

Environmental and spatial effects on coastal stream fishes in the Atlantic rain forest

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Abstract

Contemporary and historical factors influence assemblage structure. The environmental and spatial influences acting on fish organization of rain forest coastal streams in the Atlantic rain forest of Brazil were examined. Fish (and functional traits such as morphology, diet, velocity preference, body size), environmental variables (pH, water conductivity, dissolved oxygen, temperature, stream width, flow, depth, substrate), and altitude were measured from 59 stream reaches. Asymmetric eigenvector maps were used to model the spatial structure considering direction of fish movements. Elevation played an important role—fish abundance, biomass, and richness all decrease with increasing elevation. Fish communities are influenced by both environmental and spatial factors, but downstream movements were shown to be more important in explaining the observed spatial variation than were bidirectional and upstream movements. Spatial factors, as well as environmental variables influenced by the spatial structure, explained most of the variation in fish assemblages. The strong spatial structuring is probably attributable to asymmetric dispersal limitation along the altitudinal profile: Dispersal is likely to be more limiting moving upstream than downstream. These fish assemblages reflect scale-dependent processes: At the stream-reach scale, fish respond to local environmental filters (habitat structure, water chemistry, and food supply), which are in turn influenced by a larger scale, namely the altitudinal gradient expected in steep coastal mountains. Thus, environmental drivers are not independent of spatial factors, and the effects of local factors can be confounded across the altitudinal gradient. These results may have implications for conservation, because downstream reaches are often neglected in management and conservation plans.

Abstract in Portuguese is available with online material.

KEYWORDS

altitude, asymmetric eigenvector maps, dispersal limitation, environmental filtering, fish metacommunities, fish movement, tropical streams conservation, variation partitioning

1 | INTRODUCTION

Understanding the factors structuring biological communities is a continuing challenge in ecology, since many factors can operate simultaneously and over different spatial scales in determining community composition. The species pool from which local communities are drawn is influenced by contemporary factors such as biotic interactions and environmental constraints imposed by habitat features, as well as by biogeographic factors that may restrict or promote colonization opportunities, as well as speciation (Jackson, Peres-Neto, & Olden, 2001). Over the past decade, metacommunity theory has provided fresh perspectives on the mechanisms and processes that regulate the spatial organization of species, in particular by recognizing that local communities are connected to each other by movement between different communities via dispersal processes playing out across different spatial scales (Heino et al., 2015; Holyoak, Leibold, Mouquet, Holt, & Hoopes, 2005; Leibold et al., 2004; Logue, Mouquet, Peter, & Hillebrand, 2011).

Fish communities are structured non-randomly over space (Jackson et al., 2001), as many species of fish often require different habitats to complete their life cycles, making movement across space an essential ingredient in species persistence at given locations (Blanck, Tedesco, & Lamouroux, 2007). Many factors can exert strong influences on the structure of the ichthyofauna in streams, so both local environmental constraints and dispersal processes are important and should be evaluated together to better understand the structuring of fish metacommunities (De Macedo-Soares, Petry, Farjalla, & Caramaschi, 2009, Falke & Faush, 2010, Cetra, Petrere, & Barrella, 2017, Pérez-Mayorga, Casatti, Teresa, & Bregão, 2017). The relative importance of local environmental conditions and dispersal to fish community organization will be influenced by the spatial context (Geheber & Geheber, 2016), as differences among communities may arise depending on the spatial distribution of stream sites and even the spatial extent of the aquatic ecosystems under consideration (Nakagawa, 2014; Sály & Erős, 2016).

The eastern Brazilian coastal basins harbor an extraordinary diversity of fish (>500 species, Thomaz & Knowles, 2018), mainly of small body size, with many cases of endemism resulting from isolation promoted by the mountainous relief (Menezes et al., 2007). Many species have an intimate association and dependence on the adjacent forested landscape, which acts as a key food source (a spatial subsidy) for stream fishes (Gonçalves, Braga, & Casatti, 2018). Although several studies on stream fish communities have been conducted in past decades in our general region (see Abilhoa, Braga, Bornatowski, & Vitule, 2011), there is still a very large gap in basic information (e.g., feeding, reproduction, dispersal) on many species in the fish assemblages in this region.

In the Brazilian Atlantic Forest, it is well known that fish assemblages are influenced by local habitat structure (Abilhoa et al., 2011; Mazzoni, Fenerich-Verani, Caramaschi, & Iglesias-Rios, 2006; Terra, Hughes, & Araújo, 2016) such as depth, water velocity, and substrate (Ferreira, Silva, Gonçalves, & Petrere, 2014; Gonçalves & Braga, 2012). The importance of spatial structure in the organization of

fish assemblages is revealed by species zonation along an upstream–downstream gradient of environmental heterogeneity (Balon & Stewart, 1983; Ferreira & Petrere, 2009; Hynes, 1970; Mazzoni & Lobón-Cerviá, 2000; Rahel & Hubert, 1991). The streams of this system display a continual shift in physical features from headwaters to mouths opening into the ocean, likely driving changes in the species composition of aquatic communities, as crystallized in the river continuum concept (RCC) (Vannote, Minshall, Cummins, Sedell, & Cushing, 1980).

Coastal headwater streams from southeast Brazil are located on very steep and ancient Precambrian mountains in the Serra do Mar (Almeida & Carneiro, 1998). These mountains may reach altitudes over 2,000 m (Por & Lopes, 1994), and along the altitudinal gradient, the slope can quickly increase up to very steep grades, as much as 75%, over just a few kilometers. Some streams spring up in the mountains and flow directly into the sea, while others, especially downstream reaches, drain an extensive Pleistocene alluvial plain, which is less than four meters above sea level (Por, 2004; Por & Lopes, 1994). Over geological time scales, it is likely that many of these streams have stayed disconnected (Lima & Ribeiro, 2011), though some may have shared the same paleodrainages during sea level retreats (Thomaz & Knowles, 2018). Thus, landscape and geographical constraints are expected to limit the dispersal of fish (Jaramillo-Villa, Maldonado-Ocampo, & Escobar, 2010) and so channel the processes of metacommunity formation (Heino et al., 2015). Coastal streams provide a good system exploring the interplay of environmental constraints and dispersal processes of organisms as determinants of community structure.

The topographic variation imposed by altitude is reflected in the abiotic conditions of local aquatic environments. Headwater communities are subject to different environmental filters than are downstream communities (Pouilly, Barrera, & Rosales, 2006). The relative importance of species sorting by abiotic conditions (which occurs when species are unable to cope with particular environmental constraints) and dispersal processes for fish community organization vary greatly among aquatic ecosystems (Datry et al., 2016; Heino et al., 2015). In the Brazilian coastal streams system, with strong elevational differences over relatively short distances, altitude serves as a proxy for the distinct upstream–downstream regions typically found in coastal drainages (doubtless reflecting many abiotic and biotic factors changing simultaneously along the gradient).

Stream fishes that undergo altitudinal variation are subject to changes in community structure in a non-random way (Hynes, 1970). Functional ecology is an emerging approach that has been proven to be a powerful tool to predict species compositional changes across gradients of environmental conditions (Villegger, Brosse, Mouchet, Mouillot, & Vanni, 2017). Some biological attributes such as locomotion and food acquisition are useful to describe functions performed by fish, and prior work shows that fish morpho-anatomical traits strongly correlate with species habitat use and trophic ecology (Gatz, 1979; Watson & Balon, 1984). As hypothesized by Townsend and Hildrew (1994) in their classic model of river habitat templates, the attributes of local communities (as measured in suites of major

functional traits) should converge predictably when environmental conditions are similar. We will examine how the functional traits of our communities vary across the altitudinal gradient.

Human impacts change fish assemblages (Casatti et al., 2012) hindering the understanding of historical ecological patterns (Terra et al., 2016), and such impacts are pervasive across the tropics. Studies of small, non-impacted tropical streams are still scarce (e.g., Cilleros, Allard, Vigouroux, & Brosse, 2017) probably due to the difficulty of accessing these environments, and their increasing scarcity due to human impacts. The objective of this study is to characterize the factors that seem to govern fish assemblage structure in non-impacted Atlantic Forest coastal streams. We addressed the specific question: How much of the variability in fish assemblages is explained by environmental rather than spatial factors? Considering metacommunity theory, we hypothesized that species sorting (a niche-based mechanism controlled by biotic and abiotic factors, such as competition or environmental filtering) would regulate the fish metacommunities if the variation in the structure of fish assemblages were explained by environmental factors, that is, local habitat characteristics. We determined the functional similarity among fishes to identify the relationship between species traits and environmental factors that could be responsible for assemblage structure. Conversely, dispersal processes would be more important if spatial factors explained observed variation better than the local environmental factors. Abstractly, one can imagine three modes of directionality in dispersal leading to community assembly: downstream, bidirectional, and upstream movements. We hypothesized that downstream movements should be more important in the studied stream network, due to the dispersal by fish promoted by the often-strong downward flow of water along the steep elevation gradient. This bias in dispersal could occur over both ecological and evolutionary time scales.

2 | METHODS

2.1 | Study area

The non-impacted stream study sites are situated in the Juréia-Itatins Reserve, a mosaic of conservation areas protecting Atlantic rain forest located on the south coast of the State of São Paulo, Brazil (24°18', 24°32'S and 47°00', 47°30'W) (Figure S1). The climate of this region is classified as predominantly wet without a pronounced dry season, and the average annual rainfall and temperature are 2,277 mm and 21.4°C, respectively (Tarifa, 2004).

The Juréia-Itatins Reserve contains several steep mountains that rise up to 1,240 m, and the altitudinal gradients on these mountains can abruptly fall to alluvial plains not exceeding 5 m (Por, 1986; Souza & Souza, 2004). Headwaters may reach an altitude of 600 m, even over distances less than 4 km. The reserve is delimited by a set of mountains contained within the Serra do Mar known as Serra dos Itatins (the northern boundary), and Serra da Juréia (the southern boundary). Reflecting these differences in topography, along with heterogeneity in bedrock, soil composition, and vegetation types, a

diverse river system is found in the Juréia-Itatins Reserve, with three distinct local aquatic environments: (a) clearwaters (nutrient poor with pH ~ 6) from very steep Precambrian mountains with dense ombrophilous forest, (b) blackwaters (rich in humic substances with pH ~ 4) from Pleistocenic lowlands with herbaceous/shrubby forest, called *restinga*, that covers sandy podzolic soils, and (c) brackish waters from estuarine areas with mangrove forest (Gonçalves & Braga, 2012; Por, 1986; Por & Lopes, 1994).

2.2 | Sampling

Sampled sites included 59 clearwater locations, comprising 23 stream systems (sensu Allan & Castillo, 2007) from first to fourth order at a scale based on 1:10,000 mapping (Figure S1). These were selected to encompass the altitudinal profile of stream environments in the reserve, that is, upper (above 100 m), middle (between 15–100 m), and lower (up to 15 m) reaches of coastal streams. Sampling included the period when rainfall is less intense (from June to August, Tarifa, 2004) on 19 sites during July 2009, and 40 different sites during June 2013. Sites sampled in 2009 were not sampled again in 2013, and sites of a given drainage were sampled in the same year.

Fish were caught using an electrofisher unit (500 V DC), and two dip nets (mesh size 2 mm), along 50-m reaches, using one passage of the equipment without a block seine. The dip nets were handled by two people who walked slowly upstream, in the opposite direction to the direction of the stream flow, up to the upper limit of the selected reach.

Fish specimens were anesthetized with benzocaine, fixed in 10 percent formalin, and then kept in 70% ethanol until analysis. In the laboratory, fish specimens were identified, counted, and weighed. Vouchers are deposited in the fish collection of Universidade Estadual Paulista (UNESP), São José do Rio Preto, São Paulo, Brazil (DZSJRP 13234–13258, 20728–20740).

We measured seven functional traits (Table 1) in 19 species that were represented by a sufficient number of specimens (≥ 10) to obtain quantitative traits, following Casatti et al. (2015). Traits were associated with vertical habitat use, trophic ecology, velocity preference, and body size. We obtained fish measurements with a digital caliper. Fin areas were obtained by contouring the fins over graph paper. For species with accentuated sexual dimorphism, such as *Phalloceros harpagos* and *P. reisi*, we measured only females for procedure standardization. *Synbranchus marmoratus* was excluded from functional analysis due to it not having pectoral fins. We obtained functional traits related to feeding through stomach content analysis, previous studies, and the published literature. We obtained velocity preference and body size from the literature.

We measured pH, conductivity ($\mu\text{S}/\text{cm}$), dissolved oxygen (mg/L), and water temperature (°C), before fish sampling. Habitat variables measured at each site were stream width (m), flow (m/s), depth (m), and the percentage of the predominant bottom type (in mm), as clay <0.05, sand 0.05–2, gravel 2–10, pebble 10–100, rock

TABLE 1 Description and interpretation of each functional trait measured in the stream fish species of Juréia-Itatins reserve

Traits	Statistical type	Description and interpretation
Compression index	Quantitative	Maximum height of the body divided by its maximum width. High values may indicate a laterally compressed fish inhabiting lentic habitats ¹
Relative area of pectoral fin	Quantitative	Pectoral fin area divided by body area. High values indicate slow swimmers, which use pectoral fins to perform maneuvers and breakings, or fish inhabiting fast waters, which use them as airfoils to deflect the water current upward to remain firmly attached to the substrate ¹
Pectoral fin aspect ratio	Quantitative	Maximum length of the pectoral fin divided by its maximum width. High values indicate long fins, typical of fish that swim for long distances ¹
Eye position	Quantitative	Distance from the middle of the eye to the base of the head, divided by head height. High values indicate dorsally located eyes, typical of benthic fish ¹
Diet	Fuzzy	Feeding items were allochthonous insects, detritus, autochthonous insects, fish, and periphyton. Each feeding item was coded as 0, 1, or 2, depending on its predominance in the stomachs of each species sample. 0 = item absent or rare in species diet, 1 = item consumed, although not the most representative in species diet, 2 = dominant item in the diet ^{3,4,5,6,7}
Velocity preference	Ordinal	Values of 0, 1, or 2 were assigned to each species, according to its preference for current speed: 0 = slow, 2 = intermediate, and 3 = fast ^{3,4,5}
Standard length classes	Ordinal	Distance from the tip of the nose to the end of the last vertebrae. Values of 1, 2, or 3 were assigned to each species, according to the most common size class for adults. ² 1 = up to 50 mm, 2 = from 51 to 100 mm, 3 = larger than 100 mm

¹Watson and Balon (1984);

²Froese and Pauly (2019);

³Sabino and Castro (1990);

⁴Sabino and Silva (2004);

⁵Oyakawa, Akama, Mautari, and Nolasco (2006);

⁶Gonçalves and Cestari (2013);

⁷Gonçalves et al. (2018).

100–300, boulder >300 mm, bedrock, and plant debris. Replicate measurements of stream width and flow, channel depth, and bottom type were taken in the same 50-m stream reaches where fish were sampled. Ten contiguous linear transects were set up for the physical measurements, one every 10 m of the 50-m stretch. We also recorded the elevation (m) of each sample site, as well as its geographic position using a GPS device; the locations were plotted in topographic maps (scale of 1:10,000) using ArcGIS 9.3 (Environmental Systems Research Institute (ESRI) 2009), to facilitate spatial analyses.

2.3 | Data analysis

We started our analysis by exploring whether different aggregate variables of community structure (abundance, biomass, species richness) change as a function of the elevation gradient, using simple linear regression models.

To explore the role of environmental factors on fish distribution, we performed redundancy analysis (RDA) with the environmental variables.

The relative importance of local environmental variables and spatial factors in structuring the metacommunity was evaluated using partial redundancy analysis (pRDA) (Borcard, Gillet, & Legendre, 2011; Legendre & Legendre, 1998). Partial RDA is a multivariate

analogue of partial linear regression (Borcard et al., 2011), useful to investigate the processes that determine the abundance and species composition of assemblages among locations (Cottenie, 2005; Cottenie, Michels, Nuytten, & Meester, 2003; Logue et al., 2011). The method decomposes the total variation; that is, it evaluates how much of the total variation in the community matrix can be attributed to environmental [E] or spatial [S] variables, according to its components: combined variation [E + S], environmental variation [E], spatial variation [S], environmental variation without the spatial component [E|S], and spatial variation without the environmental component [S|E]. Therefore, we can evaluate the relative influence of environmental and spatial factors in explaining the variation of fish community structure. Statistical significance of the components was evaluated by Monte Carlo permutation tests (999 permutations). We calculated the percentage of the variation not explained by the variables considered ($1 - [E + S]$), and the variation from correlations between environmental and spatial factors ($[E \text{ with } S] = [E] - [E|S] = [S] - [S|E]$).

Fish abundance was treated as the dependent data matrix in both the RDA and pRDA. The mean values of the habitat measurements, and the spatial structure (described below) were the explanatory data matrices. Fish data were Hellinger-transformed, and habitat variables were standardized (following Legendre & Gallagher, 2001).

The environmental variables were forward-selected using a double-stopping criterion (α and R^2_{adj}) for inclusion in the model so

as to ensure parsimony and to avoid possible correlations among the predictor variables (Borcard et al., 2011). Therefore, forward selection was stopped if an environmental variable reached $\alpha > 0.05$ or if it increased the adjusted coefficient of multiple determination R^2_{adj} of the model over the value of the R^2_{adj} of the global model containing all environmental variables (Blanchet, Legendre, & Borcard, 2008a), using the `forward.sel` function of `packfor` (Blanchet, Legendre, & Gauthier, 2013). Clay was infrequently encountered in the field samples and thus excluded from the analyses.

The spatial distribution of fish species was modeled using the asymmetric eigenvector maps (AEM) framework, which is an eigenfunction-based spatial filtering technique, proposed by Blanchet, Legendre, and Borcard (2008b). We used the geographic eigenfunctions created

by AEM to model the spatial structure of the studied stream sites. An advantage of this method is that it incorporates directionality in processes linking sites (here fish dispersion) by construction of a connection diagram linking the sites (each link is called edge herein). A sites-by-edges matrix was constructed using binary coding: Linked sites received code 1, whereas unlinked sites received code 0.

For each directional approach (downstream, bidirectional, and upstream movements), we computed a Euclidean distance matrix using the sites-by-edges matrix calculated from the connection diagram, and then a principal coordinate analysis (PCoA) using that matrix (`pcoa` function in the `ape` package) (Paradis, Claude, & Strimmer, 2004). To select the eigenfunctions representing the spatial structure, we ran an automatic stepwise model selection using permutation tests.

TABLE 2 Stream fish species registered in 59 sites of Juréia-Itatins reserve and its respective acronyms

Order	Family	Species	Acronym
Characiformes	Curimatidae	<i>Cyphocharax santacatarinae</i>	Csan
	Crenuchidae	<i>Characidium lanei</i>	Clan
		<i>Characidium pterostictum</i>	Cpte
		<i>Characidium schubarti</i>	Csch
		<i>Deuterodon iguape</i>	Digu
	Characidae	<i>Hollandichthys multifasciatus</i>	Hmul
		<i>Hyphessobrycon griemi</i>	Hgri
		<i>Mimagoniates microlepis</i>	Mmic
		<i>Oligosarcus hepsetus</i>	Ohep
		<i>Hoplias cf. malabaricus</i>	Hmal
Siluriformes	Callichthyidae	<i>Scleromystax barbatus</i>	Sbar
		<i>Scleromystax prionotos</i>	Spri
	Loricariidae	<i>Kronichthys heylandi</i>	Khey
		<i>Pseudotothyris obtusa</i>	Pobt
		<i>Rineloricaria</i> sp.	Rsp
		<i>Schizolecis guntheri</i>	Sgun
	Pseudopimelodidae	<i>Microglanis cf. parahybae</i>	Mpar
	Heptapteridae	<i>Acentronichthys leptos</i>	Alep
		<i>Pimelodella transitoria</i>	Ptra
		<i>Rhamdia aff. quelen</i>	Rque
<i>Rhamdioglanis transfasciatus</i>		Rtra	
Gymnotiformes	Gymnotidae	<i>Gymnotus pantherinus</i>	Gpan
Cyprinodontiformes	Aplocheilidae	<i>Atlantirivulus santensis</i>	Asan
	Poeciliidae	<i>Phalloceros harpagos</i>	Phar
		<i>Phalloceros reisi</i>	Prei
Synbranchiformes	Synbranchidae	<i>Synbranchus aff. marmoratus</i>	Smar
Cichliformes	Cichlidae	<i>Crenicichla cf. tinguí</i>	Ctin
		<i>Geophagus brasiliensis</i>	Gbra
Gobiiformes	Eleotridae	<i>Dormitator maculatus</i>	Dma
		<i>Eleotris pisonis</i>	Epis
	Gobiidae	<i>Awaous tajasica</i>	Ataj
		<i>Bathygobius soporator</i>	Bsop

To complement the evaluation of fish assemblage structure, we analyzed fish functional traits. The fish functional similarity was represented in a graph resulted from PCoA using a matrix of functional distance among species which is generated through the generalization of Gower's distance, according to Pavoine, Vallet, Dufort, Gachet, and Daniel (2009). This analysis was conducted using the `dist.ktab` function in the `ade4` package (Dray & Dufour, 2007).

All analyses were conducted in R, version 3.0.3 (R Core Team, 2014).

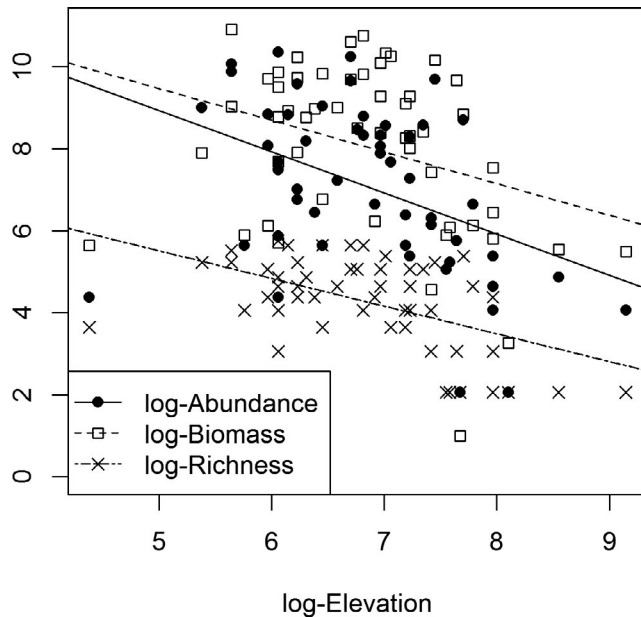


FIGURE 1 Simple linear regressions of fish abundance ($r = -.46$, $p = .001$), biomass ($r = -.32$, $p = .017$), and richness ($r = -.45$, $p < .001$) as a function of elevation. Data were log-transformed

3 | RESULTS

We encountered a total of 32 fish species (Table 2) and 3,623 individuals. Fish abundance and biomass as well as species richness were negatively correlated with elevation, showing that abundance, biomass, and species richness all decrease as elevation increases (Figure 1).

Environmental variables varied between upper and lowermost sites, indicating habitat heterogeneity along the gradient of elevation (Table 3). Overall, the uppermost sites had coarser substrates (bedrock and boulders) and faster flow, whereas the lowermost sites were sandier and deepest with more plant debris and low pH (Table 3).

The following five variables were significant and selected to comprise the environmental data matrix used in subsequent modeling: conductivity ($p = .001$), elevation ($p = .001$), temperature ($p = .001$), flow ($p = .014$), and depth ($p = .016$). Fifteen, twelve, and five eigenfunctions modeled by AEM were used to create the spatial explanatory matrix used in pRDA analysis, considering downstream, bidirectional, and upstream dispersion, respectively.

Redundancy analysis of fish abundance constrained by five forward-selected environmental variables (reduced model) explained 30.8% ($R^2_{adj} = 30.8$, $p = .001$) of the variation in fish assemblages. The ordination plot indicated some patterns in fish assemblage structure that were influenced by environmental factors (Figure 2). For instance, *Characidium schubarti* was associated with higher elevations, which have faster and deeper waters, whereas *Mimagoniates microlepis* was found in lower elevations with lentic, shallow, and warmer waters. For some species, such as *Characidium lanei* and *Characidium pterostictum*, the scores produced by ordination were closer to the origin, revealing that these species were found more or less everywhere below high altitudes, despite environmental differences among middle and lower sites.

Variance partitioning showed that the total amount of variation in the fish distribution explained by the environmental and spatial

Variables	Upper sites	Middle sites	Lower sites
pH	6.72 ± 0.51	6.72 ± 1.22	6.55 ± 4.29
Conductivity (μS/cm)	31.60 ± 15.90	27.12 ± 15.49	43.45 ± 0.05
Dissolved oxygen (mg/L)	9.82 ± 1.33	10.56 ± 1.72	9.35 ± 0.15
Water temperature (°C)	19.90 ± 1.70	19.92 ± 1.31	20.65 ± 0.72
Stream width (m)	5.26 ± 2.46	4.47 ± 2.64	4.66 ± 22.70
Stream flow (m/s)	0.10 ± 0.08	0.07 ± 0.05	0.04 ± 1.16
Stream depth (m)	0.26 ± 0.16	0.19 ± 0.07	0.26 ± 1.81
Bottom type (%)			
Sand	5.93 ± 7.24	17.30 ± 14.30	46.48 ± 29.69
Gravel	3.94 ± 5.90	9.40 ± 10.31	10.19 ± 14.85
Pebble	10.80 ± 8.90	24.81 ± 17.35	10.78 ± 14.54
Rock	14.40 ± 11.03	23.96 ± 19.23	12.38 ± 15.11
Boulder	35.43 ± 22.00	8.43 ± 11.02	2.85 ± 6.70
Bedrock	23.48 ± 25.12	5.31 ± 10.45	0.26 ± 0.65
Plant debris	6.03 ± 7.26	10.78 ± 8.39	16.89 ± 14.62

TABLE 3 Mean values (±SD) for environmental variables at upper, middle, and lower stream reaches

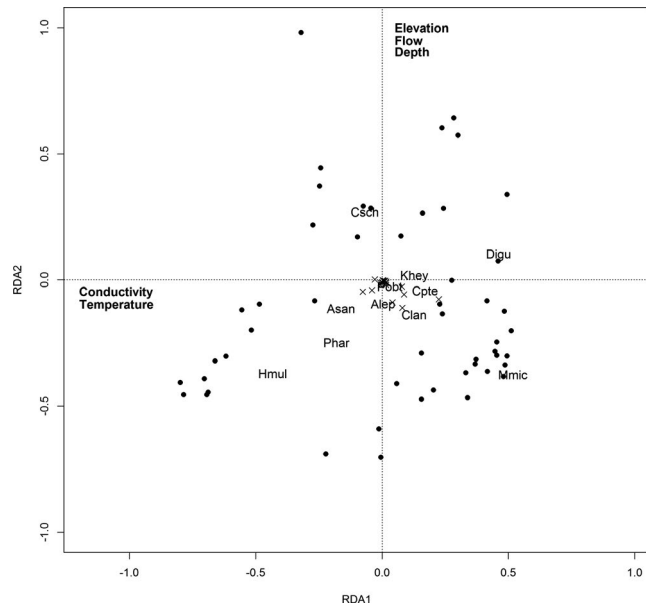


FIGURE 2 A redundancy analysis triplot of fish abundance constrained by five statistically significant environmental variables: conductivity ($p = .001$), elevation ($p = .001$), temperature ($p = .001$), flow ($p = .005$), and depth ($p = .028$). Percentages of explanation: axis 1 = 46.5% and axis 2 = 26.7%. Sites are represented by black dots. Species acronyms are presented in Table 1

factors [E + S] was 48%, $\approx 43\%$, and 32%, considering downstream, bidirectional, and upstream movements, respectively. The environmental factor was responsible for 24.3%, 24.2%, and 24.3% of the variation, contrasting with $\approx 42\%$, $\approx 36\%$, and $\approx 22\%$ produced by the spatial structure [S], considering downstream, bidirectional, and upstream movements, respectively (Figure 3).

The PCoA plot indicated some patterns that were influenced by fish functional traits (Figure 4). The first axis of PCoA ordered the selected species in relation to their swimming ability in faster or slower waters and the use of vertical strata. The feeding traits influenced the similarity as well as the dissimilarity among species. Periphyton and autochthonous insects were preyed upon mainly by benthic fishes that inhabit fast waters represented by the Loricariidae, Callichthyidae, and Crenuchidae. Detritus and allochthonous insects were important for species that explored the water column (nektonic species), occasionally exploring the stream bottom (nektobenthic species) in slow water sites. The Poeciliidae and most of the Characidae represented these species. The second PCoA axis ordered the fishes according to their body size.

4 | DISCUSSION

Stream fish organization in the studied coastal streams is influenced by both environmental and spatial factors, but the magnitude of influence of the environment or space depends on what one hypothesizes about the directionality of movements (downstream, bidirectional, or upstream). Environmental factors themselves may have a spatial signal, so that these fish assemblages reflect processes

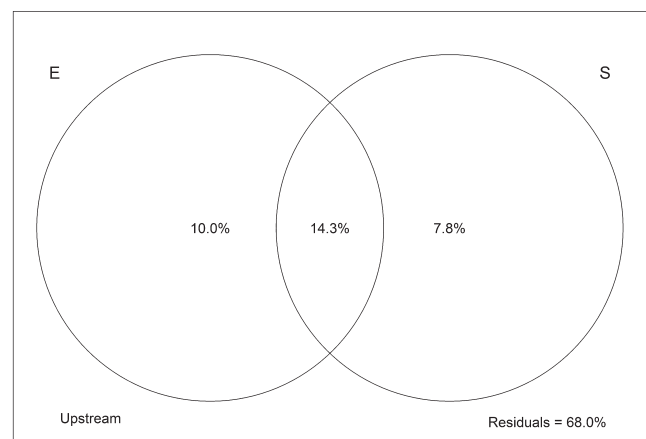
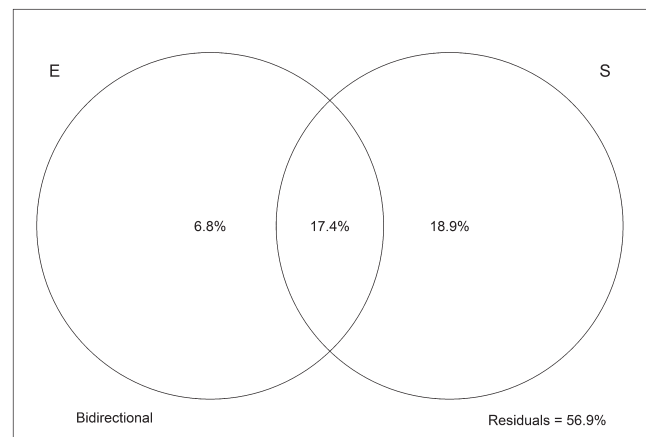
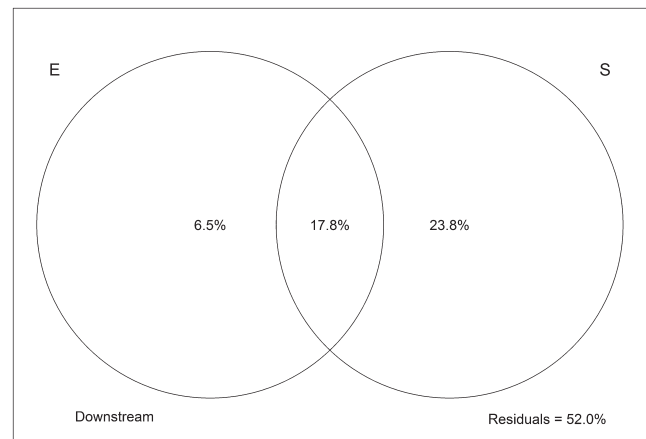


FIGURE 3 Venn diagrams showing the partition of the total variation in the studied stream fish assemblages explained by the environmental variables (E) and the spatial factors (S), considering downstream, bidirectional, and upstream movements

at different scales: At the stream-reach scale, fish respond to local environmental filters (habitat structure and water chemistry), which are themselves influenced by a larger scale, the altitudinal gradient, as is connectivity via dispersal. Overall, upstream segments have characteristically fast flow, deep pools, and substrates dominated by boulders and bedrocks, whereas middle reaches of moderate elevation have a wider diversity of substrate and mesohabitats (pools and riffles), and finally, the lower sites have slow flow and sandier

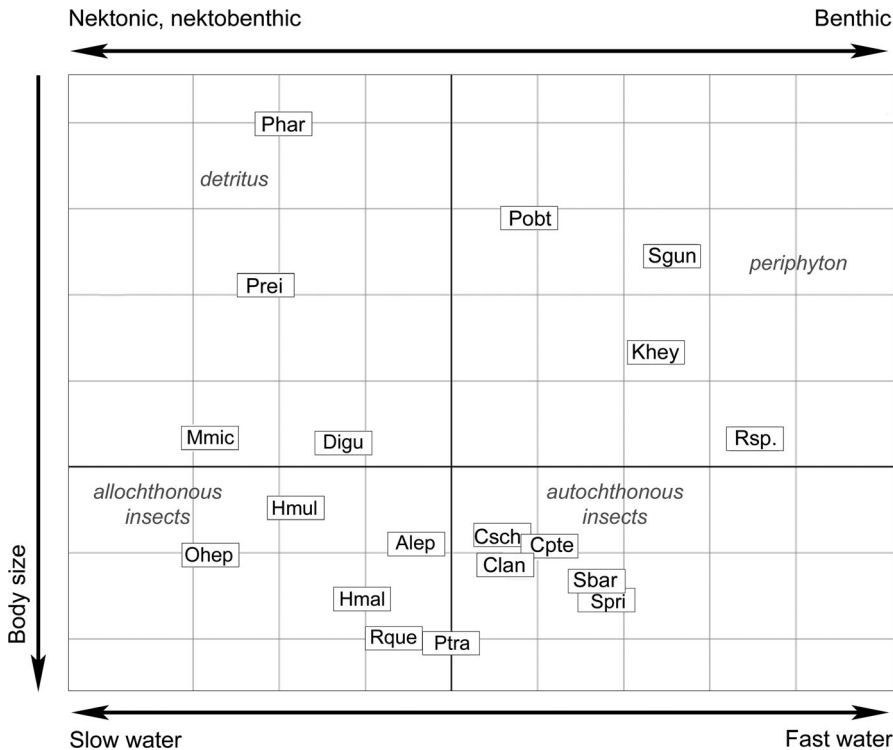


FIGURE 4 A principal coordinate analysis biplot representing the functional distance among fish species, according to their habitat use (horizontal axis), body size (vertical axis), and diet. Some food items were less representative in fish diet and are not shown. Species acronyms are shown in Table 2

bottoms (Gonçalves & Braga, 2012). Thus, environmental patterns describing variation in local conditions are not independent of spatial factors, and the effects of local processes can be confounded with the spatial (altitudinal) gradient.

Our results show that both spatial factors and environmental variables correlated with spatial structure, explained the majority of the variation of the studied fish assemblage structure. A major goal of metacommunity ecology is to unravel the relative contributions of environmental factors and space in explaining the organization and spatial patterning of ecological communities (Heino et al., 2015; Leibold & Chase, 2018). In our study, local environmental variables can explain better the fish organization of headwaters, while spatial factors that favor dispersal (particularly downstream) seem to have a strong influence on community organization downstream (e.g., the main stem). Comparable patterns have been found by Carvalho and Tejerina-Garro (2014) and Vitorino, Fernandes, Agostinho, and Pelicice (2016). In seeming contrast to our results, Terra et al. (2016) and Cetra et al. (2017) showed environmental control dominated over spatial importance in the Atlantic Forest coastal stream fishes. However, our study covered a larger area compared to these studies, and Cetra et al. (2017) in any case sampled exclusively upstream locations. Thus, what seems to be the relative importance of local factors and dispersal may depend in part on the spatial distribution of the sites being studied, as well as on the overall spatial extent contained within a study (Heino et al., 2015; Sály & Erős, 2016). Nakagawa (2014) convincingly demonstrated that the relative importance ascribed to environmental and spatial factors differs among scales and that scaling down may increase the perceived importance of environmental variables. Moreover, because fish can actively disperse both upstream and downstream—but dispersal is potentially greater

downstream than upstream—our study considered potential asymmetries in fish movements, which made the influence of space quite evident in the organization of the fish fauna.

The influence of space on the organization of the ichthyofauna depended on the direction of fish movement: The importance of space was greater than the habitat characteristics for those models that assumed downstream or bidirectional movements, whereas it was equal for models assuming upstream movements. Compared to upper reaches, fish movements would be facilitated more downstream due to the spatial hierarchization of the river network and the overall steep inclines present at higher altitudes (Hitt & Angermeier, 2008). Downstream sites at the studied area are more interconnected, and it is plausible to conclude that downstream movements would be more important because the downward flow direction along the steep elevation gradient would facilitate fish dispersal, for instance, during flash floods that sharply increase water flow (Chapman & Kramer, 1991). Migration can be motivated by a search for places with better conditions (Schlosser, 1991; Welcome, 1969). Upstream movements may be important for the reproduction and population maintenance of some species (Mazzoni & Iglesias-Rios, 2012; Mazzoni, Pinto, Iglesias-Rios, & Costa, 2018; Mazzoni, Schubart, & Iglesias-Rios, 2004), say by avoiding predation. Reciprocal migration is believed to reflect the interplay of temporal variation in local conditions and spatial heterogeneity among sites (Holt & Fryxell, 2011).

A combination of constraints on dispersal and elevated extinction risks explains fish absence in almost 30% of sites (6 of 21 sites) in our uppermost locations. This possibility further highlights that dispersal limitation can have an important implication for fish spatial structuring in our system. Heino et al. (2015) argued that

headwater streams are relatively isolated: Fish presumably would need to cross the terrestrial landscape to reach other headwaters, or move downstream and then upstream across long distances. Resistance of flow may also impede movements upstream and thus the colonization of headwaters (Baguette, Blanchet, Legrand, Stevens, & Turlure, 2013). High extinction rates and low community persistence are expected for such habitats, considering that headwater streams do not have an upstream source to provide immigrants and buffer extinction (Heino et al., 2015). Occasional multi-annual dry periods could even make these habitats disappear for a while. Moreover, it is important to consider the effect of watersheds on fish assemblages. Coastal drainages of the Atlantic Forest harbor many fish species endemic to this biome (Nogueira et al., 2010) as a consequence of the presence of several independent drainages (Abilhoa et al., 2011). This means that even nearby drainages may have dissimilar fish assemblages. Spatial constraints on dispersal are likely very important in the organization of the fish fauna in this region.

Elevation played an important role for fish abundance and biomass, and species richness declined sharply as elevation increased. In studies elsewhere in the Neotropics, species richness has been shown to rapidly decrease with altitude, for example, in tropical streams in the Colombian Andes (Jaramillo-Villa et al., 2010), and in Costa Rica (Lorion, Kennedy, & Braatne, 2011), and other studies have shown dominance by just a few species at high elevations (Askeyev et al., 2017; Braga, 2004; Mazzoni et al., 2006). It is noteworthy that these patterns changed over very short distances and differences in elevations in our studied site (5–140 m), compared to patterns reported from the Colombian Andes (258–2,242 m) (Jaramillo-Villa et al., 2010), and even with the Costa Rican river (up to 500 m) (Lorion et al., 2011).

Considering that biological communities change in a predictable way along the longitudinal course of the river (as encapsulated in the celebrated RCC hypothesis of Vannote et al., 1980), one may hypothesize that the altitudinal gradient represents an important environmental filter either for fishes or their food resource (and possibly other biotic factors, such as predators). The attributes of headwaters (as noted above) may act as environmental filters favoring a few species with morphological adaptations for maintaining position near the stream bottom, escaping the worst of the flow (Winemiller, Agostinho, & Caramaschi, 2008). Fish with these morphological requirements are represented in the studied streams by the periphytivorous benthic grazers (Loricariidae) with a dorso-ventrally flattened body and a ventral mouth they use to scrape periphyton from bedrock and to maintain attached to the bottom, as well as the crenuchids that have a fusiform body, as well as large and strong pectoral fins they use to support the fast flow. These Crenuchidae species feed on aquatic insect larvae that in turn consume detritus derived from coarse particulate organic matter, possibly provided by the dense surrounding forest (Gonçalves et al., 2018). On the other hand, nektonic and nektobenthic fishes that have a laterally flattened body, terminal mouth, and feed on detritus were associated with slow waters (typical of the lowermost reaches). According to

RCC (Vannote et al., 1980), it is expected that detritivory prevails at downstream reaches where the accumulation of fine particulate organic matter (FPOM) is greater. Although organic matter occurs at all reaches, FPOM is more abundant in downstream backwaters (Bowen, 1983) similar to the places where the poecilids *P. harpagos* and *P. reisi* were commonly found in Juréia. The caracids *Mimagoniates microlepis* and *Hollandichthys multifasciatus* are nektonic fishes with a laterally flattened body, and a upturned mouth, which feed mainly on terrestrial insects; so, their occurrence may reflect the availability of food resources, given that terrestrial insects are more abundant at middle reaches (Gonçalves & Braga, 2012; Gonçalves et al., 2018) which provide slow flow water pool mesohabitats where such food can drift and accumulate. Therefore, it is reasonable to expect that the observed environmental influence on fish structure may also reflect correlated changes of food supply along elevation, not only habitat structure. Thorp, Thoms, and DeLong (2006) developed the riverine ecosystem synthesis model, where fish zonation results from the interplay of fluvial geomorphology and hierarchical patch dynamics. Our finding that both local abiotic conditions and directional spatial influences appear to be a play in these Brazilian Atlantic rain forest streams is consistent with this theoretical synthesis.

We caution that our study involves a descriptive, statistical analysis of patterns in species distributions across these Atlantic rain forest streams. Documenting these patterns is just the first stage in teasing out the complex causal nexus that gives rise to them. As Blanchet et al. (2008b) note with respect to their development of the AEM technique, permitting asymmetry in spatial relationships among sites: “Dominant ... current directions [can] cause the appearance of gradients in physical conditions whereas biogeographical gradients can be the result of historical events.” The asymmetric spatial influences discerned by this technique, as in our study, could reflect either short-term dispersal processes, operating year-by-year, or longer-term adaptive and evolutionary responses. Teasing these apart would be a significant, albeit challenging, objective for follow-up studies of our systems.

This improved understanding of how fish communities are spatially structured by elevation, influenced by both environmental and spatial factors depending on the direction of fish movement, may have important conservation implications. The studied streams are located in a legally protected area of the coastal complex of Serra do Mar, which has permitted us to aim at understanding the factors responsible for structuring the fish communities in a relatively pristine environment—which are increasingly scarce in this region of the Neotropics. However, most of the protected and preserved areas of the Atlantic Forest cover regions that include only headwaters (Baptista, Dorvillé, Buss, & Nessiamian, 2001) located above 100 m (100 m is the legal limit of the Serra do Mar above which human occupation is prohibited), which also turn out to be zones where fish diversity (Gonçalves & Braga, 2012) and also aquatic insects (Baptista et al., 2001) are lower. Consequently, the aquatic fauna located on the coastal plain (the most species-rich sites, and also probably the source pool for the species in our communities) are more susceptible to anthropogenic impacts such as deforestation (which may

homogenize aquatic habitats (Casatti et al., 2012)) and urbanization (Peressin, Gonçalves, & Cetra, 2018), since the biggest cities in Brazil (e.g., Sao Paulo, Rio de Janeiro) are near the coast and their expansion surely affects the integrity of the lowermost stream reaches that are easy to access and perturb. Because fish populations require different habitats to persist through time via migratory responses to temporal variation (Schlosser, 1991), our findings reinforce the importance of spatial heterogeneity and connectivity between stream reaches to maintain the metacommunity dynamics of fish, and thus the integrity of this important dimension of tropical biodiversity. With increasing fragmentation of aquatic habitats (Pelicice et al., 2017; Reis et al., 2016), these are important issues to consider in conservation and restoration plans, not only in Atlantic Forest (Terra et al., 2016), but also elsewhere around the world.

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DISCLOSURE STATEMENT

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated. Fish sampling protocol was approved by IBAMA/ICMBio (#37489-1/2, #15744) and COTEC (#260108-015.708/2012, #260108-000.197/2008). We followed all applicable ethical and legal guidelines for the care and use of animals.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.sxksn02zj> (Gonçalves, Holt, Christman, & Casatti, 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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