Neotropical Ichthyology

Original article https://doi.org/10.1590/1982-0224-2023-0030

Fish responses to multiple scales in coastal blackwater Atlantic Forest streams in Southeast Brazil

Correspondence:
Katharina Eichbaum Esteves
kesteves.ke@gmail.com

Mariana Landucci Giongo[1], Maria Letizia Petesse[1] and Katharina Eichbaum Esteves[2]

Environmental factors act at multiple spatial scales in a hierarchical manner to shape the organization of biota. However, the relative influence of different scale-related factors is poorly known, especially in Atlantic Forest Blackwater streams. Therefore, we herein aimed to evaluate local, landscape and spatial factors that shape fish assemblages in 14 blackwater restinga coastal Atlantic Forest streams under natural conditions and verify species occurrence patterns among four sub-basins during the low-precipitation season. When we combined local, landscape and spatial factors, variance partitioning explained a high proportion of variation in species matrix. Local variables pH and Total Dissolved Solids explained most of the variability, and these were the most important factors in determining fish community structure. Significant differences in fish assemblage structure among the four sub-basins were observed, and *Mimagoniates microlepis*, *Phalloceros harpagos*, and *Hollandichthys multifasciatus* were the species that most contributed to this dissimilarity. The important contribution of local predictors, the high number of endemic species herein recorded, the presence of an endangered species (*Spintherobolus broccae*), and near pristine conditions, may be used as baseline conditions for the assessment of similar environments.

Keywords: Acidic streams, Ichthyofauna, Neotropical streams, Restinga, Variance partitioning.

Submitted July 4, 2022
Accepted May 29, 2023
by Lilian Casatti
Epub July 10, 2023, 2023

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

Neotrop. Ichthyol.
vol. 21, no. 2, Maringá 2023

---

[1] Programa de Pós-Graduação em Aquicultura e Pesca, Instituto de Pesca, Secretaria da Agricultura e Abastecimento do Estado de São Paulo. Av. Conselheiro Rodrigues Alves, 1252, Vila Mariana, 04014-900 São Paulo, SP, Brazil. (MLG) marilanduccig@gmail.com, (MLP) mlpetesse@gmail.com.

[2] Centro de Pesquisa em Recursos Hídricos e Pesqueiros, Instituto de Pesca, Secretaria da Agricultura e Abastecimento do Estado de São Paulo. Av. Conselheiro Rodrigues Alves, 1252, Vila Mariana, 04014-900 São Paulo, SP, Brazil. (KEE) kesteves.ke@gmail.com (corresponding author).

Fatores ambientais atuam em múltiplas escalas espaciais de forma hierárquica, moldando a organização da biota. Todavia, as influências relativas de fatores relacionados a diferentes escalas são ainda pouco conhecidas, especialmente em riachos de águas pretas da Mata Atlântica. Investigamos como os fatores locais, da paisagem e espaciais, moldam as assembleias de peixes em 14 riachos costeiros de restinga de águas pretas da Mata Atlântica sob condições naturais, verificando os padrões de ocorrência de espécies em quatro sub-bacias durante a estação de baixa precipitação. A partição de variância explicou uma alta proporção de variação na matriz de espécies ao combinar fatores locais, de paisagem e espaciais. As variáveis locais pH e Sólidos Totais Dissolvidos explicaram a maior parte da variabilidade e foram os fatores mais importantes na estruturação da comunidade de peixes. Foram observadas diferenças significativas na estrutura da assembleia de peixes entre as quatro sub-bacias, sendo que *Mimagoniates microlepis*, *Phalloceros harpagos* e *Hollandichthys multifasciatus* foram as espécies que mais contribuíram para essa dissimilaridade. A importante contribuição dos preditores locais, o alto número de espécies endêmicas e a presença de uma espécie ameaçada (*Spintherobolus broccae*) indicam condições próximas das pristinas dos riachos, podendo estes ser usados como referência para a avaliação de ambientes semelhantes.

Palavras-chave: Ictiofauna, Partição de variância, Restinga, Riachos neotropicais, Riachos ácidos.

INTRODUCTION

Metacommunity theory has been widely used to understand how the complex spatial structure of river networks mediates the relative influences of local and regional control on species composition. This framework considers that processes act at multiple spatial scales, and that community composition is subject to the interaction between local environmental conditions (both biotic and abiotic) and dispersal driven regional effects (Brown *et al*., 2011). Another interpretation is linked to the Niche Theory, which predicts that resources and conditions dictate the distribution of species over space and time (Hutchinson, 1957), which, together with local conditions and species' dispersion abilities influence community structure (Cottenie, 2005). Thus, multiscale approaches have been considered good tools to gain a better understanding of broader scales that affect the composition of aquatic communities (Frissell *et al*., 1986; Schlosser, 1991), and may help identify the most appropriate scales and environmental factors for the management of aquatic ecosystems (Roth *et al*., 1996).

Stream communities are largely determined by the structure and dynamics of the physical stream habitat, together with the pool of species available for colonization (Wevers, Warren, 1986). Conditions at smaller spatial scales are constrained by processes at larger spatial scales (O'Neill *et al*., 1989). As such, multiple spatial scales act hierarchically to shape the biota's organization (Compin, Ceréghino, 2007; Stephenson, Morin, 2009). At the local scale, for example, fish assemblage structure is regulated by both abiotic factors such as chemical characteristics of water and physical features of the stream channel, and biotic interactions, such as competition and predation (Gebrekiros, 2016). Since these factors determine conditions for the survival of these organisms, they may help predict the structure of fish communities (Gerhard *et al*., 2004; Terra *et al*., 2013). At the same time, however, both abiotic and biotic factors are subject to complex, dynamic and context-dependent mechanisms that affect fish communities. For instance, local variables in headwaters can largely control fish assemblages, but this depends on environmental heterogeneity and overall connectivity of the watersheds (Henriques-Silva *et al*., 2019).

Recent studies using variation partitioning have demonstrated a relatively small, but statistically significant, unique effect of spatial variables on the similarity of aquatic communities (De Bie *et al*., 2012). However, the relative importance of spatial distance as a predictor of local community composition remains to be elucidated. Environmental factors that affect species distributions are also spatially structured, and they have become evident at large-scale ecoregion comparisons (Van Sickle, Hughes, 2000) and between drainage basins (Brown, Lomolino, 1998; Matthews, 1998), either historically by the differences in species pool, or dispersal limitations (Cottenie, 2005; Mykrä *et al*., 2007). Spatial context also determines the relative importance of local environmental conditions and dispersal of the fish community (Geheber, Geheber, 2016), as well as the similarity of assemblages among sampling sites, which decreases with increasing spatial distance (Legendre, 1993; Dray *et al*., 2006). In this sense, knowledge of connections among drainage basins will lead to an understanding of the major distribution patterns of fishes (Hocutt, Wiley, 1986) since physiography may govern fish distribution and abundance (Pflieger *et al*., 1981).

The Atlantic Rain Forest, which originally extended continuously along the Brazilian east coast, is today a patchwork of fragments (11.4 to 16%) (Ribeiro *et al*., 2009), but still considered a global biodiversity hotspot (Myers *et al*., 2000). Blackwater rivers and clearwater rivers are the main river types of the Atlantic Rainforest (Por, 1992). They harbor a high richness of fish species, consisting of 89 genera and 269 species, 70% of which are endemic (Abilhoa *et al*., 2011). The most important reason for this diversity and endemicity is the isolating effect exerted by mountains (upstream) and sea (downstream) among coastal river basins (Bizerril, 1994; Menezes *et al*., 2007). Half of these species are small in size and complete their life cycle entirely in streams (Abilhoa *et al*., 2011).

Most studies on community structure, distribution and influence of local variables on fish assemblages have been performed in clearwater Atlantic Forest rivers (Gerhard *et al*., 2004; Mazzoni *et al*., 2006; Terra *et al*., 2016; Gonçalves, Perez-Mayorga, 2016; Teshima *et al*., 2016; Wolff, Hahn, 2017; Gonçalves *et al*., 2018). Despite several studies on fish assemblages of blackwater rivers (Ferreira, Petrere Jr., 2009; Gonçalves, Braga, 2012; Ferreira *et al*., 2014; Esteves *et al*., 2019), an expanding basin-wide perspective would provide a better foundation for understanding the factors that govern fish assemblage structure in these rivers. This view is highlighted by the unique conditions of blackwater rivers, including high humic content, decreased pH, low nutrients (Por, 1992), low water velocities, fine-particulate substrate (Ferreira *et al*., 2014) and their origin at low altitudes in the Coastal Plain Forest or Restinga Forest. Restingas are herbaceous/shrubby coastal sand-dune habitats that represent one of the faces of the Atlantic Rain Forest (Marques *et al*., 2015). They occur over Brazilian coastal plains and are formed by marine sediments originated from the Quaternary (CONAMA, 1999).

Lowland streams in coastal regions are also strongly influenced by proximity to the sea with faunal transitions occurring over distances of only a few kilometers on the coastal alluvial plains (Winemiller, Leslie, 1992). Thus, as observed for other studies, simple ecological processes such as dispersal, spawning migration and reproduction can lead to strong distance–decay relationships, whereby the similarity of assemblages decreases with increasing spatial distance of the sampling sites (Legendre, 1993; Dray *et al*., 2006).

Multiscale influences on Atlantic Forest fish communities performed in clearwater streams have shown a predominance of local (Terra *et al*., 2016) and spatial variables, explaining most of the variation in fish assemblages (Teshima *et al*., 2016; Gonçalves *et al*., 2019). However, in blackwater streams multiscale influences are still poorly known, providing the rationale for this study. We aimed to understand the contributions of environmental and spatial factors in describing the variance of fish assemblages in blackwater streams located in a region subject to the isolating effect of mountains and sea among coastal river basins. We predicted that local factors would be significant in assemblage structuring because in least modified watersheds, landscape variables can be expected to contribute little to explaining the fish assemblage structure (Barbosa *et al*., 2019). Also, because of the particular conditions of blackwater streams, it is expected that local conditions provide for rare organisms that are specially adapted to life in low-pH environments. As we selected an area considered small to medium in extension, we hypothesized that the contribution of environmental factors is larger than that of spatial factors, because the contribution of spatial factors is predicted to decline with decreasing geographical extent. More specifically, we herein aimed to determine a) the relative contribution of site-scale (local variables), landscape and spatial configuration in explaining variability of fish assemblages; b) the local and/or landscape variables that best predict stream fish composition, and c) the patterns of fish assemblages in different coastal sub-basins. The outcomes of this study are important for understanding how fish assemblages are structured in Atlantic Forest blackwater streams, directing efforts for conservation of aquatic biodiversity.

MATERIAL AND METHODS

Study area. We sampled 14 blackwater streams located in the coastal plain of São Paulo State (Southeast Brazil) where meandering rivers occur in a low declivity region. The sampled streams are of 1st and 2nd order and originate at low altitudes in a region between marine and coastal mountain (Serra do Mar) environments. Sites belong to four sub-basins: Itapanhaú, Itaguaré, Guaratuba, and Una (Tab. 1). The first three sub-basins are located in the Baixada Santista Hydrographic Basin (Ribeiro, 2018), while the Una is located on the northern coast sub-basin. All sub-basins are included in the Ribeira do Iguape Ecoregion *sensu* Abell *et al.* (2008). The criteria used to select the sampling sites were accessibility, adequacy for electrofishing, salinity ≤ 0.05 ppm and good conservation status of the streams. Thus, we considered only sites located in areas with well-preserved stretches of High Dry Restinga Forest and sub-montane and/or lowland rain forest where intense human activities are absent. Maximum urban occupation attained 10.9% at one site of the Itapanhaú River sub-basin because of the proximity of a sewage treatment plant (Tab. 1).

Most sites were located in the municipalities of Bertioga and São Sebastião, covering the Conservation Unit “Parque Estadual das Restingas de Bertioga” (PERB), a private area known as “Fazenda Jimbuíbas”, and an area close to the “Rio Silveira Indigenous Reserve” in the municipality of São Sebastião (Fig. 1). Created in 2010, the PERB consists of 9,312.32 hectares (Fundação Florestal, 2018) and is a Conservation Unit housing 97% of the remaining Restinga Forest of Baixada Santista (Fundação Florestal, 2022). This vegetation refers to the set of physiognomically distinct plant communities under marine and fluvial-marine influence, occurring on coastal sandy deposits (Cerqueira, 2000). Ecological interest in the PERB stems from its rich diversity of environments, including the Itaguaré and Guaratuba sub-basins and the eastern segment of the Itapanhaú River sub-basin. Vegetation consists of Dense Ombrophilous Forest and Pioneer Formations (Instituto Ekos Brasil, 2008). The climate in the Bertioga region is characterized as tropical with precipitation throughout the year (Af). Average annual temperature is around 24°C, and rainfall is 3,200 mm (Köppen, 1948). The highest average rainfall values occur in January, February and March, and the lowest in June and July, revealing a water surplus throughout the year.

The Una River sub-basin is located in the northern coastal Hydrographic Basin of São Paulo State, covering 12,060 ha. Approximately 80% of this basin’s area is found within state park boundaries with important natural remnants of the Atlantic Forest (Instituto Ekos Brasil, 2008). The average temperature recorded for the low-rainfall season in this region (April to September) was 18.33 °C in 2016, along with cumulative precipitation of 593.06 mm (CIIAGRO, 2021).

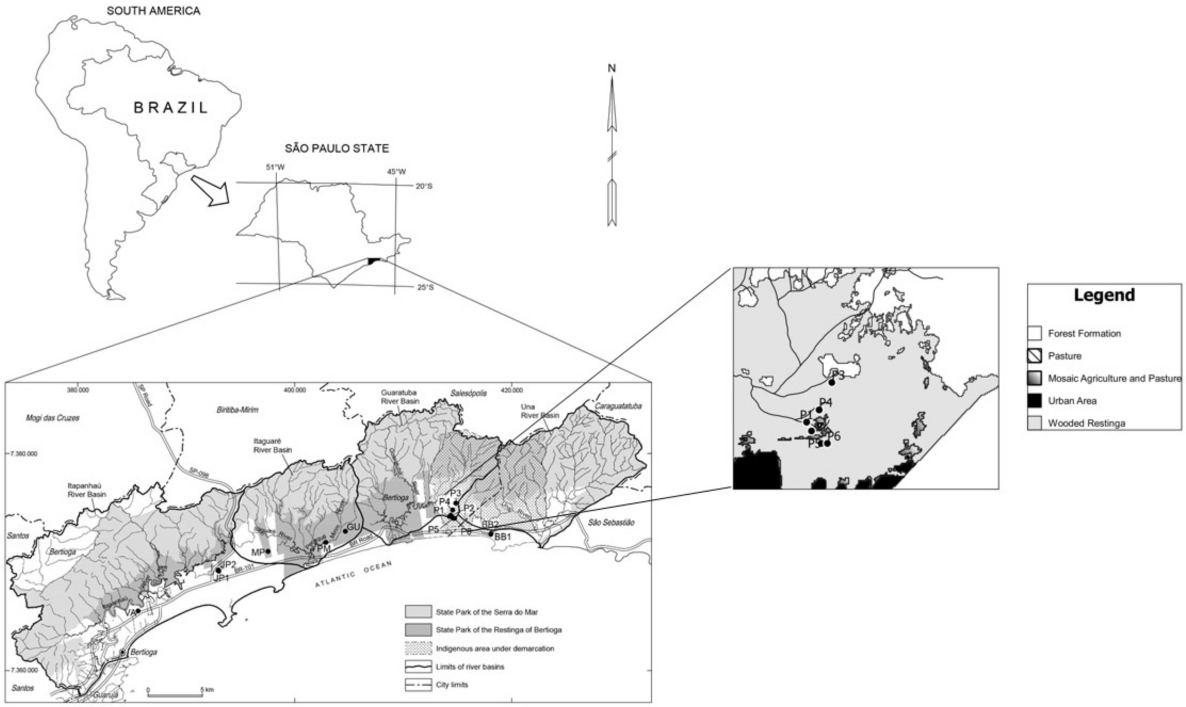

FIGURE 1 | Location of the study area in the coastal region of the state of São Paulo, indicating the Baixada Santista and Northern Coast basins and the distribution of the sampling sites in the Itapanhaú (JP1, JP2, VA), Itaguaré (MP, PM, GU), Guaratuba (P1–P6), and Una (BB1, BB2) sub-basins (Adapted from Esteves *et al*., 2019). In detail, sites of the Guaratuba sub-basin and main landscape types.

TABLE 1 | River Basins, catchment size (hectares), sampling locations and main characteristics of sampling sites in the Municipalities of Bertioga and São Sebastião, SP. Urb % = percentage of urbanization; NF % = percentage of Native Forest; AR % = percentage of Areas under Regeneration; HrDf = High Restinga Dry Forest; FODT = Lowland Rainforest, FODM = Dense Sub-Montane rainforest (Adapted from Esteves *et al*., 2019). *Sites located within the Parque Estadual Restingas de Bertioga (PERB). **Sites within private properties; +proximity of villages/roads. Vegetation types according to França, Rolim (2000); Instituto Ekos Brasil (2008) and Pinto-Sobrinho *et al.* (2011).

Sub-basin	Catchment Area (ha)	Stream	Distance from the sea (km)	Acronym	% Urb	% NF	% AR	Dominant vegetation	Coordinates
Guaratuba	11.3	Peralta 1**	1.75	P1	0.4	75.7	19.1	FaR, FODT	23°44'27.1"S 45°50'28.5"W
		Peralta 2**	1.87	P2	0.4	66.6	28.8		23°44'23.7"S 45°50'24.6"W
		Peralta 3**	2.97	P3		99.6			23°43'47.6"S 45°50'07.9"W
		Peralta 4**	2.35	P4	0.2	79.4	18.7		23°44'08.0"S 45°50'18.3"W
		Peralta 5**	1.57	P5	0.4	69.1	26.5		23°44'33.0"S 45°50'16.8"W
		Peralta 6**	1.56	P6	0.4	63.9	32.6		23°44'33.0"S 45°50'11.8"W
Itaguaré	9.04	Maneco Pinto*	3.1	MP		100.0		FaR, FbRb	23°46'08.2"S 46°00'20.4"W
		Perequê Mirim*	1.7	PM	4.2	95.5			23°45'42.6"S 45°57'11.8"W
		Gumercindo*	2.16	GU	0.4	98.8			23°45'09.9"S 45°56'08.2"W
Itapanhaú	14.9	João Pereira 1*+	3.17	JP1	10.9	89.0		FaR	23°47'06.6"S 46°03'01.2"W
		João Pereira 2*+	3.29	JP2	3.5	96.4			23°47'03.0"S 46°03'03.6"W
		Vila Agaó*+	1.98	VA	10.2	78.7			23°49'03.8"S 46°07'25.3"W
Una	12.06	Bora Bora 1+	0.39	BB1	4.2	81.4		FODT, FODM	23°45'21.8"S 45°48'14.6"W
		Bora Bora 2+	0.46	BB2	3.1	89.5			23°45'19.4"S 45°48'13.6"W

Sampling design and environmental variables. Data on fish, water and habitat characteristics were obtained during the period of low rainfall between the months of July and September 2016. This season is associated with a continuously falling water level and decreasing interconnection among habitats. In each stream, a continuous stretch of 100m was selected in the middle-downstream section, and the following local parameters were recorded at a single point along that reach: temperature (°C), pH, conductivity (µS.cm^{-1}), turbidity (NTU), dissolved oxygen (mg. L^{-1}) and total dissolved solids (mg. L^{-1}), using a Horiba model U-5000G multiparameter probe. In addition, subsurface water collection was performed for the analysis of total phosphorus (mg. L^{-1}), dissolved organic carbon (DOC) (mg. L^{-1}), total organic carbon (TOC) (mg. L^{-1}) and total iron (mg. L^{-1}), according to APHA/AWWA/WEF (2012). Water velocity was obtained using the float method (Marques, Argento, 1988), which provides an estimate of the maximum surface water velocity. For this calculation, we launched a float three times and measured the time required to pass through a 5 m section.

Other local variables related to instream features were recorded for each stream at five 20 m transects, including wetted width (m), depth (m), fish shelter (algae, aquatic plants, pieces of wood > 3 m, pieces of wood < 3 m, leaf banks, roots, boulders overhanging vegetation and artificial structures) (%), pools (%), smooth flow (slow surface and low turbulence) (%), high trees within the riparian zone (2 m distance from the stream; height

> 5 m; diameter at breast height > 3 m) (%), grasses and trunks (%), sand (0.06–2 mm) (%), gravel (2–64 mm) (%), and fines (silt/clay/mud – %), and the means calculated for each site. The methodology used to record habitat structures was adapted from the physical habitat assessment protocol modified by Callisto *et al.* (2002) and estimated visually.

Landscape variables were measured using the percentage cover of urban areas (houses, roads, sewage treatment plant), native forests, areas under regeneration (shrubs, bushes and small trees), deforested areas (clearings, sandbanks, dirt roads), rivers and beaches within a 500-m radius of the sampling point. Measurements were performed according to Tibúrcio *et al.* (2016), using satellite images for the year of 2016 and measurement tools from Google Earth, v. 7.3. Spatial data were calculated considering watercourse distance between sampling sites as recommended by Landeiro *et al.* (2011). We used drainage shapefiles and performed measurements on QGis 3.4 (QGIS Development Team, 2018).

Fish community sampling. Fish sampling was conducted from downstream to upstream with electrofishing equipment (Honda EUi10 Generator, 1000 W, CA), exploring all types of microhabitats along the 100 m reaches (Mazzoni *et al*., 2000). Blocking nets were used to prevent the escape of the most mobile species. For each site, three successive removals were used (Zippin, 1958) since three passes have proven to be adequate for obtaining quantitative data in Atlantic Forest streams (Mazzoni *et al*., 2000). The reach length of 100 m was set considering previous studies that evaluated the efficiency of electrofishing in small streams of the Neotropical region in reaches varying from 50 to 80 m in length (Mazzoni *et al*., 2000; Teixeira-de Mello *et al*., 2014). Forty channel widths were recommended by Terra *et al*. (2013) to estimate species richness in clearwater rain forest streams, but we could not sample greater extensions because of downstream marine influences and/or inaccessibility of upstream sections.

We separated fish into plastic boxes, anesthetized in eugenol solution, fixed in a 10% formalin solution and transferred to 70% ethanol after 10 days. For species taxonomy, we used the identification keys of Britski (1972) and Britski *et al.* (1984). Specialists from the Museu de Zoologia of the Universidade de São Paulo (MZUSP) and Universidade Estadual de Campinas (UNICAMP) confirmed fish identification. Voucher specimens were deposited in the Museu de Zoologia of the UNICAMP (ZUEC).

Data analysis. To compare fish assemblage similarity based on abundance data among sub-basins, we used a nonmetric multidimensional scaling analysis (NMDS). We applied the Bray-Curtis distance measure that is suggested for abundance data and considered the NMDS valid for a stress value < 0.2 (Clarke, Warwick, 1994). To test for statistical difference among the communities of the different sub-basins, we ran a non-parametric similarity analysis (ANOSIM) on the raw abundance data using 9999 permutations with a significance level of $\alpha = 0.05$. In this test, the R value varies between 0 and +1.0. Values close to "1.0", suggest dissimilarity among groups, while values close to "0" mean low separation among groups (Clarke, Warwick, 1994). A value of $p < 0.05$ indicates that the R value observed was not randomly obtained. We also used a SIMPER analysis to evaluate which taxa contributed most to the dissimilarity among streams from the four sub-basins. All analyses were performed on PRIMER 7 software (Clarke, Gorley, 2006).

Variance partitioning. Because species composition and environmental variables are spatially structured, we used variance partitioning (pRDA) to evaluate the relative contribution of 13 local and six landscape variables, including the spatial data matrix (W matrix) as a conditional value within the RDA. This method evaluates how much of the change in species abundance can be attributed to the changes in environmental variables (at local and landscape scale), and spatial variables as well as how much variability is shared among them (Borcard *et al*., 2011). According to Landeiro *et al*. (2011), our spatial matrix was represented as the network distance, *i.e*., the distance between the sampling points following the watercourse. We extracted spatial variables for inclusion into the model through the Analysis of Principal Coordinates of Neighborhood Matrix (PCNM). Following the step-by-step procedures of Borcard *et al*. (2011), we generated the PCNM variables and then calculated the Euclidean distance between points following the watercourse, using the 'dist' function in the R programming environment v. 4.2.2 (R Development Core Team, 2022). Based on the resulting Euclidean distance matrix, a truncation threshold was calculated using the maximum value of the minimum spanning tree using the 'spantree' function (Sedgewick, 1990) from the 'vegan' package (Oksanen *et al*., 2022) in R. The truncation limit was based on the minimum distance connecting all sample points resulting from the 'spantree' and it was used as a reference to calculate a PCoA (Principal Coordinate Analysis) of the truncated matrix. From this PCoA, only the positive eigenvalues were retained for use as spatial predictors represented as PCNM variables (Dray *et al*., 2006; Borcard *et al*., 2011).

Prior to the statistical modeling, the three predictive matrices (local, landscape and spatial) were evaluated for the levels of collinearity among them. To accomplish this, we calculated Pearson correlation coefficients for all pairs of variables using the 'color' function in R and excluded one of the variables with $r > 0.70$ (Dormann *et al*., 2013). Then, the predictive matrices containing only less correlated variables ($r < 0.70$) were individually subjected to a 'forward selection' using the 'ordistep' function from the 'vegan' package (Oksanen *et al*., 2022) in R to select the most important predictive variables that would explain the species matrix (Blanchet *et al*., 2008). Thus, we selected the significant variables ($p < 0.05$) of the three matrices as the most important to integrate the final datasets (Blanchet *et al*., 2008). Accordingly, the final explanatory matrices used in the variance partition models and pRDAs (Partial Redundancy Analysis) were composed of the following variables: local matrix: pH and TDS; landscape matrix: areas under regeneration; spatial matrix: PCNM1 (axis 1 of the PCNM).

To check the relative importance of local, regional and spatial variables for community composition, we performed three variance partitionings using the 'varpart' function of the 'vegan' package (Oksanen *et al*., 2022). This function partitions the variance of the dependent matrix Y (*e.g*., species composition) against the predictive matrices using redundancy analysis (RDA) ordering (Borcard *et al*., 1992; Legendre, Legendre, 1998). The significance of the contribution of the individual fractions (local, regional and spatial matrices) that quantify the variance in species composition was evaluated by applying the 'anova' function in R on partial RDA models (pRDAs) calculated using the 'rda' function of the 'vegan' package. Prior to the analysis of variance partitioning and the pRDAs, data from the species composition matrix were standardized using the Hellinger transformation, thereby avoiding statistical bias imposed by high abundances of few species (Legendre, Gallagher, 2001).

We also evaluated the possible influence of spatial autocorrelation on our results by applying multiscale ordination (MSO) on the RDA models using the 'mso' function from the ‘vegan’ package (Wagner, 2004; Borcard *et al*., 2011). For this, we applied the ‘MSO’ over a global RDA model containing all predictive matrices (local, landscape, and spatial) and over the individual pRDAs for each matrix. The MSO combines multivariate variograms with ordinations (simple or canonical), allowing the user to assess whether the variables of the predictive matrices exert a spatial autocorrelation effect on the response matrix and to identify in which distance classes this effect is significant (Wagner, 2003, 2004).

RESULTS

Environmental variables and fish communities. The studied streams presented unique characteristics, having dark and acidic waters, high values of DOC, TOC and conductivity, low flow and a predominance of native forest, followed by areas under regeneration (Tab. 2).

Twenty species belonging to 13 families and seven orders were collected in the 14 streams of the four sub-basins. The highest richness was that of the Characiformes, contributing 74.1% of the total abundance, followed by the Siluriformes (Tab. 3). The most abundant species recorded were *Mimagoniates microlepis* (Steindachner, 1877), which contributed with 55.4% of the captures, followed by *Hollandichthys multifasciatus* (Eigenmann & Norris, 1900), *Phalloceros harpagos* Lucinda, 2008, and *Pseudotothyris obtusa* (Miranda Ribeiro, 1911), representing 75.9% of the total abundance. *Cyphocharax santacatarinae* (Fernández-Yépez, 1948), *Hoplias malabaricus* (Bloch, 1794), and *Geophagus brasiliensis* (Quoy & Gaimard, 1824) were occasional species. Total abundance varied among sub-basins with the highest values in the Una sub-basin and lowest values in the Itapanhaú sub-basin.

NMDS analyses showed that fish communities were distinct among sub-basins, especially when considering the Guaratuba sub-basin in relation to the others (Fig. 2). The stress value for this analysis was 0.07, indicating a powerful representation of the sample patterns (Clarke, Warwick, 1994). This distinction was confirmed by the similarity analysis (ANOSIM) ($R = 0.333$; $p = 0.02$) with significant differences between Guaratuba x Itapanhaú ($p = 0.03$) and Guaratuba x Itaguaré ($p = 0.03$) sub-basins. According to SIMPER analysis, the species that most contributed to these dissimilarities were *M. microlepis* and *P. harpagos* (Itapanhaú x Guaratuba – 30.9 and 19.4%, respectively) and *M. microlepis* and *Dormitator maculatus* (Bloch, 1792) (Guaratuba x Itaguaré – 31.8 and 12.4%, respectively) (Tab. 4).

Predictors of fish composition. Variance partitioning analysis indicated that the three predictive matrices (local, landscape and spatial) together explained 58.6% of the variance in the composition of fish communities and the model was statistically significant ($F = 2.73$, $P = 0.001$). All fractions (local, spatial, landscape) had a significant influence on the variance of fish community composition, but the local variable had the highest R^2_{adj} (37%), explaining the greatest amount of variance in the fish community (Tab. 5). Within this amount, the pure local variable explains 17% of the variance, and the rest is shared among the other components: [local + landscape], [local + spatial], and [local + landscape + spatial], which explained 4.2, 1.6, and 15%, respectively (Fig. 3). We

TABLE 2 | Maximum, minimum, mean and standard deviation (SD) of local and regional environmental variables obtained for 14 blackwater Atlantic Forest streams during the period of low rainfall (June-September/2016) along the coast of São Paulo State. The most important variables selected for the variance partitioning procedure (pRDA) are indicated.

Environmental variables	Acronym	Minimum	Maximum	Mean	SD	Selected Variables (pRDA)
Local Variables						
Temperature (ºC)	T	17.00	21.37	19.31	1.30	
pH	pH	3.67	6.37	4.92	1.12	X
Conductivity (µS.cm $^{-1}$)	C	66.0	208.00	104.71	36.73	
Turbidity (NTU)	Tu	0.00	22.65	4.63	6.38	
Dissolved oxygen (mg.L^{-1})	DO	1.34	10.15	5.55	2.76	
Total Dissolved Solids (mg.L^{-1})	TDS	46.00	135.00	68.5	23.00	X
Total Iron (mg. L^{-1})	TI	0.14	2.05	0.61	0.49	
Total Posphorus (mg. L^{-1})	TP	0.01	0.22	0.06	0.06	
Dissolved Organic Carbon (mg.L^{-1})	DOC	9.88	87.10	34.92	28.92	
Total Organic Carbon (mg.L^{-1})	TOC	13.1	93.6	40.17	29.84	
Width (m)	W	1.03	5.80	2.16	1.17	
Depth (m)	D	0.16	0.39	0.29	0.07	
Water speed (m.s^{-1})	WS	0.00	0.73	0.06	0.19	
Fish shelter (%)	FS	22.00	33.50	28.00	3.30	
Pools (%)	P	0.00	26.00	7.44	8.16	
Smooth flow (%)	Sm	67.00	100.00	89.75	9.85	
High trees (%)	HT	15.50	72.50	37.31	15.22	
Grasses and trunks (%)	GT	45.00	67.50	55.00	7.35	
Sand (%)	S	12.00	73.00	44.08	18.75	
Gravel (%)	G	0.00	38.00	7.48	10.33	
Fines (%)	F	9.00	88.00	46.95	24.99	
Landscape variables						
Urban (%)	Ur	0.29	10.94	3.54	3.64	
Native Forest (%)	NF	63.91	100.00	84.24	12.27	
Areas under Regeneration (%)	AR	18.71	32.63	25.30	5.46	X
Deforestation (%)	De	0.29	4.89	2.49	1.66	
Beach (%)	B	5.73	12.69	9.21	3.48	
River (%)	R	6.21	6.21	6.21	0.00	

TABLE 3 | Fish species abundance during the low-precipitation season in 14 blackwater streams in the Itapanhaú, Itaguaré, Guaratuba, and Una sub-basins located along the coast of São Paulo State. *Atlantic Forest endemic species (Menezes *et al.*, 2007); +endangered species (MMA, 2022). Voucher specimens were deposited in the Museu de Zoologia of the Universidade Estadual de Campinas (ZUEC).

Order/Family	Species	Voucher	Acronym	Abundance					
Sub-basin		specimens		Una	Itapanhaú	Guaratuba	Itaguaré	Total	%
Characiformes									
Characidae	*Deuterodon taeniatus* (Jenyns, 1842)	16633	*Dete*			7		7	0.33
	Deuterodon iguape Eigenmann, 1907*	17322	*Deig*		2			2	0.09
	Hollandichthys multifasciatus (Eigenmann & Norris, 1900)*	16629	*Homu*	13	38	119	3	173	8.13
	Hyphessobrycon griemi Hoedeman, 1957*	16637	*Hygr*	13	4	16	7	40	1.88
	Mimagoniates microlepis (Steindachner, 1877)*	16632	*Mimi*	493	193	281	214	1181	55.47
	Spintherobolus broccae Myers, 1925*+	16636	*Spbr*		12	5	64	81	3.80
Crenuchidae	*Characidium lanei* Travassos, 1967*	16630	*Chla*	42	19	3	28	92	4.32
Curimatidae	*Cyphocharax santacatarinae* (Fernández-Yepéz, 1948)*	17004	*Cysa*				1	1	0.05
Erythrinidae	*Hoplias malabaricus* (Bloch, 1794)	17320	*Homa*				1	1	0.05
Cyprinodontiformes									
Poeciliidae	*Phalloceros harpagos* Lucinda, 2008	16638	*Phha*	19	98	1	27	145	6.81
Rivulidae	*Atlantirivulus santensis* (Köhler, 1906)*	17318	*Atsa*	7	1	11		19	0.89
Gobiiformes									
Eleotridae	*Dormitator maculatus* (Bloch, 1792)	16640	*Doma*		3		47	50	2.35
Gymnotiformes									
Gymnotidae	*Gymnotus pantherinus* (Steindachner, 1908)*	16631	*Gypa*	3		60	1	64	3.01
Cichliformes									
Cichlidae	*Geophagus brasiliensis* (Quoy & Gaimard, 1824)	16641	*Gebr*		1			1	0.05
Siluriformes									
Callichthyidae	*Callichthys callichthys* (Linnaeus, 1758)	17319	*Caca*			2		2	0.09
	Scleromystax barbatus (Quoy & Gaimard, 1824)*	16635	*Scba*	9	7	8	5	29	1.36
Heptapteridae	*Acentronichthys leptos* Eigenmann & Eigenmann, 1889*	16628	*Acle*	42	7	55	4	108	5.07
	Rhamdia quelen (Quoy & Gaimard, 1824)	16639	*Rhqu*		2		3	5	0.23
Loricariidae	*Pseudotothyris obtusa* (Miranda Ribeiro, 1911)*	17317	*Psob*		27	34	58	119	5.59
Synbranchiformes									
Synbranchidae	*Synbranchus marmoratus* Bloch, 1795	17321	*Syma*			3	6	9	0.42
	TOTAL			**641**	**414**	**605**	**469**	**2129**	

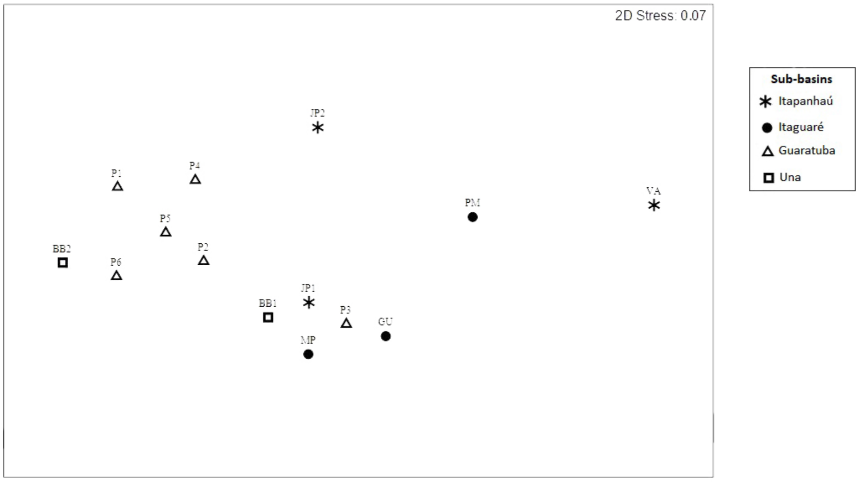

FIGURE 2 | Nonmetric Multidimensional Scaling (NMDS) plot of Axis 1 and Axis 2 of the total fish density of 14 blackwater streams. Stream codes according to Tab. 1.

TABLE 4 | Analysis of similarity percentage (SIMPER) for fish species with pairing among sub-basins, showing the species that determine group dissimilarity. Subscripts indicate sub-basins containing the highest abundance of each species. Only higher-contributing species are shown. Ita= Itapanhaú, Itg = Itaguaré, Gua = Guaratuba, and Una sub-basins. *Indicates groups with significant dissimilarities ($p<0.05$).

Species/Sub-basin	Una x Ita	Una x Gua	Ita x Gua*	Una x Itg	Ita x Itg	Gua x Itg*
Average dissimilarity	87.5	76.6	83.2	86.1	79.5	84.5
	% contribution					
Mimagoniates microlepis	45.3_{Una}	54.2_{Una}	30.9_{Ita}	49.2_{Una}	34.0_{Itg}	31.8_{Itg}
Characidium lanei						
Spintherobolus broccae				7.3_{Itg}	8.9_{Itg}	8.9_{Itg}
Acentronichthys leptos	17.0_{Una}	10.3_{Una}	8.8_{Gua}	8.5_{Una}		
Phalloceros harpagos	15.5_{Ita}		19.4_{Ita}		15.5_{Ita}	
Hollandichthys multifasciatus		13.3_{Gua}	15.1_{Gua}			10.1_{Gua}
Dormitator maculatus				10.7_{Itg}	13.0_{Itg}	12.4_{Itg}
Pseudotothyris obtusa						7.6_{Itg}

found no significant spatial correlation of residuals in pRDA models according to MSO diagnoses, indicating that our models have residual independence and homogeneity.

In Fig. 4 we performed an RDA with the best predicted variables for fish composition elected from the local, landscape and spatial matrices (pH, TDS, areas under regeneration and PCNM1). The percentage of variance explained by the first two axes was 30.6 and 20.14%, respectively. Some species, such as *Acentronichthys leptos* Eigenmann & Eigenmann, 1889, *Gymnotus pantherinus* (Steindachner, 1908), and *H. multifasciatus*, were associated with areas under regeneration and occurred in sites with low pH, characteristic of the Guaratuba sub-basin. On the other hand, *M. microlepis*, *P. obtusa*, *Scleromystax barbatus* (Quoy & Gaimard, 1824) and *Characidium lanei* Travassos, 1967 occurred mainly in sites with low total dissolved solids. *Phalloceros harpagos* occurred in sites with higher pH and *Dormitator maculatus* (Bloch, 1792) in sites with higher TDS.

TABLE 5 | Results of partial redundancy analysis (pRDA) for fish species composition predicted by local, landscape, and spatial variables in Atlantic Forest blackwater streams. a = fraction of exclusive explanation of local variables; b = fraction of exclusive explanation of landscape variables; c = fraction of exclusive explanation of spatial variables; d = fraction of shared explanation between local and landscape variables; e = fraction of shared explanation between landscape and spatial variables; f = fraction of shared explanation between local and spatial variables; g = fraction of shared explanation between local, landscape and spatial variables; h = residuals; df = degrees of freedom; R^2 = r-squared; R^2 adj = adjusted r-squared; p = p-value of F.

	df	R^2	R^2 adj	F	P	Residual Variance
[a+d+f+g] = LOCAL	2	0.47	0.37	4.92	0.001	0.30
[b+d+e+g] = LANDSCAPE	1	0.22	0.16	3.56	0.003	0.45
[c+e+f+g] = SPATIAL	1	0.22	0.15	3.44	0.010	0.45
[h] = Residuals			0.65			

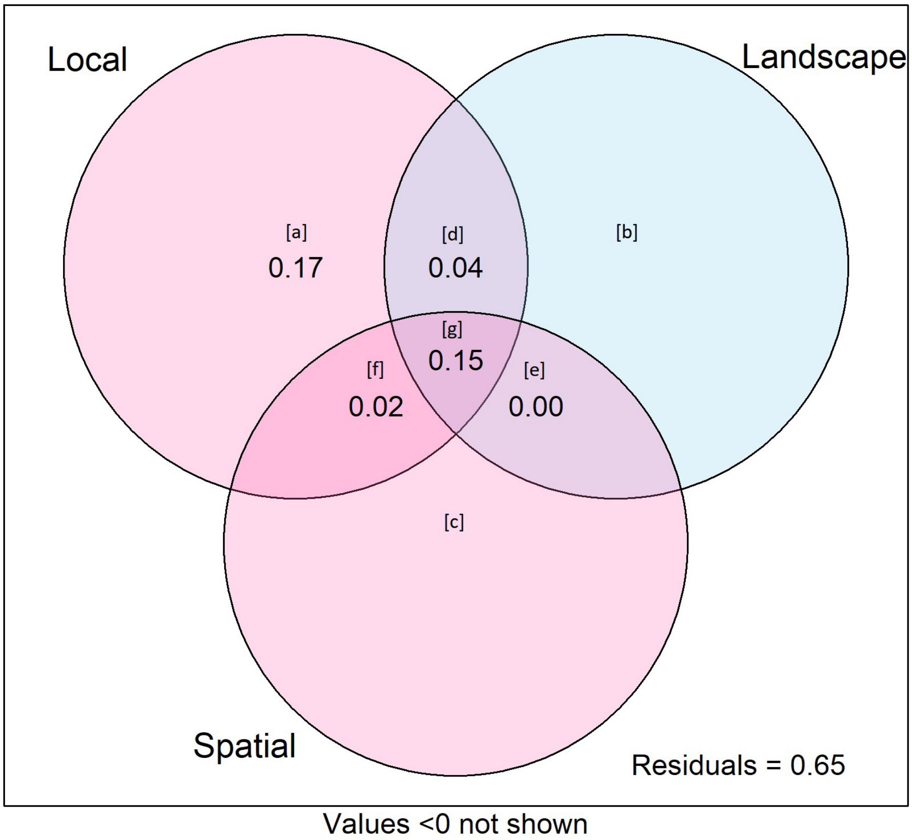

FIGURE 3 | Venn diagram showing the variance partition of local, regional and spatial variables in explaining the composition of fish communities. **a** = fraction of exclusive explanation of local variables; **b** = fraction of exclusive explanation of landscape variables; **c** = fraction of exclusive explanation of spatial variables; **d** = fraction of shared explanation between local and landscape variables; **e** = fraction of shared explanation between landscape and spatial variables; **f** = fraction of shared explanation between local and spatial variables; **g** = fraction of shared explanation among local, landscape and spatial variables.

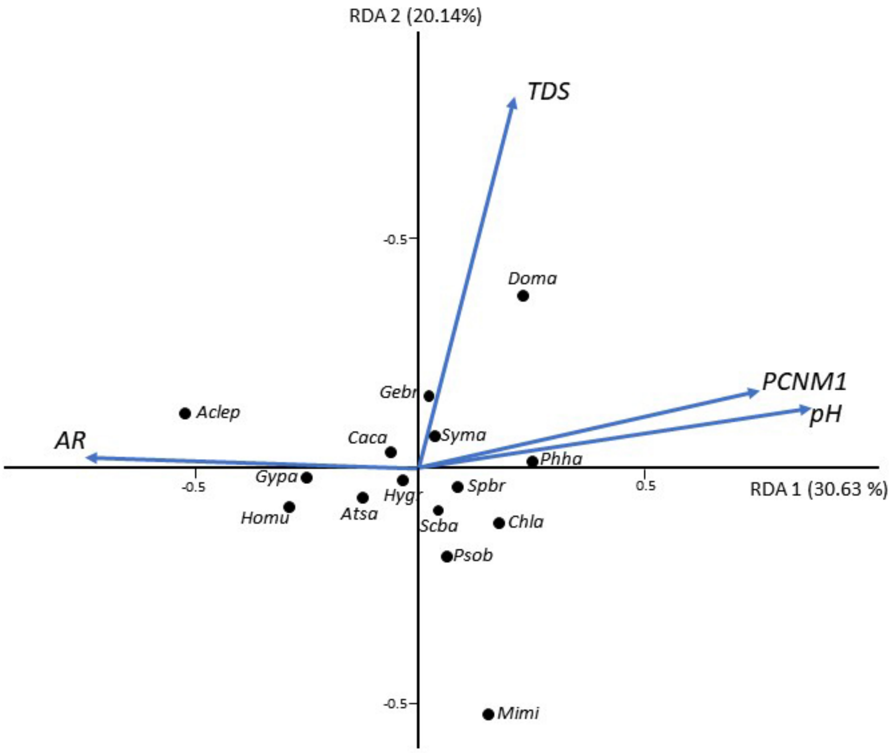

FIGURE 4 | Redundancy analysis (RDA) explaining the relationship between selected local, landscape, and spatial variables and fish species. Vector lines indicate the relationship of significant environmental variables to the ordination axis. TDS – Total Dissolved Solids; AR – Areas under Regeneration; PCNM1 – Spatial Component represented by the Principal Coordinates of Neighbor Matrices. Species are indicated by black dots. Acronyms according to Tab. 3

DISCUSSION

We found that environmental variables at the local scale best predicted fish abundance of stream fish assemblages in blackwater streams. The two most important selected local factors in our study, pH and TDS are apparently related to the main characteristics of blackwater rivers which are rich in humic substances and form complexes with iron, aluminum, calcium and magnesium (Krachler *et al*., 2019). The pH is known to have a strong effect on fish communities (Jackson *et al*., 2001), indicating that it is probably the main environmental filter for them, as also observed by Gonçalves, Braga (2012) in blackwater Atlantic Forest streams. Total Dissolved Solid (TDS) levels, a measurement of inorganic salts, organic matter and other dissolved materials in water (Weber-Scannell, Duffy, 2007), were high when compared to blackwater rivers from the Amazon (Duncan, Fernandes, 2010). These conditions may be important in maintaining fish diversity, as changes in TDS may exclude less tolerant species and cause shifts in biotic communities (Weber-Scannell, Duffy, 2007).

The lower importance of the “pure” landscape scale, compared to that of local scale, has been commonly reported in several other neotropical streams (Lemke, Suárez, 2013;

Junqueira *et al*., 2016; Terra *et al*., 2016; Barbosa *et al*., 2019), while other studies found contrasting results concerning their relative importance (Weigel *et al*., 2006; Ferreira *et al*., 2007; Cunico *et al*., 2012). Although these studies were performed in different river types, it is known that local and landscape factors may be context-dependent by their relationship to the spatial scale investigated (Junqueira *et al*., 2016) and the degree of system preservation (Dias, Tejerina-Garro, 2010). Thus, the higher importance of local variables in our study may be explained by the relatively uniform landscape conditions since streams were, in general, located in areas with well-preserved vegetation. Also, as organic acidity of naturally acidic waterways is reliant on the input of large amounts of allochthonous organic matter such as Dissolved Organic Carbon and leaf litter (Holland *et al*., 2012), linkages between local factors as the riparian flora and the aquatic environment are of fundamental importance.

Shared variation between local and landscape factors was also observed in our study, suggesting that landscape variables had a complementary effect in explaining variance in fish assemblages. In addition, areas under regeneration represented the only landscape predictor that influenced our model, and seems to be the one giving the best evidence of human-induced changes, especially in the Guaratuba sub-basin, where fine substrate was dominant. Landscape variables are known to create and maintain local habitats, influencing sedimentation and water regime, oxygen, and habitat properties, consequently impacting biodiversity (Blevins *et al*., 2013). For instance, native forests play a vital role in physical channel heterogeneity by supplying large wood, branches, litter and roots to aquatic systems (Allan, 2004; Jackson *et al*., 2015), creating mesohabitats and microhabitats along stream channels, as well as increasing marginal and instream habitat complexity (Harvey *et al*., 2018). On the other hand, modification of natural conditions can contribute to the input of unconsolidated substrate to the stream channel (*i.e*., siltation) (Wantzen, Mol, 2013).

Spatial effects were significant, but the "pure" spatial fraction did not explain the variation in the composition of the assemblages. This could be explained by the different processes by which metacommunities are organized and connected, including such mechanisms as species sorting, mass effects and dispersal limitation (Heino *et al*., 2015). Also, spatial processes, which can be important at very large and very small spatial extent, depend on fish dispersal ability and the influence of local and landscape predictors (Heino *et al*., 2015). Our study covered a 65 km stretch along the coast, an area that might be considered small to medium, covering regions "across streams" and "across drainage basins". Considering that a possible connection among adjacent localities may occur during the rainy season, some species may have sufficient dispersion capacity to generate a 'mass effect', whereby high dispersal rates homogenize communities to some degree at neighboring localities, irrespective of their abiotic and biotic environmental conditions (Heino *et al*., 2015). This hypothesis may be confirmed by the presence of several Characidae species, which perform reproductive migrations, as described by Mazzoni *et al.* (2004) and Mazzoni, Iglesias-Rios (2007) for Atlantic Forest streams. More specifically, they have found evidence of a group of fishes termed "Long Movement group", which moved at least 6 km within 60 days. Nevertheless, another mechanism such as dispersal limitation, which increases with spatial distance between sites, may also structure fish communities and, consequently, explain highest dissimilarities between the most distant sites as Vila Agaó and Bora Bora 2.

In this respect, our analyses should be viewed with caution as they represent an ecological snapshot, and seasonal or more sampling-intensive studies would help to clarify the variability of the spatial and temporal correlates. Also, since sampling sites in the present study were at sea level, spatial factors and environmental variables are not comparable to those of most studies performed in clearwater coastal Atlantic Forest streams, studied along longitudinal gradients (Ferreira *et al*., 2014; Terra *et al*., 2016; Gonçalves *et al*., 2019). However, Gonçalves *et al.* (2019) highlight the importance of dispersal processes in Atlantic Forest streams, particularly downstream, which seem to have a strong influence on community organization.

Differences in community composition were confirmed by the NMDS, which showed distinct fish composition among the four sub-basins, especially between the Guaratuba and both Itaguaré and Itapanhaú sub-basins, indicating dissimilarities within the same ecoregion (Ribeira do Iguape) *sensu* Abell *et al.* (2008). Although some authors state that a similarity among ichthyofauna is expected to occur between ecoregions (Hughes *et al*., 1987; Rohm *et al*., 1987), others imply that local factors within an ecoregion are more important (Van Sickle, Hughes, 2000; Herlihy *et al*., 2006). Fish species may show distinct preferences for different habitats, giving rise to distinct fish assemblages, which may be related to such variables as depth, pools and riffles, and substrate, as well water quality, such as oxygen, pH, conductivity and temperature (Gebrekiros, 2016).

Streams from the Guaratuba sub-basin were characterized by the presence of fine substrate and very acidic conditions, and dissimilarities between this sub-basin and both Itaguaré and Itapanhaú sub-basins were attributed mainly to the characid *M. microlepis*. This species was dominant in our study and is among the most abundant species in Atlantic Rain Forest streams (Esteves, Lobón-Cerviá, 2001; Barreto, Aranha, 2005), occurring both in clear and blackwater streams (Weitzman, Menezes, 1994). As this is an insectivorous surface feeder forming schools, usually associated with deep pools (Esteves, Lobón-Cerviá, 2001), its occurrence in regions with lower TDS indicates a preference for the most distant sites from the sea, essentially because proximity to the sea results in higher levels of water conductivity (Por, 2004) and, hence, high related TDS values.

Phalloceros harpagos, *H. multifasciatus*, and *D. maculatus* also contributed to the dissimilarities among sub-basins, indicating their association with different environmental conditions. *Phalloceros harpagos* has been defined as an indicator of deeper areas, like pools, favoring colonization owing to higher amounts of trunks, branches and leaf litter (Rezende *et al*., 2010), which were common conditions within the studied streams. On the other side, *D. maculatus* can be found in streams considered as transitional environments between the estuarine-riverine and the estuarine mixing zones (Abilhoa *et al*., 2011). The occurrence of a group of species associated with very acidic streams and fine sediment in the Guaratuba basin (*H. multifasciatus*, *G. pantherinus*, *A. leptos*) indicates a strong adaptation to these harsh conditions, which were also influenced by the proximity of areas under regeneration.

In conclusion, results showed differences in composition and structure among sub-basins that revealed distinct ecological requirements of some species, suggesting, in turn, environmental heterogeneity among streams determine the wider structural patterns of ichthyofauna. They also suggest that the contribution of local predictors to these blackwater streams holds the greatest importance in maintaining their fish assemblages, especially given that 60% of the recorded species are endemic, including one Endangered (EN) species (*Spintherobolus broccae* Myers, 1925) (MMA, 2022), and one classified as Data Deficient (DD) by the Brazilian federal list of endangered species (*H. multifasciatus*) (ICMBio, 2018). Also, the Atlantic Forest concentrates the largest number of threatened fishes, representing 35% of the total endangered species at the national level (Castro, Polaz, 2020). This situation draws attention to the importance of consistent conservation efforts, especially when coupled with the paucity of knowledge that exists about blackwater Atlantic streams located in restinga areas and the presence of rare organisms especially adapted to life in low-pH environments. In addition, restinga forests are considered highly fragmented, and little attention has been given to ensure the maintenance of their diversity and processes (Marques *et al*., 2015). Nonetheless, many of the studied streams were located within a conservation area (PERB) harboring 98% of the remnants of the restinga forests found within the Baixada Santista Hydrographic Basin (Banzato *et al*., 2012). Thus, the nearly pristine conditions of our study seem to be essential for conserving fish species, and to achieve this, the heterogeneity found among sub-basins seems to be important in maintaining fish biodiversity.

Environmental modifications, such as land use, may directly affect the characteristics of water (*e.g*., pH level), influencing fish preferences for reproduction habitat (Dei Tos *et al*., 2002) and determining fish growth (Ferreira *et al*., 2001). Thus, alterations in the studied streams could result in the elimination of fish species which are adapted to low pH and, consequently, modify fish composition. From a conservation perspective, then, this study may provide subsidies for species management in other blackwater Atlantic Forest streams and may be used as a baseline condition for the assessment of similar environments. Maintaining spatial heterogeneity and connectivity between stream reaches is also recommended in order to preserve the metacommunity dynamics of fish in these restinga remnants, which are under constant human pressure.

ACKNOWLEDGMENTS

The authors thank the the Instituto de Pesca (APTA/SAA) for providing the infrastructure; the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) for financial support (Proc. 2015/26728–6) and scholarship provided to MLG (Proc. 2017/21915–8); the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), for a scholarship to MLG (Finance Code 001); Écio S. Diniz for help with statistical analysis; Maressa H. N. Costa, Marcelo H. C. da Silva, Sergio L. Silva, Ronaldo F. Bernardino, Luiz Evangelista and Renato H. C. da Silva for help in the fieldwork; João B. P. da Silva, Marizete R. dos Santos, and Bolivar Barbanti, who assisted during the collections; Oswaldo T. Oyakawa and Flávio C. T. Lima for help in identifying fish species; Mirna Ferracini for map drawing and the Peralta group for allowing us to perform part of the study on their property.

REFERENCES

- **Abell R, Thieme ML, Revenga C, Bryer M, Kottelat M, Bogutskaya N *et al.*** Freshwater ecoregions of the world: A new map of biogeographic units for freshwater biodiversity conservation. Bioscience. 2008; 58(5):403–14. https://doi.org/10.1641/B580507
- **Abilhoa V, Braga RR, Bornatowski H, Vitule JRS.** Fishes of the Atlantic Rain Forest streams: Ecological patterns and conservation. In: Grillo O, Verona G, editors. Changing diversity in changing environment. Intech; 2011. p.259–82. https://doi.org/10.5772/24540
- **Allan JD.** Landscapes and riverscapes: the influence of land use on stream ecosystems. Annu Rev Ecol Evol Syst. 2004; 35:257–84. https://doi.org/10.1146/annurev.ecolsys.35.120202.110122
- **American Public Health Association (APHA), American Water Works Association (AWWA), Water Environment Federation (WEF).** Standard methods for the examination of water and freshwater. Washington, D.C.: APHA/AWWA/WEF; 2012.
- **Banzato BM, Favero JM, Arouca JAC, Carbonari JHB.** Análise ambiental de unidades de conservação através dos métodos swot e gut: O caso do Parque Estadual Restinga de Bertioga. Rev Bras Gest Ambient. 2012; 6(1):38–49.
- **Barbosa HO, Borges PP, Dala-Corte RB, Martins PTA, Teresa FB.** Relative importance of local and landscape variables on fish assemblages in streams of Brazilian savanna. Fish Manag Ecol. 2019; 26(2):119–30. https://doi.org/10.1111/fme.12331
- **Barreto AP, Aranha JMR.** Assemblage of freshwater fishes of Atlantic Forest: Composition and spatial distribution (Guaraqueçaba, Paraná State, Brazil). Acta Sci Biol Sci. 2005; 27(2):153–60. https://doi.org/10.4025/actascibiolsci.v27i2.1326
- **De Bie T, De Meester L, Brendonck L, Martens K, Goddeeris B, Ercken *et al.*** Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. Ecol Lett. 2012; 15(7):740–47. https://doi.org/10.1111/j.1461-0248.2012.01794.x
- **Bizerril CRSF.** Análise taxonômica e biogeográfica da ictiofauna de água doce do leste brasileiro. Acta Biol Leopold. 1994; 16:51–80.
- **Blanchet FG, Legendre P, Borcard D.** Forward selection of explanatory variables. Ecology. 2008; 89(9):2623–32. https://doi.org/10.1890/07-0986.1
- **Blevins ZW, Effert EL, Wahl DH, Suski CD.** Land use drives the physiological properties of a stream fish. Ecol Indic. 2013; 24:224–35. https://doi.org/10.1016/j.ecolind.2012.06.016
- **Borcard D, Gillet F, Legendre P.** Numerical ecology with R. New York: Springer; 2011.
- **Borcard D, Legendre P, Drapeau P.** Partialling out the spatial component of ecological variation. Ecology 1992; 73(3):1045–55. https://doi.org/10.2307/1940179
- **Britski HA, Sato Y, Rosa ABS.** Manual de identificação de peixes da região de Três Marias (com chaves de identificação para os peixes da bacia do São Francisco). Brasília: Companhia de Desenvolvimento do Vale do São Francisco – CODEVASF; 1984.
- **Britski HA.** Peixes de água doce do Estado de São Paulo: Sistemática. In: Branco SM, editor. Peixes de água doce do estado de São Paulo: Sistemática, Poluição e Piscicultura. São Paulo: Comissão Interestadual da Bacia Paraná-Uruguai, Faculdade de Saúde Pública da USP e Instituto de Pesca, Poluição e Piscicultura; 1972. p.79–108.
- **Brown BL, Swan CM, Auerbach DA, Campbell Grant EH, Hitt NP, Maloney KO *et al.*** Metacommunity theory as a multispecies, multiscale framework for studying the influence of river network structure on riverine communities and ecosystems. J North Am Benthol Soc. 2011; 30(1):310–27. https://doi.org/10.1899/10-129.1
- **Brown JH, Lomolino MV.** Biogeography. Sunderland: Sinauer; 1998.
- **Callisto M, Ferreira WR, Moreno P, Goulart M, Petrucio M.** Aplicação de um protocolo de avaliação rápida da diversidade de habitats e atividades de ensino e pesquisa (MG-RJ). Acta Limnol Bras. 2002;14(1):91–98.
- **Castro RMC, Polaz CNM.** Small-sized fish: the largest and most threatened portion of the megadiverse neotropical freshwater fish fauna. Biota Neotrop. 2020; 20(1):313–24. https://doi.org/10.1590/1676-0611-BN-2018-0683

- **Centro Integrado de Informações de Agronegócios (CIIAGRO).** Portal agrometeorológico e hidrológico do Estado de São Paulo [Internet]. São Paulo; 2021. Available from: http://www.ciiagro.org.br
- **Cerqueira R.** Biogeografia das restingas. In: Esteves FA, Lacerda LD, editors. Ecologia de restingas e lagoas costeiras. Macaé, Rio de Janeiro, Brasil: NUPEM/UFRJ; 2000. p.65–75.
- **Clarke KR, Gorley RN.** PRIMER v6: User Manual/ Tutorial. Plymouth: Primer-E; 2006.
- **Clarke KR, Warwick RM.** Changes in marine communities: an approach to statistical analysis and interpretation. Plymouth: Plymouth Marine Laboratory; 1994.
- **Compin A, Ceréghino R.** Spatial patterns of macroinvertebrate functional feeding groups in streams in relation to physical variables and land-cover in Southwestern France. Landscape Ecol. 2007; 22:1215–25. https://doi.org/10.1007/s10980-007-9101-y
- **Conselho Nacional do Meio Ambiente (CONAMA).** Resolução 261/1999 [Internet]. 1999. Available from: http://www.mma.gov.br/port/conama/res
- **Cottenie K.** Integrating environmental and spatial processes in ecological community dynamics. Ecol Lett. 2005; 8(11):1175–82. https://doi.org/10.1111/j.1461-0248.2005.00820.x
- **Cunico AM, Ferreira EA, Agostinho AA, Beaumord AC, Fernandes R.** The effects of local and regional environmental factors on the structure of fish assemblages in the Pirapó basin, Southern Brazil. Landsc Urban Plan. 2012; 105(3):336–44. https://doi.org/10.1016/j.landurbplan.2012.01.002
- **Dei Tos C, Barbieri G, Agostinho AA, Gomes LC, Suzuki HI.** Ecology of *Pimelodus maculatus* (Siluriformes) in the Corumbá reservoir, Brazil. Cybium. 2002; 26:275–82. https://doi.org/10.26028/cybium/2002-264-003
- **Dias AM, Tejerina-Garro FL.** Changes in the structure of fish assemblages in streams along an undisturbed-impacted gradient, upper Paraná River basin, Central Brazil. Neotrop Ichthyol. 2010; 8(3):587–98. https://doi.org/10.1590/S1679-62252010000300003
- **Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G *et al*.** Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography. 2013; 36(1):27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x
- **Dray S, Legendre P, Peres-Neto PR.** Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecol Modell. 2006;196(3–4): 483–93. https://doi.org/10.1016/j.ecolmodel.2006.02.015
- **Duncan WP, Fernandes MN.** Physiochemical characterization of the white, black, and clearwater rivers of the Amazon Basin and its implications on the distribution of freshwater stingrays (Chondrichthyes, Potamotrygonidae). Panam J Aquat Sci. 2010; 5(3):454–64.
- **Esteves KE, Lobón-Cerviá J.** Composition and trophic structure of a fish community of a clear water Atlantic rainforest stream in southeastern Brazil. Environ Biol Fish. 2001; 62(4): 429–40. https://doi.org/10.1023/A:1012249313341
- **Esteves KE, Silva MHC, Nanini-Costa MH, Petesse ML.** Organization of fish assemblages in blackwater Atlantic Forest streams. Neotrop Ichthyol. 2019; 17(1):1–12. https://doi.org/10.1590/1982-0224-20180120
- **Ferreira AA, Nuñer APO, Esquivel JR.** Influência do pH sobre ovos e larvas de jundiá, *Rhamdia quellen* (Osteichthyes, Siluriformes). Acta Sci Biol Sci. 2001; 23(2):477–81.
- **Ferreira FC, Petrere Jr. M.** The fish zonation of the Itanhaém river basin in the Atlantic Forest of Southeast Brazil. Hydrobiologia. 2009; 636(1):11–34. https://doi.org/10.1007/s10750-009-9932-4
- **Ferreira FC, Silva AT, Gonçalves CS, Petrere Jr. M.** Disentangling the influences of habitat structure and limnological predictors on stream fish communities of a coastal basin, southeastern Brazil. Neotrop Ichthyol. 2014; 12(1):177–86. https://doi.org/10.1590/S1679-62252014000100019
- **França FS, Rolim SG.** Estrutura de um trecho de floresta de restinga no município de Bertioga (SP). In: Watanabe S, editor. Anais do V Simpósio de Ecossistemas Brasileiros: Conservação, vol. 3. São Paulo: ACIESP; 2000. p.84–91.

- **Frissell CA, Liss WJ, Warren CE, Hurley MD.** A hierarchical framework for stream habitat classification: Viewing streams in a watershed context. Environ Manage. 1986; 10:199–214. https://doi.org/10.1007/BF01867358
- **Fundação Florestal.** Parque Estadual Restinga de Bertioga - Plano de Manejo [Internet]. São Paulo; 2018. Available from: http://arquivos.ambiente.sp.gov.br/fundacaoflorestal/2019/01/plano-de-manejo-pe-restinga-de-bertioga.pdf
- **Fundação Florestal.** Parque Estadual Restinga de Bertioga [Internet]. São Paulo; 2022. Available from: https://www.infraestruturameioambiente.sp.gov.br/fundacaoflorestal/parque-estadual-restinga-de-bertioga/
- **Gebrekiros ST.** Factors affecting stream fish community composition and habitat suitability. J Aquac Mar Biol. 2016; 4(2):00076. https://doi.org/10.15406/jamb.2016.04.00076
- **Geheber AD, Geheber PK.** The effect of spatial scale on relative influences of assembly processes in temperate stream fish assemblages. Ecology. 2016; 97(10):2691–704. https://doi.org/10.1002/ecy.1503
- **Gerhard P, Moraes R, Molander S.** Stream fish communities and their associations to habitat variables in a rain forest reserve in southeastern Brazil. Environ Biol Fish. 2004; 71:321–40. https://doi.org/10.1007/s10641-004-1260-y
- **Gonçalves CS, Braga FMS.** Changes in ichthyofaunal composition along a gradient from clearwaters to blackwaters in coastal streams of Atlantic Forest (southeastern Brazil) in relation to environmental variables. Neotrop Ichthyol. 2012; 10(3):675–84. https://doi.org/10.1590/S1679-62252012000300022
- **Gonçalves CS, Braga FMS, Casatti L.** Trophic structure of coastal freshwater stream fishes from an Atlantic rainforest: evidence of the importance of protected and forest-covered areas to fish diet. Environ Biol Fish. 2018; 101(6):933–48. https://doi.org/10.1007/s10641-018-0749-8
- **Gonçalves CS, Holt RD, Christman MC, Casatti L.** Environmental and spatial effects on coastal stream fishes in the Atlantic rain forest. Biotropica. 2019; 52(1):139–50. https://doi.org/10.1111/btp.12746
- **Gonçalves CS, Pérez-Mayorga MA.** Peixes de riachos da Estação Ecológica Juréia-Itatins: estrutura e conservação. Unisanta Biosci. 2016; 5:42–55.
- **Guedes D, Barbosa LM, Martins SE.** Composição florística e estrutura fitossociológica de dois fragmentos de floresta de restinga no município de Bertioga, SP, Brasil. Acta Bot Bras. 2006; 20(2):298–311. https://doi.org/10.1590/S0102-33062006000200006
- **Harvey GL, Henshaw AJ, Parker C, Sayer CD.** Reintroduction of structurally complex wood jams promotes channel and habitat recovery from overwidening: Implications for river conservation. Aquat Conserv. 2018; 28(2):395–407. https://doi.org/10.1002/aqc.2824
- **Heino J, Melo AS, Siqueira T, Soininen J, Valanko S, Bini LM.** Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. Freshw Biol. 2015; 60(5):845–69. https://doi.org/10.1111/fwb.12533
- **Henriques-Silva R, Logez M, Reynaud N, Tedesco PA, Brosse S, Januchowski-Hartley SR *et al.*** A comprehensive examination of the network position hypothesis across multiple river metacommunities. Ecography. 2019; 42:284–94. https://doi.org/10.1111/ecog.03908
- **Herlihy AT, Hughes RM, Sifneos JC.** Landscape clusters based on fish assemblages in the conterminous USA and their relationship to existing landscape classifications. Am Fish Soc Symp. 2006; 48: 87–112.
- **Hocutt CH, Wiley EO.** The zoogeography of North American freshwater fishes. New York: John Wiley and Sons; 1986.
- **Holland A, Duivenvoorden LJ, Kinnear SHW.** Naturally acidic waterways: Conceptual food webs for better management and understanding of ecological functioning. Aquat Conserv Mar Freshw Ecosyst. 2012; 22(6):836–47. https://doi.org/10.1002/aqc.2267

- **Hughes RM, Rexstad E, Bond CE.** The relationship of aquatic ecoregions, river basins, and physiographic provinces to the ichthyogeographic regions of Oregon. Copeia. 1987; 1987(2):423–32. https://doi.org/10.2307/1445780
- **Hutchinson GE.** Concluding remarks. Cold Spring Harb Symp Quant Biol. 1957; 22:415–27. http://dx.doi.org/10.1101/SQB.1957.022.01.039
- **Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio)**. Livro Vermelho da Fauna Brasileira Ameaçada de Extinção: Volume VI - Peixes. Brasília: ICMBio/MMA; 2018.
- **Instituto Ekos Brasil.** Diagnóstico socioambiental para criação de unidades de conservação polígono Bertioga: relatório final [Internet]. São Paulo; 2008. Available from: http://assets.wwfbr.panda.org/downloads/diagnostico_socioambiental_para_criacao_de_unidades_de_conservacao.pdf
- **Jackson CR, Leigh DS, Scarbrough SL, Chamblee JF.** Herbaceous *versus* forested riparian vegetation: Narrow and simple *versus* wide, woody and diverse stream habitat. Riv Res Appl. 2015; 31(7):847–57. https://doi.org/10.1002/rra.2783
- **Jackson DA, Peres-Neto PR, Olden JD.** What controls who is where in freshwater fish communities – the roles of biotic, abiotic, and spatial factors. Can J Fish Aquat Sci. 2001; 58(1):157–70. https://doi.org/10.1139/f00-239
- **Junqueira NT, Macedo DR, Souza RCR, Hughes RM, Callisto M, Pompeu PS.** Influence of environmental variables on stream fish fauna at multiple spatial scales. Neotrop Ichthyol. 2016; 14(3):e150116. https://doi.org/10.1590/1982-0224-20150116
- **Köppen GW.** Climatologia. México: Fundo de Cultura Econômica; 1948.
- **Krachler R, Krachler R, Valda A, Keppler BK.** Natural iron fertilization of the coastal ocean by “blackwater rivers”. Sci Total Environ. 2019; 656:952–58. https://doi.org/10.1016/j.scitotenv.2018.11.423
- **Landeiro VL, Magnusson WE, Melo AS, Espírito-Santo HMV, Bini LM.** Spatial eigenfunction analyses in stream networks: Do watercourse and overland distances produce different results? Freshw Biol. 2011; 56(6):1184–92. https://doi.org/10.1111/j.1365-2427.2010.02563.x
- **Legendre P, Gallagher E.** Ecologically meaningful transformations for ordination of species data. Oecologia. 2001; 129:271–80. https://doi.org/10.1007/s004420100716
- **Legendre P, Legendre L.** Numerical ecology. Amsterdam: Elsevier Science BV; 1998.
- **Legendre P.** Spatial autocorrelation: trouble or new paradigm? Ecology. 1993; 74(6):1659–73. https://doi.org/10.2307/1939924
- **Lemke AP, Súarez YR.** Influence of local and landscape characteristics on the distribution and diversity of fish assemblages of streams in the Ivinhema River basin, Upper Paraná River. Acta Limnol Bras. 2013; 25(4):451–62. https://doi.org/10.1590/S2179-975X2013000400010
- **Marques JSM, Argento SF.** O uso de flutuadores para avaliação da vazão de canais fluviais. Geociências. 1988; 7:173–86.
- **Marques MCM, Silva SM, Liebsch D.** Coastal plain forests in southern and southeastern Brazil: ecological drivers, floristic patterns and conservation status. Braz J Bot. 2015; 38:1–18. https://doi.org/10.1007/s40415-015-0132-3
- **Matthews WJ.** Patterns in freshwater fish ecology. New York: Chapman and Hall; 1998.
- **Mazzoni R, Fenerich-Verani N, Caramaschi EP.** Electrofishing as a sampling technique for coastal stream fish populations and communities in the southeast of Brazil. Rev Bras Biol. 2000; 60(2):205–16. https://doi.org/10.1590/S0034-71082000000200003
- **Mazzoni R, Fenerich-Verani N, Caramaschi EP, Iglesias-Rios R.** Stream-dwelling fish communities from an Atlantic rain forest drainage. Braz Arch Biol Technol. 2006; 49:249–56. https://doi.org/10.1590/S1516-89132006000300010
- **Mazzoni R, Iglesias-Rios R.** Patterns of investment of the reproductive strategy of two stream-dwelling Characidae. Braz J Biol. 2007; 67(4):695–99. https://doi.org/10.1590/S1519-69842007000400015
- **Mazzoni R, Schubart SA, Iglesias-Rios R.** Longitudinal segregation of *Astyanax janeiroensis* in rio Ubatiba: a Neotropical stream of south-east. Ecol Freshw Fish. 2004; 13(3):231–34. https://doi.org/10.1111/j.1600-0633.2004.00062.x

- **Menezes NA, Weitzman SH, Oyakawa OT, Lima FCT, Castro RMC, Weitzman MJ.** Peixes de água doce da Mata Atlântica. São Paulo: Museu de Zoologia da Universidade de São Paulo; 2007.
- **Ministério do Meio Ambiente (MMA).** Portaria MMA nº 148, de 7 de junho de 2022 [Internet]. Brasília; 2022. Available from: https://www.icmbio.gov.br/cepsul/images/stories/legislacao/Portaria/2020/P_mma_148_2022_altera_anexos_P_mma_443_444_445_2014_atualiza_especies_ameacadas_extincao.pdf
- **Myers N, Mittermeier RA, Mittermeier CG, Fonseca GAB, Kent J.** Biodiversity hotspots for conservation priorities. Nature. 2000; 403:853–58. https://doi.org/10.1038/35002501
- **Mykrä H, Heino J, Muotka T.** Scale-related patterns in the spatial and environmental components of stream macroinvertebrate assemblage variation. Global Ecol Biogeogr. 2007; 16(2):149–59. https://doi.org/10.1111/j.1466-8238.2006.00272.x
- **O'Neill RV, Johnson AR, King AW.** A hierarchical framework for the analysis of scale. Landscape Ecol. 1989; 3:193–205. http://dx.doi.org/10.1007/BF00131538
- **Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P *et al.*** Vegan: Community ecology package. R package version 2.6-4m [Internet]; 2022. Available from: https://CRAN.R-project.org/package=vegan
- **Pflieger WL, Schene MA, Haverland PS.** Techniques for the classification of stream habitats, with examples of their application in defining the stream habitats of Missouri. In: Armantrout NB, editor. Acquisition and utilization of aquatic habitat inventory information. Bethesda: American Fisheries Society; 1981. p.362–68.
- **Pinto-Sobrinho FA, Souza CRG, Mogollon JEJB.** Análise estrutural de florestas de restinga associadas a depósitos marinhos pleistocênicos e holocênicos na bacia do rio Itaguaré, Bertioga (SP). Rev I Geol. 2011; 32(1–2):27–40. https://doi.org/10.5935/0100-929X.20110003
- **Por FD.** Sooretama, the Atlantic rainforest of Brazil. The Netherlands: SPB Academic Publishing; 1992.
- **Por FD.** Hidrobiologia da Juréia e da baixada do Ribeira: rios e manguezais. In: Marques OAV, Duleba W, editors. Estação Ecológica Juréia-Itatins: ambiente físico, flora e fauna. Ribeirão Preto: Holos; 2004. p.51–57.
- **QGIS Development Team.** QGIS geographic information system. Chicago, IL: Open Source Geospatial Foundation Project; 2018. Available from: https://qgis.org/en/site/
- **R Development Core Team.** R: A language and environment for statistical computing, version 4.2.2. Vienna, Austria: R Foundation for Statistical Computing; 2022. Available from: https://www.r-project.org/
- **Rezende CF, Moraes M, Manna LR, Leitão RP, Caramaschi EP, Mazzoni R.** Mesohabitat indicator species in a coastal stream of the Atlantic rainforest, Rio de Janeiro-Brazil. Rev Biol Trop. 2010; 58(4):1479–87. https://doi.org/10.15517/rbt.v58i4.5425
- **Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM.** The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biol Conserv. 2009; 142(6):1141–53. https://doi.org/10.1016/j.biocon.2009.02.021
- **Ribeiro RB.** Relatório de situação dos recursos hídricos da Baixada Santista 2018. Santos: Comitê da Bacia Hidrográfica da Baixada Santista (CBH-BS) [Internet]. São Paulo; 2018. Available from: https://sigrh.sp.gov.br/public/uploads/documents/CBH-BS/13787/rs-2018-bs.pdf
- **Rohm CM, Giese JW, Bennett CC.** Evaluation of an aquatic ecoregion classification of streams in Arkansas. J Freshw Ecol. 1987; 4(1):127–40. https://doi.org/10.1080/02705060.1987.9665169
- **Roth NE, Allan JD, Erickson DL.** Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landscape Ecol. 1996; 11:141–56. https://doi.org/10.1007/BF02447513
- **Schlosser IJ.** Stream fish ecology: a landscape perspective. Bioscience. 1991; 41(10):704–12. https://doi.org/10.2307/1311765
- **Sedgewick R.** Algorithms in C. Boston: Addison Wesley; 1990.

- **Stephenson JM, Morin A.** Covariation of stream community structure and biomass of algae, invertebrates and fish with forest cover at multiple spatial scales. Freshw Biol. 2009; 54(10):2139–54. https://doi.org/10.1111/j.1365-2427.2008.02142.x
- **Teixeira-de Mello F, Kristensen EA, Meerhoff M, González-Bergonzoni I, Baattrup-Pedersen A, Iglesias C *et al*.** Monitoring fish communities in wadeable lowland streams: Comparing the efficiency of electrofishing methods at contrasting fish assemblages. Environ Monit Assess. 2014; 186:1665–77. https://doi.org/10.1007/s10661-013-3484-9
- **Terra BF, Hughes RM, Araújo FG.** Fish assemblages in Atlantic Forest streams: the relative influence of local and catchment environments on taxonomic and functional species. Ecol Freshw Fish. 2016; 25(4):527–44. https://doi.org/10.1111/eff.12231
- **Terra BF, Hughes RM, Francelino MR, Araújo FG.** Assessment of biotic condition of Atlantic Rain Forest streams: a fish-based multimetric approach. Ecol Freshw Fish. 2013; 34:136–48. https://doi.org/10.1016/j.ecolind.2013.05.001
- **Teshima FA, Mello BJG, Ferreira FC, Cetra M.** High β-diversity maintains regional diversity in Brazilian tropical coastal stream fish assemblages. Fish Manag Ecol. 2016; 23(6):531–39. https://doi.org/10.1111/fme.12194
- **Tibúrcio GS, Carvalho CS, Ferreira FC, Goitein R, Ribeiro MC.** Landscape effects on the occurrence of ichthyofauna in first-order streams of southeastern Brazil. *Acta* Limnol Bras. 2016; 28:e2. https://doi.org/10.1590/S2179-975X2515
- **Van den Wollenberg AL.** Redundancy analysis. An alternative for canonical correlation analysis. Psychometrika. 1977; 42:207–19. https://psycnet.apa.org/doi/10.1007/BF02294050
- **Van Sickle J, Hughes RM.** Classification strengths of ecoregions, basins and geographic clusters for aquatic vertebrates in Oregon. *J* North Am Benthol Soc. 2000; 19:370–84.
- **Wagner HH.** Direct multi-scale ordination with canonical correspondence analysis. Ecology. 2004; 85(2):342–51. https://doi.org/10.1890/02-0738
- **Wagner HH.** Spatial covariance in plant communities: integrating ordination, variogram modeling, and variance testing. Ecology. 2003; 84(4):1045–57. https://doi.org/10.1890/0012-9658(2003)084[1045:SCIPCI]2.0.CO;2
- **Wantzen KM, Mol JH.** Soil erosion from agriculture and mining: A threat to tropical stream ecosystems. Agriculture. 2013; 3(4):660–83. https://doi.org/10.3390/agriculture3040660
- **Weber-Scannell PK, Duffy LK.** Effects of total dissolved solids on aquatic organisms: A review of literature and recommendation for salmonid species. Am J Environ Sci. 2007; 3(1):1–06. https://doi.org/10.3844/ajessp.2007.1.6
- **Weigel BM, Lyons J, Rasmussen PW, Wang L.** Relative influence of environmental variables at multiple spatial scales on fishes in Wisconsin's warmwater nonwadeable rivers. Am Fish Soc Symp. 2006; 48:493–511.
- **Weitzman SH, Menezes NA.** As espécies de *Glandulocauda* e *Mimagoniates*, peixes glandulocaudíneos do Brasil, Paraguai e nordeste do Uruguai. Habitat. 1994; 1:1–08.
- **Wevers MJ, Warren CE.** A perspective on stream organization, structure, and development. Arch Hydrobiol. 1986; 108(2):213–33. https://doi.org/10.1127/archiv-hydrobiol/108/1986/213
- **Winemiller KO, Leslie MA.** Fish communities across a complex freshwater-marine ecotone. Environ Biol Fishes. 1992; 34:29–50. https://doi.org/10.1007/BF00004783
- **Wolff LL, Hahn NS.** Fish habitat associations along a longitudinal gradient in a preserved coastal Atlantic stream, Brazil. Zoologia. 2017; 34:e12975. https://doi.org/10.3897/zoologia.34.e12975
- **Zippin C.** The removal method of population estimation. J Wildl Manag. 1958; 22:82–90.

AUTHORS' CONTRIBUTION

Mariana Landucci Giongo: Investigation, Methodology, Writing-original draft, Writing-review and editing.

Maria Letizia Petesse: Formal analysis, Methodology, Supervision, Writing-review and editing.

Katharina Eichbaum Esteves: Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Writing-review and editing.

ETHICAL STATEMENT

Sampling license was provided by the Instituto Florestal do Estado de São Paulo (SMA Process: 260108–003286/2016) and the Sistema de Autorização e Informação em Biodiversidade (SISBIO, No 54432–1). All sampling and handling procedures were approved by the Animal Experimentation Ethics Committee of the Instituto de Pesca/APTA/SAA (License No 05/2016) in accordance with their protocols for the ethical and methodological use of fish.

COMPETING INTERESTS

The author declares no competing interests.

HOW TO CITE THIS ARTICLE

- **Giongo ML, Petesse ML, Esteves KE.** Fish responses to multiple scales in coastal blackwater Atlantic Forest streams in Southeast Brazil. Neotrop Ichthyol. 2023; 21(2):e230030. https://doi.org/10.1590/1982-0224-2023-0030

Neotropical Ichthyology

OPEN ACCESS

SBI
Official Journal of the
Sociedade Brasileira de Ictiologia