 \pm 73.2$  in 2010 and  $879 \text{ g/m}^2 \pm 116.2$  in 2015) of large-bodied TEP endemic piscivorous species and the high functional diversity represented mainly by vulnerable species. The dominance in density and biomass of regional endemic species exemplifies the high endemism level within the TEP. High levels of fish biomass and functional richness suggest that Malpelo is one of the most pristine and vulnerable sites within the TEP region. Thus, Malpelo Island represents a baseline for untouched assemblages in this marine province, as well as a priority area for conservation at the national and international level.

## **Introduction**

Understanding temporal and spatial variations of assemblages and the influence of biotic and abiotic factors on communities are among the most important goals in community ecology (Jones and Syms 1998; Ricklefs 2006). This interest arises due to the fact that each species perceives the environment on a unique range of scales and thus responds individually to environmental variability (Levin 1992). Species often show a patchy distribution over a range of temporal and spatial scales as a result of different evolutionary (dispersal, speciation and extinction) and ecological (environmental tolerances, habitat choice and species

interactions) processes operating at those scales (Ricklefs 2004). Although several studies have been key to understanding these questions on tropical reefs (Mora et al. 2003; Connolly et al. 2005; Parravicini et al. 2013), our knowledge on the influence of these processes in structuring reef fish communities in the Tropical Eastern Pacific (TEP) is still scarce. Few studies in this region have examined the regional reef fish assemblage, but they have primarily focused on range size distribution (Mora and Robertson 2005a), latitudinal variation in species richness (Mora and Robertson 2005b), and the delineation of biogeographic provinces based on species composition (Robertson and Cramer 2009). One aspect of reef fish ecology that is receiving increasing attention in other regions is that of functional diversity (Stuart-Smith et al. 2013). While this topic has begun to be studied in the TEP (Alvares-Filip and Reyes-Bonilla 2006, Aguilar-Medrano and Calderón-Aguilera 2015), these studies have been carried out mostly on coastal locations of the northern portion of the region (Gulf of California and Mexican Pacific), whereas no study has examined functional diversity on an oceanic island of the TEP. The study of functional aspects of communities, especially in areas with little or no local human influence, such as isolated oceanic islands, has only recently been receiving increased attention (Sandin et al. 2008; Mora et al. 2011; Williams et al. 2015). These studies point to specific characteristics shared by oceanic islands, such as high productivity (Gove et al. 2016), high levels of endemism, reduced gene flow among populations (Hachich et al. 2015), and high density of top predators (Sandin et al. 2008), all of which convert these islands into important natural laboratories to studies of marine communities. Additionally, these islands because of their isolation are often nearly untouched by humans, and may exhibit features, such as "inverted biomass pyramids", typical of pristine places (Trebilco et al. 2013).

Despite the importance of remote oceanic islands as the last pristine marine sites, the number of studies focused on their marine communities is low (Friedlander and DeMartini 2002; Sandin et al. 2008; Williams et

al. 2015). This is in part linked to logistical constraints imposed by the remote location of these islands, which increase the costs and difficulties of acquiring quantitative data of the marine communities and local factors that influence the species composition (Dawson 2015; Luiz et al. 2015), such as wave exposure, depth, and anthropogenic influence, among others. This lack of information is most evident in regions with high geographic isolation, such as the TEP, whose isolation from the central Pacific by the Eastern Pacific Barrier (EPB) and from the Caribbean by the closure of the Isthmus of Panama, has led to high endemism but low richness at the species level (Zapata and Robertson 2007; Robertson and Cramer 2009).

Malpelo Island is a small remote island located in the TEP region, which has low reef fish species richness compared to oceanic islands in the Indo-Pacific and Caribbean Regions (Kulbicki et al. 2013). Malpelo, together with the Revillagigedos, Clipperton, Cocos and Galapagos islands define a biogeographical sub-province distinct from the coastal adjacent regions, due to the presence of a small number of island endemics and a high number of transpacific species (Robertson and Cramer 2009). Currently, this island is the only Marine Protected Area (MPA) in the Colombian Pacific recognized as a World Heritage site since 2006 owing to its unique characteristics and importance as a stepping-stone for marine wildlife between the continent and other oceanic islands of the TEP (McCosker and Rosenblatt 1975).

Additionally this island has a high endemism and a high concentration of sharks and mega-fauna (Bessudo et al. 2011). Malpelo Island is also part of “Eastern Tropical Pacific Marine Conservation Corridor”, an international marine conservation initiative that additionally include the Galápagos, Gorgona, Coiba and Cocos Islands. Despite its status as a World Heritage Site and MPA, populations of large fishes have drastically decreased around Malpelo due to illegal fishing activities around the island (Soler et al. 2013). This type of impact has never been

locally evaluated despite the increasing human population and its continuing appetite for natural resources.

Our objective here is to describe the temporal and spatial variation in species richness, functional richness, density and biomass of the Malpelo Islands reef fish assemblages based on data obtained in two years. More specifically, this study aims to answer the following questions: 1) How did the species richness, functional richness, density and biomass of the fish assemblages vary between 2010 and 2015? 2) How do these same attributes vary spatially across the island? 3) What is the relative importance of endemic species vs widely distributed species in terms of total density and biomass? 4) How do wave exposure and depth influence the species richness, functional richness, density and biomass of fishes concentrated in different trophic groups, size classes and geographic distribution classes across the island? 5) How does the functional structure of the fish assemblage vary across three different scales (i.e. regional species pool, local species pool, and species observed in underwater visual censuses)? 6) Are the fish assemblages in Malpelo more redundant or vulnerable when compared to the TEP regional species pool, given their isolation level and small habitat area?

## **Materials and Methods**

### **Study Area**

This study was carried out at Malpelo Island (4°00'05" N, 81°36'30" W; Fig. 1-1), a protected Sanctuary of Marine Fauna and Flora, located 377 km from the nearest reef habitat (Gorgona Island) and 395 km off the coast of Colombia (Fig. 1-1). The oceanic waters surrounding Malpelo are seasonally influenced by four currents: the North Equatorial Countercurrent, the South Equatorial Countercurrent, the Colombia Current, and the Panama Cyclonic Current (Rodríguez-Rubio et al. 2007). The annual mixing period of these currents depends on the

variation of the Intertropical Convergence Zone, with the degree of mixing depending on long-term cycles such as the El-Niño Southern Oscillation (Rodríguez-Rubio and Schneider 2003). This island is of volcanic origin and is subjected to constant erosion of its coastal cliffs. The seabed around the island is dominated by steep walls and mostly covered by loose boulders resulting from landslides, though there are some small terraces with underdeveloped coral formations (Zapata and Vargas-Ángel 2003).

Fieldwork was conducted during two SCUBA diving expeditions, one in 2010 and another in 2015. During these expeditions, we sampled four sites around the island (one site in 2010 and four sites in 2015), which were classified into ‘sheltered’ and ‘exposed’ according to wave exposure and prevailing winds. The ‘sheltered sites’ of “El Arrecife” (AR) and “La Nevera” (LN) are unique sites in Malpelo in the sense that they are characterized by coral development and structural complexity (Zapata and Vargas-Ángel 2003; Chasqui and Zapata 2007). On the other hand, the ‘exposed’ sites of “Bajo de Junior” (BJ) and “Pared del Náufrago” (PN) are mainly rocky reefs with low structural complexity, formed by large boulders and vertical walls, with comparatively lower coral cover (*personal observations*: Fig. 1-1).

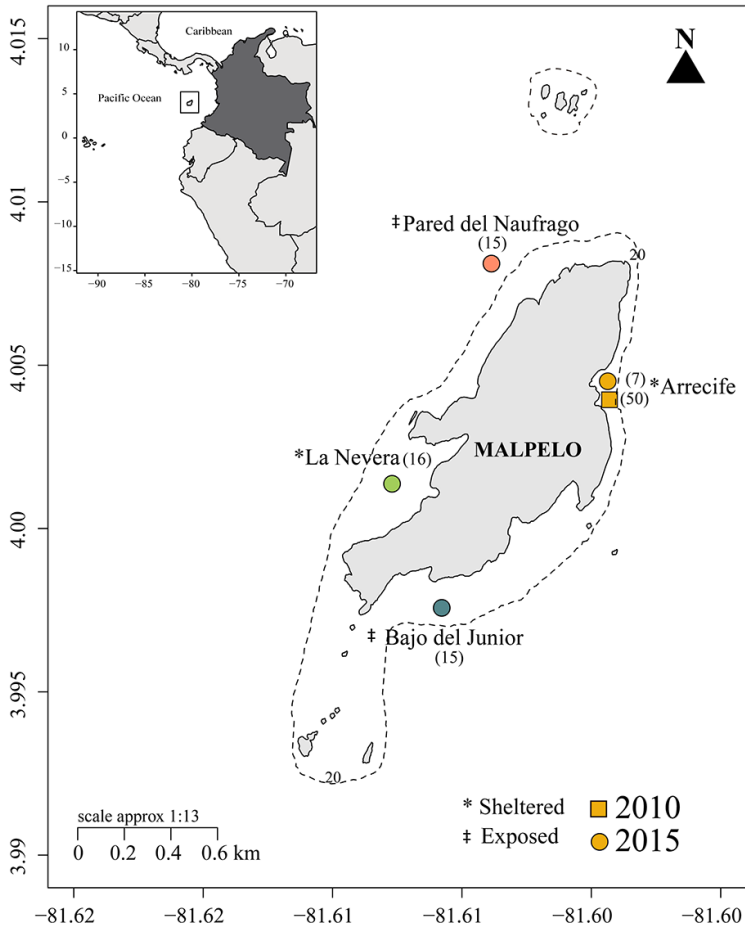


Figure 1-1: Map of Malpelo Island showing the four sampling sites. The map also indicates the location El Arrecife, which was visited both 2010 and 2015, as well as exposed and sheltered sites. Numbers within parenthesis represent the total number of underwater visual censuses. The dashed line represents the 20 m isobaths



## Reef Fish Assemblages

We estimated reef fish species, density and biomass for 103 underwater visual censuses (UVCs) along transects of 40 m<sup>2</sup> (20x2 m). This sampling involved identifying, counting and estimating the size (total length in cm) of all fishes observed both in the water column and on the bottom along the 20m-long transect (see Floeter et al. 2007). We had two sampling schemes, one for comparing temporal and the other for testing spatial variation in reef fish assemblages. For the temporal analysis, we carried out 50 UVCs at El Arrecife location in 2010 and repeated the sampling at the same location in 2015, but made only 7 UVCs. To compare spatial variation in reef fish assemblages, we sampled three more locations (totaling 4 locations) in 2015. Therefore, our spatial analysis was restricted to the 2015 sampling whereas temporal changes in reef fish assemblages are specific to El Arrecife location.

Multiple UVCs were performed in each location in shallow (7–17 m) and deep (17–30 m) area, and allowed the estimation of species richness, as well as density and biomass for each species (Fig. 1-1). We estimated the weight of each fish using the allometric length-weight conversion  $W = a \times TL^b$ , where parameters  $a$  and  $b$  are species-specific constants, TL is the estimated total length in cm, and W is weight in grams. Length-weight parameters ( $a$  and  $b$ ) were obtained for each species from FishBase (Froese and Pauly 2016). All shark and ray species were excluded from the analysis since they may disproportionately increase the biomass values, especially in transects with small areas (Ward-Paige et al. 2010). Finally, based on Rubio et al. (1992) and Robertson and Allen (2016), we also compiled a reef fish checklist (i.e. all species that are reported in a place) for Malpelo to compare the characteristics of the local and regional species pools.

## **Geographic Distribution**

All reef fish recorded during the UVCs and from the checklists were classified into six classes according to their geographic distribution (Robertson and Allen 2016): (1) Species endemic to Malpelo (LOC); (2) species that occur only in one or more of the TEP oceanic islands (ITEP); (3) species restricted to the TEP (on both continental coast and islands: CTEP); (4) species shared with the Central Pacific (CP); (5) species with occurrence in the TEP and Atlantic Ocean (AT); and (6) species with circumglobal distribution (CG).

## **Fish Functional Richness**

All species were classified according to six different life-history traits using functional properties defined by Mouillot et al. (2014): (1) Species maximum body size: <7 cm, 8–15 cm, 16–30 cm, 31–50 cm, 51–80 cm or >80 cm; (2) Mobility: sedentary (including territorial species), mobile or very mobile; (3) Period of activity: diurnal, nocturnal, or both; (4) Schooling: solitary, pairing, small groups (3–20 individuals), medium groups (20–50 individuals) or large groups (>50 individuals); (5) Position in the water column: benthic (species associated with the bottom), bentho-pelagic, or pelagic and (6) Trophic group: herbivores-detritivores (feed upon turf and filamentous algae and/or detritus), macroalgae-feeders (large fleshy algae and/or seagrass), sessile invertebrate feeders (e.g. corals, sponges, ascidians), mobile invertebrate feeders (benthic prey, such as crabs and mobile mollusks), planktivores (small organism in the water column), piscivores (fish and cephalopods) or omnivores (both vegetal and animal material). Functional Entities (FE.s) were defined as a combination of the six life history traits. We used the number of FE.s as a proxy for the functional richness of each fish census.

## Statistical Analysis

### *Temporal analysis*

To quantify temporal changes in fish assemblages, we compared UVCs from El Arrecife between 2010 and 2015. As the number of UVCs sampled varied between these periods (50 in 2010 and 7 in 2015; AR: Fig. 1-1), we randomly sampled 7 UVCs from 2010 and repeated this procedure 999 times to estimate mean differences in richness, density, biomass, and FE.s richness of comparable sample sizes. This procedure simulates a sample-based rarefaction procedure that enables temporal comparisons of reef fish assemblage parameters while controlling for sample size differences (Gotelli and Colwell 2001). We explored the temporal variations of fish density and biomass using GLM with Gamma distribution since these data are positive and continuous and tend to have a log-normal distribution (Zuur et al. 2009).

### *Spatial analysis*

We explored the spatial variations in fish assemblages among the four sampling sites in the 2015 survey using rarefaction curves (species richness and functional richness) and generalized linear mixed model – GLMM - (fish density and biomass) with a Gamma distribution. We considered depth classes (shallow and deep) and sites as fixed factors, while transect were defined as a random factor to attempt to account for spatial autocorrelation. We used a Gamma distribution in all of the above models as density and biomass are overdispersed, positive and continuous response variables (Zuur et al. 2009). We used a Tukey test for testing the difference observed in the GLMMs, using the function “*glht*” within the package *multcomp* (Hothorn et al. 2008). Finally, we compared the contribution of local endemic species vs non-endemic species within the same family to density and biomass per transect using Mann-Whitney *U*-tests.

We evaluated the effect of wave exposure and depth on species richness, functional richness, density and biomass classified into different (1) trophic groups, (2) size classes and (3) geographic distribution levels, with permutational Multivariate Analyses of Variance (PERMANOVA) using wave exposure (2 levels: sheltered and exposed) and depth (2 levels: shallow and deep) as factors (Anderson 2001). The PERMANOVAs were performed using a Bray-Curtis dissimilarity distance matrix. The statistical significance of the PERMANOVA was tested with 999 permutations under a reduced model and type II (conditional) sums of squares (Anderson et al. 2008). PERMANOVA analyses were made using the function “adonis” within the package *vegan* (Oksanen et al. 2015). To explore the multivariate patterns observed in the PERMANOVA test, we used a Redundancy Analysis (RDA) to graphically display the influence of the above factors (wave exposure and depth class) on the species richness, functional richness, density and biomass of the reef-associated fish assemblages.

We used the six life history traits assigned to each species observed in 2015 to compare the multidimensional functional space occupied by the regional species pool (species with occurrence in the TEP), the local species pool (species registered in local checklist), and species detected in UVCs. The multidimensional functional space was built from a Principal Coordinates Analysis (PCoA) using a Gower’s distance dissimilarity matrix, which allows mixing qualitative and quantitative data (Villéger et al. 2008; Mouillot et al. 2014). The intent was to understand potential links between three levels of spatial organization and the decrease in functional richness according to isolation level (Bender et al. 2016). Finally, we analyzed the redundancy within functional entities for both the local checklist and the assemblages determined by UVCs and the proportion of vulnerability (functional entities with only one species). To test whether the functional richness observed at each scale (TEP pool, checklist and UVCs) was significantly different from the functional richness of a random subset of species, we

used null models based on randomization of species pools. To simulate a realistic pool of species in each realm, the number of species per taxonomic order was kept constant in the random choice process (999 iterations). Random matrices were generated through the “oecosimu” function available in the *vegan* R package (Oksanen et al. 2015). All statistical analyses were performed in R software version 3.2.4 (R Core Team 2016).

## Results

### *Temporal analysis*

A total of 87 species (37 families) was recorded during the two surveys. We found during the 2010 survey, 70 species (35 families), whereas in 2015 we found 65 species (29 families). Richness ranged from 5 to 30 species per transect. We detected higher species richness and functional richness in 2015 compared to 2010 (Fig. 1S-1 A, B). We also observed some exclusive species for each year, 22 species in 2010 and 16 in 2015 (Table 1S-1). Species exclusive to 2010 were mainly piscivores and mobile invertebrate feeders (41% each), planktivores (13.6%) and omnivores (4.4%; Table 1S-1). On the other hand, the exclusive species in 2015 were mainly mobile invertebrate feeders (43.7%), planktivores (31.3%), piscivores (12.5%), herbivores-detritivores and omnivores (6.3% each; Table 1S-1). We found differences in density (2010:  $9.30 \text{ ind/m}^2 \pm 0.68 \text{ s.e.}$ ; 2015:  $9.77 \text{ ind/m}^2 \pm 0.7 \text{ s.e.}$ ) and biomass (2010:  $706.2 \text{ g/m}^2 \pm 73.2 \text{ s.e.}$ ; 2015:  $879 \text{ g/m}^2 \pm 116.2 \text{ s.e.}$ ) between sampling years (GLM: p-value < 0.05; Fig. 1S-1 C, D). The species that most contributed to the total density for both years were the regional endemics: *Chromis atrilobata*, *Apogon atradorsatus*, *Cirrhitichthys oxycephalus* and *Paranthias colonus* (Table 1S-1). In terms of biomass, the dominant species were the regional endemic *Lutjanus viridis*, *L. jordani*, *Gymnothorax dovii*, *Paranthias colonus*, and the circumglobal *Seriola rivoliana* (Table 1S-1).

### *Spatial analysis*

We found a higher species richness in “El Arrecife” (AR), followed by “La Nevera” (NV), “Bajo de Junior” (BJ) and “Pared del Náufrago” (PN) (Fig. 1-2A), but no difference was detected for functional richness (Fig. 2b). The mean density found in 2015 was 5.95 ind/m<sup>2</sup> and varied from 0.02 to 140.4 ind/m<sup>2</sup> (Table 1S-1). There was a significant difference in mean density among sampling sites, but not between the two depth classes (GLMM: p-value < 0.05; Fig. 1-2C). AR and NV were the most different sites (Tukey test: p-value < 0.05; Fig. 1-2C), and were also the sites that presented the highest mean densities (15.1 ind/m<sup>2</sup> and 10.2 ind/m<sup>2</sup>, respectively), whereas PN and BJ had a lower mean density (9.01 ind/m<sup>2</sup> and 7.58 ind/m<sup>2</sup>, respectively; Fig. 1-2C). The mean biomass in 2015 was 872 g/m<sup>2</sup> and varied from 5.03 to 2683.0 g/m<sup>2</sup> (Table 1S-1). There was a significant difference in mean biomass among sampling sites, but not between the two deep sites (GLMM: p-value < 0.05; Fig. 1-2D). BJ and AR presented significantly higher biomass values (Tukey test, p-value < 0.05; 1730 g/m<sup>2</sup> and 1212 g/m<sup>2</sup>; Fig. 1-2D), whereas NV and PN had lower mean biomass values (474 g/m<sup>2</sup> and 229 g/m<sup>2</sup>; Fig. 1-2D).

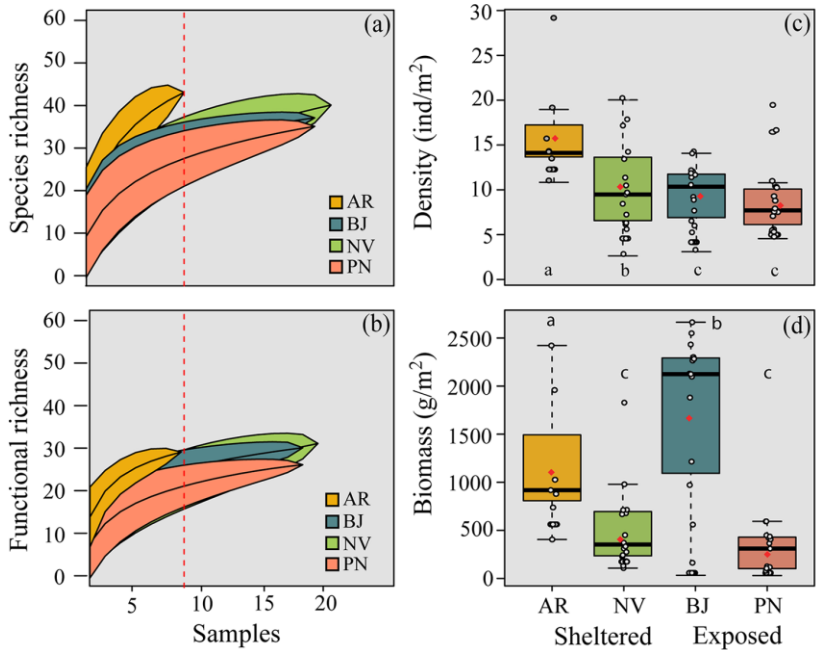
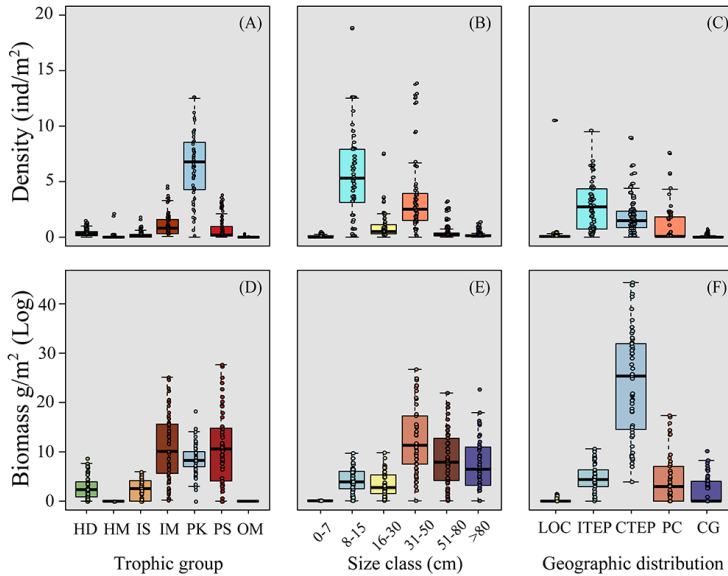


Figure 1-2: Comparison among the four sampling sites in 2015. A) Species richness, B) Functional richness, C) Density and D) Biomass. Each color represents a different site. Boxplots show medians (black line), mean (red diamond), upper and lower quartiles, and 95% confidence intervals. Letters show statistical groupings (Tukey post hoc) with boxplot having different letters being significantly different. Boxplot with the same letter are not significantly different. Red lines in A and B, represent the standardized number of surveys. Each point represents an underwater visual census. Sites around of Malpelo Islands “AR” El Arrecife, “NV” La Nevera, “BJ” Bajo del Junior, and “PN” Pared del Naufrago.

Planktivores accounted for 64.8% of all individuals recorded, followed by mobile invertebrate feeders (22.6%), piscivores (8.96%), herbivores-detritivores (2.63%), macroalgae-feeders, sessile invertebrate feeders and omnivores (<1% each; Fig. 1-3A). The most common size class among the fish assemblages was 8-15 cm (47.64%) followed by the classes of 31-50 cm (35%), 16-30 cm (10.5%), 51-80 cm (5.06%), >80cm (1.56%) and 0-7 (<1%; Fig. 1-3B). Species present in one or

more of the TEP oceanic islands (ITEP) were the most important for density (59.4%; Fig. 1-3C), followed by species with wide distribution in the TEP (CTEP; 29.6%), species shared with the central Pacific (PC; 10.33%), endemics (LOC), and circumglobally distributed species (CG; <1%). Species shared with the Atlantic Ocean were not observed during the 2015 sampling (Table 1S-1). In terms of biomass, piscivores were the most important (54.6%), followed by planktivores (23.3%), mobile invertebrate feeders (16.7%), sessile invertebrate feeders (3.3%), herbivores-detritivores (1.9%), macroalgae-feeders, and omnivores (<1%; Fig. 1-3D). The size class with the highest biomass was 31-50 cm (48.7%), followed by the class of 51-80 cm (26.6%), >80 cm (21.3%), 8-15 cm (2.2%), 16-30 cm (1.2%), and 0-7 cm (<1%; Fig 1-3E). Species considered as CTEP had the largest contribution to biomass (82%), followed by CG species (10.5%), PC (4.3%), ITEP (3.1%) and LOC (<1%; Fig. 1-3F).





**Figure 1-3:** Comparison of density and biomass during the 2015 sampling in Malpelo Island. A) Density per trophic groups. B) Density per size classes. C) Density per geographic distribution classes. D) Biomass per trophic groups. E) Biomass per size classes. F) Biomass per geographic distribution classes. Each color represents a different class. Boxplots show medians (black line), upper and lower quartiles, and 95% confidence intervals. Each point represents an UVC. Trophic groups: herbivores-detritivores (HD), macroalgae-feeder (HM), sessile invertebrate feeders (IS), mobile invertebrate feeders (IM), planktivores (PK), piscivores (PS) and omnivores (OM). Geographic distribution: Circum-global (CG), Pacific (PC), coastal Tropical Eastern Pacific (CTEP), restricted to oceanic islands in Tropical Eastern Pacific (ITEP) and local endemic (LOC).

Our results show that both wave exposure and depth influenced the fish assemblages of Malpelo (PERMANOVA:  $p$ -value  $< 0.05$ ; Table 1). However, the magnitude and direction of these effects varied. For instance, wave exposure was the unique factor that influenced species richness of several trophic groups, size classes and geographic distribution classes (Table 1). Species richness was concentrated in sheltered places (Fig. 1-4A, B, C). Functional richness observed for different trophic groups, size and geographic distribution classes was

influenced exclusively by wave exposure, which was concentrated in sheltered and shallow places (Fig. 1-4D, E, F; Table 1). Density observed for the different trophic groups, size and geographic distribution classes was influenced by depth and interaction of depth and wave exposure (Table 1), and was also concentrated in sheltered and shallow places (Fig. 1-5G, H, I). Finally, the biomass observed for the different trophic groups, size and geographic distribution classes were influenced by both wave exposure and depth, and was concentrated in exposed and deep places (Fig. 1-5J, K, L; Table 1).

During the UVCs we observed 80% (four out of five) of all endemic species reported from Malpelo: *Axoclinus rubinoffi*, *Acanthemblemaria stephensi*, *Lepidonectes bimaculatus* and *Halichoeres malpelo* (the fifth endemic, the gobiid *Chriolepis lepidota*, has never been observed after its initial collection of two individuals with rotenone in 1972; Findley 1974). Local endemic species and non-endemic species differed in their contribution to density (Wilcoxon's test,  $W = 320$ ,  $p < 0.01$ ) and biomass (Wilcoxon's test,  $W = 107$ ,  $p < 0.01$ ), being lower for local endemic than for those non-endemic species within the same families (Fig. 1S-2 A B). Among endemic species, the most important in terms of density was *A. rubinoffi* (0.013 ind/m<sup>2</sup>), followed by *H. malpelo* (0.011 ind/m<sup>2</sup>), *L. bimaculatus* (0.008 ind/m<sup>2</sup>) and *A. stephensi* (0.001 ind/m<sup>2</sup>). For biomass, the most important endemic species was *H. malpelo* (0.27 g/m<sup>2</sup>), followed by *L. bimaculatus* (0.004 g/m<sup>2</sup>), *A. rubinoffi* (0.003 g/m<sup>2</sup>) and *A. stephensi* (0.0004 g/m<sup>2</sup>; Table 1S-1). Among the endemic species observed during the sampling, three are mobile invertebrate feeders (75%) and one is planktivore (25%). Three of these endemic species are in the 0-7cm size class (*A. rubinoffi*, *A. stephensi*, and *L. bimaculatus*), whereas *H. malpelo* is in the 8-15 cm size class.

Table 1. The influence of depth and exposure on species richness, functional richness, density and biomass of reef fishes for each trophic group, size and geographic distribution classes in 2015. Significant values ( $p < 0.05$ ) in bold.

Source	Species richness				Functional richness				Density				Biomass			
	<i>df</i>	SS	F	P	<i>df</i>	SS	F	P	<i>df</i>	SS	F	P	<i>df</i>	SS	F	P
<b><i>Trophic group</i></b>																
Depth	1	0.22	2.29	0.08	1	0.09	2.01	0.11	1	0.36	3.12	<b>0.02</b>	1	1.18	6.02	<b>0.001</b>
Exposure	1	0.02	0.45	<b>0.03</b>	1	0.25	5.2	<b>0.002</b>	1	0.25	2.19	0.06	1	1.02	5.23	<b>0.002</b>
Depth:Exposure	1	0.02	0.37	0.8	1	0.11	2.24	0.07	1	0.26	2.27	0.06	1	0.38	1.93	0.08
<b><i>Size classes</i></b>																
Depth	1	0.14	2.53	0.52	1	0.16	3.09	0.06	1	0.37	3.23	<b>0.01</b>	1	1.08	5.35	<b>0.01</b>
Exposure	1	0.32	6.01	<b>0.001</b>	1	0.27	5.23	<b>0.003</b>	1	0.25	2.12	0.07	1	1.11	5.48	<b>0.01</b>
Depth:Exposure	1	0.08	1.54	0.19	1	0.07	1.45	0.22	1	0.46	3.92	<b>0.01</b>	1	0.31	1.52	0.16
<b><i>Geographic distribution classes</i></b>																
Depth	1	0.1	2.17	0.1	1	0.11	2.45	0.08	1	0.51	4.48	<b>0.03</b>	1	1.3	7.41	<b>0.01</b>
Exposure	1	0.32	6.76	<b>0.02</b>	1	0.24	5.15	<b>0.003</b>	1	0.19	0.16	0.16	1	0.99	5.64	<b>0.01</b>
Depth:Exposure	1	0.01	0.33	0.79	1	0.01	0.31	0.81	1	0.24	2.11	0.1	1	0.33	1.89	0.11

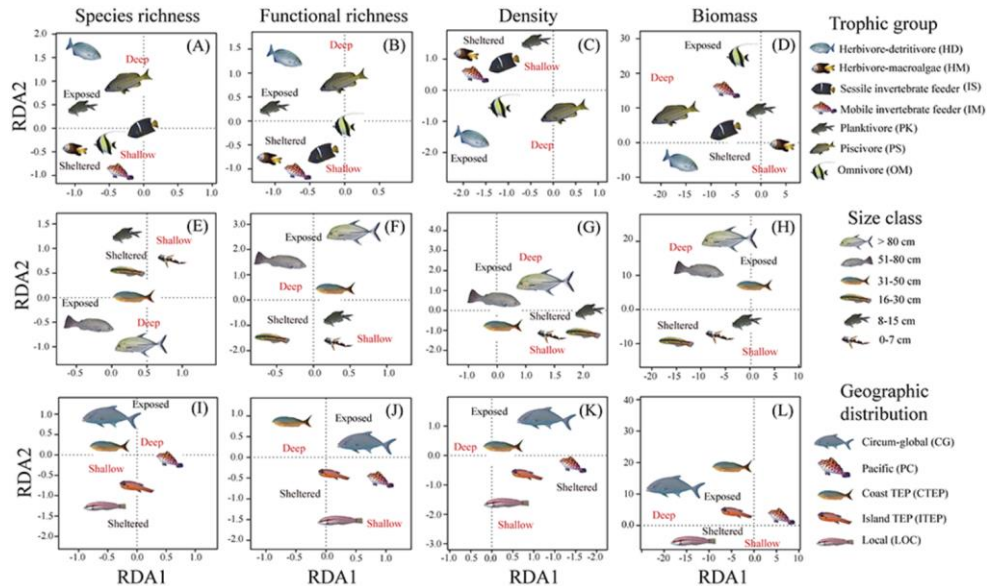


Figure 1-4: Redundancy analysis biplots representing the influence of environmental factors wave exposure (Exposed and Sheltered: Black labels) and depth classes (Shallow and Deep: Red labels) on the species richness (A, E, I), functional richness (B, F, J), density (C, G, K) and biomass (D, H, L) for each trophic group, size class and geographic distribution class. Each fish figure represents the most common species observed in each level.

The Malpelo fish checklist represented 35% of the reef-associated species in the TEP, and the species recorded during our UVCs represented 15% of those TEP species (Fig. 1-5A). The proportion of functional entities (FE.s) present in the TEP was respectively 60% for the Malpelo checklist (121 FE.s) and 30% for the UVCs (62 FE.s; Fig. 1-5A). The high number of FE.s found in the species checklist of Malpelo occupied a large proportion of the functional volume calculated for the TEP region, while the functional volume calculated for UVCs occupied the central part of the total TEP volume (Fig. 1-5B). The most common species trait combination reported in the checklist of Malpelo was: sedentary species, diurnal, solitary, bottom-dweller, 8-15 cm and mobile invertebrate feeder, such as *Cirrhitichthys oxycephalus*, whereas for the UVCs the most frequent trait combination was: mobile species, diurnal, solitary, bottom-dweller, size class 51-80 cm and mobile invertebrate feeder, such as *Bodianus diplotaenia*. The proportion of FE.s with at least two species changed with scale: 60% of FE.s from the regional pool, 22% from the local checklist and only 10% from the species observed in the UVCs (Fig. 1-6A). Finally, we observed that the fish assemblage registered in local checklist and observed in UVCs at Malpelo was disproportionally represented by vulnerable FE.s (Null model p-value < 0.01; Fig. 1-6B).

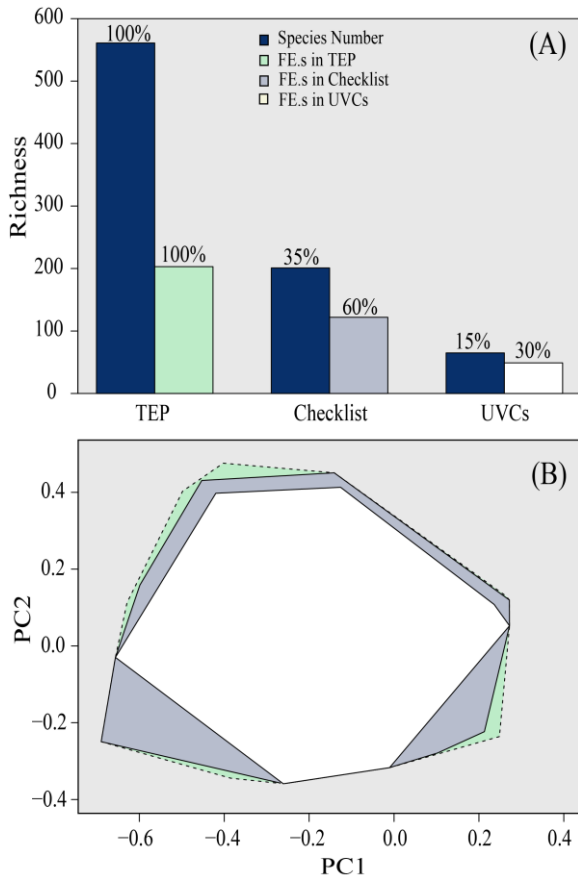


Figure 1-5: Comparison of the functional richness of Malpelo Island in relation to the regional species pool and the local pool (Checklist and UVCs). A) Number of species (dark blue bars) and number of functional entities (FE.s) found in the regional pool (light green bar), in the Malpelo checklist (gray bar), and in the UVCs (white bar). B) Representation of the first and second, component axes of the functional volume across the three levels with the corresponding convex hull. Dashed lines in light green represent the FE.s occurring in the entire TEP, gray color represents FE.s observed in Malpelo checklists and white represents FE.s observed during the UVCs.

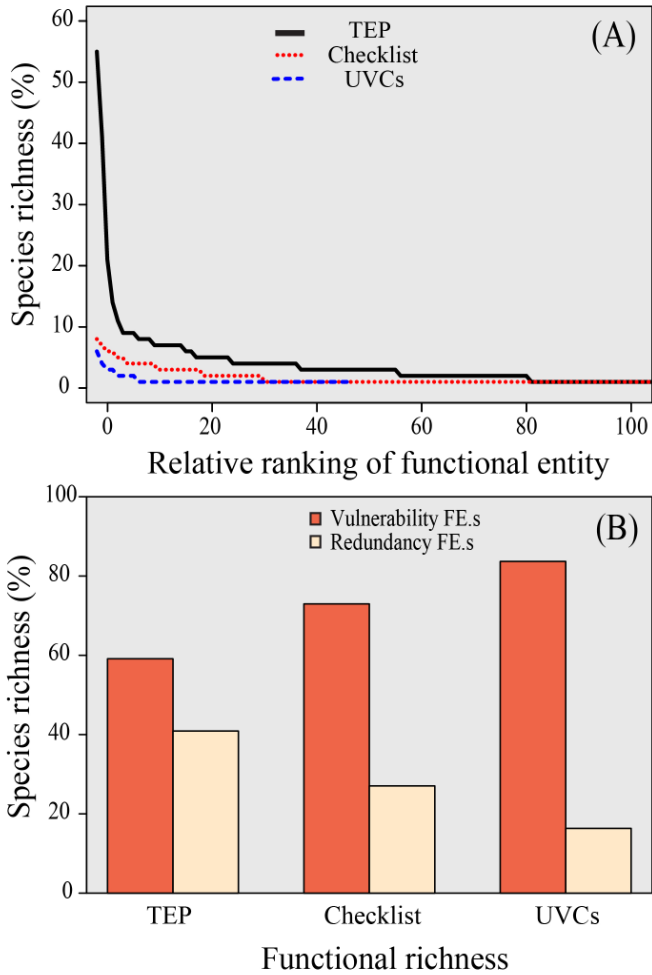


Figure 1-6: Species richness related to the number of functional entities in different scales. A) Perceptual species richness related to relative ranking of functional entities (FE.s), representing across the TEP region (black solid line), Malpelo checklists (red line), and UVCs (dashed blue line). B) Proportion of vulnerable FE.s for each scale: regional species pool, Malpelo checklist and UVCs.

## **Discussion**

The composition of reef fish assemblages at Malpelo was different between the two years sampled (48 species in common: 55.2%), which can be associated with changes in oceanographic features, such as upwelling (Luiz et al. 2015; Gove et al. 2016). This factor probably increased primary production thus favoring planktivores (McClanahan and Branch 2008), which presented a high density and the highest richness in 2015. These differences could also be associated with natural variations in species abundance (McGill et al. 2007; Locey and White 2013), which may have affected the detectability of species during the UVCs (i.e., the common and abundant species being the most observed during surveys). However, our findings showed that such turnover was among different trophic groups, which could suggest a change in the trophic structure of the assemblage over time. The number of species detected during our UVCs (87 species in two years) is lower than for nearby oceanic islands, such as Galapagos (171 species of reef fish excluding elasmobranchs; Edgar et al. 2004) and Cocos Island (102 species of reef fish excluding elasmobranchs; Friedlander et al. 2012). These differences are likely to be associated with the local species pool, which is smaller in Malpelo (202 species) compared to these islands (Galapagos: 291 species and Cocos: 236 species; Robertson and Allen 2016), as well as differences in sampling protocols (i.e. our transects were smaller and less numerous than those in other studies). The dominance of a small number of species in density and biomass during the two sampling years is consistent with general patterns observed for diversified assemblages, where abundance or biomass are dominated by a restricted number of species, most other species being uncommon to rare (Gaston et al. 1997; Hubbell 2001; Mouillot et al. 2013).

Our results showed a variation in species richness, density and biomass across four sampling sites in 2015, which could be associated with particular features at each site. For instance, “El Arrecife” and “La Nevera” are unique sites in Malpelo with sheltered areas that allow the development of high coral cover and great structural complexity (Zapata



and Vargas-Ángel 2003; Chasqui and Zapata 2007). Such features tend to favor small species (e.g. *A. atradorsatus*, *C. oxycephalus* and *T. lucasanum*) that can more easily find shelter and food within coral branches. The two other sites, “El Bajo de Junior” and “Pared del Náufrago”, are mainly rocky reefs with low structural complexity, formed by large boulders and vertical walls, with comparatively low coral cover (*personal observations*). These types of reefs tend to favor the presence of medium and large-bodied species, usually in high densities. On the other hand, the lack of difference in the functional richness observed among sites reflects the functional homogenization despite taxonomic differences and the lack of influence from environmental factors on the functional structure of fish assemblages at such a small spatial scale. Moreover, it can be related to the wide home range of a number of species which travel around the island, mainly schooling and large species in search of food, cleaning service or refuge (Quimbayo et al. 2014; 2016).

Despite the differences observed among sites, density and biomass were dominated by planktivores and piscivores respectively, which is consistent with other MPAs on oceanic islands. These places often support local upwellings, which may bring nutrients favorable to plankton and therefore favor plankton feeders (Gove et al. 2016). In addition, these islands are under little human influence, which allows the concentration of large species (Sandin et al. 2008; Aburto-Oropeza et al. 2011; Edgar et al. 2011; Longo et al. 2015). The low contribution of mobile invertebrate feeders to biomass could be related to the fact that all these species were mainly small and presented low densities in Malpelo. The low density and biomass values for species classified as herbivores-detritivores, macroalgae-feeders, sessile invertebrate feeders and omnivores could be associated both with the low number of these species within the TEP species pool as well as with local conditions (bottom dominance by calcareous algae) which may not favor the presence of these groups at Malpelo. A comparison of the biomass values found in Malpelo with those from other oceanic islands

considered as pristine (Fig. 1S-3), indicates that Malpelo even when excluding elasmobranchs, is remarkable for its high concentration of large species such as groupers, jacks, moray eels and snappers. The proportion of piscivores on Malpelo is comparable to what is found on other islands, which are considered as pristine such as Chagos and Cocos Island (Fig. 1S-3). On the other hand, Malpelo differs from these islands because of the low contribution of herbivores and the high contribution of plankton feeders to its total biomass.

The considerable contribution of regional endemics (CTEP) to density and biomass could be associated with the high level of endemism observed in the TEP (Zapata and Robertson 2007; Robertson and Cramer 2009; Kulbicki et al. 2013). Species belonging to the CTEP group are rather large. Large species tend to be found in higher proportions on small isolated islands (Kulbicki et al. 2015), which may in part explain the contribution of CTEP species to density or biomass on Malpelo. On the other hand, the high contribution to density of species endemic to TEP islands (ITEP) could be related to the importance of endemics in systems such as the Hawaiian islands (DeMartini and Friedlander 2004), Easter Island (Friedlander et al. 2013), and Kermadec (Cole et al. 1992). The low density values observed for endemic species in Malpelo (four species: LOC) are opposite to those patterns observed for the ITEP species. The reasons for this difference are unknown, but a comparative analysis of their phylogeny may reveal major differences in their evolutionary history. In Malpelo, the density of the LOC endemic species reported here is 0.034 ind/m<sup>2</sup>. However, when performing censuses focused on these LOC endemic species, Chasqui et al. (2011) registered an average of 0.27 ind/m<sup>2</sup>, almost eight times higher than ours. These differences are likely to be associated with the type of census used by Chasqui et al (2011), which focused exclusively on these endemic species and was adapted for the analysis of populations of small-bodied species. The contribution in density of transpacific species in the fish assemblages of Malpelo (9.3%), supports the findings of Robertson and Cramer (2009), who

highlighted that these species form a sizeable part of the total reef fish assemblages in TEP oceanic islands. The presence and importance of species with circumglobal distribution in biomass reflects the specific traits of these species, such as large body size, unspecialized diet, high reproductive capacity and long pelagic larval duration (Luiz et al. 2012), which favor their dispersal and colonization of isolated areas.

Wave exposure and depth played an important role in the fish distribution at Malpelo. Shallow sheltered areas presented high species richness, functional richness and abundance, whereas exposed and deep sites were dominated by large-bodied species. These results support those found by Dominici-Arosemena and Wolff (2006), who observed a decrease in abundance of planktivorous species such as *Chromis atrilobata*, territorial herbivores such as *Stegastes arcifrons* and small species as depth increases. According to them, such a relationship would be due to a decrease in both food (plankton, algae) and refuge. Similar patterns have been observed in other oceanic islands of the Pacific (Friedlander and Parrish 1998; Friedlander et al. 2016) and Atlantic Oceans (Pineiro et al. 2011; Luiz et al. 2015). The increase in biomass in exposed or deep places is related to space requirements of large species, which use mostly areas of high spatial relief with strong hydrodynamics (Friedlander and Parrish 1998; Schultz et al. 2014).

The large number of FE.s found in both species checklist and UVCs are evidence of a high functional richness, despite the fact that only 35% and 15% of the regional species pool were recorded in the local checklist and the UVCs, respectively. These results suggest that the relatively high functional richness observed at Malpelo is not related to taxonomic richness, but to the high endemism of the TEP (Mora and Robertson 2005a). These results also support the idea that functional richness is different from taxonomic richness regarding the theory of island biogeography (which considers the effects of area and isolation), since, despite its small area and long distance from the coast, Malpelo harbors a high proportion of the regional FE.s. This result supports the

findings of Bender et al. (2016) who observed that isolated places possess a subset of functional richness of the regional functional pool, which is independent of taxonomic richness. The high overlap found among the functional spaces of the TEP, the local species checklist and UVCs, is related to similar overlaps found at a much wider scale by Mouillot et al. (2014) who compared the functional volume across realms for reef fish assemblages. This suggests a high conservatism of ecological functions across scales and calls attention to the vulnerability of the fish assemblages of Malpelo as they have a high proportion of vulnerable FE.s. When a species that constitutes a vulnerable FE.s disappears or becomes so rare that it no longer fulfills its ecological role, there is a loss in function that may have larger consequences than the same fate for a species belonging to a redundant FE.s as the latter may be replaced by another species within its FE.s.

Finally, our study presents for the first time an assessment of the density, biomass, taxonomic and functional structure of fish assemblages at Malpelo Island a World Heritage site. The high biomass values composed mainly by piscivorous species endemic to the TEP, as well as a high functional vulnerability, suggests that this island is still in a very pristine state and represents a baseline for untouched assemblages in this marine province, as well as a priority area for conservation. Additionally, our study provides new information about the density and biomass of local and regional endemic species, which confirms that regional endemics may constitute a large share in isolated systems of the TEP region.

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## Supplementary Material

Table 1S- 1. Density and biomass estimates of fish species recorded during underwater visual census (103 transects) in two different years (2010 and 2015). Species are ranked in decreasing order according to densities observed during the 2010 survey. Trophic group: herbivores-detritivorous (HD), macroalgal-feeder (HM), sessile invertebrate feeders (IS), mobile invertebrate feeders (IM), planktivores (PK), piscivorous (PS) and omnivores (OM). Geographic distribution: Circum-global (CG), Pacific (PC), coastal of Tropical Eastern Pacific (CTEP), only in oceanic island in Tropical Eastern Pacific (ITEP) and local endemic (LOC).

Species	Density 2010 (individuals per m <sup>2</sup> ) ± s.e.	Density 2015 (individuals per m <sup>2</sup> ) ± s.e.	Biomass 2010 (grams per m <sup>2</sup> ) ± s.e.	Biomass 2015 (grams per m <sup>2</sup> ) ± s.e.	Trophic Group	Geographic Distribution
<i>Chromis atrilobata</i>	3.32 ± 0.491	1.022 ± 0.321	78.05 ± 12.347	12.35 ± 1.561	PK	CTEP
<i>Apogon atradorsatus</i>	1.147 ± 0.122	2.65 ± 0.326	5.4 ± 0.643	0.64 ± 1.208	PK	ITEP
<i>Cirrhitichthys oxycephalus</i>	0.985 ± 0.08	0.963 ± 0.181	15.22 ± 1.632	1.63 ± 0.993	IM	PC
<i>Paranthias colonus</i>	0.881 ± 0.158	2.495 ± 0.267	39.59 ± 6.271	6.27 ± 16.16	PK	CTEP
<i>Stegastes arcifrons</i>	0.523 ± 0.059	0.156 ± 0.026	37.89 ± 4.441	4.44 ± 0.585	HD	ITEP
<i>Lutjanus viridis</i>	0.483 ± 0.093	0.433 ± 0.107	36.48 ± 6.675	6.68 ± 39.169	FC	CTEP
<i>Thalassoma lucasanum</i>	0.45 ± 0.059	0.685 ± 0.182	7.54 ± 1.224	1.22 ± 0.716	IM	CTEP
<i>Bodianus diplotaenia</i>	0.222 ± 0.036	0.107 ± 0.025	31.38 ± 5.04	5.04 ± 3.498	IM	CTEP
<i>Holacanthus passer</i>	0.168 ± 0.022	0.076 ± 0.015	35.59 ± 6.03	6.03 ± 6.096	IS	CTEP
<i>Myripristis leiognathus</i>	0.144 ± 0.042	0.003 ± 0.002	10.6 ± 3.042	3.04 ± 0.043	PK	CTEP

<i>Ophioblennius steindachneri</i>	0.127 ± 0.024	0.028 ± 0.006	4.11 ± 0.786	0.79 ± 0.104	HD	CTEP
<i>Johnrandallia nigrirostris</i>	0.116 ± 0.024	0.142 ± 0.035	15.87 ± 3.716	3.72 ± 2.029	IM	CTEP
<i>Halichoeres malpelo</i>	0.055 ± 0.013	0.011 ± 0.004	2.92 ± 0.685	0.69 ± 0.088	IM	LOC
<i>Mulloidichthys dentatus</i>	0.055 ± 0.014	0.111 ± 0.043	4.77 ± 1.353	1.35 ± 25.893	IM	CTEP
<i>Stegastes beebei</i>	0.05 ± 0.013	0.055 ± 0.014	3.71 ± 0.969	0.97 ± 0.18	HD	ITEP
<i>Stegastes acapulcoensis</i>	0.037 ± 0.024	0.004 ± 0.002	2.23 ± 1.49	1.49 ± 0.05	HD	CTEP
<i>Lutjanus jordani</i>	0.035 ± 0.035	0.271 ± 0.099	9.65 ± 9.653	9.65 ± 60.203	FC	CTEP
<i>Gymnothorax dovii</i>	0.034 ± 0.005	0.028 ± 0.004	99.81 ± 18.93	18.93 ± 5.63	FC	CTEP
<i>Sphyraena idiaestes*</i>	0.03 ± 0.03		14.41 ± 14.406		FC	PC
<i>Sufflamen verres</i>	0.03 ± 0.004	0.021 ± 0.004	5.44 ± 1.067	1.07 ± 0.993	IM	CTEP
<i>Halichoeres melanotis*</i>	0.028 ± 0.011		1.33 ± 0.553		IM	CTEP
<i>Halichoeres discolor</i>	0.026 ± 0.008	0.004 ± 0.002	1.33 ± 0.393	0.39 ± 0.05	IM	CTEP
<i>Dermatolepis dermatolepis</i>	0.024 ± 0.006	0.08 ± 0.023	9.45 ± 3.103	3.1 ± 16.673	FC	CTEP
<i>Plagiotremus azaleus</i>	0.022 ± 0.007	0.055 ± 0.032	0.57 ± 0.173	0.17 ± 0.142	IM	CTEP
<i>Epinephelus labriformis</i>	0.016 ± 0.003	0.02 ± 0.004	7.66 ± 1.647	1.65 ± 2.697	FC	CTEP
<i>Lepidonectes bimaculatus</i>	0.016 ± 0.004	0.008 ± 0.003	0.02 ± 0.004	0.004 ± 0.002	IM	LOC
<i>Arothron meleagris</i>	0.014 ± 0.002	0.012 ± 0.003	5.7 ± 1.154	1.15 ± 0.912	IM	PC
<i>Mycteroperca olfax</i>	0.014 ± 0.003	0.011 ± 0.002	9.32 ± 2.492	2.49 ± 3.473	IM	ITEP
<i>Lutjanus inermis</i>	0.013 ± 0.013	0.146 ± 0.074	0.51 ± 0.51	0.51 ± 29.546	PK	CTEP

<i>Serranus tico</i>	0.008 ± 0.003	0.004 ± 0.002	0.59 ± 0.231	0.23 ± 0.021	FC	ITEP
<i>Opistognathus panamaensis</i>	0.008 ± 0.003	0.005 ± 0.005	0.23 ± 0.088	0.09 ± 0.022	PK	CTEP
<i>Caranx melampygus</i>	0.007 ± 0.002	0.009 ± 0.007	7.26 ± 2.627	2.63 ± 8.661	FC	PC
<i>Haemulon maculicauda*</i>	0.007 ± 0.007		0.32 ± 0.324		IM	CTEP
<i>Cirrhitus rivulatus</i>	0.007 ± 0.002	0.013 ± 0.004	11.41 ± 4.599	4.6 ± 3.765	IM	CTEP
<i>Seriola rivoliana</i>	0.007 ± 0.003	0.016 ± 0.005	38.57 ± 20.05	20.05 ± 36.062	FC	CG
<i>Labrisomus dendriticus</i>	0.006 ± 0.002	0.017 ± 0.004	0.3 ± 0.105	0.11 ± 0.063	IM	ITEP
<i>Axoclinus rubinoffi</i>	0.006 ± 0.003	0.014 ± 0.004	0.01 ± 0.003	0.003 ± 0.001	IM	LOC
<i>Acanthurus xanthopterus</i>	0.006 ± 0.006	0.005 ± 0.002	4.46 ± 4.464	4.46 ± 3.092	HD	PC
<i>Elagatis bipinnulata</i>	0.006 ± 0.002	0.002 ± 0.002	5.63 ± 3.34	3.34 ± 1.712	FC	PC
<i>Heteroconger klausewitzii*</i>	0.004 ± 0.004		2.29 ± 2.291		PK	ITEP
<i>Malacanthus brevisrostris*</i>	0.004 ± 0.003		0.25 ± 0.124		IM	PC
<i>Odontoscion xanthops*</i>	0.004 ± 0.002		0.52 ± 0.341		PK	CTEP
<i>Aulostomus chinensis</i>	0.003 ± 0.002	0.006 ± 0.002	0.97 ± 0.687	0.69 ± 0.719	FC	PC
<i>Cantherhines dumerilii</i>	0.003 ± 0.001	0.001 ± 0.001	1.43 ± 0.642	0.64 ± 0.594	IM	PC
<i>Rypticus bicolor*</i>	0.003 ± 0.001		0.35 ± 0.209		FC	CTEP
<i>Diodon holocanthus*</i>	0.002 ± 0.001		0.94 ± 0.496		IM	CG
<i>Diodon hystrix</i>	0.002 ± 0.001	0.0001 ± 0.001	3.43 ± 1.876	1.88 ± 1.852	IM	CG
<i>Fistularia commersonii</i>	0.002 ± 0.001	0.003 ± 0.001	0.7 ± 0.345	0.35 ± 0.846	FC	PC

<i>Melichthys niger</i>	0.002 ± 0.001	0.002 ± 0.001	0.83 ± 0.632	0.63 ± 0.402	PK	CG
<i>Heteropriacanthus cruentatus</i> *	0.002 ± 0.001		0.41 ± 0.294		IM	CG
<i>Lutjanus novemfasciatus</i> *	0.002 ± 0.001		2.03 ± 1.476		FC	CTEP
<i>Scorpaena mystes</i>	0.002 ± 0.001	0.001 ± 0.001	0.25 ± 0.184	0.18 ± 0.622	FC	CTEP
<i>Thalassoma grammaticum</i> *	0.002 ± 0.002		0.05 ± 0.046		IM	CTEP
<i>Canthigaster punctatissima</i>	0.001 ± 0.001	0.017 ± 0.008	0.03 ± 0.02	0.02 ± 0.001	IM	CTEP
<i>Kyphosus vaigiensis</i> *	0.001 ± 0.001		0.03 ± 0.032		HM	ATL
<i>Lutjanus argentiventris</i>	0.001 ± 0.001	0.013 ± 0.008	0.49 ± 0.371	0.37 ± 5.678	IM	CTEP
<i>Novaculichthys taeniourus</i> *	0.001 ± 0.001		0.23 ± 0.194		IM	PC
<i>Prionurus laticlavus</i>	0.001 ± 0.001	0.008 ± 0.003	0.62 ± 0.483	0.48 ± 1.531	HD	CTEP
<i>Serranus psittacinus</i> *	0.001 ± 0.001		0.09 ± 0.063		FC	CTEP
<i>Strongylura scapularis</i> *	0.001 ± 0.001		0 ± 0.003		FC	CTEP
<i>Zanclus cornutus</i>	0.001 ± 0.001	0.002 ± 0.001	0.42 ± 0.358	0.36 ± 0.965	OM	PC
<i>Arothron hispidus</i>	0.001 ± 0.001	0.001 ± 0.001	0.23 ± 0.226	0.23 ± 0.575	IM	PC
<i>Bothus mancus</i> *	0.001 ± 0.001		0.41 ± 0.413		FC	PC
<i>Cephalopholis panamensis</i> *	0.001 ± 0.001		0.39 ± 0.385		FC	CTEP
<i>Gymnomuraena zebra</i>	0.001 ± 0.001	0.001 ± 0.001	0.3 ± 0.303	0.3 ± 0.289	FC	PC
<i>Gymnothorax castaneus</i> *	0.001 ± 0.001		1.72 ± 1.717		FC	CTEP
<i>Halichoeres nicholsi</i> *	0.001 ± 0.001		0.03 ± 0.026		IM	CTEP

<i>Melichthys vidua</i> *	0.001 ± 0.001		0.27 ± 0.27	PK	PC
<i>Muraena lentiginosa</i> *	0.001 ± 0.001		0.04 ± 0.041	FC	CTEP
<i>Oxycirrhites typus</i> *	0.001 ± 0.001		0.03 ± 0.032	IM	PC
<i>Abudefduf troschelii</i>	0.001 ± 0.001		0.008 ± 0.008	PK	CTEP
<i>Acanthemblemaria stephensi</i>	0.001 ± 0.001		0.0004 ± 0.0002	PK	LOC
<i>Alectis ciliaris</i>	0.001 ± 0.001		0.77 ± 0.573	FC	CG
<i>Aluterus scriptus</i>	0.0004 ± 0.0004		0.38 ± 0.387	PK	CG
<i>Balistes polylepis</i>	0.0004 ± 0.0004		0.82 ± 0.827	IM	CTEP
<i>Canthidermis maculata</i>	0.009 ± 0.006		12.35 ± 8.262	PK	CG
<i>Canthigaster janthinoptera</i>	0.0004 ± 0.0004		0.001 ± 0.002	OM	PC
<i>Caranx sexfasciatus</i>	0.001 ± 0.001		1.10 ± 1.101	IM	PC
<i>Halichoeres chierchiae</i>	0.001 ± 0.001		0.02 ± 0.018	IM	CTEP
<i>Hoplopagrus guentherii</i>	0.0004 ± 0.0004		0.32 ± 0.321	IM	CTEP
<i>Kyphosus ocyurus</i>	0.0004 ± 0.0004		0.0001 ± 0.0001	HD	PC
<i>Microspathodon dorsalis</i>	0.001 ± 0.001		0.1 ± 0.094	IM	CTEP
<i>Myripristis berndti</i>	0.001 ± 0.001		0.25 ± 0.176	PK	PC
<i>Ostracion meleagris</i>	0.001 ± 0.001		0.15 ± 0.123	IM	PC
<i>Pseudobalistes naufragium</i>	0.0004 ± 0.0004		1.67 ± 1.674	IM	CTEP
<i>Trachinotus stilbe</i>	0.002 ± 0.002		0.0001 ± 0.0001	FC	CTEP
<b>Mean total</b>	<b>9.30±0.68</b>	<b>9.77±0.7</b>	<b>706.2±73.2</b>	<b>879±116.2</b>	

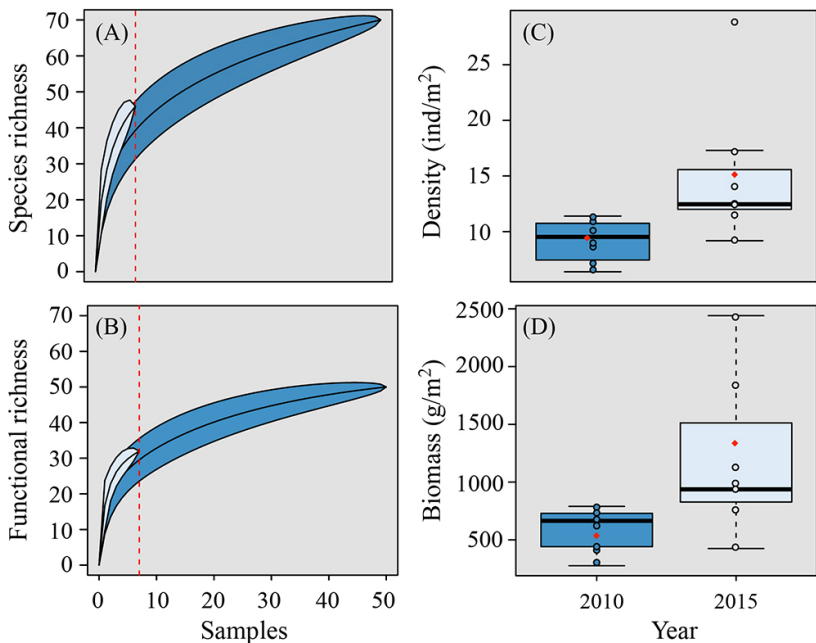


Figure 1S- 1. Comparison between the two sampling years 2010 and 2015. A) Species richness, B) functional richness, C) density and D) biomass. Each color represents a different year (dark blue for 2010 and light blue for 2015). Boxplots show medians (black line), mean (red diamond), upper and lower quartiles, and 95% confidence intervals. Red lines in A and B, represent the standardized number of surveys. Each point represents an underwater visual census.



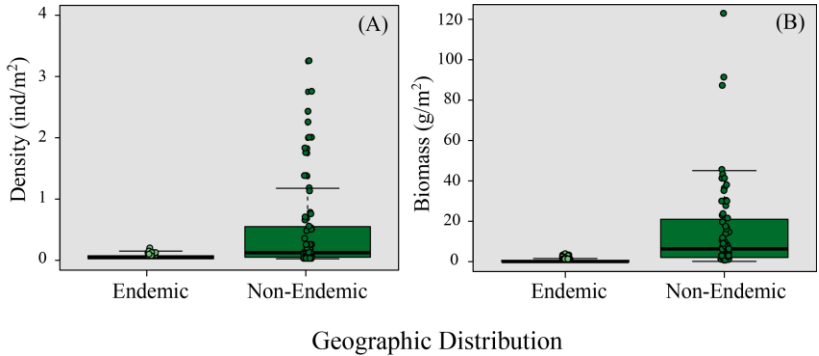


Figure 1S- 2. Comparison of the density (A) and biomass (B) between endemic species and non-endemic species. Only families that have endemic species were considered for this comparison. Boxplots show medians (black line), upper and lower quartiles, and 95% confidence intervals. Each point represents an UVC.

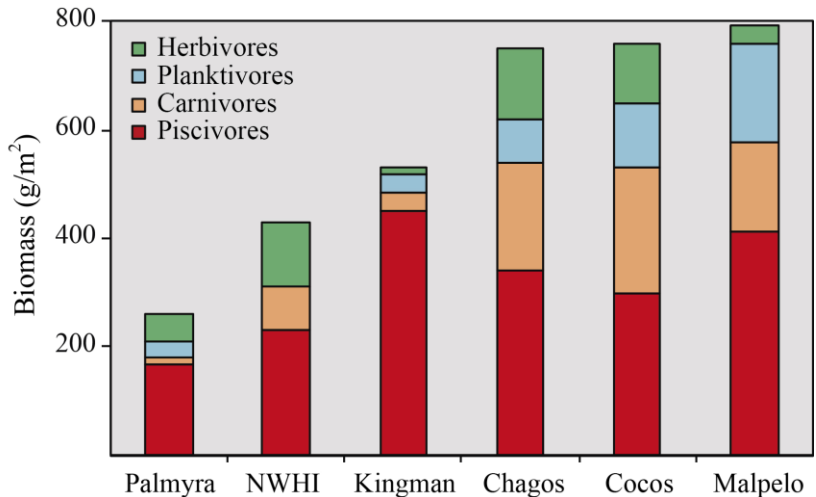


Figure 1S- 3. Comparison of the biomass from Malpelo Island with others oceanic islands considered as pristine. Each color represents a different trophic group of fish assemblage.

## CAPÍTULO 2

### **Determinants of Fish Assemblages in Tropical Oceanic Islands**

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## **Determinants of Fish Assemblages in Tropical Oceanic Islands**

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## **Abstract**

**Aim:** To test the relative influence of biogeographic, energetic, and anthropogenic factors on species richness (SR), functional dispersion (FD), density of individuals (DE), and biomass (BS) of fish assemblages at 18 oceanic islands.

**Location:** Eastern Pacific and Atlantic Ocean.

**Methods:** We estimated SR, FD, DE and BS of fish assemblages from 1527 underwater visual censuses performed at 88 sites. We used linear models to estimate the effects of biogeographic (island area, distance to the nearest reef and local fish species pool), energetic (sea surface temperature and primary productivity), and anthropogenic (protection level, distance from the mainland and resident human density) factors on SR, FD, DE, and BS.

**Results:** Fish DE was highest near the equator, and BS was highest in islands from the Eastern Pacific, which are influenced by strong upwelling regimes. SR and FD were similar across islands. In the TEP, small to medium-sized mobile invertebrate feeders and planktivores yielded the highest DE, whereas piscivores of medium body size contributed the most to BS. In the Atlantic, DE was concentrated in small and medium sized planktivorous species, while BM was dominated by both omnivores and planktivores. SR was positively related to area, primary productivity, distance from mainland, and protection level. FD was dependent on distance from nearest reef and mainland and protection level. DE and BS were positively related to local distance from nearest reef, local species pool, and primary productivity.

**Main conclusions:** Biogeographic, energetic and anthropogenic factors are important drivers of fish assemblages in tropical oceanic islands. Oceanic islands with high primary productivity, relative isolation, and strong protection tend to yield high SR, FD and a considerable concentration of BM of reef fishes. The relative effects of these drivers varied between provinces, highlighting the importance of the interactions between large-scale and local factors on structuring fish assemblages.

## Introduction

Efforts to understand the mechanisms responsible for variation in biodiversity over broad spatial scales have produced general hypotheses related to habitat size, differential speciation and extinction rates, physiological and energetic constraints, as well as dispersal (Brown *et al.*, 2004; Mittelbach *et al.*, 2007; Mittelbach & Schemske, 2015). Although the mechanisms are not well understood, striking patterns materialize at large scales whereby environmental and geographical clines predict the number and density of species in a given area. For instance, in the marine realm, tropical reef fish present the highest species richness in areas with high coral area available (Parravicini *et al.*, 2013), whereas their population densities are determined mainly by species richness and available energy (Barneche *et al.*, 2016).

As a relatively new predictive factor, anthropogenic impacts have gained considerable importance in the last 50 years due to high extinctions rates. In particular, sharks and other large top predators have been driven to locally extinct in places by fishing pressure (Luiz & Edwards, 2011), yielding a negative effect of human population density on biodiversity and ecosystem functioning (Mora *et al.*, 2011). Understanding the mechanisms that control spatial variation in species diversity may help improve predictions of how biodiversity will respond to environmental change and other human impacts, and to design and implement effective conservation strategies (Mellin *et al.*, 2016). Given the breadth of factors known to affect biodiversity, a modern approach is to compare the relative predictive power of multiple competing theories.

Biological diversity cannot be described by a single parameter; rather multiple dimensions of diversity must be assessed and tested against the proposed predictors to evaluate the robustness of macroecological and biogeographical theories (e.g. Whittaker *et al.*, 2008). However, theories usually focus on a single biodiversity metric, usually species richness or

density of individuals, and avoid the use of multiple parameters, such as biomass, rates of endemism, or parameters linked to ecological function and phylogenetic diversity (Kulbicki *et al.*, 2013; Mouillot *et al.*, 2014; Floeter *et al.*, 2017). Field observation of reef fishes allows the collection of a wide range of such parameters. Here, we rely on an extensive data set based on underwater visual censuses of reef fish assemblages from isolated islands at the large scale to quantify the relative strength of major macroecological and evolutionary predictions, and understand some possible mechanisms driving the variation in fish species richness, functional dispersion, density of individuals and biomass.

Oceanic islands are those that have never been connected to the mainland and encompass a wide range of topography, size, age, available area, nutrients, and levels of isolation, yielding a variety of unique habitats (MacArthur & Wilson, 1967). Combining these factors allows robust comparison of how varied selection pressures result in complex evolutionary trajectories of species assemblages (Brown, 2014). Due to differential colonization, speciation, and extinction rates, oceanic islands are excellent candidates for ecological and evolutionary studies (Warren *et al.*, 2015). However, most studies to date involved terrestrial organisms, whereas the marine realm remains poorly studied. This has been due in part to logistical difficulties imposed by remote locations and the fact that the underwater environment is subjected to additional research constraints compared to terrestrial ecosystems (Dawson, 2015).

Historically, island faunas have been disproportionately affected by habitat destruction, fragmentation, overfishing and the introduction of invasive species (Triantis *et al.*, 2010). Despite this vulnerability, isolated islands can still harbor the last pristine marine habitats, therefore offering unique opportunities to observe habitats with little or no history of anthropogenic disturbance (Sandin *et al.*, 2008). It is therefore crucial to study marine organisms in these natural laboratories

and continue testing current and new theories with integrative approaches that include marine organisms. In particular, it is relevant to contrast the predictions of the macroecological and biogeographic theory, which reflect historical processes, with current trends in the distribution and effects of human impacts on island faunas.

Tropical reef fishes are the most diverse marine vertebrate group with over 6,000 species worldwide (Kulbicki *et al.*, 2013). Their distributions vary widely (Parravicini *et al.*, 2013), and they are usually characterized by high functional diversity (Mouillot *et al.*, 2014) and high economic importance for human populations (Mora *et al.*, 2011). However, little is known about how reef fish assemblages are organized around oceanic islands, or how biogeographic, energetic, and anthropogenic factors may structure these assemblages. During the last decade, several studies have shown that both predatory and herbivorous fish species are present in high densities and biomass at remote islands from the Indo-Pacific (Sandin *et al.*, 2008), Central Pacific (Williams *et al.*, 2015), and Caribbean regions (Newman *et al.*, 2006). Only recently have the fish assemblages at islands of the Tropical Eastern Pacific and Tropical Atlantic been explored (e.g. Luiz *et al.*, 2015; Quimbayo *et al.*, 2017b). To date no attempt has been made at large-scale comparisons of fish assemblages on oceanic islands and the factors determining general spatial patterns of species richness, functional dispersion, density of individuals and biomass.

We examined the relative influence of a set of biogeographic, energetic, and anthropogenic factors on the structure of reef fish assemblages from highly isolated oceanic islands in five marine provinces (Tropical Eastern Pacific-North, Tropical Eastern Pacific-South, Southwestern Atlantic, Central Atlantic, and Tropical Eastern Atlantic). We expected that biogeographic factors would have the strongest influence on species richness and functional dispersion, and a lower effect on reef fish density and biomass. Second, all reef fish assemblage metrics (species



richness, functional dispersion, density, and biomass) should be maximized in locations with high energy availability (primary productivity) and thermal stability. Third, islands with little human influence or impact, high environmental protection level and isolation from the mainland should have higher density and biomass of fish, especially top predators and large-bodied species, whereas species richness and functional dispersion should show little variation in response to these anthropogenic factors.

## **Material and methods**

### ***Study region***

Our study comprised 18 tropical oceanic islands from two oceans (Pacific and Atlantic; Fig 2-1) located between latitude 38°N and 22°S, encompassing two marine biogeographic provinces in the Pacific and three in the Atlantic (Fig. 2-1). These provinces have been classified according to endemism, diversity and species composition (Robertson & Cramer, 2009; Kulbicki *et al.*, 2013). Most islands in our study are of volcanic origin with low reef development (Hachich *et al.*, 2015; Cortés *et al.*, 2017), the exception being Clipperton and Rocas, which have been formed by biogenic processes (e.g. Kikuchi & Leão, 1997; Cortés *et al.*, 2017). We considered only oceanic islands with independent isobaths (up to 50 m), and that were strong influence by upwelling gradients dividing reef fish faunas (specifically in the Galapagos islands the fauna are subdivided into central and southern subgroups; Witman *et al.*, 2010).

### ***Fish surveys***

We obtained data on fish assemblages from 1527 underwater visual censuses (UVCs), performed at 88 sites between 2006 and 2016 (Table 2S-1). The sampling consisted of visually identifying, counting and estimating the size (total length in cm) of all actinopterygian fish species

observed both in the water column and on the bottom using belt transects (Brooks, 1954). The area per transect varied among islands between 40 and 250 m<sup>2</sup> (see Data Analysis; Table 2S-1), whereas transects depth varied between 5 and 25 m (97% of UVCs, only 3% were in deeper depths). We estimated the weight of each individual fish using the allometric length-weight conversion  $W = a \times TL^b$ , where  $W$  is the fish weight (grams), parameters  $a$  and  $b$  are species-specific constants, and  $TL$  is the visually estimated total length in cm. Length-weight parameters were obtained for all species from FishBase (Froese & Pauly, 2016). In cases where species coefficients were not available, we used coefficients of congeneric species that were phylogenetically or morphologically similar. We calculated the length-weight relationship for *Melichthys niger*, since this species is very abundant in the Atlantic oceanic islands, and was not available in FishBase.

### ***Fish traits and assemblage functional index***

We classified all fish species according to six different life-history traits (Table 2S-2). These traits have been successfully used to describe functional aspects of reef fish assemblages and vulnerability (e.g. D'agata *et al.*, 2016; Bender *et al.*, 2017). We used the functional dispersion parameter “FD” as it quantifies the functional variation of reef fish assemblages by incorporating the relative abundance of species and qualitative and quantitative functional data types with a Gower’s distance dissimilarity matrix (Villéger *et al.*, 2008). Overall, FD quantifies the average distance of individual assemblages to the group weighted centroid in a multivariate functional trait space and is independent of species richness (Laliberte & Legendre, 2010).

### ***Response and factors***

We considered the influence of biogeographic factors on reef fish assemblages, including surface area of the shallow shelf area between 0

and 50 m depth (based upon Gridded Bathymetric Data GEBCO 30 arc-second grid; [http://www.gebco.net/data\\_and\\_products/gridded\\_bathymetry\\_data/gebco\\_30\\_second\\_grid/](http://www.gebco.net/data_and_products/gridded_bathymetry_data/gebco_30_second_grid/)), the regional and local species pool (Rpool and Lpool: Kulbicki *et al.*, 2013), and distances from the nearest reef (DReef: orthodromic distance between islands or reefs). Area serves as a proxy for habitat size and diversity, DReef represents isolation from nearby islands, and Lpool and Rpool describe the potential pool of species from the entire island and from the greater biogeographical provinces for each surveys.

For energetic factors hypothesized to predict species composition of fish assemblages, we compiled annual mean sea surface temperature (SST) and primary productivity (PP) estimated from mean surface chlorophyll *a* values, for each island. Both variables were estimated from satellite data averaged between 2002 and 2009 from BIO-oracle database at a resolution of 5 arcmin (Tyberghein *et al.*, 2012). Anthropogenic factors included human density (HumD: human population divided by the land surface area of the island), environmental protection status (Prot: as defined by the International Union for Conservation of Nature, IUCN red list), and distance from mainland (DistM: orthodromic distance between each island and the nearest continent). The IUCN red list environmental protection status consists of six categories: Strict natural reserve, Wilderness area, National Park, Natural Monument and natural feature, Habitat management area, and Species management area (World Database on Protected Areas, available at <http://www.protectedplanet.net>; see Table 3S-2 for further details).

### ***Data analysis***

As the number of UVCs and transect dimensions varied among oceanic islands (Table 2S-1), we produced a set of simulations to standardize the sampling effort for each island. First, we identified the island with the smallest sampled area in our dataset (Clipperton with 1250 m<sup>2</sup> surveyed; Table 2S-1), and then restricted the sampled area in all the other islands

to this limit, defined as the minimal sampled area (MSA). For each island, we then randomly sub-sampled UVCs from different locations until reaching the MSA. As multiple combinations of UVCs can compose the same MSA, we repeated this procedure 999 times to estimate mean values of species richness (SR), functional dispersion (FD), density (DE) and biomass (BS) in each island. FD was estimated using the function *dbFD* within the R package 'FD' (Laliberté *et al.*, 2015). At each simulation step, we modeled the four response variables against predictor variables using ordinary least square models. All selected predictors were scaled to mean zero and unity standard deviation so that all estimated parameters varied from -1 to +1 and were directly comparable as an effect size. We also ensured low multicollinearity from our models by excluding highly correlated variables ( $|r| > 0.70$ ; Fig. 2S-1). In order to quantify the relative importance of each predictor in each simulation step, we applied a hierarchical partitioning analysis using the function *hier.part* from the R package 'hier.part' (Walsh & Mac Nally, 2015). We used an additive partition based on canonical redundancy analysis and assuming linear relationships to evaluate the influence of each set of factors on metrics of fish assemblages. We retained parameter estimates from all analyses in each simulation step and then used their mean and standard deviation as a measure of their effect on each response variable. This procedure is analogous to sample-based rarefaction and enables comparison between the effect of each predictor on reef fish assemblage variables while controlling for differences in sample size (Gotelli & Colwell, 2001). We considered a predictive factor to have a significant effect if its 95% confidence interval did not overlap zero (i.e., if zero was not within the confidence interval then the effect was considered significant), which is similar to procedures adopted in null model analysis. We did not observe spatial autocorrelation in our analysis as measured by Moran's I index (Fig. 2S-2), calculated using the function *Moran.I* from the 'ape' package (Paradis *et al.*, 2004). All statistical analyses were performed in the R environment, version 3.2.4 (R Core Team, 2016).

## Results

Species richness displayed little differences among the five provinces (Fig. 2-1A). Galapagos-Central (TEPS) and St Paul's Rocks (SWA) yielded the highest and the lowest values of species richness, respectively (Table 2S-4). Functional dispersion varied among regions (Fig. 2-1B), the highest values were observed in the TEPN and TEPS and the lowest values in the TEA (Fig. 2-1B; Table 2S-4). In contrast, density of individuals varied widely among islands. The highest densities were recorded near the Equator (Malpelo, St Paul's Rocks, Rocas Atoll, Principe and São Tomé Fig. 2-1C), and the lowest densities were observed at high latitudes or on very isolated islands (e.g. Clipperton; Table 2S-4). The highest biomass values were observed in the TEPS (Fig. 2-1D; e.g., Galapagos-South: 1087 g/m<sup>2</sup>, Malpelo: 879 g/m<sup>2</sup>, Cocos: 850 g/m<sup>2</sup>). Fish biomass in the Atlantic Ocean was much lower than in the TEP (Fig. 1D), although some islands including St Paul's Rocks, Trindade, Martin Vaz, and Ascension had values of up to 480 g/m<sup>2</sup> (Table 2S-4). Trophic and size structure showed little variation relative to species richness, but varied widely amongst islands relative to density of individuals and biomass (Fig. 2S-3).

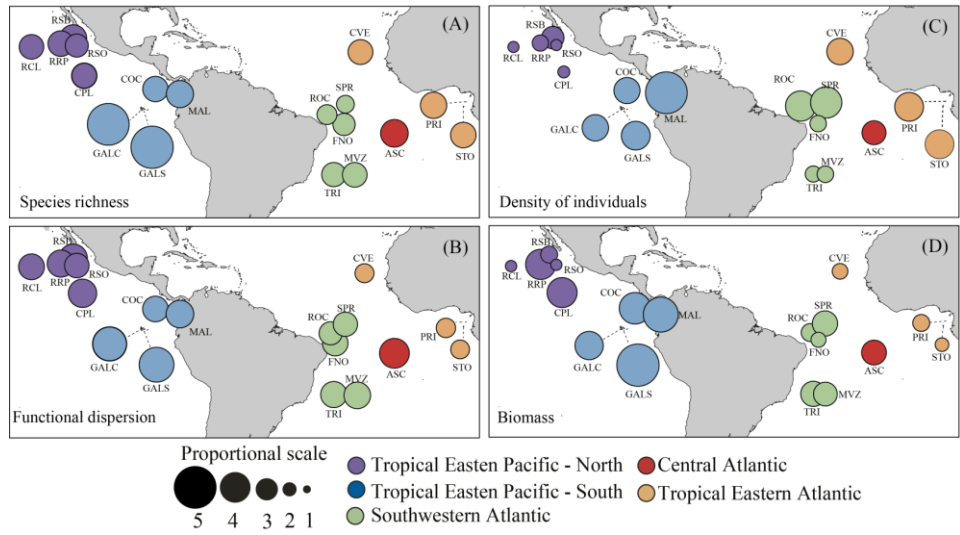


Figure 2- 1. Variation of assemblage metrics of reef fish at oceanic islands. (A) Species richness; (B) Functional dispersion; (C) Density of individuals; (D) Biomass. Each color represent a marine province. All circles are proportional. Oceanic islands: Revillagigedos-Clarion “RCL”, Revillagigedos-Roca Partida “RRP”, Revillagigedos-San benedicto “RSB”, Revillagigedos-Socorro “RSO”, Clipperton “CPL”, Cocos “COC”, Malpelo “MAL”, Galápagos-Central “GALC”, Galápagos-South “GALS”, St Paul’s Rocks “SPR”, Rocas Atoll “ROC”, Fernando de Noronha “FNO”, Trindade “TRI”, Martin Vaz “MVZ”, Ascension “ASC”, Cape Verde “CVE”, Principe “PRI”, São Tomé “STO”.

Our results indicated that each assemblage metric was influenced by a different set of biogeographic, energetic, and anthropogenic factors (Fig. 2-2; Fig. 2S-4). For instance, species richness was positively influenced by available area (Area), primary productivity (PP), distance from the mainland (DistM), and protection level (Prot; Fig. 2-2A), with 47% of variation explained by energetic factors, specifically by PP (Fig. 2-2B; Table 2-1). The positive relationship between species richness and DistM (Fig. 2-2A) was influenced by high richness values found in the Galapagos islands (Table 2S-4, Fig 2S-4). Contrastingly, species richness presented a negative relationship with human density (HumD; Fig. 2-2A), though this factor explained a low proportion of variance (Table 2-1). Functional dispersion was positively related to protection level, DistM, and DReef (Fig. 2-2C; Fig. 2S-4), but anthropogenic factors explained most of the variance in this metric (Fig. 2-2D). Density of individuals was low in large oceanic islands, as well as those distant from the mainland and with high protection level (Fig. 2-2E). On the other hand, density of individuals was higher in islands that were far from the closest reef and had high PP and local richness (Fig. 2-2E). Energetic factors accounted for 55% of the variance in density of individuals (Fig. 2-2F), of which PP was the most important factor (Table 2-1). Fish biomass was higher in islands far from the mainland and from the nearest adjacent reef, with high primary productivity and with high local richness (Fig 2-2G, Table 2-1). Energetic factors explained most of the variance in biomass, with PP being the most important single factor (Fig. 2-2H; Table 2-1). Functional dispersion was primarily determined by anthropogenic factors (Fig 2-2; Table 2-1), a result that did not support our first hypothesis. Density of individuals and biomass were determined mainly by energetic factors, confirming our second hypothesis. Finally, our results extended our third hypothesis because anthropogenic factors influenced not only density of individuals and biomass, but also species richness and functional dispersion.

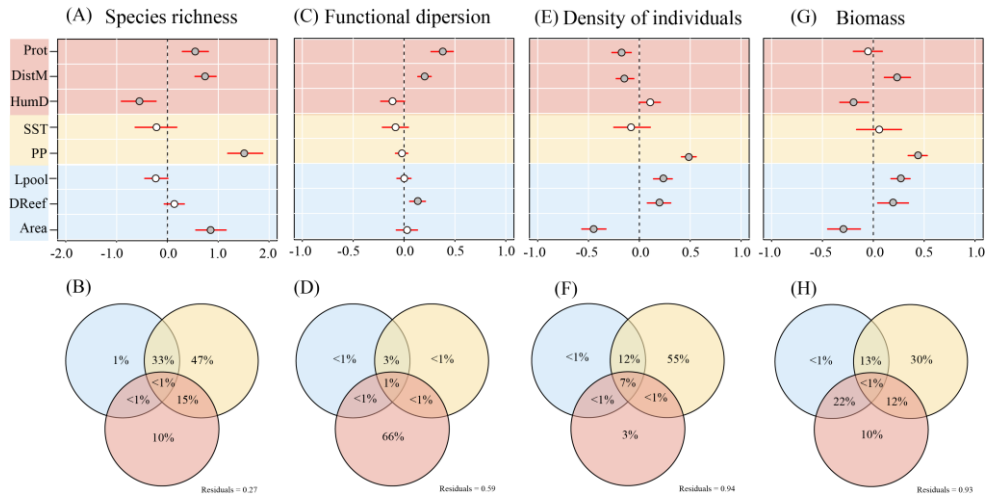


Figure 2- 2. Patterns and drivers of reef fish species richness (A-B), functional dispersion (C-D), density of individuals (E-F), and biomass (G-H) at the studied oceanic islands. Standardized effect sizes of biogeographic, energetic and anthropogenic factors (dots). Parameter estimates are simple models posterior median values, 95% uncertainty intervals (red lines). Gray dots indicate significant values, whereas white dots are not significant. Venn diagram represented assemblage metric and biogeographic (blue), energetic (yellow) and anthropogenic (red) drivers considered in this study. Percentages indicate the proportion explain to each driver.



Table 2- 1. Proportion of the variation explained by each biogeographic, energetic and anthropogenic factor considered in linear models. SR=Species richness, FD= Functional dispersion, DE= Density of individuals, BS=Biomass.

<b>Factor</b>	<b>SR (%)</b>	<b>FD (%)</b>	<b>DE (%)</b>	<b>BS (%)</b>
Area	21.2	4.66	9.32	7.95
Distance from nearest reef	1.99	8.25	7.34	11.7
Local Pool	2.67	3.31	6.76	7.95
Primary productivity	41.7	1.52	51.3	29.1
Sea surface temperature	14.8	6.33	3.85	7.48
Human density	4.11	26.5	6.56	13.1
Distance from mainland	9.98	16.5	8.68	18.4
Protection level	3.33	32.84	6.14	4.24

## **Discussion**

We quantify the relative strengths of the three main groups of predictors explaining reef fish assemblages across tropical oceanic islands using four complementary response metrics (fish species richness, functional dispersion, density of individuals and biomass). By using a large data set from isolated oceanic islands and applying an integrative analytical framework for comparing fish assemblage metrics, we confirmed several of our predictions and uncovered several unexpected results concerning the effects of anthropogenic, energetic, and evolutionary factors on fish faunas.

All islands except Galapagos had low variation in species richness (SR) and functional dispersion (FD), as well as stable proportions of species richness per trophic group and size classes across islands (see Fig. S3). This low variation could result from similar features among islands,

such as high isolation (>200 km from mainland), volcanic origin, underdeveloped coral formations, and distance from major biodiversity centers of marine organisms (Indo-Pacific for TEP and Caribbean for SWA and TEA). Indeed, isolated oceanic islands are known to support depauperate fish faunas but high functional diversity (Quimbayo *et al.* 2017b). The Galapagos islands are clearly an example, as its large surface size, its high diversity of benthic substrates (Edgar *et al.*, 2011), and seasonal upwelling events (Stuart-Smith *et al.*, 2013), contrast with characteristics of the other oceanic islands. The Galapagos islands may also represent a stepping stone to marine fauna between the coastal TEP and the Central Pacific, which could explain the high proportion of non-specialized species in these islands (Edgar *et al.*, 2004). In contrast, the low FD values observed in all TEA islands reflect both the low species richness in this province and a homogenization of fish faunas throughout of all its extent (Kulbicki *et al.*, 2013). This implies low functional redundancy (i.e., few species performing the same ecological function), and a high vulnerability of such ecosystems, since the loss of any given species probably signifies the loss of a unique function to the ecosystem (Mouillot *et al.*, 2014). Functional vulnerability peaks in remote islands where fish faunas are only a very small subset of species found within the marine province (Bender *et al.*, 2017).

The density of individuals (DE) and biomass (BS) of reef fishes were low in large, isolated and species-poor islands. On the other hand, small islands also harbored high densities and biomass of small-sized planktivorous species (e.g., Malpelo and St Paul's Rocks islands; Luiz *et al.*, 2015; Quimbayo *et al.*, 2017b). This result can be associated with fact that oceanic islands act as oases in the open sea, attracting large predators and pelagic schooling fishes in search for food, cleaning services and/or refuge, with widely roaming species aggregating along with resident reef species to allow high concentrations of DE and BS (Quimbayo *et al.*, 2017a). Another hypothesis is that small and isolated oceanic islands support a higher proportion of large-sized species than

large and connected island because they serve as stepping-stones and refuges to large migrant and pelagic species (Jacquet *et al.*, 2017). Fish assemblages inhabiting oceanic islands usually comprise species with wide geographic ranges and a combination of traits (e.g., large body size, long pelagic larval duration, high swimming capacity, and plastic diet) that favor colonization and dispersal processes (Luiz *et al.*, 2012). Isolated fish assemblages from these islands may also experience reduced predation and competition for resources, hence favoring selective pressure for large body sizes on isolated oceanic islands. Terrestrial and deep-sea organisms, for instance, exhibit gigantism on oceanic islands and deep zones, a pattern known as the Island Rule (Lomolino, 1985; McClain *et al.*, 2006). These hypotheses, however, require further evaluation.

Primary productivity was a key factor positively influencing SR, DE and BS of reef fish assemblages at oceanic islands. The high PP around these islands can be linked to the Island Mass Effect (Gove *et al.*, 2016), which induces high plankton concentrations and primary production, as well as high densities of benthic species that process dead plankton and fecal material. This planktonic production may therefore favor planktivores, detritivores, and benthic invertivore fish species. These results support both the species-energy hypothesis and population abundance hypothesis, as high levels of species diversity and abundance can be found due a combination of high energy availability (i.e., PP) and the thermal stability characteristic of tropical areas (Brown, 2014). However, some islands (e.g. those from the TEA province), had low biomass values despite high a PP, which may be explained by intense rates of fishing activities (Cinner *et al.*, 2016), and/or to limited habitat (e.g. area available) and low recruitment of fish species.

Large predators and herbivores comprise a large proportion of fish faunas on oceanic islands and are also the main target of most fisheries, leading us to conclude that the low SR and BS found in densely populated islands results from anthropogenic pressures. Studies in the

Indo-Pacific (Sandin *et al.*, 2008), and the Caribbean (Newman *et al.*, 2006) reported a dramatic decline in fish biomass linked to the accessibility from the nearest human settlement and a short distance from source to market, since assemblages closer to human population centers are more disturbed than isolated ones or that have restricted access (D'agata *et al.*, 2016). The high values of SR and BS we observed around isolated islands with minimal human impacts (e.g., Roca Partida, Clipperton, Cocos, Malpelo and Galapagos) corroborate the mechanism of human pressure as a driver of reef fish assemblages at oceanic islands.

Low fish densities were found on the most isolated islands, which is contrary to the effect found for the other metrics. This could be linked to specific features of these islands such as topography, low available area, high isolation level, and low coral diversity (Luiz *et al.*, 2015; Quimbayo *et al.*, 2017b), in addition to the predictions of Island Biogeography Theory (MacArthur & Wilson, 1967). Although human presence reduces fish abundance and biomass, our results suggest that strong protections are effective at maintaining high levels of SR, FD, and BS. In this manner, the creation of new marine protected areas is key to prevent the depletion of marine fish stocks or fish extinctions in marine environments (at least in isolated oceanic islands). As a low number of species are performing the same function on oceanic island (Bender *et al.* 2017), the extirpation or extinction of a single or a few species would result in complete loss of potentially important functions for the entire island (Quimbayo *et al.*, 2017b). The values reported here for SR, FD, DE, and BS of fish assemblages from isolated islands with minimal anthropogenic impacts could be used as baselines for reef assemblages from these regions in future comparative studies evaluating anthropogenic effects on reef fish assemblages.

Overall, we observed that the variation in fish assemblages metrics estimated from field censuses is poorly explained by the set of biogeographic factors usually known to influence the regional diversity of reef fishes (Kulbicki *et al.*, 2013; Parravicini *et al.*, 2013; Mouillot *et al.*, 2014). Interestingly, whereas SR and DE are strongly influenced by energetic factors, mainly primary productivity, FD and BS are mainly determined by anthropogenic factors evaluated here. Thus, these results suggest that the relative effects of these drivers vary between different metrics of fish assemblage structure. This highlights the importance of considering the combination of a wide set of ecological, biogeographical and anthropogenic factors with a range of metrics (e.g. SR, DE, FD, BS), to explain large-scale patterns in reef fish assemblages.

## **Conclusions**

Our study focused on determining and quantifying the relative strength of different predictors in explaining reef fish species richness, functional dispersion, density of individuals and biomass for a wide range of oceanic islands. We found that biogeographic factors were not very effective at predicting SR and FD. In contrast, distance from mainland and island area were quite good predictors for DE and BS. We interpret this as dual effects of ecological/biogeographical and anthropogenic factors in response to isolation in which smaller and more remote islands are less likely to receive colonists from outside sources (MacArthur & Wilson, 1967), yet those species that do arrive also enjoy relaxed human impacts such as fishing and pollution. We also identified PP as an important driver for all fish assemblage metrics, this result being persistent across a broad range of situations. Although oceanic islands with high levels of anthropogenic pressure not only support lower DE and BS, but lower FD, the degree of isolation and conservation of oceanic islands is important in maintaining high species richness, functional dispersion and biomass over broad spatial scales.

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## **Statement of authorship**

J.P.Q., M.S.D., M.K., T.C.M and S.R.F., conceived the study. J.P.Q., S.R.F., H.T.P., E.S., R.W.L., O.A.O., A.A.B., I.M., F.R.Z., F.A.Z. compiled the datasets. J.P.Q., and M.S.D. analyzed the data. J.P.Q., M.S.D., M.K., T.C.M., R.W.L., and A.F.J wrote the first draft, and all authors contributed to the final draft.

## **List of brief titles of items in the supplementary material**

Quimbayo et al – Supplementary material

- a. Table S1-S4
- b. Figures S1-S3
- c. Supplementary references

## DATA ACCESSIBILITY STATEMENT

All data and R code (data manipulation and analyses) can be found at Dryad and will be available upon publication.

## BIOSKETCH

**Juan P. Quimbayo** is interested in macroecology, conservation, behavior, functional diversity, and evolution of fishes, computational biology, and reproducible transparency in science.

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## Supplementary material

Table 2S- 1. List of oceanic islands analyzed within this study located in five different marine provinces. Tropical Eastern Pacific - North (TEPN), Tropical Eastern Pacific – South (TEPS), Southwestern Atlantic (SWA), Central Atlantic (CA) and Tropical Eastern Atlantic (TEA). UVCs: underwater visual census.

Province	Oceanic Island	Code	Latitude	Longitude	Sites	Year	Total UVCs	Area UVCs (m <sup>2</sup> )
TEPN	Clarion	RCL	18.35	-114.729	2	2006	24	250 & 50
TEPN	Roca Partida	RRP	18.962	-112.052	1	2006	14	251 & 50
TEPN	San Benedicto	RSB	19.3343	-110.823	2	2006	22	252 & 50
TEPN	Socorro	RSO	18.729	-110.965	4	2006	27	253 & 50
TEPN	Clipperton	CLP	10.2981	-109.2183	3	2008	25	50
TEPS	Cocos	COC	5.5300	-87.0548		2014	32	40
TEPS	Malpelo	MAL	3.9950	-79.6076	4	2015	51	40
TEPS	Galapágos-Central	GALC	-0.5308	-90.6924	8	2014	14	250
TEPS	Galapágos-South	GALS	-1.2941	-90.4379	4	2014	8	250
SWA	St Paul's Rocks	SPR	0.8988	-29.3110	4	2011	65	40
SWA	Rocas Atoll	ROC	-3.8552	-33.8110	11	2012	156	40
SWA	Fernando de Noronha	FNO	-3.8536	-32.4054	8	2007	89	40

SWA	Trindade	TRI	-20.5453	-29.1941	10	2009	252	40
SWA	Martin Vaz	MVZ	-20.4741	-32.8568	1	2013	47	40
CA	Ascension	ASC	-7.9333	-14.4167	3	2015	81	40
TEA	Cape Verde - Santa Luzia	CVE	16.7611	-24.7340	9	2009	198	40
TEA	Príncipe	PRI	1.6184	7.4038	7	2016	137	40
TEA	São Tomé	STO	0.1905	7.6149	7	2006	139	40

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Table 2S- 2. List of traits considered for each reef fish species observed in underwater visual censuses.

<b>Traits</b>		<b>Categories</b>						
1	Trophic Group	HD	HM	SI	SM	PK	PS	OM
2	Máx. Body Size (cm)	0-7	8--15	16-30	31-50	51-80	>80	
3	Schooling	Solitary	Pair	Small groups (3-20 ind)	Medium groups (20-50 ind)	Large groups (>50 ind)	Both	
4	Period of activity	Diurnal	Nocturnal	(day/night)				
5	Position in the water column	Pelagic	Bentho-pelagic	Benthic				
6	Mobility	Very mobile	Mobile	Sedentary				

Table 2S- 3. Biogeographic (area, distance from nearest reef, and species richness from of the local species pool), energetic (Mean sea surface temperature - SST, and primary productivity) and anthropogenic factors (human density, distance from mainland, and protection level) considered in the comparative analyses of reef fish assemblages on oceanic islands. Each superscript represents one reference of local checklist of the different islands: (1) Robertson & Allen (2016) (2) Fourri re et al. (2014); (3) Rubio et al. (1992); (4) Kulbicki et al. (2013); (5) Floeter et al. (2008); (6) Simon et al. (2013); Wirtz et al. (2014); Wirtz et al. (2007). Tropical Eastern Pacific - North (TEPN), Tropical Eastern – South (TEPS), Southwester Atlantic (SWA), Central Atlantic (CA) and Tropical Eastern Atlantic (TEA).

Province	Oceanic Island	Area (Km <sup>2</sup> )	Distance from nearest reef (Km)	Local pool	Mean SST* (�C)	Primary productivity* (mg m <sup>-3</sup> )	Hum. Density (ind/km <sup>2</sup> )	Distance from mainland (Km)	Protection level‡
TEPN	Clarion	31.4	314	136 <sup>1</sup>	25.98	25.95	0	700	4
TEPN	Roca Partida	0.014	100	119 <sup>1</sup>	25.98	26.10	0	459	4
TEPN	San Benedicto	6.76	55.68	139 <sup>1</sup>	25.98	26.19	0	402	4
TEPN	Socorro	184.39	100	141 <sup>1</sup>	25.98	26.33	0.244	460	4
TEPN	Clipperton	12.62	945	119 <sup>2</sup>	28.29	31.62	0	1080	3
TEPS	Cocos	34.35	550	284 <sup>1</sup>	28.04	31.44	0.23	490	4
TEPS	Malpelo	3.5	380	202 <sup>1,3</sup>	26.92	47.80	2.29	395	4
TEPS	Galap�gos-Central	8985	35	203 <sup>1</sup>	26.32	63.60	0.19	965	3
TEPS	Galap�gos-South	281.2	55	178 <sup>1</sup>	21.25	63.59	0.36	965	3

SWA	St Paul's Rocks	0.032	630	59 <sup>4,5</sup>	27.40	31.18	0.001	1010	1
SWA	Rocas Atoll Fernando de	7.036	145	123 <sup>4,5</sup>	27.23	7.41	0.57	288	4
SWA	Noronha	33.79	145	151 <sup>4,5</sup>	27.53	23.33	89.14	345	3
SWA	Trindade	13.77	50	154 <sup>4,5</sup>	25.64	14.99	3.63	1150	2
SWA	Martin Vaz	3.93	50	64 <sup>6</sup>	25.64	15.08	12.72	1200	2
CA	Ascension Cape Verde - Santa	111.6	1130	107 <sup>7</sup>	25.89	23.61	7.89	1500	2
TEA	Luzia	58.27	10	269 <sup>5</sup>	24.46	49.13	35.45	800	1
TEA	Príncipe	1111.2	161.4	204 <sup>5</sup>	27.27	40.93	4.5	216	1
TEA	São Tomé	11181.13	161.4	204 <sup>5,7</sup>	27.27	40.50	132.92	250	1

\* Data extracted from BioOracle (REF)

‡ Data extracted from IUCN



Table 2S- 4. Mean and standard deviation of each assemblage metric estimated for each oceanic island located in five marine provinces. Tropical Eastern Pacific - North (TEPN), Tropical Eastern Pacific – South (TEPS), Southwestern Atlantic (SWA), Central Atlantic (CA) and Tropical Eastern Atlantic (TEA).

Province	Oceanic Island	Species richness (spp/m <sup>2</sup> )	Functional dispersion	Density (ind/m <sup>2</sup> )	Biomass (g/m <sup>2</sup> )
TEPN	Clarion	0.12 ± 0.08	2.02 ± 0.20	1.42 ± 1.58	114 ± 217
TEPN	Roca Partida	0.18 ± 0.16	2.02 ± 0.09	4.16 ± 2.61	797 ± 65.3
TEPN	San Benedicto	0.14 ± 0.11	2.33 ± 0.15	2.24 ± 2.14	253 ± 569
TEPN	Socorro	0.11 ± 0.07	2.24 ± 0.19	1.05 ± 0.91	110 ± 189
TEPN	Clipperton	0.27 ± 0.06	1.74 ± 0.01	1.57 ± 0.55	797 ± 496
TEPS	Cocos	0.31 ± 0.07	2.16 ± 0.01	5.71 ± 3.85	850 ± 743
TEPS	Malpelo	0.35 ± 0.13	2.49 ± 0.02	10.12 ± 5.59	879 ± 863
TEPS	Galapágos-Central	0.40 ± 0.02	2.32 ± 0.07	5.89 ± 3.59	710 ± 363
TEPS	Galapágos-South	0.39 ± 0.01	2.28 ± 0.17	6.99 ± 4.68	1087 ± 690
SWA	St Paul's Rocks	0.10 ± 0.06	1.97 ± 0.05	7 ± 3.40	559 ± 310
SWA	Rocas Atoll	0.31 ± 0.08	1.91 ± 0.04	6.89 ± 3.67	288 ± 351
SWA	Fernando de Noronha	0.27 ± 0.08	1.94 ± 0.05	2.23 ± 1.49	198 ± 153
SWA	Trindade	0.29 ± 0.08	2.05 ± 0.07	2.34 ± 1.11	495 ± 360
SWA	Martin Vaz	0.28 ± 0.07	2.03 ± 0.03	2.2 ± 0.88	560 ± 350
CA	Ascension	0.37 ± 0.08	2.15 ± 0.03	4.82 ± 1.82	545 ± 251
TEA	Cape Verde	0.30 ± 0.08	1.11 ± 0.11	5.95 ± 6.27	223 ± 273
TEA	Príncipe	0.33 ± 0.09	1.28 ± 0.09	6.96 ± 5.07	247 ± 217
TEA	São Tomé	0.31 ± 0.09	1.42 ± 0.14	7.09 ± 6.86	173 ± 310

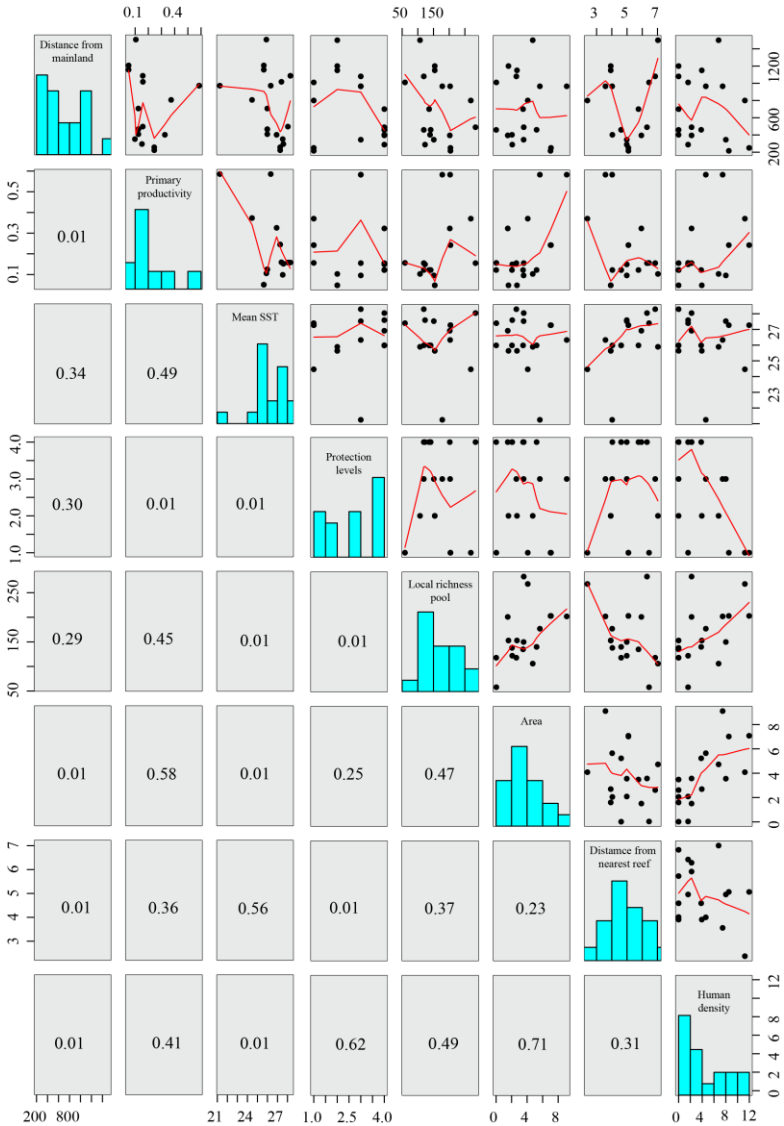


Figure 2S- 1 Correlation plot of candidate continuous covariates before accounting for collinearity

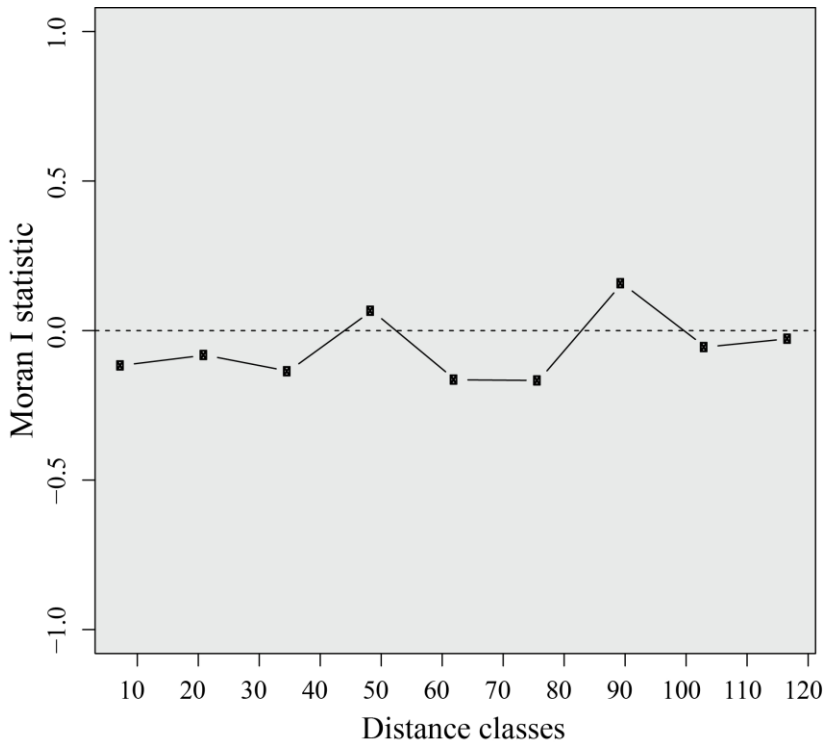


Figure 2S- 2. Plot exploring spatial autocorrelation of our analysis using Moran's I index

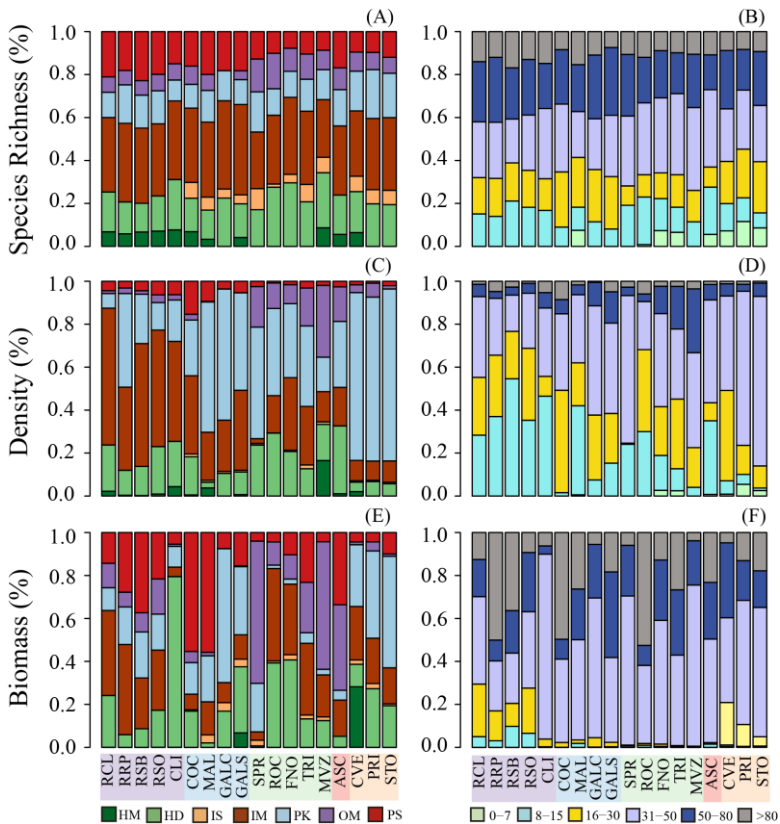


Figure 2S- 3. Comparison among the proportion of trophic groups (A, C, E) and size classes (B, D, F) observed at each oceanic island. Revillagigedos-Clarion (RCL), Revillagigedos-Roca Partida (RRP), Revillagigedos-San Benedicto (RSB), Revillagigedos-Socorro (RSO), Clipperton (CLI), Cocos (COC), Malpelo (MAL), Galapagos-Central (GALC), Galapagos-South (GALS), St Paul’s Rocks (SPR), Rocas Atoll (ROC), Fernando de Noronha (FNO), Trindade (TRI), Martin Vaz (MVZ), Ascension (ASC), Cape Verde (CVE), Principe (PRI), São Tomé (STO).

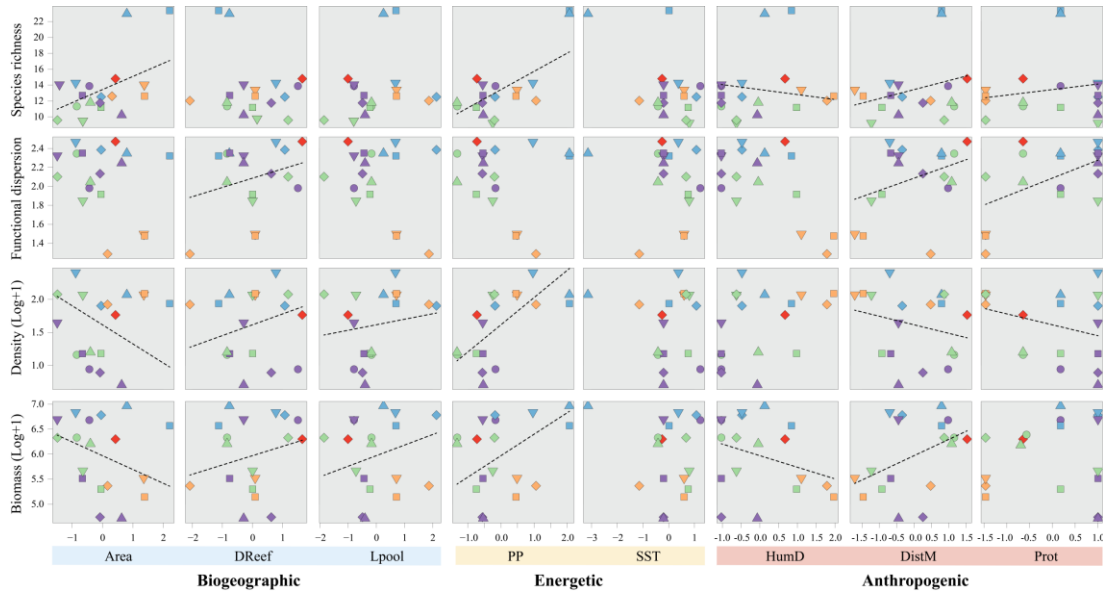


Figure 2S- 4. Linear correlation among assemblage metrics and biogeographic, energetic and anthropogenic factors. Each point represents an oceanic island and each color a marine province. Tropical Eastern Pacific - North (Purple), Tropical Eastern Pacific – South (Blue), Southwestern Atlantic (Green), Central Atlantic (Red) and Tropical Eastern Atlantic (Orange).

## Capítulo 3

### **Dedicated cleaners structure marine mutualistic networks**

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**Title**

Dedicated cleaners structure marine mutualistic networks

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## **Abstract**

A persistent challenge in ecology is to unravel the interplay between ecological and evolutionary processes shaping species interactions at the community level. We studied marine cleaning mutualism between species that feed upon ectoparasites and injured tissues of other species in 20 localities around the Atlantic and the Eastern Pacific. We show that dedicated cleaner species are key in driving the asymmetry of mutualistic interactions at the community level. Since dedicated cleaners rely exclusively on cleaning for feeding, they interact with most client species available and so tend to be at the core of the network; in contrast, facultative cleaners explore other resources and engage in cleaning more opportunistically, so tend to target the most common clients. We found that biological traits of cleaners—position in the water column, body and school sizes—play a role in defining their cleaning interactions. More importantly, we found that marine communities with only facultative cleaners are generally not structured, whereas dedicated cleaners are the main contributors for the interaction asymmetry that assembles cleaning networks into nested architectures. Our study illustrates how species distribution at a macroecological scale and local trophic niche can interact and influence the structure of ecological networks.

**Keywords:** nestedness, mutualism, ecological networks, macroecology

## **Introduction**

Recent years have seen a surge in the study of the structure of biological interaction networks, since they can reveal how ecological and evolutionary mechanisms have shaped niche and degree of specialization of the interacting species [1]. In marine habitats, a conspicuous positive biotic interaction is cleaning mutualism, in which a cleaner species feeds on ectoparasites and dead/injuries tissue from the body of another, client species [2]. Such mutual benefits are key for population and community processes (e.g. promoting local species abundance, diversity and health) [2]. Approximately 259 species of two taxa (fish, shrimp) engage in cleaning behaviour, some do so only



opportunistically or when juvenile ('facultative cleaners') while others specialise in cleaning throughout their lifetime ('dedicated cleaners') [3]. As a foraging activity for cleaners, the patterning of cleaning interactions within a marine community can give insights on their ecological niche [4,5].

In tropical and subtropical waters, cleaning mutualism at the species level are influence by multiple factors—e.g. species abundance, morphological traits, diet, size, behaviour [3-5,7]. However, an outstanding question is how biological traits of cleaners specifically contribute to the overall structure of the mutualistic network at the community level. Only recently we began to appreciate that cleaning interactions may be distributed asymmetrically within the community [5,6]. Notably, the interactions of low-connected cleaner/client species tend to be a proper subset of the interactions of the highly connected cleaner/client species, leading to the so-called nested pattern [6]. However, these studies are restricted in geographical range, leaving two critical gaps: 1) how widespread these network patterns are at the global scale; and 2) which biological trait, if any, determines a key cleaner species at the local scale. The pervasiveness and drivers of nestedness in cleaning networks are therefore uncertain. Exploring how cleaner species richness varies across communities, and how cleaners exploit clients as food resources locally, can ultimately help unravelling how ecological and evolutionary processes interact and contribute to the structure cleaning mutualisms.

Considering marine cleaning network at a large, macroecological scale, we postulate that 1) biological traits of cleaners can influence the emergent structure of the cleaning network, and that 2) such networks would display a nested structure in communities where dedicated cleaners occur. Our hypotheses are based on the fact that biological traits of cleaners are key for their cleaning efficiency [4,7]. Therefore, we tested whether their exclusivity to cleaning (i.e., being facultative or dedicated cleaner) along with a range of other traits that could be sought

by clients—taxa, advertising coloration, water column position, body and school size—affect the number of client species they interact with, and so contribute for the emergence of nestedness in cleaning networks.

## Material and methods

We collected and compiled data on cleaning interaction among species (electronic supplementary material, Table 3S-1) from 20 marine habitats in the Atlantic and Eastern Pacific (figure 3-1a). We depicted local interactions as two-mode networks in which set of nodes representing cleaners were linked to another set of clients whenever the former was observed removing ectoparasites, injured tissue, and/or mucus from the body surface, gills or buccal cavity of the latter (figure 3-2) [2]. We estimated nestedness based on overlap and decrease fill (NODF) [8] and assessed its significance using a benchmark distribution generated by a null model based on the empirical data [9] (electronic supplementary material).

We tested whether biological traits of cleaners influenced network structure using Linear Mixed Models (LMM; Gaussian distribution) in which Nestedness Contribution was a function of the cleaners' biological traits (fixed factors) and locality (random factor). To estimate the contribution of each cleaner species to nestedness, we compared the observed NODF of their entire network with the null distribution of NODF values obtained when randomizing only the interactions of a target cleaner using z-scores ( $> 0$  indicated positive,  $< 0$  indicated negative contribution) [10] (electronic supplementary material, Table S2). As the LMMs independent variables, we considered the following six functional descriptors for cleaning success (figure 3-2; electronic supplementary material, Table 3S-3): Taxa (vertebrate/invertebrate), associated with how efficient the cleaning service is [2]; Type (dedicated/facultative), indicating how much a cleaner depends on cleaning for feeding [3]; Coloration (number of body colours),

influencing how conspicuous a cleaner is for its clients [7]; Body size (cm), influencing diet composition (large and small species usually prey on different items [11]); Water column position (bottom/medium/top) influencing frequency of cleaning (bottom cleaners have less access to clients [12]); and School size (solitary, pair, small (3–20), medium (20–50), large (>50 individuals)) influencing the time needed to clean a client [2]. We built two models, one using data from all 20 localities; another using data from localities in which the cleaning network were significantly more nested than expected by chance, and contained both dedicated and facultative cleaners (Table 3-1).

## **Results**

We recorded 56 cleaner species: 50 fish, 6 shrimps; 85% facultative, 15% dedicated. Dedicated cleaners were concentrated in the Caribbean and Southwestern Atlantic, while facultative cleaners were distributed homogeneously across localities (figure 3-1*a*). Cleaner richness was higher near the equator (e.g. Rocas Atoll, São Tomé), but no trend of decreasing richness towards high latitudes was evident (e.g. Banyuls, New Zealand; figure 3-1*a*). The ratio cleaner/client species was similar between localities with only facultative cleaners and localities with both types (figure 3-1*b,c*). While dedicated cleaners are not always central in their networks (figure 1*b*), overall they contribute the most to nestedness (electronic supplementary material, Table 3S-2).

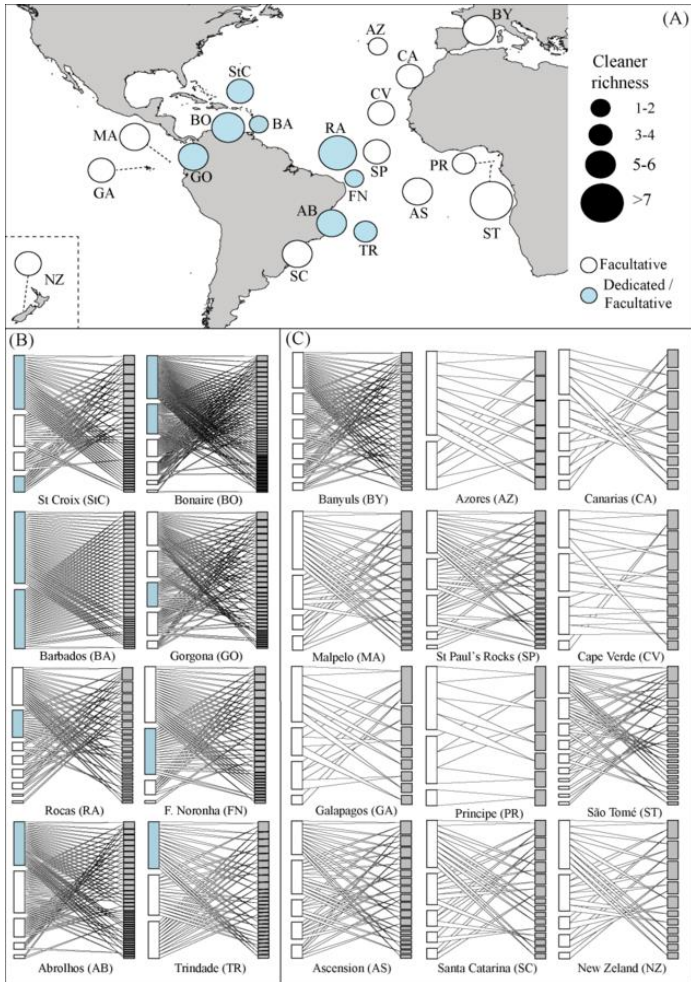


Figure 3- 1 (A) Distribution of the 20 localities sampled for marine cleaning mutualism, with sizes proportional to richness of cleaner species. (B) Cleaning networks in with both dedicated (blue) and facultative cleaners (white) linked to clients (grey) by binary links whenever they were observed interacting. (C) Networks in localities with only facultative cleaners.

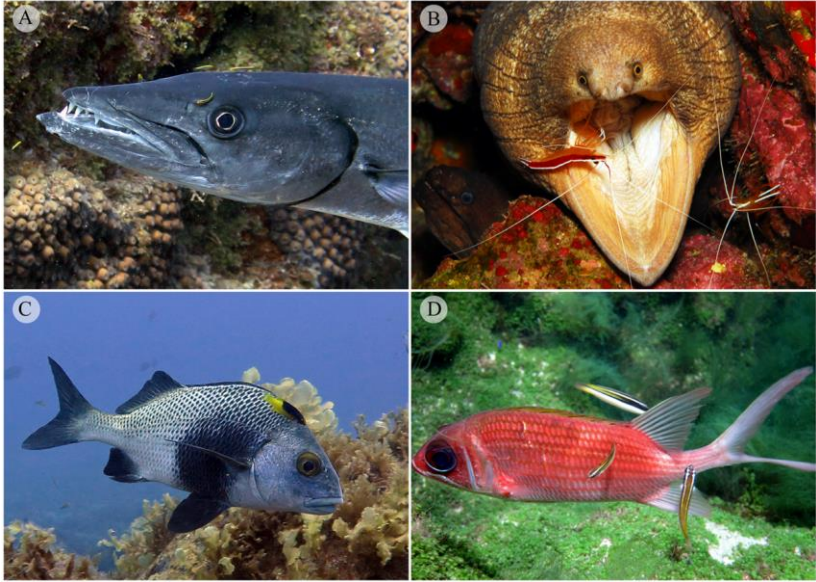


Figure 3- 2. Mutualistic interactions between client and cleaner species, illustrating the six biological traits considered: taxa, type, coloration, body size, water column position, and school size. (A) Four dedicated cleaners with small body size and aposematic coloration (*Elacatinus phthirophagus*) clean the head of a Great Barracuda (*Sphyraena barracuda*) off the Fernando de Noronha archipelago (Photo: Floeter SR). (B) A pair of white-striped cleaner shrimp (*Lysmata grabhami*) clean the mouth of a Brow Moray (*Gymnothorax unicolor*) near the substrate off Ascension Island (Photo: Brown J). (C) A solitary facultative cleaner *Bodianus rufus* cleans a Black Margate (*Anisotremus surinamensis*) in the water column around the Fernando de Noronha archipelago (Photo: Floeter SR). (D) A small-sized group of small juveniles of the facultative cleaner fish *Thalassoma noronhanum* cleans Squirrelfish (*Holocentrus adscensionis*) off the Rocas Atoll (Photo: Quimbayo JP).

Networks with dedicated cleaners tended to be nested and have high NODF values, different than networks with only facultative cleaners (figure 3-3). Nested networks were characterized by a core of cleaners interacting with most clients, along with peripheral cleaners interacting with the highly connected clients. Eight out of 20 localities contained dedicated and facultative cleaners, 75% of which were significantly more nested than expected by chance ( $p < 0.001$ ; figure 3-3a). In contrast,

most localities with only facultative cleaners were not nested ( $p > 0.05$ , except Cape Verde, New Zealand; figure 3-3b). The biological traits that better explained cleaners' contribution to nestedness in all networks were cleaner type (dedicated), body size (small), water column position (medium), school size (large; Table 3-1). Cleaner taxa (shrimp/fish) did not influence nestedness. Moreover, the only biological trait that influenced nestedness in networks with both facultative and dedicated cleaners was cleaner type (Table 3-1).

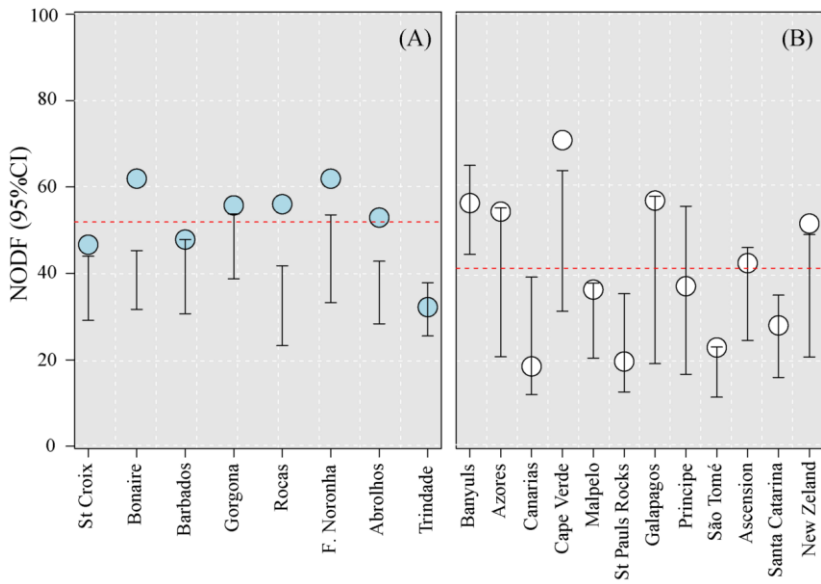


Figure 3- 3. Nestedness (NODF) of cleaning networks in (A) localities with both dedicated and facultative cleaner species (left), and (B) in localities with only facultative cleaners (right). Red-dashed lines represent mean NODF values. Significantly nested networks display NODF values beyond the 95% confidence intervals generated by null models (whiskers). Localities are ordered by decreasing latitude.

Table 3- 1. Coefficients of two Linear Mixed Models (LMM) for Nestedness Contribution of cleaners as a function of their biological traits (fixed factors) and locality (random factor). LMM1 included data from all 20 localities; LMM2 considered data from localities where the cleaning network was nested and contained both dedicated and facultative cleaners. Bold font indicates p-values < 0.05.

Biological traits	Nested Contribution					
	LMM1			LMM2		
	Estimate	<i>t</i> -value	<i>p</i> -value	Estimate	<i>t</i> -value	<i>p</i> -value
Taxa						
<i>Fish</i>	-0.81	-1.32	0.190	-0.17	-0.17	0.859
<i>Shrimp</i>	0.24	0.52	0.600	-0.80	-1.12	0.270
Cleaner type						
<i>Facultative</i>	1.85	4.17	0.191	1.78	2.15	0.882
<i>Dedicated</i>	<b>2.66</b>	<b>5.49</b>	<b>0.001</b>	<b>1.95</b>	<b>2.32</b>	<b>0.029</b>
Colouration	0.01	0.08	0.930	-0.03	-0.82	0.420
Body size	<b>-0.03</b>	<b>-3.03</b>	<b>0.003</b>	0.31	1.01	0.323
Water column position						
<i>Bottom</i>	-3.01	-3.59	0.210	0.45	1.15	0.991
<i>Medium</i>	0.32	0.92	0.020	0.62	1.32	0.837
<i>Top</i>	-2.20	-2.27	0.410	0.79	1.49	0.140

School size						
<i>Large</i>	<b>1.19</b>	<b>2.21</b>	<b>0.030</b>	1.30	1.53	0.138
<i>Medium</i>	0.14	0.38	0.690	-0.64	-0.95	0.351
<i>Pair</i>	-0.06	-0.15	0.870	-0.19	-0.28	0.779
<i>Solitary</i>	-0.03	-0.09	0.920	-0.26	-0.51	0.613



## Discussion

Our findings showing that cleaning interactions in marine communities with dedicated cleaners often have a nested architecture highlight this cleaner type as key in structuring global mutualistic networks. Dedicated cleaners rely exclusively on cleaning interactions to obtain food, consequently they target most of clients locally available and emerge as generalists, highly-connected cleaners in the system. Facultative cleaners, in contrast, exploit other food sources and may engage in cleaning with fewer species—the most common, or other clients as opportunities arise. This asymmetry leads to nested pattern in communities where dedicated and facultative cleaners co-occur [6]. However, in localities with only facultative cleaners—sometimes richer in cleaner species—the use of clients as resource tend to overlap, hindering the emergence nestedness. This can be associated with the more flexible diet of facultative cleaners, which only clean sporadically, i.e. during juvenile stages, or when the predation risk is low [2,3]. These findings suggest that nested structures are not as widespread in marine mutualistic networks as earlier thought [6].

Beyond nestedness, all localities contained few cleaners, many clients, and some degree of heterogeneity in the distribution of interactions among them. This is probably related to morphological or behavioural adaptations of cleaner species, which are fundamental for the success of cleaning mutualism. For instance, dedicated fish cleaners (e.g. *Elacatinus* spp.) have lateral body stripe that increase signalling and contrast between the cleaners and background [7]. Some facultative cleaners form large groups on corals, sponges or big rocks which call the attention of clients [12]. Despite cleaning services being performed by two groups that are morphologically distinct, both—fishes and shrimps—have similar ability to perform rapid mouth gape cycles on individual prey items at the client's body, and small body size that facilitates interaction with a range of clients of different sizes [3,13].

In addition to niche-related traits of cleaners, another central factor influencing cleaning mutualism at the macroecological scale is richness of cleaner species [6]. Since dedicated cleaners are important for the network structure, their occurrence determines differences across communities. The lack of dedicated cleaners in Eastern Atlantic suggests these lineages have not emerged in this region. This may be due to the isolation from the biodiversity centre in the Atlantic Ocean (the Caribbean [14]) limiting dispersal, or to the lack of specialised lineages (e.g., coral-feeders are thought to be the first functional group with morphological adaptations to feed on ectoparasites [15]). Moreover, the predominance of dedicated cleaners in communities near to the equator suggest these organisms may have low tolerance to cold water and low colonization capacity, due to their small body size and habit of living close to cleaning stations at the sea bottom [16]. Although cleaner richness is high in communities with only facultative cleaners, this functional role may not be as efficiently performed as in the communities with dedicated cleaners which may provide a more rewarding service for clients [5]. In the Indo-West Pacific, for example, the omnipresent *Labroides dimidiatus* is such a specialized, skilled dedicated cleaner [17] that almost leave no room for facultative cleaners despite the higher local species richness compared to our localities. Overall, by exploring empirical patterns of cleaning mutualism in marine communities, our study illustrates how ecological and evolutionary processes operating at different spatiotemporal scales can interact and influence the structure of mutualistic networks.

## **Ethics statement**

Data came from literature and non-invasive observations only.

## **Data Accessibility**

Data can be found at Dryad:

<http://datadryad.org/review?doi=doi:10.5061/dryad.t1097>

## **Competing interests**

We have no competing interests.

## **Authors' Contributions**

JPQ, MC conceived the study; JPQ, SRF collected data (field and literature); JPQ, MC, MSD analysed data; JPQ, MC wrote the manuscript; MSD, SRF reviewed manuscripts. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

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## **Supplementary Methods S1.**

### *Data sampling*

To conduct a quantitative assessment of cleaning interactions across biogeographical regions, it is necessary to use taxa with sufficient diversity within all regions, good taxonomical resolution and reliable data on geographical distributions [1]. Two comprehensive reviews published in the last 20 years [2,3] considered the ecological and evolutionary aspects of cleaning interactions and provided detailed lists of fish and shrimp species that engage in cleaning behaviour across biogeographical regions. Based on the listed species, we surveyed nearly 200 other references to compile cleaning interactions from published peer-reviewed articles and grey literature (monographies, technical reports, dissertations and theses). We focused on studies that provide interaction matrices with several cleaner and client species, discarding the studies reporting a single cleaner species. Additionally, we have analysed cleaning interactions from our own field observations in five localities (Table S1). During dedicated SCUBA dive surveys, we counted cleaning events, defined as the removal of ectoparasites, injuries tissue, and/or mucus by a cleaner species from the body, gills or buccal cavity of a client species. Each cleaning event began when physical contact between cleaner and client was initiated and ended when either the cleaner or the client withdrew.

Table 3S- 1. Localities and richness of cleaner and client species analysed this study.

Province/Locality	Latitude	Longitude	Richness of cleaner species	Richness of client species	References
<b><i>Caribbean</i></b>					
Barbados	13°05	59°36	2	38	[4]
Bonaire	12°11	68°15	6	49	[5]
St Croix	17°73	64°44	4	32	[6]
<b><i>Central Atlantic</i></b>					
Ascension Island	7°56	14°25	5	18	[7]
<b><i>Mediterranean</i></b>					
Banyuls	42°28	3°07	6	19	[8]
<b><i>North Atlantic</i></b>					
Azores	38°30	28°00	2	8	[9]
Canarias	28°06	15°24	4	9	[10]
<b><i>South Pacific</i></b>					
New Zealand	41°17	174°27	5	11	[11]
<b><i>Southwestern Atlantic</i></b>					
Abrolhos	17°92	38°81	5	38	[12]
Fernando de Noronha	3°85	32°40	2	26	[13]
Rocas Atoll	3°85	33°81	8	23	[14]
Santa Catarina	27°59	48°59	5	15	This study
St Paul's Rocks	0°89	29°31	4	10	This study
Trindade Island	20°54	29°19	3	27	This study
<b><i>Tropical Eastern Atlantic</i></b>					
Cape Verde	16°76	24°73	4	13	[15]
Principe	1°61	7°40	3	6	This study
São Tomé	0°19	6°61	10	16	[15]
<b><i>Tropical Eastern Pacific</i></b>					

Galápagos	0°53	90°69	4	8	This study
Gorgona Island	2°96	78°14	5	32	[16]
Malpelo	3°99	79°61	5	19	[17]

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## Supplementary Methods S2.

### *Cleaning network topology*

We described the mutualistic interactions between cleaner and client species in each site using binary two-mode networks [18]. A mutualistic network was represented by an adjacency matrix  $\mathbf{M}$  in which an elements  $m_{ij} = 1$  when the cleaner species  $i$  interacts with the client species  $j$ , and  $m_{ij} = 0$  otherwise. In the network representation, nodes representing individual cleaner species were linked to those representing client species whenever a cleaner has been found empirically to remove ectoparasites, diseased tissue, and/or mucus from the body surface, gills or buccal cavity of the clients [19].

We evaluated the large-scale structure of the cleaning networks of each locality with a nestedness metric based on overlap and decrease fill of the adjacency matrix (*NODF*; [20]). A nested network structure indicated heterogeneity in the distribution of mutualistic interactions within a locality, with some more generalist cleaner species cleaning most of the clients, along with more specialist cleaner species cleaning a subset of the clients with which the more generalist cleaners interact [21].

We assessed the significance of nestedness with a null model approach [22]. We built benchmark distributions of nestedness values for the cleaning network of each locality by calculating *NODF* for 1,000 theoretical adjacency matrices of same size (i.e. number of cleaner and client species) and connectance (i.e. proportion of realized cleaning interactions). We used an algorithm that randomizes cleaning



interactions among species based on their empirical interactions (i.e. row and column sums; see [23]). Each cell of the theoretical adjacency matrix had a probability of being filled that was proportional to the number of interactions of both cleaners and clients, defined as:  $c_{ij} = \frac{1}{2} \left( \frac{P_i}{C} + \frac{P_j}{R} \right)$ , where  $P_i$  = number of cleaners that have interacted with the client  $i$  (row sums);  $P_j$  = number of client species cleaned by the cleaner  $j$  (column sums);  $C$  = number of cleaner species (columns); and  $R$  = number of client species (rows). The nestedness network structure of a locality was considered significant when its empirical *NODF* value lied outside of the 95% confidence intervals of the *NODF* benchmark distribution.

### **Supplementary Methods S3.**

#### *Contribution of cleaner species to nestedness*

To evaluate the contribution each cleaner species to the nested pattern, we defined whether the interactions of a given cleaner change the overall nestedness of the network, controlling for differences in the observed number of interactions. For each species in a given network we compared the *NODF* of the entire network with the *NODF* obtained when we randomized only the interactions of that target species (method developed by [24]). To randomize the target species' interactions, we used the same null model described above [23]. When the *NODF* of a network in which the interactions of the target species  $i$  were randomized was consistent and close to the *NODF* of the original network, the species  $i$  was deemed as a strong contributor to the nested pattern. To compare *NODF* values, we used z-scores, in which values greater than 0 indicated that a species contributed positively to increase the nestedness of the entire network, and values less than 0 indicate otherwise. The contribution of each cleaner species for the nestedness of the network of all localities are presented in the Table S2.

Table 3S- 2. Contribution each cleaner species to nestedness of cleaning networks of all 20 studied localities.

<b>Province/Locality</b>	<b>Cleaner species</b>	<b>Nested contribution</b>
<b><i>Caribbean</i></b>		
Barbados	<i>Elacatinus evelynae</i>	2.216
	<i>Elacatinus prochilos</i>	1.781
Bonaire	<i>Elacatinus spp</i>	4.203
	<i>Periclimenes pedersoni</i>	3.373
	<i>Bodianus rufus</i>	1.777
	<i>Thalassoma bifasciatum</i>	1.560
	<i>Stenopus hispidus</i>	0.413
St Croix	<i>Pomacanthus paru</i>	0.322
	<i>Elacatinus evelynae</i>	2.408
	<i>Bodianus rufus</i>	0.150
	<i>Thalassoma bifasciatum</i>	-0.979
	<i>Periclimenes pedersoni</i>	-0.527
<b><i>Central Atlantic</i></b>		
Ascension Island	<i>Bodianus insularis</i>	2.033
	<i>Pomacanthus paru</i>	1.537
	<i>Lysmata grabhami</i>	-0.015
	<i>Chaetodon sanctaehelenae</i>	0.077
	<i>Thalassoma ascensionis</i>	-0.447
<b><i>Mediterranean</i></b>		
Banyuls	<i>Symphodus melanocercus</i>	1.904
	<i>Symphodus mediterraneus</i>	-1.696
	<i>Symphodus ocellatus</i>	-0.253
	<i>Coris julis</i>	-2.334
	<i>Symphodus tinca</i>	-0.322
	<i>Ctenolabrus rupestris</i>	-1.621

**North Atlantic**

Azores	<i>Coris julis</i>	1.107
	<i>Thalassoma pavo</i>	0.839
Canarias	<i>Thalassoma pavo</i>	-0.967
	<i>Lysmata grabhami</i>	-0.044
	<i>Stenorhynchus lanceolatus</i>	-0.543
	<i>Diplecogaster tonstricula</i>	-0.996
	<i>Coris julis</i>	-1.119

**South Pacific**

New Zealand	<i>Coris sandageri</i>	1.885
	<i>Halichoeres spp</i>	1.722
	<i>Coris picta</i>	-0.273
	<i>Pseudolabrus luculentus</i>	-0.927
	<i>Pseudolabrus miles</i>	-0.371

**Southwestern Atlantic**

Abrolhos	<i>Elacatinus figaro</i>	3.028
	<i>Pomacanthus paru</i>	3.008
	<i>Anisotremus virginicus</i>	-0.573
	<i>Chaetodon striatus</i>	-1.201
	<i>Gramma brasiliensis</i>	-1.179
Fernando de Noronha	<i>Elacatinus phthirophagus</i>	2.463
	<i>Pomacanthus paru</i>	0.471
	<i>Bodianus pulchellus</i>	-1.293
Rocas Atoll	<i>Thalassoma noronhanum</i>	3.247
	<i>Elacatinus phthirophagus</i>	2.305
	<i>Lysmata grabhami</i>	-0.357
	<i>Stenopus hispidus</i>	-0.656
	<i>Pomacanthus paru</i>	0.665
	<i>Stegastes rocasensis</i>	0.816
	<i>Abudefduf saxatilis</i>	-0.224

	<i>Acanthurus chirurgus</i>	-0.051
Santa Catarina	<i>Anisotremus virginicus</i>	1.109
	<i>Pomacanthus paru</i>	0.465
	<i>Diplodus argenteus</i>	-0.393
	<i>Lysmataa ankeri</i>	-1.467
	<i>Abudefduf saxatilis</i>	-1.470
St' Pauls Rocks	<i>Stegastes sanctipauli</i>	0.856
	<i>Lysmata grabhami</i>	-0.839
	<i>Pomacanthus paru</i>	-0.657
	<i>Chromis multilineata</i>	-1.350
Trindade Island	<i>Elacatinus pridisi</i>	0.207
	<i>Bodianus rufus</i>	0.742
	<i>Thalassoma noronhanum</i>	-0.420
<b><i>Tropical Eastern Atlantic</i></b>		
Cape Verde	<i>Bodianus speciosus</i>	2.558
	<i>Coris atlantica</i>	1.275
	<i>Thalassoma pavo</i>	0.818
	<i>Canthigaster capistrata</i>	0.348
Principe	<i>Bodianus speciosus</i>	0.735
	<i>Thalassoma pavo</i>	0.721
	<i>Microspathodon frontalis</i>	-1.178
São Tomé	<i>Bodianus speciosus</i>	0.756
	<i>Lysmata grabhami</i>	2.297
	<i>Bodianus pulchellus</i>	0.152
	<i>Chaetodon robustus</i>	-0.371
	<i>Coris atlantica</i>	0.069
	<i>Thalassoma newtoni</i>	-0.141
	<i>Abudefduf taurus</i>	0.063
	<i>Abudefduf saxatilis</i>	-1.227

	<i>Spicara melanurus</i>	-1.107
	<i>Lysmata spp</i>	-0.708
<b><i>Tropical Eastern Pacific</i></b>		
Galápagos	<i>Bodianus diplotaenia</i>	1.573
	<i>Johnrandallia nigrirostris</i>	0.274
	<i>Holacanthus passer</i>	0.569
	<i>Thalassoma lucasanum</i>	1.044
Malpelo	<i>Johnrandallia nigrirostris</i>	1.683
	<i>Bodianus diplotaenia</i>	1.424
	<i>Lepidonectes bimaculata</i>	-0.830
	<i>Holacanthus passer</i>	0.870
	<i>Thalassoma lucasanum</i>	-1.132
Gorgona Island	<i>Johnrandallia nigrirostris</i>	-0.161
	<i>Thalassoma lucasanum</i>	1.034
	<i>Tigrigobius spp</i>	1.082
	<i>Bodianus diplotaenia</i>	1.730
	<i>Holacanthus passer</i>	0.410

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#### **Supplementary Methods S4.**

##### *Biological traits of cleaners*

We classified all cleaner species according to the following six life-history traits that included behaviour, functional and morphological properties (Table S3).

- 1) Taxa: fish (vertebrate) and shrimps (invertebrates). Species in these groups vary both morphologically and in their efficiency in providing cleaning services [2].

- 2) Type: dedicated or facultative. Dedicated cleaners are species that depend exclusively on cleaning activities to obtain food, while facultative cleaners performed this activity sporadically or only juvenile stages [3].
- 3) Size: maximum body size (cm) reported in online databases [25,26]. Body size influences diet composition, with large cleaners usually preying on different items than smaller ones [27].
- 4) Coloration: number of body colours. Colour determines how conspicuousness of cleaners, including signalling to clients and contrast with background [28].
- 5) Water column position: bottom, medium, or top. Position in the water column influences the frequency of cleaning interaction: cleaners more associated to the bottom interact with fewer clients, as opposed to cleaners that stay higher in the water column [6,13].
- 6) School size: solitary, pair, small (3-20), medium (20-50), and large (> 50 individuals). Number of grouped cleaner individuals influence the efficiency of the cleaning services., in which larger schools are typically quicker than smaller ones.

Table 3S- 3. Biological traits of fish and shrimp cleaners considered in this study. Cleaners are organized by taxa and presented in alphabetical order. Water position: bottom (B), medium (M), and top (T); Schooling: solitary (S), pair (P), small (S), medium (M), and large (L).

Family/Species	Taxa	Type cleaner	Maximum body size (cm)	Number of body colours	Water position	Schooling
<b><i>Fishes</i></b>						
<b>Acanthuridae</b>						
<i>Acanthurus chirurgus</i>	Fish	Facultative	39	2	M	M
<b>Centranchidae</b>						
<i>Spicara melanurus</i>	Fish	Facultative	30	2	T	L
<b>Chaetodontidae</b>						
<i>Chaetodon robustus</i>	Fish	Facultative	14.5	3	M	P
<i>Chaetodon sanctaehelenae</i>	Fish	Facultative	18	3	M	P
<i>Chaetodon striatus</i>	Fish	Facultative	16	2	M	P
<i>Johnrandallia nigrirostris</i>	Fish	Facultative	20	3	B	M
<b>Gobiesocidae</b>						
<i>Diplecogaster tonstricula</i>	Fish	Facultative	3	3	B	S
<b>Gobiidae</b>						

<i>Elacatinus evelynae</i>	Fish	Obligate	4	4	B	F
<i>Elacatinus figaro</i>	Fish	Obligate	3.4	3	B	F
<i>Elacatinus phthirophagus</i>	Fish	Obligate	3.2	3	B	F
<i>Elacatinus pridisi</i>	Fish	Obligate	2.8	2	B	F
<i>Elacatinus prochilos</i>	Fish	Obligate	4	2	B	F
<i>Elacatinus spp</i>	Fish	Obligate	4	2	B	F
<i>Tigrigobius spp</i>	Fish	Obligate	3	4	B	S

#### **Grammatidae**

<i>Gramma brasiliensis</i>	Fish	Facultative	6.6	2	B	F
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#### **Haemulidae**

<i>Anisotremus virginicus</i>	Fish	Facultative	40.6	3	M	F
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#### **Labridae**

<i>Bodianus diplotaenia</i>	Fish	Facultative	76	4	B	S
<i>Bodianus insularis</i>	Fish	Facultative	33	1	M	S
<i>Bodianus pulchellus</i>	Fish	Facultative	28.5	3	M	S
<i>Bodianus rufus</i>	Fish	Facultative	40	2	M	S
<i>Bodianus speciosus</i>	Fish	Facultative	50	3	M	S
<i>Coris atlantica</i>	Fish	Facultative	15	2	M	F



<i>Coris julis</i>	Fish	Facultative	30	3	M	F
<i>Coris picta</i>	Fish	Facultative	25	4	B	M
<i>Coris sandageri</i>	Fish	Facultative	25	3	M	F
<i>Ctenolabrus rupestris</i>	Fish	Facultative	18	2	M	F
<i>Halichoeres sp</i>	Fish	Facultative	22	4	M	M
<i>Pseudolabrus luculentus</i>	Fish	Facultative	17	1	B	S
<i>Pseudolabrus miles</i>	Fish	Facultative	27.2	2	B	S
<i>Symphodus mediterraneus</i>	Fish	Facultative	9	3	M	S
<i>Symphodus melanocercus</i>	Fish	Facultative	14	2	M	F
<i>Symphodus ocellatus</i>	Fish	Facultative	12	4	M	F
<i>Symphodus tinca</i>	Fish	Facultative	44	2	M	M
<i>Thalassoma ascensionis</i>	Fish	Facultative	10	2	M	M
<i>Thalassoma bifasciatum</i>	Fish	Facultative	15	4	M	M
<i>Thalassoma lucasanum</i>	Fish	Facultative	15	3	B	F
<i>Thalassoma newtoni</i>	Fish	Facultative	25	2	M	M
<i>Thalassoma noronhanum</i>	Fish	Facultative	13.3	3	M	M
<i>Thalassoma pavo</i>	Fish	Facultative	25	3	M	M

### **Pomacanthidae**

<i>Holacanthus passer</i>	Fish	Facultative	35.6	4	B	S
<i>Pomacanthus paru</i>	Fish	Facultative	41.1	2	M	P
<b>Pomacentridae</b>						
<i>Abudefduf saxatilis</i>	Fish	Facultative	22.9	3	M	F
<i>Abudefduf taurus</i>	Fish	Facultative	25	2	M	F
<i>Chromis multilineata</i>	Fish	Facultative	12	2	T	L
<i>Microspathodon frontalis</i>	Fish	Facultative	31	2	B	S
<i>Stegastes rocasensis</i>	Fish	Facultative	8.5	2	M	S
<i>Stegastes sanctipauli</i>	Fish	Facultative	9	2	M	S
<b>Sparidae</b>						
<i>Diplodus argenteus</i>	Fish	Facultative	37.8	2	M	F
<b>Tetraodontidae</b>						
<i>Canthigaster capistrata</i>	Fish	Facultative	15	3	M	S
<b>Tripterygiidae</b>						
<i>Lepidonectes bimaculata</i>	Fish	Facultative	5	3	B	S
<b>Shrimps</b>						
<b>Inachoididae</b>						
<i>Stenorhynchus lanceolatus</i>	Shrimp	Facultative	5	2	B	P

**Lysmatidae**

<i>Lysmata ankeri</i>	Shrimp	Facultative	6.8	2	B	F
<i>Lysmata grabhami</i>	Shrimp	Facultative	6	2	B	F
<i>Lysmata spp</i>	Shrimp	Facultative	6	2	B	F

**Palaemonoidea**

<i>Periclimenes pedersoni</i>	Shrimp	Obligate	3	3	B	M
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**Stenopodidae**

<i>Stenopus hispidus</i>	Shrimp	Facultative	6	3	B	P
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## **Conclusão geral**

Diante dos resultados apresentados ao longo dos três capítulos desta tese, conclui-se que estudos sobre os fatores que influenciam a estruturação e manutenção das comunidades de peixes recifais em ambientes tropicais são diversos e que estes envolvem diferentes escalas espaciais. Por exemplo, no capítulo 1, demonstrou-se que fatores locais como a profundidade e nível de exposição a ondas são dois mecanismos que influenciam sobre a densidade e biomassa de peixes recifais. Isto pode ser devido a que sítios com maior profundidade e exposição, apresentam uma alta concentração de indivíduos grandes, incrementando a biomassa, enquanto lugares protegidos e com menor profundidade são dominados por espécies pequenas, apresentando altas densidades, mas baixa biomassa. Por outro lado, observou-se que a riqueza funcional e biomassa em uma ilha oceânica é elevada devido à pouca influência humana e a nível de isolamento, o qual ao limitar o número de espécies que colonizam este ambiente, eleva a redundância funcional pois uma função é cumprida por uma espécie.

Adicionalmente, demonstrou-se no capítulo 2 que fatores biogeográficos, energéticos e antropogênicos influenciam os padrões de riqueza de espécies, diversidade funcional, densidade e biomassa de peixes observados em ilhas oceânicas tropicais. No entanto a magnitude do efeito que cada um destes fatores exerce sobre as métricas anteriores da comunidade variam significativamente. Por exemplo, fatores biogeográficos tais como a área disponível e a distância ao recife mais próximo foram importantes individualmente, porém ao explorar seus efeitos conjuntamente, estes explicaram pouco a variação das métricas. Alternativamente, fatores energéticos e antropogênicos foram importantes tanto individualmente como em conjunto. Estes resultados sugerem que os padrões observados na riqueza de espécies, diversidade funcional, densidade e biomassa de peixes em ilhas oceânicas são o resultado de processos que ocorrem em escalas regionais.

Finalmente, demonstrou-se no capítulo 3 que as interações de limpeza entre peixes e outros organismos são um importante processo local que determina o nível de aninhamento de algumas comunidades recifais. Estes resultados apontam que os atributos das espécies têm um papel fundamental no desenvolvimento destas interações nos ambientes recifais.

Em conclusão os ambientes recifais tropicais apresentam uma ampla variedade de processos locais e regionais que determinam a estrutura e manutenção da diversidade. Outros componentes da diversidade como a diversidade funcional, densidade e biomassa devem ser mais utilizados pois estes oferecem uma visão mais ampla sobre os processos de dispersão, colonização, especiação e extinção.