ARTICLE

Taxonomic and functional diversity patterns of stream fish assemblages from Brazilian Atlantic Rain Forest

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Abstract

Disentangling the hierarchical structure of river systems and multi-scale environmental effects is essential for understanding freshwater fish community structure and function. We sampled 70 stream stretches to investigate how the taxonomic and functional composition and diversity of fish assemblages responded to the environment considering a hierarchical organisation of streams in three Brazilian watersheds (Upper Sorocaba, Upper Paranapanema and Upper Ribeira de Iguape). Functional diversity indicated that stream fish community function was independent of the watershed. The most critical environmental variable was substrate gradient. In streams with a consolidated substrate, equitability and functional dispersion were low due to invertivores occurring in this type of substrate. Our results highlight the importance of local environmental filters for shaping streams fish assemblages across different basins. This shaping was more evident when functional descriptors of assemblages were analysed, thereby reinforcing the importance of an approach based on traits as a tool to elucidate local community assembly processes at broader spatial scales.

KEYWORDS
environmental factors, functional diversity, hierarchy, stream conservation

1 | INTRODUCTION

Understanding the contribution of local and regional factors in the distribution, abundance and composition of species is an old and exciting question in community ecology (MacArthur & Wilson, 1967). Recently, given the increase in anthropogenic pressures on natural ecosystems, the answer to this question can help decision-makers in conservation and restoration actions (Palmer et al., 2014) and inland recreational fishery management (Carpenter et al., 2017). Local and regional factors can act in a complementary way (Gonçalves-Souza et al., 2014), with environmental and biotic constraints (local factors) being prevalent if dispersal mechanisms (regional factors) allow organisms to find habitat patches for species establishment (Leibold et al., 2004). Moreover, actions related

to fisheries sustainability may depend on the relationship between local and large-scale factors (Rypel & David, 2017). Generally, managers can control small-spatial-scale factors through harvest regulation, modifications to hydrologic structures, invasive species prevention, land management and in-stream habitat management (Carpenter et al., 2017). In contrast, large-scale spatial factors can be uncontrollable, such as climate change, macroeconomics, political shifts and war (Carpenter et al., 2017). At low levels of climate change, a large part of the harvest of a climate-sensitive species may be sustainable, provided that high-quality local habitat supports high biomass production (Rypel, 2014; Rypel & David, 2017). However, if climate effects are more intense, management would require a substantial reduction in harvest to sustain the fishery (Carpenter et al., 2017; Grafton, 2010).

Analysis of fish assemblage structure is helpful for inland fishery management where fish diversity is high, and fish catches tend to be multispecies (Cetra & Petrere, 2001). For example, the management of the Arapaima sp. positively affected the structure and composition of fish assemblages in floodplain lakes of the central Amazon Basin (Medeiros-Leal et al., 2021). On the contrary, in the rich species assemblage from the Tonle Sap Lake (Cambodia), changes in inland fisheries management coincided with substantial changes to floodplain habitats and increases in fishing pressure, threatening fish stocks (Chan et al., 2020).

Due to the multifaceted nature of biodiversity, predictions of assemblages using uniquely taxonomic descriptors provide an incomplete picture of assemblage structure that limits understanding of community assembly processes (Pavoine et al., 2011). In this way, given the high variability inherent in most natural communities, recent emphasis has shifted from a taxonomic approach to a functional perspective in which species traits are the primary focus (Casatti et al., 2015; Hoeinghaus et al., 2007; Poff & Allan, 1995; Roa-Fuentes et al., 2019; Teichert et al., 2018). The structure of biological communities assembled in hierarchical systems is crucial to understand, such as streams in drainage networks (Ganio et al., 2005). One advantage of using functional descriptors of communities in multi-scale studies is that convergent patterns may be more easily verified (Ibáñez et al., 2009). Similar environmental filters may select assemblages functionally redundant across basins, even though they differ in species composition (Hoeinghaus et al., 2007).

Stream fish studies of functional diversity have ranged in scale from ecoregions (Carvalho & Tejerina-Garro, 2015; Teresa & Casatti, 2017) to mesohabitats (Pessoa et al., 2021; Teresa & Casatti, 2012). Furthermore, catchment (Nakamura et al., 2018; Pease et al., 2012) and stream (Pereira et al., 2021) scales are adopted. On a land-use scale with a degradation gradient, riparian and watershed land use had little influence on stream fish taxonomic and functional diversity (Casatti et al., 2015; Larentis et al., 2021; Montag et al., 2019). However, land-use activities in the catchment, riparian and local scales modified instream habitat and influenced stream fish communities (Dala-Corte et al., 2016). Stream bottom substrate was an essential predictor of stream fish functional diversity (Casatti et al., 2015; Dala-Corte et al., 2016). In a preserved landscape, functional composition changed with increasing total annual rainfall to change stream substrates from litter-dominated to free sand (Borba et al., 2021).

We propose that environmental gradients can explain the taxonomic and functional structures of stream fish communities. While the hierarchical basin effect influences measures of taxonomic diversity, the convergent process of community assembly will affect functional descriptors of communities. Specifically, we expect that variation in the taxonomic composition of species has a regional effect that is represented by the hydrographic basin. Local assemblages of species are classified according to a biogeographic pattern (Hoeinghaus et al., 2007). On the contrary, functional diversity models will indicate the same local factors that filter stream fish assemblages, regardless of geographic region (Hoeinghaus et al., 2007). We will test these predictions of taxonomic and functional diversity in streams in three Brazilian river basins, by considering the spatial organisation that is naturally nested in sub-basins. Our findings will hopefully be useful to managers by providing tools for monitoring the sustainability of fish assemblages that support valuable fisheries.

## 2 | METHODS

2.1 | Study area and stream stretches

The Maciço de Piedade, Brazil, has a highly heterogeneous relief that contributes to numerous small-sized watercourses. In this region, the drainage basin is topographically separated by the Serra de Paranapiacaba, which represents a geographical barrier to adjacent river basins of the Sorocaba, Paranapanema and Ribeira de Iguape (Figure 1). The river basin of the Sorocaba River is characterised by a well-developed industry and a population density of about 140 inhabitants/km². The Alto Paranapanema river basin is agricultural, a population density of about 30 inhabitants/km², with about 15% of native vegetation and headwaters covered by reforestation areas, mainly *Eucalyptus* and natural forests. In the hydrographic basins of the Ribeira de Iguape River, about 60% is native vegetation, and a population density of about 15 inhabitants/km².

Environmental data and fish were sampled in the dry period in 2010–2013 (July to November) to limit effects of seasonal differences. In the dry season, relationships between fish assemblages and water were expected to be more robust, because flows are low and fish can be captured more efficiently (Pease et al., 2012; Pinto et al., 2006).

Each stream stretch consisted of a 70-m long reach encompassing at least one pool-riffle sequence. Stream stretches were selected to include a diverse range of physical habitats (Fryirs & Brierley, 2013). Seventy stream stretches were sampled in the Sorocaba River basin ($n = 17$), Alto Paranapanema River basin ($n = 31$) and the Ribeira de Iguape River basin ($n = 22$). The width of stream stretches averaged 4.7 m ($SD = 2.4$ m) and depth averaged 24.1 cm ($SD = 14.3$ cm). Stream stretches were chosen by inspecting 1:50,000 scale maps and during field trips. All points were geo-referenced using a handheld GPS (Garmin eTrex).

2.2 | Environmental variables

Instream variables were recorded during onsite surveys within every 70-m reach before fish sampling along three perpendicular, equidistant (i.e. 20–25 m) transects. Transects were selected to represent the upper, middle and lower sections of each reach. Sampling was focused on the presence of structures that promote natural cover, such as large rocks, boulders, fallen trees, submerged logs or branches that fish use for shelter, feeding or nest building. Substrate was classified into seven categories, and abundance was estimated visually at 1-m intervals from left to right along each transect. Within these intervals, total depth was measured. Flow velocity was measured with a mechanical General Oceanics model 2030 flowmeter (General Oceanics,
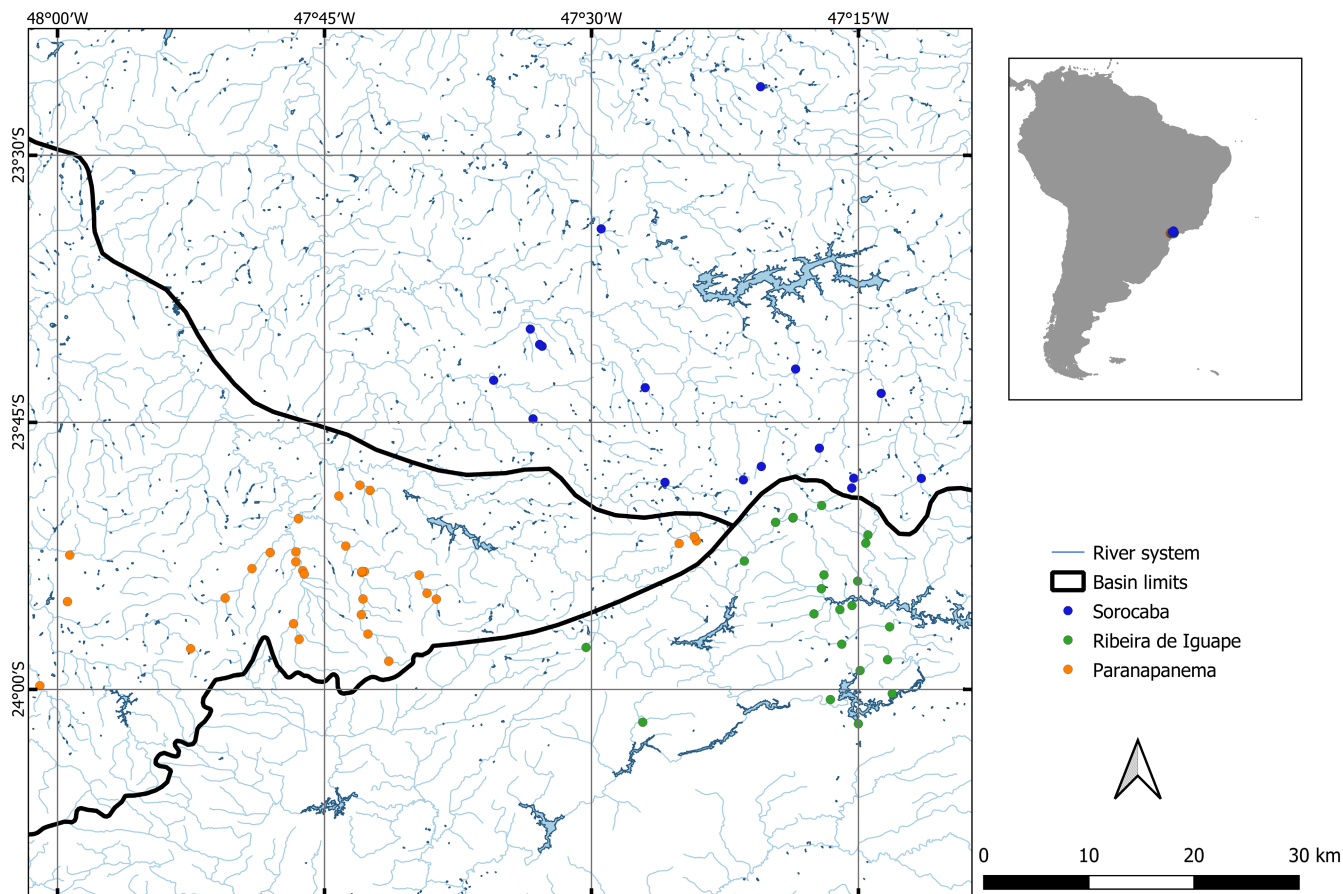
FIGURE 1 Study area and stream reaches that cross the Atlantic Forest of south São Paulo state, Brazil, from adjacent basins of the Paranapanema, Ribeira de Iguape and Sorocaba rivers sampled in 2010–2013.

Miami, FL, USA) in the middle of the water column. Bank stability was visually estimated as the percentage of rocks, tree roots, tree trunks, steep slopes and exposed soil in both banks at three transects. Riparian vegetation coverage was estimated through the intensity of shade provided to the reach (0%–25%; 25%–50%; 50%–75%; and above 75%). Local land cover was classified into natural vegetation, agriculture, pasture and urban (Table 1).

2.3 | Fish sampling

Fish were captured (License no. 13352–1 SISBIO/IBAMA/MMA) during daytime, from 8 a.m. to 4 p.m., in an upstream direction with a single pass of electrofishing using a portable generator (Yamaha, model EF2600, 2.3 kVA, 60 Hz) linked to a current rectifier. A generator with a power of 2000 W was connected to an AC voltage transformer with 200 V input and 500 V output.

2.4 | Fish assemblage variables

To characterise the functional composition of fish assemblages, fish were grouped into categories based on their: (1) position in the

water column (benthopelagic and demersal); (2) trophic group (carnivores, herbivore-detritivores, omnivores and invertivores); and (3) body size (cm) (Oyakawa et al., 2006, Casatti et al., 2012, Froese & Pauly, 2015 and personal observations; Table 2). Three complementary, uncorrelated, functional diversity indices (Villéger et al., 2008) were computing using the three fish traits (i.e. position in the water column, trophic group and size): (1) functional richness (Fric) represents the functional space occupied by the community; (2) functional evenness (Feve) represents the regularity in species abundance distribution and position in multidimensional functional space; and (3) functional dispersion (Fdis) represents the mean distance in multidimensional trait space of individual species to the centroid of all species (Laliberté & Legendre, 2010). In addition, community-level means of trait values (CWM) were computed as an index of functional composition (Lavorel et al., 2008) (dbFD function, *FD* package, R Core Team, 2020).

2.5 | Data analyses

The first axis of the detrended correspondence analysis (DCA) from the species abundance by stream stretches matrix represented the species composition (Figure 2). Principal component analysis (PCA)

| | River basin | | | | | |
| | Paranapanema | | Ribeira de Iguape | | Sorocaba | |
Variable	Mean	SD	Mean	SD	Mean	SD
Channel morphology						
Width (m)	5.59	2.57	4.2	1.59	3.57	2.09
Depth (cm)	37.39	13.93	25.24	9.23	31.15	14.83
Velocity (m s^{-1})	0.23	0.15	0.29	0.13	0.21	0.17
Substrate						
Leaf litter (%)	9	9	5	4	10	6
Silt (%)	7	10	5	5	9	10
Sand (%)	16	17	3	3	15	15
Wood debris (%)	9	7	20	15	17	15
Gravel (%)	21	11	22	17	18	14
Pebbles (%)	14	10	11	9	7	7
Cobbles (%)	11	10	13	12	6	9
Boulders (%)	14	20	21	17	16	18
PCA1	0.60	1.77	−0.23	1.01	−0.80	1.08
Bank stability						
Vegetation (%)	25	21	21	17	13	16
Rocks (%)	11	22	13	18	16	26
Roots (%)	10	9	10	7	3	4
Trunks (%)	2	4	5	5	2	4
Steep stones (%)	43	24	42	21	43	26
Bare soil (%)	10	13	9	13	24	22
Riparian cover						
0–25 (%)	49	33	32	32	40	36
26–50 (%)	21	25	11	17	19	21
51–75 (%)	17	23	10	19	7	15
76–100 (%)	11	20	47	40	32	42
Local and land cover						
Vegetation (%)	53	33	78	30	53	30
Agriculture (%)	15	24	1	3	7	18
Pasture (%)	16	29	7	23	12	18
Urbanisation (%)	16	24	15	23	28	23
PCA1	−0.54	1.52	0.98	1.83	−0.29	2.04

on the correlation matrix of substrate categories and surrounding environment (bank stability, riparian vegetation coverage and local land coverage) was used to reduce the number of variables and identify the most critical environmental gradients among stream stretches.

To test whether fish assemblages responded to environmental gradients, nine metrics related to taxonomic and functional diversity facets were considered. Taxonomic variables included (i) species composition (DCA1); (ii) species richness (S); and (iii) equitability (J). Functional variables included: (iv) functional richness (Fric); (v) functional evenness (Feve); (vi) functional dispersion (Fdis); and three functional compositions (i.e. community-level weighted means of trait values, CWM): (vii) trophic group (TG); (viii) body size (BS); and (ix) water column (WC).

Multiple linear regression models were adjusted to test the relative influence of basin and environmental covariables (substrate, depth, width, velocity and surrounding) on fish assemblage variables (composition, richness, equitability, functional richness, functional evenness, functional dispersion, CWM body size and CWM trophic group). Stream stretches were nested within sub-basins (SB = 12) in mixed-effects models (lme function, *nlme* package, R Core Team, 2020). Random effects were evaluated using the random intercept model (Zuur et al., 2009).

A variance inflation factor (VIF) was used to test for multicollinearity of variables in the complete model with all covariables. The VIF values in all complete models were minor than four, indicating no multicollinearity (Logan, 2010). All possible sub-models were

TABLE 2 Fish species captured in 70 stream reaches that cross the Atlantic Forest of south São Paulo state, Brazil, from adjacent basins of the Paranapanema, Ribeira de Iguape, and Sorocaba rivers sampled in 2010-2013. Column water: benthopelagic (1) and demersal (0). Trophic group: carnivore (1), herbivore-detritivores (2), invertivores (3), and omnivores (4)

					River basin		
	Code	Water column	Trophic group	Body size (cm)	P	RI	S
CHARACIFORMES							
Astyanax lacustris (Lütken, 1875)	Alac	0	4	10.6	16	0	77
Psalidodon bockmanni (Vari & Castro, 2007)	Pboc	0	4	7	91	0	47
Psalidodon fasciatus (Cuvier, 1819)	Pfas	0	4	16.8	187	62	163
Psalidodon paranae (Eigenmann, 1914)	Ppar	0	4	11.3	193	3	105
Bryconamericus iheringii (Boulenger, 1887)	Bihe	0	4	11.4	0	0	61
Piabarchus stramineus (Eigenmann, 1908)	Pstr	0	3	11.4	29	0	0
Characidium gomesi (Travassos, 1956)	Cgom	0	3	6.5	83	0	60
Characidium pterostictum (Gomes, 1947)	Cpte	0	3	7.4	0	361	0
Characidium schubarti (Travassos, 1955)	Csch	0	3	5.3	307	0	0
Characidium zebra (Eigenmann, 1909)	Czeb	0	3	6.4	55	0	68
Deuterodon iguape (Eigenmann, 1907)	Digu	0	4	9.8	0	340	0
Hoplias malabaricus (Bloch, 1794)	Hmal	0	1	55.2	17	5	13
Psalidodon anisitsi (Eigenmann, 1907)	Pani	0	3	6	7	78	15
Piabina argentea (Reinhardt, 1867)	Parg	0	4	6.8	60	10	4
SILURIFORMES							
Cetopsorhamdia iheringi (Schubart & Gomes, 1959)	Cihe	1	3	10.6	36	0	40
Hypostomus ancistroides (Ihering, 1911)	Hanc	1	2	21	87	48	84
Imparfinis borodini (Mees & Cala, 1989)	Ibor	1	3	15.7	85	0	0
Imparfinis mirini (Haseman, 1911)	Imir	1	3	8.5	248	1	112
Isbrueckerichthys epakmos (Pereira & Oyakawa, 2003)	Iepa	1	2	10.3	0	182	0
Neoplecostomus yapo (Zawadzki, Pavanelli & Langeani, 2008)	Nyap	1	2	11	97	7	40
Phenacorhamdia tenebrosa (Schubart, 1964)	Pten	1	3	6.7	20	0	0
Pimelodella avanhandavae (Eigenmann, 1917)	Pava	1	3	9.6	383	0	13
Pimelodella transitoria (Miranda Ribeiro, 1907)	Ptra	1	3	13	0	54	0
Rhamdia quelen (Quoy & Gaimard, 1824)	Rque	1	1	47.4	34	21	17
Rineloricaria pentamaculata (Langeani & de Araujo, 1994)	Rpen	1	2	13	62	0	0
Cambeva davisi (Haseman, 1911)	Cdav	0	3	6.2	52	0	21
Cambeva zonata (Eigenmann, 1818)	Czon	0	3	5.5	0	55	0
GYMNOTIFORMES							
Gymnotus carapo (Linnaeus, 1758)	Gcar	0	3	76	4	2	1
Gymnotus pantherinus (Steindachner, 1908)	Gpan	0	3	23.6	0	187	0
Gymnotus sylvius (Albert & Fernandes-Matioli, 1999)	Gsyl	0	3	8.4	10	2	4
CYPRINODONTIFORMES							
Phalloceros reisi (Lucinda, 2008)	Prei	0	4	2.7	188	449	649
SYNBRANCHIFORMES							
Synbranchus marmoratus (Bloch, 1795)	Smar	1	1	50	8	0	5
PERCIFORMES							
Geophagus brasiliensis (Quoy & Gaimard, 1824)	Gbra	0	4	28	49	0	142
Geophagus iporangensis (Haseman, 1911)	Gipo	0	4	10	0	44	0
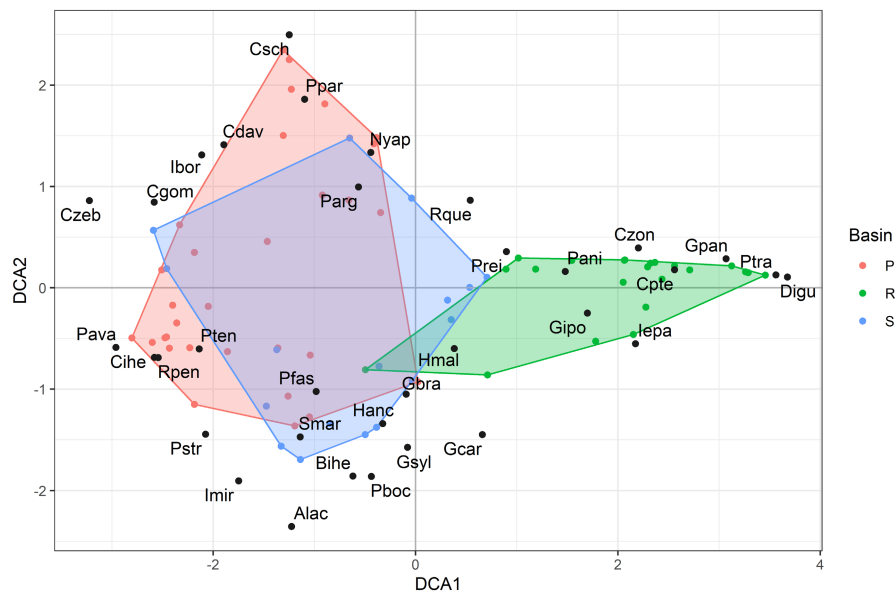
FIGURE 2 First two axes of a detrended correspondence analysis (DCA) with fish species in 70 stream reaches that cross the Atlantic Forest of south São Paulo state, Brazil, from adjacent basins of the Paranapanema (P), Ribeira de Iguape (R) and Sorocaba (S) rivers sampled in 2010–2013. Species identification with code is in Table 2.

generated using the dredge function in the *MuMIn* package (R Core Team, 2020) (Garibaldi et al., 2014). The Akaike information criterion (AIC) was used to choose the best fitting model, which can be interpreted as a measure of the distance between each model and a "true" model that is not necessarily known (Anderson, 2008). The relative importance of independent variables was evaluated with Akaike weights for each covariate among all models with that co-variate (sw function, *MuMIn* package, R Core Team, 2020; Figure S8). The probability ratio between the best (w) and each reduced model (w0, i.e. when all parameters except b0 are set to zero) was used to determine the number of times the chosen model was parsimonious. Logistic regression was used to model the relationship between CWM water column and environmental covariables (glm function, family = *binomial, stats* package, R Core Team, 2020).

3 | RESULTS

Across all locations, 34 fish species and 6060 individuals were collected (Table 2). Streams in the Paranapanema basin had higher species richness and abundance, with 26 species and 2408 individuals, and species richness ranging from three to 15. Streams in the Sorocaba basin had 22 species, and species richness ranged between five and nine. Streams in the Ribeira de Iguape basin had 19 species, and species richness ranged from three to 10. Six species represented about 52% of total individuals captured, including *Phalloceros reisi* (21%), *Psalidodon fasciatus* and *Pimelodella avanhandavae* (7%), *Characidium pterostictum, Imparfinis mirini* and *Deuterodon iguape* (6%).

The DCA1 explained 13.1% of total variation in species, and 6.26 standard deviations reflected heterogeneity of species composition. Paranapanema and Sorocaba streams had negative site scores and shared *Psalidodon fasciatus, Pimelodella avanhandavae* and *Imparfinis mirini*. In contrast, Ribeira de Iguape streams had positive site scores, characterised by exclusive fish species, *Deuterodon iguape* and *Characidium pterostictum* (Figure 2).

The substrate PCA1 axis explained 28% of the variation among the stream stretches and represented the unconsolidated-consolidated gradient. PCA1 axis from surrounding environment characterised the gradient poor-good surrounding accounted for 28% of the total variation of the data (Tables S1 and S2).

Basin and substrate gradient were the most critical factors affecting fish assemblage taxonomic and functional structure (Table 3). The regional effect of river basins affected all taxonomic diversity components, including taxonomic structure of fish assemblages from Paranapanema, Ribeira de Iguape, and Sorocaba river basins in the Brazilian Atlantic Forest.

Species composition was negatively related to substrate and depth gradient (Table 3, Figure S10). In contrast, species richness (S) increased with velocity (Table 3, Figure S11), while equitability increased with width and decreased with substrate and depth (Table 3, Figure S12).

Basins did not affect functional evenness (Feve) or functional richness (Fric), which suggests that stream fish assemblages from Paranapanema, Ribeira de Iguape and Sorocaba river basins were functionally similar. However, functional richness (Fric) decreased with surrounding environment and width gradients, so large stream stretches were characterised by stable banks, high riparian vegetation coverage and natural vegetation coverage of local land (Table 3, Figure S13).

Functional dispersion (Fdis) decreased with substrate and depth gradients and increased with width, so that consolidated substrate decreased and stream stretches were deep and narrow (Table 3, Figure S14). The regional effect of river basins affected functional diversity, as in the case of streams of the Ribeira River basin, which had the smallest Fdis values (Figure S9).

In streams of the Sorocaba River basin, omnivores were more prevalent than invertivores in stream fish assemblages (Figure S9). Community-level weighted means of trophic groups decreased with substrate and surrounding environment gradients (Figure S15). The omnivore trophic group assemblage occurred in streams with

TABLE 3 Best-fitting mixed-effects models for basin and covariables (standard error), probability of the best model (w) and model parsimonious (w/w0) for 70 stream reaches that cross the Atlantic Forest of south São Paulo state, Brazil, from adjacent basins of the Paranapanema, Ribeira de Iguape and Sorocaba rivers sampled in 2010–2013

| Dependent variable | Basin | Environmental covariables | | | | | w | w/w_0 |
		Substrate	Velocity	Depth	Surrounding	Width		
Taxonomic diversity								
Composition	+	−0.23 (0.06)		−0.01 (0.01)			0.35	$5.94*e^6$
Species richness	+		2.56 (1.59)				0.09	150.88
Equitability	+	−0.06 (0.02)		−0.002 (0.001)		0.05 (0.01)	0.26	159.11
Functional diversity								
Richness					−0.58 (0.18)	−0.29 (0.15)	0.15	173.28
Dispersion	+	−0.10 (0.05)		−0.01 (0.003)		0.08 (0.03)	0.18	5.34
Functional composition								
Trophic group	+	−0.05 (0.03)			−0.06 (0.02)		0.16	103.92
Body size					−0.37 (0.20)		0.11	1.58
Water column		0.56 (0.19)					0.02	893.35

unconsolidated substrate, where the bank was unstable, riparian vegetation was poor and local land coverage had no natural vegetation (Table 3).

Community-level weighted means of body size decreased with surrounding environment gradients (Table 3, Figure S16) and CWM water column increased with substrate gradients, so benthopelagic assemblages were more frequent on consolidated substrate (Table 3, Figure S17).

The residuals are symmetrically distributed, tending to cluster towards the middle of the plot, clustered around the lower single digits of the y-axis. In general, there are not any clear patterns (Figures S1–S7).

4 | DISCUSSION

Our results revealed that local environmental gradients and regional biogeographic factors determined how taxonomic and functional diversity of stream fish assemblage differed in three Brazilian river basins. Models of taxonomic diversity suggested an essential role of regional scale, whereby local assemblages were sorted according to a biogeographic pattern (Hoeinghaus et al., 2007). By contrast, in our functional diversity models, stream fish assemblages were described by the same ecological filters regardless of geographic region. In functional diversity analysis, Hoeinghaus et al. (2007) suggested equal roles of local and larger scales factors and habitat templates irrespective of geographic area.

A substrate gradient contributed the most to predicting stream fish functional and taxonomic structure in our study of Brazilian rivers, as in other studies. For example, the percentage of coarse substrate in the stream bottom was a significant predictor of species richness, diversity and functional redundancy that indicated more preserved conditions in an agroecosystem that harbour a gradient of degradation in southeastern Brazil (Casatti et al., 2015). Furthermore, in south Brazilian grasslands, functional diversity decreased with substrate siltation with a replacement of benthic and lithophilic species by significant more morphologically similar nektonic fish (Dala-Corte et al., 2016). Consolidated substrate types (large rocks, boulders, fallen trees, submerged logs and branches) promote natural cover that can be used for shelter, feeding or nest building (Matthews, 1998). Functional and species richness was not related to substrate in our study, which suggests that species in streams with consolidated substrate are functionally redundant and packed in a specific position of multidimensional functional space as invertivores. The CWM trophic group in our study decreased along the substrate gradient, as an omnivore–invertivore gradient. The benthopelagic assemblage represented by aquatic invertivores were favoured in streams with consolidated substrate by benefiting from higher availability of aquatic macroinvertebrates in complex substrate streams (Angermeier & Schlosser, 1989).

In our study of Brazilian rivers, positive species–volume relationships did not explain the relationship between species richness and depth, unlike other studies. Rather, higher species diversity in pool

habitat was due to the habitat complexity and volume being related to a combination of submerged vegetation and substrate (Langeani et al., 2005). In our study, velocity was positively associated with species richness. This environmental variable is essential for promoting ecological heterogeneity, with micro-habitat hydraulics playing a vital role as a template for stream fish life-history strategies (Blanck et al., 2007; Poff & Allan, 1995).

The surrounding gradient decreased functional richness and CWM trophic group and body size in our study of Brazilian rivers, in contrast to other studies that have shown land-use activities are an essential environmental filter resulting in functionally redundant communities (Bordignon et al., 2015; Casatti et al., 2015; Dala-Corte et al., 2016; Larentis et al., 2021; Montag et al., 2019). We attributed the discrepancy to a loss of tolerant and generalist species in well-preserved surrounding streams that tended to be more abundant in degraded streams (Teresa & Casatti, 2012). Our study represented these species by CWM trophic groups. The omnivore trophic group includes species with high phenotypic plasticity that explore resources available in degraded habitats (Casatti et al., 2012), and the invertivore group that includes species of small body size.

In summary, we showed the relationship of stream fish assemblage structure with environmental gradient, within a hierarchical drainages network. We showed that similar filters in different basins produced assemblages with similar functional diversity even with different species composition. By doing this, we highlighted the importance of local environmental variables as consistent filters across biogeographically distinct basins. Our findings suggest how assemblage structure changes depending on which aspect of biodiversity is considered, thereby reinforcing the importance of an approach based on traits as a powerful tool to elucidate local community assembly processes at broader spatial scales.

4.1 | Management implications

The ecological relationship between species richness and productivity is far from resolved, although species-rich ecosystems are likely more productive (Duffy et al., 2007) and therefore more likely to support inland fisheries that depend on ecosystem productivity (Welcomme, 2008). In theory, complex systems are more stable, so maintenance of complexity is related to species richness (MacArthur, 1955). Unfortunately, stream fishes are not important for inland fisheries, given the small size and low biomass produced, although they represent about 50% of Brazilian freshwater fish biodiversity (Buckup, 2021). Maintaining fish biodiversity in higher elevation basins will be reflected in rivers and reservoirs further down river basins (Vannote et al., 1980). Regionally, species diversity between streams is more important than local diversity, thereby indicating the conservation importance of multiple streams that make up the upper reaches of watersheds (Teshima et al., 2016). Habitat loss is a primary concern identified for all South American river

basins (Barletta et al., 2015). In a historic moment with factors on a large spatial scale in an uncontrollable context (i.e. climate change, macroeconomics and war) (Carpenter et al., 2017), the present study showed the importance of substrate composition and a preserved surrounding environment in maintaining functional and taxonomic diversity.

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare that are relevant to the content of this article.

DATA AVAILABILITY STATEMENT

The data are from FAPESP 2009/53056–8.

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SUPPORTING INFORMATION

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