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**BIOGEOGRAFIA DE ILHAS MARINHAS ATRAVÉS DA
ABORDAGEM FUNCIONAL**

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ABORDAGEM FUNCIONAL**

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Este trabalho é dedicado ao meu grande amor pelo mar

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“Toda grande caminhada começa com um simples passo”

Buda

RESUMO

A riqueza de espécies tem sido amplamente abordada visando entender os padrões que estruturam as comunidades biológicas. No entanto esta abordagem oferece uma visão incompleta do funcionamento do ecossistema, já que ela assume que as espécies são equivalentes, e perdas na diversidade são raramente compreendidas apenas analisando a riqueza de espécies. Considerando essa incompleta visão e o contínuo declínio da biodiversidade devido as interferências humanas, abordagens que levam em consideração o papel funcional das espécies no ecossistema, são chaves para compreender os processos evolutivos e ecológicos que determinam uma comunidade. A Teoria de Biogeografia de Ilhas é comumente abordada em estudos de diversidade taxonômica, porém estudos que abordam essa teoria em relação a diversidade funcional ainda são escassos. Trabalhos que visam entender como a diversidade funcional das espécies respondem às variações ambientais são cruciais para prever os efeitos das mudanças ambientais nos atributos, e por consequência, no funcionamento dos ecossistemas. Sendo assim, o objetivo deste estudo foi investigar a diversidade funcional de peixes recifais em setenta e duas ilhas oceânicas ao redor do globo que diferem em área atual, área passada, idade e no grau de isolamento. Mais especificamente, este estudo avaliou padrões nos índices funcionais de riqueza (FRic), divergência (FDiv), equitabilidade (FEve), redundância (FOR) e vulnerabilidade (FVul) das assembleias de peixes recifais nessas ilhas. Para este objetivo foi utilizado dados de ocorrência de espécies. Posteriormente cada espécie foi classificada de acordo com seus atributos biológicos para então construir um espaço multidimensional usando uma matriz de dissimilaridade de Gower e Análise de Coordenadas Principais (PCoA). Os índices funcionais (FRic, FDiv, FEve, FOR e Fvul) foram estimados para cada ilha oceânica a fim de verificar sua possível relação entre estes e a área submersa atual e passada da ilha, idade e grau de isolamento através de um modelo de regressão Beta. Nossos resultados demonstraram que a área atual, isolamento e idade influenciam nos padrões de diversidade funcional de peixes recifais em ilhas oceânicas tropicais. Foi observado um efeito positivo da área aos índices FRic, FDiv e FOR, uma vez que esses índices são correlacionados a riqueza de espécies. Por outro lado, a área teve um efeito negativo no FVul e FEve. O isolamento do continente teve um efeito positivo sobre o FVul e FEve, enquanto teve um efeito negativo sobre o FOR e FRic, podendo estar relacionado a menor riqueza de espécies em ilhas mais distantes da

costa. Da mesma forma, uma maior intensidade de filtros ambientais atuando ao longo do isolamento podem ter influenciado a relação positiva entre FEve e isolamento. O fator idade da ilha apresentou uma relação negativa com a FVul e positiva com FOR, possivelmente devido a ilhas antigas contarem com um maior tempo de colonização, aumentando o número de espécies dentro das entidades funcionais. A distribuição dos índices foi divergente entre os reinos biogeográficos, sendo que FRic, FDiv e FOR foram maiores nos reinos Indo-Pacífico Central, Pacífico Central e Índico Ocidental, enquanto os outros índices foram maiores nos reinos do TEP e Atlântico. Tal padrão sugere a influência do refúgio no arquipélago indo-australiano durante o período do quaternário e da proximidade atual do centro de origem das espécies de peixes recifais. Através desses resultados foi possível observar que a diversidade funcional segue um padrão semelhante a riqueza de espécies em relação à teoria de biogeografia de ilhas. Por fim, a integração da ecologia funcional na biogeografia de ilhas fornece uma melhor compreensão sobre a distribuição dos atributos biológicos em função das características do habitat.

Palavras-chave: Ilhas oceânicas, Diversidade funcional. Peixes recifais.

ABSTRACT

Species richness has been widely addressed to understand the patterns that structure biological communities. However, this approach provides an incomplete vision into ecosystem functioning, since it assumes that species are equivalent, and biodiversity loss is not completely understood through the species richness analysis. Considering this incomplete perception and the continuous decline in biodiversity due to human interference, approaches taking into account the functional species role are key to understanding the evolutionary and ecological processes that determine a community. Theory of Island Biogeography (TIB) is commonly addressed in studies of taxonomic diversity, but studies of TIB through functional diversity approach are still scarce. Studies that aim to understand how functional diversity responds to environmental changes are crucial to predict the effects of these changes on species traits, and consequently, on the ecosystems functioning. Thus, the goal of this study was to investigate the functional diversity of reef fish on seventy-two tropical oceanic islands that differ in current and past area, age and isolation of mainland. More specifically, this study aimed to evaluate the indices of functional richness (FRic), divergence (FDiv), evenness (FEve), over-redundancy (FOR) and vulnerability (FVul) of reef fish assemblage in these islands. In order to achieve that, species occurrence data was used, and each species was classified according to their biological traits to build a multidimensional space using a Gower dissimilarity matrix, and a Principal Coordinate Analysis (PCoA). Finally, the indices of FRic, FDiv, FEve, FOR and FVul were applied to each sample (i.e. oceanic islands) to verify the relationship between response variables (i.e. functional indices) and explanatory variables (i.e. current area, past area, age, and degree of isolation) through Beta regression model. Our results demonstrate that current area, isolation, and age influence patterns of functional diversity of reef fishes on tropical oceanic islands. A positive effect of area on the FRic, FDiv, and FOR indices was observed since these indices are correlated with species richness. On the other hand, the area had a negative effect on FVul and FEve. Isolation from the continent had a positive effect on FVul and FEve, while had a negative effect on FOR and FRic, which could be related to lower species richness in isolated islands. Likewise, a greater intensity of environmental filters acting along the isolation may influence the positive relationship between FEve and isolation. The island age showed a negative relationship with FVul and a positive

relationship with FOR, possibly due to older islands have a longer colonization time, increasing the number of species within the functional entities. The indices distribution was divergent between the biogeographic realms, with FRic, FDiv, and FOR being higher in the Central-Indo Pacific, Central Pacific, and Western Indian, while the other indices were higher in the TEP and Atlantic realms. This pattern suggests the influence of refuge in the Indo-Australian archipelago during the Quaternary period and also the closeness of the current reef fish centre of origin. Through these results, it is possible to observe that the functional diversity follows a similar pattern to species richness in relation to the Theory of Island Biogeography. Finally, integration of functional ecology in island biogeography provides a better understanding of biological traits distribution depending on the habitat characteristics.

Keywords: Oceanic islands. Functional diversity. Reef fish.

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1. Introdução geral

A perda da biodiversidade é cada vez mais frequente nos ambientes marinhos devido à constante necessidade das populações humanas por recursos, a qual cresce de forma exponencial (Mora et al., 2011). Este crescimento exponencial tem sido evidente em habitats como recifes de coral, onde a constante remoção de predadores de topo e grandes peixes herbívoros tem induzido mudanças de fases nestes habitats, como por exemplo, os quais passaram de ambientes dominados por corais, para ambientes cobertos de macroalgas (Estes et al., 2011, Sandin et al. 2008). Tradicionalmente, para acessar o status da biodiversidade têm sido utilizadas medidas clássicas baseadas na riqueza taxonômica e abundância das espécies (e.g. McNeely 2002). No entanto essas métricas oferecem uma visão incompleta do funcionamento do ecossistema, já que estas assumem que as espécies são equivalentes e perdas na diversidade são raramente compreendidas apenas pela riqueza de espécies (Weiher, 2011). Dada esta lacuna de conhecimento, abordagens que quantifiquem a diversidade funcional vêm sendo usadas para compreender melhor o funcionamento dos ecossistemas e as possíveis consequências na perda da diversidade. Essas métricas descrevem as espécies baseado em seus atributos e seus papéis dentro do habitat, permitindo um melhor entendimento sobre o funcionamento ecossistêmico dos ambientes marinhos (Weiher, 2011).

A diversidade funcional emergiu há aproximadamente 20 anos através de um debate sobre como a biodiversidade promove o funcionamento do ecossistema (Weiher, 2011; Diaz & Cabido 2001). Apesar desse debate ter sido um pouco controverso, através dele se iniciou um grande interesse em medir e quantificar a diversidade funcional. Sendo em 1999 publicado o primeiro trabalho relacionando medidas e as funções ecossistêmicas (ver Walker et al., 1999). Logo após, diversos trabalhos desenvolveram medidas para acessar a diversidade funcional (e.g. Mason et al., 2003; Petchey & Gaston 2002; Mouillot et al., 2005)

A abordagem funcional considera o conceito de nicho desenvolvido por George E. Hutchinson (Hutchinson, 1957), o qual descreve o nicho como um hipervolume n-dimensional que inclui todos os fatores bióticos e abióticos com os que interagem os organismos. Desta forma o nicho envolve todos os recursos presentes do ambiente e as adaptações dos organismos, em n-dimensões onde cada dimensão representa uma relação, em outras palavras o nicho funcional de cada espécie. A diversidade funcional

pode ser definida como a variação das espécies que coexistem baseado em seus atributos funcionais (Weiher, 2011). Estes atributos funcionais são definidos a partir de características morfológicas, comportamentais, tróficas e entre outras, que influenciam a performance da espécie e, por consequência, afetam o funcionamento do ecossistema (Mouillot et al., 2014). Os atributos funcionais podem ser classificados de acordo com a qualidade de informação (Petchey et al., 2006), como as informações de alta qualidade *hard traits*, que são informações diretas sobre padrões de uso de recurso (e.g. dieta, modo de forrageio), ou de baixa qualidade *Soft traits* que são informações indiretas geralmente usadas para compilar dados de uma grande quantidade de indivíduos (e.g. tamanho corporal; Petchey et al., 2006). O conjunto desses atributos forma uma entidade funcional, e em nível de comunidade, várias espécies podem se encaixar na mesma entidade funcional. E através das entidades funcionais é possível estimar diferentes índices da diversidade funcional

Os índices de diversidade podem ser divididos em três componentes primários, sendo eles, riqueza funcional, divergência funcional e equitabilidade funcional (Mason et al., 2005). Apesar desses três componentes antepor-se ao surgimento de novos índices, quando juntos, eles continuam sendo os mais adequados para acessar a diversidade funcional (Mouchet et al., 2010). A riqueza funcional pode ser definida como o volume preenchido em um espaço n-dimensional ocupado por uma comunidade (Villéger et al., 2008). Também conhecido por *Convex hull* volume, esse convexo é o perímetro de um polígono no qual é construído a partir de pontos que são os valores de atributos mais extremos das espécies. O algoritmo determina os pontos mais extremos, ligando-os e formando o convexo e posteriormente calcula o volume dentro do convexo. Sendo esse valor a medida de riqueza funcional (Villéger et al., 2008). Ela pode ser considerada alta quanto mais distantes forem os pontos (entidades funcionais), aumentando o volume do espaço funcional. A divergência funcional representa o grau que o táxon mais abundante está longe do centro de gravidade da assembleia em um espaço funcional, devido a valores de atributos extremos (Villéger et al., 2008). A divergência funcional é alta quando as espécies mais abundantes têm valores de atributos extremos, ou seja, ficando mais longe do centroide. Por outro lado, é considerada baixa quando as espécies mais abundantes têm atributos funcionais próximos ao centro de gravidade (Villéger et al., 2008). A equitabilidade funcional, mede a regularidade da distribuição das abundâncias das espécies no espaço funcional diminuindo quando a abundância ou as distâncias funcionais são menos regulares (Villéger et al., 2008). Portanto, quando as abundâncias forem

melhores distribuídas entre as espécies e as distâncias funcionais forem mais uniformes, maior será o índice de equitabilidade funcional. Enquanto que a divergência e equitabilidade funcional podem também levar em consideração a abundância relativa das espécies, ou seja, a contribuição de cada espécie é proporcional à sua abundância (Villéger et al., 2008). Além dos índices já mencionados, outros índices surgem com intuito de acessar outros aspectos da diversidade funcional, tais como: redundância funcional e vulnerabilidade funcional (Mouillot et al., 2014).

A diversidade funcional vai além da diversidade taxonômica, pois ela permite integrar tanto processos evolutivos associados aos atributos das espécies e como processos ecológicos associados ao papel que cada espécie desempenha no ecossistema, permitindo assim uma melhor compreensão sobre as regras de montagem que estruturam as comunidades (Mouillot et al., 2007). A estruturação das comunidades ocorre através de processos em diferentes escalas de tempo e espaço (Floeter et al., 2018). Processos como diversificação e especiação estariam por detrás dos padrões de diversidade funcional encontrados em escala global, todavia, levando em consideração o tempo evolutivo para gerar tal padrão (Floeter et al., 2018). Por outro lado, processos a nível regional, como a seleção (e.g. competição) e filtros abióticos (e.g. temperatura), moldam as comunidades locais de acordo com seus atributos funcionais (Floeter et al., 2018). Os atributos funcionais das espécies estão diretamente relacionados aos seus nichos e, conseqüentemente, com a repartição de recursos dentro de uma comunidade local (Mouillot et al., 2007).

A redundância ou vulnerabilidade funcional de um atributo, por exemplo 'tamanho corporal', pode variar em função da área e isolamento do local (Jacquet et al., 2016), seguindo a teoria de biogeografia de ilhas (TBI). A TBI proposta por Robert MacArthur & Edward Wilson em 1967, descreve que a riqueza local de espécies em ilhas é o resultado do balanço entre o número de espécies que já ocorrem previamente, a taxa de novas espécies através do processo de imigração e especiação, e a taxa de extinção. Esses processos ocorrem em resposta a duas principais variações ambientais, o tamanho da área e o grau de isolamento em que o sistema está inserido. Em adição a TBI, foi postulada a Teoria Dinâmica Geral de Biogeografia de Ilhas Oceânicas (Whittaker et al., 2008), que inclui a idade como um fator importante para a riqueza de espécies dado ao longo tempo geológico que permite maior colonização e especiação de espécies. Como resultado, é esperado uma maior riqueza de espécies em ilhas com grandes áreas, antigas

e pouco distantes em relação a ilhas com áreas pequenas, mais novas e mais isoladas. Ao passo que há uma menor taxa de imigração em locais mais isolados, podem ocorrer processos evolutivos como a diversificação, levando a especiação e ao aumento do número de espécies endêmicas. Mais recentemente, um novo modelo proposto por Fernández-Palacios et al. (2015), objetivou incorporar as implicações ecológicas e biogeográficas dos ciclos glaciais do Pleistoceno nos modelos biogeográficos anteriormente mencionados. O *glacial-sensitive model* (GSM) leva em consideração que a biodiversidade encontrada nas ilhas atualmente é resultado dos ciclos do nível do mar. Essas alterações no nível do mar tiveram efeitos sobre as configurações das ilhas oceânicas, como a área, elevação e o isolamento, influenciando nas taxas e padrões de imigração e extinção, e por consequência na riqueza de espécies (Fernández-Palacios et al., 2015).

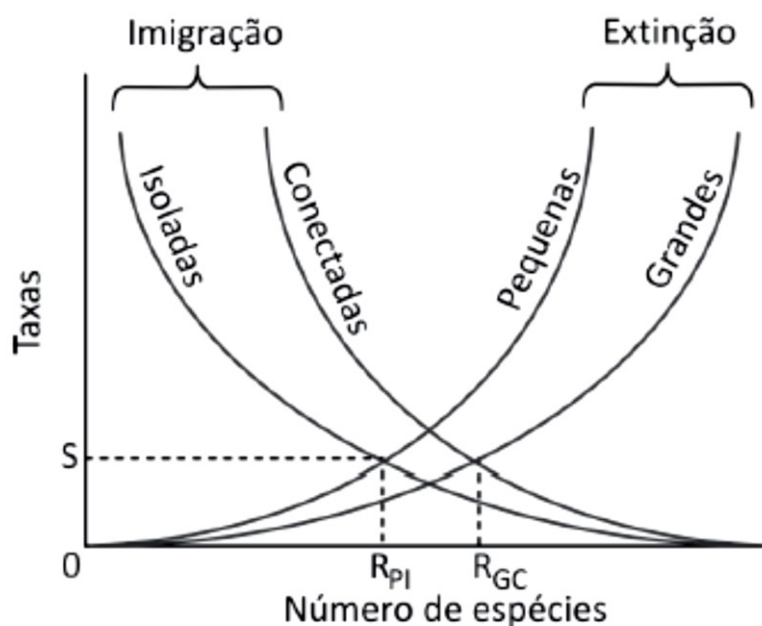


Figura 1: Modelo conceitual da Teoria de Biogeografia de Ilhas retirado de Ferreira et al. (in prep.)

No sistema marinho, a biogeografia de ilhas foi analisada em múltiplos táxons e em diferentes escalas espaciais (Hachich et al., 2015, 2020; Pinheiro et al. 2017). A relação espécie-área foi observada para peixes recifais (Hachich et al., 2015; Parravicini et al., 2013; Bellwood & Hughes, 2001) e para invertebrados (Pérez-Ruzafa et al. 2005;

Ávila et al. 2018). Uma vez observado que ilhas grandes possuem maior riqueza de espécies quando comparado com ilhas pequenas, tal padrão segue ao sistema terrestre. Por outro lado, a relação espécie-isolamento para grupos marinhos não parece ser universal, essa variação é devida à maior capacidade de dispersão de algumas espécies marinhas, fazendo com que a relação espécie-isolamento seja dependente da escala e dos táxons (Hachich et al., 2015; 2020). Apesar de poucos estudos marinhos sobre a relação espécie-idade, esta parece seguir o padrão dos sistemas terrestres (e.g. Hachich et al., 2015; Velasquez et al., 2018). Tal padrão pode ser explicado pelo tempo para acumulações de espécies, sendo equivalente a explicação do sistema terrestre.

Nas últimas décadas muitos estudos utilizam a TBI para tentar entender a variável área e isolamento como um processo ecológico determinando a riqueza de espécies (e.g. Quinn & Harrison 1988; Blackburn et al., 2016). Entretanto, por levar em consideração apenas a riqueza taxonômica, essa teoria assume que as espécies sejam iguais, ou seja, equivalentes funcionalmente. Em recente estudo abordando a influência dessa teoria (i.e. área e isolamento) sobre o atributo funcional ‘tamanho corporal’, foi observado que recifes pequenos e isolados apresentam maior proporção de espécies de peixes com elevado tamanho corporal em comparação com recifes grandes e conectados (ver Jacquet et al., 2016).

A partir desse contexto, trabalhos que visam entender como a diversidade funcional das espécies respondem à variação ambiental são cruciais para prever os efeitos das mudanças ambientais sobre os atributos, e por consequência, efeitos no funcionamento dos ecossistemas. Contudo, até o momento não foram realizados estudos que abordem a influência da TBI sobre uma gama de atributos funcionais das espécies de peixes recifais. Sendo assim o objetivo deste estudo foi investigar a diversidade funcional de peixes recifais em 72 ilhas oceânicas localizadas ao redor do globo que diferem em área, idade e no grau de isolamento. Mais especificamente, nós esperamos que (i) ilhas grandes, conectadas e antigas serão positivamente relacionadas com a riqueza funcional, a divergência funcional e a redundância funcional, (ii) enquanto ilhas pequenas, isoladas e novas serão negativamente relacionadas a esses índices e positivamente com equitabilidade e vulnerabilidade funcional (Fig 1).

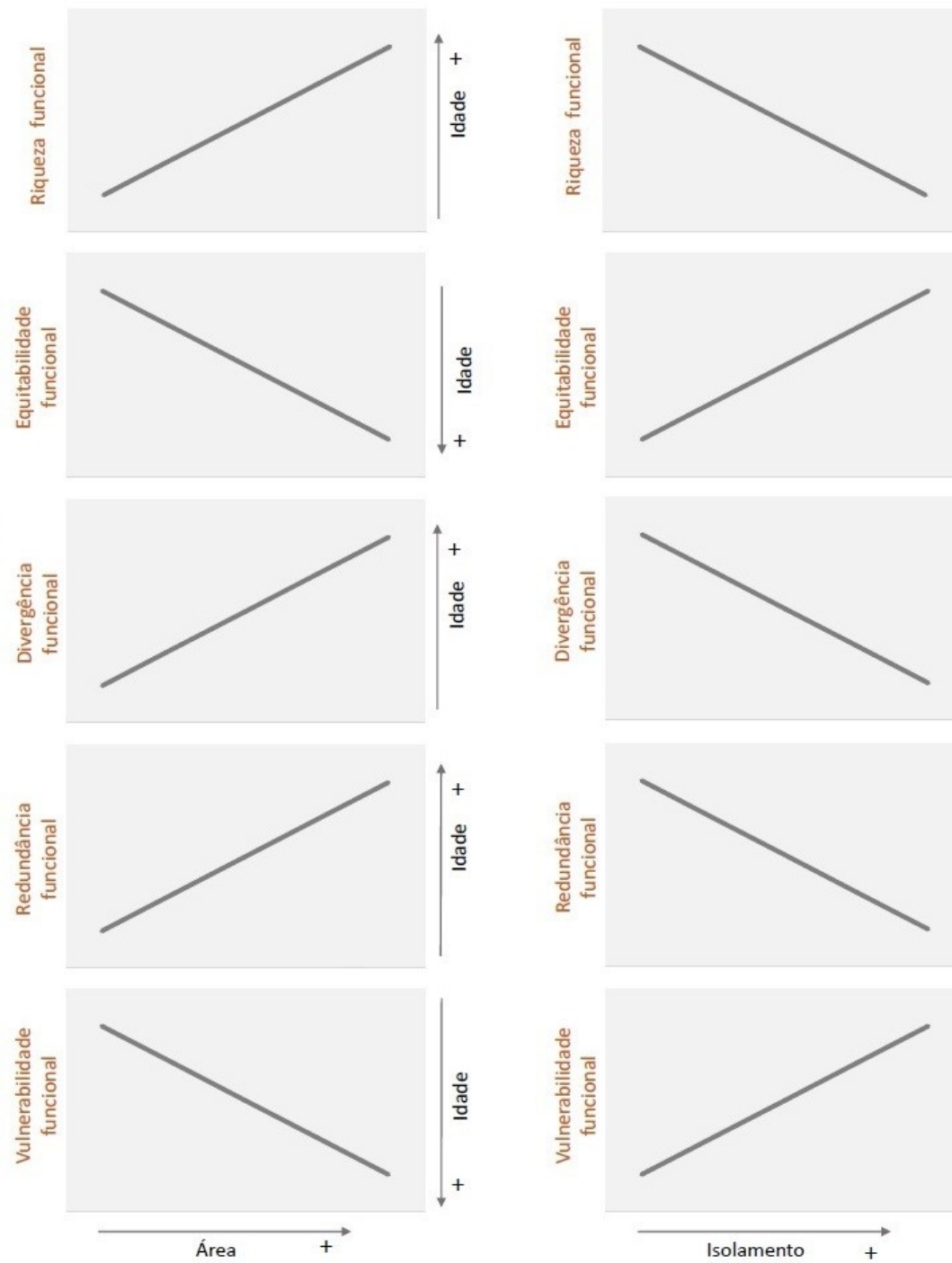


Figura 2: Relações hipotéticas entre riqueza funcional, equitabilidade funcional, divergência funcional, redundância funcional, vulnerabilidade funcional, e os fatores biogeográficos: área, idade e isolamento.

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2. Capítulo único: *A trait-based approach to marine island biogeography*

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A trait-based approach to marine island biogeography

Running head: Functional Marine Island Biogeography

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Keywords: Functional diversity, reef fish, area island, isolation, age island, oceanic islands.

Abstract**Aim**

The Theory of Island Biogeography (TIB) is among the most well-known patterns that explain species distribution. However, how this theory can explain the functional diversity in remote habitats, such as oceanic island, remains a challenge. Here, we evaluated how functional diversity of reef fish in oceanic islands vary according to past and current island features.

Location

Tropical oceanic islands.

Major taxa studied

Reef fish

Methods

We tested whether the following five functional metrics: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), functional over-redundancy (FOR), and functional vulnerability (FVul) are influenced by island features (i.e., age, isolation, current and past area). We combined literature data and online repositories to gathered occurrence data and traits of reef fish assemblages in oceanic islands. We used beta regressions to evaluate the effect of island features over functional metrics.

Results

Overall, we identify a positive effect of area on the FRic, FDiv and FOR, whereas a negative effect on the FVul and FEve. The isolation from mainland had a positive effect on the FVul and FEve, whereas a negative effect on the FOR and FRic. Island's age holds a positive effect on FOR, whereas negative effects on FVul. FRic, FDiv and FOR shows a positive relation with species richness, while, FEve and FVul had a negative relation. The FRic, FDiv and FOR were higher in the Central-Indo Pacific, Central Pacific, and Western Indian, whereas other indices were higher in TEP and Atlantic realms.

Main conclusions

Our results demonstrated that island features, such as current area, isolation, and age also influence on functional diversity patterns of reef fishes in tropical oceanic islands, extends the TIB towards a functional approach. Furthermore, our results provide a parsimonious explanation to functional distribution in remote habitats and open new perspectives to integrate species traits into simple models.

1. Introduction

The Theory of Island Biogeography (TIB) predicts that local species richness results from a balance between immigration and extinction rates (MacArthur & Wilson, 1967). This process occurs due to immigration rates to be altered based on island isolation, and extinction rates which vary according to island area (MacArthur & Wilson, 1967; Whittaker et al., 2017). In addition to these drivers, the General Dynamic Theory of Oceanic Island Biogeography (GDM) considers that the geological age of islands is an important driver that regulate the species richness (Whittaker et al., 2008), speciation and extinction in these habitats (Pinheiro et al., 2017). Recently, the glacial-sensitive model (GSM; Fernández-Palácios et al., 2016) shown that sea-level cycles can also influence island's biodiversity, since these alter the available area, elevation and isolation, and consequently the patterns of immigration, speciation, and extinction (Fernández-Palácios et al., 2016; Pinheiro et al., 2017; Ávila et al., 2019). Although these theories have provided important insights to understanding the processes determining assemblage rules in islands, these only take into account the taxonomic approach and explored patterns in territorial organisms. Thus, disentangling the intrinsic features of marine species and the drivers regulating their functional diversity is still challenging. This will require a comprehensive functional approach that takes count species traits, since these intrinsic features may suggest the functional role development by each species (Mouillot et al., 2014; Bellwood et al., 2019).

The functional approach has been recognized as an effective tool to study biodiversity and to better understand the role of species in ecosystem mechanisms (McGill et al., 2006). Furthermore, functional biogeography provides an important framework for analysing large-scale patterns in trait combinations (Mouillot et al., 2014). Despite advances in functional diversity studies concerning the marine environment (e.g., Villéger et al., 2011; Stuart-Smith et al., 2013; Mouillot et al., 2014), little attention has been given to functional marine island biogeography, because species richness has dominated our “way of thinking” on global biodiversity patterns. For instance, studies have showed a strong positive relationship between species richness of marine organisms with available area and island age (Bellwood & Hughes, 2001; Pérez-Ruzafa et al., 2005; Parravicini et al., 2013; Hachich et al., 2015; Ávila et al., 2018); while, species–isolation relationship does not seem to prevail, because marine species generally have higher

dispersal capacity than territorial organisms (Hachich et al., 2015, 2020). Although some studies have postulated that marine communities in islands exhibit a reduce functional combination of traits because these are taxonomic subsets from the mainland (Bender et al., 2017), the effect of island features remain largely unexplored. Here, we tackle this issue evaluating how past and current island features (i.e., area, isolation and age) influence functional diversity of reef fish the most diverse vertebrate assemblages on Earth.

The functional diversity of a given community may comprise several components which provide different details on the mechanisms that operate in the formation of communities and ecosystem functioning (Mason et al., 2005; Villéger et al., 2008; Mouillot et al., 2013). For instance, the functional richness “FRic” is influenced mainly by environmental filters (e.g., isolation) that controlling the presence or absence of trait (i.e., species) in a community (Villéger et al., 2008). The functional evenness “FEve” and functional divergence “FDiv” respond more to local-scale factors (i.e., interactions between species) which can determine how the abundance or biomass of a species is distributed within a community (Bello et al., 2013). On the other hand, the functional over-redundancy “FOR” and functional vulnerability “FVul”, are emerging faces that can provide empirical evidence on speciation processes, since the exclusiveness of a trait or not is consequence the evolutionary drivers (Mouillot et al., 2014). Thus, understanding how each component of functional diversity responds to past and current island features is crucial to unrevealing the processes structuring marine communities and ecosystem functioning.

Here, we compiled a compressive dataset of local reef fish checklists and traits from 72 tropical oceanic islands with two goals in mind. We firstly describe the global patterns of distribution of the functional components in tropical oceanic islands. As observed in the taxonomic approach, we expected that large and connected islands have a high functional richness, functional divergence, and functional over-redundancy, because these islands have a higher variety of habitats and the probability be colonized favour a high diversity with different traits. In contrast, we expected that small and isolated islands have a higher functional evenness and functional vulnerability because these islands will be shaped by limiting similarity – when two species cannot coexist due to their similarities, and to compete for the same limited resource –, resulting in a high

evenness in species traits composition (Hachich et al., 2020). In the same way, it is expected in isolated and small islands to find few species possessing the same set of traits – species that fit into the same functional entity – because the species island pool is only a small subset from the coastal areas (Bender et al., 2017), and thus contributing to a context of functional vulnerability. We also expected that old island have a high functional richness and functional over-redundancy and low functional evenness, functional divergence and functional vulnerability because species in old islands have a longer colonization time, which increases the number of species and functions in the community and reducing the divergence between these functions. Second, we describe the relationships between the functional components (i.e., FRic, FEve, FDiv, FOR, FVul) and the local species richness reported in each tropical oceanic island. We expected a positive correlation between functional richness, functional over-redundancy and functional divergence with species richness, since both functional components are dependent of the local pool. In contrast, we expected a negative effect of species richness on the functional vulnerability and functional evenness, since the increase of species richness favour more species performing the same function.

2. Materials and Methods

2.1. Study region

Our study comprised seventy-two tropical oceanic islands from six marine biogeographical realms (Figure 1). These marine realms include the Western Indian, Central-Indo Pacific, Central Pacific, Tropical Eastern Pacific, Western Atlantic and Eastern Atlantic (sensu; Kulbicki et al., 2013). All the islands considered in this study never had a connection with the mainland and they are mostly the volcanic origin with low reef development (Dawson, 2015). On the other hand, due to high isolation and small area, these islands have subset reef fish assemblages (Bender et al., 2017). We considered each archipelago as a sample unit since there is no significant difference in species composition amongst the archipelago's islands (Hachich et al., 2015; Bernardi et al., 2014). The area in these islands goes from 3.5 to 36.7 km², age amongst 0.5 to 91 Ma, and distance from the mainland range from 227 to 5.380 km (Table S1)

2.2. Reef fish assemblages and species traits

We gathered reef fish checklists of oceanic islands from articles, online repositories, books and monographs compiled by GASPAR (General Approach to Species-Abundance Relationships) group. Additionally, we compiled information on the six species traits defined by Mouillot et al. (2014). To Atlantic and Tropical Eastern Pacific were obtained data from Quimbayo et al. (2021), and to other provinces were databases, books and online repositories (Mouillot et al., 2014). These functional traits have been successfully used to infer the functional role of each reef fish species within its habitats (Bender et al., 2017; Quimbayo et al., 2019). These traits were: Maximum body size: < 7 cm, 8–15 cm, 16–30 cm, 31–50 cm, 51–80 cm or > 80 cm; Mobility: sedentary, territorial species, mobile and very mobile; Period of activity: diurnal, nocturnal, or both; Gregariousness: solitary, pairing, small groups of 3–20 individuals, medium groups of 20–50 individuals or large groups > 50 individuals; Position in the water column: benthic, benthopelagic, or pelagic species; Trophic group: herbivores-detritivores, macroalgae-feeders, sessile invertebrate feeders, mobile invertebrate feeders, planktivores, piscivores or omnivores.

2.3. Functional components

The indices analysed correspond to the primary components of functional diversity (Mason et al., 2005). Functional richness (FRic) measures the volume filled in an n-dimensional space occupied by a community; Functional evenness (FEve) measures the regularity of species distribution in functional space. FEve decreases when functional distances are less regular; Functional divergence (FDiv) for presence and absence data relates to the distance between species distribution of convex hull and the centre of gravity (Villéger et al., 2008). Functional divergence will be high when distances are similar to species from the centre of gravity. Additionally, we estimated functional over-redundancy, where many species fit into the few functional entities and therefore possibly perform the same functions. Lastly, functional vulnerability, where only one or a few species have the same combination of biological attributes (Mouillot et al., 2014).

2.4. Environmental data

For all islands, we estimated the current area that corresponds to the shallow shelf area down to 200 m, a depth which is traditionally defined as shallow-water habitats (Lalli & Parsons, 1997; Hachich et al., 2020), based upon Gridded Bathymetric Data GEBCO 30 arc-second grid (www.gebco.net/data_and_products/gridded_bathymetry_data/gebco_30_second_grid). We also calculated the past area based on the last glaciation, where the sea level decreasing 120 m from the current sea level (Fernández-Palacios et al., 2016). Hence, we estimated again the shallow shelf area down to 200 m depth, which means that we use the isobaths 320 m as a proxy to the past area. Island age was considered a time estimate of an island emerging from the surface, this data was compiled from the literature. Isolation was measured through the distance from each island to the nearest mainland point, this data was assessed through satellite images (Table S1).

2.5. Data Analyses

We used the six life-history traits assigned to each species to build the multidimensional functional space occupied by each local species pool (species registered in local checklist). The multidimensional functional space was built from a Principal Coordinates Analysis (PCoA) using Gower's distance dissimilarity matrix, which allows mixing qualitative and quantitative data. Through functional space it was possible to calculate the Functional Richness (FRic), which corresponds to the volume of

multidimensional space. We also calculated the Functional Evenness (FEve) and Functional Divergence (FDiv). These analyses were performed using *multidimFD* function from Mouillot et al. (2013). We also calculated Functional Over-redundancy (FOR) and Functional Vulnerability (FVul) of the reef fish community. This analysis was performed using *species_to_FE* and *FE_metrics* functions from Mouillot et al. (2013). We examined the quality of functional space that would reflect our life-history trait space, using the *quality_funct_space* R function. As expected, the quality of representation increased with the number of axes (Figure S1) (Maire et al., 2015). We kept only the first four axes for the convenience of graphical representation and because they represented more than 70% of the explained variance in the data.

To evaluate potential collinearity among the different island features (i.e., past and current area, age, and isolation), we used Pearson correlations, considering a correlation coefficient < 0.7 as a cut-off value for keeping island features (i.e., predictors) in the models. The past area showed an autocorrelation with the current area (Figure S2), thus we removed this variable from the models. Additionally, we estimated the variance inflation factor (VIF) using the “vif” function from the *car* package (Fox and Weisberg, 2019) to ensure that predictors were not correlated with each other, considering a value < 3 as a cut-off.

We employed beta regressions to evaluate how functional components of reef fish were influenced by island features (i.e., past and current area, age, and isolation). These models were built using the “betareg” function from *betareg* package (Cribari-Neto & Zeileis, 2010). This type of model was used because the values from functional components varied in a standard unit interval (0-1). We also included the quadratic term of age, area and isolation to investigate whether a non-linear relationship better fits data on the functional indices. Finally, we did the linear models with a smooth on the x predictor variable ($I(x^2)$), to test the effect of species richness on the different components the functional diversity of reef fish in oceanic islands. All the analyses and figures were performed in R software (R Core Team).

3. Results

A total of 4632 species and 569 functional entities belong to 157 families were observed in all the tropical oceanic islands. The functional richness (FRic) and functional over-redundancy (FOR) range between 0.12 – 0.83 and 0.33 – 0.56 respectively, being highest in the Central-Indo Pacific, Central Pacific and Western Indian realms than in the Atlantic and Tropical Eastern Pacific (Figure 1). In contrast, the functional evenness (FEve) and the functional vulnerability (FVul), which range between 0.22 – 0.66 and 0.46 – 0.85 respectively, showing its highest value in the Tropical Eastern Pacific and Atlantic, whereas the other realms exhibited low values (Fig 1). Finally, the functional divergence (FDiv) that range 0.74 – 0.85 was high in the Central-Indo Pacific, Central Pacific, Tropical Eastern Pacific and Western Indian but low in all realms within the Atlantic (Figure 1).

Our results indicated that current area, age and isolation from the mainland were important predictors that explain the variation in the functional components of the functional diversity of reef fishes observed in oceanic islands (Figure 3). The magnitude and direction of predictors varied among functional components. For instance, current area had a positive effect on FDiv and FOR, and marginally significant on FRic ($p=0.07$), whereas the isolation had a negative effect on FRic, FDiv, and FOR (Fig 3). In contrast, we observed a positive effect of isolation on FEve and FVul, but negative effect the current area on these two components. The island age had a positive effect on FOR, whereas presented a negative effect on FVul (Figure 3). The species richness had a positive relationship with the FRic, FDiv and FOR, whereas a negative effect on the FEve and FVul (Figure 2).

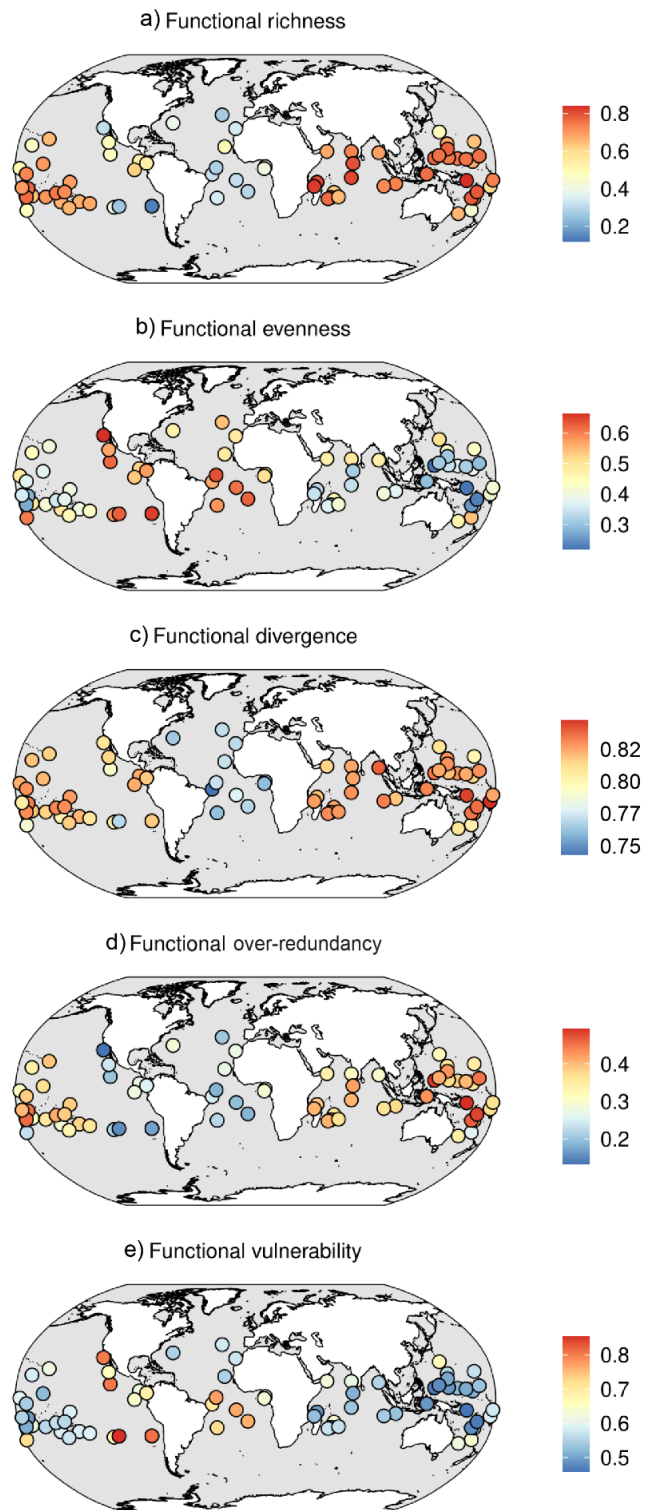


Figure 1: Distribution of reef fish functional diversity at 72 oceanic islands worldwide. (a) Functional richness, (b) Functional evenness, (c) Functional divergence, (d) Functional over-redundancy and (e) Functional vulnerability. Each point represents an oceanic island and the colours represent the variation of functional values

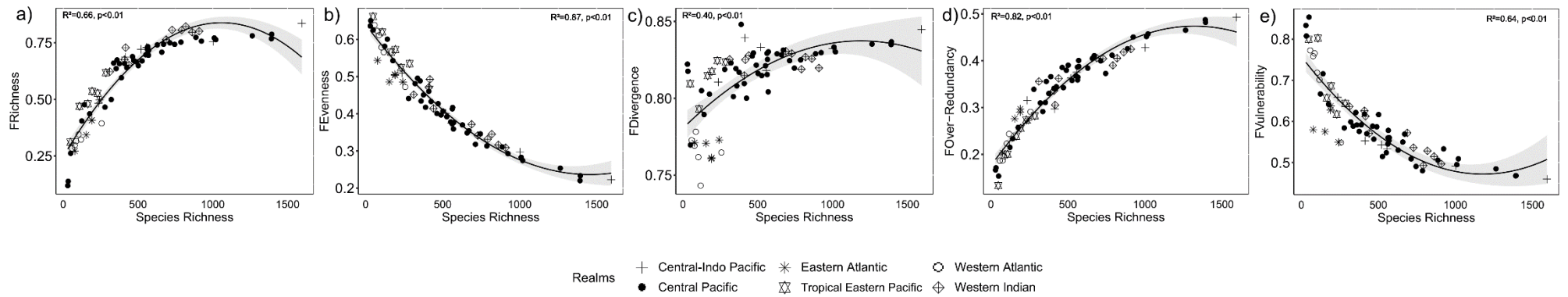


Figure 2: Relationships between species richness and functional indices. (A) Functional richness, (B) Functional evenness, (C) Functional Divergence, (D) Functional over-redundancy and (E) Functional vulnerability. Each point represents an oceanic island and each symbol represent a specific realm. The shaded areas represent confidence intervals of the regressions.

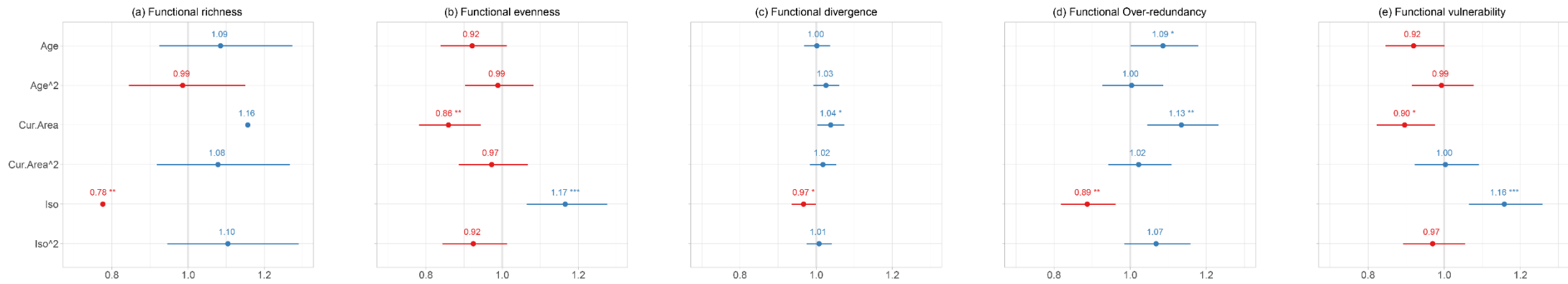


Figure 3: Mean effects of Age, Age², Current area, Current area², Isolation from mainland and Isolation from mainland² factors on the reef fish functional diversity from tropical oceanic islands worldwide. Results for (a) Functional richness, (b) Functional evenness, (c) Functional divergence, (d) Functional over-redundancy and (e) Functional vulnerability. Circles represent mean parameter estimates and lines represent 95% confidence intervals. Red lines indicate values below zero and blue lines indicate values above zero. * indicate significant mean values.

4. Discussion

In this study, we analysed the response of reef fish assemblages to past and current island features (i.e., age, isolation, past and current area) using five functional components (i.e., functional richness, functional evenness, functional divergence, functional over-redundancy, and functional vulnerability) in tropical oceanic islands. Our findings showed island's features as key drivers explaining the functional diversity of the reef fish in oceanic islands. The singularity of oceanic islands features can lead to non-random processes of biological communities' structure. Environmental filtering (e.g. barriers) and local filtering (e.g. competition) could shape the functional reef fish structure on these systems. Furthermore, our results revealed a high disparity in the distribution of functional components among the marine realms, which suggests a strong historical and evolutionary signal in the functional diversity of reef fish assemblages in tropical oceanic islands.

4.1 Environmental and local filtering acting on functional diversity

The positive effect of the area on the FRic supports our initial hypothesis since large areas have more habitats types, higher ecosystem productivity and higher niches available that favour high colonization and speciation rates (Whittaker & Fernández-Palacios, 2008; Hachich et al., 2015) and consequently a high combination of species traits. This positive pattern has been observed in plants, birds, ants and spiders (Ding et al., 2013; Whittaker et al., 2014; Zhao et al., 2020). On the other hand, a decrease in FRic was observed according to isolation, confirmed our first hypothesis, following the species-isolation relationships (SIR) where the number of species decreases with isolation. Even though to reef fishes, isolation does not seem to predict species richness pattern (Hachich et al., 2015), we found this prediction for functional richness. The species distribution will depend on dispersal ability which is associated with body size and pelagic larval duration (Luiz et al., 2012, 2013) and have more influence by environmental conditions.

The association between the dispersion capacity of the organism and the different environmental filters that limited the arrival of many species in isolated islands, may results in a subset species with different attributes increasing the vulnerability and

reducing redundancy (Bender et al., 2017; Hachich et al., 2020). Hence, we observed that functional vulnerability showed higher values in small and isolated islands than in large and connected islands. The mid-Atlantic ridge islands of Ascension and St. Helena Islands, even with large areas, both showed high vulnerability due to their fish composition, being among the most isolated places in the world (Floeter et al., 2008). In terms of geographic range of species, it is known that dispersal ability is influenced by larval traits (Luiz et al., 2013). To reef fishes, the trait pelagic larval duration (PLD) is considered a determinant of dispersal ability (Mora et al., 2012), and adult traits may influence the establishment and persistence of species in isolated places, such as body size, schooling behaviour, and nocturnal activity (Luiz et al., 2013). Thus, winner dispersers and species who own part of these adult traits are favoured and can overcome barriers, great distances and have the ability to settle in remote islands.

Our results also showed that the regularity of species in the functional space (i.e. Functional evenness) decreases according to area, which presents an opposite pattern that found in SAR to marine organisms (Hachich et al., 2015). Thus, the functional evenness is possibly somehow related to species richness variations. We observed that functional evenness increases in more isolated islands and more depauperate fauna, as in the case of mid-Atlantic ridge islands (Figure 1). We hypothesize that local filtering (e.g. competition) in this place, is a driver that explains the low functional similarity and consequently the high functional evenness of functional entities. This may explain limiting similarity of species traits (greater functional evenness) found as one moves from more connected to isolated reef areas. The species in large and more connected islands are disproportionally distributed, concentrated in certain areas of the functional space, i.e. lower functional evenness, such as the islands of Central-Indo Pacific and Central Pacific. We hypothesize that these islands accommodate more functionally similar species due to a combination of higher colonization from the source pool and more niches available in three-dimensional reefs of the Indo-Pacific, which allows similar species to colonize and persist.

Island age has been documented as an important predictor that explains the functional diversity of terrestrial systems. According to Borregaard et al. (2017), in the most advanced stage of island age, habitat loss would lead to fewer niches available and greater competition between species with similar traits, thus, increasing extinction rates.

However, for marine systems, an opposite scenario is expected. Once the erosion of the islands progresses, the submerged area tends to increase (Ávila et al., 2019; Pinheiro et al., 2017). Thus, it is expected that marine functional diversity found on old islands follow the patterns of larger islands. Furthermore, it is expected that greater colonization time and establishment found in old islands favour the inclusion of species and add the number of species inside the functional entities, increasing the FOR and reducing the FVul.

4.2 Historical and evolutionary signal in the functional diversity

The region of the Indo-Australian archipelago is known to hold the greatest species of tropical marine biodiversity and this pattern have been strongly influenced by the Quaternary period (Pellissier et al., 2014). The Indo-Australian archipelago maintained a refuge and was the source of recolonization, and hence also to high speciation rates being drivers responsible for shaping the current worldwide reef fish richness patterns (Pellissier et al., 2014). The impact of the past on reef fish diversity of Indo-pacific realms could lead to the higher functional richness (FRic), functional divergence (FDiv) and functional over-redundancy (FOR) values since these indices are highly correlated with species richness (Figure 2). Contrarily, TEP and Atlantic realms hold the lowest values of these functional components, which are dependent on species richness. This makes sense once these realms had the highest levels of isolation from the refuge, and consequently, little diversity and diversification of reef fish assemblages (Pellissier et al., 2014).

Despite large and more connected islands had a high influence on FOR, we need to consider that the effect of the Quaternary period on the Indo-Pacific and Central Pacific, help increase the FOR of reef fishes in these places. Nevertheless, in species-rich places, we cannot ignore that this redundancy can be packed disproportionately (i.e. the most species are packed inside few functional entities leading to over-redundancy). Thus, despite higher taxonomic richness, functional vulnerability, even being lower, cannot be overlooked once the loss of a few species may affect some functions (Mouillot et al., 2014). Besides the FOR pattern, we also expected the highest FDiv in communities with a large functional space (i.e. high FRic) due to a great distance between the centroid of functional space and extreme functional entities. We found a lower FDiv as one moves from regions close to quaternary refugia to areas isolated from refugia. In fact, little diversified and isolated islands of the Atlantic had the lowest FDiv pattern, while Central-

Indo Pacific, Central Pacific, and Western Indian realms carry on a higher FDiv value, and also in some small islands of TEP. These regions hold a range of species with specific traits due to the great species diversification arising from the centre of origin and diversification (Mora et al., 2003).

5. Conclusion

We demonstrated that island features are key drivers that explain the functional diversity of the reef fish in oceanic islands, extent important theories, such as the Theory of Island Biogeography (TIB), the General Dynamic Theory of Oceanic Island Biogeography (GDM) and Glacial-Sensitive Model (GSM) within the functional approach. The increase of island areas influences habitat heterogeneity and niche availability. Similarly, the old islands keep these habitat types according to the increase of the geological age, favouring a high combination of species traits. Beyond habitat conditions, species are also influenced by isolation level and may be filtered according to functional traits linked to colonization and establishment. Furthermore, we found a high disparity in the distribution of functional indices among marine realms, which suggests a large influence of historical and evolutionary factors on the functional diversity of reef fish assemblages on tropical oceanic islands. Finally, the pattern found in this study offers new insights, showing that functional indices of reef fishes tend to follow the biogeographic drivers suggested by the Theory of Island Biogeography. Thus, we suggest the functional approach use in classical theories, since this approach recognises the distinct species characteristics, and comprehends the intrinsic role of species both in the community structure and in the ecosystem functioning. This study also comprised the first step towards the use of new metrics in the Theory of Island Biogeography, which can be further expanded in studies of other marine taxa.

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Data availability statement

Data of species traits can be found at the <http://doi.org/10.5281/zenodo.4455016>

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Supplementary material

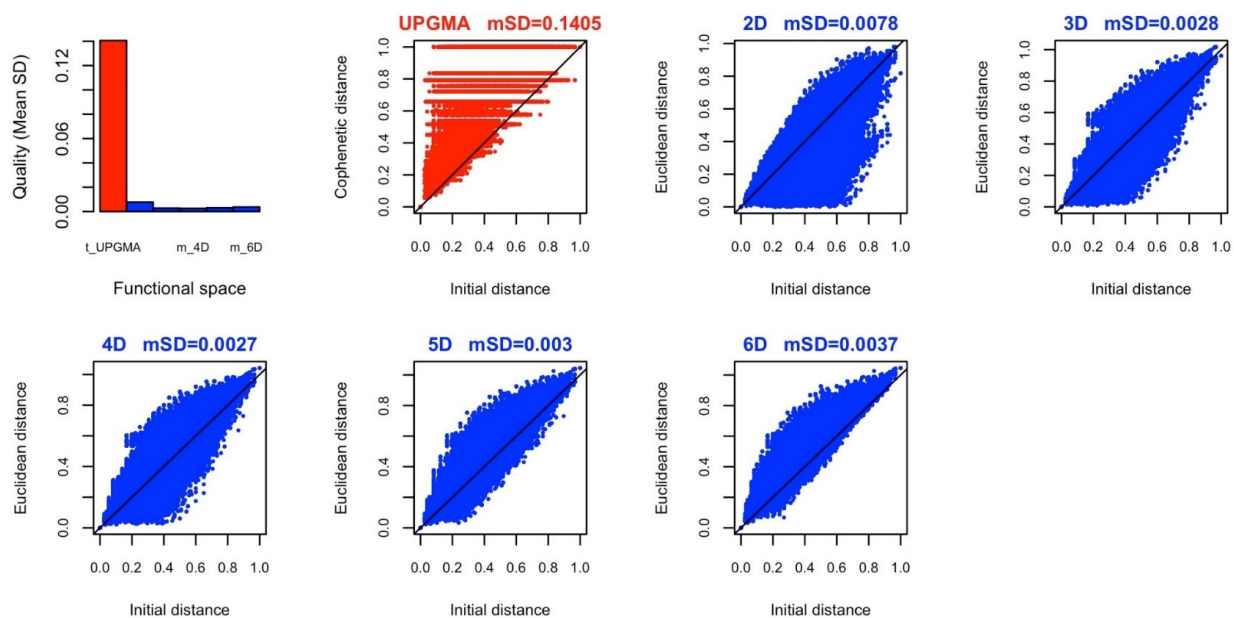


Figure S1: Representation of quality of functional space. The first panel (Top-left) shows the quality of six functional spaces calculated for a dataset of 4632 reef fish species described with six functional traits. The second panel (from top-left) is the UPGMA dendrogram and the other panels are multidimensional spaces built using a principal coordinates analysis.

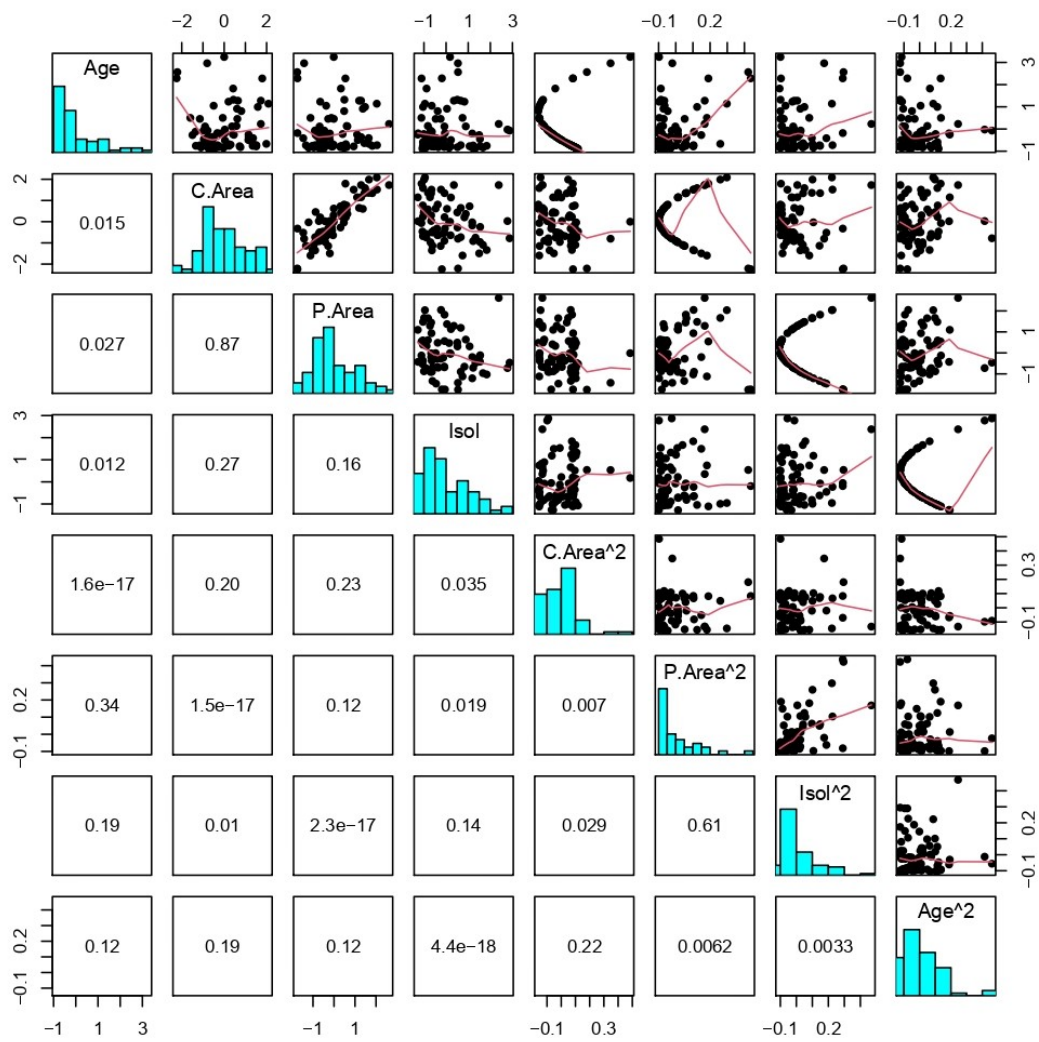


Figure S2: Correlation plot of candidate continuous covariates

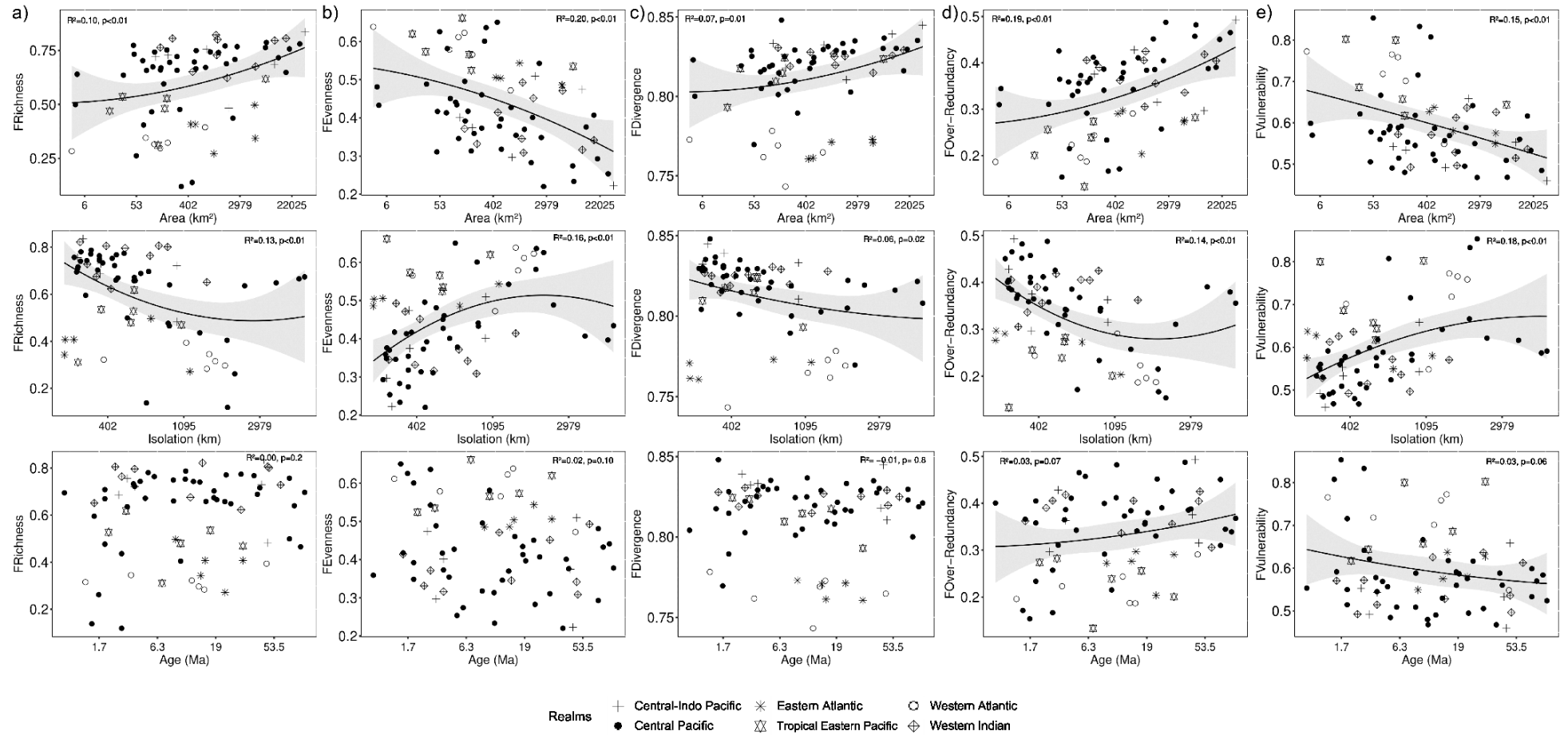


Figure S3: Relationships among biogeographic factors (area, isolation and age) and functional indices. (A) Functional richness, (B) Functional evenness, (C) Functional Divergence, (D) Functional over-redundancy and (E) Functional vulnerability. Each point represents an oceanic island and each symbol represent a specific realm. The shaded areas represent confidence intervals of the regressions.

Table S1: List of oceanic islands analysed in this study. Functional indices values and biogeographic factors considered in the comparative analyses of reef fish assemblages in each oceanic island. Western Atlantic (WAtl), Eastern Atlantic (EAtl), Western Indian (WInd), Central-Indo Pacific (CIPac), Central Pacific (CPac) and Tropical Eastern Pacific (TEP).

Realm	Oceanic island	Species richness	Functional richness	Functional divergence	Functional evenness	Func. Over-redundancy	Functional vulnerability	Isolation (km)	Area (km ²)	Past area (km ²)	Age (Ma)
WInd	Aldabra	792	0.81	0.82	0.33	0.39	0.49	394	218.3	169.4	2.58
CIPac	Ambon islands	1002	0.76	0.83	0.30	0.43	0.49	271	815.5	447.9	3.40
CIPac	Andaman Nicobar	414	0.69	0.84	0.47	0.30	0.55	364	11283.2	1332.0	2.80
WAtl	Ascension	86	0.32	0.78	0.61	0.20	0.77	1659	108.3	78.0	1.15
CPac	Australes Islands	337	0.66	0.80	0.50	0.29	0.59	448	137.5	53.1	8.74
EAtl	Azores	77	0.27	0.77	0.54	0.20	0.58	1188	1082.6	727.7	22.57
CPac	Baker and Howland	321	0.50	0.82	0.48	0.31	0.60	521	4.2	6.2	70.10
WAtl	Bermuda	257	0.39	0.76	0.47	0.29	0.55	1133	773.4	54.7	47.00
EAtl	Cabo Verde	242	0.50	0.77	0.49	0.27	0.55	712	5277.1	1975.9	9.09
EAtl	Canaries	154	0.34	0.77	0.49	0.28	0.58	227	5368.1	1841.2	14.50
WInd	Carajos Island	312	0.62	0.83	0.45	0.36	0.64	420	1817.3	199.4	30.00
WInd	Chagos	728	0.81	0.83	0.34	0.40	0.54	788	17654.4	2692.1	48.00
CIPac	Christmas	557	0.73	0.82	0.37	0.38	0.53	367	183.6	96.2	43.00
CPac	Chuuk	629	0.74	0.83	0.37	0.38	0.53	281	1300.9	35.2	14.30
TEP	Clipperton	108	0.47	0.79	0.62	0.20	0.80	1062	18.4	21.6	31.00
CIPac	Cocos Keeling	520	0.72	0.83	0.40	0.36	0.54	998	113.2	33.7	4.00
TEP	Cocos TEP	230	0.53	0.82	0.52	0.27	0.62	565	176.1	55.3	2.20
WInd	Comores Mayotte	819	0.82	0.83	0.35	0.41	0.53	279	1175.9	464.2	15.00
CPac	Cook Islands	563	0.70	0.82	0.41	0.36	0.56	352	68.7	33.1	18.50

CPac	Desventuradas	30	0.12	0.82	0.64	0.17	0.83	1950	307.5	162.7	3.00
CPac	Easter island	124	0.40	0.80	0.58	0.22	0.67	1937	70.9	87.9	10.00
WAtl	F Noronha	118	0.32	0.74	0.57	0.24	0.70	382	181.8	51.5	12.30
TEP	Galapagos	285	0.62	0.82	0.53	0.28	0.64	571	8042.6	7845.6	3.31
CPac	Gambier	490	0.67	0.82	0.40	0.38	0.59	4998	540.9	47.9	19.44
TEP	Guadalupe Island	48	0.31	0.81	0.66	0.13	0.80	271	124.9	96.9	7.00
CPac	Hawaii	502	0.65	0.82	0.41	0.39	0.62	3699	17611.6	38777.3	25.00
CPac	Ifaluk and around	745	0.74	0.82	0.35	0.37	0.49	305	109.0	41.8	12.70
CPac	JFernandez Islands	33	0.14	0.82	0.65	0.17	0.81	670	468.4	520.7	1.40
CPac	Jonston atoll	279	0.47	0.82	0.44	0.34	0.58	907	97.5	11.7	85.00
CPac	Kermadec	141	0.48	0.79	0.60	0.23	0.72	892	290.3	377.9	2.00
CPac	Kosrae	527	0.67	0.81	0.39	0.36	0.51	460	140.0	49.7	2.00
WInd	La Reunion	688	0.76	0.83	0.37	0.41	0.57	702	136.4	185.5	3.00
WInd	Laccadives	417	0.73	0.83	0.49	0.31	0.61	307	1211.9	393.6	60.00
CPac	Line islands	552	0.70	0.82	0.38	0.37	0.52	690	509.0	198.6	91.20
CPac	Lord Howe	410	0.66	0.81	0.46	0.34	0.62	579	261.4	6.2	15.97
CPac	Loyalty Islands	659	0.71	0.83	0.35	0.40	0.55	270	2446.3	671.3	2.00
WInd	Maldives	862	0.80	0.83	0.32	0.42	0.51	506	11380.6	12315.8	4.00
TEP	Malpelo	193	0.54	0.82	0.57	0.26	0.69	369	30.9	33.7	17.30
CPac	Mariana North	471	0.67	0.83	0.43	0.34	0.56	571	787.2	629.6	5.00
CPac	Mariana South	887	0.77	0.83	0.31	0.43	0.51	500	47.7	116.5	30.00
CPac	Marquesas	463	0.69	0.83	0.40	0.39	0.59	622	1762.2	3186.8	40.00
CPac	Marshall Islands	924	0.76	0.83	0.29	0.45	0.53	259	20138.2	604.5	70.00
WInd	Mauritius	909	0.80	0.82	0.31	0.42	0.50	886	1250.5	547.1	48.94
CPac	New Caledonia	1264	0.78	0.84	0.25	0.47	0.48	282	30003.0	5737.2	5.30
CPac	Niue	354	0.64	0.82	0.49	0.31	0.62	2443	32.0	26.0	3.40
CPac	Norfolk	177	0.44	0.80	0.54	0.26	0.64	1354	2263.6	380.4	3.00
CIPac	Ogasawara	236	0.48	0.81	0.51	0.32	0.66	1000	1930.5	2228.7	48.00

CPac	Palau	1392	0.77	0.83	0.22	0.49	0.47	451	2668.8	536.2	37.70
CPac	Phoenix	562	0.72	0.83	0.37	0.39	0.55	440	260.7	115.7	4.00
CPac	Pitcairn and Ducie	360	0.67	0.81	0.43	0.36	0.59	5381	101.7	80.5	18.44
CPac	Pohnpei	713	0.75	0.82	0.32	0.40	0.51	360	547.7	137.4	8.70
EAtl	Principe Island	191	0.41	0.76	0.50	0.30	0.64	229	531.8	86.7	15.70
CPac	Rapa Island	376	0.66	0.82	0.45	0.33	0.58	569	79.6	51.7	22.47
TEP	Revillagigedos	165	0.48	0.81	0.57	0.24	0.66	546	162.0	128.5	10.00
WInd	Rodrigues Island	440	0.65	0.83	0.41	0.36	0.57	1484	478.5	18.0	1.50
CPac	Rotuma Island	389	0.60	0.85	0.42	0.37	0.59	301	155.5	47.5	1.50
CPac	Sala y Gomez	50	0.26	0.77	0.63	0.15	0.85	2146	53.2	29.5	1.70
CPac	Samoa	1010	0.77	0.83	0.28	0.45	0.49	322	1676.5	684.8	23.00
EAtl	Sao Tome	190	0.41	0.76	0.51	0.29	0.63	257	443.5	158.8	31.00
CPac	Society Islands	671	0.74	0.83	0.35	0.41	0.57	360	946.1	195.4	4.50
WInd	Socotra	410	0.68	0.81	0.47	0.34	0.63	346	5429.1	2705.1	12.00
CIPac	Solomon Islands	1595	0.84	0.84	0.22	0.49	0.46	290	36727.1	12064.5	45.00
WAtl	St Helena	77	0.30	0.77	0.62	0.19	0.76	1885	228.0	136.5	14.00
WAtl	St Paul's Rocks	58	0.28	0.77	0.64	0.19	0.77	1485	3.5	3.5	15.50
CPac	Tonga	1020	0.76	0.83	0.27	0.46	0.51	360	7947.9	3686.6	6.00
WAtl	Trindade Island	103	0.35	0.76	0.58	0.22	0.72	1532	77.0	49.2	3.70
CPac	Tuamotu Islands	571	0.72	0.83	0.38	0.39	0.56	272	13160.7	3943.8	41.80
CPac	Tuvalu Gilbert	565	0.73	0.83	0.42	0.36	0.58	377	48.8	14.0	3.90
CPac	Vanuatu	1394	0.79	0.84	0.23	0.48	0.47	323	8280.7	5585.8	11.00
CPac	Wake	425	0.64	0.80	0.43	0.34	0.57	909	4.5	6.1	76.26
CPac	Wallis Island	570	0.69	0.80	0.36	0.40	0.55	267	195.9	71.0	0.50
CPac	Yap	787	0.75	0.82	0.31	0.41	0.48	427	175.6	10.8	10.90

Table S2: Functional indices value for each marine realm analysed in this study. Western Atlantic (WAtl), Eastern Atlantic (EAtl), Western Indian (WInd), Central-Indo Pacific (CIPac), Central Pacific (CPac) and Tropical Eastern Pacific (TEP).

Realm	Species richness	Functional richness	Functional divergence	Functional evenness	Functional Over-redundancy	Functional Vulnerability
EAtl	348	0.51	0.78	0.39	0.36	0.51
WAtl	380	0.47	0.78	0.39	0.35	0.51
TEP	413	0.67	0.83	0.43	0.33	0.55
WInd	1557	0.84	0.83	0.23	0.49	0.46
CIPac	1968	0.86	0.85	0.19	0.52	0.44
CPac	2771	0.86	0.84	0.15	0.56	0.41

3. Conclusão

Neste estudo, demonstramos que os fatores área, isolamento e a idade das ilhas foram importantes preditores no padrão de diversidade funcional de peixes recifais encontrado em ilhas oceânicas, seguindo o padrão postulado pela Teoria de Biogeografia de Ilhas clássica. A área das ilhas está diretamente relacionada a heterogeneidade do habitat e disponibilidade de nichos, e o aumento desses fatores reflete na maior riqueza e redundância funcional das espécies. Além das condições do habitat, as espécies estão sujeitas ao nível de isolamento das ilhas, sendo filtradas de acordo com seus atributos funcionais ligados a capacidade de colonização e estabelecimento, refletindo no padrão de equitabilidade e divergência funcional. Porém, ao passo que ilhas antigas apresentam mais tempo para colonização, foi observado uma relação negativa com a FVul e positiva com FOR, possivelmente devido a ilhas antigas contarem com um maior tempo de colonização, aumentando o número de espécies dentro das entidades funcionais.

A alta disparidade na distribuição dos índices funcionais entre os reinos marinhos, sugere uma grande influência de fatores históricos e evolutivos na diversidade funcional de assembléias de peixes recifais em ilhas tropicais oceânicas. Os padrões de diversidade funcional encontrados para os reinos Pacífico central, Indo-pacífico central, e Indico ocidental podem estar refletindo o efeito do refúgio durante o período do quaternário e da proximidade do atual centro de origem das espécies de peixes recifais. Além disso, o isolamento do centro de origem e a baixa diversidade de espécies no Atlântico e Pacífico Leste Tropical, influenciam no padrão de diversidade funcional oposto aos demais reinos.

Além disso, nosso estudo também observou a influência da riqueza taxonômica sobre os índices de diversidade funcional. A riqueza funcional, redundância funcional e a divergência funcional são componentes altamente dependentes da riqueza local de espécies, necessitando de várias espécies com o mesmo conjunto de atributos biológicos para gerar redundância nas entidades funcionais, por exemplo. Ao passo que a equitabilidade funcional e a vulnerabilidade funcional são negativamente correlacionadas a riqueza de espécies, uma vez que quanto menos espécies em um local, maior será a vulnerabilidade, tendo apenas uma espécie compondo cada entidade funcional.

O presente estudo foi o primeiro a abordar a Teoria de biogeografia de ilhas marinhas através da perspectiva da diversidade funcional para o grupo de peixes recifais e através da abordagem funcional permitiu entender os mecanismos (i.e. filtros ambientais, filtros bióticos) que estruturam essas assembleias em ilhas oceânicas que diferem em tamanho, grau de isolamento e idade. Por fim, cada vez mais há uma compreensão da importância de estudos funcionais dentro da ecologia marinha e em diferentes escalas e táxons. Portanto, os resultados encontrados nesse estudo oferecem novos *insights* para futuros estudos na ecologia marinha e principalmente relacionados à teoria de biogeografia de ilhas e a diversidade funcional de peixes recifais. Além disso, corresponde ao primeiro passo no uso de novas métricas na teoria de biogeografia de ilhas além da clássica métrica taxonômica. Dessa forma, nós sugerimos o uso da abordagem funcional em teorias clássicas, uma vez que essa nova abordagem considera que as espécies apresentam características distintas, podendo compreender o papel intrínseco das espécies tanto na estruturação das comunidades como no funcionamento do ecossistema.