Neotropical Ichthyology
Original article
https://doi.org/10.1590/1982-0224-2025-0035

Functional diversity and ecological patterns of reef fish assemblages across depth gradients in oceanic islands of the Brazilian Province

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Environmental gradients and geography are key drivers of biodiversity and community assembly in reef ecosystems. To investigate how biogeography and depth gradients shape reef fish assemblages, we analysed two Southwestern Atlantic oceanic archipelagos: Fernando de Noronha, larger and closer to the continent, and Saint Peter and Saint Paul, smaller and more isolated. Using mixed-gas rebreather dives to depths of 120 m, we conducted visual censuses of 6,982 individuals across 95 species and categorized assemblages by depth strata: shallow, upper, and lower mesophotic zones. We expected fish assemblages to be structured by predictions of Island Biogeography Theory and environmental gradients: larger, nearer island, and shallower reefs, sustaining higher species and functional richness while smaller and isolated island, and deeper reefs harbouring higher functional originality and specialization. Our results revealed assemblages geographically and depth-structured, with the lower mesophotic zone more isolated. While Fernando de Noronha exhibited higher overall species richness, Saint Peter and Saint Paul unexpectedly showed greater functional richness, particularly in shallow and lower mesophotic zones, alongside higher functional originality and specialization. These findings highlight the combined evolutionary and ecological processes shaping insular reef fish assemblages and underscore the need to integrate functional diversity into conservation of deep and isolated reefs.

Keywords: Endemism, Functional traits, Marine conservation, Mesophotic ecosystems, Theory of island biogeography.

Submitted March 10, 2025
Accepted December 10, 2025
Epub April 27, 2026

Associate Editor Luiz Osmar
Section Editor Luiz Osmar
Editor-in-chief José Birindelli

Online version ISSN 1982-0224
Print version ISSN 1679-6225

Neotrop. Ichthyol.
vol. 24, no. 1, 2026

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Gradientes ambientais e a geografia são fatores-chave na determinação da biodiversidade e na estruturação das comunidades em ecossistemas recifais. Para investigar como a biogeografia e os gradientes de profundidade moldam as comunidades de peixes recifais, analisamos dois arquipélagos oceânicos do Atlântico Sul-Ocidental: Fernando de Noronha, maior e mais próximo do continente, e São Pedro e São Paulo, menor e mais isolado. Utilizando mergulhos em circuito fechado de gases mistos até 120 m de profundidade, realizamos censos visuais de 6.982 indivíduos de 95 espécies, categorizadas por estratos de profundidade: raso, mesofótico superior e mesofótico inferior. Esperávamos que as assembleias de peixes fossem estruturadas de acordo com as previsões da Teoria da Biogeografia de Ilhas e gradientes ambientais: ilhas maiores e mais próximas e recifes rasos sustentando maior riqueza funcional e de espécies, enquanto ilhas menores e isoladas e recifes mais profundos apresentariam maior originalidade e especialização funcional. Nossos resultados revelaram assembleias estruturadas geograficamente e por profundidade, com o estrato mesofótico inferior mais isolado. Enquanto Fernando de Noronha apresentou maior riqueza de espécies geral, São Pedro e São Paulo exibiu, inesperadamente, maior riqueza funcional, especialmente nos estratos raso e mesofótico inferior, além de maior originalidade e especialização funcional. Esses achados destacam os processos evolutivos e ecológicos combinados que moldam as comunidades recifais insulares e reforçam a necessidade de integrar a diversidade funcional na conservação de recifes profundos e isolados.

Palavras-chave: Atributos funcionais, Conservação marinha, Ecossistemas mesofóticos, Endemismo, Teoria da Biogeografia de Ilhas.

INTRODUCTION

Depth gradients have emerged as a key factor influencing the assembly of reef fish communities on a global scale (Jankowski *et al*., 2015; Rocha *et al*., 2018; Pinheiro *et al*., 2023), offering valuable insights into how environmental and biogeographic processes shape biodiversity. Mesophotic ecosystems (MEs), which occur between 30 and 150 m, are particularly relevant in this context. These ecosystems exhibit high species turnover, reduced biodiversity, and significant shifts in trophic structure with increasing depth (Pinheiro *et al*., 2016; Rocha *et al*., 2018; Pimentel *et al*., 2022), reflecting the interplay between environmental conditions (*e.g*., temperature, light availability, turbidity, reef rugosity), and biological interactions (*e.g*., predation, competition, habitat selection), that govern species distribution. For instance, in tropical reef systems, depth-related decreases in light and temperature have been shown to limit the distribution of herbivorous fish, while complex reef structures provide refuges that reduce predation pressure and allow higher species coexistence (Nemeth, Appeldoorn, 2009; Smallhorn-West *et al*., 2017; Williams *et al*., 2019). By exploring the functional connections between shallow and deep reef habitats, including the role of depth-related fish endemism, we can better understand how these ecosystems contribute to assemblage structure and ecosystem processes (Lindfield *et al*., 2016; Simon *et al*., 2016).

Understanding depth-related processes requires approaches that extend beyond species counts, focusing on the functional role organisms play within ecosystems. In marine environments, fishes are key regulators of food webs and nutrient cycling, underscoring the value of functional approaches for ecological and conservation studies (Ives, Hughes, 2017; Albouy *et al*., 2019; Auber *et al*., 2022). Biodiversity is now widely understood to encompass genetic, phylogenetic, and functional dimensions, rather than being limited to species richness (Cardinale *et al*., 2012; Mouillot *et al*., 2013a). Functional diversity, in particular, has emerged as a powerful tool for predicting ecosystem responses to environmental changes, as it directly reflects the traits that mediate species' interactions with their environment (Villéger *et al*., 2008; Yeager *et al*., 2017). As anthropogenic impacts on ecosystems intensify, functional approaches are increasingly used in conservation biology to better preserve ecosystem functionality and resilience (Buisson *et al*., 2013; Parravicini *et al*., 2021). Examining the functional traits of fish assemblages across habitats and regions provides critical insights into the ecological consequences of species loss and helps pinpoint areas where conservation efforts should be prioritized (Mouillot *et al*., 2013a; Parravicini *et al*., 2014).

This functional perspective is particularly relevant when examining isolated marine ecosystems, such as Fernando de Noronha Archipelago and Saint Peter and Saint Paul Archipelago, which stand out as critical study sites, where recent discoveries of new species have expanded our understanding of biogeography and biodiversity patterns in Brazilian oceanic islands (Souza *et al*., 2015; Pinheiro *et al*., 2018a; Pimentel *et al*., 2020; Mincarone *et al*., 2022). These locations are about 600 km apart, exhibiting unique characteristics. Fernando de Noronha, the larger archipelago, harbours higher species richness and shares more species with the continental reefs (Pimentel *et al*., 2020). In contrast, Saint Peter and Saint Paul Archipelago, characterized by its extreme isolation and small insular area, displays higher rates of endemism (Rosa *et al*., 2016). Both historical and current levels of isolation are acknowledged as key factors influencing the distribution patterns of reef fish species (Floeter *et al*., 2008; Parravicini *et al*., 2013, Ferrari *et al*., 2023) and the composition of assemblages on oceanic islands (Bender *et al*., 2017; Quimbayo *et al*., 2019).

These unique features underline the ecological significance of both archipelagos, emphasizing the need for tailored conservation efforts. Reef are the most diverse marine ecosystem and support extremely high biodiversity in addition to providing ecosystem services that benefit humans (Graham, Nash, 2013; Harborne *et al*., 2017; Hughes *et al*., 2017; Brandl *et al*., 2019). However, these ecosystems are rapidly degrading due to multiple anthropogenic impacts, which increases the urgency for effective management (Bellwood *et al*., 2004; Pinheiro *et al*., 2023). Importantly, both archipelagos are part of Marine Protected Areas, with zones designated as no-take and sustainable use (Pimentel *et al*., 2020). However, despite their scientific and economic significance, management predominantly focuses on shallower no-take zones, highlighting the need to extend protection to deeper habitats, particularly those beyond 50 m (Jacquemont *et al*., 2024). Additionally, studying assemblage structure across depth gradients is crucial to understanding how biodiversity and ecosystem processes vary with depth, providing valuable insights to inform conservation strategies.

In this study, we investigated how depth and biogeographic factors (*e.g*., isolation, habitat availability and species composition), shape the functional structure of reef fish assemblages in two oceanic islands of the Southwestern Atlantic Ocean. Following the Theory of Island Biogeography (MacArthur, Wilson, 1967), we expect Fernando de Noronha, being larger and closer to the continent, to sustain higher species and functional richness due to greater habitat diversity and connectivity to the continental coast (Pinheiro *et al*., 2018b). In contrast, the smaller and more isolated São Pedro and São Paulo Archipelago is predicted to harbours lower species richness but higher functional originality and specialization, reflecting stronger ecological filtering and higher endemism (Floeter *et al*., 2008; Ferrari *et al*., 2023). Additionally, within both archipelagos, we predict that species and functional richness will decline with increasing depth, consistent with environmental constraints and turnover processes along depth gradients (Rocha *et al*., 2018; Lesser *et al*., 2019; Pinheiro *et al*., 2023).

MATERIAL AND METHODS

Study site. We sampled two oceanic islands in the Brazilian Province: Saint Peter and Saint Paul's Archipelago (SPSPA), situated about 1,010 km from the northeastern Brazilian coast (00°55'N 29°21'W), and Fernando de Noronha Archipelago (FNA), located 345 km off the northeastern Brazilian coast (03°50'S 32°25'W) (Fig. 1). Both locations are part of a mosaic of marine protected areas, containing both sustainable-use and no-take zones. Whereas SPSPA is inhabited by only four people (researchers and military), FNA is relatively close to the mainland and is the most accessible oceanic island in Brazil, with over 3,000 residents and receiving over 100,000 tourists every year (Cristiano *et al*., 2020).

The shallow (≤ 30 m depth) marine zone of SPSPA consists of rocky shores covered by macroalgae, coralline algae, turf, and bryozoans (Magalhães *et al*., 2015). The mesophotic component of the SPSPA reef system is composed mainly by vertical rocky walls and reef habitat dominated by sponges and black corals (Rosa *et al*., 2016). Saint Peter and Saint Paul's Archipelago is directly influenced by the surface South Equatorial Current, which flows westwards, and the Equatorial Undercurrent, flowing eastwards at depths between 40 and 150 m (Rosa *et al*., 2016). The presence of strong up and downwelling currents increases the amount of nutrients in the water and favours the occurrence of many pelagic species, forming an important fishing ground (Pinheiro *et al*., 2020). Additionally, SPSPA is the world's smallest remote tropical archipelago, formed by a group of small rocky islands (Vaske Jr. *et al*., 2005).

Fernando de Noronha is the largest Brazilian oceanic archipelago and consists of 21 islands and islets. The main island has two distinct sides: the leeward side, locally known as the "inside sea" facing north-west; and the windward side, locally known as the "outside sea" facing southeast, which receives constant winds and is strongly influenced by the low nutrient waters of the South Equatorial current (Martins *et al*., 2021). FNA reef ecosystems comprise a mosaic of habitats, where the shallow reefs (≤ 30 m) are composed of volcanic rocks, mainly covered by turf algae and brown macroalgae, with a low coral cover (Aued *et al*., 2018; Pimentel *et al*., 2020). The deeper reefs are mainly covered by sponges, scleractinian corals and the insular edge platform is followed by a steep wall, characterizing the lower mesophotic reefs (Pimentel *et al*., 2020).

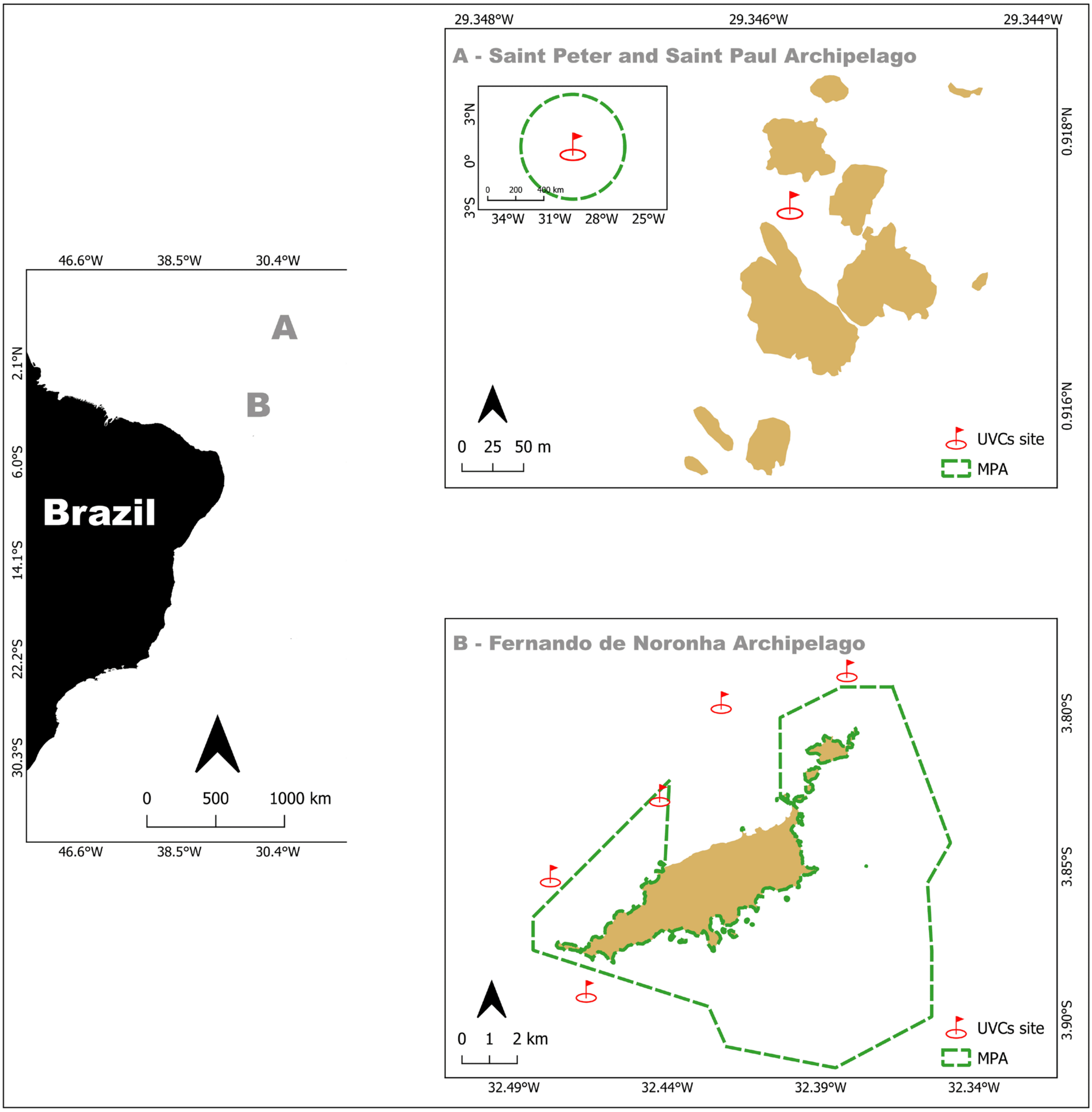

FIGURE 1 | Location of the Saint Peter and Saint Paul Archipelago and Fernando de Noronha Archipelago, Brazil (South-western Atlantic).

Data sampling. We assessed the reef fish assemblages by underwater visual censuses (UVC). A total of 87 belt transects (20 x 2 m) were conducted across different depths by using closed-circuit mixed gas rebreather dives in shallow and mesophotic ecosystems. Different sampling strategies were adopted in each island due to differences in island sizes and shelf width, which also affected the technical diving logistics (Tab. **S1**). Due to a larger shelf, five diving sites ranging from 4 to 112 m depth were sampled around FNA in 2019, while just one site covering a depth gradient spanning 9–107 m was sampled at SPSPA in 2017. The samples were classified into three strata: shallow, 0–30 m, and upper (31–60 m) and lower mesophotic (61–120 m deep).

Data analysis. To assess whether sampling effort was comparable across depths, we first constructed rarefaction curves (Fig. **S2**) using the "iNEXT" package (Hsieh *et al*., 2016). The analyses were conducted using total abundance data at the transect scale. Data was Hellinger-transformed and dissimilarity matrices between pairs of transects were computed using Bray-Curtis distances. To evaluate patterns in assemblage structure, we first performed a Principal Coordinates Analysis (PCoA). We then tested the effects of depth and location using a Permutational Multivariate Analysis of Variance (PERMANOVA), with dissimilarities calculated using '*vegdist*' function and PERMANOVA performed with '*adonis2*'. Also, we measured species' contribution to dissimilarities between the strata trough a Similarity Percentages (SIMPER) analysis, using the '*simper*' function. All multivariate analyses were performed using the "vegan" package (Oksanen *et al*., 2017).

We used afunctional diversity approach to assess differences in the structure of fish assemblages between the two studied archipelagos and their responses to environmental gradients (Mouillot *et al*., 2013). Six traits were selected to describe the morphological, behavioural, and biological functions of the reef fish species surveyed (Mouillot *et al*., 2014): size class (0–7 cm, 7.1–15 cm, 15.1–30 cm, 30.1–50 cm, 50.1–80 cm, > 80 cm), home range (sedentary, mobile and very mobile), diel activity (day, night and both), schooling (solitary, pair, small, medium and large school), water position (high, low and bottom) and diet (herbivores, omnivores, carnivores, planktivorous, mobile invertebrates feeders and sessile invertebrates feeders), (see Tab. **S3**). The functional traits have been compiled from available literature (Quimbayo *et al*., 2021) and FishBase (Froese, Pauly, 2024).

First, we calculated pairwise species trait distances using the Gower distance metric using '*funct.dist*' function in "mFD" package (Magneville *et al*., 2022), which is appropriate for datasets containing mixed trait types (Gower, 1971). The resulting distance matrix was then used to build the functional trait space for each assemblage, across locations (FNA and SPSPA) and depth strata, as well as for the global species pool, defined as all species recorded in both locations. The '*quality.fspaces*' function was used to assess the quality of functional space, leading to the decision to calculate trait space across two axes (PC4 and PC5, Tab. **S4**). We used Principal Coordinate Analysis (PCoA) to visualize the functional trait space occupied by fish assemblages, with polygons delineating the functional distances among species within each transect. At the transect level, we computed four functional α-diversity indices using the '*alpha.fd.multidim*' function: functional richness (FRic), based on species presence, and functional specialization, divergence and originality, all weighted by species abundance. These indices capture different aspects of the ecological niche (spatial, temporal, trophic dimensions), and were used to evaluate how the functional structure of assemblages' changes with depth. Functional richness, measured by the diversity of the species biological traits presented in the studied assemblages, represents the niche space occupied by the species within a community (Villéger *et al*., 2008), and it was used to test whether functional space contracts with decreasing species richness at greater depths and geographical isolation. Additionally, functional divergence refers to the degree of ecological differentiation between assemblages, with higher values indicating lower overlap in ecological/functional traits, which imply greater difference in resource use and the ecological niches among species (Mason *et al*., 2005). Furthermore, functional originality quantifies the distinctiveness of a species' traits within the community, reflecting how rare or unique a species trait is. A species tends to be less original as it shares more traits with others, which in turn increases redundancy (Pavoine *et al*., 2017). Thus, assemblages with higher originality values are characterized by lower redundancy, since the functions provided by these species are less likely to be replaced by others (Kondratyeva *et al*., 2019). Functional specialization indicates how traits can restrict the niche use of a species (Ferry-Graham *et al*., 2002), *i.e*., species with highly specialized traits are limited to narrower sets of resources or habitats, whereas generalist species can exploit a broader range. Together, these functional metrics allow us to explore the effects of depth and regional endemism on the assemblages. Finally, to assess the significance of differences in functional indices (richness, specialization, divergence and originality), across depth zones and between locations, we performed a Kruskal-Wallis test (Kruskal, Wallis, 1952). All analyses were performed in R v. 4.3.2 (R Development Core Team, 2023).

RESULTS

Taxonomic structure of the fish assemblages. We conducted a total of 85 transects across depths ranging from 4 to 111 m. In FNA, 4,600 individuals representing 63 species were recorded across 54 transects, whereas in SPSPA, 2,376 individuals belonging to 31 species were recorded across 31 transects (Tab. **S1**). The reef fish assemblages were both geographically and depth-structured (Fig. 2), with the lower mesophotic zone more isolated, and a small overlap between upper and shallow strata. The PERMANOVA (Tab. **S5**) results showed a significant effect of depth ($R^2 = 0.34$, $p = 0.001$), location ($R^2 = 0.18$, $p = 0.001$) and their interaction ($R^2 = 0.08$, $p = 0.001$), in the structure of the reef fish assemblages. A total of 49 species occurred exclusively in FNA, while 17 were only recorded in SPSPA; 17 species were limited to shallow reefs, while 41 were unique to MEs (Tab. **S6**). Although a marked separation was identified, some degree of convergence can be observed between islands and along the depth gradient, such as the dominance of planktivorous species in all strata. In shallow waters, *Azurina multilineata* and *Melichthys niger* were found in both islands, while *Tosanoides aphrodite* and *Chromis vanbebberae* predominate in their deeper waters (Fig. 2). Moreover, *Paranthias furcifer* was the most important contributor to the dissimilarities between the lower mesophotic and upper mesophotic zones of FNA (Tab. **S7**), accounting for 14% of the dissimilarity. *Holocentrus adscensionis* and *Thalassoma noronhanum* contributed most to the similarity between shallow and upper mesophotic zones of this same island (7% and 5%, respectively). In SPSPA assemblages, *A. multilineata* was the largest contributor to the dissimilarity in shallow and lower mesophotic zones (41% of dissimilarity). In upper and lower mesophotic zones, accounted for 33% of the dissimilarity, followed by *M. niger* (10%) and *Choranthias salmopunctatus* (8%).

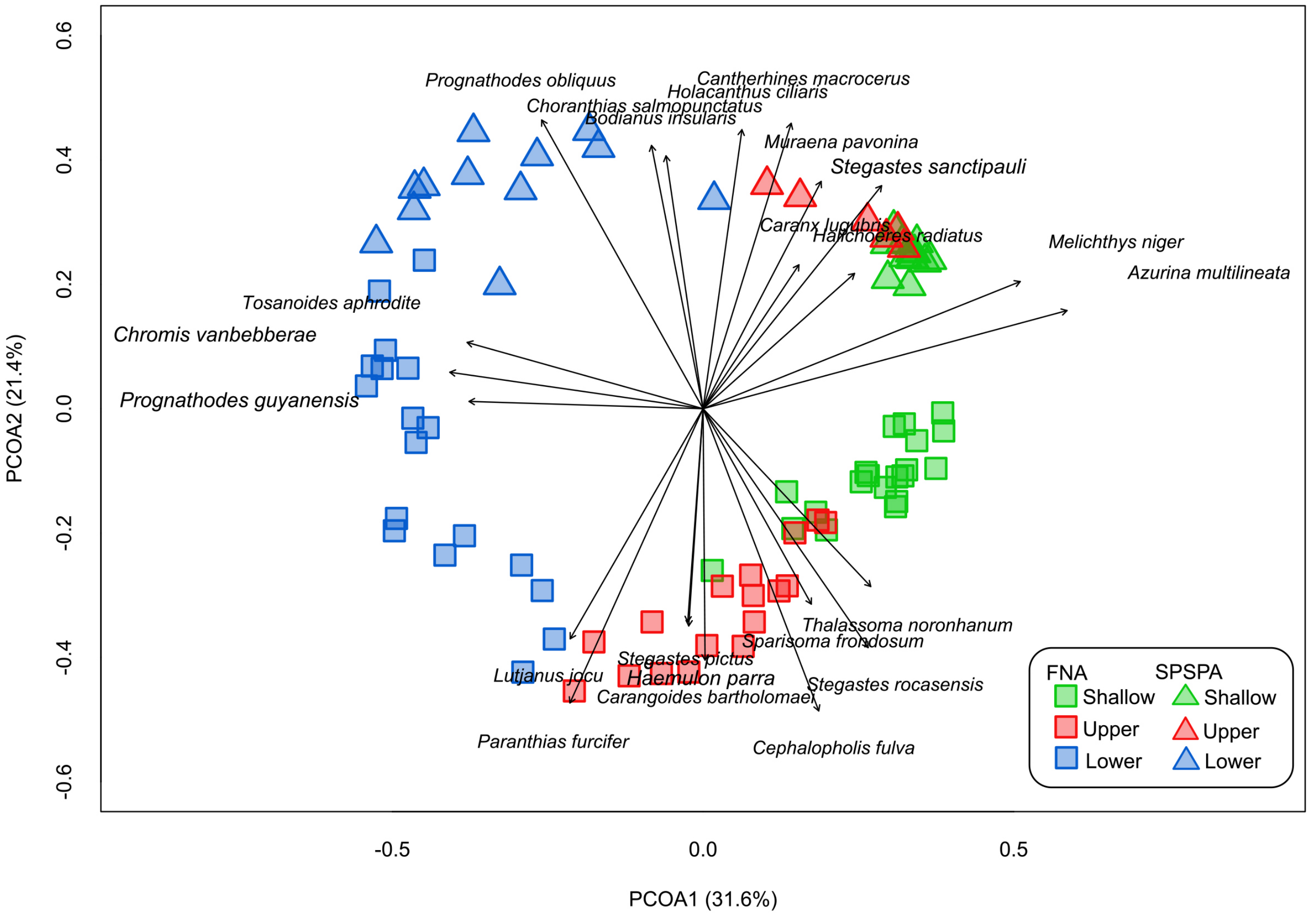

FIGURE 2 | Principal Coordinate Analysis (PCoA) performed on species abundance by transect. Each symbol represents one transect. Axis 1 represents the depth while axis 2 represents the locations. The plotted species are those with r2 greater than or equal to 10%.

Functional structure of the fish assemblages. Fish assemblages exhibited significant differences in species and functional richness across islands and depth strata (Kruskal-Wallis test: $p < 0.001$). Higher values of species richness were recorded in FNA (Fig. 3), compared to SPSPA, except in the lower mesophotic zone, where SPSPA showed a slightly higher richness (mean: 7.1) than FNA (mean: 6.5). In contrast, functional richness showed an inverse result. SPSPA presented higher functional richness values in both shallow (Fric: 0.32) and lower mesophotic zone (Fric: 0.26), compared to FNA (Fric shallow: 0.22; Fric lower: 0.23). For both locations, the upper mesophotic exhibited the highest functional richness (FNA Fric: 0.36; SPSPA Fric: 0.34).

Functional specialization (Fig. 4) increased with depth in both archipelagos, with SPSPA showing lower overall values (SPSPA: Fspe: shallow: 0.32; upper: 0.33; lower: 0.34; and FNA: Fspe: shallow: 0.31; upper: 0.34; lower: 0.48). Functional originality showed a different pattern: SPSPA had consistently higher originality values across all depth strata (*e.g.*, Fori: shallow: 0.16; upper: 0.19; lower: 0.14), whereas FNA showed lower values across the gradient (Fori: shallow: 0.14; upper: 0.12; lower: 0.04). No significant differences (Kruskal-Wallis test: $p > 0.001$), were observed for functional divergence between locations or depth strata.

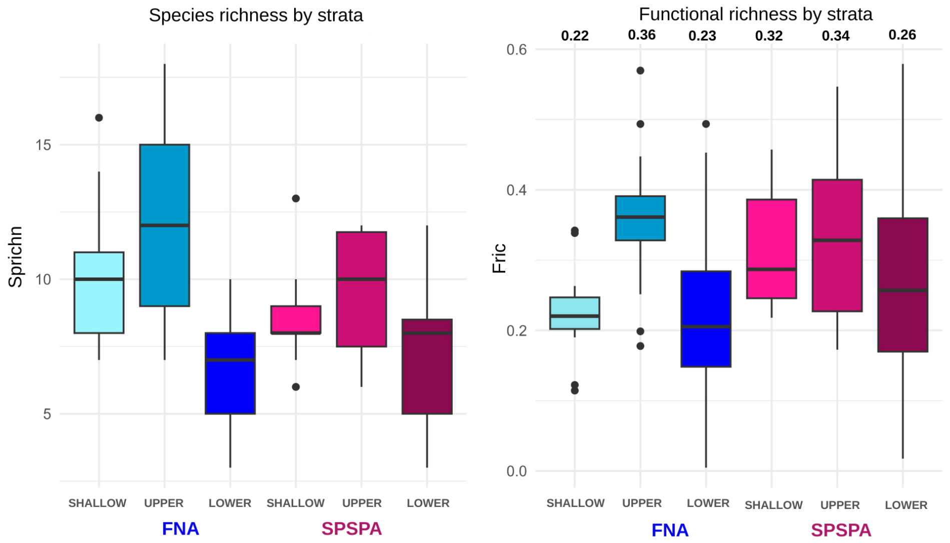

FIGURE 3 | Boxplot of median and quartiles of species and functional richness. Species Richness (Sprichn): total number of species present in each transect. Functional richness (Fric) indicates the proportion of functional space filled by species of each depth strata. The numbers above the bars indicate the average value of the indices at each strata.

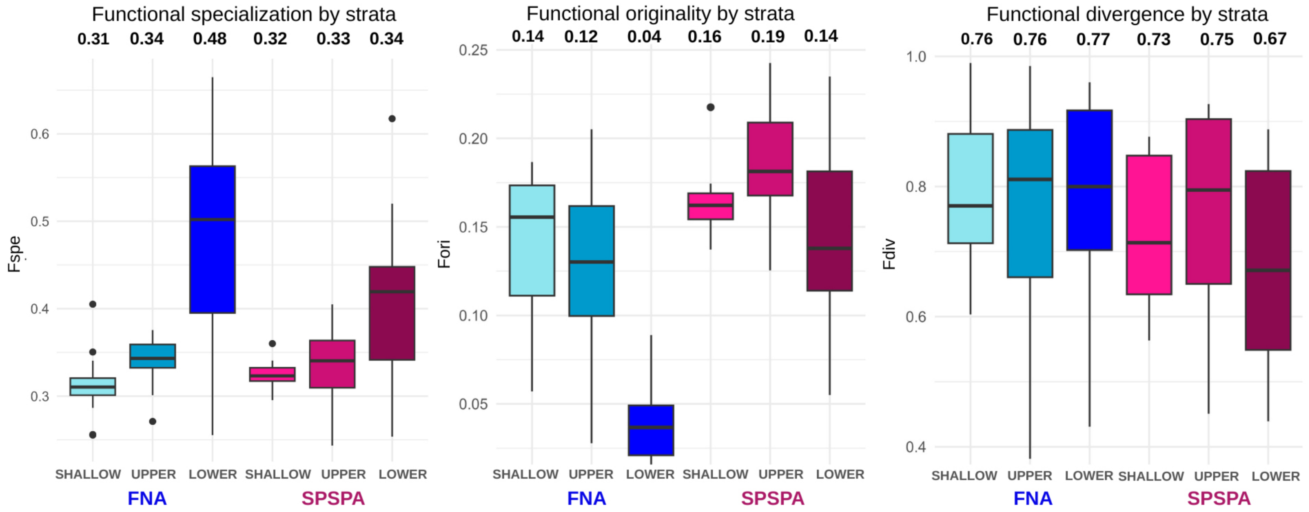

FIGURE 4 | Boxplot of median and quartiles of multidimensional functional indices by island and depth strata. Functional specialization (Fesp) corresponds to the average distance weighted by abundance to the average position of the species of the global set. Functional originality (Fori) is measured by the average weighted distance to the closest species of the global set of species. Functional divergence (Fdiv) means the proportion of abundance supported by the species with the most extreme functional traits. The numbers above the bars indicate the average value of the indices at each strata.

DISCUSSION

As expected, the reef fish assemblages investigated were structured by island and depth, influenced by the evolutionary history of each location and environmental characteristics, which change along the depth gradient. Many species typically found in mesophotic zones prefer cooler temperatures, while others are associated with shallower and warmer waters. Thus, overlap between the shallow and upper mesophotic zones could be attributed to species that display ontogenetic shifts, such as *Stegastes*, whose juveniles can recruit in deeper reefs, exploiting a broader range of habitats (Ferreira *et al*., 1998; Gajdzik *et al*., 2016; Rosa *et al*., 2016). Additionally, species with broader bathymetric distributions, such as *Lutjanus jocu* and *Bodianus insularis*, can thrive across multiple depth strata, thus contributing to the observed similarities between shallow and deeper zones (Rosa *et al*., 2016; Pimentel *et al*., 2022). Conversely, distinct patterns emerge in the lower mesophotic, likely driven by species shifts frequently found along the depth gradient, in response to environmental changes (Rocha *et al*., 2018; Pinheiro *et al*., 2023; Gragnolati *et al*., 2024). We found that the lower mesophotic of both islands shared species like *Chromis vanbebberae* and *Tosanoides aphrodite*. Nevertheless, we observed that FNA presented widespread species, such as *Paranthias furcifer* and *Prognathodes guyanensis*, showing a positive relationship with greater depths, whereas SPSPA showed local endemics, like *Prognathodes obliquus* and *Choranthias salmopunctatus*. Therefore, these deeper ecosystems support distinct ecological assemblages with low connectivity with shallower areas, where SPSPA is more isolated, while FNA receives colonizers from both the isolated island (SPSPA) and the continental shelf.

The comparison between the two archipelagos revealed clear distinctions in their fish assemblages, with FNA exhibiting a higher taxonomic richness than SPSPA. These patterns align with previous expectations regarding differences in island size and isolation, which are known to influence species diversity in coral reef ecosystems (Bellwood, Hughes, 2001; Parravicini *et al*., 2013; Ferrari *et al*., 2023). Larger and more complex environments typically support a broader range of species, offering more habitats and resources for ecological interactions (Mora *et al*., 2003; Hachich *et al*., 2015; Velasquez *et al*., 2018). In contrast, smaller and more isolated islands often show lower biodiversity due to limitations in available resources and space (Hachich *et al*., 2015; Velasquez *et al*., 2018). These differences in species richness could also be attributed to the geological age of each archipelago, as described in the General Dynamic Theory of Oceanic Island Biogeography (Whittaker *et al*., 2008; Pinheiro *et al*., 2018a). Under this framework, island age influences habitat availability, with younger islands providing more newly formed substrates and older islands experiencing gradual habitat loss through erosion and subsidence. Therefore, FNA, younger, larger, and closer to the continental shelf likely provides a wider range of habitats and more opportunities for species colonization (Hachich *et al*., 2015). In contrast, SPSPA, an older, smaller, and highly isolated island, may have reduced and more spatially restricted habitats due to long-term geological degradation and subsidence, supporting fewer species (Luiz *et al*., 2012).

Interestingly, contrary to our initial expectations, functional richness in SPSPA exceeded that of FNA. In such contexts, this pattern may emerge from the need of different species to efficiently utilize limited resources and minimize competition, particularly in resource-poor and isolated environments (Mason *et al*., 2005; Mendes *et* *al*., 2019). Additionally, we observed greater species richness at upper mesophotic depths for both islands, suggesting that specific depth zones may facilitate higher diversity and functional richness than initially anticipated. Although different from widescale patterns (Pinheiro *et al*., 2023), a hump-shaped pattern of richness distribution along the depth gradient has already been described for corals, suggesting the existence of local dynamics such as disturbance frequency and/or competitive exclusion (Roberts *et al*., 2019). This finding highlights the complexity of ecological interactions in these systems and emphasizes that the diversity of functional groups is not necessarily linearly related to species richness (Halpern, Floeter, 2008). In fact, our results contrast with those of Ferrari *et al*. (2023), who analysed the fish composition (presence/absence data) of 72 oceanic islands around the world, without incorporating depth-related variation, and reported a positive correlation between species and functional richness. The lack of this positive relationship could be related to differences in the evolutionary history and assembly rules, as previously suggested by Pinheiro *et al*. (2023), when comparing species vs functional richness patterns of Pacific and Atlantic MEs. Here, this apparent decoupling may reflect the presence of fewer, yet more functionally distinct species, potentially resulted from environmental filtering and the strong selective pressures typical of small, isolated, and resource-limited systems (Hachich *et al*., 2015). Additionally, differences in sampling scale and consequently species pools may also contribute to the discrepancy in the relationship between taxonomic and functional richness.

The occupation of the available functional space indicates the degree of complementarity among the species (Mouillot *et al*., 2014). A uniform occupation of functional space by a rich assemblage is often associated with ecological resilience (Mouillot *et al*., 2014), since the presence of multiple species playing the same functions can confer greater stability to ecosystems under environmental disturbances (Mouillot *et al*., 2013). However, evolving in geographic isolation and under intense limitation of available area, the remote SPSPA assemblage reached high levels of functional originality, especially in mesophotic zones. The predominance of assemblages with high levels of functional originality in a low-diversity environment may indicates little functional plasticity and redundancy, which potentially makes the assemblage more vulnerable to environmental changes (Robinson *et al*., 2022; Huang *et al*., 2024).

Conversely, the lower functional diversity found in the richer FNA suggests that species are more densely packed (patch distribution) within the functional space, indicating a redundancy also found in richer faunas (Mouillot *et al*., 2014). This pattern may reflect the ecological filtering effect of oceanic islands and specific geographic characteristics of the archipelago, such as its large size and proximity to the continental shelf (Mora *et al*., 2003). While the oceanic environment constrains the ecological traits and species composition of those able to reach and establish in these areas (Pinheiro *et al*., 2018a; Mazzei *et al*., 2021), these geographic characteristics may also favour species packing through higher levels of colonization. High migration levels decrease opportunity for speciation in oceanic islands (Luiz *et al*., 2012; Pinheiro *et al*., 2017; Mazzei *et al*., 2021), probably driving lower originality levels compared to SPSPA.

Variations in habitat availability and usage along the depth gradient can lead to different levels of specialization (Jankowiski *et al*., 2015). The highest values of functional specialization observed in the lower mesophotic strata of both islands suggest that in deeper zones, the species are more specialized in their ecological functions. This result may be attributed to the more restricted or stable conditions found at greater depths, where the competition for specific resources favours the development of specialized traits (Wilson *et al*., 2008; Lesser *et al*., 2009). High species richness on shallow reefs is often linked to environmental characteristics, including physical factors such as high structural complexity, temperature, light availability, and hydrodynamics (Wood, 2001; Pereira-Filho *et al*., 2011; Francini-Filho *et al*., 2013). These conditions create diverse habitats that support a variety of species. Additionally, ecological factors such as benthic cover and species interactions, along with biogeographic influences like provinciality and regional enrichment, play a significant role (Pinheiro *et al*., 2023). These factors may promote shifts in niche breadth, resulting in species to become more specialized in response to local conditions (Lesser *et al*., 2018).

While FNA's larger size and higher biodiversity might provide some resilience to their assemblages, the growing impacts of the local population and increasing tourism might counterbalance the benefits of the protection offered by the national park (Mello *et al*., 2025). Indeed, both archipelagos are susceptible to disturbances like climate change, habitat degradation, and overfishing. SPSPA, with its smaller size and higher levels of endemism, faces even greater risks due to limited habitat availability and lower colonization opportunities. These anthropogenic threats could impact the biodiversity metrics studied mainly through the removal of predator, specialist and sensible species, decreasing both taxonomic and functional richness. Therefore, conservation efforts in oceanic islands like FNA and SPSPA must account for the unique ecological dynamics and the vulnerability of these ecosystems. Expanding protection measures to include deeper zones and incorporating functional diversity into conservation plans is critical (Giglio *et al*., 2018; Pereira *et al*., 2020; Jacquemont *et al*., 2024). By understanding the functional roles of species, particularly in relation to depth gradients, conservation strategies can be more effectively tailored to maintain ecosystem services, protect biodiversity, and ensure the resilience of these ecosystems in the face of ongoing environmental changes.

ACKNOWLEDGMENTS

We would like to thank Tyler A. Phelps who, together with HTP and LAR, did the sampling for this work. We thank Guilherme Loyola da Cruz for creating the map used in this article. We are grateful to our friend M. Vilella and the staff at his Pizzaria Namoita for all their care during our stay in Noronha, and to K. V. Bastos (CIUFES) and R. Francini-Filho (CEBIMar-USP) for help with logistics.

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AUTHORS' CONTRIBUTION

Julia Marx: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing-original draft, Writing-review and editing.

Caio R. Pimentel: Funding acquisition, Investigation, Writing-review and editing.

Luiz A. Rocha: Data curation, Funding acquisition, Investigation, Resources, Writing-review and editing.

Hudson T. Pinheiro: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing-original draft, Writing-review and editing.

FUNDING INFORMATION

We thank Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP; 2019/24215–2) and the California Academy of Sciences through the Hope For Reefs Initiative for funding. JM and HTP received FAPESP fellowships (2022/08684–5 and 2021/07039–6, respectively). This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) - finance code 001. CRP also thanks the Fundação Estadual de Amparo à Pesquisa do Estado do Espírito Santo for the PhD scholarship (54/2018) and CAPES for the PDSE fellowship (88881.362262/2019–01). We are grateful to NGO Voz da Natureza for supporting the project, and to Fundação Grupo Boticário de Proteção à Natureza for funding.

ETHICAL STATEMENT

Not applicable.

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are available from the corresponding author, upon reasonable request.

AI STATEMENT

The authors did not use any AI-assisted technologies in the creation of this manuscript or its figures.

COMPETING INTERESTS

The authors declare no competing interests.

SUPPLEMENTARY MATERIAL

Supplementary material **S1**
Supplementary material **S2**
Supplementary material **S3**
Supplementary material **S4**
Supplementary material **S5**
Supplementary material **S6**
Supplementary material **S7**

HOW TO CITE THIS ARTICLE

- **Marx J, Pimentel CR, Rocha LA, Pinheiro HT.** Functional diversity and ecological patterns of reef fish assemblages across depth gradients in oceanic islands of the Brazilian Province. Neotrop Ichthyol. 2026; 24(1):e250035. https://doi.org/10.1590/1982-0224-2025-0035

Neotropical Ichthyology

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