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Assembly processes of fish communities on estuarine and oceanic beaches along the Brazilian coast using taxonomic and functional ß-diversity

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ABSTRACT

Understanding how deterministic niche (traits and environment-driven) and stochastic neutral (randomness and dispersal-driven) processes shape communities is essential for predicting biodiversity. We investigated taxonomic and functional β-diversity in fish assemblages from oceanic and estuarine beaches along the Brazilian coast to test assembly processes. We hypothesized that: (H1) Community assembly varies latitudinally, influenced by temperature, regional factors, and beach type. Niche processes are expected to dominate in estuarine beaches due to environmental gradients, while neutral processes should prevail on oceanic beaches where physical and chemical conditions are more stable and connectivity with the sea is higher; (H2) Niche processes dominate in the Transition and Warm Temperate regions, where steeper environmental gradients are present. In contrast, neutral processes prevail in the Tropical region, driven by temperature stability and greater species dispersal. Using Mantel tests and null model simulations, we found that niche-based processes predominated at latitudinal scale in both beach types, partially rejecting H1. High taxonomic turnover and functional nestedness indicate species replacement with reduced functional diversity. Oceanic beaches, characterized by high water dynamism, showed niche-driven patterns based on β-diversity components. In estuarine beaches, strong local environmental gradients drove niche-based turnover, although nestedness suggested some neutral influence. At regional scale, niche processes were stronger in oceanic beaches of the Transition and Warm Temperate regions, while neutral dynamics dominated in the Tropical region, supporting H2. In estuarine beaches, niche-based processes predominated regionally, though less intensely. These findings show that niche and neutral processes jointly shape fish communities, varying by region and habitat, and underscore the need for region-specific conservation strategies. Estuarine beaches require protection for disturbance-sensitive species, while oceanic beaches benefit from maintaining connectivity. Niche-driven communities are more vulnerable to local impacts, whereas neutral-driven ones are more resilient but still rely on dispersal. Effective coastal management should prioritize connectivity in tropical regions and focus on local conditions and habitat diversity in temperate and transitional zones, supporting targeted, evidence-based conservation under climate and human pressures.

1. Introduction

Sandy beaches are dynamic and ecologically important habitats that support diverse coastal fish assemblages, particularly as nurseries for early life and subadult stages (Blaber and Barletta, 2016; Fulford et al., 2020). Yet, the ecological processes shaping fish communities in sandy beaches are still poorly understood, which hinders efforts to identify priority habitats and develop effective conservation strategies (Capp Vergès et al., 2022). Understanding how these factors drive spatial variation in biodiversity is crucial for developing effective conservation and management strategies in coastal ecosystems facing increasing anthropogenic pressures and climate change.

Fish assemblages in coastal systems are shaped by a combination of deterministic (niche-based) and stochastic (neutral) processes (Chase and Myers, 2011; Ford and Roberts, 2018). Deterministic processes, such as environmental filtering and species interactions, tend to dominate in heterogeneous environments by selecting species with traits adapted to local conditions (Mouillot et al., 2007; Cadotte and Tucker,

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2017). In contrast, stochastic processes such as dispersal limitation, ecological drift, and random colonization, play a stronger role in environmentally homogeneous or highly connected habitats, where community composition becomes less predictable (Shoemaker et al., 2020; Mori et al., 2018).

Estuarine and oceanic beaches provide a natural gradient for investigating these processes. Estuarine beaches, characterized by high environmental variability (e.g., salinity fluctuations, structural heterogeneity), impose strong filters that promote trait-based community assembly (Henriques et al., 2017; Whitfield, 2020). Oceanic beaches, with high hydrodynamics, but more stable salinity and substrate conditions, and stronger connectivity with the open sea, tend to favor stochastic assembly mechanisms, such as dispersal and ecological drift (Ricklefs, 1987; Olds et al., 2018).

Understanding how these processes operate across spatial scales is essential for effective biodiversity conservation. At local scales, community structure is shaped by immediate environmental drivers, such as habitat complexity, salinity, and biotic interactions (Franco and Santos, 2018; Camara et al., 2020). At broader scales, historical, evolutionary and climate factors define regional species pools and biogeographic patterns, such as the latitudinal diversity gradient, where species richness declines with increasing latitude (Anderson et al., 2011; Jackson and Blois, 2015; Gaston, 2000; García-Girón et al., 2020). Integrating local and regional perspectives is essential to understanding the interplay between environmental filtering, dispersal and diversification processes (Halpern et al., 2008; Clavel et al., 2011; Zhang et al., 2024). These insights are particularly important for identifying critical nursery habitats for juvenile and subadult fish, whose use of sandy beaches environment remains poorly understood (Halpern et al., 2008; Blaber and Barletta, 2016).

β-diversity, particularly its components of turnover (species replacement) and nestedness (species loss), is a powerful tool for evaluating spatial variation in community composition and the relative importance of niche and neutral mechanisms (Baselga, 2010; Anderson et al., 2011). Taxonomic β-diversity captures differences in species richness and composition, whereas functional β-diversity reflects differences in the ecological roles species play, offering insights into community resilience and ecosystem functioning (Petchey and Gaston, 2006; Laureto et al., 2015). Assessing both dimensions together allows for a more nuanced understanding of biodiversity patterns and the processes shaping them (Mason et al., 2005; Stuart-Smith et al., 2013; Fang et al., 2025). For instance, turnover dominance may indicate environmental heterogeneity selecting distinct species, whereas nestedness dominance suggests filtering that favours generalists or resilient species (Villéger et al., 2012). Simulated fish communities under neutral and niche-based extinction scenarios can further clarify how those patterns relate to assembly processes (Fang et al., 2025).

Sandy beaches fish assemblages are particularly suitable for identifying assembly processes through taxonomic and functional β-diversity due to their relatively low species richness and strong environmental gradients, which simplify the detection of turnover and nestedness patterns (Defeo and McLachlan, 2005; Baselga, 2010; Legendre and De Cáceres, 2013; Soininen et al., 2018). The predominance of physical drivers over biotic interactions provides clearer insights into how environmental filtering and stochasticity shape community composition across spatial scales (Chase and Myers, 2011; McLachlan et al., 2018). Moreover, their high temporal and spatial variability offers natural experimental gradients that allow repeated testing of community assembly mechanisms in a more controlled and interpretable way than in more complex ecosystems (Able, 2005; Olds et al., 2018; Ford and Roberts, 2018; Whitfield, 2020; Capp Vergès et al., 2022; Montanyès et al., 2023).

The Brazilian coast, extending from 0° to 33°S, offers an exceptional natural laboratory for investigating large-scale biodiversity patterns and their underlying drivers. The region encompasses diverse environmental gradients and distinct biogeographic provinces, providing opportunity to examine how community structure responds to varying climatic conditions, habitat types and degree of connectivity with marine and estuarine systems (Palacio, 1982; Seeliger et al., 1997; Blaber and Barletta, 2016). Previous studies have documented latitudinal gradients in fish diversity across bays, lagoons, and oceanic beaches along this coastline (Araújo and Azevedo, 2001; Araújo et al., 2018). However, little is known about how different types of beaches—oceanic and estuarine—mediate the assembly of fish communities across these gradients.

This study evaluates how niche and neutral processes shape the taxonomic and functional β-diversity of fish assemblages along the Brazilian coast within a latitudinal and regional framework. Specifically, we tested two hypotheses: (H1) Community assembly varies along the latitudinal gradient, influenced by temperature, regional environmental factors, and beach type, with niche processes prevailing in estuarine beaches due to stronger local environmental gradients, whereas neutral processes dominate on oceanic beaches due to more stable physical and chemical conditions and greater connectivity with the sea; and (H2) Niche processes are more prominent in the Transition and Warm Temperate regions, where environmental gradients are steeper, while neutral processes dominate in the Tropical region, driven by temperature stability, ecological drift, and higher species dispersal. We also expect that climatic gradients, distinct coastal species pools, dispersal, and local environmental conditions interact to influence the predominance of these processes, which are not mutually exclusive. By addressing these questions, we aim to advance the understanding of fish community assembly and contribute to biodiversity conservation along one of the world's most extensive and environmentally diverse coastlines.

2. Material and methods

2.1. Study area

The following regions were outlined along the coast of Brazil (Fig. 1): **Tropical Region** – Extending from the northern/northeastern to the upper southeastern coastline of Brazil at north of the Rio de Janeiro State (0–22°S). This coastline features a vast continental shelf with warm waters from the Equatorial and Brazilian currents. The average water temperature ranges from 26 to 31 °C, tide height varies between 2 and 7 m, and annual precipitation ranges from 1700 to 3200 mm (Moraes et al., 2005). This region encompasses various ecosystems, including mangroves and coral reefs. The northeastern coastline, with a regular profile, is interrupted by estuaries and river deltas. **Transition Region** – Extending from the northern coastline of Rio de Janeiro State (22°S) to Cabo de Santa Marta (28.6°S), marking the boundary between the Tropical and Warm Temperate regions. In this area, the tropical climate gradually shifts to a transitional climate before reaching the warm temperate conditions in the far south. The average water temperature ranges from 20 to 28.6 °C, tide height varies between 1.5 and 2.7 m, and annual precipitation ranges from 1700 to 3000 mm (Cerda and Castro, 2014). **Warm Temperate Region** – From the southern Cabo de Santa Marta (28.6°S) to the Chuí estuary (33.7°S). The Subtropical Convergence formed by the mix of the Brazil and Falklands Currents presents temperate characteristics. The average water temperature ranges from 13 to 20 °C, tide height ranges from 0.4 to 1.5 m, and annual precipitation ranges from 1300 to 1500 mm (Palma and Matano, 2009; Johannessen et al., 1967).

2.2. Distribution and occurrence of fish species

An extensive search was conducted on Google Scholar (keywords: fish, sandy beach, estuarine, Brazil) to gather available information on the occurrence of fish in estuarine or oceanic beaches along the entire Brazilian coastline, from the mouth of the Amazon River (0°S) to Chuí estuary (33.7°S). For inclusion in our database, we filtered studies that

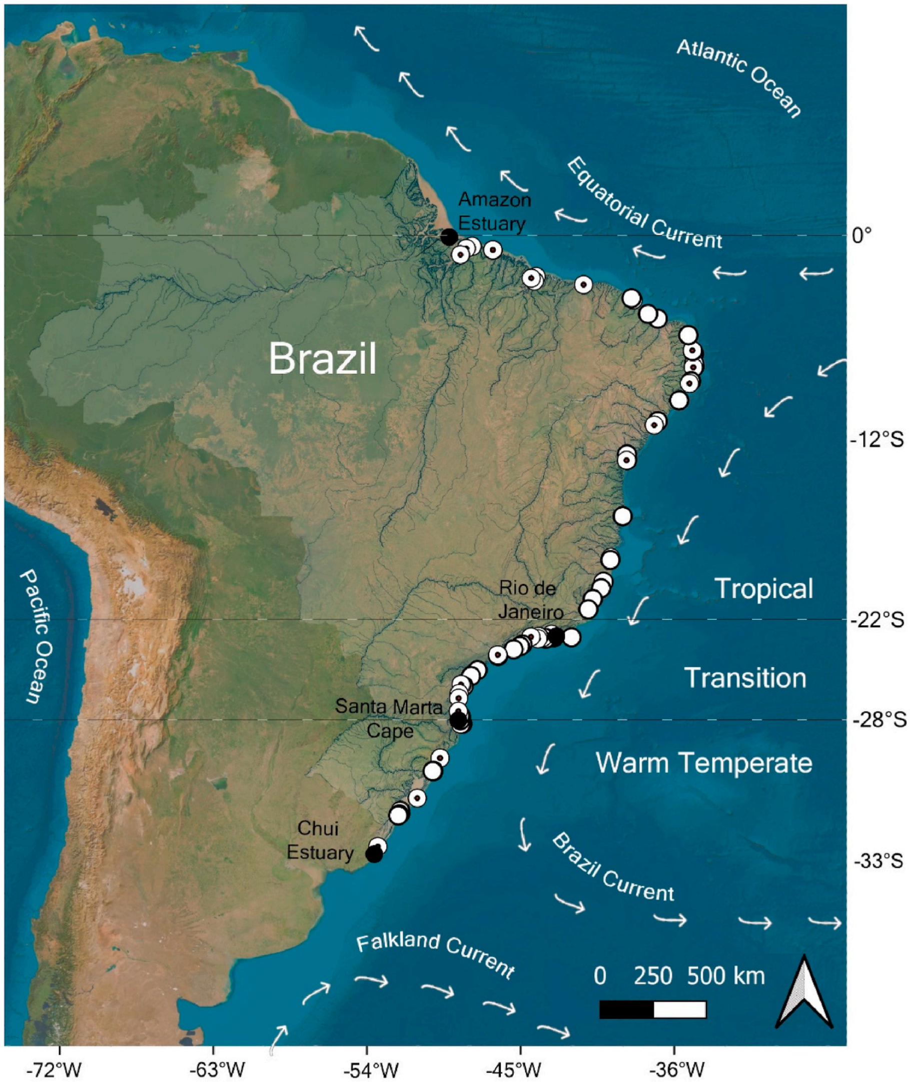

Fig. 1. Study area showing the beaches sampled in the three regions: (Tropical, Transition, and Warm Temperate) along the Brazilian coast. White circles represent oceanic beaches; white circles with a black dot represent estuarine beaches. Black circles represent the boundaries of the considered regions.

(1) used beach seine as the collection method, except on the north coast, where seine net was not available and only gillnets were used for a few collections; (2) provided a complete list of species, and (3) included sampling replicates in the sampled region. In regions with numerous articles, we selected the most comprehensive ones with the highest number of species, ensuring a balanced sampling design, considering the number of articles from other locations. From each selected article, we extracted information on (i) species presence/absence; (ii) geographic coordinates; (iii) beach type (oceanic or estuarine). The final dataset includes a total of 100 articles (Table S1 in the Supplementary Information), revealing 454 fish species inhabiting Brazilian sandy beaches, whether oceanic or estuarine (Table S2). These articles covered 52 estuarine beaches (22 – Tropical, 16 – Transition, 14 – Warm Temperate) and 48 oceanic beaches (16 – Tropical, 18 – Transition, 14 – Warm Temperate) (Fig. 1, Table S1).

2.3. Functional diversity

For functional diversity analysis, seven (7) functional traits were assigned to each of the 454 species in the database (Table S3). We selected traits that reflect habitat use, life history, and trophic and reproductive ecology, which are expected to respond to environmental changes and influence ecosystem functioning —that is, the roles and processes shaped by species' traits, including interactions among organisms and with their environment—with a focus on functional effect traits (Mori et al., 2018; Fulford et al., 2020). These traits play key roles in mediating species interactions and ecological processes. For example, reproductive guilds influence recruitment dynamics, population resilience, and the timing and location of reproductive effort, all of which affect community turnover and the stability of fish populations (Winemiller, 1989; Lowerre-Barbieri et al., 2011). Among these selected traits, five are categorical (body shape, position in the water column, trophic and reproductive guilds, caudal fin shape), one is categorized (habitat use: freshwater, brackish, marine), and one is continuous (maximum body size). Since truly diadromous fish are absent in the Neotropical region, we chose to use the habitat categories of freshwater, brackish, and marine, allowing species to be classified into one, two, or all three of these categories. All traits were identified using a combination of published data and information available in Fishbase (Froese and Pauly, 2021) extracted using the R package rfishbase (version 3.1.6; Boettiger et al., 2012).

To estimate functional diversity, we used Gower distance (Gower, 1966) to calculate pairwise functional distances between species, as our original trait matrix (Table S3) includes a mix of categorical and continuous variables. We then performed a Principal Coordinates Analysis (PCoA) based on this distance matrix and used the first three

PCoA axes to quantify functional diversity (Villéger et al., 2008; Laliberté and Legendre, 2010).

2.4. Data treatment

2.4.1. Decomposition of taxonomic and functional β-diversity

Fish occurrence data were used to calculate taxonomic and functional β-diversity, as well as their decomposition into turnover and nestedness. Taxonomic β-diversity and its components were calculated using the beta. pair function (pairwise dissimilarities based on incidence), which generates three distance matrices, accounting for (1) turnover (replacement), (2) nestedness, and (3) total dissimilarity (i.e., the sum of the two components) (Baselga, 2010). The fish data matrix was combined with the trait matrix to calculate functional β-diversity and its decomposition into turnover-replacement and a nestedness components, using the functional. beta.pair function. This function returns a list with three dissimilarity matrices: (1) turnover, (2) nestedness, and (3) total dissimilarity (i.e., β-diversity or the sum of both components).

The correlations between taxonomic and functional β-diversity, as well as between their respective components, were tested using the Mantel permutation test, a statistical test that evaluates the correlation between two matrices. The partial Mantel test was used to test the correlation between two matrices while controlling for the effect of a third. Partial Mantel tests were performed controlling for the effect of geographic distance and differences in species richness between sites.

2.4.2. Null model of β-diversity correlation coefficient

To test the strength of correlations between taxonomic and functional β-diversity, fish assemblages were permuted under random extinction assembly processes, following Si et al. (2016). We simulated the null model under the "Random Extinction" process, maintaining species occupancy while randomizing species richness (i.e., the random row, fixed column algorithm, or the 'c0′ algorithm) (Jonsson, 2001; Miklós and Podani, 2004). Each simulation was run 100 times. If random extinction is the primary process driving fish assemblage assembly, we expect the observed correlation coefficients (Pearson's r) to fall within the null distributions obtained under the random extinction scenario. Conversely, if random extinction is not the process driving fish assemblage assembly, we expect the observed correlation coefficients to fall outside the null distributions obtained under the random extinction scenario. R scripts for randomization tests simulating random extinction processes were employed following Si et al. (2016), using the "betapart" (Baselga and Orme, 2012), "FD" (Laliberté and Legendre, 2010), and "vegan" (Oksanen et al., 2013) packages. All analyses were conducted in the R environment v. 3.5.1 (R Core Team, 2018).

3. Results

3.1. Fish assemblage composition

Across the 48 oceanic beach sites, a total of 313 fish species were recorded, spanning 35 orders, 80 families, and 187 genera (Table S2). The estuarine beaches, comprising 52 sites, exhibited even greater diversity, with 401 species identified across 35 orders, 87 families, and 229 genera.

When analyzed by region, the Tropical region hosted 309 species on estuarine beaches and 231 species on oceanic beaches. In the Transition region, 205 species on estuarine beaches and 204 species on oceanic beaches. In the Warm Temperate region we recorded 194 species on estuarine beaches and 159 species on oceanic beaches.

3.2. Latitudinal pattern

On oceanic beaches, taxonomic β-diversity ranged from 0.07 to 0.98, with a mean value of 0.80 (±0.002 SE). The mean turnover (0.69) was higher than the nestedness-resultant component (0.11), contributing 86 % to taxonomic β-diversity, while nestedness accounted for 14 %. Functional β-diversity ranged from 0.05 to 0.92, with a mean value of 0.56 (±0.005 SE). On average, turnover (0.20) was lower than the nestedness component (0.36), contributing 36 % to functional β-diversity, while nestedness accounted for 64 %. The mean values of taxonomic and functional β-diversity in oceanic beaches differed significantly ($F = 1858$; $p < 0.001$), with taxonomic β-diversity showing higher values. Taxonomic turnover was significantly greater than functional turnover ($F = 6718$; $p < 0.001$), whereas functional nestedness exceeded taxonomic nestedness ($F = 1026$; $p < 0.001$) (Table S4, Fig. S1 in Supplementary Information).

On estuarine beaches, taxonomic β-diversity ranged from 0.16 to 1, with a mean value of 0.82 (±0.002 SE). The mean turnover (0.73) exceeded the nestedness component (0.09), contributing 89 % to taxonomic β-diversity, while nestedness accounted for 11 %. Functional β-diversity ranged from 0.07 to 0.91, with a mean value of 0.57 (±0.004 SE). The mean functional turnover (0.29) was slightly higher than the nestedness component (0.27), contributing 51 % to functional β-diversity, while nestedness accounted for 49 %. The mean values of taxonomic and functional β-diversity in estuarine beaches differed significantly ($F = 2079$; $p < 0.001$), with taxonomic β-diversity being higher (Fig. 2). Taxonomic turnover was significantly greater than functional turnover ($F = 4124$; $p < 0.001$), while functional nestedness exceeded taxonomic nestedness ($F = 921$; $p < 0.001$) (Table S4, Fig. S1).

The Mantel test revealed significant correlations ($p < 0.001$) between taxonomic and functional β-diversity and their components (turnover and nestedness) on both oceanic and estuarine beaches. Notably, the highest correlation was observed between taxonomic and functional nestedness on oceanic beaches, while the lowest correlation occurred between these components on estuarine beaches. (Table 1, Fig. 2).

Partial Mantel tests, controlling for geographic distance and differences in species richness between sites, also revealed significant correlations. When the effect of geographic distance was removed, the correlation between taxonomic and functional β-diversity remained unchanged in both types of beaches, but their components, turnover and nestedness, increased more markedly on oceanic beaches. When removing the effect of differences in species richness, there was a marked reduction in all correlations for β-diversity and its components on oceanic beaches. In estuarine beaches, a decrease was observed in the relationship between taxonomic and functional β-diversity, while an increase was noted in their components of turnover and nestedness.

After removing the effects of geographic distance and differences in species richness, the most significant correlations were observed between taxonomic and functional β-diversity (0.49), as well as the turnover component (0.49), on estuarine beaches, and between taxonomic β-diversity and nestedness (0.59) on oceanic beaches (Table 1).

3.3. Regional patterns – oceanic beaches

Tropical - Taxonomic β-diversity ranged from 0.12 to 0.93, with a mean value of 0.78 (±0.007 SE). The mean turnover (0.65) was higher than the nestedness component (0.13), contributing 83 % to taxonomic β-diversity, while nestedness accounted for 17 %. Functional β-diversity ranged from 0.1 to 0.87, with a mean value of 0.51 (±0.01 SE). On average, turnover (0.15) was lower than the nestedness-resultant component (0.36), contributing 29 % to functional β-diversity, while nestedness contributed 71 %. The means between taxonomic and functional β-diversity were significantly different ($F = 268$; $p < 0.001$), with taxonomic β-diversity showing higher values. Taxonomic turnover was significantly greater than functional turnover ($F = 977$; $p < 0.001$), while functional nestedness was significantly greater than taxonomic nestedness ($F = 102.7$; $p < 0.001$) (Fig. S2).

Transition - Taxonomic β-diversity ranged from 0.53 to 0.9, with a mean value of 0.77 (±0.006 SE). The mean turnover (0.63) was higher

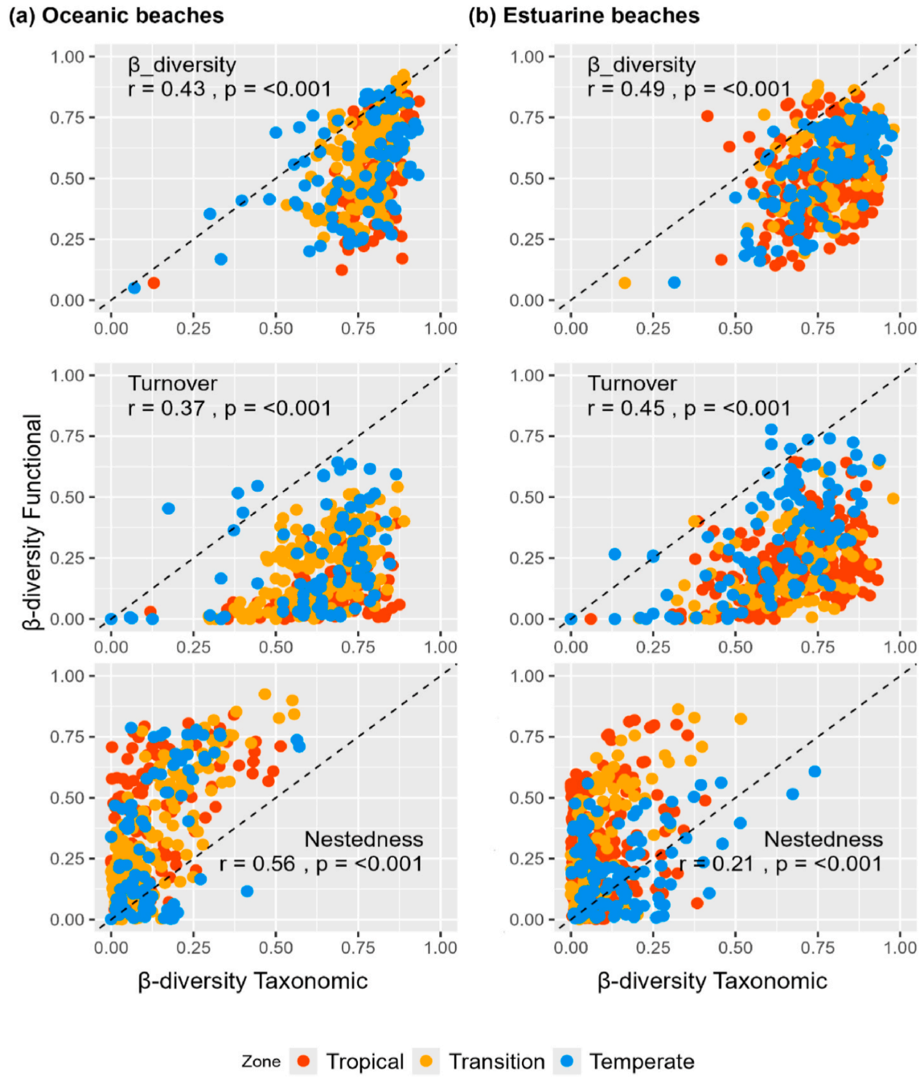

Fig. 2. Correlations between taxonomic and functional β-diversity for fish assemblages on oceanic beaches (a) and estuarine beaches (b), including their turnover and nestedness components. Each plot displays Pearson correlation coefficients and the corresponding Mantel test p-values ($p < 0.001$). Point colours represent different zones: Tropical (red), Transition (orange), and Warm Temperate (blue). The black dashed line indicates the identity line ($y = x$). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Mantel and partial Mantel test results for the components of taxonomic and functional β-diversity. Partial Mantel tests account for the effects of differences in species richness and geographic distance between sites. Values represent Pearson correlation coefficients and the associated p-values (***$p < 0.001$).

	Mantel test	Partial Mantel test	
		Geographic distance	Difference in species richness
Oceanic Beaches			
Taxonomic vs Functional β-diversity	0.43***	0.43***	0.23***
Taxonomic vs Functional turnover	0.37 ***	0.43***	0.29***
Taxonomic vs Functional nestedness	0.56 ***	0.59***	0.18**
Estuarine beaches			
Taxonomic vs Functional β-diversity	0.49 ***	0.49***	0.43***
Taxonomic vs Functional turnover	0.45***	0.47***	0.49***
Taxonomic vs Functional Nestedness	0.21 ***	0.23***	0.24***

than the nestedness-resultant component (0.14), contributing 81 % to taxonomic β-diversity, while nestedness accounted for 19 %. Functional β-diversity ranged from 0.22 to 0.91, with a mean value of 0.56 (±0.01 SE). On average, turnover (0.21) was lower than the nestedness-resultant component (0.35), contributing 38 % to functional β-diversity, while nestedness contributed 62 %. The means between taxonomic and functional β-diversity were significantly different ($F = 222$, $p < 0.001$), with taxonomic β-diversity showing higher values. Taxonomic turnover was significantly greater than functional turnover ($F = 664.2$, $p < 0.001$), while functional nestedness was significantly greater than taxonomic nestedness ($F = 96.31$, $p < 0.001$) (Fig. S2).

Temperate - Taxonomic β-diversity ranged from 0.07 to 0.93, with a mean value of 0.75 (±0.01 SE). The mean turnover (0.61) was higher than nestedness (0.13), contributing 81 % to taxonomic β-diversity, while the nestedness component represented 19 %. Functional β-diversity ranged from 0.16 to 0.78, with a mean value of 0.49 (±0.03 SE). On average, turnover (0.20) was lower than nestedness (0.29), contributing 41 % to functional β-diversity, while nestedness accounted for 59 %. The means values of taxonomic and functional β-diversity differed significantly ($F = 111.3$; $p < 0.001$), with taxonomic β-diversity being higher. Taxonomic turnover was significantly greater than functional turnover ($F = 271.4$; $p < 0.001$), whereas functional nestedness was significantly greater than taxonomic nestedness ($F = 36.86$; $p < 0.001$) (Fig. S2).

3.3.1. Mantel test

In the Tropical region, the Mantel test revealed a significant correlation between functional β-diversity and taxonomic β-diversity, as well as between their components (turnover and nestedness), with the highest correlation observed between taxonomic and functional nestedness (Table 2). After removing the effect of geographic distance, these correlations remained largely unchanged. However, when controlling for differences in species richness between sites, partial Mantel tests revealed a sharper decrease in the correlation between taxonomic and functional β-diversity (0.30) and turnover (0.18), while the correlation between taxonomic and functional nestedness became non-significant (Table 2).

In the Transition region, taxonomic and functional β-diversity, along with their components, showed significant correlations, with the highest correlation observed between taxonomic and functional nestedness. After removing the effect of geographic distance did not change the correlation between taxonomic and functional β-diversity, and their components. However, when the effect of differences in fish species richness was removed, a strong decrease although significant in these correlations was found which the strongest correlation been recorded between taxonomic and functional turnover (Table 2).

In the **Temperate region,** taxonomic and functional β-diversity, along with their components, were significantly correlated, with the highest correlations observed between taxonomic and functional nestedness. After removing the effects of geographic distance and species richness differences between sites, partial Mantel tests still indicated significant correlations. While removing the effect of geographic distance had little impact on these correlations, removing the effect of species richness caused all correlations to decrease sharply, although they remained significant, with the strongest values still found between taxonomic and functional nestedness (Table 2).

Table 2
Mantel tests between taxonomic and functional β-diversity components for oceanic beaches. Partial Mantel tests account for differences in species richness and/or geographic distance between sites. The values are Pearson correlation coefficients and the associated p-values from the Mantel tests (***$p < 0.001$).

	Mantel test	Partial Mantel test	
		Geographic distance	Diff. Difference in species richness
Tropical			
Taxonomic vs Functional β-diversity	0.52***	0.52***	0.30***
Taxonomic vs Functional turnover	0.35 ***	0.31***	0.18*
Taxonomic vs Functional nestedness	0.58 ***	0.57***	0.01n.s.
Transition			
Taxonomic vs Functional β-diversity	0.47***	0.50***	0.21*
Taxonomic vs Functional turnover	0.57***	0.58***	0.36**
Taxonomic vs Functional nestedness	0.80***	0.80***	0.32**
Warm Temperate			
Taxonomic vs Functional β-diversity	0.56***	0.58***	0.21*
Taxonomic vs Functional turnover	0.54 ***	0.59***	0.38**
Taxonomic vs Functional nestedness	0.69 ***	0.67***	0.42***

3.4. Regional patterns – estuarine beaches

Tropical - Taxonomic β-diversity ranged from 0.41 to 0.94, with an average value of 0.77 (±0.006 s. e.). The average turnover (0.68) was greater than nestedness (0.09) and contributed 88 % to taxonomic β-diversity, while the nestedness component contributed 12 %. Functional β-diversity ranged from 0.1 to 0.83, with an average value of 0.51 (±0.001). The average turnover (0.22) was lower than the nestedness component (0.28) and contributed 45 % to functional β-diversity, while nestedness contributed 55 %. The averages between taxonomic and functional β-diversity were significantly different ($F = 439.9$; $p < 0.001$), with higher values for taxonomic β-diversity. Taxonomic turnover was significantly higher than functional turnover ($F = 1248$; $p < 0.001$), while functional nestedness was significantly higher than taxonomic nestedness ($F = 202.3$; $p < 0.001$) (Fig. S3).

Transition - Taxonomic β-diversity ranged from 0.16 to 0.97, with an average value of 0.75 (±0.01 s. e.). The average turnover (0.64) was greater than nestedness (0.11) and contributed 70 % to the taxonomic β-diversity, while the nestedness component contributed 30 %. Functional β-diversity ranged from 0.12 to 0.83, with an average value of 0.52 (±0.01 s. e.). On average, turnover (0.20) was lower than nestedness (0.32) and contributed 39 % to the functional β-diversity, while nestedness contributed 61 %. The means between taxonomic and functional β-diversity were significantly different ($F = 126.4$; $p < 0.01$), with higher values for functional β-diversity. Taxonomic turnover was significantly different from functional turnover ($F = 358.5$; $p < 0.001$), with higher values for taxonomic turnover, while functional nestedness was significantly higher than taxonomic nestedness ($F = 67.35$; $p < 0.001$) (Fig. S3).

Temperate - Taxonomic β-diversity ranged from 0.31 to 0.97, with a mean value of 0.76 (±0.01 s. e.). The average turnover (0.62) was higher than the component resulting from nestedness (0.14), contributing 81 % to the taxonomic β-diversity, while the nestedness component contributed 19 %. Functional β-diversity ranged from 0.07 to 0.81, with a mean value of 0.54 (±0.01). On average, turnover (0.34) was greater than nestedness (0.20), contributing 63 % to functional β-diversity, while nestedness contributed 37 %. The means between taxonomic and functional β-diversity were significantly different ($F = 143.3$; $p < 0.001$), with higher values for functional β-diversity. Taxonomic turnover was significantly greater than functional turnover ($F = 107.4$; $p < 0.001$), while functional nestedness was significantly greater than taxonomic nestedness ($F = 10.25$; $p < 0.001$) (Fig. S3).

3.4.1. Mantel test

In the Tropical region, the Mantel test revealed significant correlations between taxonomic and functional β-diversity, as well as between their components (turnover and nestedness). The highest correlation was found between taxonomic and functional turnover. After removing the effects of geographic distance and differences in species richness between sites, partial Mantel tests still indicated significant correlations. Removing the effect of geographic distance caused the correlation between taxonomic and functional β-diversity and between taxonomic and functional turnover to decrease, while nestedness remained unchanged. When the effect of species richness differences was removed, the correlation between taxonomic and functional β-diversity decreased, while the correlation between their components (turnover and nestedness) increased (Table 3).

In the Transition region, taxonomic and functional β-diversity, along with their components, were significantly correlated according to the Mantel test, with the highest correlation observed between taxonomic and functional nestedness. After controlling for geographical distance and differences in species numbers between sites, partial Mantel tests revealed both significant and non-significant correlations. Specifically, after accounting for geographical distance, the correlation between taxonomic and functional β-diversity, as well as their turnover components, increased, while the nestedness component remained unchanged.

Table 3
Mantel tests examining the relationships between taxonomic and functional β-diversity components for estuarine beaches. Partial Mantel tests control for differences in species richness and/or geographical distance between sites. The values represent Pearson correlation coefficients and the corresponding p-values for the Mantel tests (*p < 0.05, **p < 0.01, ***p < 0.001).

	Mantel test	Partial Mantel test	
		Geographic distance	Difference in species richness
Tropical			
Taxonomic vs. Functional β-diversity	0.30 **	0.20**	0.25**
Taxonomic vs Functional turnover	0.51***	**0.41*****	0.57 ***
Taxonomic vs Functional nestedness	0.26***	0.25**	0.31**
Transition			
Taxonomic vs Functional β-diversity	0.45**	0.51**	**0.28 n.s.**
Taxonomic vs Functional turnover	0.40**	0.42**	0.38**
Taxonomic vs Functional nestedness	0.72***	0.72***	0.33**
Warm Temperate			
Taxonomic vs Functional β-diversity	0.66***	0.42***	0.62 ***
Taxonomic vs Functional turnover	0.58***	0.31**	0.63***
Taxonomic vs Functional nestedness	0.35***	0.29**	0.50**

However, after controlling for differences in fish species numbers, the correlation between taxonomic and functional β-diversity became non-significant, with a notable decrease in the correlation of their components, especially nestedness. (Table 3).

In the Warm Temperate region, taxonomic and functional β-diversity, along with their components, were significantly correlated, with the highest correlation observed between taxonomic vs. functional β-diversity. After removing the effect of geographical distance, the correlation between taxonomic and functional β-diversity and their components decreased but remained significant. When controlling for differences in fish species richness, the correlation between taxonomic and functional β-diversity decreased, while the correlation between their taxonomic and functional components increased, all remaining significant and exhibiting higher correlations compared to the influence of geographical distance (Table 3).

3.5. Null model of β-diversity correlation coefficients

3.5.1. Latitudinal pattern

For oceanic beaches, randomization tests across all collected sites (the entire Brazilian coast) showed that the observed correlation coefficients for taxonomic vs. functional β-diversity, and its components (turnover and nestedness), were outside the null distributions (Fig. 3). This indicates that the observed patterns significantly differed from the null expectations of random extinction.

For estuarine beaches, randomization tests showed that the observed nestedness correlation coefficients fell within the null distributions. This indicates that the patterns match the null expectations of random extinction (Fig. 3). In contrast, for β-diversity and turnover, the observed correlation coefficients fell outside the null distributions, indicating significant deviations from the null expectations of random extinction. This suggests that β-diversity and turnover reflect a predominance of niche processes, while nestedness indicates a neutral process, with two of the three indicators suggesting that niche processes prevailed.

3.5.2. Regional pattern

On oceanic beaches, randomization tests conducted for the Tropical, Transition, and Temperate regions revealed a similar pattern in the Transition and Temperate regions. In these both regions, all the three observed correlation coefficients fell outside the null distributions, indicating significant deviation from the null expectations of random extinction. In contrast, a distinct pattern was observed in the Tropical region, where, the observed correlation coefficients for turnover and nestedness fell inside the null distributions indicating neutral processes, while for β-diversity remained outside the null distributions of random extinction, suggesting niche processes (Fig. 4). These results suggest niche processes in the Warm Temperate and Transition regions, whereas neutral processes, particularly related to turnover and nestedness dominate in the Tropical region.

On estuarine beaches, randomization test results revealed distinct regional patterns (Fig. 4). In the Tropical region, nestedness fell within the null distributions, suggesting random extinction. However, β-diversity and turnover, had observed correlation coefficients outside the null distributions, indicating significant deviations from random extinction. In the Transition region, turnover and nestedness were within the null distributions, suggesting random extinction, while β-diversity fell outside, indicating niche processes. In the Warm Temperate region, nestedness also aligned with random extinction, whereas β-diversity and turnover deviate significantly, suggesting niche processes. These results indicate that niche processes prevail in the Warm Temperate region and, to a lesser extent, in the Tropical region, while the Transition region is dominated bv neutral processes.

4. Discussion

4.1. Taxonomic and functional β-diversity

Our results reveal higher taxonomic β-diversity than functional β-diversity across estuarine and oceanic beaches along the Brazilian coast. This suggests that, latitudinally, different species perform similar ecological roles, resulting in taxonomically distinct yet functionally redundant assemblages. On oceanic beaches, wide larval and juvenile fish dispersal through currents leads to species turnover, but only functionally similar species persist due to shared environmental constraints (Layman, 2000; Borland et al., 2017; Olds et al., 2018). Thus, communities may differ taxonomically, while remaining functionally similar in traits such as trophic levels or morphology (Villéger et al., 2012; McLean et al., 2019; Fang et al., 2025). Villéger et al. (2012) found a similar pattern in the Gulf of Mexico, where high taxonomic β-diversity co-occurred with low functional β-diversity along strong environmental gradients. Likewise, Dolbeth et al. (2016) reported functional redundancy in estuaries due to physiological constraints. In contrast, local studies in semi-enclosed systems, such as tropical bays and lagoons, have reported higher functional than taxonomic β-diversity, suggesting functional differentiation at finer spatial scales (Araújo et al., 2019; Hernández-Mendonza et al., 2024). This contrasting pattern highlights the influence of spatial scale on biodiversity-function relationships (Hooper et al., 2005). It is also important to consider that the functional composition may depend on the traits used and that this may influence the relationship between taxonomic composition and ecological functions.

The predominance of taxonomic turnover and functional nestedness at the latitudinal scale suggests that species replacement exceeds species loss, yet with notable functional decline. These components reflect distinct ecological processes: turnover indicates species replacement, while nestedness signals of functional loss due to environmental filtering (Baselga, 2010; Carvalho et al., 2012; Bevilacqua and Terlizzi, 2020). Similar patterns were observed by Rbiai et al. (2024) off the South Atlantic coast of Morocco While turnover introduces new trait combinations, nestedness often results in the loss of unique traits, threatening ecosystem functions. As shown by Petchey et al. (2004) the impact of species loss on ecosystem functioning depends on food web structure and the trophic role of the lost species. Overall, these findings

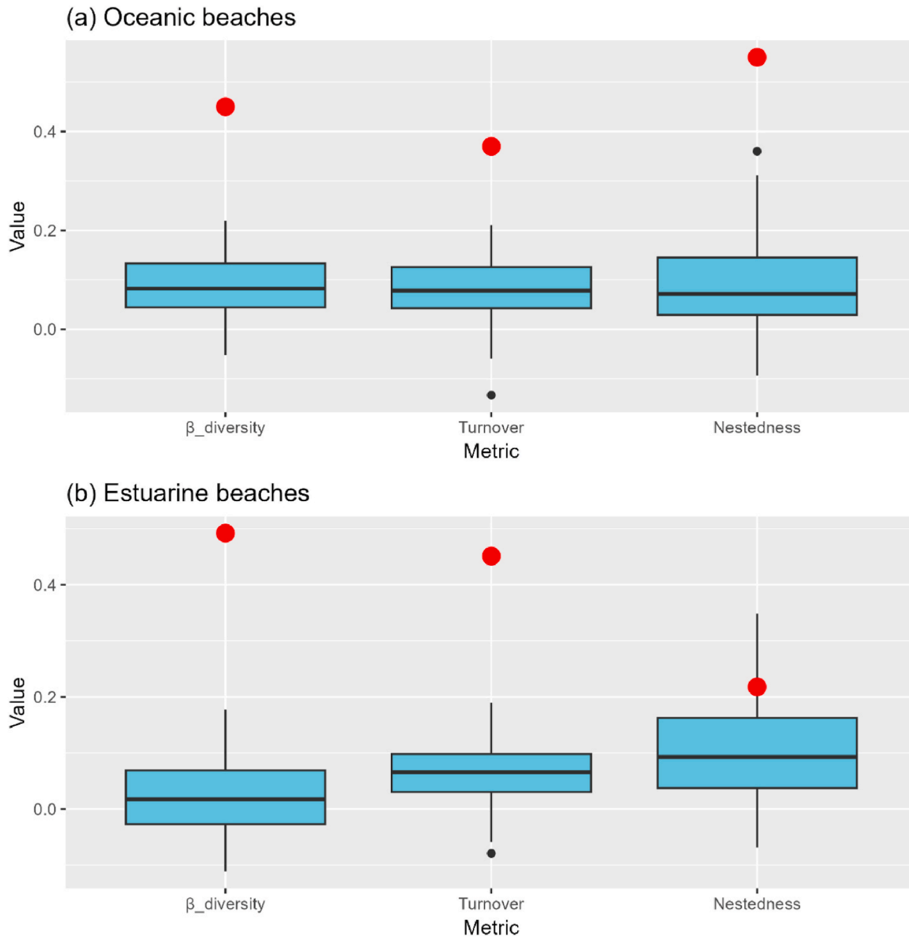

Fig. 3. Results of randomization tests for oceanic beaches (a) and estuarine beaches (b) along the entire coast, based on the null model "c0" (fixed column, random row; preserves species occupancy). Red points indicate the observed correlation coefficients between taxonomic and functional β-diversity and their turnover and nestedness components. The middle lines of the boxes represent the median values of the null distributions. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

underscore the complex dynamics between turnover and nestedness, with key implications for ecosystem stability and resilience.

The strong correlation between taxonomic and. functional turnover and the weak correlation between their nestedness in estuarine beaches likely reflect the influence of diverse local environmental drivers, such as low ocean connectivity, pronounced environmental gradients, high habitat heterogeneity, and limited species dispersal. Estuarine beaches, being shallow and variable environments, support high niche diversity and limited access to the regional species pool (Azevedo et al., 2017; Andrade-Tubino et al., 2020). In contrast, oceanic beaches are high-energy habitats but physically and chemically stable and highly connected to the regional pool, with lower niche diversity (Bernabeu et al., 2012; Borland et al., 2017). In oceanic beaches, controlling for species richness notably reduced β-diversity correlations, especially nestedness, indicating that richness strongly drives taxonomic and functional structure. This suggests that species loss does not necessarily entail functional loss, likely due to functional redundancy or broader functional diversity in species-rich communities (Ulrich and Gotelli, 2007; Maestre et al., 2011). Overall, the reduced correlation under richness control highlights that ecological functions may persist through environmental filtering and dispersal processes, even with low taxonomic diversity (Baselga, 2012; Soininen et al., 2018). This pattern may be particularly evident in oceanic beaches, where environmental conditions (e.g., salinity, substrate, wave exposure) are relatively homogeneous and select for species with similar functional traits. As a result, even when species turnover occurs, key ecological roles may be maintained, suggesting a degree of functional insurance that supports ecosystem functioning despite taxonomic change.

The high functional nestedness in oceanic beaches suggests that landscape connectivity shapes fish functional diversity, leading to a greater loss of functions. These assemblages appear as subsets of more diverse ones, reflecting spatial variations in the marine habitats. Although oceanic beaches are often considered structurally simple and homogenous (Borland et al., 2017; Henderson et al., 2020), those connected to estuarine and reef habitats can be functionally rich and productive (Henderson et al., 2022). This highlights the role of habitat proximity in structuring functional space. In contrasts, estuarine beaches showed similar levels of nestedness and turnover, indicating a more balance between function replacement and loss. The stability appears driven by dominant functional groups, where species shift in response to environmental filters, a pattern also noted by Gomes-Gonçalves and Araújo (2024) in a tropical bay.

Our study found no significant effect of geographic distance on the correlation between taxonomic and functional β-diversity or their components in oceanic beaches, at either the latitudinal or regional scales, as the Mantel and Partial Mantel tests yielded similar results. This challenges the assumption that β-diversity increases with distance in open-ocean fish communities, as it yielded essentially the same results. The generalization of β-diversity patterns in fish assemblages has been questioned, particularly the paradigm that β-diversity increases with geographic distance in open-ocean fish communities —a notion also questioned by Forget et al. (2020), who found no distance effect across

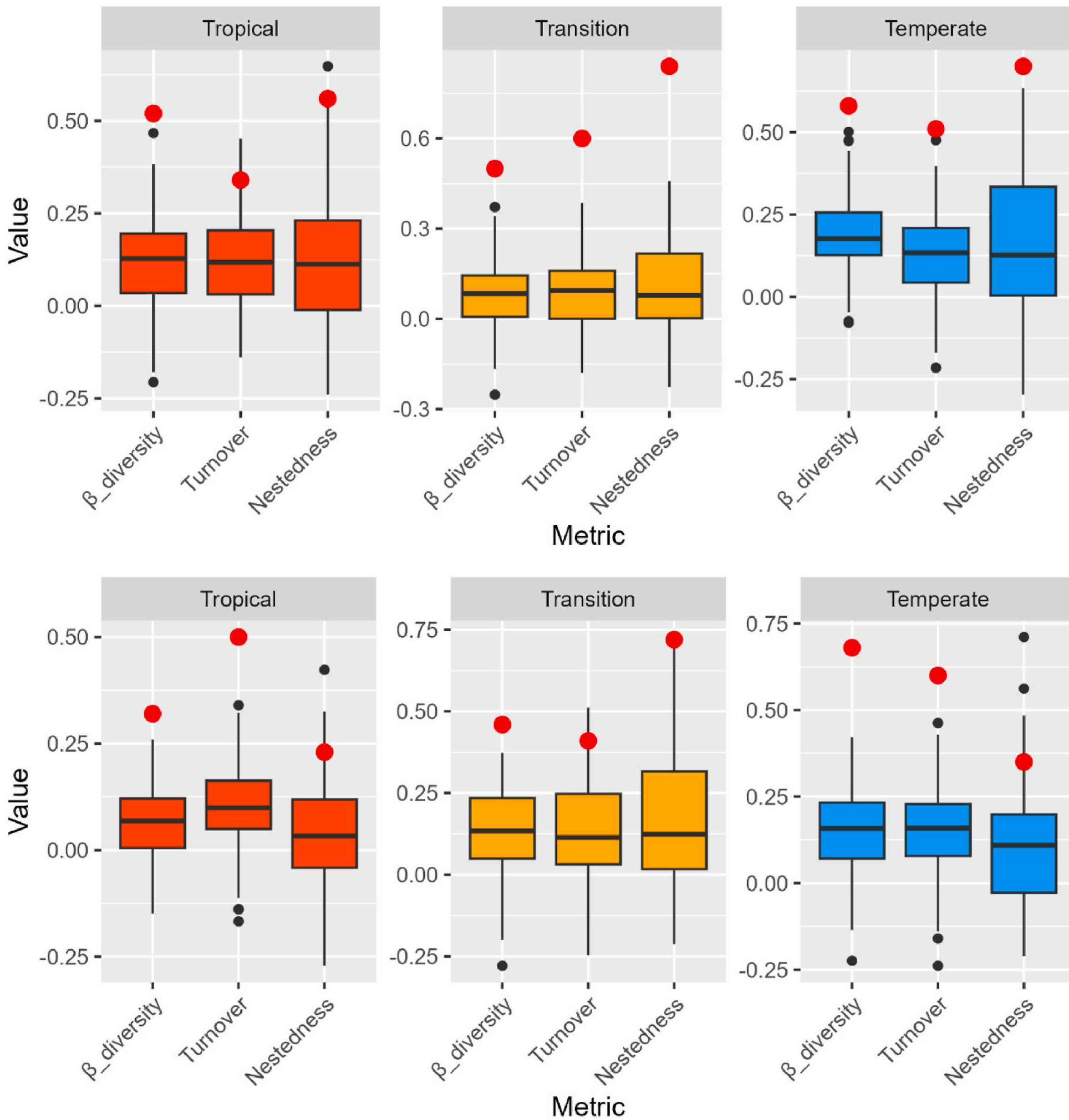

Fig. 4. Results of randomization tests by region (Tropical, Transition, and Warm Temperate) for oceanic beaches (above) and estuarine beaches (below), based on the null model "c0" (fixed column, random row; preserves species occupancy). Red points indicate the observed correlation coefficients between taxonomic and functional β-diversity and their turnover and nestedness components. Outliers are displayed as black points. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

sites up to 257 km apart. This may reflect high connectivity in oceanic systems, where larval dispersal and limited physical barriers reduce spatial turnover. In contrast, distance significantly affects estuarine beaches in the Tropical region and Warm Temperate regions, where controlling for distance sharply reduce correlations suggesting that dispersal limitation and environmental variation play a great role. While the wide extent of the Tropical region may explain its pattern, the Warm Temperate results—despite narrower latitudinal range—points to local and macroecological drivers. In such cases, effective distance may distance may reflect environmental heterogeneity more than spatial separation (McLean et al., 2021; Jarquín-;Martínez et al., 2024). Similar findings at local scales, (Araújo et al. (2019) support the broader view that environmental similarity more than geographic proximity, structures β-diversity (Rouquette et al., 2013; Graco-Roza et al., 2022; Bevilacqua et al., 2023; Jiang et al., 2024).

After controlling for species richness, the correlation between taxonomic and functional β-diversity differed by beach types. At the latitudinal scale, species richness influences β-diversity correlations on oceanic beaches but not on estuarine beaches. This effect was strongest in tropical oceanic beaches, where correlations dropped sharply—becoming non-significant for nestedness and weak for turnover. In estuarine beaches, richness effects were limited to the Transition region, where the correlations also became non-significant after adjustment. These finding highlights the context-dependent rose of species richness in shaping β-diversity patterns.

Both beach types in the Transition region exhibited the strongest correlations between taxonomic and functional nestedness, which declined significantly after accounting for species richness. This likely reflects the biogeographic boundary between Tropical and Warm Temperate regions, where taxonomic and functional diversity are lower. Functional nestedness, exceeding taxonomic nestedness, may result from geographical isolation, diversity declines with distance from biodiversity centers (Bender et al., 2017). Similar patterns were observed by Bevilacqua and Terlizzi (2020) in benthic fauna. Thus, transition zones, may reflect nested species loss shaped by proximity to tropical and temperate diversity centers.

In the Tropical and Warm Temperate estuarine beaches, correlations between taxonomic and functional β-diversity components increased after controlling for species richness, indicating that richness differences initially masked underlying patterns. This aligns with previous studies (Baselga, 2012; Loiseau et al., 2017) and underscores the importance of accounting for species richness when analyzing β-diversity.

4.2. Community assembly

At the latitudinal scale, niche processes primarily structured fish community on both oceanic and estuarine beaches, partially rejecting H1 as we expected this type of process to occur only on estuarine beaches. Taxonomic turnover dominated β-diversity in both beach types, while functional nestedness was more prominent in oceanic beaches. In estuarine beaches, both functional components contributed equally. Overall, taxonomic and functional β diversity patterns support niche-driven assembly, except for functional nestedness in estuarine beaches, which suggests neutral processes.

Environmental heterogeneity drives niche processes in estuarine beaches (Oliveira and Pessanha, 2014; Gomes-Gonçalves and Araújo, 2024), while high connectivity in both beach types likely reinforce environmental filtering and niche-based assembly. In oceanic beaches, high taxonomic turnover and functional nestedness suggest suggested species replacement shaped by habitat proximity of habitats and environmental gradients (Berkström et al., 2012; Vellend et al., 2014; Henderson et al., 2022). Connectivity with adjacent habitats, such as reefs and mangroves support this pattern (Bernabeu et al., 2012), as many species use multiple habitats (Berkström et al. (2012) and rely on estuaries (Vila-Nova et al., 2011). As a result, fish assemblages in oceanic beaches appear as nested subsets of richer communities, shaped by niche filtering and non-random functional loss. While Ford and Roberts (2018) reported strong neutral influences in fish community assembly along a tropical-temperate gradient in Australia, they found niche filtering dominant at regional scales—echoing our findings that niche processes prevail latitudinally along the Brazilian coast, except for functional nestedness in estuarine beaches, which suggests a neutral component.

At the regional scale, niche-related processes dominate in oceanic beaches of the Transition and Warm Temperate regions, supporting H2. In the Tropical region, however, H2 was only partially supported: turnover and nestedness suggested neutral processes, while overall β diversity indicate niche influences. This aligns with the view that niche and neutral processes form a continuum rather being mutually exclusive (Vellend et al., 2014; Bosch et al., 2021). Our findings reflect this gradient, with neutral processes more prevalent at low latitudes and niche filtering increasing toward higher latitudes.

In estuarine beaches, results partially rejected H2 across all regions. In the Tropical region β-diversity and turnover indicated niche processes, while nestedness suggested neutral processes. In the Transition region, turnover and nestedness pointed to neutral processes, but β-diversity indicated niche influences. In the Warm Temperate region, β-diversity and turnover supported niche processes, with nestedness reflecting neutral processes. These patterns align with Vilar et al. (2013), who found that environmental filters and dispersal shape fish communities in Brazilian estuaries. Overall, our findings underscore the interplay of niche and neutral processes, shaped by local environmental conditions across regions.

This study shows that niche and neutral assembly processes are not mutually exclusive and vary with scale and analytical approach. Along the Brazilian coast, the transition from tropical climate to warm temperate climates shapes biotic composition and ecosystem dynamics. Regional differences in species richness and taxonomic diversity reflect environmental and ecological variation (Araújo et al., 2018), while estuarine habitat complexity and filtering influence fish assemblage (Oliveira and Pessanha (2014). Recognizing the interplay between niche and neutral processes is essential for coastal biodiversity management.

While our study focuses on natural assembly processes, human activities—such as coastal development, pollution, and overfishing—can alter fish communities by removing sensitive or functionally distinct species, potentially contributing to functional nestedness or mimicking natural processes (Clavel et al., 2011; Mouillot et al., 2013). These impacts are typically greater in estuarine areas due to urban proximity, ports, and fisheries (Halpern et al., 2008; Fulford et al., 2020), whereas oceanic beaches are generally less affected (Defeo et al., 2009). Thus, human influence may partially explain the functional and compositional patterns observed.

This study advances understanding of taxonomic and functional β-diversity in coastal fish communities along the Brazilian coast, revealing how community assembly processes vary across latitude. The contrasting roles of turnover and nestedness underscore the importance of consider multiple biodiversity dimensions (Soininen et al., 2018). By testing hypotheses within an assembly framework, we highlight the influence of environmental type, geographical location, and regional species pool. These findings inform targeted conservation strategies and offer a foundation for future research on tropical coastal fish assemblages.

CRediT authorship contribution statement

Francisco Gerson Araújo: Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization. **Wagner Uehara:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Márcia Cristina Costa de Azevedo:** Writing – review & editing, Supervision, Methodology, Formal analysis. **Gustavo Henrique Soares Guedes:** Writing – review & editing, Validation, Software, Methodology, Formal analysis.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2025.107360.

Data availability

Data will be made available on request.

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