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Unraveling trait-based fish community assembly in tropical reservoirs

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Abstract

Damming of large rivers has promoted well-documented ecosystem changes that constitute critical threats to freshwater fish biodiversity. However, it is unclear how trait–environment relationships drive community assembly in older (>50 years) tropical river-reservoir systems. We assessed physical features filtering functional traits (RLQ and fourth-corner approaches) in seven tropical reservoirs along a major river, in southeastern Brazil, and correlated taxonomic and functional counterparts of local and beta diversity to assess niche-based assembly processes under prevailing environmental conditions (null model approach). Lower littoral habitat availability (smaller area, volume, and riverine influence) favored species inhabiting open areas that feed on the bottom (mostly migratory species). Downstream position (lower elevation and inflow of water from the mainstem) allowed migrators to enter the reservoirs and promoted environmental heterogeneity, favoring detritivores, invertivores, and carnivorous generalists. Total blocking of the main channel excluded most migratory species from reservoirs at upstream reaches, whereas higher riverine influence and hydrological stability (larger area, volume, and water residence time) favored small-sized sedentary species (omnivores and piscivores with parental care, mostly non-native species) in the littoral zone. Correlations differing from null expectations for alpha diversity and nestedness revealed that niche-based processes support species richness and loss under higher riverine influence and hydrological stability. Our study supports the importance of physical features to set functional spaces available for fish species, but random processes that boost taxonomic differences between reservoirs, largely related to non-native species introductions, are the primary drivers of fish assemblage structure in tropical reservoirs long-term disconnected from riverine dynamics.

KEYWORDS

freshwater fish, functional groups, null model, partitioning beta diversity, trait–environment relationships

1 | INTRODUCTION

Understanding how different processes interact to promote community assembly patterns is essential to mitigate the unprecedented

biodiversity loss related to human pressures observed currently (Su et al., 2021; Viana et al., 2016). Multidimensional ecological mechanisms underpin biodiversity patterns by driving variation in different elements of life forms (Naeem et al., 2016). Therefore, effective

advances in the knowledge of assembly processes depend on multifaceted biodiversity assessments (Altermatt et al., 2020; Zbinden et al., 2022). In the last decade, theoretical and methodological efforts have been strongly focused on simultaneously investigating the taxonomic and trait-based structure of communities (Villéger et al., 2017; Weiss & Ray, 2019). These complementary approaches allow measurement of the ecological importance of species and how their traits influence the structure and dynamic of communities, as well as their responses to human pressures (Cadotte et al., 2015).

Functional trait analysis may reveal how community structure is shaped by morphological, physiological, and behavior attributes of species that are selected along environmental gradients (Weiss & Ray, 2019). Different traits may be associated with different assembly processes and can be used to assess the importance of major deterministic processes structuring communities in space and time (Ford & Roberts, 2020). Niche processes determine that only species with suitable suits of traits occur under particular environmental conditions (environmental filtering) and species interactions (Chase & Myers, 2011). In this scenario, diversity patterns result from functional convergences and divergences along ecological gradients (Bower & Winemiller, 2019; Mouchet et al., 2013). Therefore, different patterns of community structure may arise from the interaction between different functional traits and different constraints on the number and identity of the species (Lin et al., 2021).

Mechanisms promoting assembly processes may also be revealed by taxonomic and functional measures of beta diversity expressing directional variations in species composition and functional space filled by species (Baselga, 2010; Villéger et al., 2013). Partitioning overall beta diversity into components of turnover (i.e., replacement processes) and nestedness of assemblages based on species or functional traits allows the assessment of the processes supporting such directional changes (Baselga, 2012). The strength of the concordance between taxonomic and functional components may, in turn, reveal the importance and nature of niche-based community assembly (Si et al., 2016). Likewise, neutral processes, such as ecological drift (i.e., demographic stochasticity), random dispersal, disturbances, and speciation, also influence community assembly patterns over different spatial and temporal scales (Chase & Myers, 2011; Ford & Roberts, 2018). Therefore, community structure is a product of the interaction between niche-based and stochastic assembly processes, and complementary analytical frameworks may be useful to disentangle their relative importance (Dray et al., 2014; Mori et al., 2015). The unified neutral theory of biodiversity and biogeography assumes the ecological equivalence of species under scenarios where trade-offs between performances on different competitive aspects strongly reduce the potential for competitive exclusion (Hubbell, 2006). Quantitative null models derived from this theoretical framework allow the testing of the necessity to investigate ecological differences between species to explain observed community patterns (Jonsson, 2001; Miklós & Podani, 2004).

River damming creates new ecosystems, changing physical and chemical characteristics by transforming lotic systems into lentic habitats (Agostinho et al., 2016; Granzotti et al., 2018; Tundisi &

Matsumura-Tundisi, 2003). These changes promote habitat loss, changes in resource availability, and limitation of riverine connectivity, increasing extinction risk of endemic taxa and favoring invasions by non-native species and prevalence of generalist species (Araújo et al., 2013; Fitzgerald et al., 2018; Liermann et al., 2012). Dams thus can act as environmental filters strongly selecting functional traits, and generating long-lasting changes to the structure of fish assemblages (Lima et al., 2018; Oliveira et al., 2018). The fish species most affected by reservoirs are those that migrate, whereas small-sized sedentary species with high reproductive potential and the ability to feed on the available food items are favored (Agostinho et al., 1999; Gomes & Miranda, 2001; Hoinghaus et al., 2009). Thus, alteration of the natural flow may negatively impact the taxonomic and functional structure of fish assemblages (Mattos et al., 2022). As an ultimate consequence, fish fauna homogenization by environmental filtering processes may render fish assemblages in reservoirs more distinct taxonomically than functionally (e.g., Agostinho et al., 2008; Daga et al., 2020; Oliveira et al., 2018).

We used the aforementioned framework to investigate how trait–environment relationships drive the structure of fish assemblages in seven tropical reservoirs constructed along a major riverine system in southeastern Brazil. The complex is formed by cascade reservoirs and reservoirs blocking the main channel or isolated tributaries, which differentially affect the physical and biological characteristics of the riverine system (Mattos et al., 2022). In this tropical region, spatial and temporal changes in fish diversity are primarily modulated by dispersal limitation between reservoirs, loss of native species, and non-native fish introductions (Loures & Pompeu, 2019; Pelicice et al., 2018). We thus hypothesized that (i) different physical features of reservoirs promote different local environmental conditions that filter different functional traits and favor different functional groups (FGs). Also, under similar environmental conditions (i.e., into groups of reservoirs and seasons), (ii) fish assemblages are more diverse (in reservoirs) and dissimilar (between reservoirs) taxonomically than functionally, (iii) processes of taxonomic turnover and functional nestedness are prevalent, and (iv) changes in taxonomic measures of fish diversity are decoupled from their functional counterparts, as a consequence of random processes driving colonization–extinction dynamics. Therefore, irrespective of taxonomic differences related to dispersal limitation between reservoirs and the introduction of non-native species, we expect similar functional structures under similar influences of physical features.

2 | METHODS

2.1 | Studied reservoirs

This study was performed using seven reservoirs constructed for hydroelectric generation in southeastern Brazil. All reservoirs are located in the Paraíba do Sul River (PSR), which is the main river in southeastern Brazil, providing water supply for human populations, agriculture and industry, electricity generation, sand extraction, and

fishing (CEIVAP, 2022). As a consequence, PSR is strongly affected by impoundments, and changes in land use and cover, leading to decreases in water quality and quantity (Pacheco et al., 2017). Three reservoirs directly block the main channel of the PSR (channel reservoirs; Santa Branca, Funil, and Ilha dos Pombos), three are cascade reservoirs with water diverted from the PSR (Santana, Vigário, and Pereira Passos), and one is an isolated reservoir that blocks small streams (Lajes) (Figure 1; Table S4). They are located along a gradient of altitude and also have heterogeneous features such as the year of construction, surface area, retention time, trophic state, and volume affluence (ANA, 2022). The climate is seasonal tropical with a dry winter and wet summer (Aw), according to the Köppen–Geiger classification (Kottek et al., 2006). The average annual rainfall ranges from 1250 to 1500 mm and the temperature ranges from 15 to 31°C in this area of the Atlantic rainforest.

2.2 | Fish sampling

Fish sampling was carried out during the dry (July–August) and wet (January–February) seasons of 2012 and 2013 in all reservoirs, except in Funil reservoir which was sampled in the dry and wet seasons of 2010 and 2011. Additional sampling was carried out in all reservoirs in the dry season of 2017 when morphological measurements of fishes were taken to calculate the functional traits. Three zones (upper, middle, and lower) were sampled in each reservoir. The standardized fishing sampling unit was defined as a set of three gillnets (25 × 2.0 m; stretched-mesh size 25, 50, and 75 mm between opposite knots) totaling an area of approximately 150 m², operating over

12 h. The nets were set in the late afternoon and retrieved in the following morning. The Capture per Unit Effort was defined as the total number of individuals captured per 150 m² per 12 h. The reservoirs with the largest area (Funil, Lages, and Santa Branca) were sampled using an effort of 18 sampling units (six sampling units in each zone), those with intermediate areas (Vigário, Santana, and Ilha dos Pombos) with nine sampling units (three sampling units in each zone), and the smallest reservoir (Pereira Passos) with six sampling units (two sampling unit in each zone). In total, we employed 261 samples (87 samples × 3 periods). Then the samples were averaged for each period and for each reservoir, resulting in three samples for each of the seven reservoirs (21 samples).

The collected fishes were identified to species level, measured (total length, mm), and returned to reservoirs. Vouchers were fixed in 10% formalin and then preserved in 70% ethanol after 48 h, and incorporated in the Fish Collection of the Laboratory of Fish Ecology, Universidade Federal Rural do Rio de Janeiro.

For analytical purposes, we considered the occurrences of species per reservoir in each season (wet and dry). To avoid any bias related to the sampling effort, for each season, we first constructed rarefaction curves based on the number of species per number of individuals to evaluate if the observed species richness was representative of the species pool in the study area (Gotelli & Colwell, 2001). Regardless of differences in species richness (higher in the dry season), the individual-based rarefaction curves reached an asymptote in both seasons, indicating that the regional pool of species was effectively estimated (Figure S1). We, therefore, used the presence–absence data matrices to assess species occurrences in further analysis. The rarefaction curves were based on Hurlbert's (1971) formulation and

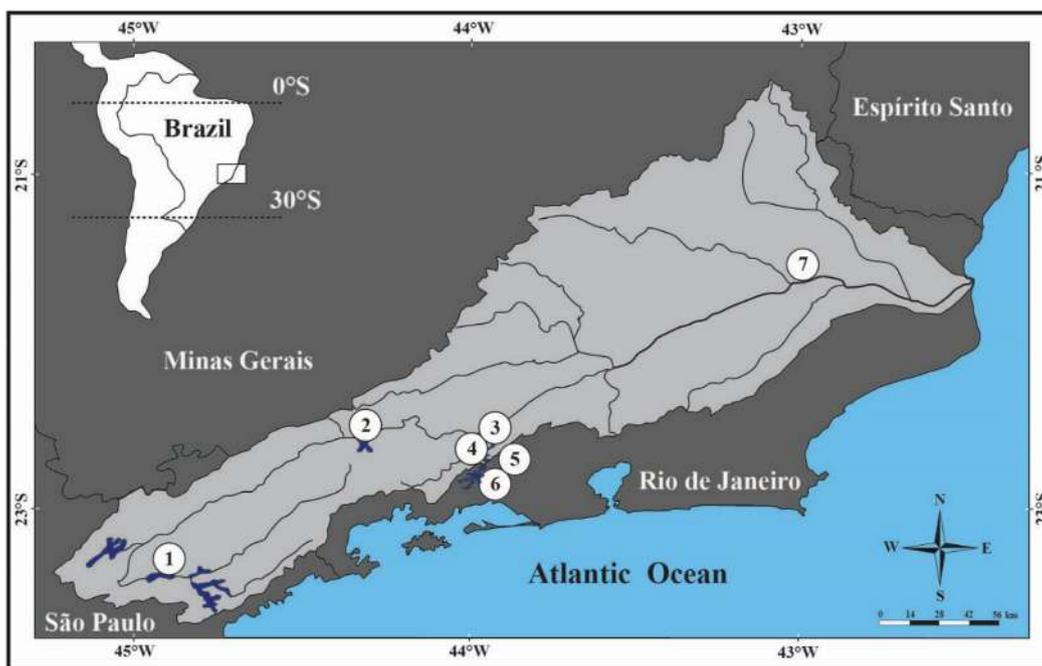


FIGURE 1 Location of the seven reservoirs (1, Santa Branca; 2, Funil, 3, Santana; 4, Lajes; 5, Vigário; 6, Pereira Passos; 7, Ilha dos Pombos) in the watershed of the Paraíba do Sul River (light gray area), southeastern Brazil. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/terms-and-conditions)]

performed in the R environment (version 4.2.1; R Core Team, 2022) using the package *vegan* (version 2.6-2; Oksanen et al., 2022).

2.3 | Environmental variables

Environmental variables obtained for each reservoir included age (years), trophic state (mesotrophic, eutrophic, or hypertrophic; Soares et al., 2008; Franco et al., 2018), and physical features represented by elevation (m), reservoir area (km²), and volume (hm³), water residence time (days), influence of river flow, and affluent flow (m³ s⁻¹) (Table S4). Age of reservoirs and physical variables were obtained for the studied period from technical reports and the website of the Sistema de Acompanhamento de Reservatórios (SAR) from the Agência Nacional de Águas e Saneamento Básico (ANA, 2022).

2.4 | Functional traits

Functional traits included ecomorphological indices (continuous variables), body size, and other ecological traits (ordinal variables) representative of behavioral characteristics related to feeding and life

history strategies (Table 1, Table S2). Morphological measures used to calculate ecomorphological traits were taken from at least five adult individuals of each one of the 34 species in seven tropical reservoirs (Table S1). All morphological measures were taken using a digital caliper with 0.1 mm precision. Ecomorphological indices expressed the contributions of fish attributes to hydrodynamic performance, swimming efficiency, feeding position, and prey detection, capture, and size (Table 1, Table S2; Brosse et al., 2021; Gatz, 1979; Giammona, 2021; Villéger et al., 2017; Watson & Balon, 1984). Body size was indicative of fish locomotion ability and metabolism, as well as their influence on ecosystem functioning based on trophic impact and nutrient cycling (Table 1, Table S2; Villéger et al., 2017). Other ecological traits were related to food acquisition and energy allocation for reproduction (Table 1, Table S2). Ecological information was obtained primarily from the FishBase online database (Froese & Pauly, 2022), complemented by several other sources (Costa et al., 2013; Guedes & Araújo, 2022; Luz-Agostinho et al., 2008; Makrakis et al., 2012; Rocha et al., 2015; Santos et al., 2010) and our combined knowledge.

We performed a Principal Coordinates Analysis (PCoA) to summarize the species trait matrix and assess the functional variation in fish assemblages. PCoA was based on a Gower distance matrix that allows numerical and categorical traits to be properly combined. The first

TABLE 1 Functional importance (proposed mechanisms linking traits to ecological functions) and codes for functional traits and their correlations with the variation in the functional space (two first axes of PCoA ordination).

Trait	Functional importance	Code	PCoA		<i>r</i> ²	<i>p</i> value
			Axis 1	Axis 2		
Ecomorphological indices						
Body elongation	Hydrodynamic performance	BE	0.613	0.790	0.57	0.001
Body transverse shape	Hydrodynamic performance	BTS	0.452	0.892	0.79	0.001
Eye size	Visual acuity and prey detection	ES	-0.975	0.222	0.10	0.202
Eye position	Fish position in water column and prey detection	EP	-0.127	-0.992	0.67	0.001
Caudal peduncle throttling	Caudal peduncle efficiency through reduction of drag	CPT	-0.840	0.543	0.07	0.316
Pectoral fin size	Pectoral fin use for swimming	PFS	0.923	-0.384	0.33	0.003
Mouth position	Feeding position in water column	MP	0.726	0.687	0.80	0.001
Oral gape proportion	Prey size and capture	OGP	-0.019	-1.000	0.53	0.001
Caudal fin shape	Caudal fin use for propulsion or direction	CFS	-0.989	0.146	0.48	0.001
Morphological trait						
Maximum body size	Locomotion ability, metabolism, trophic impacts, and nutrient cycling	BS	-0.269	0.963	0.05	0.445
Ecological traits						
Feeding habit	Food acquisition	FH	0.932	0.362	0.55	0.001
Vertical distribution	Food acquisition	VD	0.392	0.920	0.70	0.001
Mesohabitat location	Food acquisition	ML	-0.930	-0.367	0.67	0.001
Flow preference	Food acquisition	FP	-0.827	0.562	0.26	0.007
Reproductive guild	Energy allocation for reproduction	RG	0.769	-0.640	0.75	0.001
Migratory behavior	Energy allocation for reproduction	MIG	-0.721	0.693	0.54	0.001

Note: Functional traits included ecomorphological indices based on morphological measures obtained from the 34 fish species collected in seven reservoirs (Table S2), body size and ecological traits. Cut-off values (*r*² > 0.1 and nominal *p* value < 0.05) indicative of functional traits highly correlated with the PCoA axes in bold.

two PCoA axes were retained to provide a two-dimensional representation of functional differences between fish species (Figure 2; Table 1). The correlations of functional traits (vectors) with the PCoA axes were measured by the squared correlation coefficient (r^2) that expresses the maximum correlation of the vectors with the ordination configuration (999 permutations; Oksanen et al., 2022). Only the functional traits with higher correlations with the PCoA axes (considering the cut-off values of $r^2 > 0.1$ and nominal p -value < 0.05) were considered for ecological interpretation and included in further analysis.

2.5 | Taxonomic and functional diversity

Fish diversity was assessed using taxonomic and functional measures of alpha and beta diversity. Calculations were performed in the R environment (version 4.2.1; R Core Team, 2022) using the packages

FD (version 1.0-12.1; Laliberté & Legendre, 2010; Laliberté et al., 2014), and *betapart* (version 1.5.6; Baselga et al., 2022).

For each sample (reservoir per season), taxonomic alpha diversity was considered as the number of species, whereas functional alpha diversity was calculated as the volume of the convex hull filled by species in the multidimensional functional space formed by the first two PCoA axes (Laliberté & Legendre, 2010; Villéger et al., 2008).

Calculations of beta diversity used the presence-absence matrices (taxonomic perspective) combined with functional dimensions represented by the first two PCoA axes (functional perspective). Taxonomic and functional beta diversity expressed the variation in fish assemblage as measures of Sørensen pairwise dissimilarity between reservoirs within groups based on the RLQ ordination (described in Section 2.6) and on the seven tropical reservoirs per season (wet and dry) (Baselga, 2010; Villéger et al., 2013). For each pair of reservoirs, taxonomic beta diversity (i.e., Sørensen pairwise dissimilarity), measuring the variation in species composition, was partitioned into (i) spatial

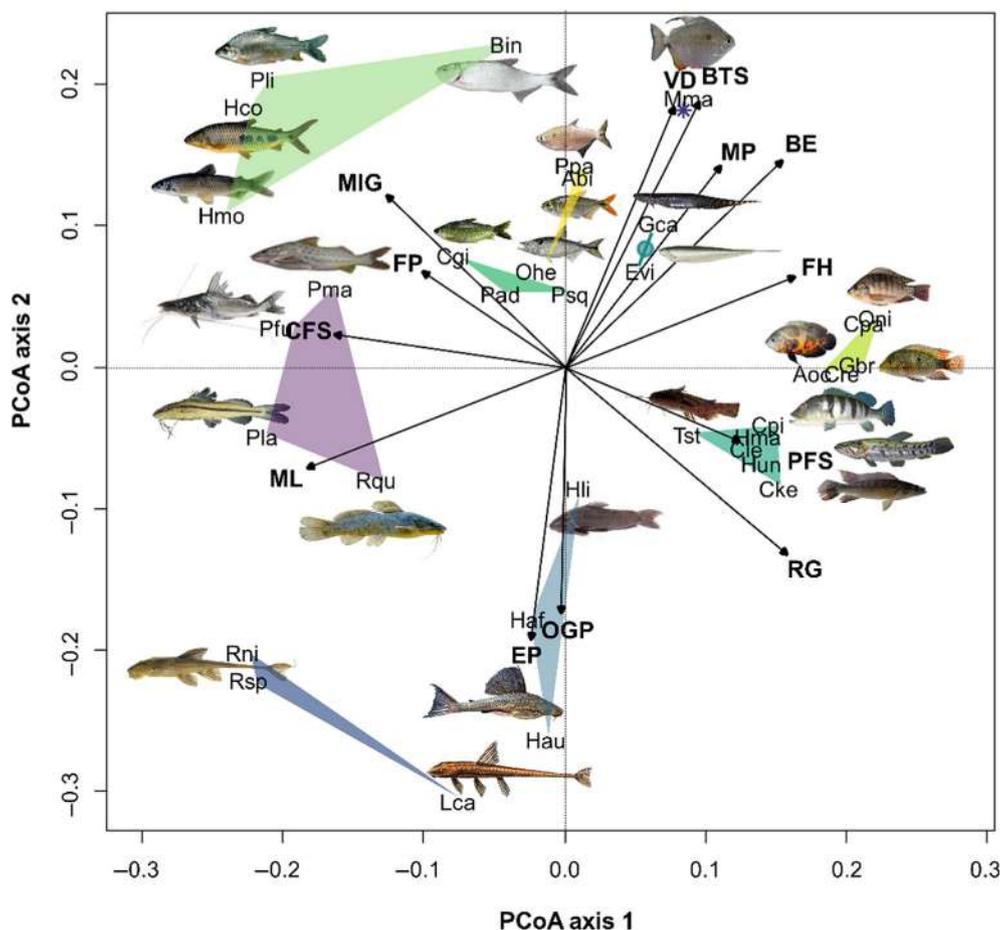


FIGURE 2 Principal coordinates analysis (PCoA) based on functional traits of fish species in seven reservoirs, in southeastern Brazil. Arrows indicate the direction and strength of the contributions of traits to species dissimilarity, with mean values at the origin. For interpretation, only the functional traits with higher correlation with the axes are displayed ($r^2 > 0.1$). Codes for functional traits are in Table 1. Polygons indicate the emergent groups created from a trait-based Gower distance matrix using the k-medoids clustering method (functional group 1—Abi, Ohe, and Ppa; functional group 2, Aoc, Cpa, Cre, Gbr, and Oni; functional group 3—Bin, Hco, Hmo, and Pli; functional group 4—Cgi, Pad, and Psq; functional group 5—Cke, Cle, Cpi, Hma, Hun, and Tst; functional group 7—Haf, Hau, and Hli; functional group 8—Lca, Rni, and Rsp; and functional group 10—Pfu, Pla, Pma, and Rqu). Symbols indicate small groups or isolated species (functional group 6—Evir and Gca and functional group 9—Mma). For species codes see Table S3. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

turnover (i.e., Simpson pairwise dissimilarity), expressing the replacement of some species by others and (ii) nestedness (i.e., a nestedness fraction of Sørensen pairwise dissimilarity), when the assemblage in the reservoir with smaller number of species is a subset of the species-richer reservoir (Baselga, 2010). Likewise, functional beta diversity (i.e., Sørensen derived pairwise dissimilarity), representative of the variation in functional strategies, was partitioned into (i) functional turnover, measured as a Simpson-derived pairwise dissimilarity and (ii) functional nestedness, measured as a nestedness fraction of Sørensen derived pairwise dissimilarity (Villéger et al., 2013). For calculation of functional beta diversity, species were plotted in the multidimensional functional space according to their respective functional trait values, and high beta diversity may result from low overlap between samples (high functional turnover) or high functional nestedness when some samples fill only a small proportion of the functional space filled by others (Villéger et al., 2013).

2.6 | Data analysis

We obtained emergent groups representative of FGs using k-medoids algorithms, a clustering approach that groups species based on the Gower distance matrix (Reynolds et al., 2006). Functional traits were centered and scaled to improve numerical stability and ensure appropriate comparisons between their relative contributions to variation (Gelman & Hill, 2007). We estimated the optimal number of clusters to be generated using the average silhouette method (i.e., average silhouette width) (Kassambara & Mundt, 2020; Rousseeuw, 1987). A hierarchically clustered heatmap based on fish species occurrence in samples (binary distance matrix) was then used to assess the distribution of species and FGs in reservoirs and seasons. For each FG, the frequency of occurrence in samples considered the sum of the occurrences (of at least one species within the group) in each reservoir per season.

Trait responses to environmental gradients were assessed using the framework proposed by Dray et al. (2014), which combines the RLQ and fourth-corner approaches. We used the multivariate RLQ approach to perform an ordination analysis on three tables: environmental variables per site (R), species occurrence per site (L), and functional traits per species (Q) (Dolédec et al., 1996). Table L was ordinated by correspondence analysis, whereas R and Q were ordinated by principal component analysis. The link between R and Q is provided by L using the site and species scores of the species ordination as row weights for R and Q , respectively. Fourth-corner analysis was performed to obtain pairwise correlations between fish traits and environmental variables (Dray & Legendre, 2008). Following Dray et al. (2014), fourth-corner analysis was also used to correlate fish functional traits and environmental variables with the first two axes of RLQ. This approach combined permutation models 2 (linking L and Q to test whether the distribution of species with fixed traits was influenced by environmental conditions) and 4 (linking L and R to test whether species composition at sites with fixed environmental conditions is influenced by species traits). The null hypothesis that fish

functional traits are not related to environmental factors is rejected if p -values <0.05 are observed for both models. All randomization tests used 49,999 permutations and p -values resulting from multiple tests were adjusted using the false discovery rate method (FDR). We used ridge plots to visualize the distributions of FGs as density functions of species scores in RLQ axes.

To assess the strength of niche-based assembly processes, we calculated Pearson correlation coefficients between taxonomic and functional measures of alpha diversity, beta diversity and its turnover, and nestedness components in reservoirs within groups based on the RLQ ordination and in the seven tropical reservoirs per season (wet and dry), and tested the significance of correlations using Mantel tests (999 permutations) (Legendre & Legendre, 2012). We then investigated if the observed patterns differed from those expected under random assembly processes using a null model approach based on Si et al. (2016). For each group of reservoirs and season, 1000 null assemblages were constructed using the non-sequential *quasiwap* algorithm (fixed-row fixed-column algorithm based on a two-step procedure) whereby matrix is first randomly filled maintaining marginal totals, and then 2×2 matrices are randomly selected and swapped (Miklós & Podani, 2004). The observed correlation coefficients were then compared with values obtained from null matrices. If random colonization and extinction are primary drivers of assembly processes in reservoirs, we expect the observed correlation coefficients to be in the 95th quantiles of the null distributions obtained under the random scenario.

All analyses were performed in the R environment (version 4.2.1; R Core Team, 2022) with the packages *vegan* (version 2.6-2; Oksanen et al., 2022), *cluster* (version 2.1.3; Maechler et al., 2022), *factoextra* (version 1.0.7; Kassambara & Mundt, 2020), *ade4* (version 2.719; Dray & Dufour, 2007), *ggplot2* (version 3.3.6; Wickham, 2016), *ggridges* (version 0.5.3; Wilke, 2021), *FD* (version 1.0-12.1; Laliberté & Legendre, 2010; Laliberté et al., 2014), and *betapart* (version 1.5.6; Baselga et al., 2022).

3 | RESULTS

3.1 | Taxonomic and FGs

A total of 34 fish species within 16 families and five orders occurred in the seven reservoirs (Table S3). Three taxonomic orders included the largest fraction of species richness: Characiformes and Siluriformes, each one with 11 species; and Cichliformes, with eight species, seven of them non-native to the study area (Table S3). As a consequence of a high concordance between families and FGs, Characiformes and Siluriformes also encompassed more FGs (Figure 2; Table S3).

Fish species were pooled into 10 FG based on traits primarily related to hydrodynamic performance, food acquisition, and energy allocation for reproduction (Figure 2; Table 1). Most species were grouped in FG5, which included piscivores with parental care, longer pectoral fin, and truncated or rounded caudal fin, typically inhabiting

reservoir (Figure 3). However, samples from a channel reservoir were grouped close to samples from the isolated reservoir, and spatial differences were primarily related to the absences of FG4 and FG8 in the former reservoir, and FG6 in the isolated reservoir (Figure 3).

3.3 | Trait–environment relationships

Functional traits representative of hydrodynamic performance, swimming ability, feeding, and energy allocation for reproduction were mostly related to elevation, and reservoir area and volume (Figure 4; Table 1). Body elongation and body transverse shape were related to elevation, with deeper and more compressed bodies occurring in higher elevations (Figure 4; Table S2). Elevation also had a positive influence on pectoral fin size which was also positively related to reservoir area and volume (Figure 4; Table S2). Mouth position and feeding habits were also positively related to these physical features, with terminal and superior mouths and the ability to obtain whatever food becomes available favored in higher elevations and larger reservoir area and volume (Figure 4; Table S2). A positive relationship was also observed between feeding habit and water residence time, indicative of feeding less restricted to benthic sources in reservoirs retaining water for longer periods (Figure 4; Table S2). Larger reservoir area and volume also favored higher investment in parental care (Figure 4; Table S2). Only the mesohabitat location had negative responses to physical features, evidencing greater importance of the littoral zone to harbor fishes in reservoirs with higher elevation, area, volume, and influence of river flow (Figure 4; Table S2).

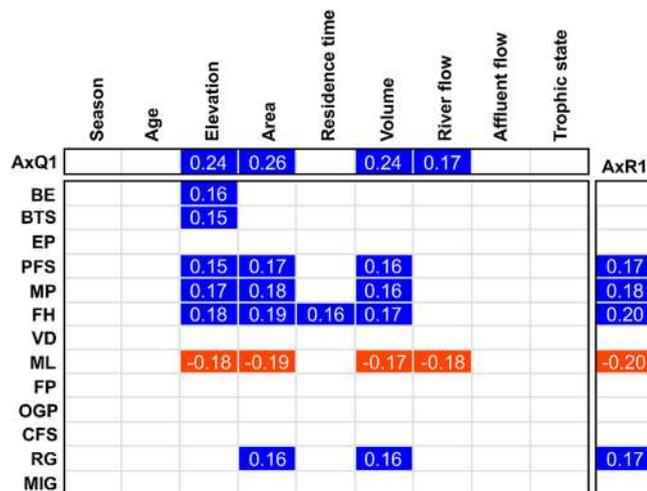


FIGURE 4 Fourth-corner analysis showing pairwise correlations between fish traits and environmental variables. Fourth-corner analysis also tested for correlations between the first RLQ axis for environmental gradients (AxR1) and traits, and the first RLQ axis for trait syndromes (AxQ1) and environmental variables. For all cases, blue and orange cells indicate significant ($p < 0.05$) positive and negative correlations, respectively. For multiple comparisons, p -values were adjusted using the false discovery rate procedure. Codes for traits are in Table 1. [Color figure can be viewed at wileyonlinelibrary.com]

Considering all species traits and environmental variables, the global randomization testing supported the strength of trait–environment relationships promoting the distribution of species (i.e., trait syndromes) and species composition in reservoirs with given environmental conditions (i.e., environmental gradients) in RLQ analysis (Table 2). The trait syndromes in RLQ axis 1 were related to elevation, reservoir area and volume, and influence of river flow, reinforcing the relevance of such physical features to promote assembly processes in the reservoirs (Figure 4). Likewise, the relationships between fish traits and the environmental gradient in RLQ axis 1 reinforced the importance of different ecological attributes of species (i.e., pectoral fin size—swimming speed; mouth position, feeding habit, and mesohabitat location—food acquisition; and reproductive guild—degree of investment in parental care) for community assembly in the reservoirs (Figure 4; Table 1 and Table S2).

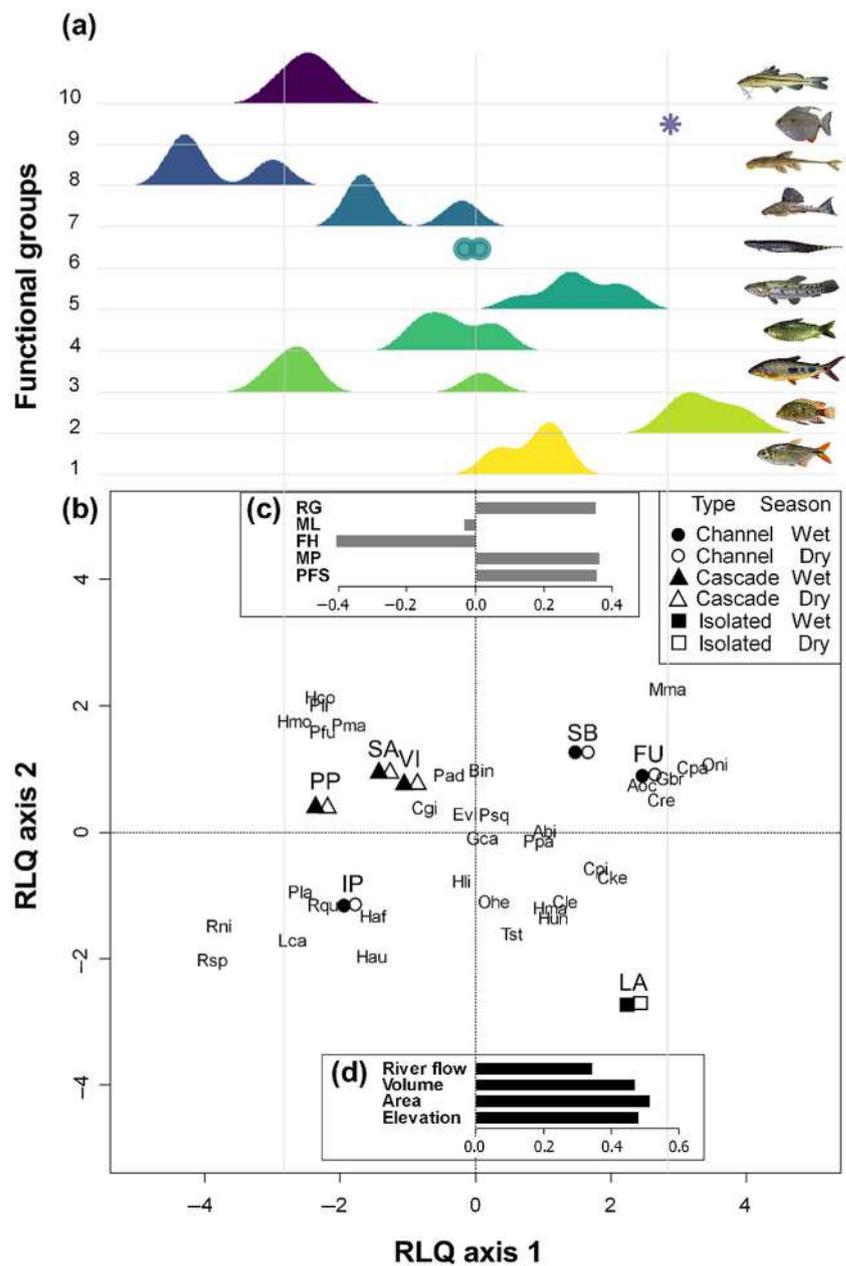
Relationships between physical features of reservoirs and fish traits related to food acquisition, energy allocation for reproduction, and swimming ability separated FGs and reservoirs in two main groups along RLQ axis 1 (Figure 5a–d; Tables 1–3). One group (R1) included cascade reservoirs characterized by lower elevation, area, volume, and river flow, and one channel reservoir, which differed from cascade reservoirs only due to the higher influence of river flow (Figure 5b,d; Table S4). This group harbored primarily FG3, FG7, FG8, FG10, and to a lesser extent FG4, mostly species with external fertilization and no parental care, inferior and subterminal mouth, and comparatively smaller pectoral fin size (Figure 5a–c; Table S2). However, FG3 (i.e., primarily detritivores inhabiting open areas) were common in cascade reservoirs, whereas species included in FG7 and FG8, mostly detritivores/algivores inhabiting the littoral or deeper zones, occurred primarily in the channel reservoir (Figure 5a–c; Table S2). Regardless of a slight response to the physical gradient, FG4 (i.e., species with detritivorous, invertivorous, or piscivorous feeding habit occurring from littoral to open areas) also occurred primarily in cascade reservoirs (Figure 5a–c; Table S2). Only FG10, composed exclusively of

TABLE 2 Results of RLQ analysis associating environmental gradients (matrix R) with trait syndromes (matrix Q) mediated by species composition (matrix L) in seven tropical reservoirs, in southeastern Brazil.

RLQ analysis	Axis 1	Axis 2
Eigenvalues	0.87	0.05
Covariance	0.94	0.22
Correlation	0.26	0.12
Projected inertia (%)	87.31	4.61
Model 2	$p < 0.001$	
Model 4	$p < 0.001$	

Note: Eigenvalues, covariance and correlation between matrices R and Q , and percentage of inertia accumulated for the first two RLQ axes. Global randomization testing the relationships between species occurrence and environmental factors (model 2) and species occurrence and fish functional traits (model 4) rejected the null hypothesis that fish functional traits are not related to environmental factors (p -value < 0.05 for both models).

FIGURE 5 Results of RLQ analysis based on the relationships between environmental variables and traits, mediated by species occurrences. The (a) density plots show the distribution of functional groups along the first RLQ axis and (b) ordination of the two first axes of RLQ analysis shows samples (reservoirs and seasons) and species distributed according to (c) trait syndromes and (d) environmental gradients. Results displayed only for traits (PFS, pectoral fin size; FH, feeding habit; ML, mesohabitat location; MP, mouth position; RG, reproductive guild) and environmental variables more related with RLQ axis 1 (fourth-corner analysis; $i > 0.15$). Symbols represent different types of reservoirs (circle, reservoirs blocking the main channel; triangle, cascade reservoirs; and square, isolated reservoir blocking small streams) and seasons (full, wet season, 2011/2013; empty, dry season, 2010/2012/2017). For species codes see Table S3. [Color figure can be viewed at wileyonlinelibrary.com]



catfishes inhabiting deeper areas, occurred in all reservoirs included in that main group, with different carnivorous species (invertivores and generalists) occurring in each type of reservoir (Figure 5a-c; Table S2).

The other group (R2) was associated with higher elevation, volume, area, and influence of river flow, including most channel reservoirs and the isolated reservoir, and different FGs that inhabit the littoral zone (Figure 5a-d; Table S4). FG1, FG2, FG5, and FG9, which include species with superior and terminal mouths and larger pectoral fin size, most of them with higher investment in parental care, occurred in all types of reservoirs (Figure 5a-c; Table S2). However, piscivorous species within FG5 were prevalent in the isolated reservoir, whereas omnivorous species included in FG2 and FG9 occurred mostly in channel reservoirs (Figure 5a-c; Table S2). Omnivores and piscivores within FG1, the only group that included only species with external fertilization and no parental care, were common in both types of reservoirs (Figure 5a-c; Table S2). For all reservoirs

included in both groups, seasonal variations in the trait-environment relationships were slight (Figure 5b). As environmental variables and functional traits were not correlated with RLQ axis 2, we considered only the groups of reservoirs based on RLQ axis 1 for further analysis.

3.4 | Taxonomic and functional contributions to fish community assembly

Taxonomic alpha and beta diversities were, as expected, generally higher than functional measures, irrespective of the groups of reservoirs based on the RLQ axis 1 (i.e., R1 and R2) and seasons (Table 3). For all groups, only functional nestedness was higher than the nestedness component of taxonomic beta diversity, but the values of median, lower, and upper quartiles were highly overlapping (Table 3).

TABLE 3 Taxonomic and functional measures of alpha diversity, and beta diversity and its components of turnover and nestedness.

Diversity measures	Groups of reservoirs		Seasons	
	R1	R2	Wet	Dry
Taxonomic				
Alpha diversity	13.5 (12.0–16.0)	13.0 (12.0–15.0)	13.0 (13.3–14.5)	20.0 (15.5–20.0)
Beta diversity	0.46 (0.42–0.50)	0.48 (0.46–0.54)	0.45 (0.42–0.46)	0.50 (0.45–0.54)
Turnover	0.40 (0.37–0.41)	0.43 (0.40–0.48)	0.40 (0.39–0.42)	0.41 (0.37–0.43)
Nestedness	0.07 (0.05–0.09)	0.08 (0.04–0.08)	0.03 (0.03–0.04)	0.09 (0.08–0.09)
Functional				
Alpha diversity	6.00 (4.88–6.46)	5.8 (4.8–6.8)	6.4 (5.4–6.6)	7.3 (5.7–7.6)
Beta diversity	0.24 (0.21–0.31)	0.27 (0.26–0.31)	0.25 (0.23–0.26)	0.30 (0.20–0.33)
Turnover	0.14 (0.10–0.19)	0.19 (0.10–0.22)	0.19 (0.16–0.20)	0.12 (0.09–0.19)
Nestedness	0.11 (0.08–0.13)	0.10 (0.07–0.14)	0.06 (0.06–0.07)	0.13 (0.10–0.14)

Note: Median, upper, and lower quartiles of measures obtained for fish assemblages in reservoirs within groups based on RLQ axis 1 (group 1, R1; group 2, R2) and in the seven tropical reservoirs per season (wet; dry). Taxonomic and functional measures with highly overlapping intervals are in bold.

TABLE 4 Correlation coefficients (Pearson's r) between taxonomic and functional measures of diversity alpha, and beta diversity and its turnover and nestedness components for fish assemblages in reservoirs within groups based on RLQ axis 1 (group 1, R1; group 2, R2) and in the seven tropical reservoirs per season (wet; dry).

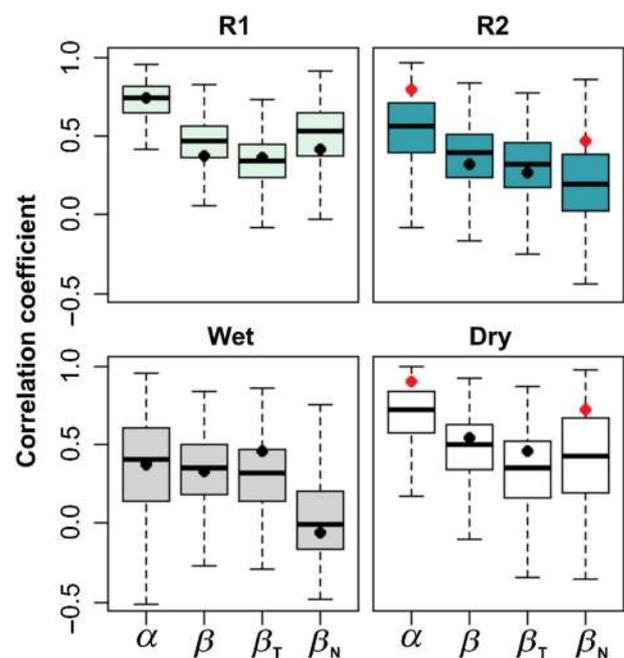
Diversity measures	Correlation coefficients			
	R1	R2	Wet	Dry
Alpha diversity	0.74	0.80	0.37	0.90
Beta diversity	0.37	0.32	0.33	0.54
Turnover	0.36	0.26	0.46	0.46
Nestedness	0.41	0.47	−0.06	0.68

Note: Significance of correlations between taxonomic and functional measures of beta diversity and their components estimated by Mantel tests. Correlations with associated p -value < 0.05 are in bold.

3.5 | Niche-related vs. stochastic assembly processes

The two groups of reservoirs based on the RLQ axis 1 (i.e., R1 and R2) had quite similar trends in correlations between taxonomic and functional measures of diversity, with higher coefficients observed with alpha diversity and to a lesser extent nestedness (Table 4). Per season, correlation coefficients were generally stronger in the dry season compared with the wet season, also as a primary consequence of alpha diversity, nestedness, and to a lesser extent beta diversity (Table 4). Except for the wet season, correlations between taxonomic and functional turnover were lower than the correlations observed for other diversity measures (Table 4). Negligible correlation coefficients were observed only for alpha diversity and nestedness in the wet season, and for turnover in R2 (Table 4).

Random assembly processes prevailed, although correlation coefficients differed from null expectations of random extinction in R2 and the dry season (Figure 6a–d). For both cases, correlation coefficients observed between taxonomic and functional measures of alpha

**FIGURE 6** Null distributions (median, lower and upper quartiles, and minimum and maximum values) resulting from randomization procedures simulating random assembly processes in reservoirs within groups based on RLQ axis 1 (group 1, R1; group 2, R2) and in the seven tropical reservoirs per season (wet; dry). Null models using the non-sequential algorithm “quasiwap” (fixed-row, fixed-column; maintains the marginal totals for null matrix) to simulate random extinction processes constrained by species richness and occupancy. Dots are the observed correlation coefficients between taxonomic and functional measures of alpha diversity (α), and beta diversity (β) and its turnover (β_T) and nestedness (β_N) components, and red dots indicate the observed correlation coefficients significantly different from null expectations of random extinction. [Color figure can be viewed at wileyonlinelibrary.com]

diversity and nestedness were higher than the 95th quantiles of the null distributions obtained under random assembly (Figure 6b,d). Therefore, spatial and temporal processes based on species richness

and loss supported niche-related community assembly in the reservoirs (Figure 6b,d).

4 | DISCUSSION

Our study demonstrated the strength of environmental filtering processes promoted by the physical features of tropical reservoirs on fish assemblages. Different types of reservoirs favored different functional traits, culminating in prevailing FGs irrespective of the number of species. In this sense, marked seasonal differences only in fish assemblage structure based on species richness reinforced the importance of spatial environmental variation to set well-defined functional spaces that may be filled with fishes irrespective of taxonomic identities. This is a critical point considering that patterns related to species richness in reservoirs are commonly linked to the introduction of non-native species (Daga et al., 2020; Franco et al., 2018), with stronger changes following impoundment observed in the tropics compared to higher latitudes (Turgeon et al., 2019). In our study, the most species-rich FGs were not the most frequent in reservoirs over space and time, and FG5, the group formed by piscivores that include native species and non-native cichlids, and FG9, a group that includes only one non-native species, an omnivorous fish inhabiting surface waters in the littoral zone, were comparatively frequent in reservoirs. These results evidence two important topics regarding non-native species: (i) their potential to replace the space occupied by native species and (ii) their capability to occupy niches not explored by native species. Both processes can promote species loss, culminating in depauperated fish assemblages typically observed over time (Agostinho et al., 1999; Loures & Pompeu, 2019).

Trait-environment relationships revealed essential mechanisms driving community assembly primarily based on the restricted availability of feeding resources and sheltered areas for breeding, commonly observed in reservoirs (Agostinho et al., 2016; Freedman et al., 2014). In this scenario, the preference for inhabiting the littoral zone in deeper reservoirs with more lentic environments (i.e., larger area and volume), regardless of the higher influence of river flow, is most likely linked to the prevalence of piscivores and omnivores that feed in the water column (i.e., terminal and superior mouths) under such conditions. Further evidence in this sense is provided by higher water residence time, indicative of more lentic conditions, favoring these feeding habits (Franco et al., 2018). Likewise, external fertilization with parental care and larger pectoral fin size, typically used to perform fanning movements that oxygenate eggs, require territorial behavior for nest guarding in the littoral zone (Bakker & Mundwiler, 2001; Lavery & Reeb, 1994). Higher elevation was also associated with these functional traits, as well as deeper and more compressed bodies, which altogether are representative of non-native species within FG2 and FG5 (cichlid species) and *Metynnis maculatus*, the only species included in FG9 and one of the most abundant species in the study area due to its ability to occupy niches not explored by other species (Uehara et al., 2015). Therefore, multiple trait-environment relationships reinforced the well-documented high

vulnerability of reservoirs to the introduction and establishment of non-native species to the detriment of native ones (e.g., Kwik et al., 2020; Loures & Pompeu, 2019; Pelicice et al., 2018; Pfauserová et al., 2021).

The importance of trait-environment relationships shaping fish assemblages was reinforced by the gradients of environmental conditions and functional traits that distinguished groups of reservoirs. The overall concordance between these emerging groups and types of reservoirs evidenced the importance of physical features to promote assembly processes (Mattos et al., 2022; Santos et al., 2017). Cascade reservoirs harbored primarily species without parental care (i.e., external fertilization and smaller pectoral fin) that inhabit open areas and feed on the bottom (i.e., primarily detritivores with inferior/subterminal mouth). Regardless of the smaller reservoir area, volume, and influence of river flow, species with migratory behavior formed the primary FG in cascade reservoirs, most likely because this closely connected serial system is supported by water diverted from the PSR. Therefore, the downstream position resulting from lower elevation and inflow of water from the mainstem river allows migratory species to enter and persist in the system (Santos et al., 2017). These hydrological features most likely also promote environmental heterogeneity favoring the prevalence of detritivores and the occurrence of carnivores (invertivores or generalists) in the system, as observed in the middle-lower reaches of the PSR (Araújo et al., 2009). At the same time, as typically observed as reservoirs age (>50 years), the deterioration of littoral habitats, already scarce in smaller areas, may prevent the occurrence of nest builders, culminating in the prevalence of species without parental care (Agostinho et al., 1999).

Sedentary fishes with more varied feeding habits (i.e., detritivores/algivores, invertivores, and generalist carnivores), typically inhabiting the littoral or deeper zones, were prevalent in the channel reservoir included in the same group as cascade reservoirs, evidencing the importance of even small environmental differences between different types of reservoirs. The Ilha dos Pombos reservoir (channel reservoir) is strongly influenced by river flow, regardless of sharing lower elevation, area, and volume with cascade reservoirs (Table S4). This system is a run-of-the-river reservoir, and its largest affluent flow (i.e., water volume that flows into the reservoir per unit time) and lowest water residence time (i.e., the amount of time that water takes to flow out of the system) contribute to reducing the decoupling from riverine dynamics, most likely promoting more niche opportunities (Freedman et al., 2014; Santos et al., 2013). Contrasting the prevalence of detritivores in cascade reservoirs with algivores and carnivores in the channel reservoir indicates the importance of more feeding areas supported by higher riverine influence (Liao et al., 2023; Miranda et al., 2019). The higher species richness in the channel reservoir compared with the cascade reservoirs reinforces this possibility (Figure 3; Uehara et al., 2015).

A more contrasting scenario was observed in the group formed by most channel reservoirs, with the prevalence of FGs inhabiting the littoral zone. Fish assemblages in channel reservoirs were primarily characterized by high investment in parental care, reinforced by the prevalence of larger pectoral fins that favor water movement within

the nest, and food acquisition in the water column (i.e., omnivore species with superior/terminal mouths). Altogether, these functional traits express the capability of maximizing the use of resources available in the littoral zone. In this sense, higher depths (mean depth >20 m) associated with higher reservoir area and volume most likely produce anoxic conditions that limit the occurrence of species associated with deeper zones, whereas the total blockage without mechanisms to enable fish passage most likely prevented species typically inhabiting open areas (mostly migrators) from colonizing channel reservoirs at higher elevations (i.e., upstream-reaches of the PSR) (Santos et al., 2013; Soares et al., 2012). As a consequence, small-sized sedentary species were common in channel reservoirs, and predation pressure in the littoral zone most likely favored species with parental care. An important point is that species with no parental care (omnivores and a piscivorous species in FG1) were native and typically occupy pelagic niches in the littoral zone, thus pre-adapted to thrive in environments created by the impoundment (Agostinho et al., 2008).

Regardless of the functional resemblance to fish assemblages in channel reservoirs, piscivorous species with a high degree of parental care prevailed in the isolated reservoir. This FG included a mix of native species and non-native cichlids, and visually oriented piscivores (mostly cichlid species) were favored in higher elevation, area, volume, and influence of river flow, as a primary consequence of the higher transparency and lower turbidity typical of larger reservoirs at upstream reaches in the PSR (Guedes & Araújo, 2022; Uehara et al., 2015). The littoral zone in the Lajes reservoir (isolated reservoir) is also characterized by higher temperature, oxygen concentration, and pH, and the substrate is covered by branches and leaves, environmental conditions strongly associated with its long water residence time (almost 300 days) (Franco et al., 2018; Guedes & Araújo, 2022). Therefore, the higher hydrological stability resulting from the long retention time most likely favors nest-building fishes, which may largely explain the prevalence of non-native species (omnivorous and piscivorous cichlids) in the group formed by the isolated and most channel reservoirs.

Physical features that distinguished two major groups of reservoirs imposed limited niche opportunities within each group, culminating in higher values of local (alpha) and beta diversity from the taxonomic than functional perspective in both groups. Higher taxonomic turnover indicated that different species occupy similar niches in different reservoirs within each group. To a lesser extent, a slightly higher functional nestedness compared to the taxonomic counterpart was indicative of the loss of niche opportunities between reservoirs under similar environmental conditions. In this sense, the low taxonomic nestedness evidenced that species loss is a process comparatively weaker than species turnover within groups of reservoirs. This scenario reinforces the importance of the physical features of reservoirs to determine the functional space to be filled by different fish species. Likewise, these results show that the loss of hydrological connectivity disrupts population flows within the riverine system, which together with the introduction of non-native species culminate in highly distinct taxonomic structures even in reservoirs close to each other (Araújo et al., 2013; Pelicice et al., 2015). The similar trends

observed per season (dry or wet) revealed that similar assembly processes operate in all reservoirs over short-term temporal dimensions, reinforcing the strength of spatial patterns.

Contrary to expected, changes in taxonomic measures of fish diversity were not decoupled from their functional counterparts, but the strength of the observed correlations varied between different environmental conditions in space and time. Except for the wet season, taxonomic and functional measures of alpha diversity in reservoirs were highly correlated, evidencing the positive relationship between the functional space and species richness. A reduction in sampling efficiency due to increased water level may partially explain the lower species richness that culminated in weak correlations between taxonomic and functional measures of alpha diversity in the wet season. However, it is more likely that environmental conditions resulting from increased water flow in the drainage basin, such as higher hydrological instability and increased turbidity, may affect the distribution of some species, such as nest-builders and visually oriented predators, by changing their ability to colonize and survive in reservoirs (Santos et al., 2010; Uehara et al., 2015). Further evidence in this sense was provided by the comparatively higher correlations between taxonomic and functional nestedness and the negligible correlation observed in the wet season when measures of nestedness were quite low and varied little between reservoirs. Therefore, as supported by the slightly higher functional nestedness, processes of species loss mediated by loss of functional space most likely operate equally in all reservoirs during the wet season.

Processes of functional and taxonomic turnover were less jointed irrespective of their higher contributions to beta diversity within groups of reservoirs and seasons. These results evidenced that moderate changes in the types of niche opportunities have slight influences on species replacement between reservoirs under similar environmental conditions. In the wet season, however, taxonomic and functional turnover were more strongly correlated, indicative of more heterogeneous environmental conditions between reservoirs determining a higher concordance between changes in functional spaces available and species replacement. The importance of different assembly processes was thus evidenced at both spatial and temporal dimensions, but niche-based community assembly was primarily based on species richness and species loss. Correlation coefficients different from null expectations only in the group formed by channel reservoirs and the isolated reservoir located in upstream reaches of the PSR evidenced that higher riverine influence promoted more niche opportunities, culminating in species-richer assemblages. As a consequence, the loss of functional space modulates processes of species loss in more isolated reservoirs under higher riverine influence. The similar scenario observed in the dry season, in turn, evidences the strength of such niche-based assembly processes in reservoirs over the PSR under more stable hydrological conditions. In this sense, the importance of species richness and loss is more likely a consequence of prevailing sedentary species (mostly non-natives) with reproductive cycles that are not triggered by flood peaks.

Our study revealed key mechanisms driving fish assemblage structure in old tropical reservoirs with different physical features. As

expected, differences in elevation, area, volume, and influence of river flow promoted different environmental scenarios that culminated in well-defined functional spaces to be filled by fish species. Trait–environment relationships distinguished two major groups of reservoirs: (i) cascade reservoirs and one reservoir blocking the main channel, characterized by lower values of elevation, area, volume, and influence of river flow, and harboring primarily species without parental care that inhabit open areas and feed on the bottom and (ii) channel reservoirs and one isolated reservoir located on upstream reaches of the PSR, characterized by opposite values of the aforementioned physical features, and prevailing FGs inhabiting the littoral zone, including fish species with high investment in parental care that feed on resources available in water column.

Environmental differences were also observed within those groups, indicating that even small differences in physical features are critical drivers of assembly patterns. Lower elevation and water diverted from the mainstem river most likely allow migratory species to enter and persist in the cascade system. Likewise, the riverine influence most likely promotes environmental heterogeneity, favoring the prevalence of detritivores and the occurrence of carnivores (invertivores or generalists), typically observed in the middle-lower reaches of the PSR. On the other hand, a comparatively reduced decoupling from riverine dynamics related to the largest affluent flow and lowest water residence time in the channel reservoir pooled with cascade reservoirs most likely favored the prevalence of fishes with more varied feeding habits (i.e., detritivores/algivores, invertivores, and generalist carnivores) inhabiting the littoral or deeper zones in this run-of-the-river reservoir. At the same time, the total blockage without mechanisms to enable fish passage most likely contributed to the prevalence of sedentary species to the detriment of migratory species. Regarding the isolated reservoir included in the group formed by most channel reservoirs, its longer water residence time most likely promoted higher transparency and lower turbidity, environmental conditions that favored the prevalence of piscivorous species with high visual acuity. In this group, a critical point is that the higher hydrological stability related to longer residence time, altogether with a higher degree of isolation (i.e., higher elevation and discontinuity of river connectivity), favored the occurrence of non-native fish species (i.e., omnivorous and piscivorous cichlids) able to explore pelagic niches in the littoral zone.

The high concordance between taxonomic and functional measures of diversity revealed how niche-based assembly processes operate under different environmental conditions. Higher taxonomic diversities compared to their functional counterparts indicated that physical features impose major environmental differences that filter different sets of functional traits highly irrespective of taxonomic identity. As a consequence, conservative functional spaces supported by prevailing environmental conditions in space and time modulate assembly processes primarily based on differences in species richness and to a lesser extent species loss. In this sense, lower contributions of nestedness compared to turnover from both taxonomic and functional perspectives are most likely a consequence of processes that

boost taxonomic differences between reservoirs, such as limited hydrological connectivity and the introduction of non-native species. High taxonomic turnover under similar environmental conditions is thus a primary consequence of random processes driving colonization-extinction dynamics, as supported by the null model approach. Therefore, trait–environment relationships support differences in species richness and processes of species loss, whereas patterns of species composition are a primary result of stochastic assembly processes. Further investigations may assess how variations in species abundance influence the prevalence of niche-based versus stochastic processes at larger spatial and temporal scales. However, our study revealed that spatially-structured mechanisms that vary only slightly with seasonal changes in hydrological regimes shape fish assemblages in older reservoirs (>50 years) with different physical features. This knowledge highlights the importance of conservation and management actions prioritizing the restoration of the structural complexity of marginal habitats and functional connectivity between reservoirs along riverine systems.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available from the authors upon reasonable request.

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