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# The role of functional ecology on Marine Protected Areas science: A global, regional and local overview

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**RAMÓN HERNÁNDEZ ANDREU**

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Tese apresentada à Universidade Estadual de Santa
Cruz, como parte das exigências para obtenção do
título de Doutor em Ecologia e Conservação da
Biodiversidade

Orientador: Carlos Werner Hackradt

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# Resumo Geral

Os ecossistemas marinhos, principalmente os recifes de corais, vêm sofrendo com os impactos antrópicos. Para minimizar os efeitos deletérios destes impactos, as áreas marinhas protegidas (AMPs) são utilizadas, no mundo todo, como uma ferramenta eficaz para proteger a biodiversidade e recuperar os ecossistemas marinhos. Entretanto, os efeitos das AMPs sobre a diversidade funcional ainda são pouco compreendidos. Portanto, este trabalho buscou avaliar o papel das AMPs na manutenção da diversidade funcional e na promoção da funcionalidade ecossistêmica de recifes de corais, à partir de suas assembleias de peixes. Baseado na hipótese de que a diversidade funcional dentro de uma AMP deve corresponder à diversidade funcional da região onde a mesma está implementada para que se possa evidenciar a efetividade das AMPs, os principais objetivos desta tese foram: ( i) entender macro-ecológicamente como as AMPs contribuem como ferramenta de proteção da funcionalidade ecossistêmica em recifes de corais; (ii) determinar como AMPs atuam na proteção da diversidade funcional de distintas comunidades de peixes recifais; e (iii) avaliar o "efeito reserva" de uma AMP considerando o efeito do habitat como um possível filtro ambiental. Os resultados indicam que globalmente, ainda que se identifique uma efetividade das AMPs, falta representatividade macro-ecológica da diversidade funcional para as assembleias de peixes nas áreas fechadas (*no take-zones*). Isso ocorre, provavelmente, pela falta de representatividade de habitats dentro das AMPs. Este padrão também é observado no Parque Nacional Marinho dos Abrolhos, onde as comunidades mostraram uma menor diversidade alfa e maior similaridade nos traços funcionais que nas áreas desprotegidas. Por outro lado, também encontramos uma relação não aleatória entre o gradiente de traços funcionais e variáveis ambientais, demonstrando que esses tem um papel na estrutura da comunidade. Podemos concluir que para conseguir que as áreas fechadas protejam toda a funcionalidade é necessário a expansão dessas áreas com uma perspectiva funcional e do ecossistema, onde sejam contemplados diferentes tipos de habitats.

**Palavras-chave:** Efeito proteção, ecologia funcional, traços funcionais, espaço funcional, peixes recifais.

## General Abstract

Marine ecosystems, mainly coral reefs, have been suffering from anthropogenic impacts. To minimize the deleterious effects of these impacts, Marine Protected Areas (MPAs) have been used around the world as an effective tool to protect biodiversity and restore marine ecosystems. However, the effects of AMPs on functional diversity are still poorly understood.Therefore, this study aimed to evaluate the role of MPAs in maintaining the functional diversity and promoting the ecosystem functionality of coral reefs, based on their fish assemblages.. Based on the hypothesis that the functional diversity within the MPA must correspond to the total functional diversity of the region where it is implemented in order to demonstrate the effectiveness of MPAs, the main objectives of this thesis were: (I) understand macro-ecologically how MPAs contribute as a tool to protect ecosystem functionality in coral reefs; (ii) determine how MPAs act to protect the functional diversity of distinct reef fish communities; and (iii) evaluate the "reserve effect" of an MPA considering the habitat effect as a possible environmental filter.. The results indicate that globally, although an MPA effectiveness is identified, there is a lack of macro-ecological representation of the functional diversity for fish assemblages in closed areas (no take-zones). This is probably due to the lack of representation of habitats within the MPAs. This pattern is also observed in the Abrolhos National Marine Park, where communities showed lower alpha richness and greater similarity of functional traits than in other unprotected areas. On the other hand, we also found that there is a non-random relationship between the gradient of functional traits and some environmental conditions that play a role in community structure. We can conclude that to get closed areas to protect all functionality, it is necessary to expand these areas, although with a functional and ecosystem perspective, where different types of habitats are contemplated.

**Keywords:** Protection effect, functional ecology, functional traits, functional space, coral reef fishes.

# Introdução Geral

O Antropoceno caracteriza-se pelas intensas atividades humanas que causam mudanças ambientais em múltiplas escalas (Steffen et al. 2011). Nos ecossistemas marinhos, as ações antrópicas como mudanças climáticas, sobrepesca, invasões de organismos, homogenização e destruição dos habitat e contaminação são alguns dos principais fatores que afetam a estrutura e a diversidade de populações marinhas (Lotze et al. 2006; Doney et al. 2012). Estas ações antrópicas podem ser os maiores estressores e interferir nas funções do ecossistema (Bellwood et al. 2003), podendo atuar de forma sinergética entre eles, selecionando diferentes traços funcionais em resposta à essas alterações (Ban et al. 2014; Hughes et al. 2018).

As funções ecossistêmicas, como a dinâmica do CaCO3, interações de herbivoria e predador-presa e os ciclos dos nutrientes (Brandl et al. 2019), são consideradas como os processos que envolvem o funcionamento do ecossistema, e são especificas e desempenhadas por espécies ou grupos de espécies (Bellwood et al. 2019), que podem ser chamadas de entidades funcionais, que tem características similares funcionalmente, que denominadas traços funcionais, e compartilham respostas a fatores ambientais ou efeitos semelhantes no funcionamento dos ecossistemas (Díaz & Cabido 2001). Existem diferentes tipos de traços: morfológicos, comportamento, fisiológicos, historia de vida, biomecânicos, filogenéticos, etc (Díaz & Cabido 2001; Petchey & Gaston 2006; Cadotte et al. 2011; Villéger et al. 2017). Com estes traços podemos quantificar a diversidade funcional das comunidades (Mouillot et al. 2013) usando índices multivariados (Petchey & Gaston 2006; Mouillot et al. 2013; Villéger et al. 2013) e definir um espaço funcional ou hipervolume (Villéger et al. 2008; Blonder 2016; Mammola et al. 2021) para explicar como as espécies e suas abundâncias estão distribuídas dentro da comunidade (Villéger et al. 2008).

Os índices multivariados de diversidade funcional foram definidos por diferentes autores na literatura atual, sendo: Riqueza Funcional (FRic, 'o volume do espaço multidimensional ocupado por todas as espécies em uma comunidade dentro do espaço funcional'); Regularidade Funcional (FEve, 'a regularidade da abundância relativa e distribuição das espécies no espaço funcional para uma determinada comunidade'); Divergência Funcional (FDiv, 'a proporção da abundância total suportada por espécies com os valores de traços mais extremos dentro de uma comunidade') em Mouillot, Graham, Villéger, Mason, & Bellwood (2013); Dispersão Funcional (FDis, 'a distância média ponderada de biomassa do centro do conjunto no espaço de nicho sintético', (Brandl, Emslie, & Ceccarelli, 2016); Especialização Funcional (FSpe, 'a distância média de uma espécie do restante do conjunto de espécies no espaço funcional'); e Originalidade Funcional (FOri, 'o isolamento de uma espécie no espaço funcional ocupado por uma determinada comunidade') (Laliberté, Legendre, & Shipley, 2015).

Uma forma para frear o impacto que ações antrópicas causam sobre a biodiversidade marinha e manter as funções do ecossistema é utilizar ferramentas de gestão espacial como as áreas marinhas protegidas, que elimina ou restringe as atividades em um área delimitada para recuperar o ecossistema (Mumby & Harborne 2010; Lotze et al. 2011), e tem o potencial de conservar o papel funcional que desempenham as diferentes especies no ecossistema (D'Agata et al. 2014). Coleman et al. (2015) justificou a importância de incluir os traços funcionais em estudos realizados em AMPs, pois eles têm um grande potencial para descobrir mudanças devido aos efeitos da proteção no habitat disponível (longo tempo) e no uso do habitat (tempo mais curto), onde podemos prever como a biodiversidade responde a essas mudanças ambientais, de habitat ou de recursos, para assim, poder entender como cada componente da diversidade funcional e função do ecossistema se comporta com as mudanças (Yeager et al. 2017).

Além disso, para cada componente da diversidade funcional existe uma relativa importância da escala e das variáveis ambientais (Mouchet et al. 2010), porque o conjunto de traços funcionais vão determinar um filtrado hierarquico das especies dependendo da abundancia relativa, primeiro por fatores ambientales a grande escala e depois por fatores ambientales a escala local e as interações biologicas (Woodward & Diament 1991, Weiher & Keddy 1995, Diaz et al. 1998). Para avaliar o efeito desses filtros na biodiversidade e na assambleia será importante usar diferentes ferramentas para medir a estrutura da comunidade (de Bello et al. 2013) e considerar a escala, que é importante para esses filtros ambientais (Yeager et al. 2017), porque a mudança do papel da espécie para um papel dominante pode ser determinada por fatores ambientais em escalas locais (Mason et al. 2011).

Esta tese é composta por 3 capítulos cujo objetivo geral é conhecer o papel que as AMPs desempenham na manutenção da diversidade funcional e na promoção da funcionalidade do ecossistema, à partir das assembleias de peixes em recifes de corais. No **primeiro capitulo**, foi avaliado numa escala global desde, um ponto de vista macro-ecológico, como as AMPs funcionam como ferramenta de proteção da funcionalidade ecossistêmica em recifes de corais. Comparamos quanta diversidade funcional estava representada dentro e fora das áreas de fechadas usando um conjunto de traços funcionais para um grande banco de dados de peixes de recife marinho pertencentes a províncias biogeográficas tropicais marinhas em todo o mundo.

No **segundo capítulo**, usamos um enfoque regional, quatro áreas de duas regiões diferentes do extremo Sul do Estado da Bahia, para avaliar se existem diferenças funcionais em assembleias de peixes recifais dentro x fora de AMPs. Procuramos um padrão que mostre se as AMPs estão influenciando a funcionalidade do ecossistema para essas áreas em cada região. Por outro lado, queremos saber se existem dissimilaridades das assambéias de peixes entre as diferentes áreas e quão original são as espécies nessas comunidades.

No **terceiro capítulo**, usamos uma escala local onde procuramos uma relação entre diversidade funcional e taxonômica, e entre traços funcionais frente as variáveis ambientais dentro e fora da uma AMP para identificar o efeito da proteção sobre a diversidade funcional. Também se existem filtros ambientais e como podem ser influenciados dependendo da proteção.

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# Capítulo 1

## Marine Protected Areas are a useful tool to protect coral reef fishes but not representative enough to conserve their functional role

Artigo submetido à Global Ecology and Biogeography

# Marine Protected Areas are a useful tool to protect coral reef fishes but not representative enough to conserve their functional role

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## Abstract

Coral reefs are one of the most affected natural systems by anthropogenic actions around the world. This can cause direct and indirect impacts on the functionality of these ecosystems. At the local level, marine protected areas (MPAs) can assist in spatial management by conserving natural resources and maintaining ecological relationships within them. No take-zones (NTZ) distributed throughout the world are considered tools for the management of fisheries resources and protection from some anthropic pressures. In the last decades, functional diversity (FD) indices have been widely used to assess ecosystem functioning, but there are no studies that evaluate FD in MPAs with a global approach. In this study, we analyse the effect of No-Take Zones on the FD and “true” diversity (TD) indices of tropical reef fish assemblages in 12 tropical biogeographic regions, and we found a significant effect of protection on these indices, although these responses were dependent of the bioregion. In general, marine protected areas preserved a lower number of species and functional entities than open access areas, and consequently functional richness protected inside them represented only partially the functional diversity in each biogeographic provinces. In addition, our results showed that herbivores respond better to protection while a higher abundance of planktivores and invertivores fishes were favoured by open fishing areas which might be revealing a “fishing down food web” effect. Thus, these results reinforce that existing NTZ are not enough to safeguard ecosystem functions on tropical reefs, reinforcing the importance of continuing expanding the number of MPAs around the world with management strategies focused on the functionality of coral reefs fish and also local/regional effective assessment. A new paradigm is necessary in the planning and creation of MPAs to safeguard ecosystem functions, because the priority is given to the protection of ecosystem functions and habitats

**Keyword:** Reef fish functional diversity, Functional traits, Protection effects, Tropical bioeographic provinces, Functional Ecology, Ecology for conservation

## Introduction

Marine ecosystems are worldwide under pressure by human activities (Halpern, 2014; McCauley et al., 2015), and one of the most threatening environment are coral reefs (Jackson et al., 2001). Climatic change, biodiversity loss, pollution, and habitat degradation are the major stressors for coral reef functioning (Bellwood, Hoey, & Choat, 2003) by removing species that belong to the same functional groups, group of equivalent species with the same ecological function (Rosenfeld, 2002). For these organisms, the ecological processes in which they participate can be affected by physical and biological changes in the ecosystem (Stella, Munday, & Jones, 2011; Wilson, Graham, Pratchett, Jones, & Polunin, 2006) due to these anthropic impacts. Brandl et al., (2019) divided the processes that engulf the functioning of the coral reef ecosystem into four pairs of processes: $CaCO_3$ dynamics (bioerosion and $CaCO_3$ production), herbivore-algae interactions (herbivory and primary production), predator-prey interactions (predation and secondary production) and nutrient cycling (nutrient uptake and nutrient release). These processes are mediated for extrinsic (environmental and anthropogenic factors) and intrinsic (species present on coral reef) drivers.

To mitigate these impacts over marine biodiversity, spatial management tools like Marine Protected Areas (MPAs) have been proposed as an effective measure to hinder the loss of marine biodiversity and allow sustainable exploitation of marine resources (Claudet et al., 2008; García-Charton et al., 2008; Pauly, Watson, & Alder, 2005). MPAs work with an ecosystem-based approach which consists in eliminate or restrict potential harmful and/or extractive activities within a delimited area, to allow ecosystem recovery (Lotze, Coll, Magera, Ward-Paige, & Airoldi, 2011; Mumby & Harborne, 2010).

MPA can aid ecosystem health by allowing biomass recovery (Aburto-Oropeza et al., 2011; Lester et al., 2009; Sala & Giakoumi, 2018), rising egg and larvae production (Planes et al., 2000), contributing to biomass exportation through spillover (for adults) (Clarke & Gorley, 2018; Goñi, Hilborn, Díaz, Mallol, & Adlerstein, 2010; Hackradt et al., 2014; Harmelin-Vivien et al., 2008), movement of juveniles and larval dispersal (Félix-Hackradt, Hackradt, Treviño-Otón, Pérez-Ruzafa, & García-Charton, 2018; Grüss, Kaplan, Guénette, Roberts, & Botsford, 2011), as well as increase ecological resilience inside their boundaries (Barnett & Baskett, 2015), and preserving habitat and biodiversity (Roberts & Hawkins, 2000).

In addition to the beneficial impacts of marine reserves over fish fauna is the conservation of functional role breadth played by different species within ecosystems (D'Agata et al., 2014) , however, there is little information available on functional diversity protected inside MPAs.

Functional diversity of reef fish assemblages has been measured through multiple multivariate indices based on species functional traits, which are defined as "*any trait directly influencing organismal performance"* (David Mouillot, Graham, Villéger, Mason, & Bellwood, 2013; Villéger, Grenouillet, & Brosse, 2013). However, some works (Villéger, Maire, & Leprieur, 2017) highlighted the necessity to incorporate the role played by each fish species in defining functional traits, which was defined as "*The function/s a species or group of species perform in a system"* (Bellwood, Streit, Brandl, & Tebbett, 2019).

Functional diversity which uses a mathematical representation of species role within the ecosystem, was described by the multi-functional space (Bellwood, Streit, Brandl, & Tebbett, 2019), using functional traits. The functional space concept has been used to explain species distribution and abundances in multiple attribute space through evaluating how species fill the multivariate space and how abundances were distributed within the community (Villéger, Mason, & Mouillot, 2008).

Currently, the studies on the functional diversity of fish are focused on evaluating spatial and temporal variation (Rincón-Díaz, Pittman, Arismendi, & Heppell, 2018), biogeographic patterns(David Mouillot et al., 2014), the effect of fisheries and benthic habitats (Cáceres, Ibarra-García, Ortiz, Ayón-Parente, & Rodríguez-Zaragoza, 2020), ecosystem functions (Brandl et al., 2019; D'Agata et al., 2014) and environmental filters (Yeager, Deith, McPherson, Williams, & Baum, 2017). On the other hand, few studies have investigated the effect o marine protected areas in functional diversity, but they are limited to data obtained from fisheries (Stezmuller, Mayon, & Martin, 2009) or restricted to trophic groups (Villamor & Becerro, 2012).

This work aims to address the hypothesis that MPAs contribute to protecting functional diversity, from a functional space point of view, in reef fish assemblages inside their boundaries. Then, our aim is to evaluate how much functional diversity is represented inside no take-zones (NTZ) areas compared to partially open or unprotected zones. To accomplish that we applied different functional diversity indices using a set of traits build for a large database of marine reef fishes belonging to marine tropical biogeographic provinces worldwide.

## Material and methods

### Data acquisition and study area

We extracted data from the Reef Life Survey database (RLS), an international network of volunteer scientists and citizens, that were previously trained to collect data on the abundance of tropical reef fishes, updated in October 2018 (Edgar & Stuart-Smith, 2018. Data download 03/10/2018) and can be accessed at https://reeflifesurvey.com. Data collection consisted of a standardized underwater visual census method using a 50 m line transect in which divers swim at constant speed (2 m/min) recording species abundances within a 5m width, totalling 250 $m^2$ of the surveyed area (for more details see [Edgar & Stuart-Smith, 2014]).

We compiled data of reef fish species and abundance from a total of 4800 transects, distributed in 12 marine tropical biogeographic provinces according to (Barneche et al., 2019). These biogeographic provinces are North-Western Indian (NWI), Western Indian (WI), Central Indo-Western Pacific (CIWP), South-Western Pacific (SWP), Central Pacific (CP), Polynesian (POL), Hawaiian (HW), Eastern island (E), Offshore Tropical Eastern Pacific (OTEP), Tropical Eastern Pacific (TEP), Caribbean (CB) and South-Western Atlantic (SWA) (Figure 1a, more details in supplementary material SM1).

Finally, we applied information available on the World Data Protected Area database (UNEP-WCMC & IUCN, 2018, download data, 3/10/2018) and can be accessed at https://www.protectedplanet.net or https://mpatlas.org (Marine Conservation Institute, 2020,last access data, 1/09/2020) to assign the level of protection to each site we retrieved data. We considered as a protected area only MPAs that had been established in the last ten years or older in order to ensure MPA effectiveness (Claudet, Pelletier, Jouvenel, Bachet, & Galzin, 2006; Edgar & Stuart-Smith, 2014)

### Fish traits

For the data compiled from the RLS project, we attributed the species' functional traits according to information available on FishBase (Froese & Pauly. 2020) and can be accessed at http://www.fishbase.org. When data was absent we searched for published information specifically for that species, and if absent, for a congeneric. We established five categorical functional traits (trophic level, maximum length, resilience, gregariousness, and spatial category) to evidence distinct functionality between reef fish species (Table S1, more details in supplementary material SM2.Appendix A and SM3).

## Functional Diversity and True Diversity indices

First, we calculate the unique combination of the five qualitative traits that define the Functional Entities (FE) of each of the 1956 species used for this study by using *species_to_FE* function of 'FD' R package (Laliberté, Legendre, & Shipley, 2015). These species were grouped into 524 different FE. Then, we combined the abundance matrix, which was transformed into a binary (presence/absence) matrix for each replicate, with a matrix of functional entities, to obtain the values of the redundancy patterns using the *FE metrics* function . They indices are described in (Mouillot et al., 2014) as Functional Redundancy (FRed) or an average number of species in each FE, Functional Over-Redundancy (FORed) or the proportion of species that are performing the same function in each FE, and Functional Vulnerability (FVul) or the proportion of FE that are only represented by one species. Subsequently, we calculated the quality of functional space, given by the functional traits, using Gower's distance matrix. The distance matrix was used to calculate the multidimensional space using principal coordinates analysis (PCoA) for a maximum of 10 dimensions, in order to evaluate the lower mean squared deviation (mSD) that represent a higher quality of the functional space (Maire, Grenouillet, Brosse, & Villéger, 2015). For this work, the highest functional space quality was achieved when species were represented by 5 dimensions (mSD = $2.7e^{-3}$).

With the coordinates matrix and abundance matrix in each sample, we computed, using the function multidimFD, the multidimensional functional diversity (FD) indices: Functional Richness (FRic), Functional Evenness (FEve), Functional Divergence (FDiv), Functional Dispersion (FDis), Functional Specialization (FSpe), Functional Originality (FOri) (Detail in supplementary material). The coordinates matrix and the multidimensional functional diversity indices were calculated using 'FD' R package (Laliberté, Legendre, & Shipley, 2015) (more details in supplementary material SM2.Appendix A).

In addition, to evaluate the relation of ecological indices with functional diversity, “true diversity” indices (sensu Jost, 2006) were calculated for reef fish assemblages by using the number of Hill (Hill, 1973) as an effective number of species. We attribute weight to species abundance so, for a weight 0 (q0) we favouring rare species, when weight 1 (q1) is applied corresponds to the effective number of common species, and finally, when a disproportionated weight is given to abundance (q2) dominant species are favoured. To calculate these indices, we use the *MetaCommunity* and *AlphaDiversity* functions of the ‘entropart’ package (Marcon & Herault, 2015).

## Data analysis

To evaluate how protection affects functional diversity indices, we applied a non-parametric permutational multivariate analysis of variance (PERMANOVA). We defined biogeographic provinces as a fixed factor with 12 levels, and Protection as a random factor with 2 levels (protected and unprotected), nested in biogeographic provinces. The FD indices were used as dependent variables, and latitude, longitude and depth as co-variable PERMANOVA was calculated with the software PRIMER v6 & PERMANOVA+ (Clarke & Gorley, 2006), based on Bray Curtis similarity distance matrix (Anderson, 2001). We applied 999 permutations and used p-value to assess the significance of the factors in our design. We used pair-wise PERMANOVA tests between the levels of a factor to identify significant differences in each level. Eastern and North Western Indian provinces were not evaluated from pair-wise analysis because of the absence of both levels of protection. Furthermore, we calculate the Response Ratio (RR) of abundance, “true diversity”, functional diversity indices and redundancy patterns for each biogeographic province between protected and unprotected areas. Moreover, to evaluate the functional space among biogeographic provinces, and how this space is filled within protected *vs* unprotected areas, we used a Bray Curtis similarity distance matrix (Anderson, 2001) of the five FD indices to calculate the PCoA.

Next, we evaluated the response of the five categorical discrete traits values (spatial category, resilience, trophic group, maximum length and gregariousness) to the protection for each biogeographic provinces. For this, we converted the abundance in density values by calculating the abundance of species between the number of replicates for protected and unprotected areas. We adjusted a binary variable to each species in which the calculated density values were higher in protected *vs* unprotected areas received value 1, and in the opposite way, we attributed the value 0. We then ran 50 BRM with the binary variable as the response variable and categorical traits values as fixed factors, and a Bernouilli error distribution. In this case, each BRM was run for 4 chain and 3,000,000 interactions with an initial warm-up phase of 50,000 and thinning interval of 10,000 using 'brms' package (Bürkner, 2018). For the prior distribution in this case we only we used "*max_treedepth*". For this analysis, we excluded species that only presented one value in each trait to avoid divergent transitions, which does not guarantee the validity of the model.

Finally, we calculate the redundancy patterns indices (redundancy, over-redundancy and vulnerability) for the trophic groups' traits. Then, we applied PERMANOVA for redundancy patterns indices of trophic groups that showed differences in protection on Bayesian analyses. We used trophic groups to evaluate any possible change in fish assemblage due to protection as some trophic groups (such as carnivores) are most target by fisheries and therefore can be more benefited from spatial closure measures such as No-Take areas (Aburto-Oropeza et al., 2011; Soler et al., 2015). For this analyses, we used the log-transformed indices using a Euclidean distance matrix, as well as latitude, longitude and depth as co-variables. Following, we represented these indices by level of protection for each biogeographic province with a non-parametric multidimensional scaling ordination.

## Results

In total, 9,364,800 individuals fishes were surveyed in 4800 transect, representing for 1,956 species. Each biogeographic province has a different pool of species, where CIWP with 1131 species was the province with the highest number of which we found 545 species in the NTZ and 1123 in the unprotected areas, collected in 145 and 1044 samples transect, respectively. Contrary, Eastern Pacific is represented by 42 species that was the one with the lowest number of species, where all were collected in the 28 sampled transects in unprotected areas because samples were not carried out in NTZ for this biogeographic province (Figure 1 and Table S2, with more detail in supplementary material SM1 and SM2, appendix B). As expected, taxonomic diversity and redundancy patterns changed between biogeographic provinces, but abundance data and most of the functional indices (except functional richness (FRic) and evenness (FEve) indices) were stable between samples in different bioregions. A positive effect of protection was found with greater abundance inside than outside MPAs. All indices tested showed a significant effect of protection, although the response for each index varied among biogeographic provinces, being Caribbean the only region in which all significant indices were greater inside MPAs, while Hawaiian and South-Western Atlantic regions the ones who did not show any significant P(B) effect (Table 1; more details in SM2, appendix C).

Table 1. PERMANOVA of Biogeographic provinces (B) and Protection level (P) on abundance, 'True diversity', multidimensional functional and redundancy patterns indices on functional entities.. Legend: df: degrees of freedom; ln(N): abundance transformer to the Neperian logarithmic, q0: diversity rare species; q1: diversity common species; q2: diversity dominant species, FRic: Functional Richness; FEve: Functional Evenness; FDiv: Functional Divergence; FDis: Functional Dispersion; FSpe: Functional Specialization; and FOri: Functional Originality, FE: Functional Entities; FRed: Functional Redundancy; FORed: Functional Over-Redundancy; FVul: Functional Vulnerability. ***: *p* ≤0.001, **: *p* ≤ 0.01, *: *p* ≤ 0.05.

| | | **ln(N)** | | **FRic** | | **FEve** | | **FDiv** | | **FDis** | | **FSpe** | | **FOri** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Sources** | df | F | p | F | p | F | p | F | p | F | p | F | p | F | p |
| **B** | 11 | 3.3 | ns | 7.0 | ** | 4.9 | * | 1.6 | ns | 0.6 | ns | 2.5 | ns | 3.0 | ns |
| **P(B)** | 10 | 10.5 | *** | 5.4 | *** | 5.4 | *** | 24.3 | *** | 6.4 | *** | 14.2 | *** | 37.8 | *** |
| **Res** | 4775 | | | | | | | | | | | | | | |

| | | **$q^0$** | | **$q^1$** | | **$q^2$** | | **FE** | | **FRed** | | **FORed** | | **FVul** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Sources** | df | F | p | F | p | F | p | F | p | F | p | F | p | F | p |
| **B** | 11 | 12.0 | ** | 7.2 | * | 5.2 | * | 20.2 | ** | 13.5 | ** | 10.7 | ** | 12.1 | ** |
| **P(B)** | 10 | 8.4 | *** | 5.5 | *** | 4.5 | *** | 7.4 | *** | 12.0 | *** | 17.0 | *** | 9.9 | *** |
| **Res** | 4775 | | | | | | | | | | | | | | |

By analyzing the functional traits space and its relation to the protection effect, it was possible to observe how much of the function diversity was represented within MPAs, and again the response was province-specific. In general, marine protected areas preserved a lower number of species and functional entities than open access areas, and consequently functional richness protected inside them represented only partially the functional diversity in each biogeographic provinces. MPAs from SWP and CIWP regions held the most efficient areas in protecting functional diversity by keeping 63 and 66% of total functional space, respectively. However, reef areas from SWA and HW presented the smallest functional trait space (less than 10%) among all provinces, nevertheless, SWA was the only region in which functional space was better represented inside (9.6%) than outside (5.7%) protected areas. The greatest differences between protected and unprotected areas were found in Polynesian region in which only 17% of species richness, 21% of functional space and 24% of functional entities existent in open areas were represented inside MPAs (Figure 1b).

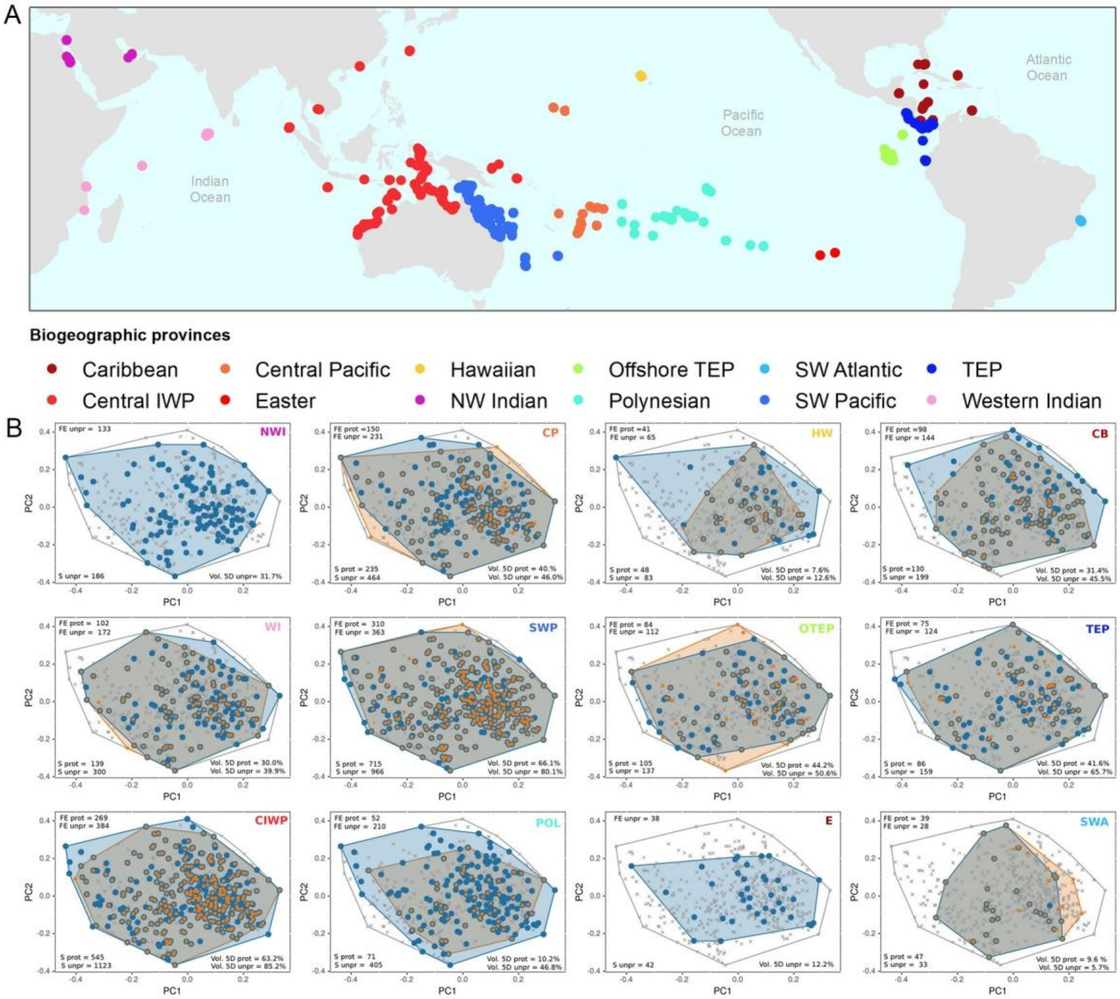

Figure 1. A) Global distribution of sites within defined for this study. Each coloured dot identify a sampled area in a specific biogeographic province and B) representation of functional space in marine protected (no-take zones) and unprotected areas for 12 biogeographic provinces (CB: Caribbean, CIWP: Central Indo-Western Pacific, CP: Central Pacific, HW: Hawaiian, OTEP: Offshore Tropical Eastern Pacific and POL: Polynesian, SWA: SouthWestern Atlantic, SWP: South Western Pacific, TEP: Tropical Eastern Pacific, WI: Western Indian). The functional space is created using PC1-PC2 and PC3-PC4 (figure S4 in SM2, appendix D) with Principal Coordinate Analysis on functional traits to represent the distribution of functional entities. Number of species (S), functional entities (FE: unique traits combinations) and functional richness (Vol. 5D: volume filled by each fish fauna, expressed as a percentage

relative of the global pool) are provided for each protection level. The global convex hull, including the 1,956 species split into 574 functional entities is in grey. The orange points represent the functional entities present in marine protected ('prot') areas, the blue points represent the functional entities in unprotected ('unpr') areas, while the orange point with blue edges represent the functional entities that share the two level protection. Grey crosses are functional entities absent in the biogeographic province

On the other hand, the response ratio, which tell us where those significant differences are, indicates that OTEP region harbor higher and significant values of functional over-redundancy (RR = 1.5, CI = 0.88 – 2.13), functional richness (RR = 0.38, CI = 0.09 – 0.66), functional entities (RR = 0.18, CI = 0.09 – 0.27) and diversity of rare species (RR = 0.26, CI = 0.03 – 0.49) inside protected areas, albeit presented high functional divergence values outside MPAs. Hawaiian province showed larger fish abundance (RR = 0.52, CI = 0.02–1.01), functional over-redundancy (RR = 0.65, CI = 0.38 – 0.91) and diversity of common (RR = 0.31, CI = 0.03 – 0.59) and dominant species (RR = 0.21, CI = 0.21 – 0.21) at protected areas. Moreover higher diversity of common species (RR = 0.54, CI = 0.45 – 0.64) and greater functional dispersion (RR = 0.17, CI = 0.15 – 0.19) values were found at Polynesian and Caribbean protected areas, respectively. For other part, diversity of common (RR = -0.35, CI = -0.49 – -0.20) and dominant species (RR = -0.51, CI = -0.75 – -0.27) were favored by absence of protection at Western Indian region. At last, fish abundance ( RR = -0.51, CI = -0.57 – -0.44) was greater at unprotected zones at Central Indo-Western Pacific (Figure 2).

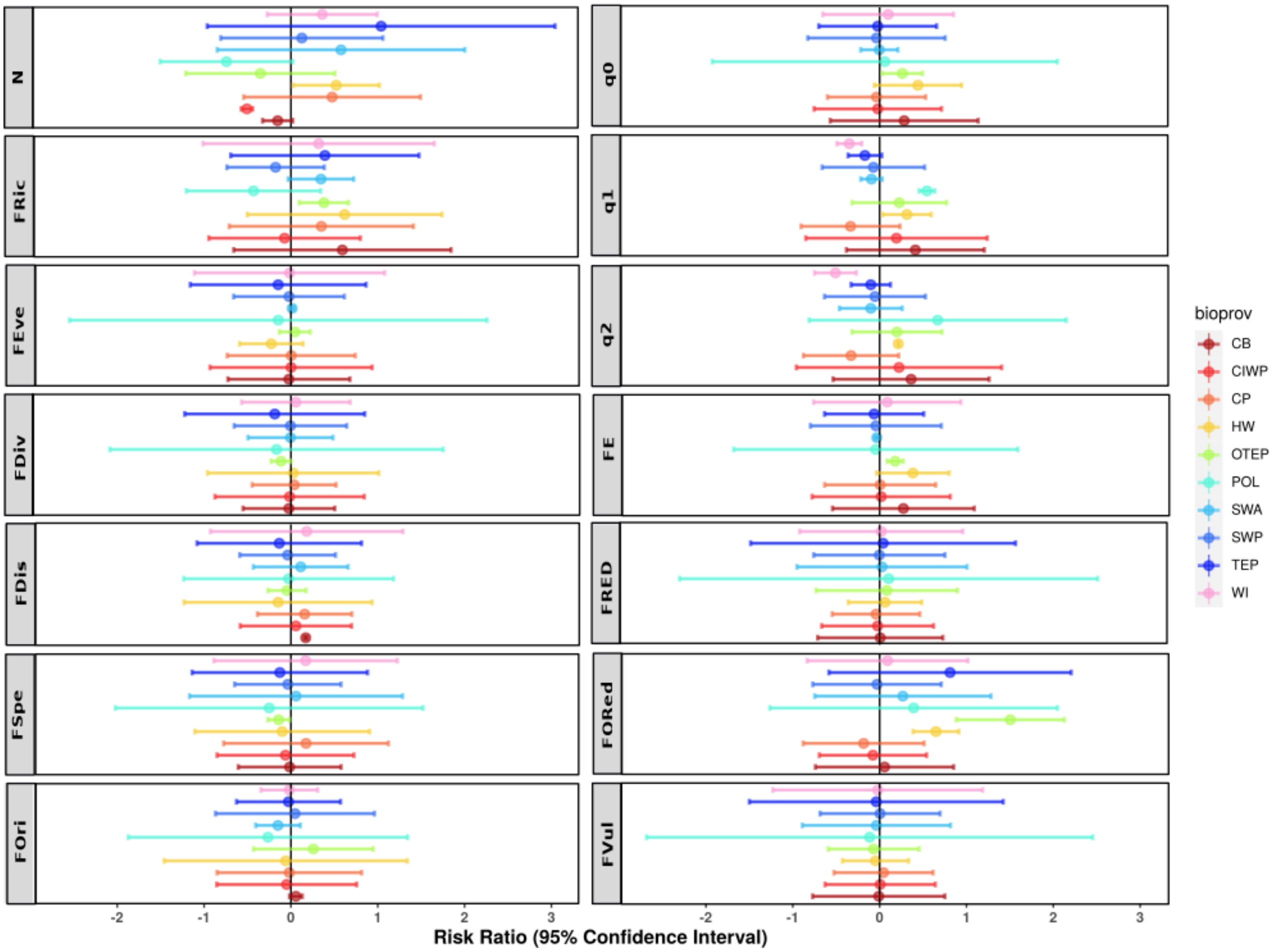

Figure 2. Response ratios (RRs) by abundance, “true diversity orders”, functional diversity indices and redundancy patterns for the each biogeographic province. Values greater than 0 indicate the effect of protection and less than 0 indicate the lack of protection effect. Bars indicate 95% confidence intervals. Bioprovinces - CB: Caribbean, CIWP: Central Indo-Western Pacific, CP: Central Pacific, HW: Hawaiian, OTEP: Offshore Tropical Eastern Pacific and POL: Polynesian, SWA: SouthWestern Atlantic, SWP: South Western Pacific, TEP: Tropical Eastern Pacific, WI: Western Indian. Indices used – N: abundance, FRic: Functional Richness, FEve: Functional Eveness, FDiv: Functional Divergence, FDis: Functional Dispersion, FSpe: Functional Specialization, FOri: Functional Originality, $q^0$: true richness, $q^1$: diversity of first order, $q^2$: diversity of second order, FE: functional entities, FRed: Functional Redundancy, FORed: Functional Over-redundancy, FVul: Functional Vulnerability

Besides how much of the functional diversity was retained inside MPAs we are interested to know which trait was favoured by the protection effect. Regarding trophic categories we found that herbivores were more prone to respond to spatial restrictions either in the Caribbean and OTEP provinces, while higher abundance of herbivores scrappers was observed only at Caribbean MPAs. Moreover, omnivores and general carnivores were more abundant at SWA protected areas. In contrast, we showed that is more likely to find higher abundance of most trophic categories in unprotected areas for the majority of biogeographic provinces, specially planktivores and invertivorous groups (Figure S5, appendix E of SM2). Larger sized fish were more abundant inside MPAs, but only at Caribbean (large and medium-large) and SWA (medium) provinces; for their part species with intermediate resilience levels and benthonic reef associated were also favoured by protection at Caribbean MPAs, while protection has affected mainly demersal reef-associated and reef attached species at SWA region. Regarding the gregariousness trait, paired species were observed in higher numbers only in TEP MPAs. On the other hand, CIWP and POL MPAs displayed the worst protection efficiency, in which all traits evaluated (maximum size, spatial and trophic classes, gregariousness and resilience) presented large values at open access areas (Figure S6-9, appendix E of SM2).

In addition, the effect of protection over redundancy patterns in each biogeographic province showed a higher redundancy, over-redundancy and vulnerability at unprotected areas, with the exception of SWA province in which MPAs harboured higher levels of all indices. Nevertheless, MPAs from SWA, SWP and OTEP, were in that order, the most efficient is reducing vulnerability proportionally to open areas (Figure 3).

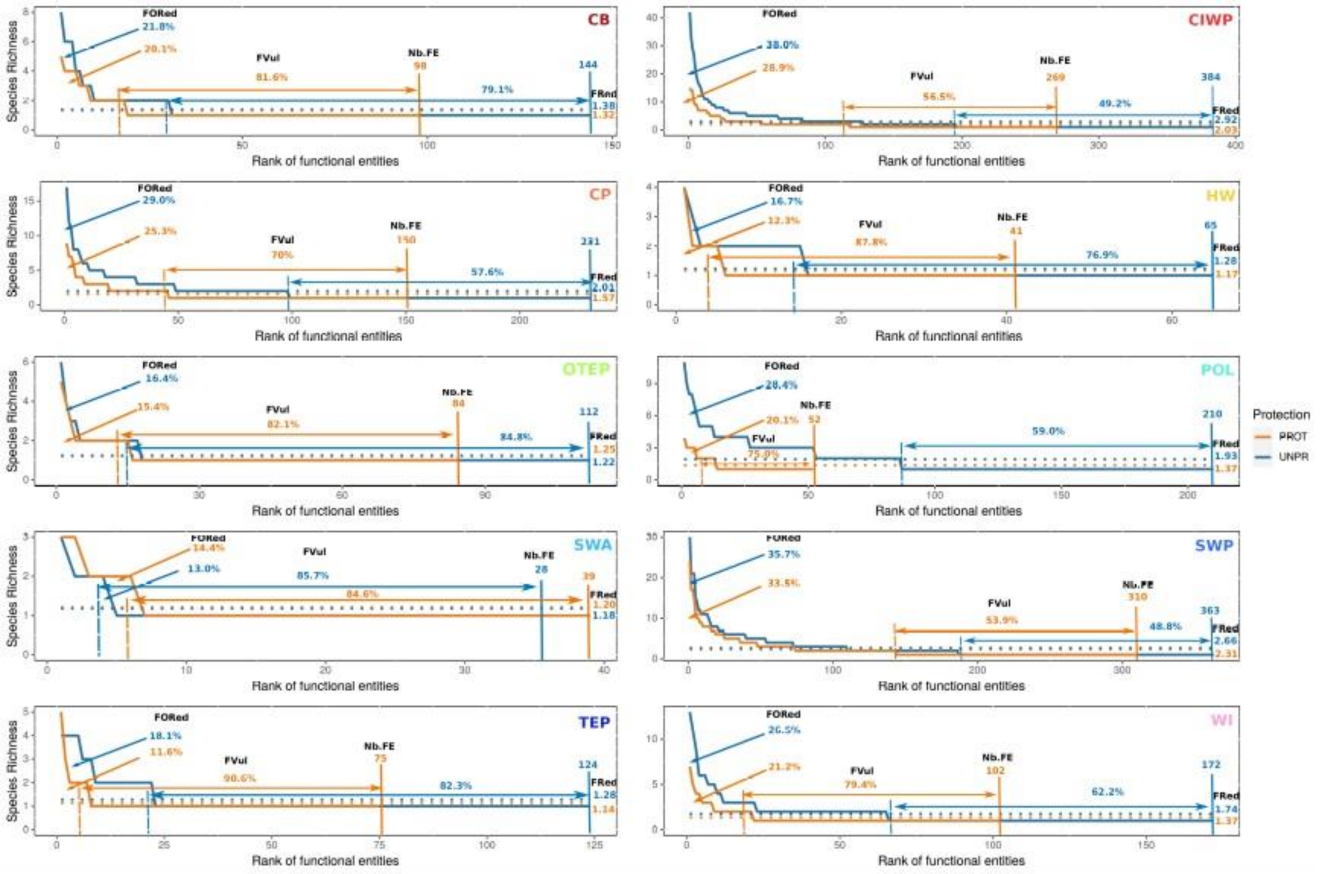

Figure 3. The redundancy patterns of the distribution of reef fish assemblages for evaluated in no take zones areas (orange) and unprotected areas (blue) for each tropical biogeographic provinces. FRed: Functional Redundancy is illustrated by the horizontal dashed line, and represents the mean of species per functional entity. FORed: Functional Over-Redundancy is the percentage of species in a functional entity that have a greater number of species than expected by redundancy. FVul: Functional Vulnerability is the percentage of functional entities that is represent by a single specie and this is illustrated for arrows. Nb_FE: the number of functional entities. CB: Caribbean, CIWP: Central Indo -Western Pacific, CP: Central Pacific, HW: Hawaiian, OTEP: Offshore Tropical Eastern Pacific, POL: Polynesian, SWA: SouthWestern Atlantic, SWP: South Western Pacific, TEP: Tropical Eastern Pacific, WI: Western Indian

In order to assess changes in redundancy patterns resulted from protection, we used the trophic groups as indicators. The permutational analysis of variance revealed differences between protection levels among trophic groups tested for all biogeographic provinces, except from SWA (Figure 4 and Table S4, apendix F of SM1). Some patterns could be observed in which redundancy and over redundancy indices followed an inverse pattern of vulnerability, but this response was dependent of the region studied. MPAs from POL, CB and CIWB provinces depicted the expected pattern, when protected areas harbored higher redundancy and/or over redundancy values, whilst vulnerability values was greater outside them. This could be observed for herbivores at CB, omnivores at CIWB and POL, for obligate corallivores at POL, for invertivores at WI, TEP and SWP, and grazing herbivores at SWP. On the other hand, the opposite response – higher redundancy and over-redundancy at unprotected zones and higher vulnerability within no-take areas – was registered for grazing herbivores and obligate corallivores at CP, for general carnivores and scrapers herbivores in TEP, and for omnivores at SWP (Figure 4 and Table S4, apendix F of SM1).

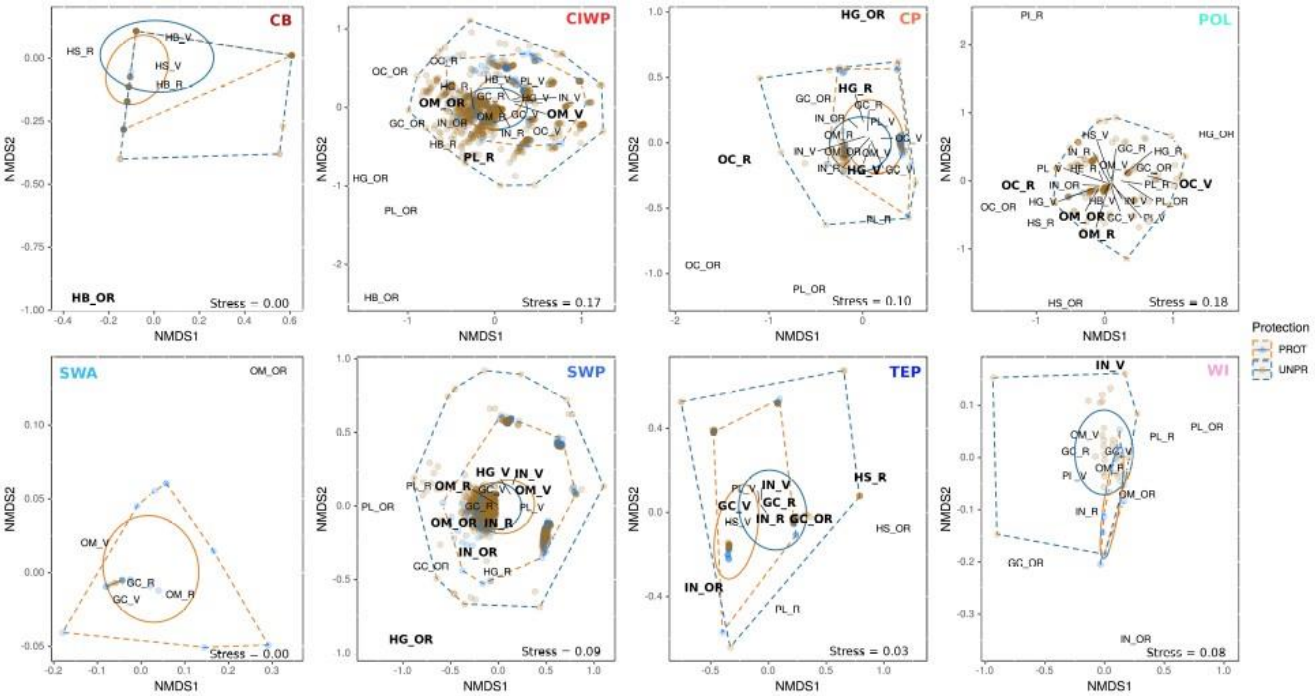

Figure 4. Non-metric multidimensional scaling (NMDS) ordination of combined redundancy indices (redundancy, vulnerability, and over-redundancy) for the trophic groups trait. Each of the biogeographic province was evaluated for different trophic groups. Orange point, ellipse and polygon represent the protected replicates, while blue point ellipse and polygon represent the unprotected replicates. The ellipses represent the standard deviation of protection level. The redundancy indices mark in bold represent the indices that are showing significant differences between levels of protection in the PERMANOVA. Bioprovinces - CB: Caribbean, CIWP: Central Indo -Western Pacific, CP: Central Pacific, POL: Polynesian, SWA: SouthWestern Atlantic, SWP: South Western Pacific, TEP: Tropical Eastern Pacific, WI: Western Indian. Trophic groups - OM: Omnivores, OC: Obligate Corallivores, PL: Planktivores, IN: Invertivores, GC: General Carnivores, HB: Herbivore, HG: Herbivore Grazers, HS: Herbivore Scrapers, PI: Piscivores. Redundancy indices - R: Functional Redundancy, OR: Functional Over-Redundancy, V: Functional Vulnerability.

## Discussion

Although the evaluation of the “reserve effect” on the reef ecosystem function is not new, this is the premier evaluation using a worldwide database of reef fish abundance together with an extensive review of marine protected areas compilation. Our hypothesis, is that MPAs contribute to protect functionality in reef systems, thus we expect to find that all functional space is represented within protected zones. However, our findings revealed, for the evaluated traits, that tropical worldwide MPAs are not representative enough to safeguard the functionality of the reef ecosystem as part of ecological functions remains unprotected outside MPAs boundaries worldwide.

Despite the ecological and socioeconomic effects worldwide recognized for MPAs, a theoretical benefit expected from protection is the enhance of ecosystem resilience protecting the species functional role (Myers, Baum, Shepherd, Powers, & Peterson, 2007). The expected increase of fish diversity due to protection, and therefore the consequent redundancy of fish species executing the same ecological function, which gives the reef system a higher resilience against environmental changes (García-Charton et al., 2008). This would result in higher ecological functional indicators such as functional richness (FRic), specialization (FSpe), divergence (FDiv), dispersion (FDis), evenness (FEve), redundancy (FRed) and over-redundancy (FORed) within managed areas. On the other hand, it is expected that functional originality (FOri) and vulnerability (FVul) are greater outside them. For example, a low FRic would indicate that there is a reduction in the productivity of the ecosystem, due to the fact that there are resources that are not being exploited (Mason, Mouillot, Lee, & Wilson, 2005). Also, with high FSpe there would be a greater average distance among species and a greater number of specialist species (David Mouillot et al., 2013), enhancing redundancy. In the same way, a high FDiv is equivalent to a high niche differentiation of the dominant species, and therefore more efficient use of resources, which could reduce competition (Mason, Mouillot, Lee, & Wilson, 2005). Additionally, with low FDis the fish community traits would be more homogeneous (Kulbicki et al., 2013) with greater competition and fewer functional diversity. Moreover, a low FEve also could increase the opportunity for the establishment of invasive species and reduce productivity (Mason, Mouillot, Lee, & Wilson, 2005), because a functional niche may be occupied but not fully utilized. Furthermore, there may be an inverse relationship between the indices of FOri and

FVul with FRed. If there is a low of FOri the species will be functionally more similar (Buisson, Grenouillet, Villéger, Canal, & Laffaille, 2013; D. Mouillot, Culioli, Pelletier, & Tomasini, 2008) due to the loss of species with a set of unique functional traits (Brandl, Emslie, & Ceccarelli, 2016). Otherwise, the loss of redundant species can increase originality because the remaining species become exclusive in their function (Brandl et al., 2016), thus also increasing FVul. Finally, a high FOred ensures that the assembly functions are not lost if any disturbance occurs.

Nevertheless, a recent study in Nova Caledonia found that the functional diversity of pristine habitats - open isolated marine areas situated far from coastal habitats (more than 20h of travel time of nearest harbour) - are significantly higher than the most restrictive, enforced, largest and oldest marine protected area (D'Agata et al., 2016). Also, through the assessment of a network of Mediterranean MPAs composed of almost 100 protected areas, researchers found that MPAs do not encompass more functional roles than one should expect by random (Guilhaumon et al., 2015). Moreover, no increase in functional indices was observed (Brandl et al., 2016) after a hurricane impact on coral reef habitats, except the functional originality, which increased post-disturbance and was negatively related to coral cover. These important outcomes can shed light on the interpretation of our findings.

The functional space approach regards the distribution of species in multivariate functional trait space (Villéger et al., 2008). With five selected traits we found a larger number of functional entities outside the protected areas, which reveals that there are still many functions that are not protected from some anthropogenic impact such as fishery and habitat degradation. Our results highlight that worldwide MPAs located in reef environments cannot protect all ecosystem functionality. In fact, the most efficient MPAs kept only 63% of total functional space available within their boundaries and belonged to Central Indo-Western Pacific province, one of the most biodiverse regions. This is probably due that the existing no-take zones do not represent the available diversity of reef essential habitats within the seascape, and therefore some species and ultimately functional entities are not represented within their limits. Moreover, some species can be benefited from anthropic impacts as has been shown by a study evaluating six Mediterranean NTZs, which found that local species richness of cryptobenthic, pelagic, and rare fishes can be greater at impacted areas due to changes in trophic interactions (Boulanger et al., 2021; Hackradt, Félix-Hackradt, Treviño-

Otón, Pérez-Ruzafa, & García-Charton, 2020).Finally, most marine MPAs are established without previous scientific knowledge about their connectivity with other areas, habitat mapping, ecosystem functionality or complete biodiversity assessment (Balbar & Metaxas, 2019). Their design, size and location are chosen based on local productivity, natural beauty, economic interests, as a biodiversity hotspot, among others (Russi et al., 2016), but never considering a multi-seascape approach when habitat is the key element to protect wildlife.

Coastal zones have a long history of cumulative impacts which varies between all biogeographic realms depending on the time since humans first began to use indiscriminately marine resources (Singh et al., 2020). The result of this intense use is a depauperated fauna, especially fishes, which are worldwide in decline. Our results showed that herbivores were more prone to respond to protection than any other trophic group, mainly at Caribbean MPAs, while a higher abundance of planktivores and invertivores fishes are favoured by open fishing areas. This indicates a possible effect of "fishing down marine foodwebs" occurring at the Caribbean sea, when herbivores are heavily targeted by coastal fisheries, and consequently more affected by protection measures (Mumby et al., 2012). Though it is noteworthy not to find such an effect over carnivore species, which have far from more depleted populations than herbivores worldwide (Abesamis, Green, Russ, & Jadloc, 2014), which might indicate that among coastal tropical seas top predator species were harvested to such a level (i.e., recruitment overfishing) that their abundance did not recover even within protected areas (Valdivia, Cox, & Bruno, 2017).

About 75% of fish stocks are collapsed, over-exploited or fully-exploited and only 25% are at moderate levels of exploration or under-exploited (Mullon, Fréon, & Cury, 2005). This historical fishing exploitation prior to protection efforts resulted in a negative relationship between habitat loss and overfishing on functional diversity of fish (Cáceres et al., 2020). Reef fish are subjected to intense anthropogenic disturbance besides the direct removal provided by fisheries (Azzurro et al., 2010; Munday et al., 2010), even inside no-take zones, resulting in deleterious effects on ecosystem functional roles. Despite the evidence that MPAs could cope better with invasive species due to increased resilience (Giakoumi et al., 2017), recent studies indicate that no differences in invasive species density or biomass could be found amongst protected vs unprotected areas (Cacabelos et al., 2020) or even that invasive species can be positively affected by MPAs (Giakoumi et al., 2017). On the other hand, there are no ecological barriers to pollutants, temperature increase or marine acidification. Therefore, cumulative anthropogenic actions at coastal zone throughout the years have caused the extinction of some ecological functions which may contribute to the higher vulnerability of most coral reef zones to adapt to climate change.

Multiple sources of anthropogenic stressors over tropical habitats can be contributing to the outcomes revealed in our work, as most marine protected areas studied rely on coastal and shallow areas of intense use throughout the years, and only recently became protected zones (i.e. the oldest MPA used in this work was Hanauma Bay, Hawaii, established in 1967). Although protection benefits could have been perceived in MPAs worldwide, only part of previously past functional entities are presented among these regions when compared to pristine habitats (D'Agata et al., 2016). These evidences might point out a scenario in which our best efforts to implement MPAs worldwide would not be enough to cope with climate change effects if its causes are not seriously addressed through political actions of gas emission reduction (to begin with) at a global scale. Our finds indicate a clear benefit effect of MPAs through bioprovinces that should be expanded and widely used as a tool of spatial ordination and must be integrated into a larger coastal management programs. Recently a global network of marine protected areas was announced as a way to promote food security enhancing 5% of MPAs total areas in coastal and conflict zones(Cabral et al., 2020), but also terrestrial potential effects over adjacent coastal and marine environments need to be considered on MPAs design (Kelleher, 1999).

Although MPAs are ecosystem-based tools, they seldom have been implemented focusing on ecosystem-based objectives, targeting mainly at the protection of one endangered species (Browman & Stergiou, 2004; Davidson & Dulvy, 2017), or a particular type of habitat or feature (Stratoudakis et al., 2019), favouring the local small scale fisheries (FAO, 2011), using the theoretical basis from terrestrial protected areas, where spatial connectivity is much more restricted than at marine environments, though more manageable. The absence of barriers imposes a management challenge to MPAs as surveillance, control and monitoring must be done continuously to guarantee effectiveness. However, it also facilitates population recovery and export of biological benefits throughout their boundaries (i.e, adults, juveniles, eggs and larvae). If implemented within a seascape perspective and together with fishing policies enforcement with hard and restricted fishing rules, scientific support, and strong surveillance, coastal MPAs can contribute to safeguarding the functional roles of coral reef ecosystems, as the more equilibrated an ecosystem is, the higher the potential to recover from large scale impacts (Arnoldi, Bideault, Loreau, & Haegeman, 2018).

Uncovering links between anthropogenic impacts and functional key groups of ecosystem is necessary to determine the causality of how protection is affecting functional diversity.. We suggest that controlled experiments be performed that contrast with our results on a global scale. These experiments could compare the functional diversity between nearby protected and unprotected areas, taking into account local and regional aspects such as environmental characteristics, positive and negative anthropic impacts, and particularities important on a small scale. With these works we could be better understand how reef ecosystems work and how local and regional characteristics influence their functionality as well as understanding what real role NTZs have in terms of functionality

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## Supplementary Material

APPENDICES

## Appendix A

Fish traits and Multidimensional functional indices

Diet as used as a categorical variable to determinate the main diet or food item; the maximum published length is a categorical variable to determinate the maximum length that is universal and predictive functional traits who can gives implicit information about the species: ecological attributes, organismal function, ontogenic (Bellwood, Streit, Brandl, & Tebbett, 2019); the resilience is a categorical variable that into account the first gonadal maturation size and fecundity estimations such as minimum number of eggs and offspring yearly (Musik 1999); the gregariousness is a categorical variable based in Mouillot et al., (2014) that showing interspecific or intraspecific social behaviour such as moving or feeding; spatial category is a categorical variable based on Harmelin, (1987) that estimate the horizontal and vertical species range of mobility. Vertical movement is related to the position a fish occupy in the water column where pelagic species have the largest vertical movement (ex. *Chromis* spp.), followed by necktonic (ex. *Abudefduf* spp.), benthic (ex. *Stegastes* spp.) and demersal species (ex. *Scorpaena* spp.). Reef associated refers to species that showed medium to large horizontal movement (ex. Acanthuridae) while reef attached are species that have little to no horizontal movement (ex. Blennnidae). These categories were attributed through behaviour video analysing of the species or a conspecific species (Table S1).

The FD indices are defined in Mouillot, Graham, Villéger, Mason, & Bellwood (2013) as: Functional Richness (FRic, '*the volume of multidimensional space occupied by all species in a community within functional space*'); Functional Evenness (FEve, *'the regularity of the relative abundance and distribution of species in functional space for a given community'*); Functional Divergence (FDiv, *'the proportion of total abundance supported by species with the most extreme trait values within a community*'); Functional Dispersion (FDis, *'Biomass-weighted mean distance from the center of the assemblage in the synthetic niche space*', (Brandl, Emslie, & Ceccarelli, 2016); Functional Specialization (FSpe, 't*he mean distance of a species from the rest of the species pool in functional space'*); and Functional

Originality (FOri*,’the isolation of a species in the functional space occupied by a given community*’) (Laliberté, Legendre, & Shipley, 2015).

Table S1. Biological functional traits, traits categories, units, type of variable and references used to defined the functional indices that describe ecological functioning in reef fish assemblages.

| Functional Traits | Trait Category | Unit | Description | Reference |
|---|---|---|---|---|
| Trophic Category | Diet | Herbivore (HERB) | Feeding on macroalgae | Bellwood et al., 2019; Floeter, Bender, Siqueira, & Cowman, 2018; Halpern & Floeter, 2008 |
| | | Herbivore grazer (HGRZ) | Feeding on superficial reef matrix | |
| | | Herbivore scraper (HSCP) | Feeding on reef matrix | |
| | | Omnivore (OMNI) | Feeding plants and animals item | |
| | | Invertivore (INV) | Feeding mobile benthic invertebrates | |
| | | Obligate corallivore (OC) | Feeding hard corals and some on soft coral | |
| | | Cleaner (CLE) | Feeding others animals organisms (ex ectoparasites) | |
| | | Planktivore (PLNK) | Feeding plakton organisms | |
| | | General Carnivore (GCAR) | Feeding invertebrates (ex. mollusc) and fish | |
| | | Piscivore (PISC) | Feeding strictly fish | |
| Maximum length | Morphology | Very small | <8 | Forese & Pauly, 2020 * |
| | | Small | 8.1-15.9 | |
| | | Medium | 16-30.9 | |
| | | Medium-Large | 31-50.9 | |
| | | Large | 51-80.9 | |
| | | Very Large | >81 | |
| Resilience | Life history | Very low | Detail in supplementary material | Musick, 1999, Forese & Pauly, 2020* |
| | | Low, | | |
| | | Medium | | |
| | | High | | |
| | | Very high | | |
| Gregariousness | Life history | Solitary | 1 individual | Mouillot et al., 2014 |
| | | Pair | 2 individuals | |
| | | Small – medium | 3-50 individuals | |
| | | Large | >50 individual | |
| Spatial Category | Habitat | Pelagic/reef associated | Detail in supplementary material | Harmelin, 1987 |
| | | Necktonic/reef associated | | |
| | | Benthonic/reef associated | | |
| | | Demersal/reef associated | | |
| | | Benthonic/reef attached | | |
| | | Demersal/reef attached | | |

* www.fishbase.org

## Appendix B

Table S2. Summary of the total number of species and samples transects by biogeographic province, differentiating the number of samples transects at each level of protection

| | CB | CIWP | CP | E | HW | NWI | OTEP | POL | SWA | SWP | TEP | WI |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| N° total species | 205 | 1131 | 488 | 42 | 89 | 186 | 171 | 410 | 48 | 1009 | 181 | 308 |
| Total sites (N° transects) | 190 | 1179 | 134 | 28 | 11 | 21 | 220 | 153 | 22 | 2378 | 425 | 39 |
| NTZ sites | 25 | 135 | 25 | 0 | 2 | 0 | 76 | 2 | 16 | 506 | 47 | 4 |
| UNPR sites | 165 | 1044 | 109 | 28 | 9 | 21 | 144 | 151 | 6 | 1872 | 378 | 35 |

## Appendix C

### PERMANOVA and Pair-wise test

In the pair-wise test, the abundance was significances differences and higher abundance in protected areas for TEP (8.2 ± 0.12, 6.99 ± 0.05) and SWP (6.75 ± 0.05, 6.74 ± 0.02), In the same way, q0 showed values higher and significances in protected areas for CB (39.4 ± 1.5, 29.8 ± 0.6), but lower in SWP (42.9 ± 1.1, 44.4 ± 0.5) and CIWP (52.3 ± 1.5, 53.6 ± 0.7). Likewise, q1 and q2 presented values higher for protected areas in CB (13.2 ±0.75, 8.63 ± 0.32; 8.44 ± 0.58, 5.75 ± 0.23, respectively) and CIWP (15.1 ± 0.53, 12.4 ± 0.19; 9.1 ± 0.4, 7.3 ± 0.12, respectively), however lower values in SWP (11.9 ± 0.32, 12.8 ± 0.18; 7.3 ± 0.2, 7.7 ± 0.1, respectively). Besides, q2 also was higher for protected areas in POL (11.6 ± 1.1, 5.9 ± 0.25). Them, the functional indices showed that FRic was higher in protected areas that in unprotected areas for CB (0.08 ± 0.008, 0.05 ± 0.002) and TEP (0.09 ± 0.006, 0.06 ± 0.002), by contrast to SWP (0.05 ± 0.002, 0.06 ± 0.001). Conversely, FDiv and FEve presented values significance higher in unprotected areas for POL (0.77 ± 0.04, 0.9 ± 0.006; 0.46 ± 0.05, 0.52 ± 0.004) and TEP (0.68 ± 0.02, 0.81 ± 0.005; 0.43 ± 0.01, 0.5 ± 0.005). In the case of FDis, for CIWP (0.46 ± 0.005, 0.44 ± 0.002) and CP (0.5 ± 0.02, 0.43 ± 0.009) the values was higher in protected areas, but in TEP (0.41 ± 0.01, 0.47 ± 0.005) was in unprotected areas. In addition, FSpe showed the same for CP (0.53 ± 0.02, 0.44 ±0.006) and WI (0.55 ± 0.03, 0.46 ± 0.008), but lower values in protected area for SWP (0.44 ± 0.001, 0.45 ± 0.003) and TEP (0.39 ± 0.01, 0.45 ± 0.004). Similarly, FOri was greater in unprotected for CIWP (0.28 ± 0.002, 0.3 ± 0.002), CP (0.29 ± 0.008, 0.3 ± 0.004), POL (0.23 ± 0.01, 0.3 ± 0.002), TEP (0.3 ± 0.005, 0.31 ± 0.002), and higher in protected areas in CB (0.32 ± 0.002, 0.3 ± 0.002), OTEP (0.36 ± 0.006, 0.28 ± 0.003) and SWP (0.31 ±0.002, 0.3 ± 0.001). On the other hand, the number of FE was higher in CB (34.6 ± 1.27, 26.4 ± 0.55) and CIWP (44.4 ± 1.1, 43.8 ± 0.5) but lower for SWP (35.2 ± 0.75, 36.8 ± 0.35) for protected areas. In the case of FRed and FORed, in protected areas was higher for OTEP (1.11 ± 0.005, 1.02 ± 0.002; 0.09 ±0.004, 0.02 ± 0.002) and TEP (1.07 ± 0.007, 1.03 ± 0.002; 0.06 ± 0.005, 0.003 ± 0.001), and lower for SPW (1.18 ± 0.005, 1.18 ± 0.002; 0.12 ± 0.003, 0.12 ± 0.001) respectively. For last, Fvul was higher for unprotected areas in OTEP (0.91 ± 0.004, 0.98 ± 0.002), POL (0.78 ± 0.06, 0.87 ± 0.004), TEP (0.93 ± 0.007, 0.97 ± 0.002), and higher for protected areas in CP (0.88 ± 0.01, 0.84 ± 0.006) and SWP (0.87 ± 0.003, 0.86 ± 0.002) (Table S3, Figures S1-3)

Table S3. Pair-wise test of abundance, true diversity indices, functional diversity indices, functional entities and redundancy patterns for protection level in each biogeographic province. CB: Caribbean, CIWP: Central Indo -Western Pacific, CP: Central Pacific, HW: Hawaiian, OTEP: Offshore Tropical Eastern Pacific, POL: Polynesian, SWA: SouthWestern Atlantic, SWP: South Western Pacific, TEP: Tropical Eastern Pacific, WI: Western Indian. ***: *p* ≤0.001, **: *p* ≤ 0.01, *: *p* ≤ 0.05.

| Variables | CB | CIWP | CP | HW | OTEP | POL | SWA | SWP | TEP | WI |
|---|---|---|---|---|---|---|---|---|---|---|
| ln(N) | 0.225 | 0.849 | 0.515 | 0.298 | 0.123 | 0.977 | 0.781 | P>U** | P>U*** | 0.306 |
| q0 | P>U** | P<U** | 0.642 | 0.196 | 0.286 | 0.176 | 0.597 | P<U*** | 0.377 | 0.941 |
| q1 | P>U** | P>U*** | 0.325 | 0.286 | 0.832 | 0.067 | 0.313 | P<U*** | 0.136 | 0.15 |
| q2 | P>U** | P>U*** | 0.365 | 0.489 | 0.614 | P>U* | 0.598 | P<U*** | 0.149 | 0.128 |
| FRic | P>U* | 0.123 | 0.194 | 0.115 | 0.587 | 0.829 | 0.371 | P<U*** | P>U* | 0.599 |
| FEve | 0.839 | 0.460 | 0.696 | 0.144 | 0.157 | P<U* | 0.896 | 0.869 | P<U*** | 0.905 |
| FDiv | 0.080 | 0.783 | 0.856 | 0.685 | 0.248 | P<U* | 0.400 | 0.211 | P<U*** | 0.066 |
| FDis | 0.244 | P>U* | P>U*** | 0.260 | 0.766 | 0.771 | 0.139 | 0.083 | P<U*** | 0.102 |
| FSpe | 0.541 | 0.394 | P>U** | 0.221 | 0.384 | 0.145 | 0.097 | P<U*** | P<U*** | P>U** |
| FOri | P>U** | P<U** | P<U* | 0.465 | P>U*** | P<U** | 0.075 | P>U** | P<U* | 0.548 |
| FE | P>U** | P>U*** | 0.965 | 0.187 | 0.711 | 0.322 | 0.495 | P<U*** | 0.086 | 0.893 |
| FRed | 0.211 | 0.413 | 0.158 | 0.921 | P>U*** | 0.061 | 0.493 | P<U*** | P>U*** | 0.774 |
| FORed | 0.256 | 0.233 | 0.152 | 0.980 | P>U*** | 0.151 | 0.442 | P<U*** | P>U*** | 0.817 |
| FVul | 0.102 | 0.288 | P>U* | 0.870 | P<U*** | P<U* | 0.618 | P>U*** | P<U*** | 0.500 |

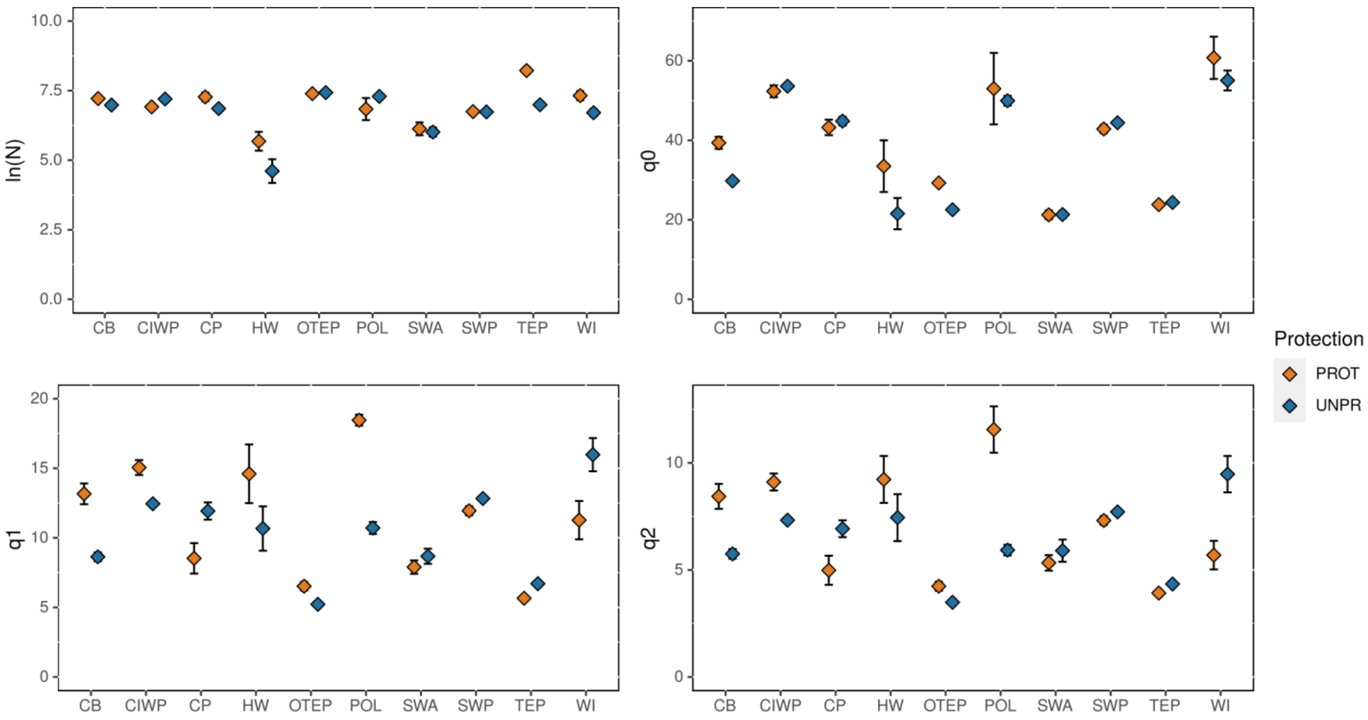

Figure S1. Mean and standard error of abundance transformer to the Neperiam logaritmic (ln (N)) and “true diversity” index: diversity q0 (rare species), diversity q1 (common species) and diversity q2 (dominant species); for the combination of factors biogeographic province and protection. CB: Caribbean, CIWP: Central Indo-Western Pacific, CP: Central Pacific, HW: Hawaii, OTEP: Offshore Tropical Eastern Pacific, POL: Polynesian, SWA: Sourth Western Atlantic, SWP: Sourth Western Pacific, TEP: Tropical Eastern Pacific, WI: Western Indian. The black point represent protected areas and grey point unprotected areas.

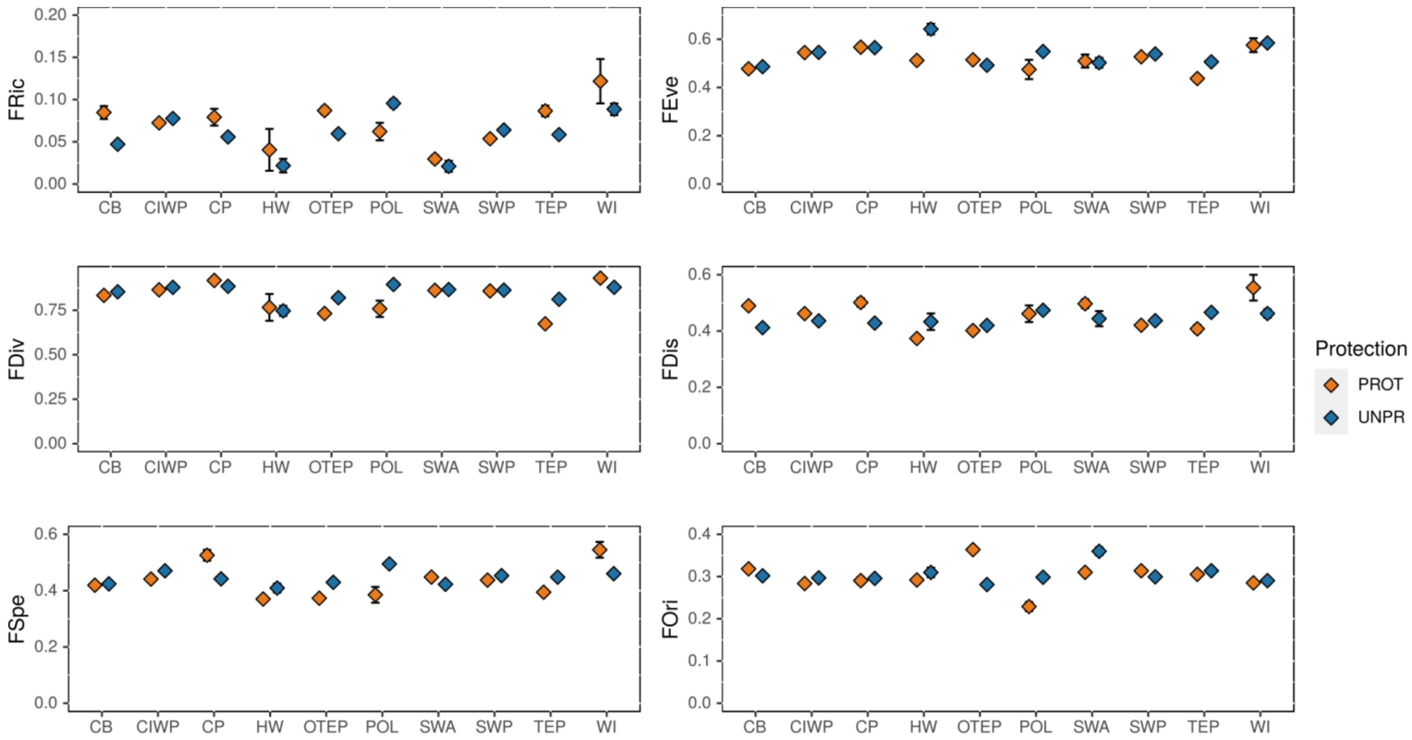

Figure S2. Mean and standard error of multidimensional functional indices FRic: Functional Richness, FEve: Functional Evenness; FDiv: Functional Divergence, FDis: Functional Dispersion, FSpe: Functional Specialization, and FOri: Functional Originality; for the combination of factors biogeographic province and protection. CB: Caribbean, CIWP: Central Indo-Western Pacific, CP: Central Pacific, HW: Hawaii, OTEP: Offshore Tropical Eastern Pacific, POL: Polynesian, SWA: Sourth Western Atlantic, SWP: Sourth Western Pacific, TEP: Tropical Eastern Pacific, WI: Western Indian. The black point represent protected areas and grey point unprotected areas.

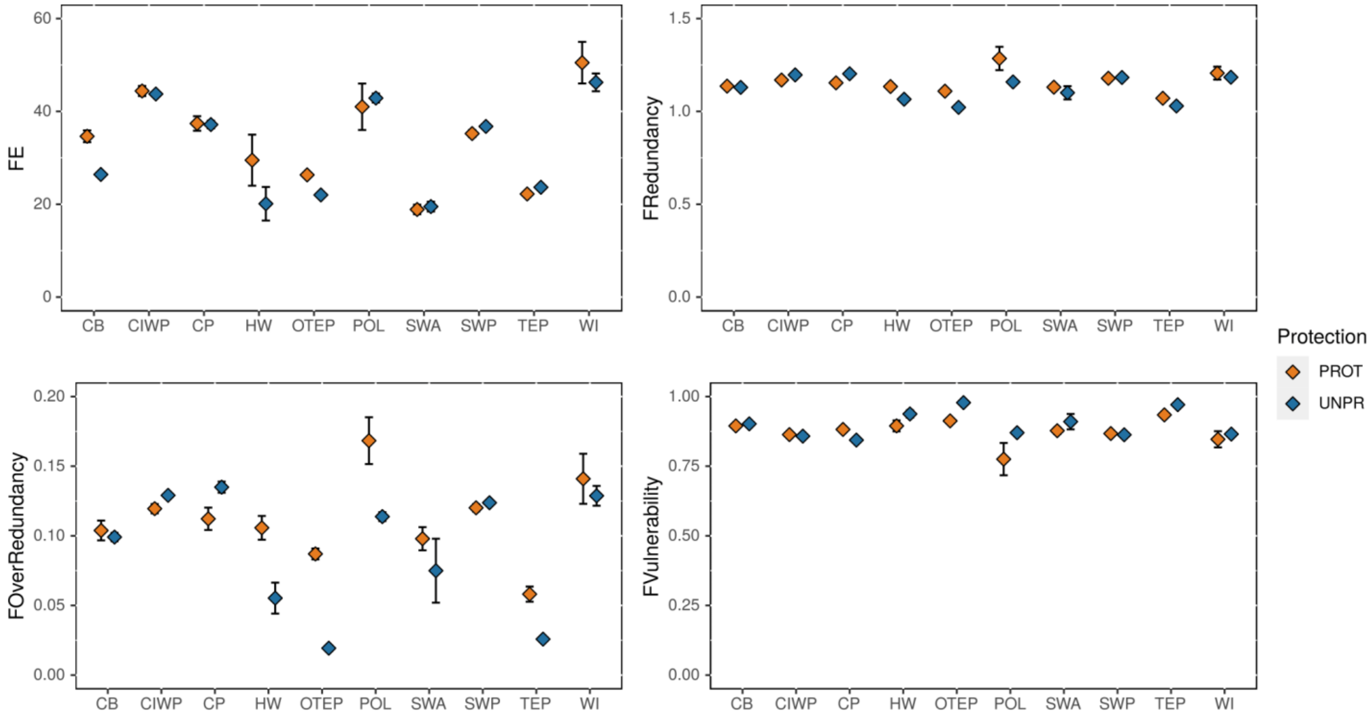

Figure S3. Mean and standard error of patterns redundancy indices FE: Functional Entities, Fred: Functional Redundancy, FORed: Functional Over-Redundancy, and FVul: Functional Vulnerability; for the combination of factors biogeographic province and protection. CB: Caribbean, CIWP: Central Indo-Western Pacific, CP: Central Pacific, HW: Hawaii, OTEP: Offshore Tropical Eastern Pacific, POL: Polynesian, SWA: Sourth Western Atlantic, SWP: Sourth Western Pacific, TEP: Tropical Eastern Pacific, WI: Western Indian. The black point represent protected areas and grey point unprotected areas.

## Appendix D

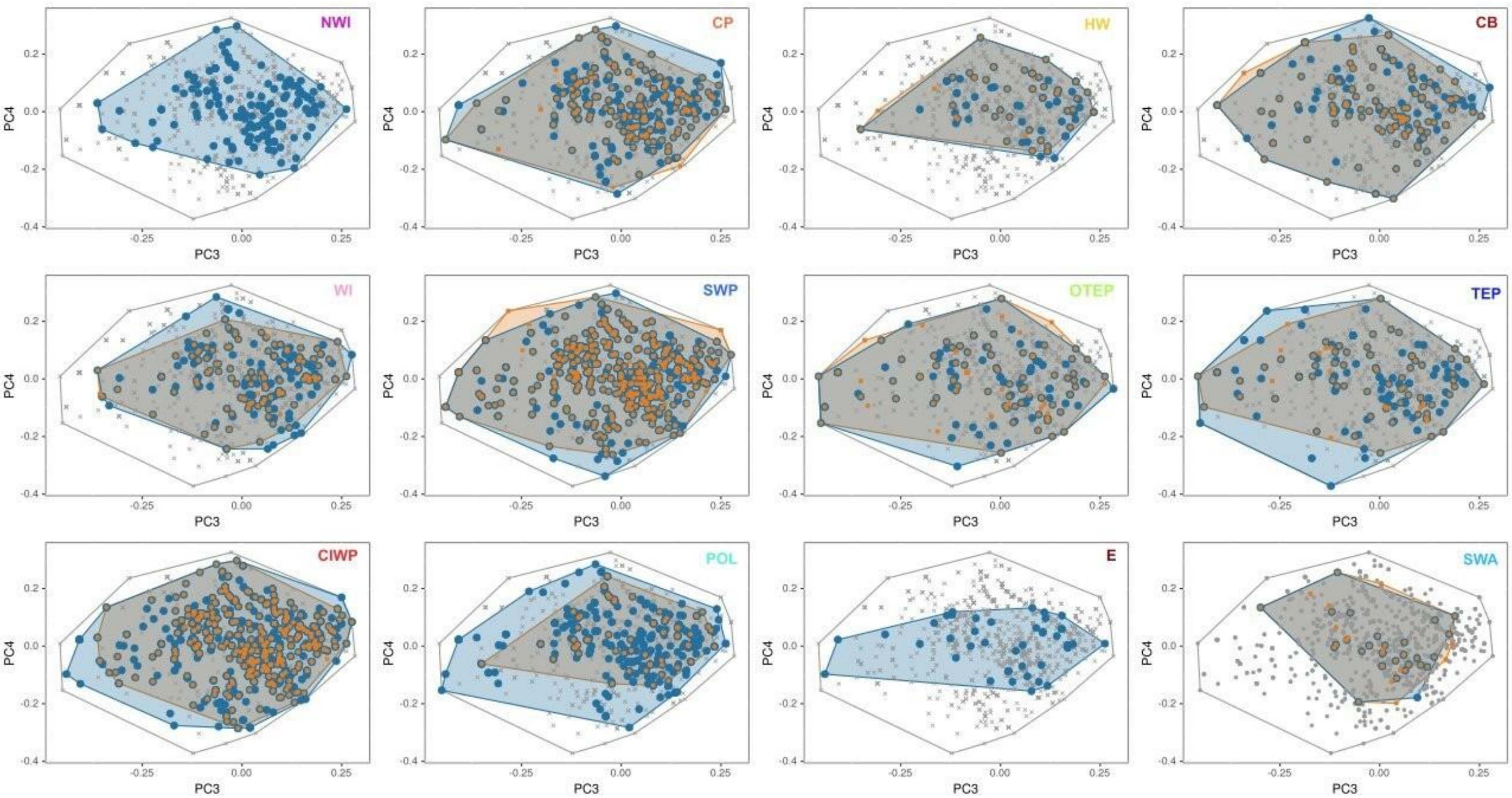

Figure S4. Representation of functional space in marine protected (no-take zones) and unprotected areas for 12 biogeographic provinces (CB: Caribbean, CIWP: Central Indo-Western Pacific, CP: Central Pacific, HW: Hawaiian, OTEP: Offshore Tropical Eastern Pacific and POL: Polynesian, SWA: SouthWestern Atlantic, SWP: South Western Pacific, TEP: Tropical Eastern Pacific, WI: Western Indian). The functional space is created using PC3-PC4 with Principal Coordinate Analysis on functional traits to represent the distribution of functional entities. The global convex hull, including the 1,956 species split into 574 functional entities is in grey. The orange points represent the functional entities present in marine protected (‘prot’) areas, the blue points represent the functional entities in unprotected (‘unpr’) areas, while the orange point with blue edges represent the functional entities that share the two level protection. Grey crosses are functional entities absent in the biogeographic province.

# Appendix E

## Functional traits in Bayesian regression models

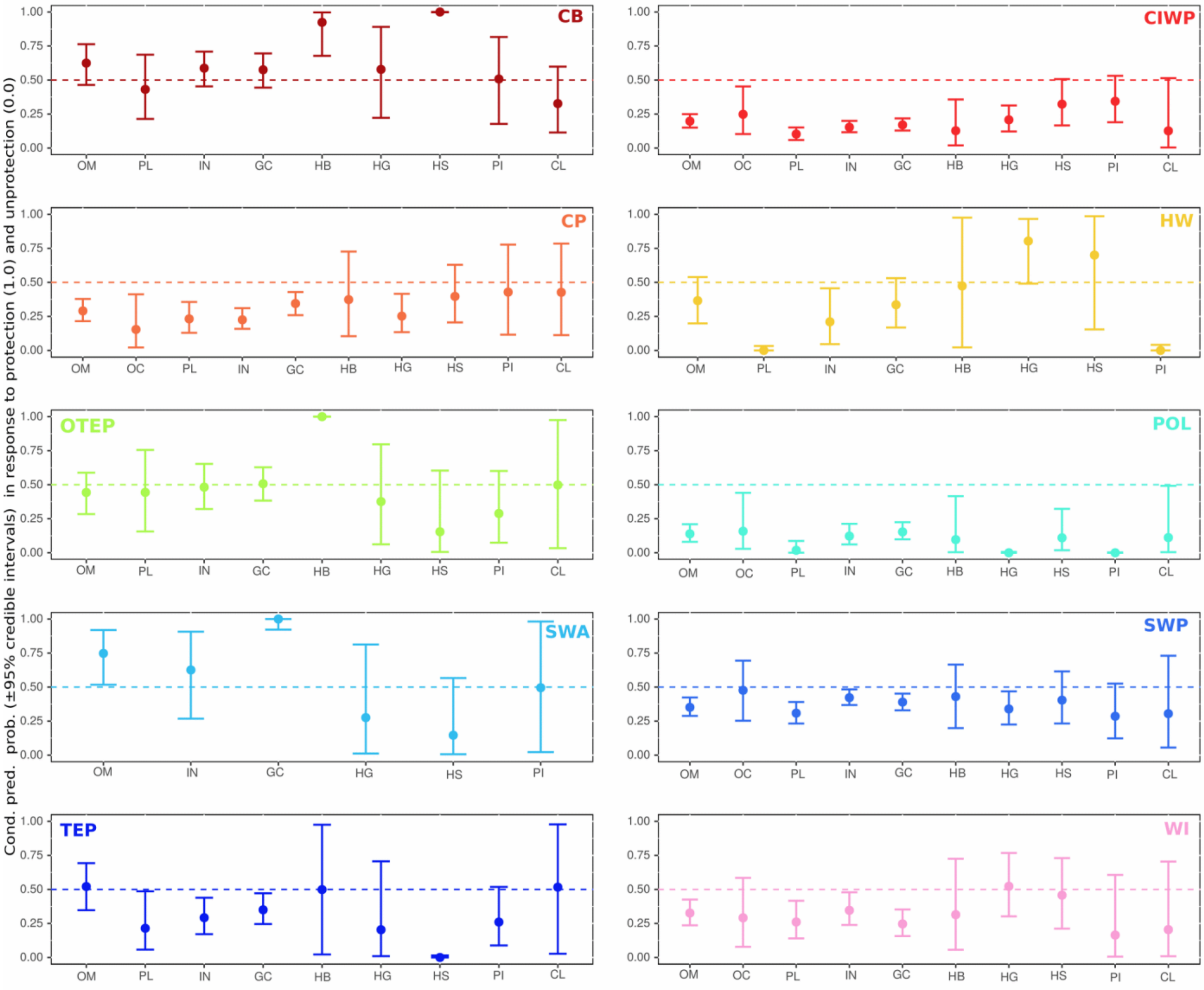

Figure S5. Predicted posterior probabilities (±95% credible intervals) from binomial Bayesian Regression Model (BRM), representing functional traits of trophic category for the factor protection and each biogeographic provinces. The line at 0.5 of the y-axis, represents the delimitation between protected and unprotected. Trophic category - OM: Omnivores, OC: Obligatory corallivore, PL: Planktivores, IN: Invertivores, GC: General Carnivores, HB: Herbivore, HG: Herbivore Grazers, HS: Herbivore Scrapers, PI: Piscivores, CL: Cleaner

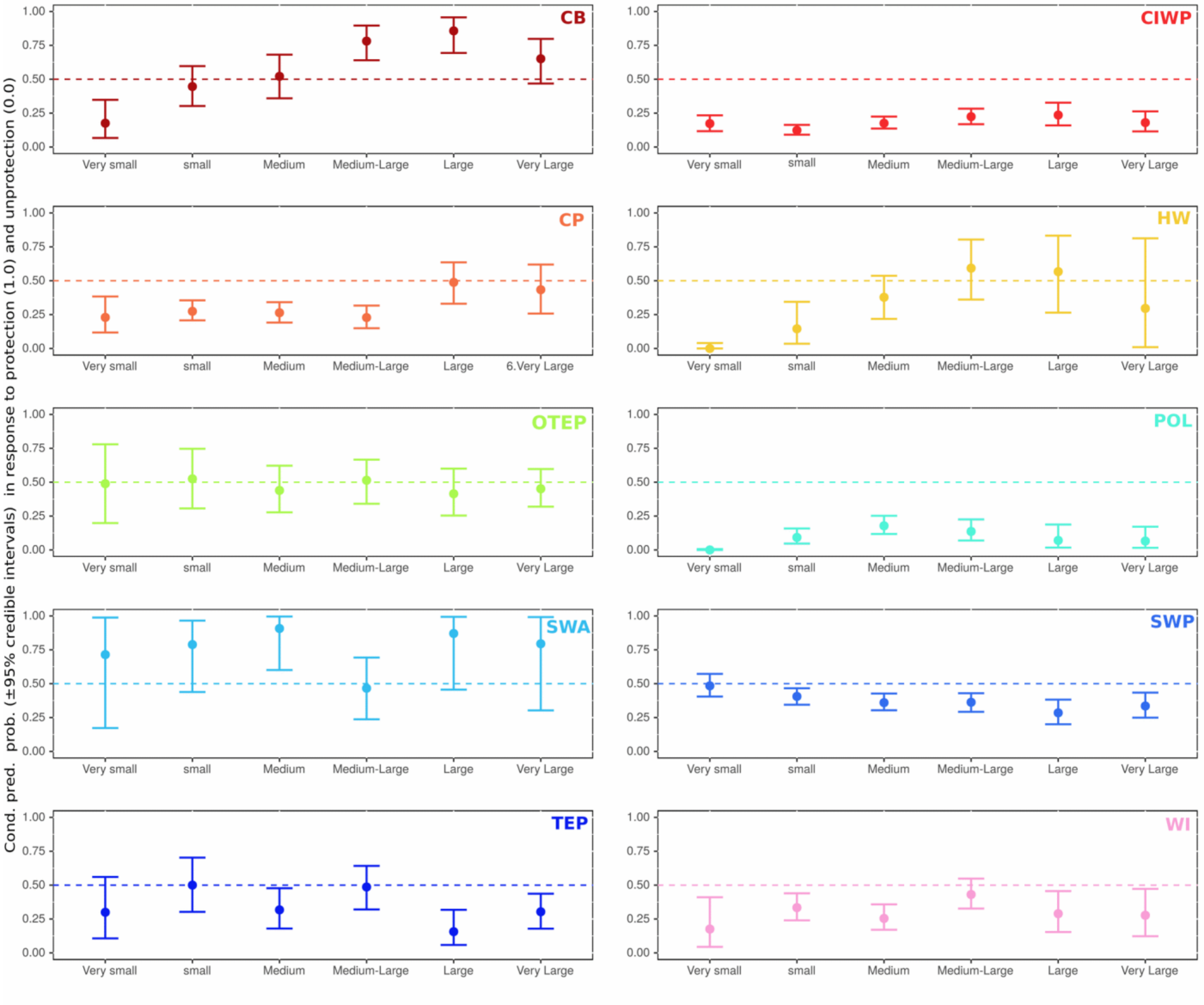

Figure S6. Predicted posterior probabilities (±95% credible intervals) from bernouilli distribution Bayesian Regression Model, representing functional traits of maximum length for the factor protection and each biogeographic provinces. The line at 0.5 of the y-axis, represents the delimitation between protected and unprotected. Very small (<8cm), small (8.1-15.9cm), medium (16-30.9cm), medium-large (31-50.9cm), large (51-80.9cm), very large (>81cm).

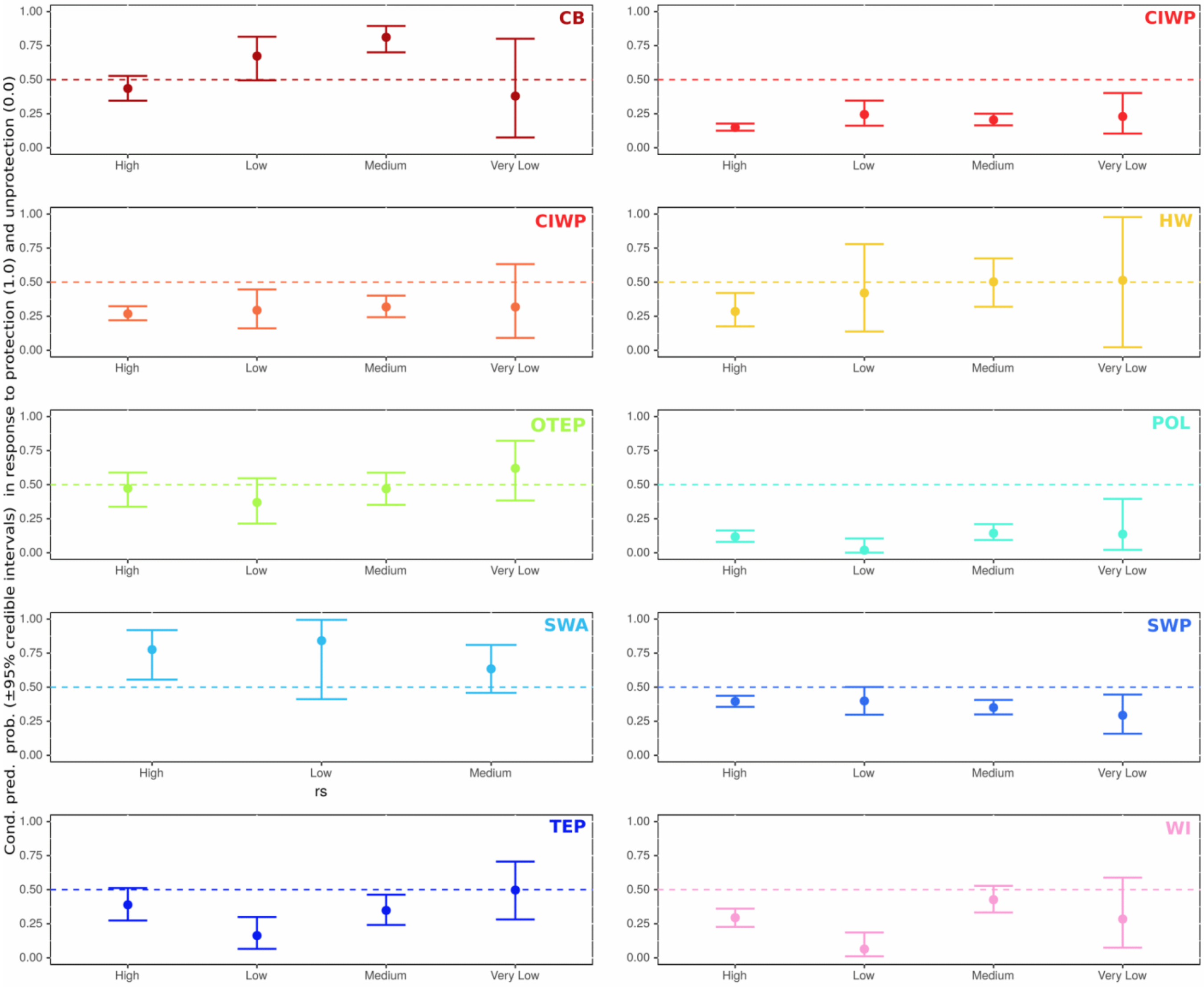

Figure S7. Predicted posterior probabilities (±95% credible intervals) from bernouilli distribution Bayesian Regression Model, representing functional traits of resilience for the factor protection and each biogeographic provinces. The line at 0.5 of the y-axis, represents the delimitation between protected and unprotected.

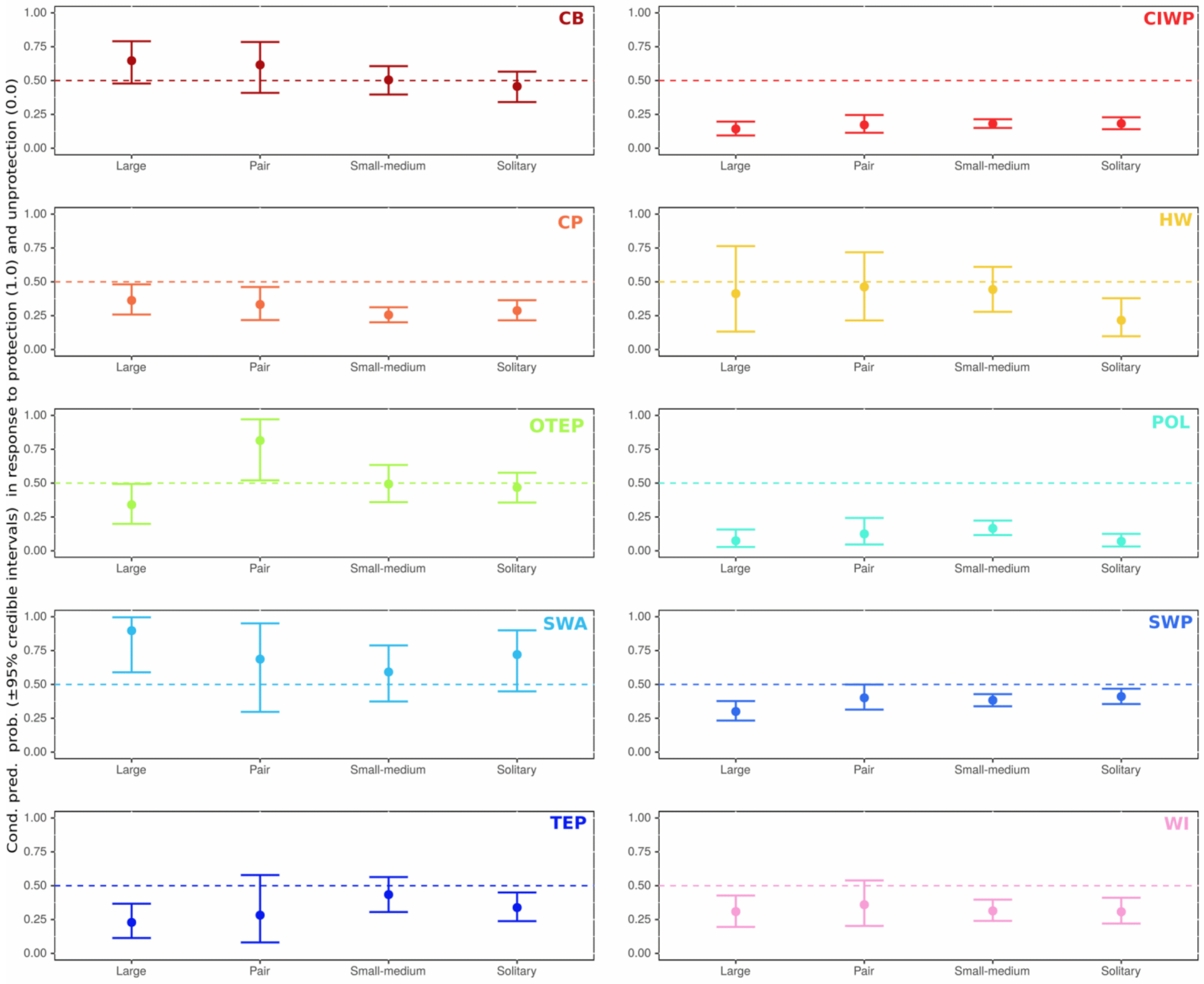

Figure S8. Conditional effects predictive probabilities (±95% credible intervals) from bernouilli distribution Bayesian Regression Model, representing functional traits of gregariousness for the factor protection. The line at 0.5 of the y-axis, represents the delimitation between protected and unprotected. Type of species gregariousness being solitary (1 individual), pair (2 individuals), small-medium (3-50 individuals), large (>50 individual).

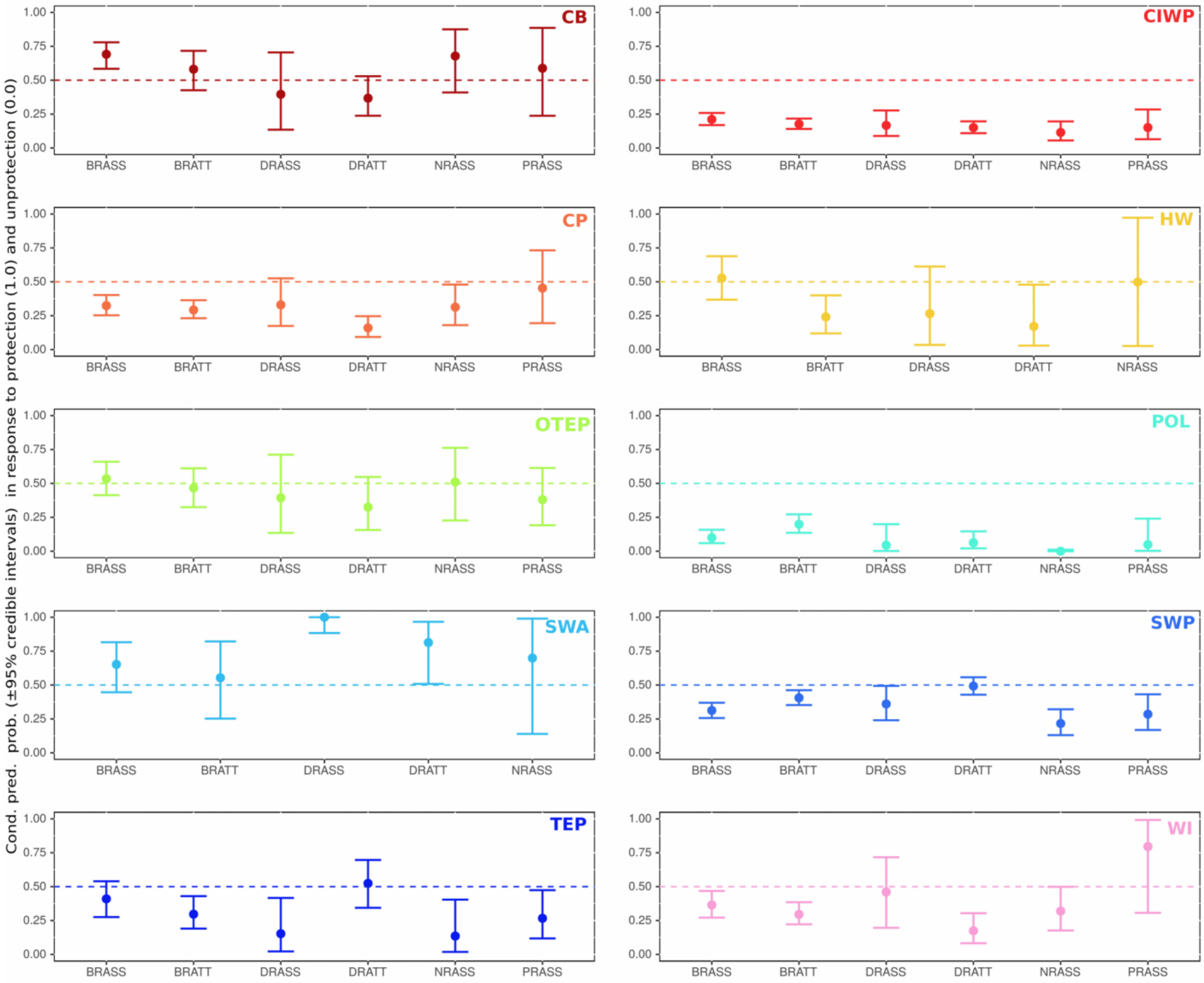

Figure SM9. Predicted posterior probabilities (±95% credible intervals) from bernouilli distribution Bayesian Regression Model, representing functional traits of spatial category for the factor protection and each biogeographic provinces. The line at 0.5 of the y-axis, represents the delimitation between protected and unprotected. Horizontal and vertical movement in the water column: BRASS: Benthic/reef associated, BRATT : Benthic/ reef attached, DRASS: Demersal/reef associated, DRATT: Demersal/reef attached, NRASS: Necktonic/reef associated, PRASS: Pelagic/reef associated

## Appendix F

Table S4. PERMANOVA of redundancy patterns for protection level in each biogeographic province for the trophic groups traits. CB: Caribbean, CIWP: Central Indo -Western Pacific, CP: Central Pacific, POL: Polynesian, SWA: SouthWestern Atlantic, SWP: South Western Pacific, TEP: Tropical Eastern Pacific, WI: Western Indian. OMNI: Omnivores, OC: Obligate Corallivores, PLNK: Planktivores, INV: Invertivores, GCAR: General Carnivores, HERB: Herbivore, HGRZ: Herbivore Grazers, HSCP: Herbivore Scrapers, PISC: Piscivores, RED: Functional Redundancy, ORED: Functional Over-Redundancy, VUL: Functional Vulnerability. ***: *p* ≤0.001, **: *p* ≤ 0.01, *: *p* ≤ 0.05.

| Sources | CB | CIWP | CP | POL | SWA | SWP | TEP | WI |
|---|---|---|---|---|---|---|---|---|
| Protection (df) | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Residual (df) | 187 | 1772 | 129 | 148 | 17 | 2373 | 420 | 34 |
| Total (df) | 191 | 1776 | 133 | 152 | 21 | 2377 | 424 | 38 |

| Variables | | CB | | CIWP | | CP | | POL | | SWA | | SWP | | TEP | | WI | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | F | p | F | p | F | p | F | p | F | p | F | p | F | p | F | p |
| OMNI | RED | - | - | 1.7 | 0.178 | 0.4 | 0.544 | 5.2 | P>U* | 3.6 | 0.063 | 39.8 | P<U*** | - | - | 2.9 | 0.099 |
| | ORED | - | - | 5.3 | P>U* | 1.7 | 0.176 | 5.8 | P>U* | 2.8 | 0.111 | 52.5 | P<U*** | - | - | 1.3 | 0.252 |
| | VUL | - | - | 4.9 | P<U* | 0.5 | 0.501 | 0.8 | 0.371 | 1.4 | 0.259 | 14.2 | P>U*** | - | - | 2.7 | 0.125 |
| OC | RED | - | - | 1.5 | 0.233 | 4.8 | P<U* | 5.1 | P>U* | - | - | - | - | - | - | - | - |
| | ORED | - | - | 2.8 | 0.095 | 0.02 | 0.886 | 2.1 | 0.101 | - | - | - | - | - | - | - | - |
| | VUL | - | - | 0.8 | 0.356 | 0.3 | 0.581 | 7.3 | P<U* | - | - | - | - | - | - | - | - |
| PLNK | RED | - | - | 4.8 | P<U* | 3.3 | 0.076 | 0.5 | 0.295 | - | - | 2.1 | 0.147 | 1.3 | 0.25 | 0.03 | 0.808 |
| | ORED | - | - | 0.9 | 0.338 | 0.1 | 0.766 | 0.1 | 0.771 | - | - | 1.3 | 0.255 | - | - | 0.1 | 0.742 |
| | VUL | - | - | 3.6 | 0.062 | 0.1 | 0.749 | 0.1 | 0.717 | - | - | 0.4 | 0.533 | - | - | 0.5 | 0.441 |
| INV | RED | - | - | 0.1 | 0.793 | 0.2 | 0.641 | 0.7 | 0.402 | - | - | 15.6 | P>U*** | 26.7 | P>U*** | 1.9 | 0.122 |
| | ORED | - | - | 0.3 | 0.61 | 0.3 | 0.606 | 1.7 | 0.195 | - | - | 15.9 | P>U*** | 66.0 | P>U*** | 0.03 | 0.872 |
| | VUL | - | - | 0.5 | 0.429 | 0.1 | 0.724 | 0.3 | 0.637 | - | - | 7.9 | P<U** | 79.8 | P<U*** | 13.8 | P<U** |
| GCAR | RED | - | - | 0.1 | 0.708 | 0.16 | 0.676 | 0.2 | 0.684 | - | - | 1.1 | 0.312 | 5.1 | P<U* | 0.01 | 0.918 |
| | ORED | - | - | 0.5 | 0.5 | 0.2 | 0.665 | 0.02 | 0.887 | - | - | 0.0 | 1 | 4.9 | P<U* | 0.001 | 0.951 |
| | VUL | - | - | 0.01 | 0.924 | 1.2 | 0.259 | 1.4 | 0.215 | - | - | 0.9 | 0.365 | 5.1 | P>U* | 0.01 | 0.93 |
| HERB | RED | 3.8 | 0.05 | 0.1 | 0.8 | - | - | 1.1 | 0.103 | - | - | - | - | - | - | - | - |
| | ORED | 6.3 | P>U* | 0.01 | 0.935 | - | - | - | - | - | - | - | - | - | - | - | - |
| | VUL | 3.2 | 0.068 | 0.01 | 0;933 | - | - | 0.9 | 0.06 | - | - | - | - | - | - | - | - |
| HGRZ | RED | - | - | 1.3 | 0.267 | 6.5 | P<U* | 0.2 | 0.468 | - | - | 0.3 | 0.599 | - | - | - | - |
| | ORED | - | - | 0.01 | 0.952 | 5.2 | P<U* | 0.2 | 0.679 | - | - | 15.1 | P>U*** | - | - | - | - |
| | VUL | - | - | 0.2 | 0.614 | 4.0 | P>U* | 1.2 | 0.129 | - | - | 8.8 | P<U** | - | - | - | - |
| HSCP | RED | 0.3 | 0.612 | - | - | - | - | 0.7 | 0.386 | - | - | - | - | 48.6 | P<U*** | - | - |
| | ORED | - | - | - | - | - | - | 0.4 | 0.206 | - | - | - | - | 0.001 | 0.913 | - | - |
| | VUL | - | - | - | - | - | - | 0.9 | 0.104 | - | - | - | - | 0.2 | 0.663 | - | - |
| PISC | RED | - | - | - | - | - | - | 0,2 | 0.707 | - | - | - | - | - | - | - | - |
| | ORED | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| | VUL | - | - | - | - | - | - | - | - | - | - | - | - | - | | - | - |

## Appendix G

### Bayesian Regression Model between ecological and functional diversity indices

Then, to find out the relationship between ecological and functional diversity indices, also we used Bayesian regression models (BRM) in which our response variables were FRic, FEve, FDiv, FDiv, FSpe, FOri, FE, FRed, FORed and FVul, and $q^0$, $q^1$ and $q^2$ as predictors. We then ran 30 BRM with different error distributions depending on the index evaluated (gaussian, log-normal, beta and zero inflated beta). Each BRM was run for 4 chain and 3,000 interactions with an initial warm-up phase of 1,500 using 'brms' package (Bürkner, 2018) . For the prior distribution we used default settings with the exception " *max_treedepth*" and "*adapt_delta*" set to 15 and 0.99, respectively.

We evaluate how the relationship between "true diversity" and functional diversity indices may be affected by the protection. We found that Fric increases significantly with an increase in diversity of rares and commons species for both levels of protection, but only for the unprotected areas that the dominant species thus influence FRic. On the contrary, we could observe that FDiv decreases with increased species diversity common in the two level protection, and the same happens in unprotected areas with the dominants species. Moreover, we showed that with an increase in commons and dominants species, the FDiv also increases for both protected and unprotected, but with rares species it only increases for open areas. Else, there is a decrease in FSpe with an increase in the diversity of rares and dominants species for unprotected areas, but with commons species this occurs both protected and unprotected areas. We also evaluated the relationship of these diversity indices with redundancy patterns and we were able to verify that the number of FE increases with increasing diversity of rare species at the two levels of protection, while the diversity of common species also causes this in protected areas and dominant species in open areas. On the other hand, FRed increases with common and dominant species in protected areas, while only dominant ones in unprotected areas. Besides, we found that in protected areas with a greater number of commons species increases the FORed while that in open areas this happens with the increase of the dominant species, but we also find that a low number of rare species can negatively affect FORed although can increase with a large number of these species. Finally, we were able to observe that with a greater number of dominant species, functional vulnerability decreases in unprotected areas(Figure S10 – 12, table S5).

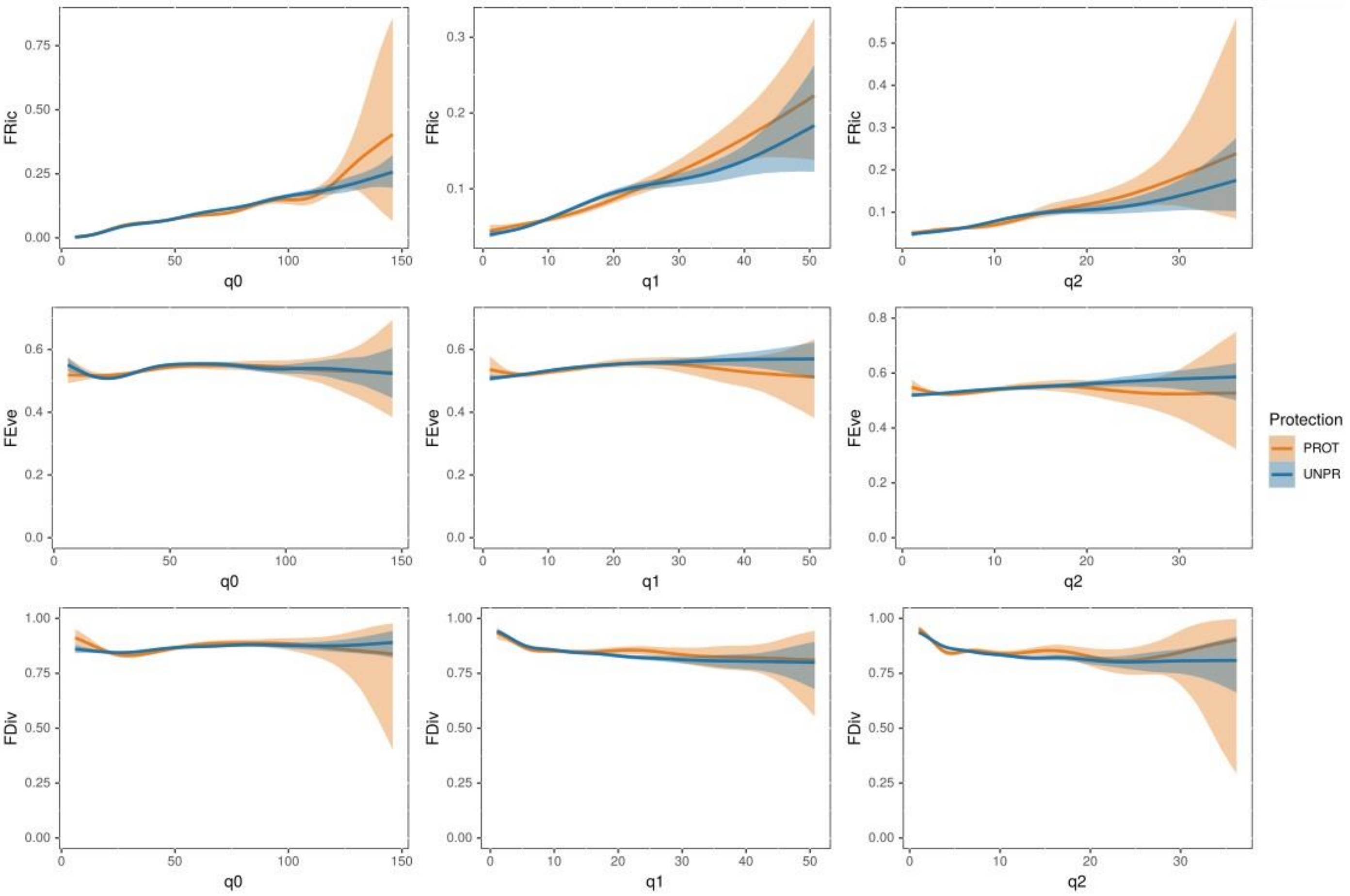

Figure S10. Conditional effects plot (±95% credible intervals) of Bayesian regression models between multidimensional functional indices and 'true diversity' ecological indices for all biogeographic provinces. q0: diversity rare species, q1: diversity common species, q2: diversity dominant species, FRic: Functional Richness (zero inflated beta distribution), FEve: Functional Evenness (beta distribution); FDiv: Functional Divergence (beta distribution).

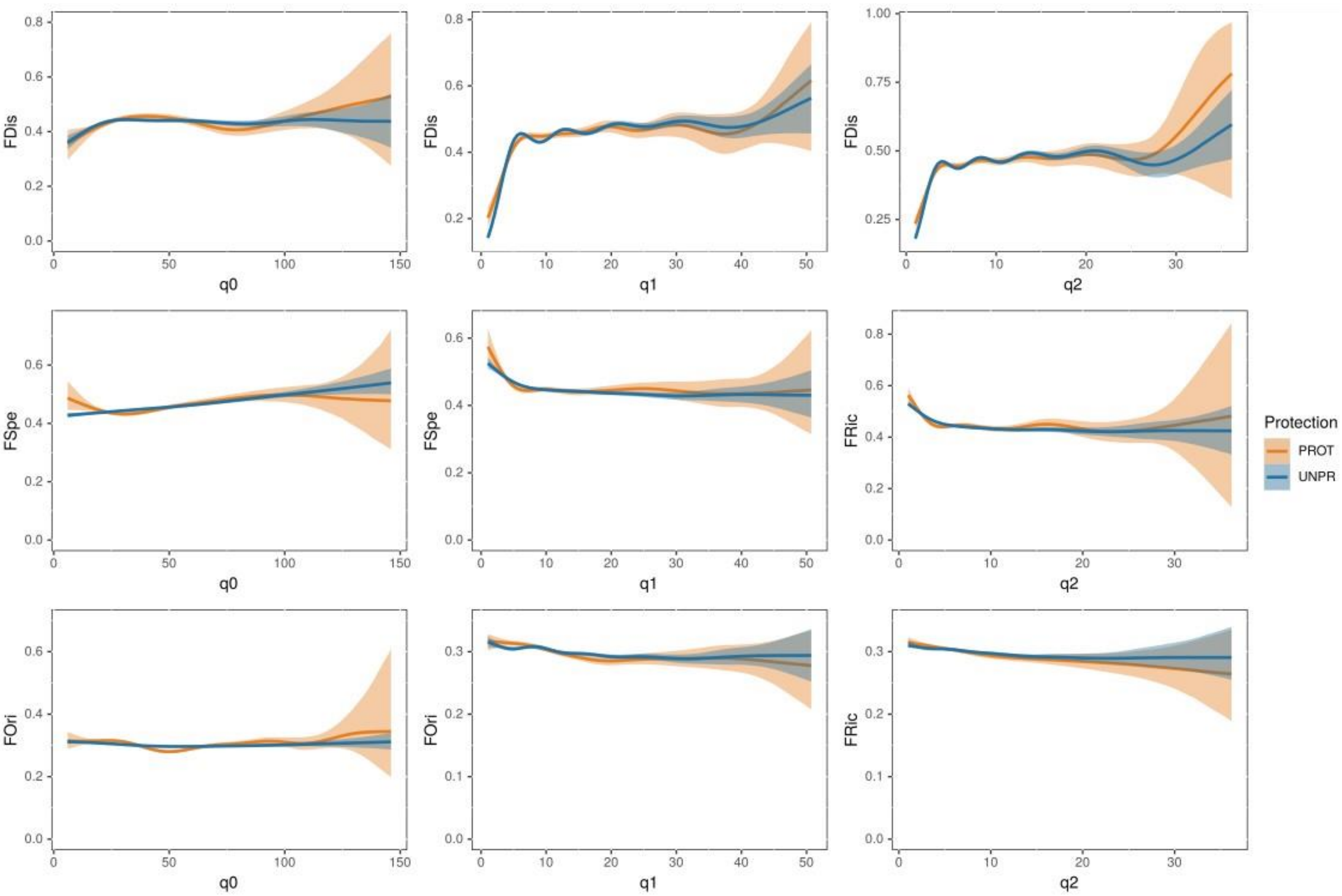

Figure S11.Conditional effects plot (±95% credible intervals) of Bayesian regression models between multidimensional functional indices and 'true diversity' ecological indices for all biogeographic provinces. q0: diversity rare species, q1: diversity common species, q2: diversity dominant species, FDis: Functional Dispersion (beta distribution), FSpe: Functional Specialization (log-normal distribution), and FOri: Functional Originality (log-normal distribution)

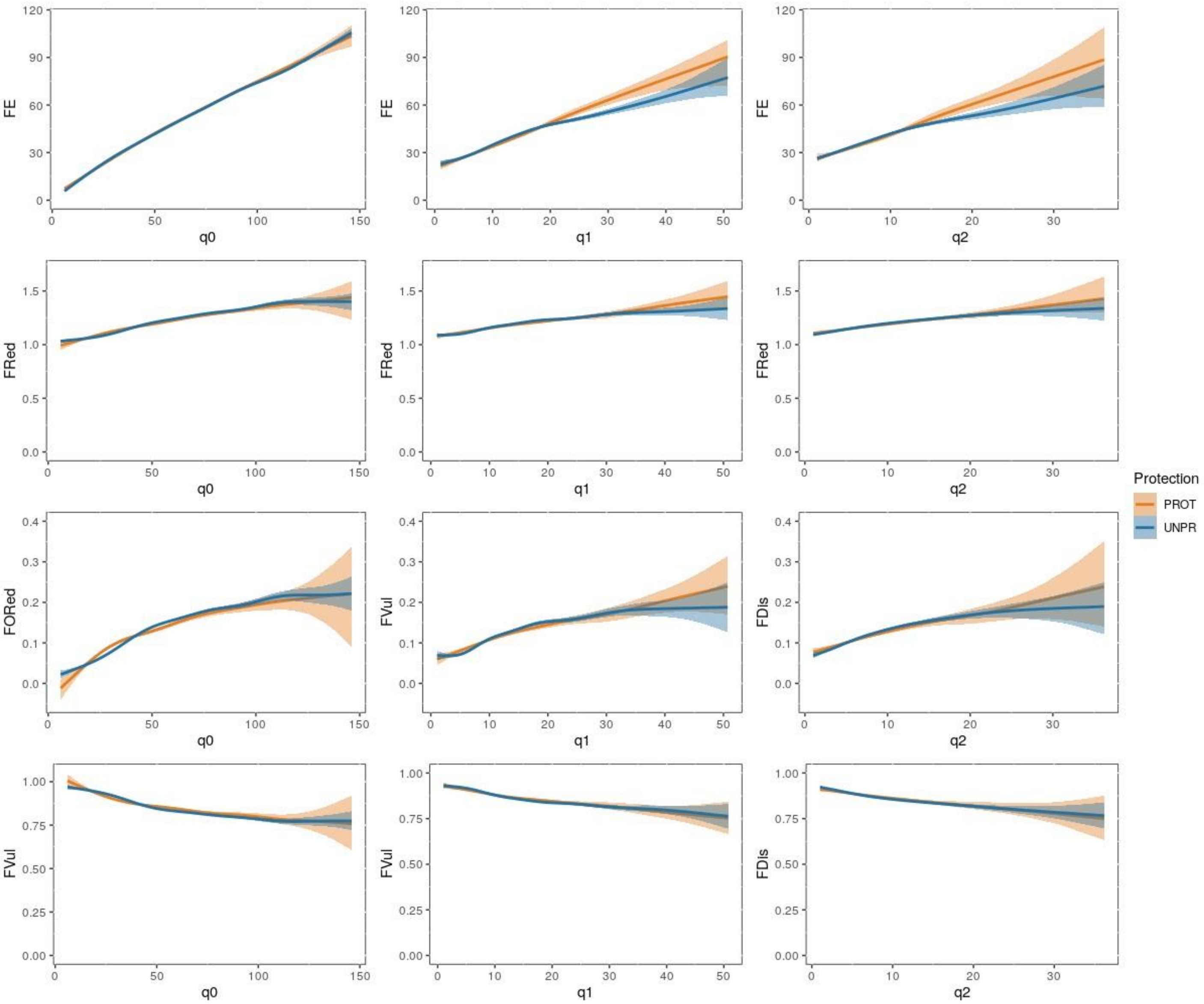
FE
FRed
FORed
FVul
FDis
q0
q1
q2
0
30
60
90
120
0.0
0.5
1.0
1.5
0.1
0.2
0.3
0.4
0.00
0.25
0.50
0.75
1.00
0
50
100
150
10
20
30
40
Protection
PROT
UNPR

Figure S12. Conditional effects plot (±95% credible intervals) of Bayesian regression models between Functional Entities, redundancy patterns and 'true diversity' ecological indices for all biogeographic provinces. q0: diversity rare species, q1: diversity common species, q2: diversity dominant species, Functional Entities (log-normal distribution), Functional Redundancy (log-normal distribution), Functional Over-Redundancy (zero inflated beta distribution, and Functional Vulnerability (gaussian distribution).

Table S5. Parameter estimates and confidence intervals for Bayesian regression models (BRM). The 95% confidence intervals are indicated by "l-95%" and "u-95%." Bulk_ESS and Tail_ESS indicates the effective sample size while Rhat indicates convergence at 1.00. "sigma" indicates the variance term of the Gaussian model.

| Model | Parameter | Estimate | l-95% | u-95% | Bulk_ESS | Tail_ESS | Rhat |
|---|---|---|---|---|---|---|---|
| **FRic (Family: zero_inflated_beta)** | | | | | | | |
| | Intercept | -1.57 | -1.57 | -1.56 | 8558 | 5018 | 1.00 |
| | Protection | 8.33 | 1.52 | 15.53 | 2199 | 3248 | 1.00 |
| | Unprotection | 7.31 | 5.53 | 9.09 | 3093 | 3891 | 1.00 |
| | sd_Protection | 2.35 | 1.21 | 4.32 | 1678 | 2932 | 1.00 |
| | sd_Unprotection | 1.76 | 1.05 | 3.04 | 1381 | 2331 | 1.00 |
| | Phi | 75.15 | 72.18 | 78.25 | 7815 | 4853 | 1.00 |
| | zi | 0.00 | 0.00 | 0.00 | 7140 | 3577 | 1.00 |
| | Bayes $R^2$ | 0.57 | 0.56 | 0.58 | | | |
| q0 | | | | | | | |
| | Intercept | -1.52 | -1.53 | -1.51 | 8674 | 4785 | 1.00 |
| | Protection | 1.53 | 0.19 | 2.9 | 3790 | 2604 | 1.00 |
| | Unprotection | 1.52 | 0.32 | 2.61 | 4137 | 3487 | 1.00 |
| | sd_Protection | 031 | 0.01 | 1.07 | 1867 | 3184 | 1.00 |
| | sd_Unprotection | 0.44 | 0.16 | 1.05 | 2046 | 3093 | 1.00 |
| | Phi | 28.2 | 29.85 | 32.43 | 7677 | 4568 | 1.00 |
| | zi | 0.0 | 0.0 | 0.0 | 8247 | 3090 | 1.00 |
| | Bayes $R^2$ | 0.18 | 0.16 | 0.20 | | | |
| q1 | | | | | | | |
| | Intercept | -1.51 | -1.52 | -1.50 | 8608 | 4887 | 1.00 |
| | Protection | 1.94 | -0.24 | 5.51 | 2445 | 2392 | 1.00 |
| | Unprotection | 1.28 | 0.12 | 2.48 | 3677 | 4370 | 1.00 |
| q2 | sd_Protection | 0.69 | 0.04 | 2.07 | 1188 | 2079 | 1.00 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | sd_Unprotection | 0.45 | 0.14 | 0.98 | 2144 | 2919 | 1.00 |
| | Phi | 28.2 | 27.1 | 29.4 | 7600 | 4276 | 1.00 |
| | zi | 0.0 | 0.0 | 0.0 | 5489 | 3127 | 1.00 |
| | Bayes $R^2$ | 0.11 | 0.09 | 0.13 | | | |
| **FEve (Family: beta)** | | | | | | | |
| | Intercept | 0.13 | 0.12 | 0.14 | 10286 | 4265 | 1.00 |
| | Protection | -0.32 | -3.43 | 1.92 | 2663 | 2049 | 1.00 |
| | Unprotection | -1.75 | -3.85 | 0.15 | 2989 | 3412 | 1.00 |
| | sd_Protection | 0.55 | 0.08 | 1.55 | 1382 | 2092 | 1.00 |
| | sd_Unprotection | 0.98 | 0.5 | 1.85 | 1739 | 2994 | 1.00 |
| | Phi | 43.9 | 42.2 | 45.7 | 7033 | 3742 | 1.00 |
| | Bayes $R^2$ | 0.05 | 0.04 | 0.06 | | | 1.00 |
| q0 | | | | | | | |
| | Intercept | 0.13 | 0.12 | 0.14 | 8335 | 3832 | 1.00 |
| | Protection | -1.12 | -4.17 | 0.91 | 1906 | 2253 | 1.00 |
| | Unprotection | 0.36 | -0.95 | 1.2 | 2095 | 1686 | 1.00 |
| | sd_Protection | 0.77 | 0.1 | 2.15 | 995 | 1469 | 1.00 |
| | sd_Unprotection | 0.27 | 0.06 | 0.81 | 1482 | 1781 | 1.00 |
| | Phi | 43.3 | 41.57 | 45.02 | 8020 | 4223 | 1.00 |
| | Bayes $R^2$ | 0.04 | 0.03 | 0.05 | | | |
| q1 | | | | | | | |
| | Intercept | 0.13 | 0.12 | 0.14 | 9730 | 4342 | 1.00 |
| | Protection | -1.0 | -4.37 | 2.11 | 3179 | 3284 | 1.00 |
| | Unprotection | 0.24 | -1.31 | 0.96 | 1374 | 1619 | 1.00 |
| | sd_Protection | 0.89 | 0.14 | 2.13 | 1475 | 1378 | 1.00 |
| | sd_Unprotection | 0.21 | 0.01 | 0.81 | 1115 | 2185 | 1.00 |
| | Phi | 42.5 | 40.8 | 44.2 | 7375 | 4428 | 1.00 |
| | Bayes $R^2$ | 0.02 | 0.01 | 0.03 | | | |
| q2 | | | | | | | |
| **FDiv (Family: beta)** | | | | | | | |
| | Intercept | 1.8 | 1.79 | 1.83 | 7958 | 4306 | 1.00 |
| | Protection | -5.9 | -16.9 | 2.6 | 2166 | 2163 | 1.00 |
| | Unprotection | -0.00 | -2.8 | 3.4 | 3023 | 2988 | 1.00 |
| | sd_Protection | 2.5 | 1.02 | 5.03 | 1887 | 2885 | 1.00 |
| | sd_Unprotection | 1.1 | 0.32 | 2.35 | 1421 | 2614 | 1.00 |
| | Phi | 15.2 | 14.6 | 15.8 | 8015 | 4421 | 1.00 |
| | Bayes $R^2$ | 0.03 | 0.02 | 0.04 | | | |
| q0 | | | | | | | |
| | Intercept | 1.82 | 1.8 | 1.84 | 6630 | 4834 | 1.00 |
| | Protection | -9.39 | -19.6 | -1.96 | 2794 | 3214 | 1.00 |
| | Unprotection | -9.73 | -13.8 | -5.8 | 3599 | 3810 | 1.00 |
| | sd_Protection | 3.44 | 1.21 | 7.06 | 1786 | 2348 | 1.00 |
| | sd_Unprotection | 3.13 | 1.7 | 5.74 | 1750 | 2586 | 1.00 |
| | Phi | 16.7 | 16.1 | 17.4 | 6667 | 4303 | 1.00 |
| | Bayes $R^2$ | 0.08 | 0.07 | 0.09 | | | |
| q1 | | | | | | | |

|  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|
|  | Intercept | 1.82 | 1.8 | 1.84 | 6680 | 4303 | 1.00 |
|  | Protection | -14.1 | -28.5 | 0.06 | 2874 | 3778 | 1.00 |
|  | Unprotection | -9.9 | -14.0 | -5.6 | 3219 | 3706 | 1.00 |
|  | sd_Protection | 6.75 | 3.56 | 11.9 | 1703 | 2718 | 1.00 |
|  | sd_Unprotection | 3.4 | 1.9 | 5.8 | 1537 | 2886 | 1.00 |
|  | Phi | 17.40 | 16.71 | 18.10 |  |  | 1.00 |
|  | Bayes R$^2$ | 0.1 | 0.09 | 0.11 |  |  |  |
| q2 |  |  |  |  |  |  |  |
| **FDis (Family: beta)** |  |  |  |  |  |  |  |
|  | Intercept | -026 | -0.27 | -0.25 | 10660 | 4538 | 1.00 |
|  | Protection | 2.71 | -1.73 | 7.63 | 2629 | 3418 | 1.00 |
|  | Unprotection | 2.28 | 0.12 | 4.83 | 3144 | 3721 | 1.00 |
|  | sd_Protection | 1.2 | 0.49 | 2.55 | 2247 | 3090 | 1.00 |
|  | sd_Unprotection | 0.97 | 0.42 | 1.93 | 1972 | 3197 | 1.00 |
|  | Phi | 23.97 | 23.03 | 24.95 | 9589 | 3796 | 1.00 |
|  | Bayes R$^2$ | 0.02 | 0.01 | 0.03 | 6305 | 4629 | 1.00 |
| q0 |  |  |  |  |  |  |  |
|  | Intercept | -026 | -0.27 | -0.25 | 7326 | 3973 | 1.00 |
|  | Protection | 15.86 | 10.39 | 21.53 | 2859 | 3564 | 1.00 |
|  | Unprotection | 22.18 | 19.64 | 24.7 | 4538 | 4052 | 1.00 |
|  | sd_Protection | 4.59 | 2.64 | 7.84 | 1619 | 2588 | 1.00 |
|  | sd_Unprotection | 7.82 | 5.03 | 12.6 | 835 | 1592 | 1.00 |
|  | Phi | 37.42 | 35.97 | 38.9 | 7007 | 3814 | 1.00 |
| q1 | Bayes R$^2$ | 0.33 | 0.316 | 0.347 |  |  |  |
|  | Intercept | -026 | -0.27 | -0.25 | 6809 | 4019 | 1.00 |
|  | Protection | 18.89 | 10.07 | 28.36 | 2546 | 3166 | 1.00 |
|  | Unprotection | 22.99 | 20.38 | 25.68 | 3507 | 3567 | 1.00 |
|  | sd_Protection | 5.53 | 3.16 | 9.42 | 1451 | 2670 | 1.00 |
|  | sd_Unprotection | 8.6 | 5.62 | 13.52 | 923 | 2027 | 1.00 |
|  | Phi | 38.4 | 36.9 | 39.9 | 5459 | 4094 | 1.00 |
|  | Bayes R$^2$ | 0.36 | 0.34 | 0.37 |  |  |  |
| q2 |  |  |  |  |  |  |  |
| **FSpe (Family: log-normal)** |  |  |  |  |  |  |  |
|  | Intercept | -0.8 | -0.81 | -0.8 | 11180 | 4204 | 1.00 |
|  | Protection | -0.76 | -2.88 | 1.04 | 2457 | 2587 | 1.00 |
|  | Unprotection | 0.33 | 0.05 | 0.65 | 2454 | 2049 | 1.00 |
|  | sd_Protection | 0.48 | 0.17 | 1.11 | 1782 | 2748 | 1.00 |
|  | sd_Unprotection | 0.06 | 0.00 | 0.2 | 1481 | 2493 | 1.00 |
|  | sigma | 0.15 | 0.14 | 0.15 | 6563 | 4389 | 1.00 |
|  | Bayes R$^2$ | 0.05 | 0.04 | 0.06 |  |  |  |
| q0 |  |  |  |  |  |  |  |
| q1 | Intercept | -0.8 | -0.81 | -0.8 | 11693 | 4218 | 1.00 |
|  | Protection | -2.75 | -5.05 | -0.76 | 2413 | 3560 | 1.00 |
|  | Unprotection | -1.36 | -2.25 | -0.58 | 2581 | 3278 | 1.00 |
|  | sd_Protection | 1.26 | 0.5 | 2.47 | 1427 | 2007 | 1.00 |
|  | sd_Unprotection | 0.46 | 0.21 | 0.92 | 1475 | 2045 | 1.00 |
|  | sigma | 0.15 | 0.14 | 0.15 | 6913 | 4681 | 1.00 |
|  | Bayes R$^2$ | 0.07 | 0.057 | 0.088 |  |  |  |

|  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|
|  | Intercept | -0.8 | -0.81 | -0.8 | 11990 | 4188 | 1.00 |
|  | Protection | -2.96 | -6.38 | 0.18 | 2660 | 3318 | 1.00 |
|  | Unprotection | -1.33 | -2.19 | -0.55 | 3409 | 4122 | 1.00 |
|  | sd_Protection | 1.7 | 0.85 | 3.18 | 1494 | 2187 | 1.00 |
|  | sd_Unprotection | 0.48 | 0.23 | 0.96 | 1320 | 2018 | 1.00 |
|  | sigma | 0.14 | 0.14 | 0.15 | 8616 | 3988 | 1.00 |
|  | Bayes $R^2$ | 0.10 | 0.086 | 0.12 |  |  |  |
| q2 |  |  |  |  |  |  |  |
| **FOri (Family: log-normal)** |  |  |  |  |  |  |  |
|  | Intercept | -1.21 | -1.21 | -1.20 | 11472 | 3770 | 1.00 |
|  | Protection | -0.06 | -3.11 | 2.56 | 2030 | 2446 | 1.00 |
|  | Unprotection | -0.03 | -0.35 | 0.36 | 3302 | 3279 | 1.00 |
|  | sd_Protection | 0.87 | 0.35 | 1.93 | 1184 | 1854 | 1.00 |
|  | sd_Unprotection | 0.1 | 0.04 | 0.24 | 2240 | 3253 | 1.00 |
|  | sigma | 0.11 | 0.11 | 0.12 | 7743 | 4396 | 1.00 |
|  | Bayes $R^2$ | 0.033 | 0.024 | 0.042 |  |  |  |
| q0 |  |  |  |  |  |  |  |
|  | Intercept | -1.21 | -1.21 | -1.20 | 11876 | 4089 | 1.00 |
|  | Protection | -0.24 | -1.23 | 0.61 | 2547 | 2306 | 1.00 |
|  | Unprotection | -0.42 | -1.30 | 0.26 | 1369 | 3608 | 1.00 |
|  | sd_Protection | 0.3 | 0.07 | 0.79 | 1384 | 2648 | 1.00 |
|  | sd_Unprotection | 0.46 | 0.07 | 1.10 | 698 | 1261 | 1.00 |
|  | sigma | 0.11 | 0.11 | 0.12 | 7220 | 4767 | 1.00 |
|  | Bayes $R^2$ | 0.028 | 0.019 | 0.03 |  |  |  |
| q1 |  |  |  |  |  |  |  |
|  | Intercept | -1.21 | -1.21 | -1.20 | 11950 | 3865 | 1.00 |
|  | Protection | -0.32 | -1.07 | 0.24 | 2695 | 1868 | 1.00 |
|  | Unprotection | -0.20 | -0.94 | 0.24 | 1340 | 1137 | 1.00 |
|  | sd_Protection | 0.13 | 0.01 | 0.44 | 1693 | 2320 | 1.00 |
|  | sd_Unprotection | 0.19 | 0.01 | 0.76 | 655 | 1304 | 1.00 |
|  | Phi | 0.12 | 0.11 | 0.12 | 6975 | 4452 | 1.00 |
|  | Bayes $R^2$ | 0.017 | 0.011 | 0.024 |  |  |  |
| q2 |  |  |  |  |  |  |  |
| **Nb_FE (Family: log-normal)** |  |  |  |  |  |  |  |
|  | Intercept | 3.5 | 3.49 | 3.5 | 7815 | 4051 | 1.00 |
|  | Protection | 7.34 | 4.22 | 10.84 | 2579 | 2947 | 1.00 |
|  | Unprotection | 8.64 | 8.03 | 9.26 | 4030 | 3999 | 1.00 |
|  | sd_Protection | 1.29 | 0.74 | 2.32 | 1750 | 2945 | 1.00 |
|  | sd_Unprotection | 1.6 | 0.98 | 2.73 | 1191 | 1641 | 1.00 |
|  | sigma | 0.06 | 0.06 | 0.06 | 6299 | 3489 | 1.00 |
|  | Bayes $R^2$ | 0.978 | 0.977 | 0.978 |  |  |  |
| q0 |  |  |  |  |  |  |  |
| q1 | Intercept | 3.49 | 3.48 | 3.51 | 9882 | 4147 | 1.00 |
|  | Protection | 2.55 | 0.32 | 4.36 | 3219 | 3101 | 1.00 |
|  | Unprotection | 1.94 | -0.05 | 3.72 | 3786 | 4296 | 1.00 |
|  | sd_Protection | 0.53 | 0.1 | 1.44 | 2376 | 2515 | 1.00 |
|  | sd_Unprotection | 0.94 | 0.41 | 1.96 | 1983 | 2979 | 1.00 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | sigma | 0.37 | 0.36 | 0.37 | 7895 | 4381 | 1.00 |
| | Bayes $R^2$ | 0.39 | 0.369 | 0.411 | | | |
| | Intercept | 3.49 | 3.48 | 3.51 | 7880 | 3961 | 1.00 |
| | Protection | 2.4 | -0.41 | 4.8 | 2804 | 2450 | 1.00 |
| | Unprotection | 2.28 | 0.67 | 3.7 | 3440 | 3055 | 1.00 |
| | sd_Protection | 0.48 | 0.02 | 1.65 | 1772 | 2648 | 1.00 |
| | sd_Unprotection | 0.53 | 0.22 | 1.23 | 2179 | 2424 | 1.00 |
| | sigma | 0.4 | 0.4 | 0.41 | 7288 | 4377 | 1.00 |
| | Bayes $R^2$ | 0.253 | 0.230 | 0.278 | | | |
| q2 | | | | | | | |
| **FRed (Family: log-normal)** | | | | | | | |
| | Intercept | 0.14 | 0.14 | 0.15 | 6278 | 3912 | 1.00 |
| | Protection | 0.66 | -0.04 | 1.33 | 2489 | 2237 | 1.00 |
| | Unprotection | 0.21 | -0.19 | 0.6 | 2612 | 3181 | 1.00 |
| | sd_Protection | 0.17 | 0.05 | 0.42 | 1500 | 2796 | 1.00 |
| | sd_Unprotection | 0.2 | 0.09 | 0.41 | 1119 | 1522 | 1.00 |
| | sigma | 0.06 | 0.06 | 0.06 | 7189 | 3690 | 1.00 |
| | Bayes $R^2$ | 0.588 | 0.577 | 0.60 | | | |
| q0 | | | | | | | |
| | Intercept | 0.15 | 0.14 | 0.15 | 8600 | 3652 | 1.00 |
| | Protection | 0.57 | 0.12 | 1.04 | 2733 | 2022 | 1.00 |
| | Unprotection | 0.10 | -0.38 | 0.54 | 3030 | 3236 | 1.00 |
| | sd_Protection | 0.11 | 0.01 | 0.36 | 1550 | 2323 | 1.00 |
| | sd_Unprotection | 0.28 | 0.09 | 0.60 | 1349 | 2109 | 1.00 |
| | sigma | 0.08 | 0.08 | 0.08 | 6756 | 4122 | 1.00 |
| | Bayes $R^2$ | 0.246 | 0.228 | 0.264 | | | |
| q1 | | | | | | | |
| | Intercept | 0.15 | 0.14 | 0.15 | 7070 | 3656 | 1.00 |
| | Protection | 0.47 | 0.08 | 0.92 | 2890 | 2443 | 1.00 |
| | Unprotection | 0.38 | 0.05 | 0.65 | 2786 | 2777 | 1.00 |
| | sd_Protection | 0.08 | 0.00 | 0.30 | 1834 | 2667 | 1.00 |
| | sd_Unprotection | 0.09 | 0.03 | 0.23 | 1962 | 2994 | 1.00 |
| | sigma | 0.08 | 0.08 | 0.09 | 8466 | 4539 | 1.00 |
| | Bayes $R^2$ | 0.158 | 0.141 | 0.176 | | | |
| q2 | | | | | | | |
| **FORed (Family: zero_inflated_beta))** | | | | | | | |
| | Intercept | -1.21 | -1.21 | -1.20 | 9743 | 4429 | 1.00 |
| | Protection | 1.31 | -1.01 | 3.12 | 2339 | 1976 | 1.00 |
| | Unprotection | -2.24 | -3.95 | -0.52 | 3043 | 3950 | 1.00 |
| | sd_Protection | 0.45 | 0.16 | 1.15 | 1902 | 2298 | 1.00 |
| | sd_Unprotection | 1.42 | 0.81 | 2.52 | 1522 | 2836 | 1.00 |
| | phi | 74.96 | 71.82 | 78.19 | 8575 | 4911 | 1.00 |
| | zi | 0.1 | 0.1 | 0.11 | 8647 | 4286 | 1.00 |
| | Bayes $R^2$ | 0.405 | 0.386 | 0.423 | | | |
| q0 | | | | | | | |
| q1 | Intercept | -1.18 | -1.19 | -1.17 | 8845 | 4280 | 1.00 |
| | Protection | 1.39 | 0.35 | 2.61 | 2849 | 2994 | 1.00 |

|  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|
|  | Unprotection | 0.61 | -0.54 | 1.43 | 2720 | 2956 | 1.00 |
|  | sd_Protection | 0.27 | 0.02 | 0.86 | 1873 | 2208 | 1.00 |
|  | sd_Unprotection | 0.35 | 0.11 | 0.89 | 1543 | 2867 | 1.00 |
|  | phi | 43.91 | 42.08 | 45.77 | 7545 | 4232 | 1.00 |
|  | zi | 0.1 | 0.1 | 0.11 | 6909 | 4431 | 1.00 |
|  | Bayes $R^2$ | 0.135 | 0.119 | 0.150 |  |  |  |
|  | Intercept | -1.17 | -1.18 | -1.17 | 8199 | 4602 | 1.00 |
|  | Protection | 1.16 | -0.06 | 2.65 | 1975 | 1687 | 1.00 |
|  | Unprotection | 0.89 | 0.09 | 1.55 | 2742 | 3085 | 1.00 |
|  | sd_Protection | 0.26 | 0.01 | 0.96 | 1572 | 1893 | 1.00 |
|  | sd_Unprotection | 0.21 | 0.06 | 0.56 | 2031 | 3187 | 1.00 |
|  | phi | 40.15 | 38.49 | 41.85 | 6319 | 4453 | 1.00 |
|  | zi | 0.1 | 0.1 | 0.11 | 6346 | 3934 | 1.00 |
|  | Bayes $R^2$ | 0.079 | 0.066 | 0.092 |  |  |  |
| q2 |  |  |  |  |  |  |  |
| **FVul (Family: gaussian)** |  |  |  |  |  |  |  |
|  | Intercept | -0.13 | -0.13 | -0.13 | 6245 | 3367 | 1.00 |
|  | Protection | -0.61 | -1.39 | 0.05 | 2496 | 1892 | 1.00 |
|  | Unprotection | -0.17 | -0.48 | 0.14 | 2821 | 3664 | 1.00 |
|  | sd_Protection | 0.18 | 0.06 | 0.46 | 1592 | 2299 | 1.00 |
|  | sd_Unprotection | 0.15 | 0.07 | 0.30 | 1445 | 2820 | 1.00 |
|  | sigma | 0.05 | 0.05 | 0.05 | 8638 | 4555 | 1.00 |
|  | Bayes $R^2$ | 0.473 | 0.458 | 0.488 |  |  |  |
| q0 |  |  |  |  |  |  |  |
|  | Intercept | -0.13 | -0.13 | -0.13 | 8249 | 3542 | 1.00 |
|  | Protection | -0.42 | -0.86 | 0.03 | 2781 | 2263 | 1.00 |
|  | Unprotection | -0.29 | -0.67 | 0.11 | 3280 | 3440 | 1.00 |
|  | sd_Protection | 0.11 | 0.01 | 0.36 | 1451 | 1565 | 1.00 |
|  | sd_Unprotection | 0.19 | 0.06 | 0.45 | 1439 | 2724 | 1.00 |
|  | sigma | 0.06 | 0.06 | 0.06 | 7644 | 4250 | 1.00 |
|  | Bayes $R^2$ | 0.1997 | 0.182 | 0.219 |  |  |  |
| q1 |  |  |  |  |  |  |  |
|  | Intercept | -0.13 | -0.13 | -0.13 | 7474 | 3817 | 1.00 |
|  | Protection | -0.33 | -0.74 | 0.10 | 2931 | 2472 | 1.00 |
|  | Unprotection | -0.39 | -0.66 | -0.10 | 3316 | 2786 | 1.00 |
|  | sd_Protection | 0.08 | 0.00 | 0.3 | 1796 | 2884 | 1.00 |
|  | sd_Unprotection | 0.08 | 0.03 | 0.2 | 1993 | 3840 | 1.00 |
|  | sigma | 0.07 | 0.07 | 0.07 | 8580 | 4730 | 1.00 |
|  | Bayes $R^2$ | 0.125 | 0.109 | 0.142 |  |  |  |
| q2 |  |  |  |  |  |  |  |

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# Capítulo 2

## The effect of protection on functional diversity of two reef fish communities in northeastern Brazilian coast.

Artigo à ser submetido para Functional Ecology

# The effect of protection on functional diversity of two reef fish communities in northeastern Brazilian coast.

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## Abstract

In the Anthropocene, human actions are causing an imbalance of ecosystem functions in the world's coral reefs. Marine protected areas (MPA) protect these ecosystems from different anthropogenic impacts. In this study, we assessed whether functional differences exist in reef fish assemblages in vs. outside MPAs at regional level. The stationary underwater visual census technique was used in two regions of the Abrolhos Bank (east coast of Brazil) to collect abundance and biomass data from reef fish assemblages. Functional indices with functional space were calculated using functional traits (maximum length, trophic level, spatial category, resilience, and gregariousness) and the hypervolume and kernel density approach. Furthermore, a beyond after-control-impact (ACI) design was used with the factors region, protection, locality, and site and PERMANOVA was applied to test differences in the variables abundance, biomass, alpha, dispersion, and regularity between these factors. For this study, we identified 99 coral reef fish species in the two regions of the Abrolhos Bank. Total abundance and biomass were significant for the region factor, especially in the southern region, and significant for the sites factor. Regarding functional diversity indices, significant differences were observed for the locality and site factor in alpha and dispersion, and only for the site factor of the regularity index. The communities of the Abrolhos National Marine Park showed lower alpha richness and greater similarity of functional traits than in the other unprotected areas, indicating not all ecosystem functions are being protected in this locality, or at least not key functions. In contrast, none of the localities revealed high space replacement values or loss or gain of space among the communities, but differences were observed for the communities in each locality. Moreover, no differences were found for originality between localities. We propose the creation of special zones within marine areas that enhance the protection of different habitats, key functional groups, and ecosystem functions.

**Keywords:** Abrolhos Bank, marine protected areas, functional traits, hypervolume, kernel density, alpha functional diversity, beta diversity, originality.

## Introduction

The ecological functioning of tropical coral reefs is being affected by increased human pressure (D'Agata et al., 2016). The extinction of some ecosystem functions due to accumulated anthropogenic actions in the coastal zone may increase the vulnerability of coral reef areas (Hernandez-Andreu et al., *in prep*). Among the main factors affecting the diversity and structure of marine populations are habitat destruction and homogenization, pollution, bio-invasion, climate change, and overfishing (Doney et al., 2012; Lotze et al., 2006). These activities have directly affected reef integrity and led to historically unprecedented changes in the structure of coral reef communities (Aronson, Macintyre, Precht, Murdoch, & Wapnick, 2002; Pandolfi et al., 2003).

Marine conservation is used to reduce and control the impact of these activities. In this regard, marine protected areas (MPA) were proposed as a management tool and swiftly became one of the most widely used mechanisms worldwide (Strain et al., 2018) to increase the protection of marine biodiversity and the conservation of marine resources (Claudet et al., 2008; García-Charton et al., 2008; Pauly, Watson, & Alder, 2005). Although MPAs are criticized in terms of their true effectiveness for protection and deficiencies in their implementation (Schiavetti, Magro, & Santos, 2012), the potential ecological benefits of strongly and fully protected MPAs are well documented (Sala & Giakoumi, 2018).

MPAs can strikingly differ depending on some factors such as the purpose for which they were created, how they are managed and applied, and the ecological and human context (Pendleton et al., 2018). For example, the efficient regulation of no-take zones (NTZ) becomes a protection factor that may directly or indirectly enable higher biomass, abundance and size of species, changes in assemblage structure (Micheli et al., 2004), exportation of biomass through spillover (for adult fish species) (Goñi, Hilborn, Díaz, Mallol, & Adlerstein, 2010; Hackradt et al., 2014; Harmelin-Vivien et al., 2008), and movement of juveniles and larval dispersal (Félix-Hackradt, Hackradt, Treviño-Otón, Pérez-Ruzafa, & García-Charton, 2018; Grüss, Kaplan, Guénette, Roberts, & Botsford, 2011), as well as safeguard ecosystem services and slow the decline of biodiversity (Halpern et al., 2015; Jones et al., 2018) in these areas. However, recent studies show that NTZs are insufficient to safeguard ecosystem functions in tropical reefs (Hernandez-Andreu et al., *in prep*).

Ecosystem function depends on the breadth of performance of the species in the ecosystem, also known as functional diversity (Naeem et al., 2012). Rosenfeld (2002) defined functional diversity according to the concept of functional space and how species are distributed based on their characteristic traits of interest, each of which represents an axis in that space. The limits of a multidimensional or hypervolume object in a multidimensional space are defined by the position of the observations for different systems (individuals, populations, species, communities, clades, regions) and a set of n independent axes (limiting resource, competition parameters, climate, resource, functional trait) (Blonder et al., 2018; Mammola & Cardoso, 2020). This concept of functional space using hypervolume, which is relevant to studies of community assemblage (Blonder, Lamanna, Violle, & Enquist, 2014), brings us closer to the concept of fundamental niche of a species proposed by Hutchinson (1957) (Blonder et al., 2018). Mammola, Carmona, Guillerme, and Cardoso (2021) differentiate two types of hypervolume, namely binary (or convex hull), where the set of observations defines the smallest convex polyhedron, and probabilistic, which detects a greater or lesser diversity within the hypervolume (Blonder, 2016). These hypervolumes allow us to identify the characteristics of the functional trait space through richness, divergence, and functional regularity metrics at different levels of organization (individuals, populations, or species) within groups (α-diversity) or between groups (β-diversity) (Mammola et al., 2021).

Our main objective was to evaluate if there are functional differences in the fish communities of six reef complexes with different levels of protection in two regions of the extreme south of Bahia. Brazil. We also sought to identify the existence of a pattern at community level that shows whether MPAs are influencing the functionality of the ecosystem for these areas in each region. In contrast, we sought to identify dissimilarities of the communities between different reef complexes and regions and the originality of the species in these communities. Moreover, we tested how the use of abundance and biomass data influences the creation of n-dimensional hypervolumes, defined by the traits, which represent the functional space.

## Material and methods

### Study sites

This study was conducted in six distinct reef systems of the marine portion of the Central Ecological Corridor of the Atlantic Forest, more specifically on the northeast coast of

Brazil, in the extreme south of the state of Bahia, as follows: i. Abrolhos National Marine Park (ANMP), ii. Parcel das Paredes Reef (PPR) and iii. Cassuruba Reef (CAR) in the south bank, iv. Recife de Fora Municipal Marine Park (RFMMP), v. Coroa Alta, Itacipanema and Alagados Reef (CAITAL), and vi. Araripe and Angaba Reef (ARAN) in the north bank. All reefs are located in the Abrolhos Bank, an extension of the continental shelf, which covers 46,000 km$^2$ with a maximum depth of 30 m and a shelf edge at around 70 m (Francini-Filho et al., 2013). This region is located on the northeast coast of Brazil and houses the most extensive and biodiverse coral reefs in the South Atlantic Ocean, with an elevated coral endemic rate (Moura et al., 2013). ANMP was established as a MPA in 1983, and it is formed by two discontinuous areas of around 91,300 hectares (882 km$^2$). The smaller area is positioned close to the coast and is located within the Parcel das Timbebas. In the larger area, positioned offshore, lies the Abrolhos Archipelago composed of five volcanic islands (Santa Bárbara, Redonda, Siriba, Sueste, and Guarita) and the Parcel dos Abrolhos that is characterized by the presence of coral reef pinnacles in the shape of mushrooms called "Chapeirões" (Leão & Kikuchi, 2005). PPR and CAR, on the other hand, are unprotected reefs formed by bank and pinnacle reefs (Moura et al., 2013), the former of which is a single large reef formation, while the latter is composed of 3 isolated reefs named Nova Viçosa, Coroa Vermelha, and Sebastão Gomes. The north bank houses Recife de Fora, a unique reef complex of 19.68km$^2$ (Tedesco et al., 2018). This locality was named the RFMMP and obtained full protection in 1997, as a preserver reef environment (Lima, Zapelini, & Schiavetti, 2021), which is equivalent to protection category II of the International Union for Nature Conservation (IUCN) Category System (Tedesco et al., 2018). The depth of the reef varies between 6 m and 8 m, with maximum depths of 15 m (Seoane et al. 2008). It has distinctive geomorphological habitats, as described in Tedesco et al. (2018), such as algal slope, tidal pool, fore reef, reef flat, back reef, patch reef, unconsolidated sediment, and reef channel. Moreover, this reef is influenced by a tidal cycle with immersion and emersion cycles of ~2 hours each per day (Seoane et al., 2008) and a marked coastal-oceanic gradient (Tedesco et al., 2018). The region includes CAITAL, composed of 3 separate reefs (Coroa Alta, Itacipanema, and Alagados) and ARAN, composed of 2 reefs (Araripe and Angaba), all of which are no deeper than 20 meters (Leão et al., 2003) (Figure 1).

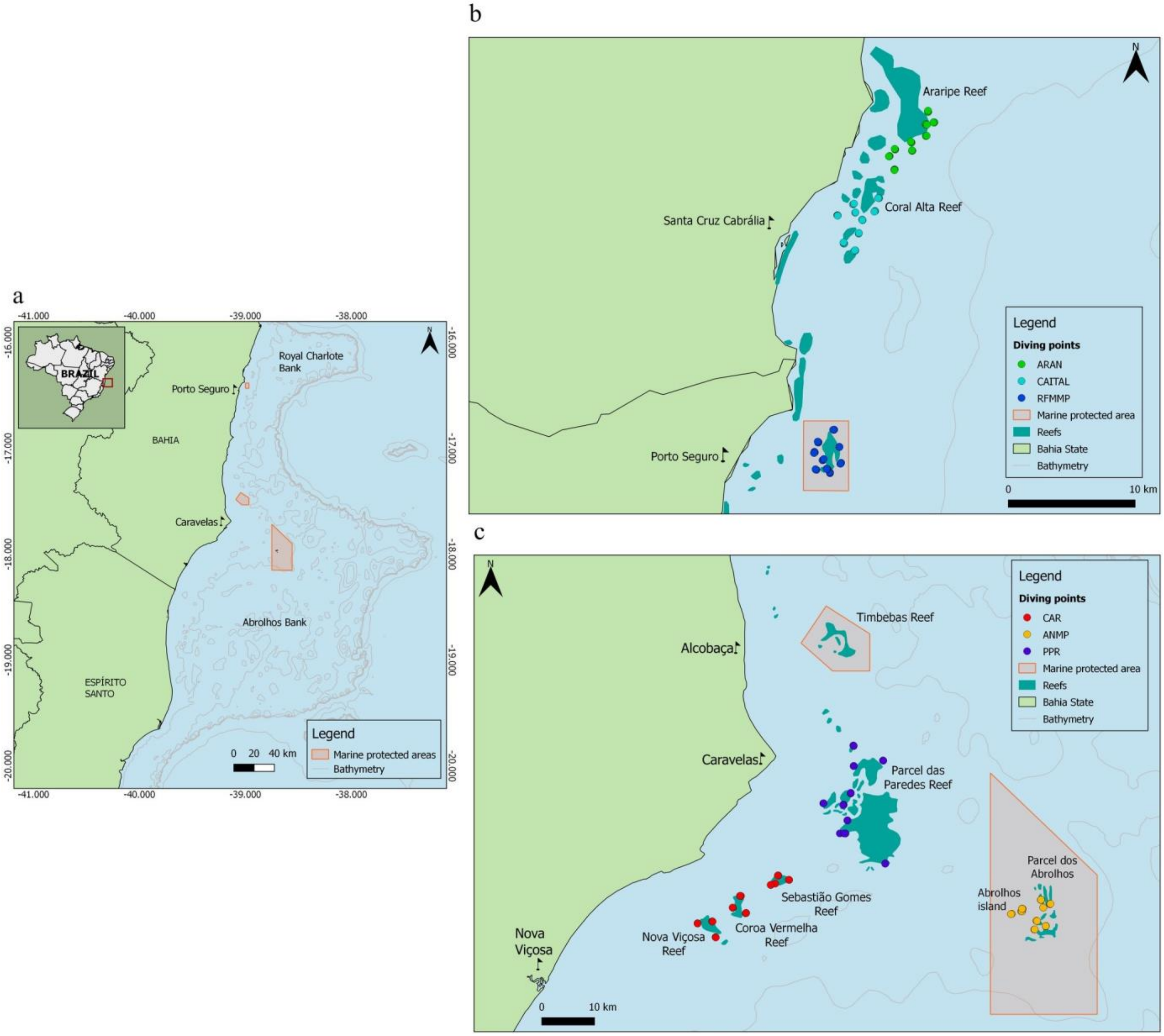

Figure 1. Map showing a) the distribution of protected and unprotected marine areas and the samples of this study in the region, b) north, and c) south of the Abrolhos Bank. The protection level is represented by the polygons and the samples by the dots

## Sampling design and data acquisition

Data were acquired using a beyond after-control-impact (ACI) (Underwood, 1997) sampling design. We defined ‘region’ as a fixed factor with 2 levels (north and south), ‘protection’ as a fixed factor with 2 levels (protected and unprotected), ‘locality’ as a random factor with 6 levels (ANMP, PPR, CAR, RFMMP, CAITAL, and ARAN) nested in ‘region’ and ‘protection’, and ‘sites’ as a random factor with 54 levels (9 per locality) nested in ‘region’, ‘protection’, and ‘locality’. Within each site (Figure 1), data were collected using 6 stationary visual censuses (cf. Minte-Vera, De Moura, & Francini-Filho, 2008) with a radius of 4 m for species >20 cm and a radius of 2 m for species <20cm. All fishes were identified at the lowest possible taxonomic level and their size was estimated in size classes of 2 cm. Fish abundance was registered in abundance classes following a geometric scale (cf. García-Charton & Pérez-Ruzafa, 2001; Hackradt, Félix-Hackradt, & García-Charton, 2011; Harmelin, 1987). Fish biomass was calculated based on length-weight parameters ($W = a \times L^b$) for each species obtained from the literature (Hackradt et al., 2011). Fish data were collected in the austral summer in January-March of 2019 for the south region and December-March of 2019/2020 for the north region.

## Functional traits

The functional traits of the species were attributed according to information available (Table S1) on FishBase or in another published material; when absent, conspecific published data were used. Five categorical functional traits (trophic level, maximum length, resilience, gregariousness, and spatial category) were established to indicate distinct functions between reef fish species. ‘Trophic level’ determines the main diet or food item; ‘maximum published length’ is a universal and predictive functional trait that provides implicit information on the ecological attributes, organismal function, and ontogeny of species (Bellwood, Streit, Brandl, & Tebbett, 2019); ‘resilience’ takes into account the first gonadal maturation size and fecundity estimations such as minimum number of eggs and offspring yearly (Musick, 1999); ‘gregariousness’ shows interspecific or intraspecific social behavior such as moving or feeding (Mouillot et al., 2014); and ‘spatial category’ estimates the horizontal and vertical species range of mobility (cf. Harmelin, 1987). Vertical movement is related to the position a fish occupies in the water column. Pelagic species have the greatest vertical movement (ex. *Chromis* spp.), followed by nektonic (ex. *Abudefduf* spp.), benthic (ex. *Stegastes* spp.), and demersal species (ex. *Scorpaena* spp.). Reef-associated refers to species that exhibit medium to large horizontal movement (ex. Acanthuridae) while reef-attached are species that have little to no horizontal movement (ex. Blennidae) (Table S2).

## Functional space

Functional diversity analysis was conducted with the general protocol developed by (Mammola et al., 2021) using BAT version 2.6.0. (Cardoso, Mammola, Rigal, & Carvalho, 2021) and hypervolume version 2.0.12. (Blonder, 2019). First, the five categorical variables of the traits were ordered using the Gower dissimilarity measure (Gower, 1971) to decrease the number of dimensions, and the results were evaluated with principal coordinate analysis (PCoA) to extract orthogonal axes for hypervolume delineation (Carvalho & Cardoso, 2020; Mammola & Cardoso, 2020). The first four PCoA axes, which cumulatively explaining 63% of the total variance, and abundance matrix were used to construct the hypervolumes with kernel.build function. For this purpose, the Gaussian method for probabilistic estimation was used with Gaussian kernel density (Mammola & Cardoso, 2020), a default bandwidth (Blonder et al., 2018). Once the hypervolumes were created for each sample, the volume of the functional space was extracted with kernel.alpha. Also, we evaluated whether the communities in the protected and unprotected areas of the two regions underwent any filtering process using the kernel.dispersion function with 'divergence' method (Mammola & Cardoso, 2020). To evaluate how the traits are distributed within the functional space, the kernel.evennes function was used, by which we compared a theoretical hypervolume where there is uniformity with the regularity of the distribution of the traits in the hypervolume of our community (Mammola & Cardoso, 2020).

Then, the dissimilarities in traits were estimated between areas by calculating the beta functional diversity with the kernel.beta function. Mammola & Cardoso (2020) defined total beta functional diversity (*βtotal*) as the sum of the following two components: the replacement of space between hypervolumes (*βreplacement*) and the difference between gain or loss of space between hypervolumes (*βrichness*). Each component is defined with ranges between 0 and 1 (identical and full dissimilarity, respectively).

Then, kernel.originality, which calculates the functional originality with the weights of species abundance and biomass in each community (Mammola & Cardoso, 2020), was used to identify if any species in the fish assemblages would provide more original traits to each of the areas and if any difference in originality existed between these areas. Species were grouped by region and the degree of species differentiation was calculated for each region. Following the methodology developed by Martínez et al. (2021), we defined delta originality to subtract the values that each species represented in each region. These values were assigned zero if the species was not present in any region. Delta originality was represented in a histogram with the values centered at zero, which indicates the species found in the two regions. The negative values are the originality of species from the south region and the positive values are the originality of species from the north region.

### Data analyses

The influence of the factors region, protection, localities, and sites was tested on log (x+1) of total abundance and biomass, alpha richness, dispersion, and evenness, obtained from the calculation of the hypervolumes of each sample with the software PRIMER v6 & PERMANOVA+ (Clarke & Gorley, 2006) based on the Bray Curtis similarity distance matrix (Anderson, 2001). We applied 9999 permutations and used the Monte-Carlo p-value to assess the significance of the factors in our design. Moreover, analysis of variance (ANOVA) was used to evaluate whether there was a set of species with a different originality between the factors.

## Results

In total, 17,899 individual fishes (equivalent to total biomass of 2,663,289.12 grams) were surveyed in 319 nested stationary visual censuses, representing 99 species. Total abundance and biomass differed and were significantly higher in the south region and sites (Table 1 and Figure 2).

Table 1. PERMANOVA for total abundance and biomass data transformed with Log(x+1). df: degrees of freedom, F: F-value and p: Monte Carlo p-value, R: region, Prot: protection, L: locality, S: sites. ***: *p* ≤0.001, **: *p* ≤0.01, *: *p* ≤0.05

| **source** | **df** | **Log (Total abundance)** | | **Log (Total biomass)** | |
|---|---|---|---|---|---|
| | | F | p | F | p |
| R | 1 | 12.7 | **0.048*** | 26.6 | **0.022 *** |
| Prot | 1 | 1.7 | 0.323 | 9.5 | 0.069 |
| R x Prot | 1 | 5.2 | 0.132 | 7.6 | 0.09 |
| L(RxProt) | 2 | 0.3 | 0.738 | 0.8 | 0.454 |
| S (L(RxProt)) | 48 | 3.0 | **0.0001***** | 2.2 | **0.0001***** |
| Residual | 265 | | | | |
| Total | 318 | | | | |

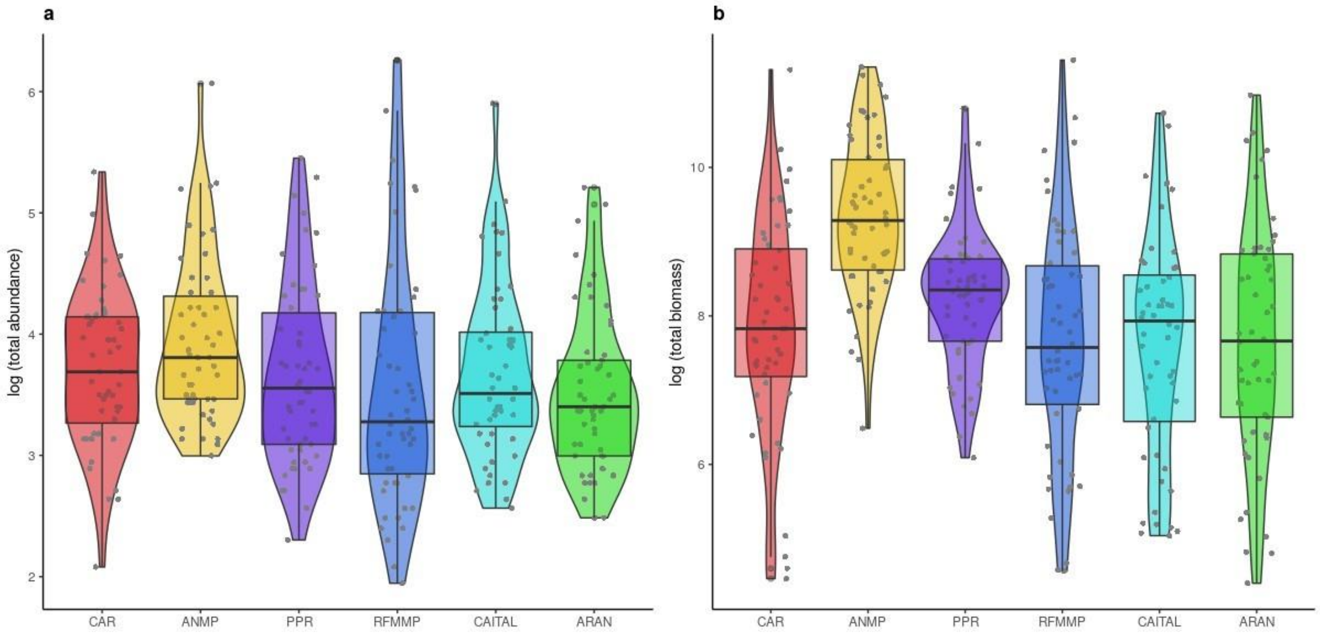

Figure 2. Box plot and violin plot of the logarithm of a) abundance and b) biomass of the underwater visual census samples of each locality. Red represents Cassuruba Reef (CAR), yellow represents Abrolhos National Marine Park (ANMPA), purple represents Parcel das Paredes Reef (PPR), dark blue represents Recife de Fora Municipal Marine Park (RFMMP), cyan blue represents Coroa Alta-Itacipanema-Alagados reefs (CAITAL), and green represents Araripe-Angaba reefs (ARAN). The grey points represent the samples.

In addition, PERMANOVA revealed that both the hypervolumes created with abundance and biomass differed significantly at locality level for the alpha functional richness and dispersion indices, but only for the random factor site in evenness (Table 2, Figure 3). For abundance, in the south region, these differences are mainly found in CAR, which has a higher alpha richness and dispersion than PPR and ANMP, and in the northern localities, where dispersion was significantly lower in ARAN than in the other two localities. However, these significant values were not found for alpha richness among the north region localities (Table 3, Figure 3-a, c). For biomass, the same response was found for alpha richness in the south and north regions as the response found for abundance; however, for dispersion, significant differences were only found among the southern localities, being higher in CAR than in the other localities, but not for the northern localities (Table 3, Figure 3d-f).

Table 2. PERMANOVA of functional diversity measures for abundance and biomass data. df: degrees of freedom, F: F-value and p: Monte Carlo p-value, R: region, Prot: protection, L: locality, S: sites. ***: *p* ≤0.001, **: *p* ≤0.01, *: *p* ≤0.05

| Sources | df | α Richness | | | | Dispersion | | | | Evenness | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Abundance | | Biomass | | Abundance | | Biomass | | Abundance | | Biomass | |
| | | F | p | F | p | F | p | F | p | F | p | F | p |
| R | 1 | 1.0 | 0.428 | 0.04 | 0.973 | 1.0 | 0.414 | 0.009 | 0.999 | 2.0 | 0.264 | 2.2 | 0.238 |
| P | 1 | 0.9 | 0.458 | 1.2 | 0.389 | 0.2 | 0.713 | 0.6 | 0.547 | 2.3 | 0.245 | 0.5 | 0.587 |
| R x P | 1 | 1.2 | 0.389 | 2.5 | 0.204 | 0.2 | 0.758 | 3.0 | 0.228 | 2.2 | 0.250 | 3.2 | 0.176 |
| L(RxP) | 2 | 6.0 | **0.002**** | 5.4 | **0.003**** | 7.0 | **0.002**** | 3.2 | **0.048*** | 0.42 | 0.710 | 1.1 | 0.356 |
| S (L(RxP)) | 48 | 1.8 | **0.0003***** | 1.6 | **0.005**** | 2.0 | **0.0002***** | 1.5 | **0.022*** | 1.5 | **0.009**** | 1.9 | **0.0001***** |
| Residual | 265 | | | | | | | | | | | | |
| Total | 318 | | | | | | | | | | | | |

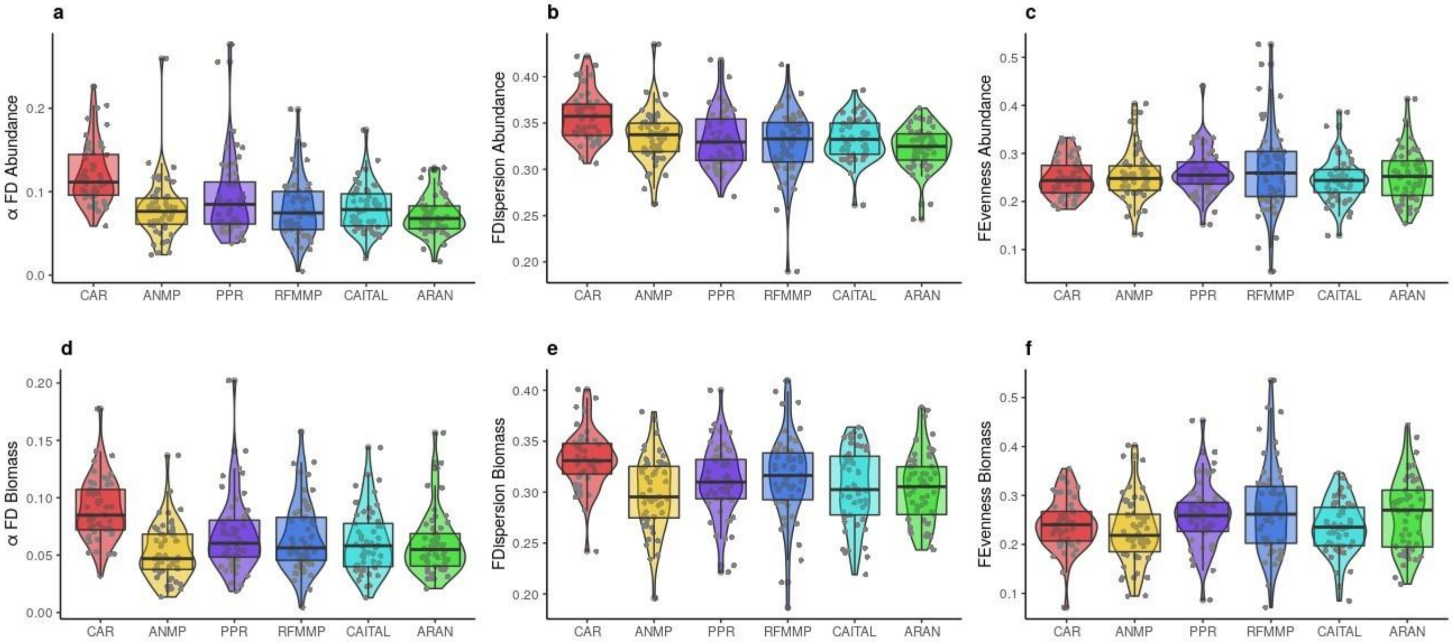

Figure 3. Box plot and violin plot of the logarithm of a) α richness, b) dispersion c) evenness for abundance data and d) α richness, e) dispersion, and f) evenness for biomass data of the underwater visual census samples of each locality. Red represents Cassuruba Reef (CAR), yellow represents Abrolhos National Marine Park (ANMPA), purple represents Parcel das Paredes Reef (PPR), dark blue represents Recife de Fora Municipal Marine Park (RFMMP), cyan blue represents Coroa Alta-Itacipanema-Alagados reefs (CAITAL), and green represents Araripe-Angaba reefs (ARAN). The grey points represent the samples.

Table 3. Summary of the average values (± standard error), functional diversity measures, and $\beta$ - diversity component in each locality for abundance and biomass data. Localities: Cassuruba Reef (CAR), Abrolhos National Marine Park (ANMPA), Parcel das Paredes Reef (PPR), Recife de Fora Municipal Marine Park (RFMMP), Coroa Alta-Itacipanema-Alagados reefs (CAITAL), and Araripe-Angaba reefs (ARAN).

| **Data** | **Region** | **Localities** | **Richness** | **Dispersion** | **Evenness** | ***βtotal*** | ***βreplacement*** | ***βrichness*** |
|---|---|---|---|---|---|---|---|---|
| Abundance | Abrolhos Bank | CAR | 0.121 ± 0.005 | 0.357 ± 0.004 | 0.249 ± 0.005 | 0.515 ± 0.003 | 0.287 ± 0.004 | 0.228 ± 0.004 |
| | | ANMP | 0.079 ± 0.005 | 0.335 ± 0.004 | 0.254 ± 0.007 | 0.535 ± 0.004 | 0.233 ± 0.004 | 0.302 ± 0.006 |
| | | PPR | 0.09 ± 0.006 | 0.333 ± 0.004 | 0.260 ± 0.006 | 0.543 ± 0.004 | 0.219 ±0.005 | 0.325 ± 0.005 |
| | Royal Charlotte Bank | RFMMP | 0.079 ± 0.005 | 0.328 ± 0.005 | 0.266 ± 0.012 | 0.543 ± 0.004 | 0.219 ± 0.005 | 0.325 ± 0.005 |
| | | CAITAL | 0.09 ± 0.003 | 0.333 ± 0.003 | 0.244 ± 0.006 | 0.551 ± 0.004 | 0.287 ± 0.005 | 0.263 ± 0.004 |
| | | ARAN | 0.071 ± 0.003 | 0.324 ± 0.003 | 0.254 ± 0.007 | 0.566 ± 0.004 | 0.312 ± 0.005 | 0.254 ± 0.007 |
| Biomass | Abrolhos Bank | CAR | 0.09 ± 0.004 | 0.332 ± 0.004 | 0.261 ± 0.01 | 0.637 ± 0.004 | 0.414 ± 0.005 | 0.223 ± 0.004 |
| | | ANMP | 0.053 ± 0.003 | 0.299 ± 0.005 | 0.228 ± 0.009 | 0.617 ± 0.004 | 0.284 ± 0.005 | 0.333 ± 0.006 |
| | | PPR | 0.068 ± 0.004 | 0.310 ± 0.005 | 0.258 ± 0.009 | 0.628 ± 0.004 | 0.313 ± 0.005 | 0.315 ± 0.004 |
| | Royal Charlotte Bank | RFMMP | 0.066 ± 0.004 | 0.315 ± 0.006 | 0.270 ± 0.01 | 0.628 ± 0.004 | 0.313 ± 0.005 | 0.315 ± 0.004 |
| | | CAITAL | 0.062 ± 0.004 | 0.305 ± 0.005 | 0.234 ± 0.007 | 0.684 ± 0.004 | 0.368 ± 0.005 | 0.316 ± 0.005 |
| | | ARAN | 0.06 ± 0.004 | 0.304 ± 0.004 | 0.261 ± 0.01 | 0.665 ± 0.004 | 0.376 ± 0.005 | 0.289 ± 0.005 |

In contrast, the hypervolumes constructed for each sample did not clearly differ between region and localities for the trait space. For abundance, *βtotal* and *βrichness,* on average, were higher between communities of ANMP and PPR than CAR in the south region, although *βreplacement* was higher in CAR. Moreover, in the north region, ARAN showed a higher *βtotal and βreplacement* but lower *βrichness,* contrary to the results for RFMMP (Figure 4a-c and Table 4). However, a different response was found for biomass, with a higher *βtotal and βreplacement for CAR and βrichness* for ANMP in the south region, and higher *βtotal for CAITAL, βreplacement* for *ARAN, and βrichness* for RFMMP and CAITAL in the north region (Figure 4d-f and Table 4).

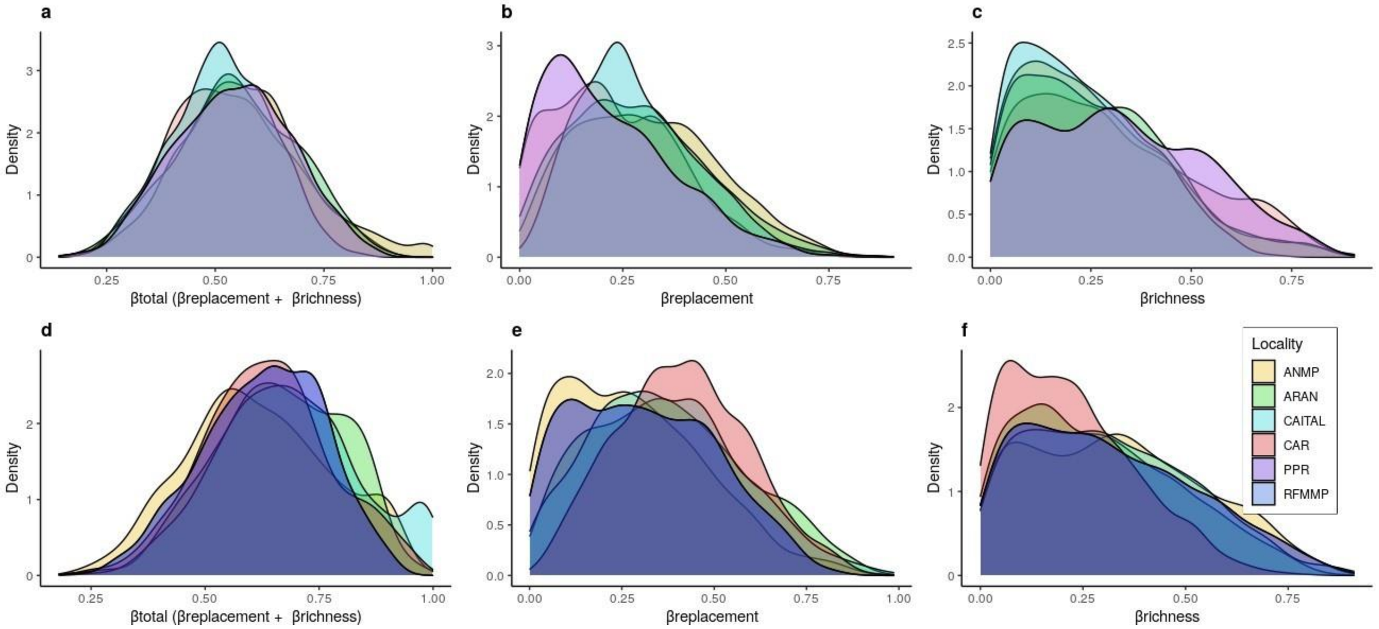

Figure 4. Density of functional beta diversity values for pairwise comparison of communities in Abrolhos National Marine Park (ANMPA), Araripe-Angaba reefs (ARAN), Coroa Alta-Itacipanema-Alagados reefs (CAITAL), Cassuruba Reef (CAR), Parcel das Paredes Reef (PPR), and Recife de Fora Municipal Marine Park (RFMMP) for a-c) abundances data and d-f) biomass data.

Moreover, ANOVA showed that there are no significant differences in originality between these localities for abundance (F = 1.29; *p*-value =0.263) and biomass (F = 1.38 *p*-value =0.227) (Figure 5a-b). Because no differences were found between areas, the species were grouped by region to evaluate delta originality, and a set of 61 species appeared in both areas. Moreover, 22 species were only found in the south region, namely *Sphyraena barracuda* and *Gymnothorax funebris,* the most original of the community, and 16 species were only found in the north region, namely *Anchova sp* and *Pempheris scomburgkii,* the most original species with abundance data (Figure 5c). For biomass, the most original were *Sphyraena barracuda* and *Hypanus americanus* in the south region and *Anchova sp* and *Pempheris scomburgkii* in the north region (Figure 5d).

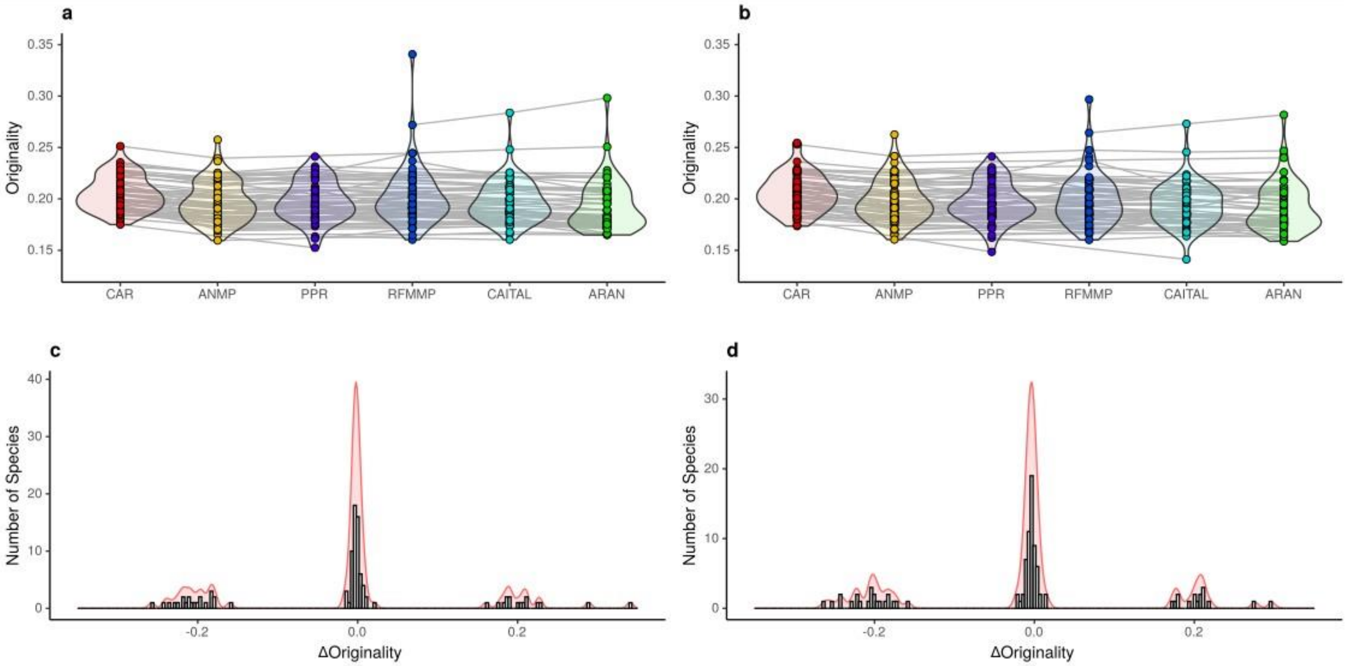

Figure 5. Violin plots of the distribution of functional originality values of species for a) abundance and b) biomass data between areas and histogram of delta originality values between species in the north and south regions for c) abundance and d) biomass data. Red represents Cassuruba Reef (CAR), yellow represents Abrolhos National Marine Park (ANMPA), purple represents Parcel das Paredes Reef (PPR), dark blue represents Recife de Fora Municipal Marine Park (RFMMP), cyan blue represents Coroa Alta-Itacipanema-Alagados reefs (CAITAL), and green represents Araripe-Angaba reefs (ARAN). Grey lines connect species between areas. Red lines show the predicted density of values according to a kernel density estimation.

## Discussion

Contrary to expectations, no differences were found between the MPA and unprotected areas for species abundance and biomass, although, a difference was found between fish communities, with higher abundance and biomass in the south region. The Abrolhos National Marine Park has a higher, albeit not significant, total biomass and abundance than the Cassuruba Reef and Parcel das Paredes Reef (unprotected areas in the south region). However, total abundance and biomass in Recife de Fora Municipal Marine Park was lower than in the unprotected areas in the north region, which may be due to a difference in habitat availability between these areas and the percentage of reefs that is fully exposed by tidal influences. Some studies, such as the study of Strain et al. (2018), revealed the importance of MPAs to directly benefit target species from local fisheries and protect some components of coral reefs when some attributes are considered during planning.

Moreover, from the functional perspective, RFMMP, CAITAL, and ARAN did not show differences, indicating that the traits represented by the hypervolumes in the communities seem to be similar for these three localities. Contrary to expectations, on average, ANMP had the lowest volume in the hypervolumes with abundance and biomass data when compared to open areas of the south region and areas of the north region. Moreover, lower dispersion was found for biomass data for ANMP when compared with CAR and PPR. Therefore, ANMP seems to have a lower diversity of traits and more species with similar traits. Apparently, no differences were found for the use of resources between the different areas since no differences were observed in the regularity of traits. These MPAs are fulfilling the role for which they were created, which is to increase the abundance and biomass of species; however, and according to the hypothesis proposed by Hernández-Andreu et al. (*in prep.*), our results clearly show that in ANMP not all ecosystem functions are being protected, or at least not key functions. Hernández-Andreu et al. (*in prep.*) found that MPAs can increase abundance of herbivores, which is an important functional group of fish due to its role in maintaining the ecosystem structure (Bellwood, Hughes, Folke, & Nyström, 2004; Hughes, Bellwood, Folke, McCook, & Pandolfi, 2007), while a higher abundance of invertivores and planktivores was observed in open areas. Therefore, the low abundance and richness of planktivore species in ANMP (Moura et al., 2021) could be a response of the hypervolumes with a smaller volume, as there is almost no representation of these functions in the ecosystems. Planktivores are species that may exhibit heterogeneity in their distribution, which is associated with their morphological characteristics (Siqueira, Morais, Bellwood, & Cowman, 2021), resources partitioned in time (diurnal and nocturnal planktivores) (Hobson, 1991), and a strong partition depending on the target resource (Siqueira et al., 2021).

In addition, we measured how the communities are functionally different from each other using decomposition of functional $\beta$-diversity that differentiates between two components, functional turnover, or functional space not shared between communities, and functional nestedness-resultant, or differences between communities due to the space occupied (Villéger, Grenouillet, & Brosse, 2013). Moreover, in terms of species, Carvalho & Cardoso (2020) calculated the decomposition of niche space with hypervolume partition for species. According to these authors, high values of replacement indicate a niche change between species, while high values of differences of niche breadth indicate a contraction/expansion of one species with another, thus revealing that niche space can be replaced by trait space. This finding, applied to the results obtained and from a community perspective, indicates the absence of a differentiated functional space in terms of abundance and biomass of coral reef communities of the two regions, represented by n-dimensional hypervolume. These communities were functionally more dissimilar in PPR and ARAN, while the communities were more similar in CAR and RFMMP for abundance, in the south and north region, respectively. However, for biomass, the greatest dissimilarity was between the communities of ANMP and RFMMP and the lowest similarity was between CAR and CAITAL. Furthermore, the replacement of space between communities for abundance data was higher in CAR and ARAN and lower in PPR and RFMMP, while for biomass, it was higher in CAR and ARAN and lower in ANMP and RFMMP. Moreover, the gain or loss of space between communities was higher in PPR and RFMMP and lower in CAR and ARAN for abundance, while for biomass, it was higher in ANMP and CAITAL and lower in CAR and ARAN. These results indicate differences between the communities in each locality, especially for biomass data compared with abundance data. However, none of the localities showed large values for space replacement or loss or gain of space between their communities, although the latter is considerable.

Originality measures whether a species is more unique as a function of the combination of traits within the hyperspace (Mammola & Cardoso, 2020). Greater functional originality was expected in the unprotected areas due to the anthropogenic impacts, as some functions would not be redundant due to the lack of more than one species to perform a specific function. We did not find a difference in originality between the localities of the regions, although differences of originality of some species were observed in each locality. Moreover, the most original species for each locality were *Carangoides bartholomei* for abundance and *Hypanus americanus* for biomass in CAR, *Gymnothorax funebris* for abundance and biomass in PPR, and *Sphyraena barracuda* in ANMPA, *Anchova sp.* in RFMMP, and *Pempheris scomburgkii* in CAITAL and ARAN for abundance and biomass data. Coincidentally, in the north region, the most original species were *Anchova sp.* and *Pempheris scomburgkii*, which are pelagic and nektonic planktivores, respectively. However, the differences of the more original species between localities in the south region could be more influenced by the top predators. When comparing *Sphyraena barracuda* with *Hypanus americanus, Gymnothorax funebris,* and *Carangoides bartholomei*, the first three species are considered general carnivores that differ from the other species of this same trophic group since they are unique for the spatial category trait, namely pelagic, demersal reef-associated, and demersal reef-attached, respectively. The fourth, *Carangoides bartholomei,* is a more unique species within the piscivores, as it shares fewer characteristics with the other species of this same trophic category. The exclusivity of these species in terms of functions may justify this greater originality, which results in lower redundancy. In this regard, Brandl, Emslie, and Ceccarelli (2016) found an increase in originality due to the loss of species redundancy after hurricane impact on coral reef habitats. In addition, the species *Sphyraena barracuda* in the south region and *Anchova sp.* and *Pempheris scomburgkii* in the north region are found at the extremes of delta originality since they occur in low abundances or are distributed in a restricted habitat (Martínez et al., 2021). According to Violle et al. (2017), they could be considered outliers. Since we did not find differences in originality between the localities, these localities may be similar to each other, as the originality of these species was able to directly influence the alpha richness of each area, as found by Villéger et al. (2013) using convex hull, by which the definition of the proportion of functional space is influenced by the combination of extreme traits.

In the present study, the input data used to calculate the indices and diversities can lead to different results. Although different types of data are not normally used for most organisms, we decided to use these two types of data because the variables abundance and biomass in fish fauna can reveal important information.

According to the results obtained here and those obtained in Hernández-Andreu et al. (*in prep*), the ANMP should be expanded to protect resource extraction on a functional basis. Further studies are needed to identify priority species and habitats when expanding the area. Although other areas show a greater functional space than ANMP, their potential in terms of functional diversity could be even greater with the creation and application of effective management plans, correct monitoring, and environmental campaigns to increase interest in protection and the environmental and socio-economic-cultural benefits of protection for society. Public policies that act directly on these "paper parks" are also required (Lima et al., 2021).

Moreover, it is important to highlight that the MPAs studied here were created with different protection objectives. The RFMMP, for example, is a small MPA created to regulate the number of visits and establish which areas of the reef can be visited, leading to the selection of one natural pool for visitation and recreational activities (Lima et al., 2021). ANMP, considered a large MPA compared to RFMMP, was created for biodiversity conservation. In this regard, a large MPA can provide greater coverage of marine ecosystems and benefit local communities with integrated management of human activities, while small MPAs alone may not cover all protection needs appropriately (Kelleher, 1999). However, a well-designed network of small, connected MPAs can meet important ecological criteria (Lausche, Laur, & Collins, 2021) for the conservation of biodiversity and its functions.

Finally, we believe that areas with a high abundance of planktivore species may be functionally important with a higher priority for conservation. Similarly, it is important to consider environmental variables for the definition of these areas since they may be influencing with some environmental filter or the composition of functional traits of fish communities. Recent studies show the importance of rhodoliths within the Abrolhos Bank (Moura et al., 2021) and that this type of habitat is also predominant in the Royal Charlotte Bank (Negrão et al., 2021). In addition, we believe that future studies on functional diversity with an MPA-approach could provide a seascape point of view that sheds light on how functional diversity acts at habitat level and which functional diversity is found within these areas. These studies could support management measures to enhance the performance of these areas in terms of functional diversity. We propose the establishment of one of these protection measures in the form of special zones within the MPA that could be named functional protected zones. These zones are represented by areas with the greatest number of ecosystem functions, different types of habitats, and key functional groups. These groups can be exclusively marine (such as corals or fish), or marine or terrestrial with direct interaction in these areas (such as seabirds or sea turtles).

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## Supplementary Material

Table S1. Biological functional traits, traits categories, units, type of variable and references used to defined the functional indices that describe ecological functioning in reef fish assemblages.

| Functional Traits | Trait Category | Unit | Description | Reference |
|---|---|---|---|---|
| Trophic Category | Diet | Herbivore (HBT) | Feeding on plant with a territorial behavior | Bellwood et al., 2019; Floeter, Bender, Siqueira, & Cowman, 2018; Halpern & Floeter, 2008 |
| | | Herbivore grazer (HGRZ) | Feeding on superficial reef matrix | |
| | | Herbivore scraper (HSCP) | Feeding on reef matrix | |
| | | Omnivore (OMNI) | Feeding plants and animals item | |
| | | General invertivore (GINV) | Feeding general invertebrates | |
| | | Mobile invertivore (MINV) | Feeding mobile benthic invertebrates | |
| | | Obligate corallivore (OC) | Feeding hard corals and some on soft coral | |
| | | Cleaner (CLE) | Feeding others animals organisms (ex ectoparasites) | |
| | | Planktivore (PLNK) | Feeding plakton organisms | |
| | | General Carnivore (GCAR) | Feeding invertebrates (ex. mollusc) and fish | |
| | | Piscivore (PISC) | Feeding strictly fish | |
| Maximum length | Morphology | Very small | <8 | Forese & Pauly, 2020 * |
| | | Small | 8.1-15.9 | |
| | | Medium | 16-30.9 | |
| | | Medium-Large | 31-50.9 | |
| | | Large | 51-80.9 | |
| | | Very Large | >81 | |
| Resilience | Life history | Very low | | Musick, 1999, Forese & Pauly, 2020* |
| | | Low, | | |
| | | Medium | | |
| | | High | | |
| | | Very high | | |
| Gregariousness | Life history | Solitary | 1 individual | Mouillot et al., 2014 |
| | | Pair | 2 individuals | |
| | | Small – medium | 3-50 individuals | |
| | | Large | >50 individual | |
| Spatial Category | Habitat | Pelagic/reef associated | | Harmelin, 1987 |
| | | Necktonic/reef associated | | |
| | | Benthonic/reef associated | | |
| | | Demersal/reef associated | | |
| | | Benthonic/reef attached | | |
| | | Demersal/reef attached | | |

Table S2. Functional traits and absence / presence information for each one species

| Specie | code_sp | Functional traits | | | | | Localities | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Spatial category | Trophic category | Resilience | Lmax | Gregariouness | ANMP | CAR | PPR | RFMMP | CAITAL | ARAN |
| Abudefduf saxatilis | ABUSAX | Nektonic/Reef Associated | OMNI | Medium | Medium | Large | x | x | x | x | x | x |
| Acanthurus bahianus | ACABAH | Benthic/Reef Associated | HGRZ | High | Medium -Large | Large | x | x | x | x | x | x |
| Acanthurus chirurgus | ACACHI | Benthic/Reef Associated | HGRZ | Medium | Medium -Large | Large | x | x | x | x | x | x |
| Acanthurus coeruleus | ACACOE | Benthic/Reef Associated | HGRZ | Medium | Medium -Large | Small-medium | x | x | x | x | x | x |
| Alphestes afer | ALPAFE | Benthic/Reef Attached | GCAR | High | Medium -Large | Solitary | - | x | - | - | - | - |
| Aluterus scriptus | ALUSCR | Benthic/Reef Associated | OMNI | Medium | Very Large | Solitary | - | - | x | - | - | - |
| Amblycirrhitus pinos | AMBPIN | Demersal/ Reef Attached | GINV | High | Small | Solitary | - | - | - | - | x | x |
| Anchoa sp | ANCSP | Pelagic/Reef Associated | PLNK | High | Small | Large | - | - | - | x | - | - |
| Anisotremus moricandi | ANIMOR | Benthic/Reef Attached | OMNI | High | Small | Small-medium | - | - | - | - | x | x |
| Anisotremus surinamensis | ANISUR | Benthic/Reef Attached | GCAR | Low | Large | Small-medium | - | - | x | - | x | x |
| Anisotremus virginicus | ANIVIR | Benthic/Reef Associated | MINV | Medium | Medium -Large | Small-medium | x | x | x | x | x | x |
| Balistes vetula | BALVET | Benthic/Reef Associated | GINV | Medium | Large | Solitary | x | - | - | - | - | - |
| Bodianus rufus | BODRUF | Benthic/Reef Associated | MINV | Medium | Medium -Large | Solitary | x | - | - | - | x | x |
| Calamus penna | CALPEN | Demersal/ Reef Associated | MINV | High | Medium -Large | Solitary | - | x | x | - | - | - |
| Canthigaster figueiredoi | CANFIG | Demersal/ Reef Associated | OMNI | High | Small | Pair | x | - | - | - | - | - |
| Cantherhines macrocerus | CANMAC | Benthic/Reef Associated | OMNI | Medium | Medium -Large | Pair | x | - | - | - | x | x |
| Cantherhines pullus | CANPUL | Benthic/Reef Associated | OMNI | High | Medium | Solitary | x | - | x | - | x | x |
| Carangoides bartholomaei | CARBAR | Pelagic/Reef Associated | PISC | High | Very Large | Small-medium | x | x | - | x | x | x |
| Caranx crysos | CARCRY | Pelagic/Reef Associated | GCAR | Medium | Large | Small-medium | x | x | - | x | x | x |
| Caranx hippos | CARHIP | Pelagic/Reef Associated | GCAR | Medium | Very Large | Small-medium | - | - | - | - | x | - |
| Caranx latus | CARLAT | Pelagic/Reef Associated | GCAR | Low | Very Large | Small-medium | - | - | - | - | - | x |
| Carcharhinus perezi | CARPER | Benthic/Reef Associated | PISC | Low | Very Large | Solitary | x | - | - | - | - | - |
| Caranx ruber | CARRUB | Nektonic/Reef Associated | GCAR | Medium | Large | Small-medium | x | - | - | x | - | x |
| Cephalopholis fulva | CEPFUL | Benthic/Reef Attached | GCAR | Medium | Medium -Large | Solitary | - | - | - | x | x | x |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Chaetodipterus faber | CHAFAB | Nektonic/Reef Associated | GCAR | Medium | Very Large | Large | - | x | - | - | - | - |
| Chaetodon ocellatus | CHAOCE | Benthic/Reef Attached | MINV | High | Medium | Pair | x | - | - | - | - | - |
| Chaetodon sedentarius | CHASED | Benthic/Reef Attached | GINV | Medium | Small | Pair | - | - | - | x | - | - |
| Chaetodon striatus | CHASTR | Benthic/Reef Attached | OMNI | High | Medium | Pair | x | x | x | x | x | x |
| Chilomycterus spinosus spinosus | CHISPI | Benthic/Reef Attached | GINV | Medium | Medium | Solitary | - | - | x | - | - | - |
| Coryphopterus glaucofraenum | CORGLA | Demersal/ Reef Attached | OMNI | High | Very Small | Solitary | x | x | x | x | x | x |
| Coryphopterus thrix | CORTHR | Demersal/ Reef Attached | OMNI | High | Very Small | Solitary | x | x | x | - | - | - |
| Cryptotomus roseus | CRYROS | Benthic/Reef Attached | HGRZ | High | Small | Small-medium | x | x | - | - | - | - |
| Doratonotus megalepis | DORMEG | Demersal/ Reef Associated | GINV | High | Small | Solitary | - | x | x | - | - | - |
| Echeneis naucrates | ECHNAU | Pelagic/Reef Associated | CLE | Medium | Very Large | Solitary | x | - | - | - | - | - |
| Elacatinus figaro | ELAFIG | Demersal/ Reef Attached | CLE | High | Very Small | Small-medium | x | x | x | x | x | - |
| Emblemariopsis signifer | EMBSIG | Demersal/ Reef Attached | MINV | Low | Very Small | Solitary | x | x | x | - | - | - |
| Epinephelus adscensionis | EPIADS | Benthic/Reef Associated | GCAR | Low | Large | Solitary | - | - | - | - | x | x |
| Epinephelus itajara | EPIITA | Benthic/Reef Associated | GCAR | Low | Very Large | Solitary | x | - | - | - | - | x |
| Epinephelus morio | EPIMOR | Benthic/Reef Associated | GCAR | Medium | Very Large | Solitary | x | x | x | x | - | - |
| Gramma brasiliensis | GRABRA | Demersal/ Reef Attached | PLNK | High | Very Small | Solitary | x | x | x | x | x | - |
| Gymnothorax funebris | GYMFUN | Demersal/ Reef Attached | GCAR | Very Low | Very Large | Solitary | - | - | x | - | - | - |
| Gymnothorax moringa | GYMMOR | Demersal/ Reef Attached | GCAR | Low | Very Large | Solitary | x | x | x | x | - | - |
| Gymnothorax vicinus | GYMVIC | Demersal/ Reef Attached | GCAR | Very Low | Very Large | Solitary | x | - | - | - | - | - |
| Haemulon aurolineatum | HAEAUR | Nektonic/Reef Associated | OMNI | Medium | Medium | Large | x | x | x | x | x | x |
| Haemulon parra | HAEPAR | Benthic/Reef Associated | GCAR | Medium | Medium -Large | Large | x | x | x | x | x | - |
| Haemulon plumierii | HAEPLU | Benthic/Reef Associated | GCAR | Medium | Large | Small-medium | x | x | x | x | x | x |
| Haemulon squamipinna | HAESQU | Benthic/Reef Associated | MINV | High | Small | Small-medium | x | - | - | x | - | x |
| Haemulon steindachneri | HAESTE | Benthic/Reef Associated | GCAR | Medium | Medium | Small-medium | - | x | - | - | x | x |
| Halichoeres brasiliensis | HALBRA | Benthic/Reef Associated | GINV | Medium | Medium -Large | Solitary | x | x | x | x | x | x |
| Halichoeres maculipinna | HALMAC | Benthic/Reef Attached | GINV | High | Medium | Solitary | - | - | - | x | - | - |
| Halichoeres poeyi | HALPOE | Benthic/Reef Attached | GINV | Medium | Medium | Solitary | x | x | x | x | x | x |
| Hemiramphus sp | HEMSP | Pelagic/Reef | GCAR | High | Medium | Large | - | - | - | x | - | - |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Associated | | | -Large | | | | | | | |
| Holocentrus adscensionis | HOLADS | Benthic/Reef Attached | GCAR | Medium | Large | Solitary | x | x | x | x | x | x |
| Holacanthus ciliaris | HOLCIL | Benthic/Reef Associated | OMNI | Low | Medium -Large | Pair | x | x | x | x | x | x |
| Hypanus americanus | HYPAME | Demersal/ Reef Associated | GCAR | Very Low | Very Large | Solitary | - | x | - | - | - | - |
| Hypleurochilus pseudoaequipinnis | HYPPSE | Demersal/ Reef Attached | MINV | High | Very Small | Solitary | - | - | x | - | - | - |
| Kyphosus sp | KYPSP | Benthic/Reef Associated | HGRZ | Low | Large | Small-medium | x | - | - | x | x | - |
| Labrisomus nuchipinnis | LABNUC | Demersal/ Reef Attached | GCAR | Medium | Medium | Solitary | x | x | - | x | x | x |
| Lutjanus alexandrei | LUTALE | Benthic/Reef Associated | GCAR | Medium | Medium | Solitary | x | x | - | x | x | x |
| Lutjanus analis | LUTANA | Benthic/Reef Associated | GCAR | Low | Very Large | Small-medium | x | x | - | - | - | - |
| Lutjanus jocu | LUTJOC | Benthic/Reef Associated | GCAR | Low | Very Large | Solitary | x | x | x | x | x | x |
| Lutjanus synagris | LUTSYN | Benthic/Reef Associated | GCAR | Medium | Large | Large | - | x | x | - | x | - |
| Malacoctenus delalandii | MALDEL | Demersal/ Reef Attached | MINV | Medium | Small | Solitary | x | x | x | x | x | x |
| Malacoctenus zaluaris | MALZAL | Demersal/ Reef Attached | MINV | Medium | Very Small | Solitary | x | x | x | x | x | x |
| Microspathodon chrysurus | MICCHR | Demersal/ Reef Attached | HBTE | Medium | Medium | Solitary | x | - | - | x | x | x |
| Mycteroperca bonaci | MYCBON | Benthic/Reef Associated | PISC | Medium | Very Large | Solitary | x | x | x | x | x | - |
| Mycteroperca interstitialis | MYCINT | Benthic/Reef Associated | PISC | Low | Very Large | Solitary | - | - | - | x | - | - |
| Ocyurus chrysurus | OCYCHR | Nektonic/Reef Associated | GCAR | Medium | Very Large | Small-medium | x | x | x | x | x | - |
| Odontoscion dentex | ODODEN | Nektonic/Reef Associated | GINV | High | Medium | Small-medium | - | x | - | - | - | x |
| Ogcocephalus vespertilio | OGCVES | Demersal/ Reef Attached | MINV | Low | Medium | Solitary | - | - | x | - | x | - |
| Ophioblennius trinitatis | OPHTRI | Demersal/ Reef Attached | OMNI | High | Very Small | Solitary | - | x | x | x | x | x |
| Orthopristis ruber | ORTRUB | Benthic/Reef Associated | GCAR | Medium | Medium -Large | Small-medium | - | - | - | - | x | - |
| Pareques acuminatus | PARACU | Demersal/ Reef Attached | GINV | High | Medium | Small-medium | x | - | x | x | - | x |
| Parablennius marmoreus | PARMAR | Demersal/ Reef Associated | OMNI | High | Very Small | Solitary | x | x | x | x | x | x |
| Parablennius pilicornis | PARPIL | Demersal/ Reef Associated | OMNI | High | Small | Solitary | x | x | - | x | x | x |
| Pempheris schomburgkii | PEMSCH | Nektonic/Reef Associated | PLNK | High | Small | Large | - | - | - | x | x | x |
| Pomacanthus arcuatus | POMARC | Benthic/Reef Associated | OMNI | Very Low | Large | Pair | x | x | x | x | x | x |
| Pomacanthus | POMPAR | Benthic/Reef | OMNI | Medium | Medium | Pair | x | x | x | x | x | x |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| paru | | Associated | | | -Large | | | | | | | |
| Priacanthus arenatus | PRIARE | Benthic/Reef Associated | GCAR | High | Medium -Large | Small-medium | - | - | - | - | x | - |
| Pseudocaranx dentex | PSEDEN | Pelagic/Reef Associated | GCAR | Medium | Very Large | Small-medium | - | x | - | - | - | - |
| Pseudupeneus maculatus | PSEMAC | Demersal/ Reef Associated | MINV | High | Medium | Small-medium | x | x | x | x | x | x |
| Rypticus saponaceus | RYPSAP | Benthic/Reef Attached | GCAR | Medium | Medium -Large | Solitary | x | - | - | - | - | x |
| Scartella cristata | SCACRI | Demersal/ Reef Attached | HBTE | High | Small | Solitary | x | - | - | - | - | - |
| Scarus trispinosus | SCATRI | Benthic/Reef Associated | HSCP | Medium | Large | Small-medium | x | x | x | x | x | x |
| Scarus zelindae | SCAZEL | Benthic/Reef Associated | HSCP | High | Medium -Large | Small-medium | x | - | x | - | x | x |
| Scomberomorus cavalla | SCOCAV | Pelagic/Reef Associated | GCAR | Medium | Very Large | Large | x | - | - | - | x | - |
| Scorpaena plumieri | SCOPLU | Demersal/ Reef Attached | GCAR | Low | Medium -Large | Solitary | - | - | - | - | x | - |
| Scomberomorus regalis | SCOREG | Pelagic/Reef Associated | GCAR | Medium | Very Large | Large | - | - | - | x | x | - |
| Serranus flaviventris | SERFLA | Demersal/ Reef Attached | GINV | High | Very Small | Solitary | x | x | x | x | x | x |
| Sparisoma amplum | SPAAMP | Benthic/Reef Associated | HSCP | High | Medium -Large | Small-medium | x | - | x | x | - | - |
| Sparisoma axillare | SPAAXI | Benthic/Reef Associated | HSCP | Medium | Medium -Large | Large | x | x | x | x | x | x |
| Sparisoma frondosum | SPAFRO | Benthic/Reef Associated | HSCP | Medium | Medium -Large | Small-medium | x | x | x | x | x | - |
| Sparisoma radians | SPARAD | Benthic/Reef Associated | HBRW | High | Medium | Solitary | x | x | - | - | - | x |
| Sphyraena barracuda | SPHBAR | Pelagic/Reef Associated | GCAR | Low | Very Large | Solitary | x | - | - | - | - | - |
| Stegastes fuscus | STEFUS | Demersal/ Reef Attached | HBTE | Medium | Small | Solitary | x | x | x | x | x | x |
| Stegastes pictus | STEPIC | Demersal/ Reef Attached | PLNK | High | Very Small | Solitary | x | - | x | x | - | - |
| Stegastes variabilis | STEVAR | Demersal/ Reef Attached | HBTE | High | Small | Solitary | x | x | x | x | x | x |
| Synodus intermedius | SYNINT | Demersal/ Reef Associated | GCAR | Medium | Medium -Large | Solitary | x | x | - | x | - | - |
| Synodus synodus | SYNSYN | Demersal/ Reef Associated | GCAR | Medium | Medium-Large | Solitary | - | - | x | x | - | - |

# Capítulo 3

## The effect of protection and environmental variables on functional diversity.

Artigo para submeter na Conservation Biology

# The effect of protection and environmental variables on functional diversity.

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## Abstract

Marine protected areas (MPA) are widely used to manage and regulate human actions, especially those that cause the degradation of marine ecosystem functions and habitats. The main objective of this study was to compare and identify the relationship between functional and taxonomic diversity and between functional traits against environmental variables inside and outside an MPA.Stationary underwater visual census in Abrolhos Bank (east coast of Brazil) was used to collect abundance and biomass data from reef fish assemblages. Functional diversity (FD) indices were established with biomass and functional entities (FE) matrix, which was calculated using functional traits (maximum length, trophic level, spatial category, resilience, and gregariousness). Likewise, PERMANOVA was applied to test differences in the variables of biomass, taxonomic diversity (TD), FD, and redundancy pattern indices between the factors protection, locality, and site. Moreover, generalized additive models (GAM) were used to evaluate the relationship between TD and FD. Finally, RLQ ordination analyses were conducted with fourth-corner analyses to establish significant correlations between environmental variables and functional traits.For this study, 83 species were identified, grouped in 72 FE. PERMANOVA revealed higher values of functional richness in the MPA and functional evenness, common species, and dominant species in unprotected localities. Furthermore, significant differences were observed among sites for functional originality. A non-random relationship was identified between the gradient of functional traits and some environmental conditions, thus serving as an environmental filter that plays a role in community structure and reef fish distribution. The local scale was important to find this non-random relationship and to establish the environmental filter.We believe ecosystem ecological functionality is important to monitor populations more effectively. Moreover, it is critical to regulate fisheries and expand and create MPAs based on the specific environmental and habitat variables of each locality.

## Keywords

Protection effect, Functional space, Functional ecology, Functional traits, Environmental condition, Abrolhos Bank

## Introduction

Marine protected areas (MPA) represent an area-based management tool widely used in all the world's coasts and oceans to address and mitigate the impact of fisheries on fish populations and protect habitat and biodiversity. When this tool is used to protect targeted species, it also supports the recovery of population abundance inside the MPA (Pollnac et al. 2010; Coleman et al. 2015) and contributes to biomass exportation to adjacent fishing zones (Harmelin-Vivien et al. 2008; Hackradt et al. 2014) Moreover, many studies have demonstrated other benefits of MPAs, such as their ecological value in protecting genetic diversity (Pérez-Ruzafa et al. 2006), habitat structure and heterogeneity (García Charton et al. 2000), enabling egg and larvae exportation to fishing zones (Crec'Hriou et al. 2010; Harrison et al. 2012), recovery of population size structure (García-Charton et al. 2008; Hackradt et al. 2014, 2020), income generation from diving tourism (Lester & Halpern 2008; Claudet et al. 2010; Rocklin et al. 2011), and the increased provision of more valuable fish species for fisheries (García Charton et al. 2017).

Worldwide, there are 13,848 MPAs covering 21,701,556 km$^2$ or only 6% of the world's oceans. Around 7% of these MPAs (1,031 in total or 2.7% of the ocean surface) are fully or highly protected. The vast majority of MPAs, however (12,817 or 3.2% of the world's oceans) are not monitored appropriately or monitoring is unknown (www.mpatlas.org accessed 17/06/21). In Brazil, where this study was carried out, 26.48% of the exclusive economic zone is under some level of protection represented by 190 MPAs. Nonetheless, only 3.3% (or 121,124 km$^2$) (MMA, 2021) are considered well managed, as also observed worldwide. MPAs in Brazil fall into 5 categories, 3 of which are equivalent to categories of the IUCN (I, II, III), namely Ecological Station (I), Biological Reserve (I), National Park (II), Natural Monument (III), and Wildlife Refuge (III).

Although the goal to protect the world's oceans is still distant, some ecological factors of MPAs must be addressed to understand how these management tools can help mitigate anthropogenic effects on fish populations and increase the resilience of the marine ecosystem (Mouillot et al. 2013). One of these factors is how much of the functional diversity existent in the marine ecosystems is represented within these areas.

Functional diversity is calculated using functional traits based on the characteristics of existing species (Trindade-Santos et al. 2020), subsequently adopted to configure a multivariate functional space that examines the distribution of these species (Villéger et al.

2008). Therefore, it is crucial to determine how many dimensions and which and how many traits will be used to ensure a proper response for the ecosystem functionality evaluation.

Ecosystem functions or structure can be affected by changes in environmental conditions (McGill et al. 2006; Conversi et al. 2015), such as those resulting from the establishment of an MPA (Coleman et al. 2015). Such ecological alterations caused by protection (long term effects) or the use of available habitats (short term effects) can be identified by calculating functional diversity based on functional traits to predict how biodiversity responds to these environmental changes (Yeager et al. 2017). Abiotic drivers can create hierarchical filters that reduce the values of traits in a community (de Bello et al. 2013; Sydenham et al. 2015), thereby restricting species distribution (Asefa et al. 2017) by selecting the species most adapted to local conditions (de Bello et al. 2013).

According to the environmental filter hypothesis proposed by Zobel (1997), species would be more similar to each other than expected randomly, as environmental conditions act as a filter that selects only some traits. For example, Córdova-Tapia et al. (2017) found that for extreme environments such as the dry season of wetlands, environmental filters played an important role in the structure of the fish community at the end of this season, regardless of the initial composition of the community, resulting in a predominant group of species. In coral reef fish, this environmental filter acted on the selection of traits such as body morphology of herbivorous species due to wave exposure (Bejarano et al. 2017) or aspect ratio of the caudal fin and diet due to depth gradient (Bridge et al. 2016). The effect of “environmental filtering” on biodiversity and community assembly should be evaluated using different tools that measure community structure (de Bello et al. 2013), together with different spatial scales (Yeager et al. 2017) since species’ roles can change to dominant due to environmental factors at local scale (Mason et al. 2011).

Given the above, the aim of this study was to answer the following questions: i) how can an MPA influence functional and taxonomic diversity of reef fish assemblages?; ii) how can environmental variables further affect reef fishes assemblages in protected vs unprotected scenarios; iii) what role do these environmental variables play in an environmental filter on reef fish assemblages? To answer these questions, functional and taxonomic indices were applied to a reef fish assemblage based on a beyond after-control-impact (ACI) approach using MPA as the “impact factor”. We also checked if the variables of complexity, habitat heterogeneity, and benthic cover can exert further influence on these indices, the functional traits, and, consequently, the ecosystem function.

## Material and methods

### Study sites

This study was conducted in the following three reef systems: i. Abrolhos National Marine Park (ANMP); ii. Parcel das Paredes Reef (PPR); and iii. Cassuruba Reef (CAR). All reefs are located in the Abrolhos Bank, an extension of the continental shelf, which covers 46,000 km$^2$ with a depth of no more than 30 m and a shelf edge of around 70 m (Francini-Filho et al. 2013). This region is located on the northeast coast of Brazil and has the most extensive and biodiverse coral reefs in the South Atlantic Ocean, as well as high rates of endemism for coral (Moura et al. 2013). The ANMP was established as a no-take zone in 1983 and it is formed by two discontinuous areas that cover around 91,300 hectares (882 km$^2$). The smaller area is close to the coast, within the Parcel das Timbebas. In the large offshore area lies the Abrolhos Archipelago composed of five volcanic islands (Santa Bárbara, Redonda, Siriba, Sueste, and Guarita) and the Parcel dos Abrolhos characterized by the presence of mushroom-shaped pinnacle reefs called “Chapeirões” (Leão & Kikuchi 2005). In contrast, PPR and CAR are unprotected bank and pinnacles reefs (Moura et al. 2013). PPR is a single large reef formation, while CAR is composed of 3 isolated reefs named Nova Viçosa, Coroa Vermelha, and Sebastão Gomes (Figure 1).

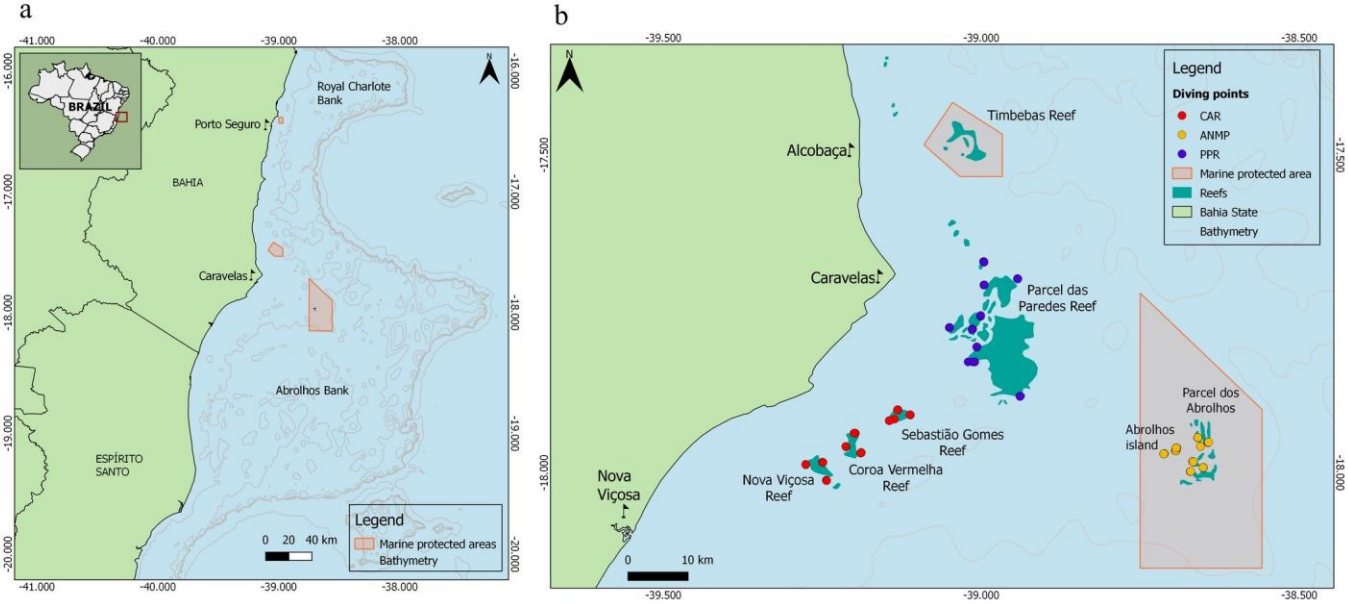


Figure 1. Map showing a) distribution of Abrolhos Bank and b) samples of this study in Cassuruba Reef (CAR), Parcel das Paredes Reef (PPR), and Abrolhos National Marine Park (ANMP). The protection level is represented by the polygons and the samples by the dots

## Sampling design and data collection

Data were collected using the beyond after-control-impact (ACI) (Underwood 1997) sampling design. ‘Protection’ was defined as a fixed factor with 2 levels (protected and unprotected), ‘locality’ as a random factor with 3 levels (ANMP, PPR, and CAR) nested in ‘protection’, and ‘sites’ as a random factor with 9 levels nested in ‘locality’. Within each site (Figure 1), data were collected using 6 stationary visual censuses (cf. Minte-Vera et al. 2008) with a radius of 4 m for species >20 cm and a radius of 2 m for species <20 cm. All fishes were identified at the lowest possible taxonomic level and their size was estimated in size classes of 2 cm. Fish abundance was recorded in abundance classes following a geometric scale (cf. Harmelin 1987; García-Charton & Pérez-Ruzafa 2001; Hackradt et al. 2011). Fish biomass was calculated based on length-weight parameters ($W = a \times L^b$) for each species obtained from the literature (Hackradt et al. 2011). Fish data were collected in the austral summer (January – March) of 2019.

Additionally, environmental data were collected and categorized into habitat heterogeneity, complexity, and benthic cover. Estimates of habitat heterogeneity were obtained by evaluating the cover percentage of consolidated reef, sand, gravel, and grassland/macroalgae. Habitat complexity was measured by the following variables: I) rugosity (visual estimates on a categorical scale of 1 to 5, with 1 being smooth and 5 highly complex); ii) slope (categorized as $0^o$-$30^o$, $30^o$-$60^o$, $60^o$-$90^o$ (cf: Félix-Hackradt et al. 2014); iii) number and size of holes (counted in 3 categories: <20cm (small), 20-50 cm (medium), and >50 cm (big), (García-Charton et al. 2004); and iv) depth (in m). These environmental variables were measured inside the visual census area by dividing the 4 m radius cylinder into 4 equal parts, except for the number and size of holes, which were counted linearly along the 8 m diameter of our stationary census area. Benthic cover was accessed using 3 photo-quadrats (Francini-Filho et al. 2008) placed randomly inside each visual census cylinder. Each photo-quadrats was approximately 0.5 $m^2$ (70 × 80 $cm^2$) and consisted of 15 high-quality photos measuring 22 × 15 cm each (cf. Francini-Filho et al. 2013). Benthic organisms were identified in higher hierarchical groups as cyanobacteria (CYAN), macroalgae (MALG), calcareous algae (CALG), ephilitical algal matrix (EAM), zoanthid (ZOAN), soft coral (SCOR), hard coral (HCOR), and other organisms (OORG) at 30 random points per photo using the Coral Point Count with Excel extensions (CPCe) program (Kohler & Gill 2006).

## Functional traits

The functional traits of the species were attributed according to information obtained (Table S1) on FishBase, in other published material, or, when absent, conspecific published data. Five categorical functional traits (trophic level, maximum length, resilience, gregariousness, and spatial category) were established to show distinct functions between reef fish species. Trophic level was used to determine the main diet or food item. Maximum published length is a universal and predictive functional trait that provides implicit information on the ecological attributes, organismal function, and ontogeny of the species (Bellwood et al. 2019). Resilience takes into account the first gonadal maturation size and fecundity estimates, such as minimum number of eggs and offspring per year (Musick 1999). Gregariousness shows interspecific or intraspecific social behavior such as moving or feeding (Mouillot et al. 2014). Lastly, spatial category estimates the horizontal and vertical migration rates of the species (cf. (Harmelin 1987). Vertical migration is related to the position fish occupy in the water column. In this regard, pelagic species exhibit the greatest vertical migration (ex. Chromis spp.), followed by nektonic (e.g. Abudefduf spp.), benthic (e.g. Stegastes spp.), and demersal species (eg Scorpaena spp.). Reef-associated species exhibit medium to high horizontal movement (e.g. Acanthuridae), while reef-attached species exhibit little to no horizontal movement (e.g. Blennnidae) (Table S2).

## Redundancy patterns, Functional Diversity and Taxonomic Diversity indices

First, the unique combination of the five qualitative traits that define the functional entities (FE) was calculated using the R function 'species_to_FE'. Then, the species occurrence matrix (presence/absence) was combined with a functional entities matrix to obtain the redundancy pattern values using the R function 'FE metrics', according to Mouillot et al. (2014), namely functional redundancy (FRed), functional over-redundancy (FORed), and functional vulnerability (FVul).

Subsequently, the quality of functional space provided by the trait FE was calculated using Gower's distance matrix. The distance matrix was used to calculate the multidimensional space by principal coordinates analysis (PCoA) for a maximum of 10 dimensions in order to evaluate the lowest mean squared deviation (mSD) that represents a higher quality of functional space (Maire et al. 2015). For this study, the highest quality of functional space occurred when species were represented by 4 dimensions ($mSD = 2.8e^{-3}$). Next, the multidimensional functional diversity (FD) indices for each sample were computed with the functional entities coordinates matrix and the biomass matrix using the function 'multidimFD'. The coordinate matrix and the multidimensional functional diversity indices were calculated using 'FD' R package (Laliberté et al. 2015). Sample replicates with a smaller number of species than functional traits were excluded. These FD indices are defined in Mouillot et al. (2013) as follows: functional richness (FRic, 'the volume of multidimensional space occupied by all species in a community within functional space'); functional evenness (FEve, 'the regularity of the relative abundance and distribution of species in functional space for a given community'); functional divergence (FDiv, 'the proportion of total abundance supported by species with the most extreme trait values within a community'); functional dispersion (FDis, 'biomass-weighted mean distance from the center of the assemblage in the synthetic niche space' (Brandl et al. 2016); functional specialization (FSpe, 'the mean distance of a species from the rest of the species pool in functional space'); and functional originality (FOri, 'the isolation of a species in the functional space occupied by a given community') (Laliberté et al. 2015).

Finally, the taxonomic indices (sensu Jost 2006) for samples were calculated using the numbers of Hill (Hill 1973) as the effective number of species to evaluate the relationship of ecological indices with functional diversity. Weight is attributed to species abundance; therefore, weight 0 ($q^0$) refers to rare species, weight 1 ($q^1$) corresponds to the effective number of common species, and a disproportionate weight is attributed to abundance of dominant species ($q^2$). We were used the *MetaCommunity* and *AlphaDiversity* functions of the 'entropart' package (Marcon & Herault, 2015), to calculate these indices

## Data analyses

The influence of factors protection, localities, and sites was tested on biomass, taxonomic diversity, multidimensional functional, and redundancy pattern indices with the software PRIMER v6 & PERMANOVA+ (Clarke & Gorley 2006) based on the Bray Curtis similarity distance matrix. To assess the significance of the tested factors, 9999 permutations were applied with the Monte-Carlo p-value. Moreover, to evaluate how much of the functional space is filled by species from protected vs unprotected areas, PCoA was calculated using a

Bray Curtis similarity distance matrix (Anderson 2001). Furthermore, the risk ratio (RR) of the effect of protection on biomass, taxonomic, and functional diversity indices, and redundancy patterns was calculated.

The relationship between taxonomic and functional diversity indices was determined using generalized additive model (GAM) with the response variables FRic, FEve, FDiv, FDiv, FSpe, and FOri and the predictors $q^0$, $q^1$, and $q^2$. These analyses were performed using gamma and beta distribution within the 'mgvc' package.

Next, we evaluated the response of the five categorical discrete trait values (spatial category, resilience, trophic group, maximum length, and gregariousness) to the protection factor. For this purpose, biomass was converted into density values (g/m$^2$) by calculating the species biomass by sampled area within the protected and unprotected sites. The density of each species in the protected and unprotected areas was calculated for each biogeographic province and adjusted to binary values, which were 1 when this density was greater for protected areas and 0 when it was greater in unprotected areas. Bayesian regression models (BRM) were employed with the Bernoulli error distribution and a run for 4 chains and 3,000,000 interactions with an initial warm-up phase of 50,000 and thinning interval of 10,000 using the 'brms' package (Bürkner 2017). For the prior distribution, in this case, only 'max_treedepth' was used. For this analysis, species that only presented one value in each trait were excluded to avoid divergent transitions, which does not guarantee the validity of the model.

In addition, we calculated the redundancy pattern indices (redundancy, over-redundancy, and vulnerability) for the trophic group trait to evaluate any possible change in fish assemblages due to protection. Then, PERMANOVA was applied for redundancy patterns indices of trophic groups that showed differences in protection in Bayesian analyses. These indices were represented by level of protection with non-parametric multidimensional scaling (NMDS) for ordination.

To evaluate how protection affects environmental variables (benthic cover, habitat heterogeneity, and complexity), PERMANOVA was used with the same sampling design and factors applied to evaluate our indices. Previously, habitat heterogeneity and benthic cover were arcsine-square root transformed ($2/\pi*\arcsine(\sqrt{x})$) and complexity data (except rugosity and slope, as they are categorical variables) were log(x+1) transformed. This analysis was applied after standardizing all the continuous and discrete variables and the category variables mentioned above without standardizing.

Finally, RLQ ordination analyses together with fourth-corner analyses were conducted to evaluate whether the environmental drivers are influencing fish structure by filtering certain species traits and to establish significant correlations between environmental variables and functional traits. Specifically, RLQ is a multivariate analysis technique that evaluates the influence between environmental factors and trait variations based on 3 types of data, namely environmental (R), species biomass (L) (log(x+1) transformation), and ecological traits (Q) (Dolédec et al. 1996; Dray et al. 2014). Before RLQ analysis, the R matrix was applied with principal components analysis (PCA), L matrix with correspondence analyses (CA), and Q matrix with the Hill and Smith ordination method that combines factors and discrete variables (Dray et al. 2014). The environmental matrix was scaled and centered. Moreover, RLQ can be considered an extension of co-inertia analysis, as biomass uses L to maximize the covariance with biomass weights and evaluates whether there is a linear combination between Q and R (Dray et al. 2014). Next, we conducted a sequential test (Model 6) based on the fourth-corner statistic that consists of a permutational test applied on two models to determine, as a null hypothesis, that environmental variables or traits are not related by the distribution of species (Dray et al. 2014). This combination comes from models 2 and 4 presented by Dray and Legendre (2008), in which model 2 tests the null hypothesis that there is no relationship between environmental conditions and the distribution of species with fixed traits, and model 4, which evaluates if there is an established relationship between some characteristics or adaptations of the species to fixed environmental conditions imposed by the site (Dray et al. 2014). We used 999 permutations and the false discovery rate to adjust *p* values in all tests. For these analyses, all the localities were evaluated together and separately.

## Result

Fish richness found in the Abrolhos Bank consisted of 83 species in 72 functional entities (FE). After evaluating how these functions are distributed in the MPA or open areas, a representation of 59 FE was identified in both. Functional space analysis revealed that these FE represented 89.9% for both areas in this space, although the same entities are not contemplated in each protected and unprotected area (Figure 2). Mean richness for sectors with stationary visual census was 13.2 ± 0.56 and 11.3 ± 0.32 species (q0), and 12.7 ± 0.52 and 10.8 ± 0.32 FE in protected and unprotected areas, respectively.

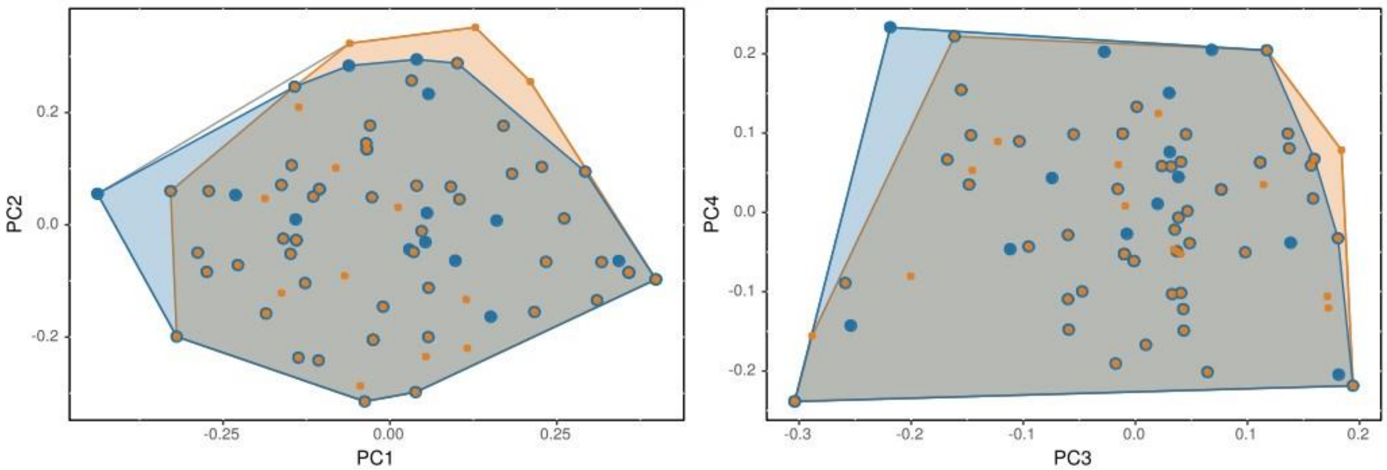


Figure 2. Representation of functional space in marine protected (no-take zone) and unprotected areas. The functional space is created using a) PC1-PC2 and b) PC3-PC4 with principal coordinate analysis on functional traits to represent the distribution of functional entities. The orange points represent the functional entities in marine protected ('prot') areas and the blue points represent the functional entities in unprotected ('unpr') areas, while the orange points with blue edges represent the functional entities that share the two levels of protection. Grey crosses are absent functional entities.

The functional and taxonomic indices did not differ for the protection factor, except functional richness (FRic), which was higher in the MPA (0.12 ± 0.01) than in the unprotected areas (0.098 ± 0.01) (Table 1). However, significant differences were observed for functional evenness (FEve) between the three localities, with higher values in the two unprotected areas (0.472 ± 0.02 for PPR and 0.361 ± 0.02 for CAR) than in the ANMP (0.326 ± 0.02). Furthermore, the richness of common and dominant species was more similar between PPR (8.1 ± 0.39; 6.3 ± 0.35) and ANMP (7.9 ± 0.4; 5.9 ± 0.34) than in CRA (6.4 ± 0.26; 4.8 ± 0.23). Finally, functional originality (FOri) differed significantly between sites with small-scale space variability (Table 1). For example, in CAR, differences of originality were observed between the least exposed area of the Nova Viçosa reef and the most exposed area of the Sebatião Gomes reef. Redundancy patterns did not show significant values for any of the evaluated factors (Table 1).

Table 1. PERMANOVA of protection level (P), locality (L), and sector (S) on biomass, taxonomic diversity, and multidimensional functional and redundancy pattern indices on functional entities. Legend: df: degrees of freedom; I, q0: rare species diversity; q1: common species diversity; q2: dominant species diversity, FRic: functional richness; FEve: functional evenness; FDiv: functional divergence; FDis: functional dispersion; FSpe: functional specialization; and FOri: functional originality, FE: functional entities; FRed: functional redundancy; FORed: functional over-redundancy; FVul: functional vulnerability. ***: *p* ≤0.001, **: *p* ≤0.01, *: *p* ≤0.05.

| Sources | df | Biomass | | FRic | | FEve | | FDiv | | FDis | | FSpe | | FOri | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | F | p | F | p | F | p | F | p | F | p | F | p | F | p |
| P | 1 | 7.41 | 0.059 | 2224.7 | ** | 0.9 | 0.51 | 14.1 | 0.157 | 14.1 | 0.153 | 50.3 | 0.075 | 7.3 | 0.2 |
| L (P) | 1 | 1.7 | 0.174 | 0.0003 | 0.998 | 9.9 | ** | 0.3 | 0.596 | 0.3 | 0.580 | 0.4 | 0.523 | 1.3 | 0.318 |
| S ((L (P)) | 24 | 2.1 | *** | 3.8 | *** | 1.2 | 0.290 | 1.3 | 0.173 | 1.3 | 0.169 | 1.5 | 0.081 | 2.0 | ** |
| Residual | 133 | | | | | | | | | | | | | | |
| Total | 159 | | | | | | | | | | | | | | |

| Sources | df | $q^0$ | | $q^1$ | | $q^2$ | | FE | | FRed | | FORed | | FVul | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | F | P | F | P | F | p | F | p | F | p | F | p | F | P |
| P | 1 | 2.5 | 0.329 | 0.2 | 0.783 | 0.006 | 0.923 | 3.5 | 0.267 | 5.4 | 0.263 | 4.4 | 0.288 | 5.7 | 0.247 |
| L (P) | 1 | 1.1 | 0.288 | 4.0 | * | 5.1 | * | 1.0 | 0.330 | 0.4 | 0.511 | 0.4 | 0.487 | 0.4 | 0.510 |
| S ((L (P)) | 24 | 4.2 | *** | 2.3 | *** | 1.9 | ** | 4.2 | *** | 1.3 | 0.157 | 1.3 | 0.156 | 1.3 | 0.162 |
| Residual | 133 | | | | | | | | | | | | | | |
| Total | 159 | | | | | | | | | | | | | | |

Moreover, the response ratio indicates the highest biomass values occurred in the protected area, (RR = 1.1, CI = 0.11 – 2.1), although the highest values for functional evenness (RR = -0.25, CI = -0.48 – -0.01), specialization (RR = -0.12, CI = -0.14 – -0.11), originality (RR = -0.3, CI = -0.43 – -0.16), and over-redundancy (RR = -0.35, CI = -0.51 – -0.18) occurred in the unprotected areas (Figure 3).

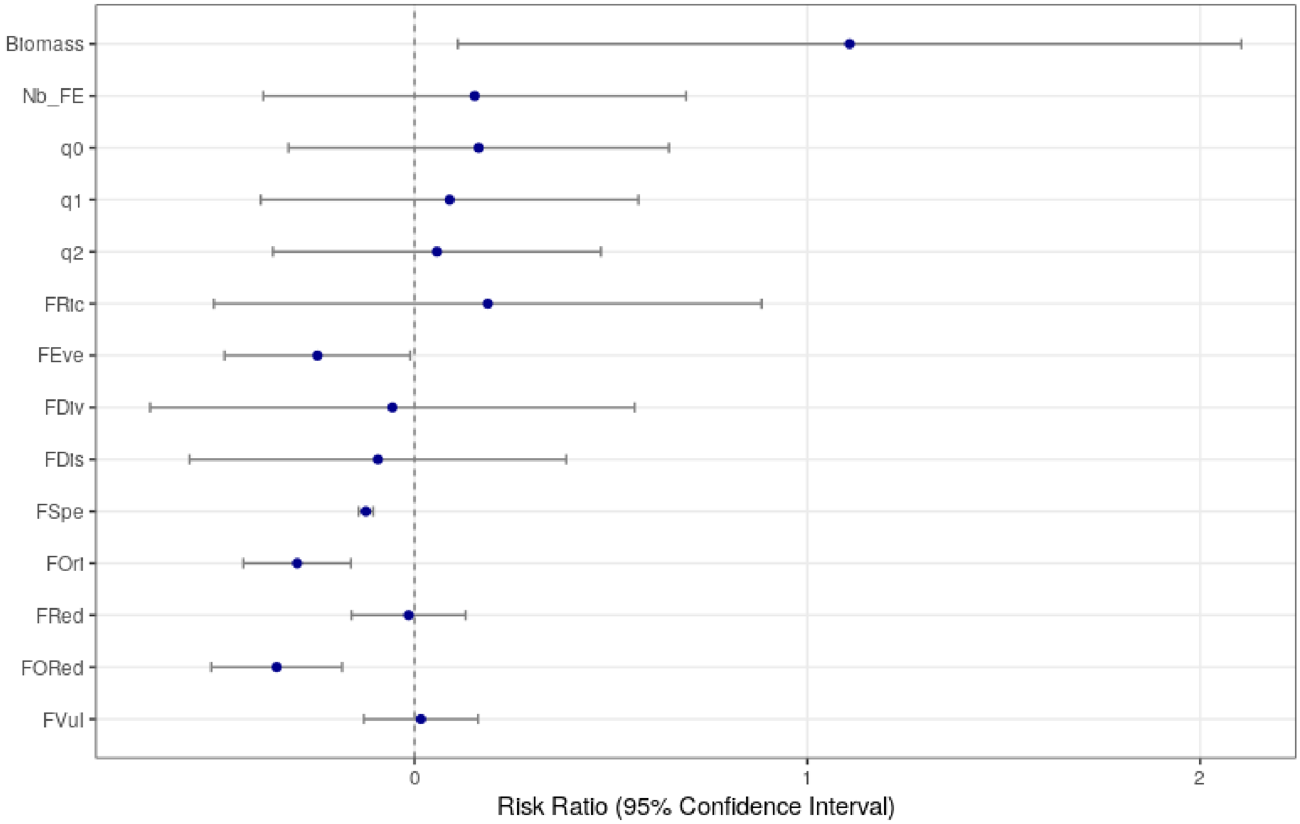


Figure 3. Response ratios (RRs) by biomass, richness of functional entities, taxonomic and functional diversity indices, and redundancy patterns. Values greater than 0 indicate the effect of protection and less than 0 indicate the effect of lack of protection. Bars indicate 95% confidence intervals. Nb_FE: functional entities, $q^0$: true richness, $q^1$: diversity of first order, $q^2$: diversity of second order, FRic: functional richness, FEve: functional evenness, FDiv: functional divergence, FDis: functional dispersion, FSpe: functional specialization, FOri: functional originality, FRed: functional redundancy, FORed: functional over-redundancy, FVul: functional vulnerability.

With regard to the manner in which functional indices behave as a function of taxonomic diversity for the two levels of protection, FRic increase significantly with an increase of rare species (q0 = P: *p*-value <0.001, U: *p*-value <0.001), common species (q1 = P: *p*-value <0.001, U: *p*-value <0.01) and dominant species diversity (q2 = P: *p*-value <0.05, U: *p*-value <0.05) for both protection factor levels. However, the FEve decreased significantly for the protection area with an increase in species for the three indices (q0: *p*-value <0.001, q1: *p*-value <0.05, q2: *p*-value <0.05), while for unprotected areas, it increased with the increase of dominant species (q2: *p*-value <0.01). Moreover, FDiv decreased with an increase of rare (q0: *p*-value <0.05) and common (q1: *p*-value <0.01) species in unprotected areas and dominant species in both areas (P: *p*-value <0.05, U: *p*-value <0.05). In the case of FDis, only an increase of rare species (q0: *p*-value <0.01) in the protected area led to an increase of this index. Conversely, for Fspe and FOri, a decrease in unprotected areas was observed with an increase of common species (FSpe: *p*-value <0.05; FOri: *p*-value <0.001) and dominant species (FSpe: *p*-value <0.01; FOri: *p*-value <0.001). (Table S3, Fig 4-5).

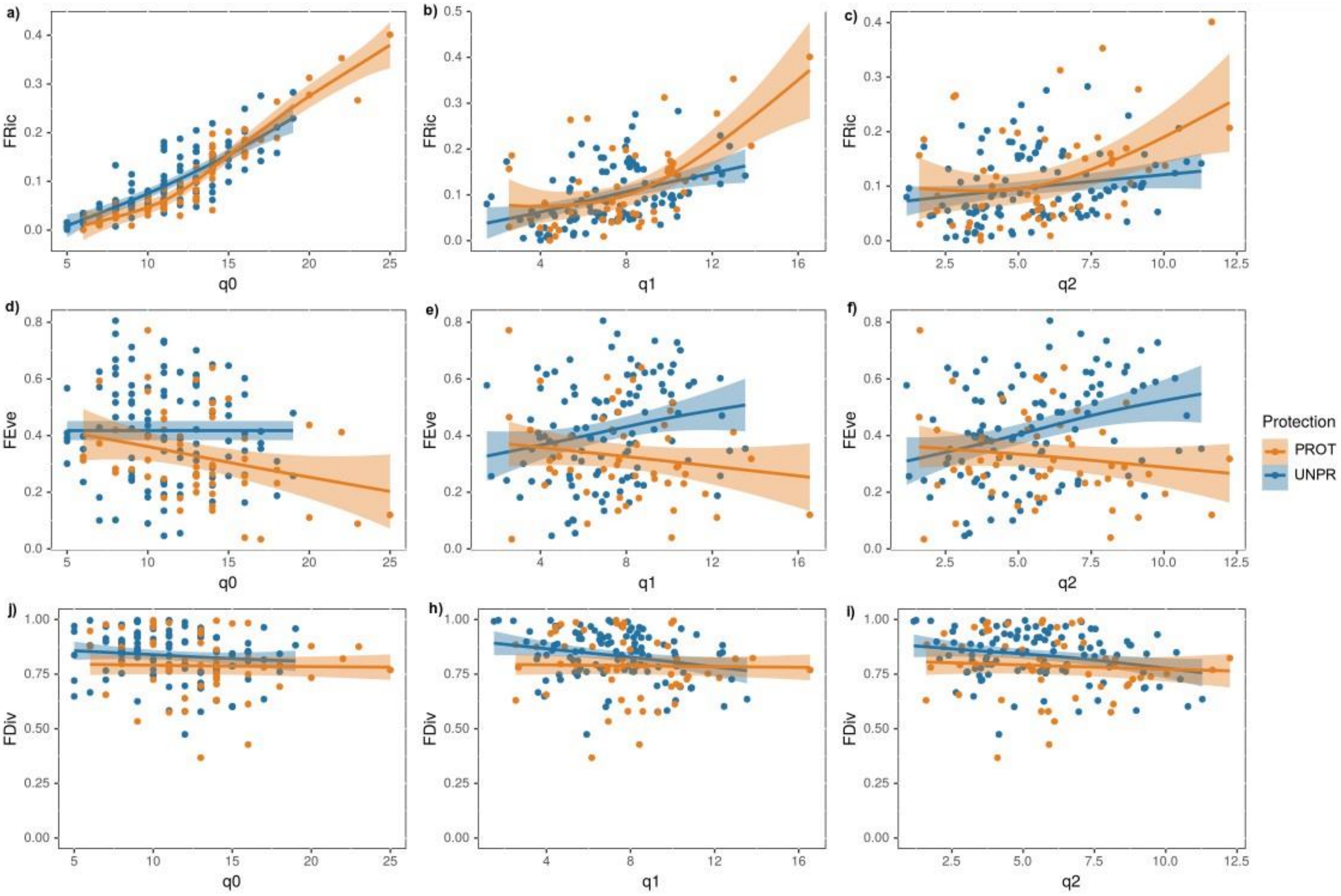


Figure 4. Generalized additive model (GAM) based on the relationship between diversity of rare (q0), common (q1), and dominant species and functional diversity indices. a-c) FRic: functional richness, d-f) FEve: functional evenness, j-i) FDiv: functional divergence. Point estimate and 95% confidence interval are represented by orange for protected areas and blue for unprotected areas.

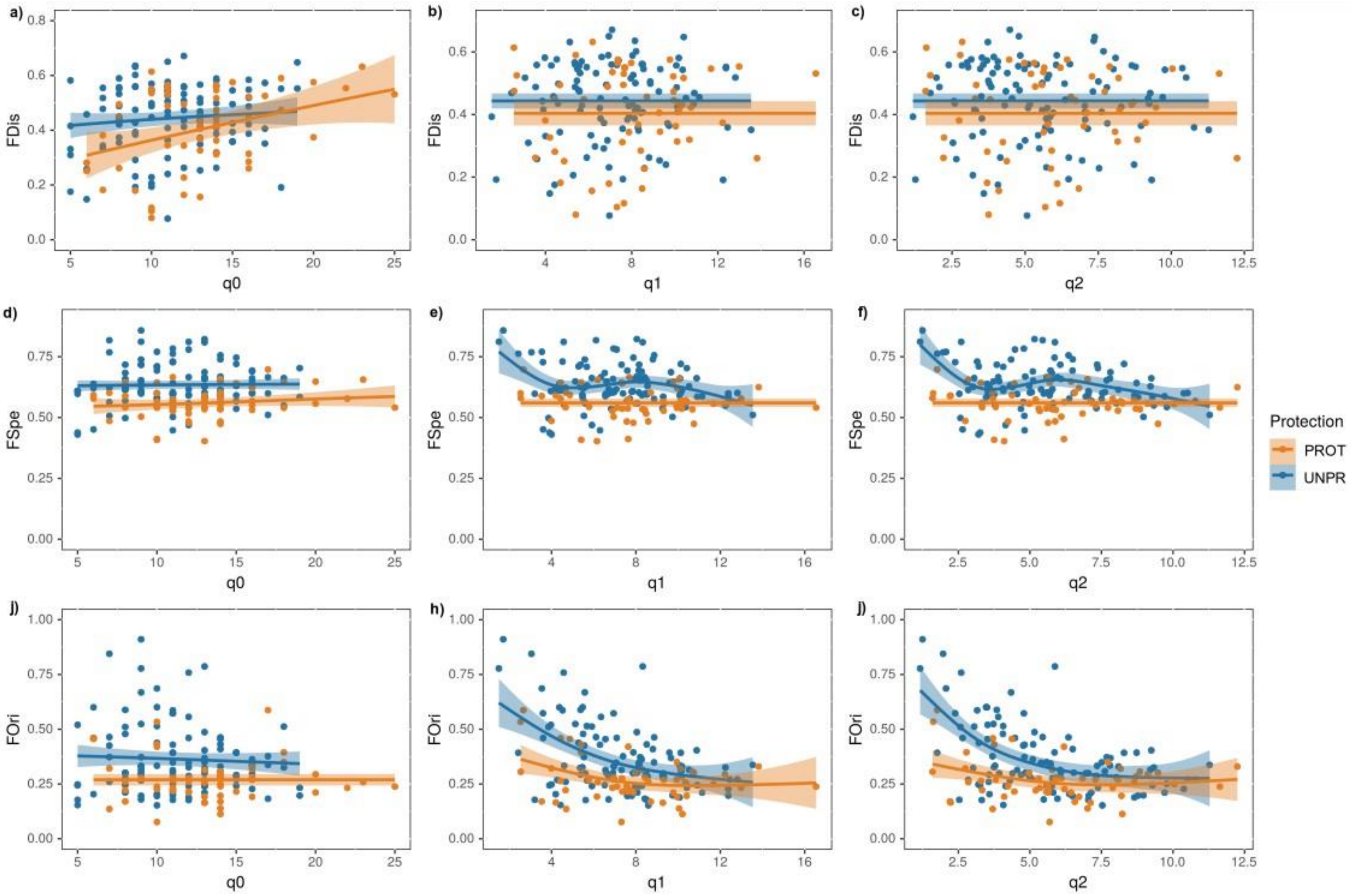


Figure 5. Generalized additive model (GAM) based on the relationship between diversity of rare (q0), common (q1), and dominant species and functional diversity indices. a-c) FDis: functional dispersion, d-f) FSpe: functional specialization, j-i) FOri: functional originality. Point estimate and 95% confidence interval are represented by orange for protected areas and blue for unprotected areas.

The Bayesian analyses of functional traits showed that some specific categories of these traits such as benthic/reef-associated species, grazer herbivores, piscivores, and planktivores had a higher species density for these categories in the protected area (Figure 6). Moreover, PERMANOVA used to evaluate the effect of protection in the redundancy patterns of the three trophic groups revealed a significant response for redundancy of planktivores (F = 106.5, *p*-value <0.05) in ANMP (Figure 7).

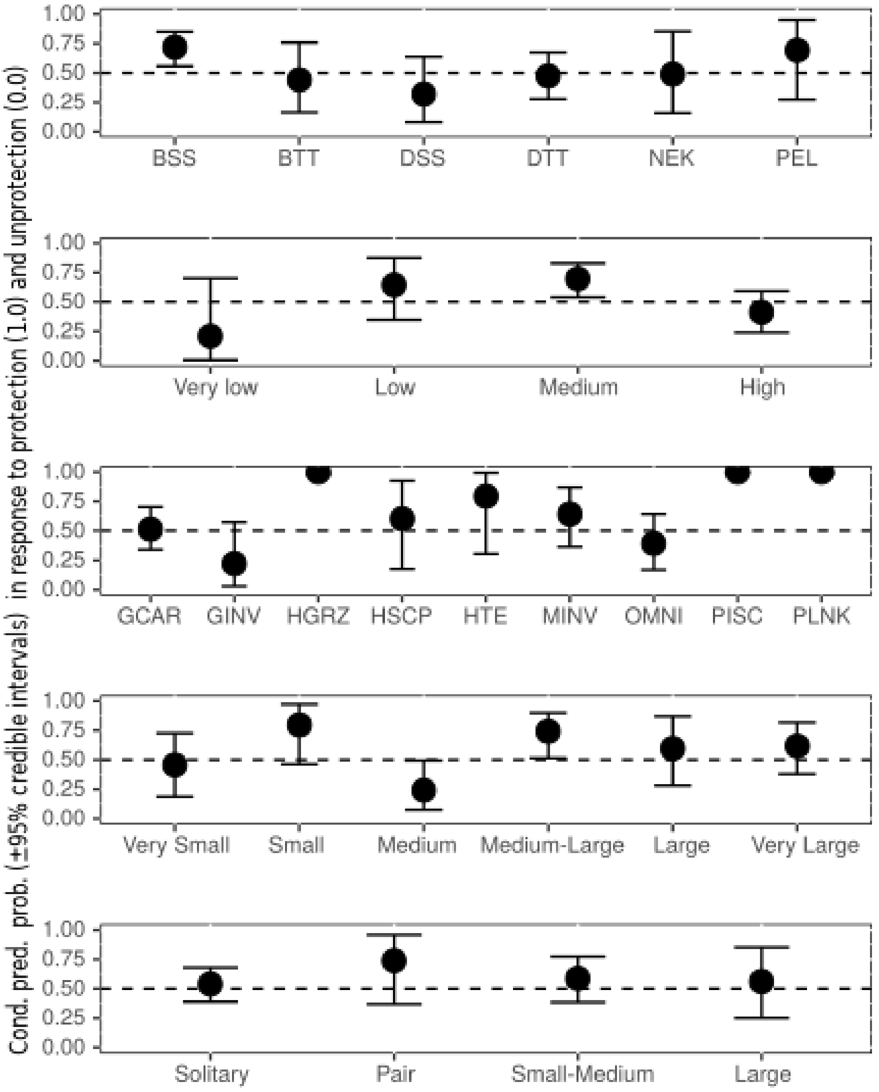


Figure 6. Predicted posterior probabilities (± 95% credible intervals) by Bernoulli distribution and Bayesian regression model, representing functional traits of a) spatial category, b) resilience, c) trophic group, d) maximum length, and e) gregariousness for the factor protection. The line at 0.5 of the y-axis represents the delimitation between protected and unprotected. Spatial category: horizontal and vertical movement in the water column: BSS: benthic/reef-associated, BTT: benthic/reef attached, DSS: demersal/reef-associated, DTT: demersal/reef attached, NEK: nektonic/reef-associated, PEL: pelagic/reef-associated. Trophic group: GCAR: general carnivores, GINV: general invertivores, HGRZ: grazers herbivores, HSCP: scraper herbivores, HTE: territorial herbivores, MINV: mobile invertivores, OM: omnivores, PISC: piscivores, PLNK: planktivores.

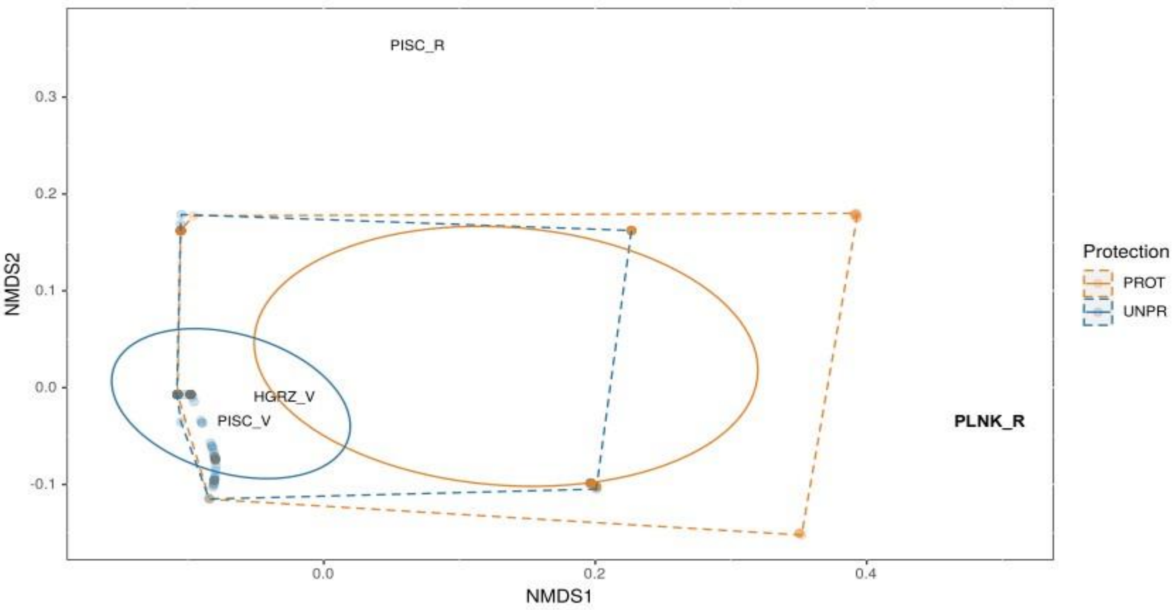


Figure 7. Non-metric multidimensional scaling (NMDS) ordination of combined redundancy indices (redundancy, vulnerability, and over-redundancy) for the trophic group trait. Orange points, ellipse, and polygon represent the protected replicates, while blue point, ellipse, and polygon represent the unprotected replicates. The ellipses represent the standard deviation of protection level. The redundancy indices in bold represent the indices showing significant differences between levels of protection in PERMANOVA. Trophic groups: PLNK: planktivores, HGRZ: herbivore grazers, PISC: piscivores. Redundancy indices: R: functional redundancy, V: functional vulnerability.

PERMANOVA of environmental variables revealed that the protected factor was not significant for any of the 3 types of variables, but it was significant for the factors locality and site in all variables together and for benthic cover, as well as for the factors site in habitat heterogeneity and complexity (Table S4). In addition, PCA used to identify how the variables are distributed spatially in each sample revealed that the samples of CAR and ANMP differ more from one another but are more similar to the samples of PPR. Variables such as rugosity, slope, depth, and % cover of HCOR, EPAM, and reef, which are more related to the ANMP samples, were also observed, as well as sand and gravel, which are more related to CAR. Moreover, the first two axes explained 33% of the variance of these variables (Figure 8).

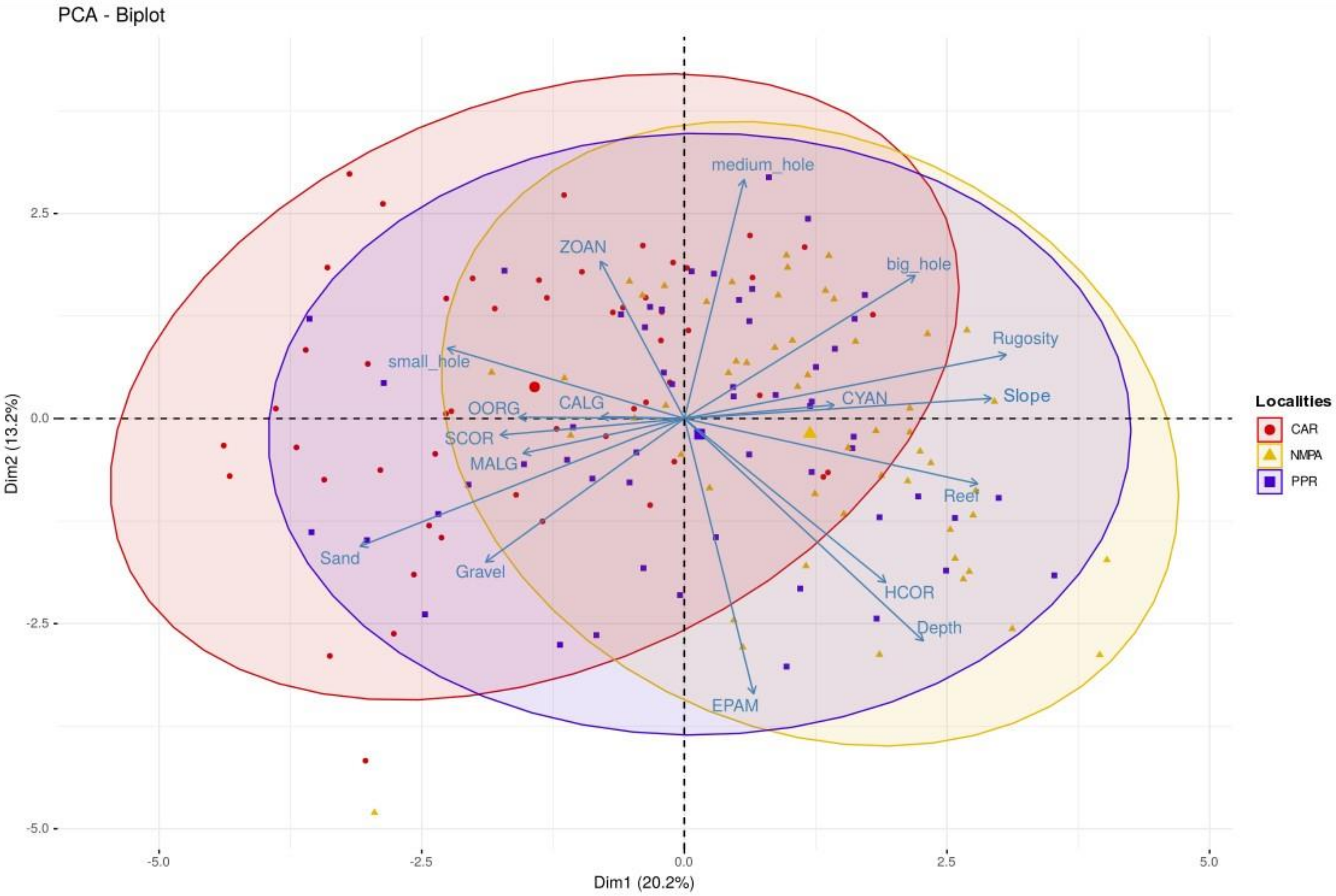


Figure 8. PCA showing the multivariate ordination for the environmental variables and samples of each locality by principal component analyses. Dim 1 and dim 2 represent the two principal axes, with variation explained in the values in parentheses.

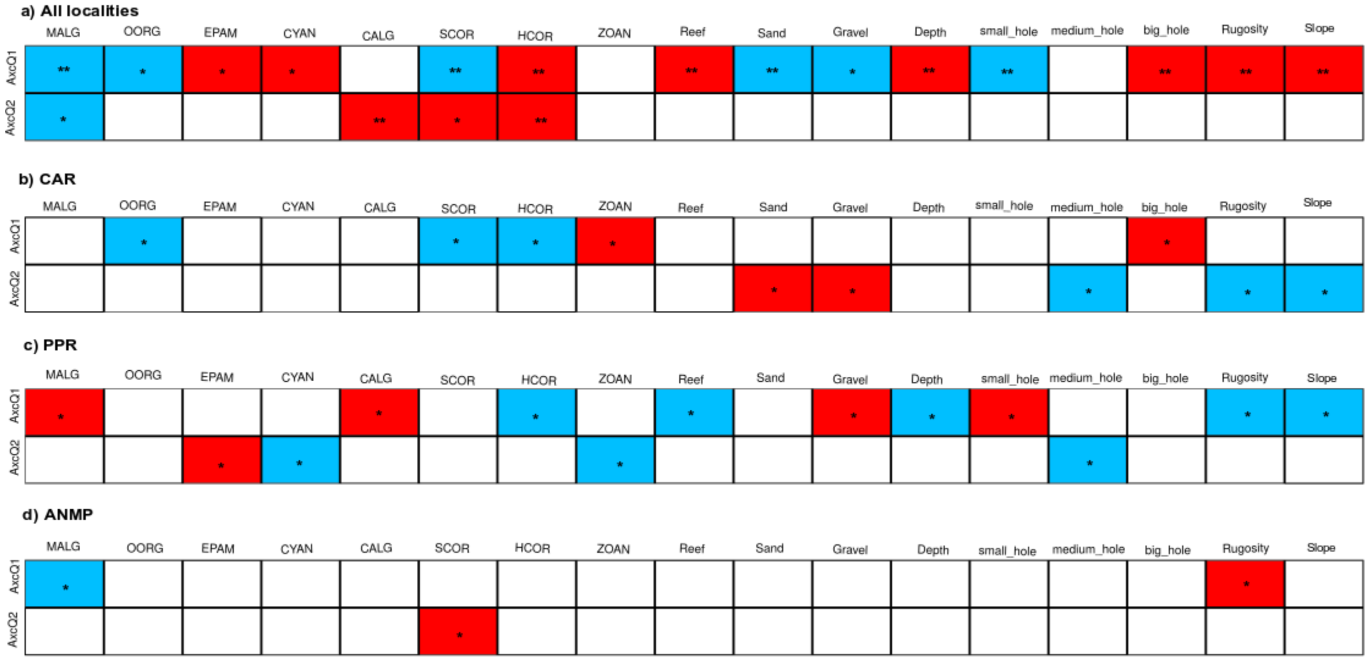
In contrast, these environmental variables were related to the functional traits and biomass of the species using RLQ analysis, revealing that the first two axes of RLQ analysis explained 55%, 70%, and 62% of variance for CAR, PPR, and ANMP, respectively, and explained 72% for all the localities together (Table 2). According to co-inertia analyses, the functional traits that most explain the variance were trophic groups, with 35.7%, 34.6%, 45.8%, and 43.9% for CAR, PPR, and ANMP and all localities together. However, for CAR, PPR, and all localities, the other trait that most explained the variance was spatial category, with 30.55%, 28%, and 23.3%, respectively, while for ANMPA, the other 4 traits explained more or less the same, varying between 13% and 15% (Table S5). Also according to co-inertia analysis, the percentage of benthic cover was the group of environmental variables that best explained this cover in CAR and ANMP, with 50.6% and 51.1%, respectively, while complexity was the environmental variable that best explained cover for PPR, with 40.2%. Considering all the localities together, cover explained 44.7% and complexity explained

38.9% (Table S5). The fourth-corner test combined with RLQ analysis showed a significant relationship between biomass distribution and all the localities, CAR, PPR, and ANMP (model 2), but no relationship between biomass distribution and biological traits (model 4). Moreover, no significant bivariate correlation was found between the specific category of traits and environmental variables (model 6) for any of the localities (Table 2).

Table 2. Summary of RLQ analysis for all localities and each locality, for the relationship between environmental variables and traits, evaluated for the biomass matrix log(x+1) transformed and traits. ***: *p* ≤0.001, **: *p* ≤0.01, *: *p* ≤0.05.

| | All localities | | CAR | | PPR | | ANMP | |
|---|---|---|---|---|---|---|---|---|
| | RLQ 1 | RLQ 2 | RLQ 1 | RLQ 2 | RLQ 1 | RLQ 2 | RLQ 1 | RLQ 2 |
| Correlation (L) | 0.252 | 0.205 | 0.238 | 0.231 | 0.257 | 0.185 | 0.225 | 0.184 |
| Projected inertia | 54.3 | 17.7 | 30.1 | 24.8 | 50.0 | 20.3 | 44.6 | 17.3 |
| Co-inertia axis (R) | 0.966 | 0.818 | 0.587 | 0.780 | 0.949 | 0.933 | 0.815 | 0.677 |
| Co-inertia axis (Q) | 0.504 | 0.644 | 0.671 | 0.624 | 0.616 | 0.674 | 0.544 | 0.626 |
| Total inertia | 0.664 | | 0.8881 | | 0.8945 | | 0.563 | |
| Model 2 | **0.001** | | **0.001** | | **0.00002** | | **0.034** | |
| Model 4 | 0.076 | | 0.401 | | 0.316 | | 0.550 | |
| Model 6 | 0.073 | | 0.366 | | 0.323 | | 0.532 | |

Nevertheless, for the first two axes of RLQ for trait and environmental variables, the fourth-corner test showed that the first trait axis (AxcQ1) of all localities was significant and negatively correlated with macroalgae, other organisms, soft coral, sand, gravel, and small holes and positively correlated with ephilitical algal matrix, cyanobacteria, hard coral, reef, depth, big holes, rugosity, and slope, while the second trait axis (AxcQ2) was negatively correlated with macroalgae and positively correlated with calcareous algae, soft coral, and hard coral. Moreover, AxcQ1 significantly and negatively correlated with other organisms, soft coral, and hard coral and positively correlated with zoanthid and big holes for CAR, while AxcQ2 significantly and negatively correlated with medium holes, rugosity, and slope and positively correlated with sand and gravel. Similarly, for PPR, AxcQ1 significantly negatively correlated with hard coral, reef, depth, rugosity, and slope and positively correlated with macroalgae, calcareous algae, gravel, and small holes, while AxcQ2 significantly negatively correlated with cyanobacteria, zoanthid, and medium holes and positively correlated with ephilitical algal matrix. Moreover, for ANMP, AxcQ1 negatively correlated with macroalgae and positively correlated with rugosity, while AxcQ2 only significantly positively correlated with soft coral (Table S6, Figure 9). This same test applied to the RLQ axes in environmental gradients and traits (AxcR1 and AxcR2) only showed a positive correlation of the pelagic (r: 0.17, *p*-value adjusted: 0.031) and piscivore (r: 0.18, *p*-value adjusted: 0.031) categories for AxcR1 in CAR.



**a) All localities**

| | MALG | OORG | EPAM | CYAN | CALG | SCOR | HCOR | ZOAN | Reef | Sand | Gravel | Depth | small_hole | medium_hole | big_hole | Rugosity | Slope |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| AxcQ1 | 🟦 ** | 🟦 * | 🟥 * | 🟥 * | | 🟦 ** | 🟥 ** | | 🟥 ** | 🟦 ** | 🟦 * | 🟥 ** | 🟦 ** | | 🟥 ** | 🟥 ** | 🟥 ** |
| AxcQ2 | 🟦 * | | | | 🟥 ** | 🟥 * | 🟥 ** | | | | | | | | | | |

**b) CAR**

| | MALG | OORG | EPAM | CYAN | CALG | SCOR | HCOR | ZOAN | Reef | Sand | Gravel | Depth | small_hole | medium_hole | big_hole | Rugosity | Slope |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| AxcQ1 | | 🟦 * | | | | 🟦 * | 🟦 * | 🟥 * | | | | | | | 🟥 * | | |
| AxcQ2 | | | | | | | | | | 🟥 * | 🟥 * | | | 🟦 * | | 🟦 * | 🟦 * |

**c) PPR**

| | MALG | OORG | EPAM | CYAN | CALG | SCOR | HCOR | ZOAN | Reef | Sand | Gravel | Depth | small_hole | medium_hole | big_hole | Rugosity | Slope |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| AxcQ1 | 🟥 * | | | | 🟥 * | | 🟦 * | | 🟦 * | | 🟥 * | 🟦 * | 🟥 * | | | 🟦 * | 🟦 * |
| AxcQ2 | | | 🟥 * | 🟦 * | | | | 🟦 * | | | | | | 🟦 * | | | |

**d) ANMP**

| | MALG | OORG | EPAM | CYAN | CALG | SCOR | HCOR | ZOAN | Reef | Sand | Gravel | Depth | small_hole | medium_hole | big_hole | Rugosity | Slope |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| AxcQ1 | 🟦 * | | | | | | | | | | | | | | | 🟥 * | |
| AxcQ2 | | | | | | 🟥 * | | | | | | | | | | | |

Figure 9. Fourth-corner tests between the first two RLQ axes for trait syndromes (AxQ1 and AxQ2) and a) all localities, b) Cassuruba Reef (CAR), c) Parcel das Paredes Reef (PPR), and d) National Marine Park of Abrolhos (ANMP). Colored squares show significant associations (red = positive; blue = negative), while no significant associations are shown in white. *P* values were adjusted for multiple comparisons using the FDR. MALG: macroalgae, OORG: other organisms, EPAM: ephilitical algal matrix, CYAN: cyanobacteria, CALG: calcareous algae, SCOR: soft coral, HCOR: hard coral, and ZOAN: zoanthid. **: *p* ≤0.01, *: *p* ≤0.05

## Discussion

This study evaluated the effect of protection using an experimental design on functional diversity by tropical reef fish in the Abrolhos Bank region. The purpose of the present study was to test, on a regional and/or local scale, the hypothesis proposed by Hernandez-Andreu et al. (in press), which suggests that all the functional space is represented in the protected areas. According to our results, the functional space was the same in protected and open areas. However, in our study, functional richness was higher in ANMP, which may indicate that resources are being better exploited by the functional groups in protected areas than in unprotected areas, possibly due to a decrease in marine fishery catches (Trindade-Santos et al. 2020). In contrast, PPR and CAR showed higher values of functional evenness than ANMP, indicating that the functional niche may be occupied but not fully utilized (Mason et al. 2005). Moreover, we found that the functional originality was different on a small spatial scale for the sampled sites, although the sites of the unprotected areas were on average greater than those of ANMP and the species were functionally more similar (Villéger et al. 2008; Buisson et al. 2013) between these protected sites, which can mean more redundancy. However, this higher originality in sites of unprotected areas may be the result of less redundancy of species, some of which could have unique functions (Brandl et al. 2016).

In terms of functional space and functional diversity indices, the functions seem to be effectively protected; however, Coleman et al. (2015) did not find these differences between protected and unprotected communities for traditional multimetric diversity indices, although they do highlight the importance of functional traits in early conservation results.

The Brazilian coral reef fish communities are characterized by different rare species throughout the coast with shared dominant and common species locally and regionally (Araújo et al. 2020). This characteristic can directly influence the functional diversity of the fish communities since the loss of rare species can lead to less redundancy (Teichert et al. 2017) or loss of unique functional entities. Araújo et al. (2020) propose that these species should be a priority in the management and design of MPAs by critical genetic pools. In this study, we sought to explore the relationship between rare, common, and dominant species with indices of functional diversity in protected and unprotected areas. We found that both Abrolhos National Marine Park and the two unprotected areas exhibit an increase in functional richness with the increase in the number of rare, common, and dominant species, although this trend is greater with rare species and within the MPA. This result may indicate that common and dominant species have greater competition for resources outside these areas, while within this MPA, the resources are greater and there is no such competition. However, rare species take advantage of resources in the same way regardless of protection. Moreover, the functional dispersion that increased with the increase of rare species confirming that rare species promoted greater functional diversity in ANMP since they have greater heterogeneity of traits for the fish community, resulting in less competition for resources among these species. However, we found niche differentiation, although the use of resources decreases with the increase of rare, common, and dominant species in unprotected areas, which only occurs with dominant species in ANMP, as shown by the functional divergence value. Furthermore, functional specialization decreased with the increase of common and dominant species in the unprotected areas, indicating that the community of these areas tends to comprise more generalist species with the increase of common and dominant species. This also occurs with the common and dominant species of the unprotected areas and common species in ANMP that tend toward lower functional originality, which suggests that these species provide redundancy to the community in these different areas. With the increase in the number of rare, common, and dominant species in ANMP, functional evenness decreases, whereas with an increase in number of dominant species in unprotected areas, functional evenness increases. In principle, this suggests that when the number of species increases, productivity is lower, the species are not taking full advantage of the niche, or there is some type of disturbance. Since biomass data was used in this case and higher biomass was observed in ANMP, a less regular community may be the answer. Legras and Gaertner (2018) discuss the precautions to consider with this index and state that the increase does not always equate to a greater regularity of branch length or abundance distribution, just as the value 1 of this index does not always have to indicate perfect inter-species regularity. Although significant differences were observed for the protection factor in our models, the percentage of variation was usually 0.

Our results showed that the biomass of grazer herbivores, piscivores, and planktivores responds to protection. The higher biomass of these groups may be related to the prohibition of extractive activities such as fishing and may signal a stable structure in the ecosystem due to the stability of the trophic web in this protected area. However, from a functional perspective, only the planktivores would be "safe" and in equilibrium within these areas due to a redundancy of trophic group, which, in the event of a disturbance, would not be compromised by the loss of a planktivore species because another would be performing that function.

In contrast, our results did not show differences in environmental variables for protection, although differences were found between localities for all variables together and benthic cover and for sites for all the environmental variables together and the three variables separately. This result indicates that the benthic cover has an important weight in these environmental variables on a larger scale, such as locality, although it also has an effect on a smaller scale, such as the heterogeneity and complexity of the habitat. According to Yeager et al. 2017, there is evidence that the scale of environmental filtering (large scale) and biotic interactions (smaller scale) influences functional diversity.

Theoretically, functional traits are expected to influence the compositional patterns of the distribution of reef species in some way. Although these traits are associated with some environmental conditions, species distribution in each locality and all localities together is determined only by environmental variables and not by functional traits. For the traits addressed in this study, when each category of each trait was directly evaluated to find a relationship with the environmental variables, a relationship was not found for each category with the environmental variables, although environmental filtering in each locality proved important for reef fish distribution. However, a relationship between the axes of the RLQ was observed for trait gradients and some environmental conditions, thus establishing a non-random relationship that suggests environmental drivers play a direct role in community structure (Cadotte 2017). Rugosity, for example, is an environmental variable that positively affects the trait gradient in ANMP. In CAR and PPR, however, rugosity was negative, possibly due to the positive relationship of these localities with the percentage of sand and gravel, which are habitats with less rugosity. In terms of scale, from a regional point of view, zoanthid or small holes, for example, did not have a significant influence, although this influence was observed for CAR and PPR separately. Curiously, scale was also important to identify a relationship between a gradient of environmental variables and some traits, as observed with the positive and significant relationship of the categories of pelagic and piscivores with the first axis of the gradient of environmental variables in CAR.

This environmental filter may also occur with other types of traits more related to life history such as life cycle, larval settlement time, and number of eggs, as, in the initial stages, there is a greater number of environmental variables and other factors. In the results found, these particularities of the environmental conditions in each locality may be favoring the realization of the niches because they may be limiting similarities between species and thereby benefiting the functioning of the communities (Frelat et al. 2018). As Cadotte and Tucker (2017) suggest, results such as those observed in this study on environmental filters may be due to the combination between local environmental conditions and local effects of competition, although these should not influence how the community is structured based on the role of environmental variables. In addition to competition, mechanisms such as exploration trophic interactions can also influence this composition (Cadotte & Tucker 2017). All the points revealed so far, such as community composition, functional relationships, trait-environmental relationships, environmental conditions and filters, and ecological interactions, among others, are important to understand the functioning of the ecosystem.

In this regard, we may need to ask the following questions: what are the main ecological functions needed to achieve these ecological goals? Are the existing functions sufficient to maintain an equilibrated and resilient ecosystem? Are these traits sufficient to explain the functionality or would it be important to include other aspects of the species such as life strategies? How can different habitats in a community influence traits? To answer these questions, a broader approach than the one presented here is needed. In recent years, methodologies such as environmental DNA have revealed the potential of this technique compared to the classical visual census in terms of species richness, diversity, and community composition (Nguyen et al. 2020; Boulanger et al. 2021; Polanco Fernández et al. 2021). There is also a greater number of studies with a seascape perspective. In this regard, a combination of both techniques and a seascape perspective could help answer these questions.

According to recent studies in the same study area as this study, MPAs without fisheries management cannot protect ecologically key species for ecosystem functioning, such as the species Scarus trispinosus (Roos et al. 2020). Some authors found that MPAs harbor important breeding habitats for this species, but the population continues to decrease, which is probably due to overfishing in nearby areas and non-compliance with MPA fishing rules (Roos et al. 2020). Moreover, as also pointed out by Azzurro et al. (2010), Guidetti et al. (2003), Munday (2004), and Munday et al. (2010), the use of ecosystem functionality to strengthen population monitoring and establish fishery regulations is critical, together with the expansion and creation of more MPAs and no-take zones. It is also important to incorporate all ecosystem functions and improve control measures in these areas to prevent direct anthropogenic impacts on the distribution and trait composition of fish species (D'Agata et al.

2014; Henriques et al. 2014). Some authors stress the importance of finding areas where the effectiveness of MPAs can encompass multiple objectives such as protect the evolutionary history and diversity of traits and minimize the risk of species extinction (Sala et al. 2021). Biodiversity is important for the ecosystem function, however, most of the MPAs are designed to protect some endangered species, key species, and traditional or cultural activity from the ecological and ethnoecological standpoint, but they are rarely designed or managed for any set of interactions that occur between the species and their functional role in the ecosystem and with these anthropogenic activities. In recent studies, Magris et al. 2021 reveal the accumulated impact on the coast, islands, and Brazilian EEZ and the need to expand marine reserves in Brazil in order to minimize current anthropogenic impacts and possible future impacts. Among the zones evaluated in the previous study, in this study, we evaluated the priority zones for the creation of new MPAs in Abrolhos Bank and expansion of ANMP. We believe that the results presented in this study could provide a functional point of view for the future creation and expansion of these areas. The ecosystem functions as a whole, therefore, it cannot be limited to the protection of functional groups or species (Bellwood et al. 2019). From a functional perspective, the management, monitoring, expansion, and creation of an MPA and/or NTZ should focus on the functions of organisms in the ecosystem.

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## Supplementary Material

Table S1. Biological functional traits, traits categories, units, type of variable and references used to defined the functional indices that describe ecological functioning in reef fish assemblages.

| Functional Traits | Trait Category | Unit | Description | Reference |
|---|---|---|---|---|
| Trophic Category | Diet | Herbivore (HBT) | Feeding on plant with a territorial behavior | Bellwood et al., 2019; (Floeter et al. 2018); (Halpern & Floeter 2008) |
| | | Herbivore grazer (HGRZ) | Feeding on superficial reef matrix | |
| | | Herbivore scraper (HSCP) | Feeding on reef matrix | |
| | | Omnivore (OMNI) | Feeding plants and animals item | |
| | | General invertivore (GINV) | Feeding general invertebrates | |
| | | Mobile invertivore (MINV) | Feeding mobile benthic invertebrates | |
| | | Obligate corallivore (OC) | Feeding hard corals and some on soft coral | |
| | | Cleaner (CLE) | Feeding others animals organisms (ex ectoparasites) | |
| | | Planktivore (PLNK) | Feeding plakton organisms | |
| | | General Carnivore (GCAR) | Feeding invertebrates (ex. mollusc) and fish | |
| | | Piscivore (PISC) | Feeding strictly fish | |
| Maximum length | Morphology | Very small | <8 | Forese & Pauly, 2020 * |
| | | Small | 8.1-15.9 | |
| | | Medium | 16-30.9 | |
| | | Medium-Large | 31-50.9 | |
| | | Large | 51-80.9 | |
| | | Very Large | >81 | |
| Resilience | Life history | Very low | | Musick, 1999, Forese & Pauly, 2020* |
| | | Low, | | |
| | | Medium | | |
| | | High | | |
| | | Very high | | |
| Gregariousness | Life history | Solitary | 1 individual | Mouillot et al., 2014 |
| | | Pair | 2 individuals | |
| | | Small – medium | 3-50 individuals | |
| | | Large | >50 individual | |
| Spatial Category | Habitat | Pelagic/reef associated | | Harmelin, 1987 |
| | | Necktonic/reef associated | | |
| | | Benthonic/reef associated | | |
| | | Demersal/reef associated | | |
| | | Benthonic/reef attached | | |
| | | Demersal/reef attached | | |

Table S2. Functional traits and absence / presence information for each one species

| Specie | Codesp | Functional traits | | | | | Localities | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Spatial category | Trophic category | Resilience | Lmax | Gregariouness | ANMP | CAR | PPR |
| Abudefduf saxatilis | ABUSAX | Nektonic/Reef Associated | OMNI | Medium | Medium | Large | x | x | x |
| Acanthurus bahianus | ACABAH | Benthic/Reef Associated | HGRZ | High | Medium-Large | Large | x | x | x |
| Acanthurus chirurgus | ACACHI | Benthic/Reef Associated | HGRZ | Medium | Medium-Large | Large | x | x | x |
| Acanthurus coeruleus | ACACOE | Benthic/Reef Associated | HGRZ | Medium | Medium-Large | Small-medium | x | x | x |
| Alphestes afer | ALPAFE | Benthic/Reef Attached | GCAR | High | Medium-Large | Solitary | - | x | - |
| Aluterus scriptus | ALUSCR | Benthic/Reef Associated | OMNI | Medium | Very Large | Solitary | - | - | x |
| Anisotremus surinamensis | ANISUR | Benthic/Reef Attached | GCAR | Low | Large | Small-medium | - | - | x |
| Anisotremus virginicus | ANIVIR | Benthic/Reef Associated | MINV | Medium | Medium-Large | Small-medium | x | x | x |
| Balistes vetula | BALVET | Benthic/Reef Associated | GINV | Medium | Large | Solitary | x | - | - |
| Bodianus rufus | BODRUF | Benthic/Reef Associated | MINV | Medium | Medium-Large | Solitary | x | - | - |
| Calamus penna | CALPEN | Demersal/Reef Associated | MINV | High | Medium-Large | Solitary | - | x | x |
| Canthigaster figueiredoi | CANFIG | Demersal/Reef Associated | OMNI | High | Small | Pair | x | - | - |
| Cantherhines macrocerus | CANMAC | Benthic/Reef Associated | OMNI | Medium | Medium-Large | Pair | x | - | - |
| Cantherhines pullus | CANPUL | Benthic/Reef Associated | OMNI | High | Medium | Solitary | x | - | x |
| Carangoides bartholomaei | CARBAR | Pelagic/Reef Associated | PISC | High | Very Large | Small-medium | x | x | - |
| Caranx crysos | CARCRY | Pelagic/Reef Associated | GCAR | Medium | Large | Small-medium | x | x | - |
| Carcharhinus perezi | CARPER | Benthic/Reef Associated | PISC | Low | Very Large | Solitary | x | - | - |
| Caranx ruber | CARRUB | Nektonic/Reef Associated | GCAR | Medium | Large | Small-medium | x | - | - |
| Chaetodipterus faber | CHAFAB | Nektonic/Reef Associated | GCAR | Medium | Very Large | Large | - | x | - |
| Chaetodon ocellatus | CHAOCE | Benthic/Reef Attached | MINV | High | Medium | Pair | x | - | - |
| Chaetodon striatus | CHASTR | Benthic/Reef Attached | OMNI | High | Medium | Pair | x | x | x |
| Chilomycterus spinosus spinosus | CHISPI | Benthic/Reef Attached | GINV | Medium | Medium | Solitary | - | - | x |
| Coryphopterus glaucofraenum | CORGLA | Demersal/Reef Attached | OMNI | High | Very Small | Solitary | x | x | x |
| Coryphopterus thrix | CORTHR | Demersal/Reef Attached | OMNI | High | Very Small | Solitary | x | x | x |
| Cryptotomus roseus | CRYROS | Benthic/Reef Attached | HGRZ | High | Small | Small-medium | x | x | - |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Doratonotus megalepis | DORMEG | Demersal/Reef Associated | GINV | High | Small | Solitary | - | x | x |
| Echeneis naucrates | ECHNAU | Pelagic/Reef Associated | CLE | Medium | Very Large | Solitary | x | - | - |
| Elacatinus figaro | ELAFIG | Demersal/Reef Attached | CLE | High | Very Small | Small-medium | x | x | x |
| Emblemariopsis signifer | EMBSIG | Demersal/Reef Attached | MINV | Low | Very Small | Solitary | x | x | x |
| Epinephelus itajara | EPIITA | Benthic/Reef Associated | GCAR | Low | Very Large | Solitary | x | - | - |
| Epinephelus morio | EPIMOR | Benthic/Reef Associated | GCAR | Medium | Very Large | Solitary | x | x | x |
| Gramma brasiliensis | GRABRA | Demersal/Reef Attached | PLNK | High | Very Small | Solitary | x | x | x |
| Gymnothorax funebris | GYMFUN | Demersal/Reef Attached | GCAR | Very Low | Very Large | Solitary | - | - | x |
| Gymnothorax moringa | GYMMOR | Demersal/Reef Attached | GCAR | Low | Very Large | Solitary | x | x | x |
| Gymnothorax vicinus | GYMVIC | Demersal/Reef Attached | GCAR | Very Low | Very Large | Solitary | x | - | - |
| Haemulon aurolineatum | HAEAUR | Nektonic/Reef Associated | OMNI | Medium | Medium | Large | x | x | x |
| Haemulon parra | HAEPAR | Benthic/Reef Associated | GCAR | Medium | Medium-Large | Large | x | x | x |
| Haemulon plumierii | HAEPLU | Benthic/Reef Associated | GCAR | Medium | Large | Small-medium | x | x | x |
| Haemulon squamipinna | HAESQU | Benthic/Reef Associated | MINV | High | Small | Small-medium | x | - | - |
| Haemulon steindachneri | HAESTE | Benthic/Reef Associated | GCAR | Medium | Medium | Small-medium | - | x | - |
| Halichoeres brasiliensis | HALBRA | Benthic/Reef Associated | GINV | Medium | Medium-Large | Solitary | x | x | x |
| Halichoeres poeyi | HALPOE | Benthic/Reef Attached | GINV | Medium | Medium | Solitary | x | x | x |
| Holocentrus adscensionis | HOLADS | Benthic/Reef Attached | GCAR | Medium | Large | Solitary | x | x | x |
| Holacanthus ciliaris | HOLCIL | Benthic/Reef Associated | OMNI | Low | Medium-Large | Pair | x | x | x |
| Hypanus americanus | HYPAME | Demersal/Reef Associated | GCAR | Very Low | Very Large | Solitary | - | x | - |
| Hypleurochilus pseudoaequipinnis | HYPPSE | Demersal/Reef Attached | MINV | High | Very Small | Solitary | - | - | x |
| Kyphosus sp | KYPSP | Benthic/Reef Associated | HGRZ | Low | Large | Small-medium | x | - | - |
| Labrisomus nuchipinnis | LABNUC | Demersal/Reef Attached | GCAR | Medium | Medium | Solitary | x | x | - |
| Lutjanus alexandrei | LUTALE | Benthic/Reef Associated | GCAR | Medium | Medium | Solitary | x | x | - |
| Lutjanus analis | LUTANA | Benthic/Reef Associated | GCAR | Low | Very Large | Small-medium | x | x | - |
| Lutjanus jocu | LUTJOC | Benthic/Reef Associated | GCAR | Low | Very Large | Solitary | x | x | x |
| Lutjanus synagris | LUTSYN | Benthic/Reef Associated | GCAR | Medium | Large | Large | - | x | x |
| Malacoctenus delalandii | MALDEL | Demersal/Reef Attached | MINV | Medium | Small | Solitary | x | x | x |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Malacoctenus zaluaris | MALZAL | Demersal/Reef Attached | MINV | Medium | Very Small | Solitary | x | x | x |
| Microspathodon chrysurus | MICCHR | Demersal/Reef Attached | HBTE | Medium | Medium | Solitary | x | - | - |
| Mycteroperca bonaci | MYCBON | Benthic/Reef Associated | PISC | Medium | Very Large | Solitary | x | x | x |
| Ocyurus chrysurus | OCYCHR | Nektonic/Reef Associated | GCAR | Medium | Very Large | Small-medium | x | x | x |
| Odontoscion dentex | ODODEN | Nektonic/Reef Associated | GINV | High | Medium | Small-medium | - | x | - |
| Ogcocephalus vespertilio | OGCVES | Demersal/Reef Attached | MINV | Low | Medium | Solitary | - | - | x |
| Ophioblennius trinitatis | OPHTRI | Demersal/Reef Attached | OMNI | High | Very Small | Solitary | - | x | x |
| Pareques acuminatus | PARACU | Demersal/Reef Attached | GINV | High | Medium | Small-medium | x | - | x |
| Parablennius marmoreus | PARMAR | Demersal/Reef Associated | OMNI | High | Very Small | Solitary | x | x | x |
| Parablennius pilicornis | PARPIL | Demersal/Reef Associated | OMNI | High | Small | Solitary | x | x | - |
| Pomacanthus arcuatus | POMARC | Benthic/Reef Associated | OMNI | Very Low | Large | Pair | x | x | x |
| Pomacanthus paru | POMPAR | Benthic/Reef Associated | OMNI | Medium | Medium-Large | Pair | x | x | x |
| Pseudocaranx dentex | PSEDEN | Pelagic/Reef Associated | GCAR | Medium | Very Large | Small-medium | - | x | - |
| Pseudupeneus maculatus | PSEMAC | Demersal/Reef Associated | MINV | High | Medium | Small-medium | x | x | x |
| Rypticus saponaceus | RYPSAP | Benthic/Reef Attached | GCAR | Medium | Medium-Large | Solitary | x | - | - |
| Scartella cristata | SCACRI | Demersal/Reef Attached | HBTE | High | Small | Solitary | x | - | - |
| Scarus trispinosus | SCATRI | Benthic/Reef Associated | HSCP | Medium | Large | Small-medium | x | x | x |
| Scarus zelindae | SCAZEL | Benthic/Reef Associated | HSCP | High | Medium-Large | Small-medium | x | - | x |
| Scomberomorus cavalla | SCOCAV | Pelagic/Reef Associated | GCAR | Medium | Very Large | Large | x | - | - |
| Serranus flaviventris | SERFLA | Demersal/Reef Attached | GINV | High | Very Small | Solitary | x | x | x |
| Sparisoma amplum | SPAAMP | Benthic/Reef Associated | HSCP | High | Medium-Large | Small-medium | x | - | x |
| Sparisoma axillare | SPAAXI | Benthic/Reef Associated | HSCP | Medium | Medium-Large | Large | x | x | x |
| Sparisoma frondosum | SPAFRO | Benthic/Reef Associated | HSCP | Medium | Medium-Large | Small-medium | x | x | x |
| Sparisoma radians | SPARAD | Benthic/Reef Associated | HBRW | High | Medium | Solitary | x | x | - |
| Sphyraena barracuda | SPHBAR | Pelagic/Reef Associated | GCAR | Low | Very Large | Solitary | x | - | - |
| Stegastes fuscus | STEFUS | Demersal/Reef Attached | HBTE | Medium | Small | Solitary | x | x | x |
| Stegastes pictus | STEPIC | Demersal/Reef Attached | PLNK | High | Very Small | Solitary | x | - | x |
| Stegastes variabilis | STEVAR | Demersal/Reef Attached | HBTE | High | Small | Solitary | x | x | x |

|  |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|
| Synodus intermedius | SYNINT | Demersal/Reef Associated | GCAR | Medium | Medium-Large | Solitary | x | x | - |
| Synodus synodus | SYNSYN | Demersal/ Reef Associated | GCAR | Medium | Medium-Large | Solitary | - | - | x |

Table S3. Generalized Additive Model (GAM) summary for to evaluate the relationship between the indices of taxonomic diversity and functional diversity. e.d.f., Estimated degrees of freedom, q0: diversity rare species; q1: diversity common species; q2: diversity dominant species, FRic: Fuctional Richness; FEve: Functional Evenness; FDiv: Functional Divergence; FDis: Functional Dispersion; FSpe: Functional Specialization; and FOri: Functional Originality.

| Model | Coefficients | (Std. Error) | t/z (F/Chi.sq) -value | p-value | Adj. R-square | e.d.f. |
|---|---|---|---|---|---|---|
| FRic ~ *f* (q0, by= prot), family =Gamma (link = "log") | Intercept | -2.49 (0.04) | -67.3 | < 0.001*** | 0.74 |  |
|  | q0 (PROT) |  | 53.2 | < 0.001*** |  | 2.480 |
|  | q0 (UNPR) |  | 59.2 | < 0.001*** |  | 3.638 |
| FRic ~ *f* (q1, by= prot), family =Gamma (link = "log") | Intercept | -2.33 (0.05) | -43.2 | < 0.001*** | 0.32 |  |
|  | q1 (PROT) |  | 6.7 | < 0.001*** |  | 1.88 |
|  | q1 (UNPR) |  | 6.5 | 0.001** |  | 4.12 |
| FRic ~ *f* (q2, by= prot), family =Gamma (link = "log") | Intercept | -2.28 (0.06) | -41.3 | < 0.001*** | 0.13 |  |
|  | q2 (PROT) |  | 3.61 | 0.028* |  | 2.09 |
|  | q2 (UNPR) |  | 5.31 | 0.022* |  | 1.00 |
| FEve ~ *f* (q0, by= prot), family =Gamma(link = "log") | Intercept | -0.94 (0.037) | -25.63 | < 0.001*** | 0.04 |  |
|  | q0 (PROT) |  | 14.8 | < 0.001*** |  | 1 |
|  | q0 (UNPR) |  | 1.4 | 0.235 |  | 1 |
| FEve ~ *f* (q1, by= prot), family =Gamma (link = "log") | Intercept | -0.95 (0.036) | -26.68 | < 0.001*** | 0.07 |  |
|  | q1 (PROT) |  | 6.53 | 0.012* |  | 1 |
|  | q1 (UNPR) |  | 2.76 | 0.052 |  | 2.49 |
| FEve ~ *f* (q2, by= prot), family =Gamma (link = "log") | Intercept | -0.951 (0.035) | -27.08 | < 0.001*** | 0.08 |  |
|  | q2 (PROT) |  | 5.04 | 0.026* |  | 1 |
|  | q2 (UNPR) |  | 10.88 | 0.001** |  | 1 |
| FDiv ~ *f* (q0, by= prot), family = betar (link = "logit") | Intercept | 1.52 (0.066) | 23.2 | < 0.001*** | 0.021 |  |
|  | q0 (PROT) |  | 2.95 | 0.107 |  | 1.30 |
|  | q0 (UNPR) |  | 4.17 | 0.041* |  | 1 |
| FDiv ~ *f* (q1, by= prot), family = betar (link = "logit") | Intercept | 1.53 (0.06) | 23.94 | < 0.001*** | 0.04 |  |
|  | q1 (PROT) |  | 3.00 | 0.08 |  | 1 |
|  | q1 (UNPR) |  | 10.72 | 0.001** |  | 1 |
| FDiv ~ *f* (q2, by= prot), family = betar (link = "logit") | Intercept | 1.54 (0.06) | 24.3 | < 0.001*** | 0.06 |  |
|  | q2 (PROT) |  | 4.44 | 0.03* |  | 1 |
|  | q2 (UNPR) |  | 12.50 | 0.014* |  | 3.44 |
| FDis ~ *f* (q0, by= prot), family = betar (link = "logit") | Intercept | -0.31 (0.045) | -6.91 | < 0.001*** | 0.04 |  |
|  | q0 (PROT) |  | 8.10 | 0.004 ** |  | 1 |
|  | q0 (UNPR) |  | 1.61 | 0.202 |  | 1 |

|  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|
| FDis ~ *f* (q1, by= prot), family = betar (link = "logit") | Intercept | -0.30 (0.045) | -6.6 | < 0.001*** | -0.01 |  |
|  | q1 (PROT) |  | 0.473 | 0.608 |  | 1 |
|  | q1 (UNPR) |  | 0.268 | 0.647 |  | 1.05 |
| FDis ~ *f* (q2, by= prot), family = betar (link = "logit") | Intercept | -0.30 (0.045) | -6.59 | < 0.001*** | - |  |
|  | q2 (PROT) |  | 0.009 | 0.979 |  | 1.1 |
|  | q2 (UNPR) |  | 0.010 | 0.923 |  | 1 |
| FSpe ~ *f* (q0, by= prot), family =Gamma(link = "log") | Intercept | -0.50 (0.02) | -42.15 | < 0.001*** | 0.04 |  |
|  | q0 (PROT) |  | 0.536 | 0.750 |  | 1.86 |
|  | q0 (UNPR) |  | 1.959 | 0.102 |  | 3.23 |
| FSpe ~ *f* (q1, by= prot), family =Gamma (link = "log") | Intercept | -0.50 (0.01) | -45.81 | < 0.001*** | 0.1 |  |
|  | q1 (PROT) |  |  | 0.244 |  | 1 |
|  | q1 (UNPR) |  |  | 0.018* |  | 3.95 |
| FSpe ~ *f* (q2, by= prot), family =Gamma (link = "log") | Intercept | -0.50 (0.01) | -46.73 | < 0.001*** | 0.12 |  |
|  | q2 (PROT) |  | 1.403 | 0.237 |  | 1.0 |
|  | q2 (UNPR) |  | 3.45 | 0.005 ** |  | 4.32 |
| FOri ~ *f* (q0, by= prot), family =Gamma(link = "log") | Intercept | -1.11 (0.03) | -32.04 | < 0.001*** | 0.03 |  |
|  | q0 (PROT) |  | 1.23 | 0.292 |  | 2.42 |
|  | q0 (UNPR) |  | 2.1 | 0.128 |  | 1.8 |
| FOri ~ *f* (q1, by= prot), family =Gamma (link = "log") | Intercept | -1.12 (0.03) | -38.38 | < 0.001*** | 0.22 |  |
|  | q1 (PROT) |  | 3.33 | 0.035** |  | 1.86 |
|  | q1 (UNPR) |  | 12.73 | < 0.001*** |  | 1.8 |
| FOri ~ *f* (q2, by= prot), family =Gamma (link = "log") | Intercept | -1.13 (0.03) | -39.36 | < 0.001*** | 0.26 |  |
|  | q2 (PROT) |  | 2.35 | 0.08 |  | 2.04 |
|  | q2 (UNPR) |  | 12.15 | < 0.001*** |  | 2.4 |

Table S4. PERMANOVA of protection level (P), locality (L) and sector (S) on environmental variables: all variables together, benthic cover, habitat heterogeneity and complexity. df: degrees of freedom.***: *p* ≤0.001, **: *p* ≤ 0.01, *: *p* ≤ 0.05.

| **Sources** | **df** | All variables |  | Benthic cover |  | Habitat heterogenity |  | Complexity |  |
|---|---|---|---|---|---|---|---|---|---|
|  |  | F | p | F | p | F | p | F | p |
| P | 1 | 0.86 | 0.572 | 0.29 | 0.859 | 7.01 | 0.077 | 1.87 | 0.389 |
| L (P) | 1 | 3.70 | **0.002**** | 6.74 | **0.002**** | 0.6 | 0.570 | 2.13 | 0.103 |
| S ((L (P)) | 24 | 3.20 | **0.0001***** | 6.28 | **0.0001***** | 3.6 | **0.0001***** | 2.01 | **0.0001***** |
| Residual | 133 |  |  |  |  |  |  |  |  |
| Total | 159 |  |  |  |  |  |  |  |  |

Table S5. Total inertia and relative contributions for two first axis of RLQ by individual functional trait and environmental variables for all localities together, Cassuruba reefs (CAR), Parcel das Paredes reef (PPR), Abrolhos National Marine Park (ANMP)

| Variable | All localities | | | CAR | | | PPR | | | ANMP | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Functional traits*** | Inertia (%) | Axis 1 (%) | Axis 2 (%) | Inertia (%) | Axis 1 (%) | Axis 2 (%) | Inertia (%) | Axis 1 (%) | Axis 2 (%) | Inertia (%) | Axis 1 (%) | Axis 2 (%) |
| Benthic reef associated | 1.1 | 1.05 | 0.44 | 1.92 | 0.39 | 4.58 | 1.04 | 0.002 | 0.78 | 0.34 | 0.15 | 0.39 |
| Benthic reef attached | 4.94 | 7.39 | 2.21 | 3.96 | 3.15 | 5.88 | 2.00 | 1.64 | 4.75 | 5.81 | 5.54 | 11.11 |
| Demersal reef associated | 6.8 | 8.50 | 0.06 | 7.14 | 2.81 | 9.46 | 10.68 | 18.85 | 4.04 | 0.94 | 0.07 | 0.249 |
| Demersal reef attached | 1.60 | 0.38 | 1.0 | 2.70 | 2.01 | 4.46 | 5.85 | 7.04 | 4.38 | 0.98 | 0.76 | 0.68 |
| Nectonik reef associated | 2.84 | 2.25 | 4.34 | 5.39 | 2.15 | 14.5 | 8.41 | 14.51 | 0.43 | 2.45 | 0.002 | 9.97 |
| Pelagic reef associted | 5.95 | 2.78 | 15.2 | 9.44 | 2.01 | 1.45 | - | - | - | 3.08 | 2.79 | 0.52 |
| Very low resilience | 1.86 | 0.11 | 6.24 | 2.54 | 1.55 | 0.003 | 3.01 | 4.61 | 0.05 | 6.40 | 1.22 | 15.51 |
| Low resilience | 2.72 | 0.73 | 7.05 | 1.04 | 0.04 | 3.01 | 1.91 | 0.20 | 2.69 | 4.44 | 2.82 | 1.14 |
| Medium resilience | 0.93 | 1.41 | 0.003 | 3.12 | 0.40 | 1.1 | 0.85 | 1.26 | 0.0001 | 0.45 | 0.008 | 1.14 |
| High resilience | 2.64 | 2.91 | 0.18 | 3.27 | 0.19 | 0.06 | 5.31 | 9.96 | 0.20 | 3.76 | 1.70 | 9.40 |
| Very small size | 1.11 | 0.31 | 0.23 | 2.60 | 0.69 | 3.65 | 3.00 | 0.31 | 0.43 | 1.57 | 0.07 | 0.004 |
| Small size | 1.30 | 0.04 | 1.88 | 1.54 | 2.20 | 0.09 | 3.18 | 0.70 | 7.49 | 0.35 | 1.74 | 1.72 |
| Medium size | 6.54 | 8.16 | 9.75 | 3.12 | 7.39 | 0.26 | 0.80 | 0.10 | 0.54 | 2.78 | 2.47 | 3.47 |
| Medium-large size | 2.15 | 3.10 | 0.25 | 1.74 | 1.27 | 0.04 | 0.92 | 0.87 | 0.003 | 2.47 | 3.58 | 2.92 |
| Large size | 0.84 | 0.04 | 1.1 | 3.50 | 0.61 | 4.73 | 0.50 | 0.02 | 0.12 | 1.80 | 0.011 | 0.64 |
| Very Large size | 1.82 | 0.2 | 4.88 | 2.02 | 5.31 | 0.14 | 5.28 | 5.76 | 5.92 | 4.45 | 5.76 | 1.20 |
| Cleaners | 0.81 | 0.05 | 0.11 | 0.04 | 0.007 | 0.0004 | 0.69 | 0.92 | 0.004 | 2.80 | 1.91 | 0.07 |
| General Carnivores | 2.51 | 2.74 | 0.86 | 2.35 | 0.71 | 2.45 | 2.86 | 0.09 | 9.97 | 6.14 | 10.92 | 0.003 |
| General Invertivores | 10.33 | 17.84 | 0.02 | 0.96 | 1.15 | 0.64 | 4.50 | 5.73 | 2.44 | 7.64 | 11.44 | 3.16 |
| Mobile Invertivores | 3.11 | 2.72 | 0.003 | 2.30 | 0.23 | 0.24 | 7.10 | 4.47 | 14.5 | 3.34 | 2.351 | 5.84 |
| Omnivores | 2.77 | 0.02 | 9.89 | 4.04 | 2.96 | 8.37 | 6.15 | 8.22 | 6.25 | 3.94 | 0.001 | 17.29 |
| Planktivores | 2.83 | 3.91 | 1.28 | 0.17 | 0.02 | 0.2 | 1.13 | 0.04 | 2.06 | 1.49 | 1.67 | 1.29 |
| Piscivores | 3.67 | 0.45 | 14.8 | 9.00 | 25.8 | 1.35 | 5.24 | 0.28 | 9.3 | 7.09 | 5.65 | 1.89 |
| Browser Herbivores | 4.68 | 4.93 | 0.47 | 6.00 | 1.23 | 11.44 | - | - | - | 0.95 | 0.19 | 0.14 |
| Territorial Herbivores | 1.52 | 0.39 | 1.51 | 1.69 | 1.58 | 2.2 | 2.61 | 0.26 | 5.88 | 1.23 | 1.30 | 0.003 |
| Scapers Herbivores | 5.98 | 7.6 | 0.002 | 6.52 | 0.12 | 12.6 | 3.13 | 2.48 | 0.53 | 9.12 | 17.80 | 0.017 |
| Grazer Herbivores | 2.57 | 3.53 | 0.008 | 2.61 | 3.23 | 1.19 | 1.23 | 0.15 | 0.46 | 2.07 | 1.68 | 3.27 |
| Solitary | 6.67 | 8.7 | 9.24 | 2.48 | 3.3 | 1.45 | 4.47 | 5.78 | 4.01 | 5.61 | 10.7 | 2.80 |
| Pair | 1.41 | 0.01 | 4.63 | 2.26 | 2.16 | 0.17 | 5.39 | 5.01 | 7.18 | 1.89 | 0.0007 | 2.33 |
| Small-medium groups | 4.89 | 7.32 | 0.004 | 2.16 | 1.12 | 0.01 | 1.30 | 0.22 | 3.65 | 3.25 | 5.6 | 0.32 |
| Large groups | 1.04 | 0.33 | 2.2 | 1.89 | 3.86 | 1.66 | 1.46 | 0.51 | 1.84 | 1.36 | 0.003 | 2.34 |
| ***Environmental variables*** | | | | | | | | | | | | |
| Macroalgae | 7.37 | 5.93 | 12.75 | 7.45 | 1.7 | 6.71 | 4.35 | 6.25 | 0.19 | 9.90 | 17.69 | 0.16 |
| EPAM | 3.57 | 2.35 | 0.11 | 4.02 | 5.25 | 1.76 | 5.89 | 1.69 | 20.56 | 7.43 | 11.74 | 2.16 |
| Cyanobacters | 4.48 | 3.78 | 0.09 | 4.03 | 0.77 | 7.3 | 5.35 | 0.85 | 15.45 | 8.52 | 11.789 | 0.80 |
| Calcareous algae | 7.60 | 1.34 | 27.58 | 6.56 | 6.69 | 2.72 | 6.22 | 9.69 | 0.41 | 2.22 | 0.02 | 0.95 |
| Soft Coral | 6.41 | 5.10 | 15.11 | 7.55 | 20.57 | 0.0004 | 2.52 | 0.51 | 0.13 | 10.6 | 10.38 | 28.2 |
| Hard Coral | 5.51 | 4.14 | 17.28 | 7.98 | 21.1 | 0.0005 | 4.28 | 4.31 | 3.11 | 5.90 | 2.39 | 16.36 |
| Zoanthids | 4.35 | 2.33 | 3.35 | 6.38 | 9.83 | 0.0037 | 5.51 | 0.18 | 23.60 | 3.49 | 1.64 | 9.58 |
| Other Organisms | 5.39 | 5.11 | 4.45 | 6.63 | 11.91 | 0.0052 | 4.64 | 0.81 | 1.13 | 3.00 | 0.41 | 1.15 |
| Reef | 5.05 | 6.45 | 0.004 | 4.79 | 0.48 | 6.54 | 6.67 | 5.59 | 0.79 | 3.56 | 0.14 | 0.2 |
| Sand | 7.68 | 9.66 | 5.37 | 5.26 | 0.68 | 17.3 | 5.48 | 3.59 | 12.05 | 7.19 | 9.26 | 0.00005 |
| Gravel | 3.75 | 2.37 | 0.59 | 5.66 | 2.76 | 11.08 | 8.85 | 7.87 | 0.04 | 3.75 | 0.001 | 11.72 |
| Depth | 6.06 | 7.25 | 3.81 | 4.16 | 1.98 | 0.99 | 4.6 | 6.95 | 2.32 | 5.70 | 3.45 | 6.00 |
| Small holes | 4.6 | 5.18 | 0.46 | 5.20 | 0.68 | 1.46 | 9.16 | 17.26 | 0.18 | 3.15 | 0.019 | 1.59 |
| Medium holes | 1.66 | 0.41 | 0.19 | 6.08 | 1.47 | 13.0 | 4.01 | 1.82 | 12.03 | 3.80 | 1.39 | 2.08 |
| Big holes | 6.82 | 9.9 | 0.53 | 6.23 | 9.28 | 1.8 | 4.02 | 3.04 | 0.45 | 4.25 | 2.82 | 0.74 |
| Rugosity | 12.14 | 19.44 | 1.02 | 5.76 | 3.13 | 14.7 | 6.46 | 7.02 | 7.46 | 13.33 | 24.22 | 8.04 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Slope | 7.56 | 9.18 | 6.26 | 6.23 | 1.8 | 14.6 | 11.99 | 22.48 | 0.07 | 4.19 | 2.66 | 1.02 |

Table S6. Summary of fourth-corner analysis to evaluate the global significance of the traits environment relationships based on the total inertia of the RLQ analysis. Tests for the links between RLQ axes and traits (“Q.axes”) and environmental variables. ***: *p* ≤0.001, **: *p* ≤ 0.01, *: *p* ≤ 0.05.

| Model | Axis | Variables | r | Std.Obs | p-value | P value adj |
|---|---|---|---|---|---|---|
| All localities | AxcQ1 | MALG | -0.1078 | -3.34 | 0.001 | **0.0034** ** |
| | | CALG | -0.05 | -1.63 | 0.111 | 0.179 |
| | | OORG | -0.10 | -2.66 | 0.004 | **0.010** * |
| | | EPAM | 0.06 | 2.57 | 0.008 | **0.016** * |
| | | CYAN | 0.08 | 2.64 | 0.007 | **0.014** * |
| | | SCOR | -0.10 | -3.09 | 0.003 | **0.008** ** |
| | | HCOR | 0.09 | 2.90 | 0.002 | **0.006** ** |
| | | ZOAN | -0.067 | -2.00 | 0.046 | 0.082 |
| | | Reef | 0.112 | 3.350 | 0.001 | **0.0034** ** |
| | | Sand | -0.137 | -3.172 | 0.001 | **0.0034** ** |
| | | Gravel | -0.068 | -2.534 | 0.01 | **0.018** * |
| | | Depth | 0.119 | 3.564 | 0.001 | **0.0034** ** |
| | | Small holes | -0.100 | 3.564 | 0.001 | **0.0034** ** |
| | | Medium holes | 0.0284 | 1.069 | 0.29 | 0.379 |
| | | Big holes | 0.139 | 4.347 | 0.001 | **0.0034** ** |
| | | Rugosity | 0.195 | 3.818 | 0.001 | **0.0034** ** |
| | | Slope | 0.134 | 3.139 | 0.001 | **0.0034** ** |
| | AxcQ2 | MALG | -0.073 | -2.231 | 0.024 | **0.045** * |
| | | CALG | 0.108 | 3.450 | 0.001 | **0.0034** ** |
| | | OORG | 0.048 | 1.265 | 0.215 | 0.323 |
| | | EPAM | - 0.0068 | -0.248 | 0.807 | 0.853 |
| | | CYAN | 0.006 | 0.203 | 0.828 | 0.853 |
| | | SCOR | 0.080 | 2.476 | 0.014 | **0.028** * |
| | | HCOR | 0.0856 | 3.555 | 0.002 | 0.0045 |
| | | ZOAN | -0.037 | -1.206 | 0.219 | 0.323 |
| | | Reef | -0.001 | -0.047 | 0.971 | 0.971 |
| | | Sand | 0.047 | 1.127 | 0.279 | 0.364 |
| | | Gravel | -0.015 | -0.590 | 0.58 | 0.7042 |
| | | Depth | -0.040 | -1.165 | 0.267 | 0.363 |
| | | Small holes | -0.014 | -0.538 | 0.612 | 0.717 |
| | | Medium holes | 0.009 | 0.333 | 0.742 | 0.8138 |
| | | Big holes | -0.015 | -0.467 | 0.65 | 0.736 |
| | | Rugosity | 0.020 | 0.408 | 0.685 | 0.7512 |
| | | Slope | 0.051 | 1.190 | 0.245 | 0.347 |
| CAR | AxcQ1 | MALG | 0.045 | 1.124 | 0.269 | 0.421 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | | CALG | -0.089 | -1.883 | 0.057 | 0.1292 |
| | | OORG | -0.119 | -2.562 | 0.012 | **0.0368 *** |
| | | EPAM | -0.0795 | -2.028 | 0.044 | 0.099 |
| | | CYAN | 0.0305 | 0.730 | 0.475 | 0.598 |
| | | SCOR | -0.157 | -4.062 | 0.001 | **0.0113*** |
| | | HCOR | -0.159 | -3.965 | 0.002 | **0.0136*** |
| | | ZOAN | 0.108 | 2.3068 | 0.018 | **0.0470 *** |
| | | Reef | -0.024 | -0.580 | 0.564 | 0.6185 |
| | | Sand | -0.027 | -0.6531 | 0.52 | 0.61858 |
| | | Gravel | -0.057 | -1.417 | 0.164 | 0.3453 |
| | | Depth | -0.048 | -1.052 | 0.32 | 0.4945 |
| | | Small holes | 0.028 | 0.614 | 0.537 | 0.6185 |
| | | Medium holes | -0.042 | -0.907 | 0.375 | 0.527 |
| | | Big holes | 0.1056 | 2.630 | 0.011 | **0.0374 *** |
| | | Rugosity | -0.0613 | -1.401 | 0.173 | 0.345 |
| | | Slope | -0.0465 | -0.893 | 0.388 | 0.527 |
| | AxcQ2 | MALG | 0.0986 | 2.151 | 0.037 | 0.089 |
| | | CALG | 0.0629 | 1.339 | 0.191 | 0.345 |
| | | OORG | 0.00875 | 0.175 | 0.858 | 0.911 |
| | | EPAM | 0.050 | 1.1223 | 0.274 | 0.421 |
| | | CYAN | 0.1030 | 2.277 | 0.024 | 0.062 |
| | | SCOR | -0.0008 | -0.00897 | 0.995 | 0.995 |
| | | HCOR | 0.025 | 0.651 | 0.549 | 0.618 |
| | | ZOAN | -0.0023 | -0.0460 | 0.97 | 0.995 |
| | | Reef | -0.0973 | -2.213 | 0.024 | 0.062 |
| | | Sand | 0.158 | 3.628 | 0.001 | **0.0113 *** |
| | | Gravel | 0.126 | 2.901 | 0.004 | **0.0194 *** |
| | | Depth | -0.0380 | -0.8319 | 0.42 | 0.549 |
| | | Small holes | -0.0460 | -0.972 | 0.346 | 0.511 |
| | | Medium holes | -0.1373 | -2.978 | 0.006 | **0.025 *** |
| | | Big holes | -0.05121 | -1.147 | 0.269 | 0.435 |
| | | Rugosity | -0.143 | -3.169 | 0.001 | **0.011 *** |
| | | Slope | -0.1455 | -2.8022 | 0.003 | **0.014 *** |
| PPR | AxcQ1 | MALG | 0.116 | 2.631 | 0.009 | **0.0255 *** |
| | | CALG | 0.1444 | 2.850 | 0.004 | **0.0151 *** |
| | | OORG | -0.041 | -0.901 | 0.368 | 0.5213 |
| | | EPAM | -0.060 | -1.334 | 0.198 | 0.3366 |
| | | CYAN | 0.0428 | 0.940 | 0.347 | 0.5144 |
| | | SCOR | -0.0332 | -0.782 | 0.452 | 0.5910 |
| | | HCOR | -0.096 | -2.24 | 0.021 | **0.047 *** |
| | | ZOAN | -0.0197 | -0.471 | 0.636 | 0.7722 |
| | | Reef | -0.109 | -2.423 | 0.013 | **0.034 *** |
| | | Sand | 0.087 | 1.988 | 0.05 | 0.106 |
| | | Gravel | 0.130 | 2.885 | 0.007 | **0.0216 *** |

| | | | | | | |
|---|---|---|---|---|---|---|
| | | Depth | -0.122 | -2.662 | 0.006 | **0.0204 *** |
| | | Small holes | 0.192 | 3.455 | 0.001 | **0.0113 *** |
| | | Medium holes | -0.062 | -1.474 | 0.142 | 0.254 |
| | | Big holes | -0.080 | -1.864 | 0.066 | 0.132 |
| | | Rugosity | -0.122 | -2.63 | 0.008 | 0.0226 |
| | | Slope | -0.219 | -3.654 | 0.001 | **0.0113 *** |
| | AxcQ2 | MALG | -0.01 | -0.227 | 0.831 | 0.866 |
| | | CALG | -0.0191 | -0.347 | 0.723 | 0.8476 |
| | | OORG | 0.0314 | 0.747 | 0.458 | 0.622 |
| | | EPAM | 0.1344 | 2.995 | 0.004 | **0.0151 *** |
| | | CYAN | -0.1165 | -2.73 | 0.003 | 0.015 |
| | | SCOR | 0.0107 | 0.312 | 0.769 | 0.866 |
| | | HCOR | -0.1440 | -3.213 | 0.002 | 0.0151 |
| | | ZOAN | -0.1440 | -3.21 | 0.002 | 0.0151 |
| | | Reef | -0.026 | -0.559 | 0.573 | 0.7493 |
| | | Sand | 0.1029 | 2.288 | 0.029 | 0.065 |
| | | Gravel | 0.0056 | 0.177 | 0.866 | 0.866 |
| | | Depth | 0.0452 | 1.063 | 0.306 | 0.4533 |
| | | Small holes | -0.0127 | -0.186 | 0.848 | 0.866 |
| | | Medium holes | -0.102 | -3.112 | 0.001 | **0.0113 *** |
| | | Big holes | 0.0199 | 0.5162 | 0.604 | 0.760 |
| | | Rugosity | -0.0809 | -1.692 | 0.105 | 0.1983 |
| | | Slope | -0.007 | -0.195 | 0.849 | 0.866 |
| ANMP | AxcQ1 | MALG | -0.155 | -3.31 | 0.001 | **0.017 *** |
| | | CALG | 0.0047 | 0.0759 | 0.946 | 0.982 |
| | | OORG | -0.023 | -0.494 | 0.632 | 0.795 |
| | | EPAM | -0.126 | -2.595 | 0.011 | 0.058 |
| | | CYAN | 0.1270 | 2.598 | 0.009 | 0.058 |
| | | SCOR | 0.119 | 2.423 | 0.012 | 0.058 |
| | | HCOR | 0.057 | 1.281 | 0.188 | 0.426 |
| | | ZOAN | 0.047 | 0.943 | 0.35 | 0.601 |
| | | Reef | 0.013 | 0.299 | 0.769 | 0.903 |
| | | Sand | -0.112 | -2.350 | 0.017 | 0.072 |
| | | Gravel | -0.001 | 0.0078 | 0.993 | 0.993 |
| | | Depth | 0.0687 | 1.4712 | 0.149 | 0.361 |
| | | Small holes | -0.005 | -0.129 | 0.889 | 0.975 |
| | | Medium holes | -0.0436 | -0.882 | 0.377 | 0.604 |
| | | Big holes | 0.062 | 1.265 | 0.211 | 0.448 |
| | | Rugosity | 0.1821 | 3.947 | 0.001 | **0.017 *** |
| | | Slope | 0.0603 | 1.2564 | 0.225 | 0.45 |
| | AxcQ2 | MALG | 0.009 | 0.282 | 0.791 | 0.903 |
| | | CALG | 0.0224 | 0.627 | 0.503 | 0.700 |
| | | OORG | 0.024 | 0.698 | 0.515 | 0.7004 |
| | | EPAM | -0.0336 | -0.935 | 0.354 | 0.601 |

| | | | | | |
|---|---|---|---|---|---|
| | CYAN | 0.121 | 3.362 | 0.002 | **0.023 *** |
| | SCOR | 0.121 | 3.362 | 0.002 | **0.022 *** |
| | HCOR | -0.092 | -2.667 | 0.006 | 0.051 |
| | ZOAN | 0.0708 | 2.067 | 0.034 | 0.1156 |
| | Reef | -0.010 | -0.245 | 0.797 | 0.9032 |
| | Sand | 0.0001 | -0.008 | 0.993 | 0.993 |
| | Gravel | 0.078 | 2.241 | 0.039 | 0.120 |
| | Depth | 0.056 | 1.665 | 0.1 | 0.261 |
| | Small holes | -0.028 | -0.858 | 0.391 | 0.6042 |
| | Medium holes | -0.0330 | -0.958 | 0.343 | 0.6018 |
| | Big holes | -0.0196 | -0.598 | 0.559 | 0.731 |
| | Rugosity | -0.064 | -1.474 | 0.138 | 0.246 |
| | Slope | -0.0732 | -2.158 | 0.028 | 0.105 |

## Conclusões

As áreas marinhas protegidas são fundamentais e essenciais para proteger os ecossistemas marinhos de ações antrópicas como a sobrepesca, destruição de habitats e contaminação, porém não sempre tem a capacidade de proteger de todos esses fatores antrópicos, como por exemplo as mudanças climáticas ou espécies bioinvasoras. No passado, esta ferramenta foi pensada, criada e aplicada, com diferentes objetivos e sem um conhecimento pleno sobre todas estás ações antrópicas. Dentro desses objetivos, não foi utilizado uma abordagem da proteção das funções do ecossistema no desenho e na gestão destas figuras de proteção, que pensamos que poderiam ajudar a proteger desses impactos antrópicos não contemplados nas atuais áreas marinhas protegidas. Só recentemente a ciência esta começando a entender melhor as interações desde um ponto de vista das funções do ecossistema, e com isso aparece uma oportunidade para investigar um novo paradigma sobre o desenho e ampliação de áreas marinhas protegidas que incluam esta abordagem. Como mostramos neste estudo, observamos que existe um padrão a nível global que mostra que as áreas marinhas protegidas atuais não estão contemplando todas entidades funcionais no seus limites, que significa que não esta protegendo todas as funções do ecossistema. Conseguimos estes resultados utilizando os índices de diversidade funcional, os quais consideramos uns indicadores ecológicos potentes para obter este tipo de respostas, e para ser utilizados na configuração de uma versão mais atualizada da ciência das áreas marinhas protegidas.

Junto destes índices, outros aspectos como os habitats e a escala, vão ser importantes para a configuração destas áreas. O primeiro, porque cada habitats vai ter uma representação diferente das especies o grupos de especies, que podem ter funções únicas que não são encontradas em outros tipos de habitats, por isso pensamos que é importante o uso de uma abordagem '*seascape*' na toma de decisões da ciência das áreas marinhas protegidas. O segundo, influenciará diretamente no anterior, porque, por exemplo, as características ambientais mudaram em função desta escala. Como encontramos neste estudo, para cada localidade existe uma peculiaridade que define as variáveis ambientais, e essas variáveis serão as que definem em grande parte a os traços funcionais, a interação das espécies o grupos com o ecossistema, e nas funções do mesmo.

Desde um ponto de vista regional e local, os bancos de Abrolhos e Royal Charlotte parecem os lugares perfeitos para avaliar e implementar uma rede de áreas marinhas protegidas que estejam conetadas e contemplem as funções do ecossistema, assim como uma ampliação das áreas existentes. Além disso, é uma grande área com recifes costeiros, e recifes e ilhas mais oceânicas e isoladas e, outras áreas com recifes e habitats ainda pouco conhecidos e estudados, como por exemplo os recifes esquecidos no sul do banco dos abrolhos, e os bancos de rodolitos no banco dos Abrolhos e Royal Charlotte. Também temos que mencionar que estas áreas sem uma efetiva gestão só ficam no papel. Isto está acontecendo atualmente com a APA Ponta das Baleias e a APA de Coroa Alta onde acontecem atividades, que estão proibidas no plano de manejo, que pode influenciar diretamente a biodiversidade e as funções do ecossistema.