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A trait-based approach to marine island biogeography

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Abstract

Aim: The Island Biogeography Theory (IBT) and its multiple extensions explain species diversity patterns in insular systems. However, how these theories can predict the functional diversity patterns in island systems remains challenging. Here, we evaluated the predictions of the IBT, the General Dynamic Theory of Oceanic Island Biogeography (GDM) and the Glacial-sensitive model of Island Biogeography (GSM) considering the functional diversity of reef fishes on islands.

Location: Tropical oceanic islands.

Taxon: Actinopterygii.

Method: We combined literature data and online repositories to gather occurrence data and traits of reef fish species for 72 tropical oceanic islands. We then calculated five functional diversity indices (functional richness 'FRic', functional evenness 'FEve', functional divergence 'FDiv', functional over-redundancy 'FOR' and functional vulnerability 'FVul'). We used generalized additive mixed models to explore relationships among species richness and functional indices. Furthermore, we built Bayesian models to evaluate relationships between the functional diversity indices and several island features (isolation from the nearest reef, past and present reef area, and geological age) and two metrics that reflect the potential influence of Quaternary climatic changes (isolation from Quaternary refugia) and historical contingency (isolation from biodiversity centres).

Results: We observed higher levels of FRic, FDiv and FOR on the Indo-Pacific islands, whereas FEve and FVul showed higher values on the Atlantic and Eastern Pacific islands. We identified positive relationships between FRic, FDiv and FOR with species richness but negative relationships with FEve and FVul. We found that past and present reef areas best explained the variation in functional diversity among islands.

Main Conclusions: The functional diversity of reef fishes on oceanic islands showed a longitudinal gradient, which can be explained by differences in the evolutionary history among marine regions. Furthermore, past and present reef areas were found to be the best predictors of reef fish functional diversity on oceanic islands, extending the IBT, GDM and GSM for marine organisms within a trait-based framework.

KEYWORDS
functional diversity, island age, island area, isolation, oceanic islands, reef fish

1 | INTRODUCTION

The Island Biogeography Theory (IBT) predicts that species richness in island systems results from a balance between immigration and extinction rates (MacArthur & Wilson, 1967). This process occurs due to (i) differential immigration rates related to island isolation and (ii) differential extinction rates related, which vary according to island area (MacArthur & Wilson, 1967; Whittaker et al., 2017). Specifically, larger islands may favour the establishment of a higher number of species because they display greater habitat diversity (Hachich et al., 2020; Weigelt et al., 2013). In addition to these island features, the General Dynamic Theory of Oceanic Island Biogeography (GDM) considers that the geological age can regulate species richness, speciation and extinction (Pinheiro et al., 2017; Whittaker et al., 2008). This is due to geological processes influencing the area, elevation, topographic complexity and isolation of islands over time, consequently affecting immigration, speciation and extinction rates (Borregaard et al., 2016). For example, plants and epiphyte communities in older islands showed a reduction in species richness due to the loss of area during natural erosion processes (Fernández-Palacios et al., 2021; Taylor & Burns, 2015), a result not found for marine organisms such as reef fishes, gastropods, echinoderms and seaweeds (Ávila et al., 2018; Hachich et al., 2015; Pinheiro et al., 2017). The glacial-sensitive model of island biogeography (GSM) added another layer of explanation to species richness patterns on islands, including climatic oscillations that altered the sea level and, consequently, island features (i.e., available area, elevation and isolation level; Weigelt et al., 2016). Thus, these changes on island features over time can also influence the connectivity and dispersal patterns of terrestrial and marine organisms (Ávila et al., 2019; Fernández-Palacios et al., 2016; Pinheiro et al., 2017; Weigelt et al., 2016). During low sea levels, reef fish populations used seamounts as stepping-stones to colonize remote islands (i.e., progression rule), while during high sea levels some fish populations remain isolated in remote habitats, favouring the evolution of endemic species (Mazzei et al., 2021; Pinheiro et al., 2017).

Historical and contemporary isolation levels have been recognized as essential drivers of reef fish species distribution patterns (Parravicini et al., 2013; Pellissier et al., 2014) and assemblages structure in oceanic islands (Bender et al., 2017; Quimbayo et al., 2019). Quaternary climatic fluctuations 2.6 million years ago were characterized by several glacial–interglacial cycles which promoted differential extinction rates for reef species (Pellissier et al., 2014). However, some areas remained stable over geological time, acting as refugia and preserving species from extinction, leaving a footprint on current reef fish distribution patterns (Pellissier et al., 2014). Moreover, locations less isolated from present biodiversity centres sustain higher connectivity leading to higher species richness than more isolated locations (Parravicini et al., 2013). Although the IBT, GDM and GSM provided important insights for the understanding of the processes shaping community assembly on islands, they mainly focused on the taxonomic dimension of biodiversity, whereas other biodiversity metrics-based on species traits remain poorly understood.

Trait-based approaches have been recognized as effective tools for studying biodiversity patterns and underlying species' role in ecosystem functioning (McGill et al., 2006; Violle et al., 2014). Global assessments have used species traits to identify biodiversity hotspots (Stuart-Smith et al., 2013), other studies used species traits to describe marine and terrestrial organisms' vulnerability to human impacts (Miatta et al., 2021). Despite these advances using species traits and functional diversity metrics to understand marine biodiversity (e.g., Mouillot et al., 2014; Stuart-Smith et al., 2013; Villéger et al., 2011), little attention has been given to marine island biogeography. Here, we tackle this issue by evaluating how past and present island features (i.e., area, isolation from nearest reef areas and age), as well as historical and contemporary isolation (i.e., isolation from Quaternary refugia and isolation from biodiversity centres) influence reef fish functional diversity on oceanic islands (i.e., islands that are not part of the continental shelf).

The functional diversity of a given community may comprise several components which provide different aspects of the mechanisms that operate in the community assembly and ecosystem functioning (Mason et al., 2005; Mouillot et al., 2013; Villéger et al., 2008). For instance, the functional richness (FRic) reveals details on the variation of species traits, which allows a better understanding on how environmental filters, such as isolation, can have an effect on community assembly (Villéger et al., 2008). In contrast, the functional evenness (FEve) and functional divergence (FDiv) better respond to local-scale factors, for example, how interactions between species can modulate communities (Bello et al., 2013). On the other hand, the functional over-redundancy (FOR) and functional vulnerability (FVul) are emerging facets that can provide empirical evidence on speciation processes, since the exclusiveness (or not) of a trait is a consequence of evolutionary drivers (Mouillot et al., 2014).

Here, we assembled three datasets that encompass reef fish occurrences on 72 oceanic islands, species traits, and historical and contemporary island features to examine three objectives. First, we described the global patterns of reef fish functional diversity indices (i.e., FRic, FEve, FDiv, FOR and FVul) on oceanic islands. Second, we examined the relationships between the functional diversity indices and the local species richness recorded on each island. Third, we considered historical and contemporary island features to test IBT, GDM and GSM predictions on functional indices of reef fish assemblages on oceanic islands. We expected a positive correlation between FRic, FDiv and FOR with species richness, since these functional indices are dependent on the local species pool (Laliberté & Legendre, 2010; Villéger et al., 2008). In contrast, we expected a negative effect of species richness on the FEve and FVul, since increasing species richness favours the possibility of more species performing the same function (Halpern & Floeter, 2008). We also expected large and connected islands (archipelagos) would display the highest levels of FRic, FDiv and FOR levels. Indeed, these large islands with extended shallow reef habitats would favour the coexistence of a greater number of species with various trait combinations (Yeager et al., 2017). The greater level of resource availability and/or habitat heterogeneity in these large reef habitats is also expected to favour the coexistence of a large number of species with similar traits (Karadimou et al., 2016). In addition to being more connected and consequently more prone to being colonized by other species, these islands are less affected by extinction processes, which helps to maintain a high-level FRic (Hachich et al., 2020). In contrast, we expected that small and isolated islands would have higher FEve and FVul because these islands would be shaped by limiting similarity—when two species cannot coexist due to their high similarities and compete for the same limited resource—resulting in high evenness regarding species traits composition (Hachich et al., 2020). We also expected that islands that had larger shallow area during the Last Glacial Maximum (LGM) 21 kya (i.e., past area) exhibited the greatest levels FRic, FDiv and FOR because large islands in the past accumulate more species than small islands (Ávila et al., 2019). Regarding island age, we expected that older islands to display the greater levels of FRic and FOR, but low FEve, FDiv and FVul because marine habitats on older islands exhibited lower extinction rates than young islands (Hachich et al., 2020). This low extinction consequently favours high species richness and diverse trait composition. Considering that reef fish assemblages in isolated locations from the Quaternary refugia and biodiversity centres are poorer (Parravicini et al., 2013; Pellissier et al., 2014), we expected that FRic, FDiv and FOR would be the smaller in isolated islands. Lastly, higher isolation from Quaternary refugia and present biodiversity centres would negatively influence reef fish species richness (Parravicini et al., 2013; Pellissier et al., 2014). We expected that FRic, FDiv and FOR would be smaller in remote islands, whereas FEve and FVul would exhibit higher values because only a small subset species and trait composition would be able to colonize these remote habitats. Our study provides a new perspective on how different island features may influence the functional diversity of reef fish assemblages on tropical oceanic islands and sheds light on the differences between marine and terrestrial island biogeography.

2 | MATERIALS AND METHODS

2.1 | Study islands

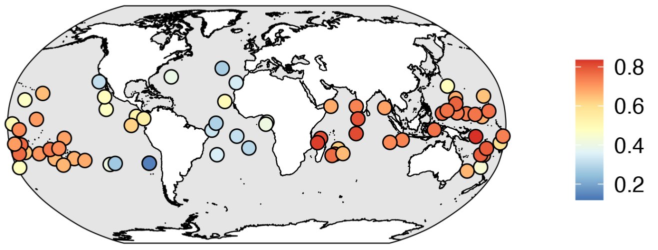
Our study comprised 72 tropical oceanic islands from four marine realms and 15 marine provinces (*sensus* Kulbicki et al., 2013; Figure 1). All the islands considered in this study are oceanic, that is, never had a connection with the mainland and are mostly of volcanic origin (Dawson, 2015). Moreover, due to their high isolation and small area, these islands comprise only subsets of regional diversity (Bender et al., 2017; Quimbayo et al., 2017). We considered each archipelago as a sample unit, since there were no significant differences in fish communities across islands within an archipelago (e.g., Channel islands of California, Galápagos Islands; Bernardi et al., 2014; Hachich et al., 2015), more specifically all local endemic species are shared among islands of the same archipelago. The area of these islands (or archipelagos) goes from 3.5 to 36,727 km^2, ages from 0.5 to 91 Ma, and their distance from nearest reef areas range from 227 to 5,381 km (Table S1).

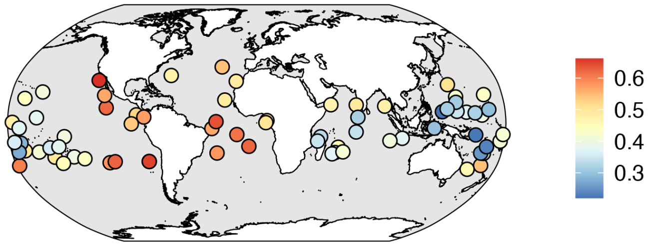
2.2 | Reef fish assemblages and species traits

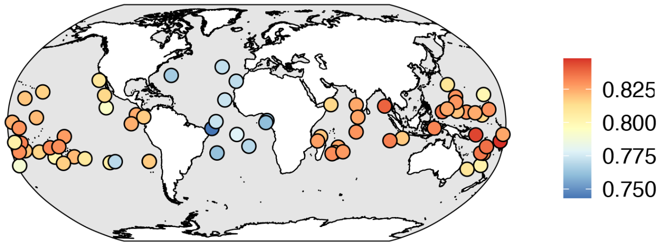
We gathered reef fish checklists of oceanic islands from articles, online repositories, books and monographs compiled by the GASPAR (General Approach to Species-Abundance Relationships) group (Kulbicki et al., 2013). In addition, we assembled information for six species traits following Mouillot et al. (2014) for each species. For the Atlantic and Tropical Eastern Pacific regions, trait data were obtained from Quimbayo, Mendes, et al. (2021) and Quimbayo, Silva, et al. (2021). For the other regions, trait data were compiled from the GASPAR group, that is, based on databases, books and online repositories (Mouillot et al., 2014). These species traits have been previously used in large-scale studies investigating the functional biogeography of tropical reef fishes (e.g., Bender et al., 2017; Quimbayo et al., 2019; Quimbayo, Mendes, et al., 2021; Quimbayo, Silva, et al., 2021). The six traits compiled were: Maximum body size: <7 cm, 8–15 cm, 16–30 cm, 31–50 cm, 51–80 cm or > 80 cm; Mobility: sedentary, territorial species, mobile and very mobile; Period of activity: diurnal, nocturnal, or both; Gregariousness: solitary, pairing, small groups of 3–20 individuals, medium groups of 20–50 individuals or large groups >50 individuals; Position in the water column: benthic, benthopelagic or pelagic species; Trophic group: herbivores–detritivores, macroalgae-feeders, sessile invertebrate feeders, mobile invertebrate feeders, planktivores, piscivores or omnivores.

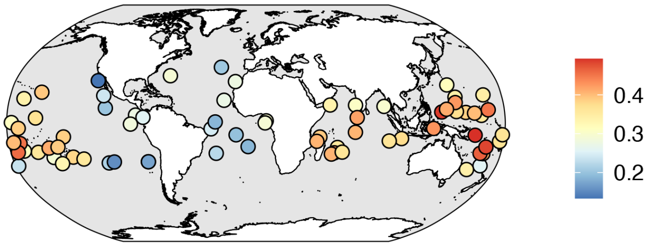
2.3 | Functional metrics

We used indices corresponding to the primary functional diversity metrics (Mason et al., 2005). The FRic measures the volume filled in an n-dimensional space occupied by a community; FEve measures the regularity of species distribution in the functional space. The FEve decreases when functional distances are less regular; FDiv for presence and absence data relates to the distance between species distribution of convex hull and the centre of gravity (Villéger et al., 2008). Functional divergence will be high when species values are far from the centre of gravity for their group. In addition, we estimated FOR and FVul based on the distribution of species in functional entities (FEs) on each oceanic island. Each FE is defined from the combination of all species traits. Thus, communities are over-redundant (FOR) when many species fit into the same FEs or are highly vulnerable (FVul) when only one or a few species are found by one FE (Mouillot et al., 2014).


(a) Functional richness


(b) Functional evenness


(c) Functional divergence


(d) Functional overredundancy

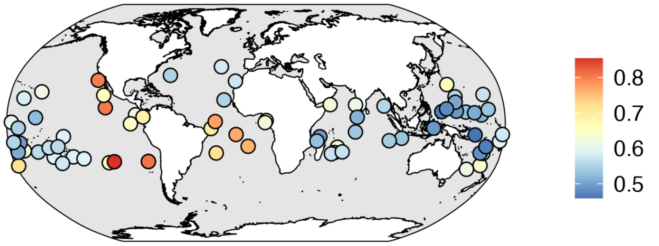

(e) Functional vulnerability

FIGURE 1 Global gradient maps of distribution of functional indices in 72 oceanic islands. (a) functional richness; (b) functional evenness; (c) functional divergence; (d) functional over-redundancy; (e) functional vulnerability. Circles with warm colors represent higher values. Robinson projection.

2.4 | Island features and geographical variables

The island features and geographical variables were selected according to several proposed hypotheses to explain the variation of species richness across islands and global distribution patterns of reef fishes. Specifically, we estimated and compiled present and past reef areas, island age and isolation (i.e., island features) to test whether IBT, GDM and GSM predictions can influence the reef fish functional diversity patterns in tropical oceanic islands. Furthermore, we compiled isolation from Quaternary refugia and isolation from biodiversity centre, two isolation metrics encompassing historical and contemporary isolation effects on reef fish species distribution.

For each island, we estimated the present area corresponding to the shallow shelf area down to 200 m. We considered this isobath because this depth has been recognized as the distribution boundary of shallow-water habitats (Hachich et al., 2015). To do this, we used the Gridded Bathymetric Data GEBCO 30 arc-second grids (www.gebco.net/data_and_products/gridded_bathymetry_data/gebco_30_second_grid). In addition, we used bathymetric data to estimate the past surface area of each island at the LGM (21,000 years ago). Specifically, we estimated the island area using the 320 m isobath because during the Late Quaternary, the sea-level decreased 120 m from the current level, possibly altering immigration, speciation and extinction rates (Weigelt et al., 2016). This approach has been used on islands in the Atlantic Ocean to estimate the effect of sea-level changes on species richness and endemism patterns of marine organisms (Ávila et al., 2018, 2019). We assembled island ages from the published works and reports (Table S1). Current isolation was measured through the distance from each island to the nearest reef area. The data were assessed through the orthodromic distance between both points (Table S1). We considered this isolation from the nearest reef areas because reef fish use mesophotic reefs as stepping-stones to colonized remote habitats (Pinheiro et al., 2017). In addition, we considered historical isolation as the distance from the nearest reef refugia across the Quaternary, because climatic oscillations during this geological period left an imprint on the global distribution of reef fish (Ottimofiore et al., 2017; Pellissier et al., 2014). To evaluate the influence of historical contingency (see Parravicini et al., 2013), we considered the distance of each island from biodiversity centres. Specifically, we considered Panama for the Eastern Pacific (Parravicini et al., 2013), the Caribbean for the Atlantic (Floeter et al., 2008) and the Indo-Australian Archipelago (IAA) for the Indo-Pacific (Kulbicki et al., 2013) as biodiversity centres.

2.5 | Data analyses

We used the six species traits assigned to each species to build the multidimensional functional trait space occupied by each local species pool (species recorded in local checklists). The multidimensional functional space was built from a principal coordinates analysis using Gower's distance dissimilarity matrix, which allows mixing qualitative and quantitative data (Podani & Schmera, 2006). Based on this functional space, we calculated the FRic, FEve and FDiv. These analyses were performed using the '*multidimFD*' function from Mouillot et al. (2013). In addition, we calculated FOR and FVul per island. This analysis was performed using '*species_to_FE*' and '*FE_metrics*' functions from Mouillot et al. (2013). We examined the quality of functional space using the '*quality_funct_space*' R function (Maire et al., 2015). We kept the first four axes because they represented more than 70% of the explained variance in the data. The results 4D functional space provided a parsimonious representation of the original distances (Figure S1).

To examine the relationships between the functional indices (i.e., FRic, FEve, FDiv, FOR and FVul) and the local species pool observed in each oceanic island, we employed generalized additive mixed models (GAMM) with Gaussian distribution. The degrees of freedom of the spline smoother function (s) were constrained to five knots (k = 5) to allow for potential non linearities, but also restricted and risk of overfitting. Furthermore, we added the 'marine province' as a random factor (random intercept model) for controlling variation associated with the different evolutionary processes of each marine province (n = 15). To do this, we used the gamm R function from the package '*mgcv*' (Wood, 2017). Posterior predictive checks are provided in the supporting information (Figure S2).

To account for the potential effect on the island ontogeny, we tested the quadratic term of island age through a linear regression (i.e., Age + Age^2) because this inclusion offers a good fit for metrics associated with evolutionary dynamics (Cameron et al., 2012; Whittaker et al., 2008). We also built linear regressions including the quadratic term to island area, isolation from Quaternary refugia, isolation of nearest reefs and isolation from biodiversity centre to investigate whether a nonlinear relationship better fits data on the functional indices. Based on the results of the linear regressions, we only observed a significant effect in both the single and quadratic terms of isolation from Quaternary refugia (Table S2).

To evaluate potential collinearity among the different island features (i.e., past, and present area, age and isolation from nearest reef areas) and isolation metrics (i.e., isolation from Quaternary refugia and isolation from biodiversity centres), we used Pearson's correlation, considering a correlation coefficient $< \pm 0.7$ (Figure S3). We considered this cut-off value for keeping island features and geographical variables in the models because values below this threshold are unlikely to involve multicollinearity in models (Dormann et al., 2013). In addition, we estimated the variance inflation factor (VIF) using the vif function from the '*car*' package (Fox & Weisberg, 2019) to ensure that predictors were not correlated with each other, considering a value <3 as a cut-off. We observed a strong correlation between past and present areas (r = 0.87, VIF = 5.02). Thus, we built two types of models considering the separated effect of each area. All predictors considered in the models were scaled using a zero mean and one standard deviation to enable the direct comparison among effect sizes.

We employed a Bayesian framework to evaluate how functional indices of reef fish were influenced by island features (i.e., past and present area, age and isolation from nearest reef areas) and isolation metrics (i.e., isolation from Quaternary refugia and isolation from biodiversity centres). Considering each area's effect separately, we built generalized linear mixed models with Gaussian distribution using bmrs R package (Bürkner, 2017). In all models, we included the quadratic term of isolation from Quaternary refugia because this term was significant in the linear regressions (Table S2) and the marine province as a random factor. The posterior distribution of model factors (i.e., island features and geographical isolation metrics) were estimated using Markov chain Monte Carlo methods by constructing four chains of 2000 steps, including a 1000-step warm-up, so a total of 3000 steps were retained to estimate posterior distribution. We considered a factor significant if their posterior 95% CIs did not overlap zero. In addition, we used Bayesian R^2 to each model's explained variation (Gelman et al., 2019). Finally, we estimated the Moran's index using residuals values of each model and geographical coordinates to explored spatial autocorrelation (Table S3). This index was estimated using the Moran. I function from the '*ape*' package (Paradis & Schliep, 2019). All the analyses and figures were performed in R software ver. 4.0.2. (R Core Team, 2020).

3 | RESULTS

A total of 4632 species and 569 FEs belonging to 157 fish families were observed on the 72 tropical oceanic islands. The functional richness (FRic) ranged between 0.12 and 0.83 and showed higher values in the Indo-Pacific (Figure 1a). The FOR ranged between 0.13 and 0.49 and showed higher values in the Indo-Pacific (Figure 1d). The functional evenness (FEve) and the functional vulnerability (FVul) indices, which ranged between 0.22–0.66 and 0.46–0.85 respectively, showed higher values in the Eastern Pacific and the Atlantic oceans (Figure 1b,d). Finally, the functional divergence index (FDiv), which ranged between 0.74 and 0.85, showed higher values in the Pacific, Eastern Pacific and Indian oceans (Figure 1b,d).

Species richness displayed a significant and positive nonlinear relationship with FRic, FDiv and FOR indices, whereas a negative relationship was found for FEve and FVul indices (Figure 2). We did not observe any significant effect of island age, isolation from nearest reefs and isolation from biodiversity centre on any functional index (Figure 3; Table S3). In contrast, past and present area, as well as the isolation from the Quaternary refugia, influenced reef fish functional indices on oceanic islands in different directions (Figure 3). For instance, past and present areas positively influenced FRic, FDiv and FOR (Figure 3a,c,d,f,h,i) but negatively influenced FEve and FVul (Figure 3b,e,g,j ; Table S3). The isolation from Quaternary refugia in the present area model negatively influenced FRic but positively affected

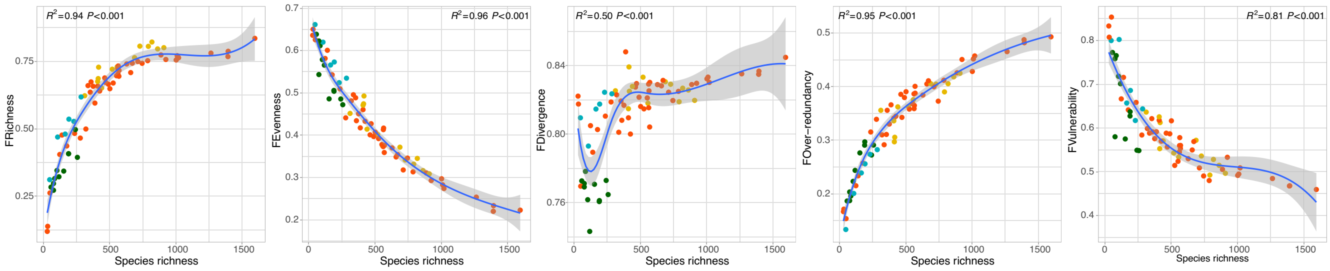


FIGURE 2 Linear regressions built from generalized additive mixed model between functional and local species pool of fish fauna in oceanic islands. Each color represents a marine realm. Atlantic (green), Eastern Pacific (light-blue), Indian (yellow), and Pacific (orange).

the FEve (Figure 3a,b; Table S3). In the past area model, the isolation from Quaternary refugia negatively influenced FRic and FOR, but positively FEve and FVul (Figure 3f,i,g,j; Table S3). Although not showing a significant effect, isolation from nearest reefs followed the same patterns of the isolation from Quaternary refugia. Based on the Bayesian estimates the amount of explained variation is considerable.

4 | DISCUSSION

This study is an empirical test of multiple extensions to the IBT, including the GDM and the GSM (Fernández-Palacios, 2016; Whittaker et al., 2008). Our results showed significant differences in functional diversity among oceanic islands. For example, islands in the Pacific exhibited a higher functional richness, functional divergence and FOR, whereas islands in the Eastern Pacific and the Atlantic presented a higher functional evenness and functional vulnerability. This strong longitudinal disparity suggests that historical and evolutionary processes played a major role in shaping the functional diversity of reef fish assemblages in tropical oceanic islands. We further observed strong relationships between local species richness and the functional diversity indices, which suggests that the functional structure of the local species pool on each island is modulated not only by regional processes but also by local ones. Lastly, our study revealed that the present-day availability of reef habitat but also during cold periods of the Quaternary are key factors driving reef fish functional structure on tropical oceanic islands.

4.1 | Relationships between species richness and functional indices

The positive relationships observed between species richness and functional richness, divergence and over-redundancy supported our initial hypothesis. These results supported the prediction that species richness influences the FRic and FOR (Mouchet et al., 2010). Increasing in species richness leads a high FRic and consequently favours an increase in FOR (i.e., different species with similar traits performing the same function). The negative relationship observed between species richness and functional evenness (FEve) suggests an uneven distribution of the fish traits on islands with high species richness compared to species-poor islands. This result confirms theoretical predictions that adding species to a speciose community tends to reduce FEve and increase the redundancy—that is, FOR (Halpern & Floeter, 2008). The high FEve found on small and remote islands suggests that species capable of arriving and colonizing these habitats have the most different traits, homogeneously within the functional space. Based on the niche theory, co-occurring species (arriving in an island over time) tend to have non-overlapping resource use to exploit local resources, a pattern exacerbated when packed in small areas. This phenomenon may be related to the optimization of resource use (habitat structure or food availability) across reef habitats, or it may be a mechanism that lessens competition among co-occurring species at smaller spatial scales. This may explain the limiting similarity of species traits (i.e., greater functional evenness in functional space) found as one moves from richer to poorer, larger to smaller, or more connected to more isolated islands. Moreover, differences among species traits can be a result of ecological filters (i.e., isolation) and specific behaviours of fish species (e.g., schooling behaviour, nocturnal habitats and rafting ability) that limit dispersal capacity and colonization of reef fish on isolated islands (Luiz et al., 2012, 2013; Mazzei et al., 2021).

The high levels of FDiv found on islands with high fish richness can be explained by the greater niche differentiation on these islands. For instance, islands in the Indo-Pacific exhibited the highest levels of FDiv, which can be related to the extensive reef area in IAA, which favoured species accumulation over time and the rise of this biodiversity hotspot (Parravicini et al., 2013). In contrast, islands in the Atlantic exhibited the lowest levels of FDiv that can be associated with the evolutionary history in this region, which is characterized by high extinction rates during the Eocene–Oligocene (Floeter et al., 2008; Siqueira et al., 2019). Islands with species-poor fish assemblages are functionally more vulnerable (higher FVul) since each function is only performed by one or few species due to ecological filters that limit colonization from the mainland (Bender et al., 2017). In contrast, islands with higher species richness are expected to have a lower functional vulnerability given that several species are grouped within FEs (Mouillot et al., 2014; Quimbayo et al., 2017).

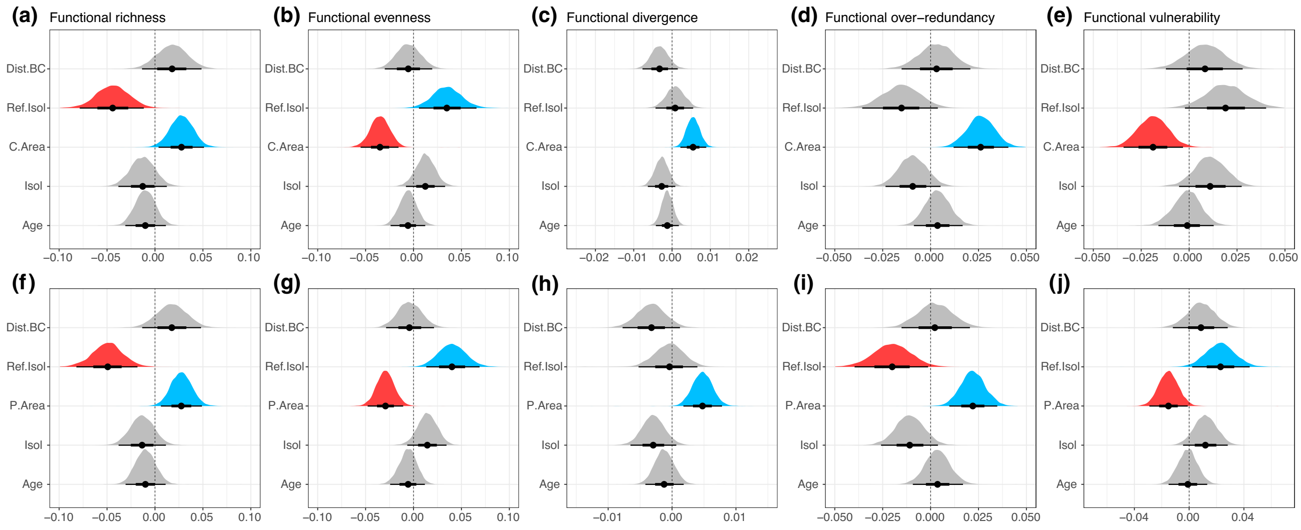


FIGURE 3 Mean effects of island features on functional indices estimated in 72 oceanic islands. (a) and (f) Functional richness using present and past area; (b) and (g) Functional using present and past area; (c) and (h) Functional divergence using present and past area; (d) and (i) Functional over-redundancy using present and past area; and (e) and (j) Functional vulnerability using present and past area. Values are standardized as effect sizes, circles represent mean parameter estimates and the lines represent 95% confidence intervals. All the effect sizes in blue represent positive relationships and the ones in red negative relationships. $^*p < 0.05$. Age, Island age; Dist.BC, Distance to biodiversity center; Isol, Isolation from nearest reef; P.Area, Present area; Ref.Isol, Isolation from Quaternary refugia.

4.2 | Effects of island features, historical and contemporary isolations on reef fish functional indices

The past and present reef areas, as well as the isolation from Quaternary refugia were the most important factors that modulate reef fish functional structure on oceanic islands in different directions. The high levels of FRic, FDiv and FOR observed in large Central Indo-Pacific islands (in the past and present) support our initial expectations because large islands tend to accumulate more species with similar traits. This pattern can be associated with both the availability of niches and with the higher colonization rates expected on large islands (Hachich et al., 2015, 2020). Several oceanic islands in these areas form large archipelagos with diverse niches and high resource availability (e.g., Fiji, New Caledonia). This scenario contributed to higher speciation rates and overlapping geographical ranges, which resulted in high levels of FRic, FDiv and FOR on islands from this region. Similar patterns have also been observed in plants, birds, ants and spiders (Ding et al., 2013; Whittaker et al., 2014; Zhao et al., 2020).

The higher connectivity of the islands of the Central Indo-Pacific with the Quaternary refugia favoured re-colonization after extinction periods (Pellissier et al., 2014), which may explain the higher values of FRic, FDiv and FOR found on these islands. The remote islands of the Atlantic and Eastern Pacific exhibited the smallest FRic values, emphasizing the effect of these historical isolations. Moreover, the present isolation of these islands (Floeter et al., 2008; Robertson & Cramer, 2009) imposes strong ecological filters on species with small body size, low pelagic larval duration, low rafting ability and specific diets (Luiz et al., 2013; Mazzei et al., 2021). Moreover, critical physical barriers also contributed to the low levels of FRic, FDiv and FOR observed on islands in the Atlantic and Eastern Pacific realm. For example, the isolation of the Atlantic realm from the Pacific by the closing of the Tethys Seaway in the so-called 'Terminal Tethyan Event' and the closure of the Isthmus of Panamá. On the other hand, the Eastern Pacific is separated by more than 3500 km from the biodiversity centre severely limiting colonization pulses from the Indo-Pacific (Floeter et al., 2008; Parravicini et al., 2013; Robertson & Cramer, 2009).

We observed higher levels of FEve and FVul in small and isolated islands from Quaternary refugia in the Atlantic and Eastern Pacific than on large and nearby islands from these historical refugia. This result supports our initial hypothesis and can be associated with recolonization limitations from the Quaternary refugia on these remote islands. Furthermore, these small and remote islands usually have fewer niches available (Ávila et al., 2019; Bender et al., 2017; Hachich et al., 2015) and their assemblages are small subsets of the regional species pool with high functional turnover due to ecological filters (i.e., isolation; Bender et al., 2017; Maxwell et al., 2022).

We did not observe any effect of island age and present isolation (i.e., based on the isolation from the nearest reef) on reef fish functional diversity. These results are opposite to our initial hypothesis, since we expected that older islands with lower isolation would exhibit higher levels of FRic, FDiv, and FOR, due to high species accumulation in these islands (Borregaard et al., 2017). We hypothesized that this lack of effect can vary according to island morphologies and historical evolutionary processes in each marine realm (Ávila et al., 2018, 2019; Ottimofiore et al., 2017; Pinheiro et al., 2017). For instance, age-progressive island chains are subject to long-term subsidence trends (e.g., Hawaii), whereas islands in stationary plates tend to form clusters and are subjected to stability or uplift trends (e.g., Cape Verde; Ávila et al., 2019). During sea-level oscillations, changes in area occur faster on chain islands than in those subjected to uplift trends independently of island age (Ávila et al., 2019). In addition, the Sea-Level-Sensitive dynamic model proposed by Ávila et al. (2019) showed that islands with different morphologies in the Atlantic were affected differently during sea-level oscillations. Volcanic older islands with narrow shallow reef areas exhibited a high extinction rate during low sea levels because all shallow areas were lost, whereas younger islands with larger shelf areas remained more stable and were refugia to marine species (Ávila et al., 2019). On the other hand, based on the absence of effects of the present isolation and biodiversity centres, we hypothesize that reef fish functional indices are not modulated via the 'progression rule' described to explain species richness and endemism on oceanic islands (Pinheiro et al., 2017). It is also possible that even younger islands of just 1 million years are already capable of having assembled a 'mature' fish assemblage over time, containing a wide variety of functional traits, such as observed on Ascension Island in the mid-Atlantic ridge. Thus, island age may not have an important role regarding reef fish functional structure on oceanic islands.

4.3 | Caveats

Although island age is an important predictor that allows inference on species accumulation processes as well as on immigration, speciation and extinction rates in the terrestrial environment, this only represents one aspect of island ontogeny. We did not observe any effect of island age despite trying to minimize this problem by building single models including a quadratic term to island age (i.e., $\text{Age} + \text{Age}^2$; see more details in Whittaker et al., 2008). Another concern related to island age is that sea-level oscillations influence the habitats and substrates of each island differently, thus resulting in mixed outcomes (Ávila et al., 2018, 2019). Thus, considering our results from single models (and literature), we suggest that future studies should include other aspects of island ontogeny such as volcanic activity and palaeo simulation of tectonic movements.

5 | CONCLUSION

Our results showed varying levels of functional diversity among marine realms, which suggests that historical and evolutionary processes left a significant imprint on present-day functional diversity of reef fish assemblages on tropical oceanic islands. Moreover, we observed a strong effect of species richness on the different functional diversity indices, emphasizing the importance of ecological filters in structuring tropical reef fish communities. Our study also showed that past and present areas are the most important island features for explaining differences in reef fish functional diversity among tropical oceanic islands. These results extend important theories, such as the IBT and the GDM. The patterns found in this study offer new insights, showing that reef fish functional diversity tends to follow the biogeographical drivers proposed by the IBT and palaeo-historical models that encompasses Quaternary climate variations. Thus, we propose that a trait-based approach can be used in re-evaluating ecological theories to unravel different aspects of ecosystem functioning in remote habitats. Lastly, it is always important to remember that a fundamental difference between the marine and terrestrial realms lies in the much greater dispersal potential and the lower number of barriers to dispersal in the oceans. Large-scale biodiversity patterns in marine and terrestrial realms results from similar processes (i.e., immigration, extinction, selection, adaptation, speciation), but their relative importance differ in terms of both timing and outcomes.

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CONFLICT OF INTEREST

There is no conflict of interest.

DATA AVAILABILITY STATEMENT

Data can be found at Zenodo GitHub repository https://doi.org/10.5281/zenodo.7316869

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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