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Disentangling spatial and environmental determinants of fish species richness and assemblage structure in Neotropical rainforest streams

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Abstract

1. Freshwater ecology templates were developed in temperate streams, but whether they also apply to tropical streams that harbour a higher biological diversity than their temperate counterparts remains uncertain. This is particularly true for tropical fish assemblages inhabiting small streams that have been less studied than larger, higher-order lowland streams.
2. Here, we disentangled the strength of spatial (longitudinal and environmental) drivers, and scale-specific (drainage basin, reach and local scale) determinants of species richness and composition of freshwater fish assemblages inhabiting small streams in French Guiana.
3. We found that species richness increased from upstream to downstream but also with increasing local habitat structural diversity independently of stream position in the upstream–downstream gradient. This pattern was shared by the two most speciose fish orders (Characiformes and Siluriformes), demonstrating that species addition rather than species replacement shaped species richness in these assemblages.
4. Species composition of fish assemblages was determined equally by their spatial structure within drainage and by the environment, and assemblages differed both with distance and along an upstream–downstream gradient. The environmental effect on species assemblages indicated by the fact that almost all environmental descriptors had slight but nonetheless significant effects on assemblage composition, probably reflecting species-specific responses to the local environment. In contrast, despite a strong micro-endemism between drainages for some taxa, assemblages were only slightly affected by river drainage identity, since widespread species were a common constituent of assemblages in all rivers.
5. We identified five species assemblages characterising different local habitat features from torrential areas to lowland muddy areas. We also distinguished fish assemblages from confluence areas with larger rivers, which differed from the other five assemblages. The fish zonation patterns we report can constitute a benchmark for future studies measuring the impact of anthropogenic disturbances on Neotropical forest streams.

KEYWORDS
drainage basin, French Guiana, freshwater fish, local scale, reach scale

1 | INTRODUCTION

The spatial patterns of biological diversity result from factors acting at different scales. According to the hierarchical filter model proposed by Tonn (1990), large or regional scale processes, related with climatic or biogeographic differences between regions, will define a species pool, i.e. a set of candidate species that could occur at smaller scale (Srivastava, 1999). From this regional species pool, species that actually occur in local assemblage are selected through local processes. Those processes encompass biotic interactions between species (predation, competition and facilitation) and the effect of the local environment on local assemblages (Jackson, Peres-Neto, & Olden, 2001). The determinant role of the local environment on species persistence relies on the Hutchinson's niche concept (Hutchinson, 1957), which still has strong support in the current development of niche modelling approaches in both terrestrial and aquatic ecosystems (e.g. Elith & Leathwick, 2009). For instance, in freshwaters, species distribution within drainage basins can be explained by the variability in the environment along the stream, especially temperature or hydromorphology, creating distinct fish assemblages across this upstream–downstream gradient. These assemblages differ either by the replacement of species due to changing environments and isolation by the distance, or by the gradual addition of species caused by a gradual increase in the size or/and in the diversity of local habitat (Ibarra et al., 2005; Rahel & Hubert, 1991). Such upstream–downstream environment-driven changes in species assemblages are consistent with some of the predictions of the River Continuum Concept (Vannote, Minshall, Cummins, Sedell, & Cushing, 1980) that set the basis for further models (e.g. the Riverine Ecosystem Synthesis: Thorp, Thoms, & Delong, 2006; the Stream Biome Gradient Concept: Dodds, Gido, Whiles, Daniels, & Grudzinski, 2015) that have informed the currently accepted integrated view of river functioning. In addition to this deterministic effect of the spatial variability on assemblages, stream fish assemblages are also influenced by the hydrological stochasticity (succession of droughts and floods or high- and low-flows between years or seasons), which can override deterministic processes (Grossman, Moyle, & Whitaker, 1982; Grossman, Ratajczak, Farr, Wagner, & Petty, 2010).

Such templates, developed in temperate rivers, have recently been extended to the tropics where the overall patterns of species richness and assemblage structure across the upstream–downstream gradient are broadly comparable to those known in temperate rivers. For instance, Araújo, Pinto, and Teixeira (2009) found an increase in species richness and a change in the species composition in fish assemblages along the upstream–downstream gradient in a large Brazilian river. Similarly, Petry and Schulz (2006) reported upstream–downstream fish zonation in the Sinos River (Southeast Brazil). However, despite an increase in research undertaken on the ecology of tropical rivers, most of information has been obtained from the lowland sections of major river systems, whereas the fish assemblages of headwater streams have been much less studied (Anderson & Maldonado-Ocampo, 2011). This bias is probably due to the easier accessibility to lowland streams for sampling and to the limited commercial interest of the, often small-bodied, fishes inhabiting low-order streams compared to the large and heavily exploited downstream species (Allan et al., 2005). However, large rivers represent only a small part of the river network. For instance, in French Guiana, more than 70% of the permanent river network is represented by streams <10 m wide (Dedieu, Allard, Vigouroux, Brosse, & Céréghino, 2014). Moreover, such small rivers host about a half of the species inhabiting each river drainage, as shown by Junk, Soares, and Bayley (2007) for the Amazon, or by Allard, Popée, Vigouroux, and Brosse (2016) for the five main Guianese river basins.

To date, most studies have been devoted to measuring the impact of human disturbance on the fish assemblages in small tropical streams (Allard et al., 2016; Dias, Magnusson, & Zuanon, 2010; Mol & Ouboter, 2004). The lack of conceptual understanding of the determinants of assemblage structure in these small streams nevertheless limits our ability to predict the fish assemblages they host and hence the impact of ongoing anthropogenic disturbances (e.g. mining, deforestation and urbanisation) on those assemblages. Here, we quantified the determinants of species richness and composition of freshwater fish assemblages in non-impacted headwater streams across the major Guianese drainages. We considered environmental determinants encompassing different hierarchical scales, from drainage basins, to reaches, to microhabitats, while considering river network connectivity that can affect fish distributions (Elith & Leathwick, 2009). We therefore predicted that local species richness (1) increases with stream size (from upstream to downstream) and (2) is higher in sites with high environmental diversity. We also tested if these predictions about determinants of diversity held for the two most speciose fish orders (Characiformes and Siluriformes) or if the global pattern observed resulted from the overlap of different responses across fish clades. Moreover, as the fish community composition differs among river drainages according to the biogeographic history of the region (Le Bail et al., 2012; Lujan & Armbruster, 2011), the pool of species inhabiting the upper reaches should be constrained by the regional context. We hence predict that species assemblage composition (3) differs primarily between drainage basins with different biogeographic histories; (4) is secondly influenced by the sites connectivity within each drainage and; (5) is finally affected by the reach position in the upstream–downstream continuum and the local scale habitat characteristics that both determine the environmental niche of the species.

2 | METHODS

2.1 | Fish data collection

We achieved complete fish inventories in 152 stream sites in French Guiana (Figure 1). All the streams considered are small (first to third order) perennial streams flowing in a primary forest environment. Their width varied between 1 and 10 m and depth from 0.1 to 1 m on average. None of the streams were disturbed by human activities as the entire drainage upstream of the sampling sites was free of

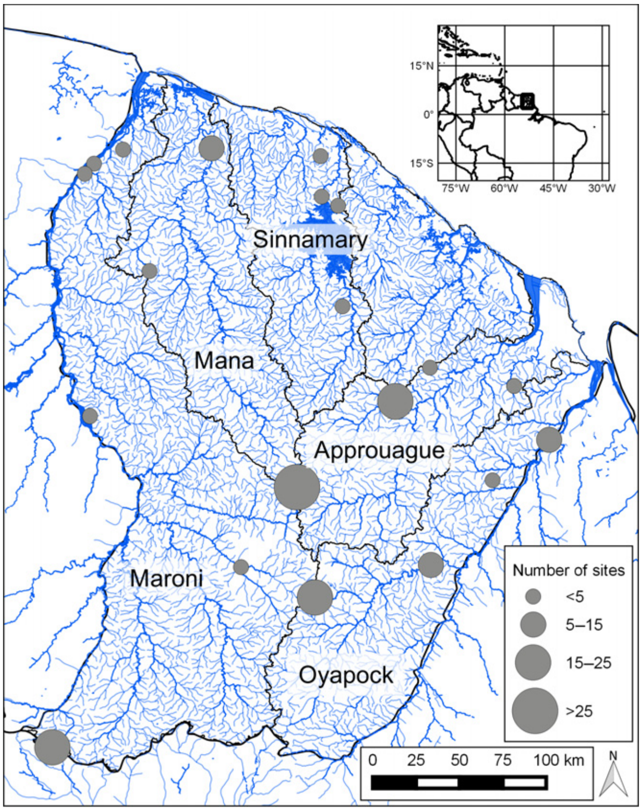

FIGURE 1 Map of French Guiana showing the location of the study sites. Point size is proportional to the number of sites sampled in each area [Colour figure can be viewed at wileyonlinelibrary.com]

settlements. The fish surveys were conducted under several different research projects conducted between 2010 and 2015, and each site was sampled once. All sites were sampled during the dry seasons to ensure similar hydrological conditions and optimal detection rate of the species (Allard et al., 2016). We did not consider inter-annual or inter-seasonal variability that would require repeated samples on the same sites at different seasons and during several years. Most of the sites are remote, and multiple sampling was not possible due to the heavy logistic needed to access to the sites. Moreover, sampling during the rainy season was not possible because of river overflows. The sampling protocol was standardised for all sites. Each site was a homogeneous hydrological unit (pool, run, riffle, rapid, waterfall), and its length was on average 27.49 ± 17.73 m (mean ± *SD*). It was proportional to stream width and was 6.48 ± 8.84 times longer than stream width. Since little is known on the home range of Neotropical tropical fishes, the length of our stream sites was the longest possible given that the streams are obstructed by fallen trees and/or dense vegetation where distinguishing fish is difficult. We nevertheless considered the length of sampled stream sites sufficient, as it was similar to that used to analyse fish assemblages in first to fifth order North American streams (Grossman, Ratajczak, Crawford, & Freeman, 1998; Hoeinghaus, Winemiller, & Birnbaum, 2007). Fish were collected using rotenone (PREDATOX®: a 6.6% emulsifiable solution of rotenone extracted from *Derris elliptica* by Saphyr, Antibes, France) a non selective piscicide, which is traditionally used to catch fishes by Amazonian tribes. Such a method is currently the only way to collect exhaustive information on local fish assemblages, because electrofishing is not efficient in those low conductivity streams (Allard et al., 2014). Nets such as seine and cast nets were not efficient in streams cluttered with fallen trees and branches and visual observation strongly underestimated nocturnal and cryptic species (Allard et al., 2014). We were therefore allowed by the authorities (French ministry of environment and National Amazonian Park) to use rotenone pending the development of an efficient alternative to this destructive method, such as environmental metabarcoding (Valentini et al., 2016). We nevertheless reduced the impact of our rotenone samples by paying a particular attention to releasing as little toxicant as possible to avoid fish mortality downstream from the section studied. This dose was sufficient to detect the entire fish community (Allard, 2014). As there is no published estimation of the efficiency of the method to measure fish abundance according to species behaviour or to environmental characteristics of the sites, we transformed species abundance into species occurrence to control for potential differences in fish capture efficiency according to sites or species as recommended by Oberdorff, Pont, Hugueny, and Chessel (2001).

In each stream, one to three subsequent sites with homogeneous hydromorphological units were selected. Subsequent hydrological units (i.e. sites) were separated using two fine mesh (4 mm) stop nets. A particular attention was devoted to set stop nets simultaneously to avoid fish movement between sites. Rotenone was released a few metres upstream of the stop net located upstream from the upstream site. When two or three subsequent sites were sampled, one or two operators were in charge of collecting fish in each site allowing collecting fish simultaneously from all the subsequent sites with a single rotenone release. At the end of each sampling session we searched for fishes lying on the bottom or hidden in the leaves and debris. In almost all sites, cryptic fish were collected, including highly cryptic Siluriformes such as *Farlowella*, *Harttiella*, *Lithoxus*, or *Ancistrus*, bottom-dwelling fishes such as *Ituglanis* or *Loricaria*, and litter-bank fishes such as small killifishes. Several species of Gymnotiformes inhabiting small Guianese streams, although known to be resistant to rotenone, were also caught.

2.2 | Description of sites

We characterised each site by three groups of variables defined according to the scale at which they were measured (Table 1). At the regional scale, we distinguished sites by drainage (from West to East: Maroni, Mana, Sinnamary, Approuague and Oyapock; Figure 1). At the reach scale, we measured chemical characteristics of the water (pH and conductivity) using pH meter (WTW pH 3110 with WTW pH-SenTix 41 electrod) and conductometer (WTW Cond 3310 with tetraCon 325 captor), and we extracted topographic metrics (distance from the source, slope and altitude) from a GIS (QGIS Development Team, 2016). At the site scale, we measured the percentage of forest canopy cover visually as in Dedieu et al. (2014) and classified each site to an hydromorphological unit (pool, run,

TABLE 1 Drainage, reach and local scale variables measured at each site. Codes used for each variable are in bold. Distance from the source, slope and altitude were derived from GIS. Conductivity and pH were measured with conductometer and pH meter in the field. Percent of forest coverage, streambed particles (Sand, Gravel, Pebble, Boulder and Bedrock) and of each shelter type (wood, aquatic macrophytes, litter, under-banks, tree roots and open water) were visually estimated. Stream width was measured on transects perpendicular to stream flow and depth was measured every metre on these transects

Scale	Variables (mean ± *SD* [min–max])	
Drainage	Identity	Maroni, Mana, Sinnamary, Approuague, Oyapock
Reach	Distance from the source (km) **(Dis)**	3.23 ± 3.71 [0.4–16]
	Slope (‰) **(Slp)**	5.24 ± 3.86 [0.49–18.8]
	Altitude (m) **(Alt)**	182.84 ± 149.45 [28.21–632.57]
	pH	5.88 ± 0.94 [3.75–7.65]
	Conductivity (μS/cm) **(Cnd)**	30.13 ± 15.84 [8.4–108]
Local	Forest cover (%) **(Foc)**	68.78 ± 29.86 [0–100]
	Hydromorphological unit	Run, riffle, rapid, fall, pool
	Streambed particle grain size (%)	Silt (<0.05 mm)
		Sand (0.05–2 mm)
		Gravel **(Grv)** (2–10 mm)
		Pebble **(Pbb)** (1–3 cm)
		Boulder **(Bld)** (3–50 cm)
		Bedrock **(Bdk)** (>50 cm)
	Available shelters (%)	Wood
		Macrophyte **(Mac)**
		Litter **(Lit)**
		Under-banks **(Ubk)**
		Tree roots **(Trt)**
		Open water **(Owa)**
	Depth (m)	Mean: 0.24 ± 0.16 [0.01–1.13] **(mDp)**
		CV: 0.43 ± 0.16 [0–0.93] **(cvDp)**
		<0.2 m
		[0.2, 0.4 m]
		[0.4 m, 0.6 m]
		[0.6 m, 0.8 m]
		[0.8 m, 1 m]
		≥1 m
	Width (m)	Mean: 3.45 ± 2.03 [0.95–10] **(mWd)**
		CV: 0.19 ± 0.12 [0–0.57] **(cvWd)**
		<2 m
		[2, 4 m]
		[4 m, 6 m]
		[6 m, 8 m]
		[8 m, 10 m]
		≥10 m

riffle, rapid and waterfall) according to Delacoste, Baran, Lek, and Lascaux (1995). We then measured the local stream habitat variables, including substratum granulometry, shelter availability and channel morphology. The substratum granulometry was described by estimating visually the percentage of streambed particle grain size cover (silt, sand, pebble, boulder and bedrock were defined according to Cailleux [1954] methodology; see Table 1 for size classes). Such visual assessment of streambed particle size clustering has often been used to analyse the relationships between freshwater fish and their physical habitat (e.g. Brosse & Lek, 2000; Grossman et al., 2006). Shelter availability (presence of wood debris, macrophytes, litter, under-banks, tree roots) was measured as a percent coverage of each shelter type as in Allard et al. (2016) and the per cent coverage without shelter was categorised as open water. Channel morphology was recorded using stream width and depth. We measured stream width on at least three transects perpendicular to the stream flow, and every 5 m if the sampled site was longer than 10 m. Stream depth was recorded every metre across transects. We then calculated the mean and the coefficient of variation (CV) of the depth and width for each site. Those local habitat variables, known to be the main predictors of fish habitat (Allard et al., 2016; Brosse & Lek, 2000; Gorman & Karr, 1978; Grossman et al., 2006) were used to analyse the species composition of the sites. In contrast, the niche theory predicts that the species diversity in a site is more related to the overall environment and its structural diversity than to its different components (Hutchinson, 1957; Kovalenko, Thomaz, & Warfe, 2011; Stein, Gerstner, & Kreft, 2014). The structural diversity of the site was estimated using the Shannon–Wiener equitability index ($-\sum_{i=1}^{S} p_i \log(p_i)/\log(S)$; Shannon, 1948). We calculated this index separately for grain size classes and percentages of shelter types. We did the same for depth and width after sorting them into six classes. A regular increment of 2 m for width and 0.2 m for depth was chosen as it provided a balanced representation of all width and depth classes (see Table 1 for classes). Those four diversity metrics were summed to obtain a single habitat structural diversity measure for each site, with a maximum value of four reflecting maximum diversity. The habitat structural diversity index and overall descriptors of the environment (distance from the source, slope, altitude, pH, conductivity, forest canopy cover and hydromorphology) were used to explain species richness patterns.

2.3 | Spatial relationships among sites within drainage basins

We described the spatial structure of the sites within individual drainages with distance-based Moran's eigenvector maps (dbMEM, Borcard & Legendre, 2002; Dray, Legendre, & Peres-Neto, 2006). We used the spatial coordinates of the sites to calculate an in-stream distance matrix using the shortest river path between sites. We then derived the dbMEM variables from the distance matrix taking into account the drainage membership of the sites (Declerck, Coronel, Legendre, & Brendonck, 2011). For each drainage, a set of dbMEM variables was computed to describe the spatial structure of the sites within the drainage. Sites from others drainages are given a zero value. We did not use Euclidean distances as they do not represent the dendritic structure of streams and thus provide irrelevant distances to explain assemblage variation for strictly aquatic species which dispersal capacities are strongly constrained by water availability (Landeiro, Magnusson, Melo, Espírito-Santo, & Bini, 2011; Yunoki & Velasco, 2016).

2.4 | Statistical analyses

To explain variation in species richness between sites, we used generalised linear-mixed effect models (GLMM) with a Poisson distribution of error terms and with a log link function to explore the relationship between species richness and environmental variables (distance from the source, slope, altitude, pH, conductivity, vegetation cover, hydromorphology and habitat structural diversity). A GLMM was preferred to a classical GLM to account for the spatially nested pattern of our data (site within reach within drainage) and to remove the dependency between sites within a reach (Rhodes, McAlpine, Zuur, Smith, & Ieno, 2009). Reach membership was treated as a random effect nested within the drainage membership random effect. Between-drainage and between-reach within drainage variations were modelled by random intercepts only. All variables were centred and scaled to *SD*. We used a model-selection approach (Burnham & Anderson, 2002) to determine the most important factors in explaining variation in species richness. No prior knowledge about the factors explaining the variation in species richness was used. We thus tested all possible combinations of the eight variables, resulting in 257 candidate models (all combinations + a null model). We used Akaike's information criterion (AIC_c; Burnham & Anderson, 2002) corrected for small samples to rank the models, with the lowest AIC_c indicating the best model, and we computed for each model its Akaike weights (w_i). As the Akaike weight of the best model was low ($w_i < 0.5$), we retained models with a ΔAIC_c to the best model ≤4. We then used model averaging to estimate parameters, standard errors (*SE*), variable relative importance and 95% confidence intervals (Burnham & Anderson, 2002). For each model, we computed marginal R^2 (R^2_m, variance explained by fixed factors) and conditional R^2 (R^2_c, variance explained by the entire model, i.e. by fixed and random factors), following Nakagawa and Schielzeth (2013). To test for congruence across clades, we repeated this analysis on the two most speciose fish orders (Characiformes and Siluriformes, that account for 45% and 30% of the species in our database respectively). Perciformes were not considered here since recent phylogenies have revealed that the previous definition of Perciformes is not valid because it included several phylogenetically distinct valid fish orders (Betancur-R et al., 2013; Sanciangco, Carpenter, & Betancur, 2016). Those valid orders did not contain sufficient species in our data to be analysed independently (see Table S1 in Supporting Information).

For composition variation, we used a detrended correspondence analysis (DCA) to select the best ordination method (ter Braak & Šmilauer, 2002) and choose between a linear (redundancy analysis) and a unimodal (canonical correspondence analysis, CCA) response. DCA revealed that a unimodal model was the most suitable (gradient length > 4 standard deviation, indicating a complete species turnover along the axis) and we thus used CCA to explore the relationships between assemblage composition variation and spatial and environmental variables (Lepš & Šmilauer, 2003).

We used variation partitioning to separate the effect of overall spatial configuration of sites (drainage-scale and dbMEM spatial variables) and the environment (reach- and site-scale) on the overall species assemblage composition (Borcard, Legendre, & Drapeau, 1992). We first selected variables using forward selection as recommended by Blanchet, Legendre, and Borcard (2008): variables were included in the CCA model as long as they did not exceed a $p > .05$ (*p*-values were assessed using 999 permutations) and if the R^2_{adj} of the tested model did not exceed the R^2_{adj} of the CCA model including all the tested variables. We then calculated the percentage of variation explained by each retained variable while taking into account all the other variables for a given scale (conditional R^2_{adj}). We then ran a final CCA with selected variables and calculated R^2_{adj} for the four components (drainage, dbMEM, reach and site) by permutations of constraining matrix using "varcanv" software (Peres-Neto, Legendre, Dray, & Borcard, 2006). We also tested if the unique parts explained by the spatial and environment components differed. We assessed significance of fractions and difference between components with 999 permutations. We performed the analysis on the entire assemblages (all the 147 species were considered) and on a reduced dataset, where rare species (occurring in less than five sites, i.e. occurrence <3% of the sites, see Table S1) were removed. In this reduced dataset 58 rare species, which might affect the quality of the CCA, were removed.

Then, to evaluate how species composition differs between sites and reaches, we classified species into groups based on their scores extracted from the two-first axes of the CCA including only reach- and local-scale variables, using *K*-means partitioning. We tested two to fifteen clusters. The final number of groups was selected based on the simple structure index (ssi), with the highest value indicating the best partition (Dolnicar, Grabler, & Mazanec, 2000). Although maximal resolution was achieved for a clustering of nine groups, five-group clustering provided similar ecological information (Figures S1 and S2). We hence considered five groups as the best compromise between species group clustering and interpretability of the results.

We then compared fish species identity between the different drainages to confront the results provided by the CCA and variation partitioning to the known differentiation of fish community composition between river drainages in French Guiana. We computed the turnover component of Jaccard's dissimilarity index between the different drainages to remove the effect of richness difference between them (Baselga, 2012). We then used the dissimilarity values in hierarchical clustering analysis with the complete linkage method, based on maximising the correlation between the original distances and the cophenetic distances (Pearson's correlation: $r = 0.86$; Farris, 1969). As for the previous analysis, we repeated these steps on Characiformes and Siluriformes, with single linkage ($r = 0.79$) and average linkage ($r = 0.81$) methods respectively.

All analyses were performed using R software (R Core Team, 2015) with the packages "adespatial" version 0.0-8 (Dray et al., 2017), "lme4" version 1.1-12 (Bates, Mächler, Bolker, & Walker, 2015), "MuMIn" version 1.15.6 (Barton, 2016) and "vegan" version 2.4-2 (Oksanen et al., 2016).

3 | RESULTS

We collected 147 species belonging to 10 orders of fish (Table S1). Characiformes and Siluriformes were the most represented orders, with 66 and 45 species respectively, and together represent more than 75% of the species. At the drainage scale, the Maroni River

TABLE 2 The eight best models retained to explain variation in species richness. The models are ranked by their Akaike's information criterion corrected for small samples (AIC_c). For each model, the variables retained are indicated by a '+'. The Akaike weigth (wi) the R^2_c and R^2_m are indicated. For each variable, the model-averaged coefficient (estimate ± *SE*), its relative importance (the sum of model w_i in which the variable is included) and its 95% confidence interval (CI) are given. R^2_m refers to the marginal R^2 (variance explained by fixed factors) and R^2_c refers to the conditional R^2 (variance explained by the entire model, i.e. by fixed and random factors)

Model	Variable							AIC_c	w_i	R^2_m	R^2_c
	Distance from the source	Altitude	Slope	Forest cover	Conductivity	pH	Diversity				
1	+	+					+	873.30	0.33	0.59	0.83
2	+	+	+				+	874.90	0.15	0.59	0.83
3	+	+		+			+	875.14	0.13	0.59	0.83
4	+	+			+		+	875.49	0.11	0.59	0.83
5	+	+				+	+	875.49	0.11	0.59	0.83
6	+	+	+	+			+	876.66	0.06	0.59	0.83
7	+	+	+			+	+	877.00	0.05	0.59	0.83
8	+	+	+		+		+	877.06	0.05	0.59	0.83
Estimate ± *SE*	0.27 ± 0.057	−0.43 ± 0.066	−0.016 ± 0.042	−0.0062 ± 0.026	0.0014 ± 0.023	0.0018 ± 0.023	0.11 ± 0.042				
Importance	1	1	0.31	0.19	0.16	0.16	1				
95% CI	0.16–0.38	−0.56 to −0.31	−0.18 to 0.075	−0.13 to 0.069	−0.10 to 0.12	−0.10 to 0.12	0.029–0.20				

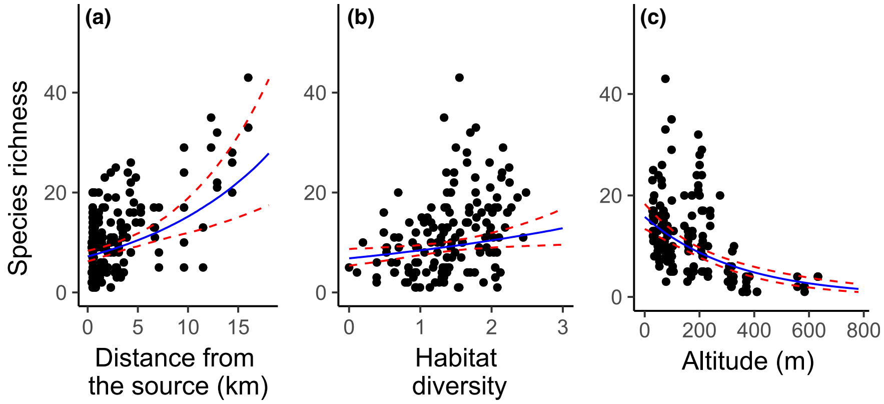

FIGURE 2 Relationships between species richness and the distance of the site from the source (a), the habitat diversity (b) and the altitude (c). Fitted values (solid lines) and 95% confidence interval (dashed lines) are derived from the averaged estimates of the Poisson generalised linear-mixed effect models [Colour figure can be viewed at wileyonlinelibrary.com]

drainage was the richest in stream species (108 species recorded), followed by the Approuague (79 species), the Sinnamary (65 species), the Oyapock (52 species) and the Mana River drainage had the lowest number of stream species (43 species). Sixty-one species were only found in a single drainage. On average, 12 (± 8) species were collected in each site, and species richness ranged from to 1 to 43 per site. Among the 257 candidate GLMM predicting species richness (see Table S2), eight were retained as the best models ($\Delta\mathrm{AIC_c} < 4$, Table 2). The distance from the source, the altitude and the habitat structural diversity were retained in the eight models, whereas the hydromorphological unit was never retained. The best model retained two reach scale variables, distance from the source and altitude, and one local scale variable, the habitat structural diversity. In this model, the variance of the intercept for the drainage random effect was null and the variance for the reach random effect was estimated at 0.15. The 95% confidence intervals of these three variables did not include zero indicating a significant effect of these variables on species richness (Table 2). In contrast, the effect of forest canopy cover, the conductivity and the pH were not significant as the 95% confidence intervals included zero for those variables. Species richness increased with the distance from the source (0.27 ± 0.057 (estimate ± *SE*); Figure 2a) and to a lower extent with habitat structural diversity (0.11 ± 0.042; Figure 2b), and decreased with the altitude (−0.43 ± 0.066; Figure 2c). Considering the two main fish orders (Characiformes and Siluriformes) showed that their species richness followed the same increasing pattern according to the distance from the source as the whole fish fauna (Tables S3 and S4; Figure S3). The species richness in Characiformes also decreased with altitude, while the species richness in Siluriformes increased with habitat structural diversity.

After independent forward selections of variables, the five reach scale variables and 14 out of the 18 local scale variables were retained (Table 3). When we partitioned variation in species composition between the three different scales and the spatial structure derived from dbMEM for the full set of species, drainage membership, reach position and local habitat characteristics explained 5.2%, 7.7% and 10.1% of the variation respectively, and the spatial component explained 10.8% of the variation (Table 4). When accounting for the other variables, the spatial structure of sites explained the highest amount of species composition variation (7.6%), local habitat characteristics and the drainage membership explained similar variation (4.1% and 4.0% respectively) and the reach-scale variables explained the lowest variation (1.9%). Overall, the spatial structure (drainage and dbMEM variables) explained a similar percentage of variation than the environment component (R^2_{adj} spatial = 10.9%; R^2_{adj} environment = 7.9%; $p = .37$). When removing the rare species (species occurring in less than five sites), the percentage of explained variation increased slightly (5% of gain) and the ranking between the different components did not differ, with the spatial component explaining the highest variation in species composition (Tables S3 and S4).

The forward selection step on all environmental variables (reach- and local-scales) excluded silt, sand, under-bank shelters, tree roots and CV of width from CCA analysis. The CCA on all assemblages constrained by all of the retained variables was significant ($F = 2.22$, $p = .001$) and the full set of constraining variables explained 13.9% of the variation in assemblage composition (raw $R^2 = 27.5\%$; Figure 3). We clustered species in five groups with the *K*-means analysis according to the simple structure index criterion (Table S1 and Figure S1). The first group of species (group 1 in Figure 3) was composed of only two species (*Hartiella* n. sp. and *Lithoxus boujardi*) that are characteristic of torrential mountainous upstream sites, with high altitude, marked slopes and waterfalls (Figure 4). Group 2 (19 species) represented species inhabiting upstream sites with less torrential and mountainous characteristics (Figure 4). Those species are replaced downstream by more ubiquitous ones (group 3, 63 species). Species in group 4 (40 species) preferentially inhabit muddy lowland streams covered by dense canopy, with a high percentage of litter and macrophytes. The last group of species contained those that mainly occur in downstream sites with wide and deep morphology and located close to the confluence with a larger river (group 5, 23 species; Figure 4). The same zonation was found when removing the rare species from the analysis (Figure S4).

Species turnover between drainages was moderate, with dissimilarities ranging from 0.13 to 0.59 (mean ± *SD*: 0.41 ± 0.14). Hierarchical classification based on species turnover separated western (Maroni and Mana) and eastern (Approuague and Oyapock) river drainages (Figure 5). The Sinnamary River drainage remained distinct

TABLE 3 Spatial, reach- and local-scales variables retained after the forward selection step and used in the variation partitioning analysis of overall fish assemblage. The cumulative R^2_{adj} value given for each variable corresponds to the R^2_{adj} of the CCA model containing the variable and all the previous ones. The conditional R^2_{adj} represents the percentage of variation explained by the selected variable while taking into account all the other variables for a given scale. Excluded variables are given in italics

Scale	Variable	Cumulative R^2_{adj} (%)	Conditional R^2_{adj} (%)
Reach	Altitude	2.8	2.7
	Distance from the source	5.4	2.1
	pH	6.8	0.4
	Conductivity	7.3	0.5
	Slope	7.7	0.3
Local	Mean width	2.2	1.2
	Open water	3.6	0.3
	Boulder	4.5	0.4
	Forest cover	5.2	0.6
	Mean depth	5.8	0.4
	Hydromorphological unit	7.2	1.7
	Macrophytes	7.7	0.6
	Depth CV	8.0	0.3
	Litter	8.4	0.7
	Pebble	8.9	0.5
	Wood	9.2	0.4
	Gravel	9.5	0.3
	Width CV	9.8	0.3
	Bedrock	10.1	0.4
	Under-bank	*10.3*	—
	Roots	*10.3*	—
	Sand	*10.2*	—
	Silt	*10.2*	—
Spatial	dbMEM 9	2.3	2.4
	dbMEM 1	4.1	1.8
	dbMEM 4	5.5	1.8
	dbMEM 5	6.6	1.2
	dbMEM 6	7.6	1.1
	dbMEM 7	8.4	1.3
	dbMEM 8	9.6	1.2
	dbMEM 3	10.2	0.6
	dbMEM 2	10.8	0.7

TABLE 4 Variation partitioning of the fish species occurrence matrix, between the four components (drainage, spatial, reach and local). This partition was achieved on the entire assemblage data after forward selection of the variables. R^2 and R^2_{adj} values are expressed in percentage

	R^2	R^2_{adj}	p
Total explained variation	44.0	25.0	
Global effects			
Drainage	8.0	5.2	.001
Spatial	16.6	10.8	.001
Reach	11.1	7.7	.001
Local	21.8	10.1	.001
Pure-effects			
Drainage	5.2	4.0	.001
Spatial	10.8	7.6	.001
Reach	4.1	1.9	.001
Local	13.0	4.1	.001
Shared effects			
Drainage ∩ Spatial	<0	<0	
Drainage ∩ Reach	1.1	1.1	
Drainage ∩ Local	3.6	<0	
Spatial ∩ Reach	1.7	1.5	
Spatial ∩ Local	2.5	1.3	
Reach ∩ Local	2.1	1.9	
Drainage ∩ Spatial ∩ Reach	<0	<0	
Drainage ∩ Spatial ∩ Local	<0	3.8	
Drainage ∩ Reach ∩ Local	<0	4.0	
Spatial ∩ Reach ∩ Local	1.8	1.4	
Drainage ∩ Spatial ∩ Reach ∩ Local	2.2	<0	
Unexplained variation	56.0	75.1	

from these two groups. Characiformes species turnover was on average slightly lower than that of the entire fauna (0.36 ± 0.13) but remained of the same magnitude (range: 0.15–0.59) and no clear distinction between the river drainages was found. In contrast, Siluriformes experienced strong turnover between river drainages (0.52 ± 0.12, range: 0.36–0.73). The distinction between the groups Mana–Maroni and Approuague–Oyapock was marked and the Siluriformes fauna of the Sinnamary River drainage remained intermediate between the two groups.

4 | DISCUSSION

Despite the marked differences in species richness and composition between tropical and temperate fish faunas (Lévêque, Oberdorff, Paugy, Stiassny, & Tedesco, 2007; Oberdorff et al., 2011), Neotropical rainforest stream fish assemblages were found to be shaped similarly to those of temperate streams. Indeed, local species richness exhibited the expected increase along the upstream–downstream gradient, which was also associated with an increase in local habitat structural diversity. Such a gradient in species richness has also been reported elsewhere in the Neotropical streams and rivers (de Mérona, Tejerina-Garro, & Vigouroux, 2012; Mol et al., 2007; Ponton & Copp, 1997; Terra, Hughes, & Araújo, 2016), but in addition to this upstream–downstream pattern, we here show that habitat structural diversity of local habitat had a positive, although slight, effect on local species richness. Habitat structural diversity includes

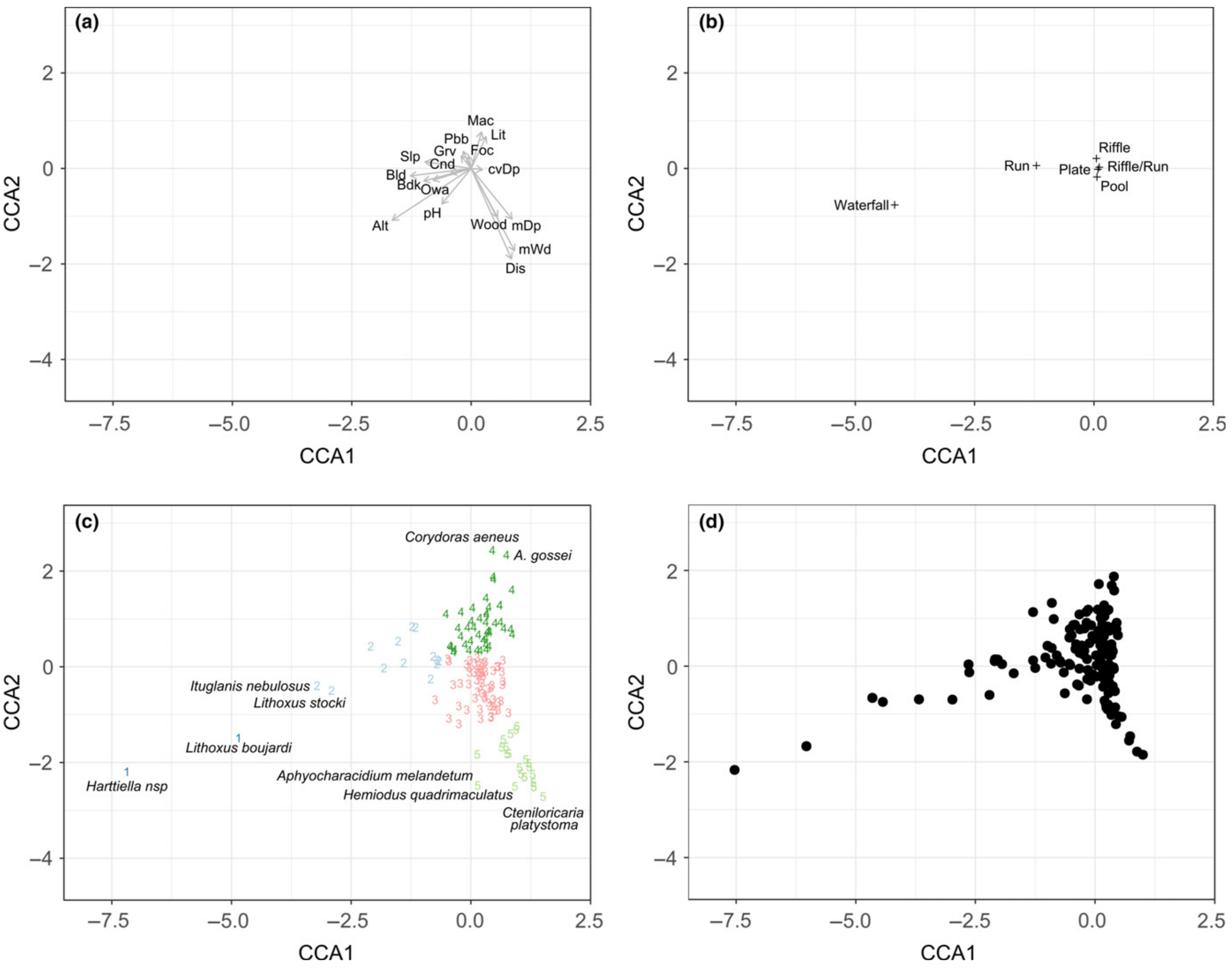

FIGURE 3 Canonical correspondence analysis (CCA) ordination illustrating fish species assemblage constrained by all environmental variables along the two-first axis (axis 1: 17% of the explained variation, $p = .001$; axis 2: 12% of the explained variation, $p = .001$). Upper left panel (a) quantitative environmental variables are represented by arrows with abbreviations as in Table 1; upper right panel (b) hydromorphological units; bottom left panel (c) species position in the CCA ordination. Species were grouped according to K-means analysis with $K = 5$. *Apistogramma gossei* is abbreviated *A. gossei*. See Table S1 for complete information about species membership for each cluster; bottom right panel (d) position of sites in the CCA ordination

a wide range of components (from flow velocity to substrate granulometry) and it thus can be described by several measurements (Gorman & Karr, 1978; Mérigoux & Ponton, 1999; Willis, Winemiller, & Lopez-Fernandez, 2004). Here, we quantified habitat structural diversity as the variability in channel morphology (width and depth), granulometry and shelter availability. Indeed, hydromorphological heterogeneity caused by local variations of the slope or by the presence of woody debris creates areas of reduced current velocity that may be used as refuges for species (Fausch, 1993). Habitat heterogeneity may also act via a trophic pathway where debris and crevices in substrate favour higher diversities of stream invertebrates and periphyton that can be consumed by a variety of fish species with different feeding modes and habits (Downes, Lake, Schreiber, & Glaister, 1998; Robson & Chester, 1999). Unlike the effect of the distance from the source, of the altitude and of the habitat structure diversity, which significantly influenced the local species richness, the role of river drainage identity was negligible. Hence, historical and macroevolutionary processes that shape the size of the species pool occurring in a river drainage (Jackson et al., 2001), hardly affected the local species richness.

Our results also highlighted that the overall species richness pattern was congruent within the two major fish orders (Characiformes and Siluriformes; Figure S3). Species richness in both orders increased from upstream to downstream. The number of Siluriformes species also increased with habitat structural diversity, but we did not detect such a relationship for Characiformes. The increase in diversity in streambed materials (grain size, shelters) primarily favoured the diversity of benthic species. Most of the Siluriformes species are benthic whereas Characiformes species often occupy open waters (Winemiller, Agostinho, & Caramaschi, 2008). This overall difference of fish position in the water column between the two orders might explain the lack of relationship between habitat

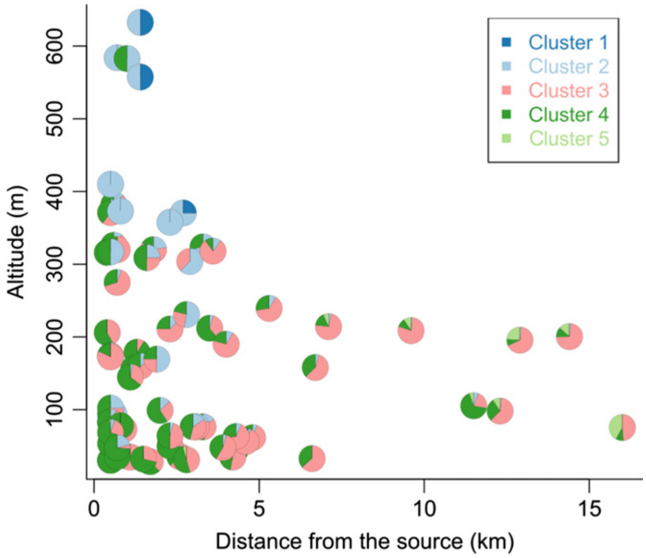

FIGURE 4 Stream sites position along the distance from the source and the altitudinal gradients. For each site, the percentage of species belonging to each cluster is represented (see Figure 3 and Table S1 for details on species clustering). Sites belonging to the same stream reach were grouped together to simplify the figure

structural diversity and Characiformes species richness. We also detected a lower richness of Characiformes in the rapids, probably due to the morphology of most Characiformes that is more suited to swimming in open waters, but less to the turbulent water of rapids (Winemiller et al., 2008). Apart from these differences, the overall fish richness pattern also holds for the two main fish orders, meaning that the overall species richness gradient resulted from a gradual increase in diversity rather than a species replacement between different fish orders.

Turning from the determinants of species richness to the determinants of assemblage composition revealed that the environment and spatial effects explained no more than 25% of the composition of species assemblages. Although this value is less than previous studies that reported a much higher explained variation (e.g. Brosse, Montoya-Burgos, Grenouillet, & Surugue, 2013; Terra et al., 2016), it should be noted that the effect we report is corrected for sample size and for the number of variables, which was not the case in previous studies. Without such correction, our explained variation reached 44% (see Table 4), a value comparable to of earlier studies. Although correcting for sample size and for the number of variables lowered the amount of variance explained, it permitted an unbiased measurement of the effect and of the importance of the environmental variables on fish assemblage composition (Peres-Neto et al., 2006), and the patterns of assemblage variation we detected were nonetheless significant. The large amount of unexplained variance recorded in the present study, but also in the literature on the determinants of fish assemblage structure in Neotropical streams (e.g. Brosse et al., 2013; Terra et al., 2015), has often been afforded to the low occurrence of most species (*c.* 75% of species occurred in <10% of the sites), a common problem in tropical community ecology (Hercos, Sobansky, Queiroz, & Magurran, 2013; ter Steege et al., 2013). Nevertheless, removing rare species (occurring in less than five sites) only slightly increased the explained percentage of variation in species composition, meaning that unexplained variance was only slightly affected by rare species. An alternative explanation is that temporal variability in the environment promotes some stochasticity in the species composition of assemblages (de Mérona et al., 2012; Grossman et al., 1982). Testing for environmental stochasticity would need repeated samples on the same sites, which is problematic given the destructive nature of rotenone sampling. The development of a non-destructive alternative to rotenone samples is therefore an urgent priority.

Among the influential determinants of assemblage composition, spatial and environmental factors explained similar amounts of variation, which contradicted our expectation that spatial factors should override environmental variables. Although almost half of the species were found in a single drainage, thereby giving rise to a strong spatial effect, the remaining half of the fauna was made up of widespread species, thus constituting a common core to all the river drainages and offsetting the role of the spatial component. This contrasts with the findings of Brosse et al. (2013) based on a few sites from the same mountainous area. In that particular case, the regional effect (drainage membership) was of primary importance to explain variation in fish assemblages. Extending our analysis the entire Guianese region therefore provided a more comprehensive view of the

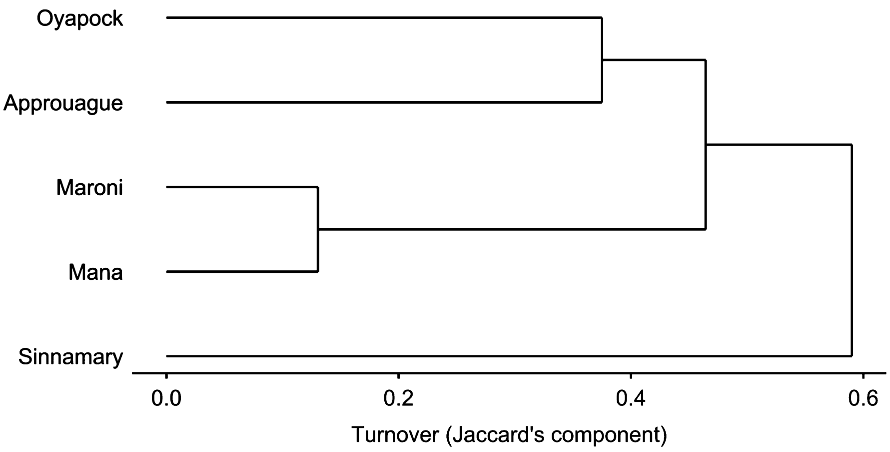

FIGURE 5 Hierarchical clustering of the species turnover between the five drainages (Jaccard's turnover component) with complete linkage method

determinants of assemblage structure, paralleling therefore the work of Garzon-Lopez, Jansen, Bohlman, Ordonez, and Olff (2014) on the scale dependence effect on tropical trees assemblages.

Although the regional determinants were not the major force driving fish assemblages, they nonetheless had a marked effect on assemblage variation. The species turnover between drainages was responsible for the clustering of the river drainages along an East-West gradient, reflecting the biogeographic history of the region (Boujard & Tito de Morais, 1992; Le Bail et al., 2012). This clustering of river drainages was mirrored in their stream fish assemblages, and was particularly marked in the Siluriformes. Indeed, a substantial part of the siluriform fauna inhabiting streams is made of strictly rheophilic taxa restricted to the upstream parts of rivers (Cardoso & Montoya-Burgos, 2009; Lujan & Armbruster, 2011). Their low dispersal ability probably accentuates the regional effect observed in the Siluriformes. This regional effect was, however, weaker compared to the spatial structure of the assemblages within each drainage, which explained the highest part of variation in assemblage composition. The low regional effect compared to the strong spatial structure within drainages probably reflects dispersal limitations between different streams belonging to the same drainage (Cilleros, Allard, Grenouillet, & Brosse, 2016; Vitorino Júnior, Fernandes, Agostinho, & Pelicice, 2016). Indeed, the main channels of the rivers and the presence of rapids can act as dispersal barriers for some small-bodied stream fishes either by way of a distance effect (Datry et al., 2016) or due to predation by—or competition with—species inhabiting large rivers (Wisz et al., 2013).

The environmental characteristics also affected species composition of fish assemblages. This effect did not result from a few environmental characteristics having a dominant effect, but rather from the combination of several environmental characteristics having slight, but nonetheless significant, effects. We therefore hypothesise that there is no consistent response of all species to environmental variables, but more probably species-specific responses to particular variables, with the result that almost all variables have some significant—albeit low—explanatory power. This multifactorial contribution of the environment to the fish community composition contrasts with the situation found in temperate streams, where the fish composition is determined by a few dominant environmental features related to stream morphology and streambed substratum size (Mesquita, Coelho, & Filomena, 2006; Nakagawa, 2014; but see Johnson, Furse, Hering, & Sandin, 2007). Although we did not identify a strong environmental gradient shaping fish assemblages, we distinguished five successive groups of species along the upstream–downstream gradient (Figure 4), revealing an upstream–downstream species succession equivalent to that reported in temperate streams (e.g. Allan & Castillo, 2007). In addition, a particular fauna was found close to the confluence with larger rivers. This last zone might be composed of a specific fish fauna (Albanese, Angermeier, & Dorai-Raj, 2004), or be a transition between streams and rivers and hence host a mixed fauna (Fernandes, Podos, & Lundberg, 2004). This last situation holds for Guianese streams where we did not detect species strictly inhabiting these zones, but a mix between stream and river fishes, with the occurrence of species usually found in large rivers such as *Hemiodus quadrimaculatus* or *Hypostomus gymnorhynchus* (Le Bail et al., 2012).

The pattern of stream fish zonation we describe could constitute a benchmark for future studies measuring the impact of anthropogenic disturbances on Neotropical forest streams. Moreover, the contribution of almost all the environmental descriptors of the local environment to both species richness and assemblage composition suggests that modifications to only a single component of the environment might alter fish assemblage composition. This is of particular importance since damming, mining and logging are already known to affect the characteristics of Neotropical streams (de Mérona, Vigouroux, & Tejerina-Garro, 2005; Dedieu et al., 2014; Dias et al., 2010), and are thus very likely to influence of both species richness and composition of stream fish assemblages.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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