ORIGINAL ARTICLE

Trait–environment relationships in Amazon stream fish assemblages

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Abstract

Studies of trait–environment relationships provide important tools for the prediction of the response of biological communities to environmental alterations. The Amazon basin presents enormous potential for the development of research on this type of relationship, given the diversity of both its fish fauna and the aquatic ecosystems this fauna inhabits. The present study investigated the association between local environmental variables and the functional traits of fish in 54 streams of six major Amazonian basins. We identified the relationship between the characteristics of the streams (channel morphology, channel habitat units, riparian vegetation cover, large woody fragments and instream cover for aquatic organisms) and fish traits related to locomotion, habitat use and feeding behaviour. The fish fauna of the broader, deeper and more slowly flowing streams was dominated by nektobenthic species that exploit autochthonous resources such as fish and invertebrates. In narrow, fast-flowing streams, by contrast, there was a predominance of benthic fishes with varying feeding habits, including periphytivorous and invertivorous species. Narrow, shady streams were inhabited by nektonic species adapted for the exploitation of resources from the marginal vegetation. The results of this study contribute to the understanding of the association between the functional structure of fish assemblages and local environmental variables in Amazonian streams. We hope that these findings will stimulate further research into the natural variation in stream fish assemblages that will ensure the development of more effective management strategies that better protect these important aquatic ecosystems.

KEYWORDS
ecomorphology, environmental filter, environmental variables, freshwater fish, functional ecology, stream habitats

1 | INTRODUCTION

The functional structure of a fish assemblage reflects the limitations imposed by environmental filters (Villéger, Brosse, Mouchet, Mouillot, & Vanni, 2017) which are the principal mechanisms that influence the biodiversity of aquatic ecosystems (Carvalho & Tejerina-Garro, 2015; Santos, 2017). Based on the niche concept, the environmental filter principle assumes that environmental conditions, such as the stream flow velocity or substrate type, act as hierarchical filters that regulate the composition of the taxa found in the regional pool and, ultimately, the local pool of species (Patrick & Brown, 2018).

The distribution of species in relation to environmental variables is the result of the interaction between the functional traits of the species and environmental conditions (Verberk, van Noordwijk, & Hildrew, 2013). In fish assemblages, for example, a high index of body depression and the mouth in a ventral position indicate species with a benthic lifestyle, which inhabit fast-flowing streams. By contrast, a high index of body compression and the mouth in a more dorsal position are traits of pelagic fishes that inhabit superficial layers of slow-flowing streams (Gatz Jr, 1979; Ribeiro, Teresa, & Casatti, 2016). However, anthropogenic impacts may alter the environmental conditions of bodies of water, leading to the loss of species due to the association between fish traits and their habitats, in particular in the case of morphologically specialised species (Villéger, Miranda, Hernández, & Mouillot, 2010) with benthic and nektobenthic habits (Dala-Corte et al., 2016).

Given this, it is important to identify the environmental variables that affect the functional structure of stream fish assemblages to ensure the adequate conservation and management of these environments (Kelley, Grierson, Collin, & Davies, 2018). The identification of these variables allows a more reliable prediction of the response of the fish community to environmental impacts (Pease, Lez-Díaz, Rodiles-Hernández, & Winemiller, 2012). While the effects of anthropogenic impacts on the distribution and abundance of stream fish are relatively well understood, much less attention has been paid to the functional traits of species (Leal et al., 2017; Leitão et al., 2018) and even less to the relationship between the functional structure of these communities and ecosystem function (Carvalho & Tejerina-Garro, 2015; Pease et al., 2012).

The Amazon region has enormous potential for the development of research on the natural variation in aquatic ecosystems, given the availability of large areas of well-preserved natural habitats and the existence of a variety of hydrographic basins, each with its own unique features and characteristics (Benone, Esposito, Juen, Pompeu, & Montag, 2017). Streams are the principal component of Amazonian drainage systems (Beighley & Gummadi, 2011) and vary considerably in their characteristics, ranging from slow-moving bodies of water on floodplains to well-defined, fast-running watercourses, with varying flow velocity (Benone et al., 2017).

This environmental heterogeneity is considered to be one of the principal factors contributing to the enormous diversity of Amazonian fish (Benone et al., 2017; Ramírez, Davenport, & Mojica, 2015). However, these systems are increasingly threatened by human activities and the relatively ineffective legislation intended to protect these bodies of water and their biota (Leal et al., 2017). Furthermore, despite being home to about half of all the fish species found in the Amazon basin, streams are still poorly studied. In this context, there is an urgent need for the understanding of the ecology of Amazonian streams, in order to develop effective measures for the mitigation of these impacts and the protection of these systems. The present study contributes to this process by identifying the associations found between local environmental variables and the functional traits of the fish assemblages found in the streams of the Brazilian Amazon region. Previous studies of fish traits in this region have all focused on either one or a few species (e.g., Freitas,

Montag, & Barthem, 2017; Silva, 2016), and none have evaluated the trait–environment relationships of an entire assemblage.

To our knowledge, this study is the first to analyse the trait–environment relationships comparatively among different Amazonian drainage basins. The broad area of the study region supported the description of features of the diversity of stream characteristics and the functional traits of stream fish throughout the Amazon basin. Three questions are analysed here: (a) Which environmental variables most influence the functional structure of the stream fish assemblages? (b) Which functional traits respond to the local variation in the environment? (c) How these functional traits are related to environmental variables? Based on the limitations imposed by environmental filters, we expected local stream variables to be associated with the functional traits of the stream fish.

2 | METHODS

2.1 | Study area

Fifty-four streams were surveyed in six major drainage basins within the Brazilian Amazon region (Figure 1): Negro (10 streams), Juruena (7), Tapajós (7), Anapu (10), Acará (10) and Capim (10). The drainage basins sampled in the present study represent the full natural diversity of the aquatic environments of the Amazon region. Benone et al. (2017) highlighted the considerable heterogeneity of these environments at both regional and local levels. All the streams are located within preserved forest in either protected areas or on properties owned by private companies. The Amazon region is covered primarily by dense *terra firme* rainforest (Barthem, Montag, & Lanna, 2004). Based on the Köppen classification system, the climate of the Acará and Capim basins is tropical humid, of the Af subtype, which is characterised by a short dry season between September and November. The climate of all the other basins is of the Am subtype, that is, tropical with monsoons and a long dry season (Peel, Finlayson, & McMahon, 2007). The region's temperature varies little over the course of the year, with annual means of 25–27°C. Rainfall levels also vary little among areas, with a mean annual precipitation of approximately 2,000 mm (Barthem et al., 2004).

2.2 | Experimental design

The samples were collected during the dry season of the years between 2012 and 2015, in first- to third-order streams. We selected streams in different microbasins in order to ensure the independence among samples. In each stream, a 150 m reach was divided into 10 longitudinal sections of 15 m by 11 equidistant cross-sectional transects. Each stream was sampled once, during the day.

2.3 | Environmental variables

We used an adapted version of the protocol of the American Environmental Protection Agency (Kaufmann, Levine, Robison, Seeliger, & Peck, 1999; Peck et al., 2006), which is used for the
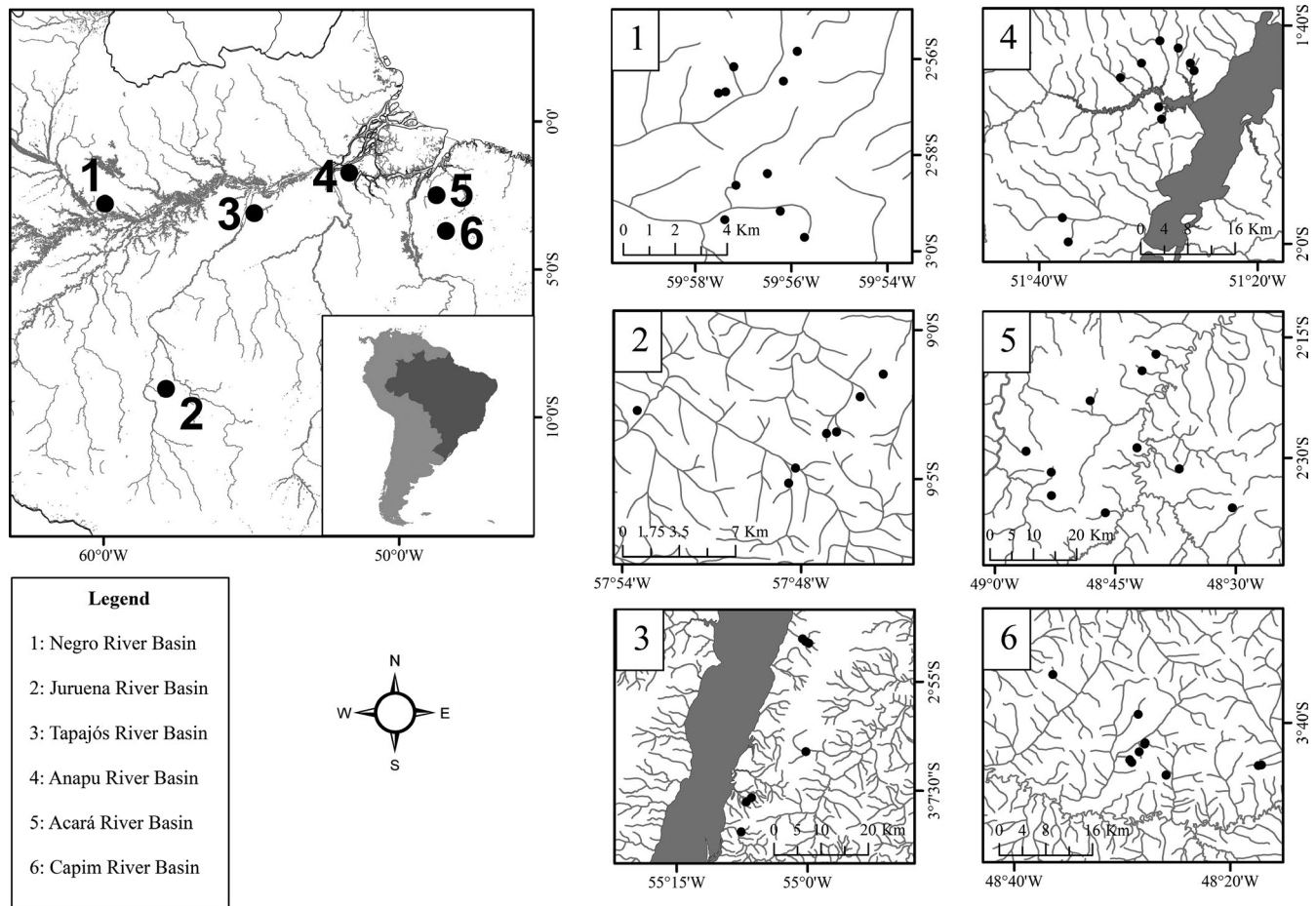
FIGURE 1 Location of the 54 streams sampled in the present study, in six major drainage basins in the Brazilian Amazon region

evaluation of physical habitats in wadeable streams, to determine the structure of the environment at each site. The data collected using this protocol were used to determine 32 environmental variables. These variables were used to evaluate the structural components of the stream habitats, including the channel morphology, substrate, channel habitat units, large woody fragments, riparian vegetation cover and instream cover for aquatic organisms (Supporting Information Table S1).

2.4 | Sampling of fish specimens

The sampling of fish specimens was approved by the UFPA Ethics Committee (CEUA no. 8293020418). Fish were captured using a circular handnet, 55 cm in diameter, with a 3-mm mesh. This type of net is considered to be an efficient method for the sampling of specimens because it permits the capture of fish in the microhabitats of small streams, including complex environments, such as the riparian cover, banks of litter and the undersides of woody fragments (Uieda & Castro, 1999). This equipment has been used successfully to assess the fish assemblages of small Amazonian streams (Ferreira, Begot, da Silveira Prudente, Juen, & de Assis Montag, 2018; Prudente, Pompeu, Juen, & Montag, 2016). Each longitudinal section was sampled by two collectors during 18 min, with a total sampling

time of 3 hr per stream. The specimens were euthanised using anaesthetic (eugenol; as required by Brazilian Civil Law 11,794/2008), fixed in 10% formalin and after 48 hr, transferred to 70% alcohol. In the laboratory, the specimens were identified using taxonomic keys (Albert, 2001; Planquette, Keith, & Bail, 1996), supported by consultations with specialists.

2.5 | Functional traits

Functional traits were determined based on ecomorphological measurements, taken from five specimens of each species sampled, when available. When fewer than five specimens were available for a given species, additional specimens were obtained from the fish collection of the Museu Paraense Emílio Goeldi in Belém, Pará (Brazil). To avoid ontogenetic effects, the specimens selected for measurement were all adults of similar size. In sexually dimorphic species, only females were selected for measurement. Fourteen standard morphometric measurements were taken from the specimens, following the protocol proposed by Winemiller (1991). These measurements were as follows: standard length, maximum body height, maximum body width, body midline height, caudal peduncle length, height, and width, head length and head height, eye height, mouth width and angle, and pectoral fin length and area.

The fin area was estimated by extending the fin on graph paper and drawing its outline, which was then digitised to estimate the area in the Image J software. This software was also used to measure the angle of the mouth based on standardised photographs of the head, based on the intersection of a line drawn along the longitudinal centre of the fish's body and a second line connecting the upper and lower maxillae. All other measurements were taken as the straight line between two reference points, always on the left side of the fish, using a 150-mm digital calliper with a precision of 0.1 mm. These measurements were used to calculate 12 functional traits, following Oliveira et al. (2010) (Supporting Information Table S2). The functional traits calculated here are expressed as unitless indices that are not influenced by the body size of the specimen (Leitão et al., 2018). These traits were first described by Gatz Jr (1979) and continue to be relevant for the understanding of features of the feeding behaviour, locomotion and habitat preferences of fish (Brejão, Hoeinghaus, Perez-Mayorga, Ferraz, & Casatti, 2017; Leitão et al., 2016).

2.6 | Data analysis

As functional traits are ineffective for the analysis of assemblage-level patterns if intraspecific variation is significant (McGill, Enquist, Weiher, & Westoby, 2006), we tested whether interspecific variation was greater than the intraspecific variation in the samples using PERMANOVA. This analysis, run in the adonis function of the vegan package (Oksanen et al., 2016) of the R program, was applied prior to testing the relationship between the traits and the environmental variables. This procedure was based on the matrix of the Euclidean distances between the ecomorphological measurements.

To ensure the effectiveness of the variables for the analysis of the environmental heterogeneity of Amazon streams, variables with a coefficient of variation of <10% were excluded from the analyses. Variables that were highly correlated (Spearman's $r \geq 0.7$, $p < 0.05$) were also omitted from the analyses. To identify the variables that contributed most to the distribution of the species and the functional composition of the assemblages, the remaining environmental variables (in three categories: channel morphology and habitat units; substrate and riparian cover; large woody fragments) were related to the biotic data using Forward selection (Blanchet, Legendre, & Borcard, 2008). Prior to this analysis, the environmental variables were standardised (mean 0, variance 1) and the abundance matrix was log $(x + 1)$ transformed. The community-weighted means (CWM) were calculated to determine the contribution of each functional trait to the streams, using the *functcomp* function in the FD package (Laliberté, Legendre, & Shipley, 2014) of the R program.

The blocks of environmental variables were used as the predictor variables in the Forward selection, while the response variables were the distance matrices of species abundance (Bray–Curtis similarity) and the CWM matrix (Euclidian distance). Only those variables that contributed significantly ($\alpha < 0.05$) to both the distribution of the species and the functional composition were included in the subsequent analyses. The Forward selection was run using the forward.

sel function, with 1,000 permutations, in the adespatial package (Dray et al., 2018) in the R program.

The analysis of the association between the functional traits and the environmental variables was based on the RLQ (Dolédec, Chessel, Ter Braak, & Champely, 1996) and Fourth-corner (Legendre, Galzin, & Harmelin-Vivien, 1997) approaches. These methods provide complementary insights into the trait–environment relationship. The RLQ analysis is used to evaluate general multivariate structures, while the Fourth-corner approach tests the significance of the bivariate associations, independently of the covariation between the traits and the environmental variables (Dray et al., 2014). The RLQ and Fourth-corner analyses were run in the R program (R Core Team, 2016) using the *rlq* and *fourthcorner* functions of the ade4 package, respectively (Dray & Dufour, 2007). Both approaches are based on the analysis of data in three matrices: the R matrix of the environmental variables for each site, the L matrix of the abundance of the species at each site and the Q matrix of the mean morphological data of the study species.

The RLQ analysis is a multivariate approach that associates environmental variables with the traits of the species based on their abundance. The first step in the RLQ comprises three independent ordinations. In the present study, following Dray et al. (2014), the matrices of environmental variables and species traits were ordinated by principal components analysis, while the species abundance matrix was ordinated by a correspondence analysis. The RLQ combines the coordinates of these three separate analyses and maximises the covariation between the environmental variables and the species traits to produce a plot of the associations.

The Fourth-corner analysis combines the R, L and Q matrices in a single matrix of bivariate associations between the traits and environmental variables and tests the significance of these associations using Monte Carlo permutation tests. Following the proposal of Dray and Legendre (2008), this analysis combined permutation models 2 and 4 and used 9,999 repetitions to test the null hypothesis (H_0), that the species traits (Q) are not related to the environmental variables (R). In permutation model 2, the sites were randomised to test the relationship between species abundance (L) and the environmental variables (R), and in permutation model 4, the species were randomised to test the relationship between species abundance (L) and their traits (Q). The null hypothesis is rejected when significant relationships are found in both permutation models. An $\alpha = 0.05$ significance level was considered in all cases.

3 | RESULTS

During the selection of the environmental variables, one variable was excluded due to a lack of variation (variation coefficient < 10%), while nine variables were correlated significantly with one other variable, and 13 were excluded by the Forward-selection analysis (Supporting Information Tables S1 and S3). The remaining nine variables represent, primarily, the differences in the composition of the substrate, the instream cover for aquatic organisms, presence of

large woody fragments, the channel morphology and channel habitat units among the six drainage basins analysed (Table 1).

A total of 15,645 fish specimens were collected during the study, representing nine taxonomic orders, 26 families and 111 species (Supporting Information Table S4). The most abundant species were *Hyphessobrycon heterorhabdus* (19% of the specimens collected), *Copella arnoldi* (18%) and *Apistogramma* gr. *regani* (10%). The orders with greatest species richness were Characiformes (47 species), Siluriformes (24) and Gymnotiformes (17). Together, these three orders contributed 79% of the species recorded in the present study. All the fish species collected were included in all the analyses, except for three species. One of these species, *Paracanthopoma parva*, was excluded due to its small size (standard length < 10 mm), which prevented adequate biometric measurement. The other two species, *Pygidianops amphioxus* and *Synbranchus marmoratus*, were omitted from this analysis due to the absence of fins, which obviously precluded the measurement of these organs.

The RLQ analysis indicated that the distribution of the species was correlated with the variation in the environment (model 2, $p < 0.001$), and was dependent on its functional traits (model 4, $p = 0.048$). These findings indicate a strong association between the environmental variables and the functional traits of the fish assemblages analysed. Axes 1 and 2 of the RLQ analysis explained 54.1% and 41.8%, respectively, of the total co-inertia found between the environmental variables and the functional traits of the fish species (Table 2).

In the first two RLQ axes, the variation in the functional structure of the assemblages was related primarily to the fish traits associated with locomotion, habitat use and feeding behaviour. The aspect ratio of the pectoral fin (Pectoral shape), the relative length of the head (Head length), the depression index of the body (Body depression) and the relative area of the pectoral fin (Pectoral area) were the principal traits associated with the variation in the functional structure of the fish assemblages (Figure 2a). The distribution of streams in the multivariate space was related primarily to the stream morphology, flow velocity and riparian vegetation cover. Specifically, the variables that most influenced this distribution pattern were the mean wetted width (Width), mean wetted area of the transect (Wetted area), glides (Glide), mean large woody fragments (Woody fragments), mean overhanging banks (Overhanging banks) and the mean total riparian cover (Riparian cover) (Figure 2b). The distribution of the streams in the multivariate space varied considerably among the drainage basins, especially in the case of the streams of the Anapu basin, which presented unique characteristics compared with all the other streams. The streams of the Juruena, Negro and Tapajós basins were highly similar to each other. The streams of the Acará and Capim basins were also broadly similar.

In the RLQ axes, Head length was associated positively with Wetted area ($p = 0.028$) and Glide ($p = 0.049$). These variables were correlated with the Anapu streams, and species such as *Aequidens epae* and *Crenicara* sp. were characterised as having relatively long heads (Figure 2a–c). Pectoral shape was related positively with stream Width ($p = 0.004$) and Woody fragments ($p = 0.001$) and negatively with Riparian cover ($p = 0.048$), and the Body depression

TABLE 1 Variables selected for analysis following the preliminary evaluation of variance and correlation. Mean and standard deviation values of variables per drainage basin are exhibited

Block of variables	Variable	Acará	Anapu	Capim	Juruena	Negro	Tapajós
Channel morphology	Mean wetted width (m)	3.44 ± 1.06	4.52 ± 2.06	2.25 ± 0.54	2.29 ± 1.08	2.01 ± 0.59	0.96 ± 0.51
	Mean wetted area of transection (width × depth) (m²)	0.63 ± 0.41	1.73 ± 0.74	0.37 ± 0.24	0.40 ± 0.29	0.23 ± 0.11	0.59 ± 0.25
Channel habitat units	Glides (%)	63.18 ± 25.00	92.00 ± 22.76	69.4 ± 14.9	46.48 ± 27.01	45.00 ± 18.08	41.71 ± 26.17
Substrate	Roots (%)	6.13 ± 5.45	6.86 ± 9.64	6.48 ± 4.70	3.13 ± 4.72	36.57 ± 9.76	22.36 ± 7.59
Riparian vegetation cover	Mean total riparian cover (%)	173.91 ± 75.33	237.59 ± 34.21	180.35 ± 23.07	246.14 ± 29.91	265.16 ± 41.55	230.84 ± 24.86
Large woody fragments	Number LWF inside bankfull channel/150 m	45.07 ± 29.7	33.47 ± 21.11	20.73 ± 13.25	12.86 ± 6.71	21.07 ± 9.00	10.86 ± 3.52
	Mean large woody fragments (>0.3 m small end diameter) (%)	24.07 ± 21.59	44.8 ± 31.11	13.14 ± 14.68	2.11 ± 3.05	4.11 ± 2.03	3.34 ± 4.90
Instream cover for aquatic organisms	Mean coarse litter (%)	36.73 ± 21.21	57.16 ± 24.94	43.45 ± 21.40	41.53 ± 23.76	19.61 ± 10.33	17.34 ± 9.57
	Mean overhanging banks (%)	2.48 ± 2.70	0 ± 0	8.86 ± 5.48	2.99 ± 1.55	1.14 ± 0.94	1.88 ± 1.65

TABLE 2 Results of the RLQ analysis comparing the environmental variables and the functional traits of the fish from 54 streams located in six major drainage basins in the Brazilian Amazon region

RLQ analysis	Axis 1	Axis 2
Eigenvalues	0.496	0.383
Covariance	0.704	0.619
Correlation	0.268	0.336
Projected inertia (%)	54.181	41.845
Monte Carlo tests (9,999 permutations)		
Model 2	$p < 0.001$	
Model 4	$p = 0.048$	

was also associated negatively with Riparian cover ($p = 0.006$). In this case, the species with relatively rounded pectoral fins and compressed bodies, such as *Laimosemion* cf. *dibaphus* and *Nannostomus marginatus*, were associated with the relatively narrow streams, with small woody fragments and shady channels, found primarily in

the basins of the Juruena, Negro and Tapajós rivers (Figure 2a–c). Pectoral area was also associated negatively with overhanging banks ($p = 0.024$), indicating that the species with relatively small pectoral fins, such as *Rineloricaria hasemani* and *Ituglanis amazonicus*, were associated with streams in which refuges formed by overhanging banks were relatively abundant, such as those of the Acará and Capim basins (Figure 2a–c).

4 | DISCUSSION

The variation in the functional structure of the fish assemblages was consistent with the observed environmental gradient, and systematic associations were identified between the functional traits of the fish and local environmental variables. The morphology of the channel, channel habitat types, riparian cover and instream cover for aquatic organisms were the features that most influenced the functional structure of the fish assemblages analysed here, mainly related to the configuration of the head, pectoral fins and body shape.
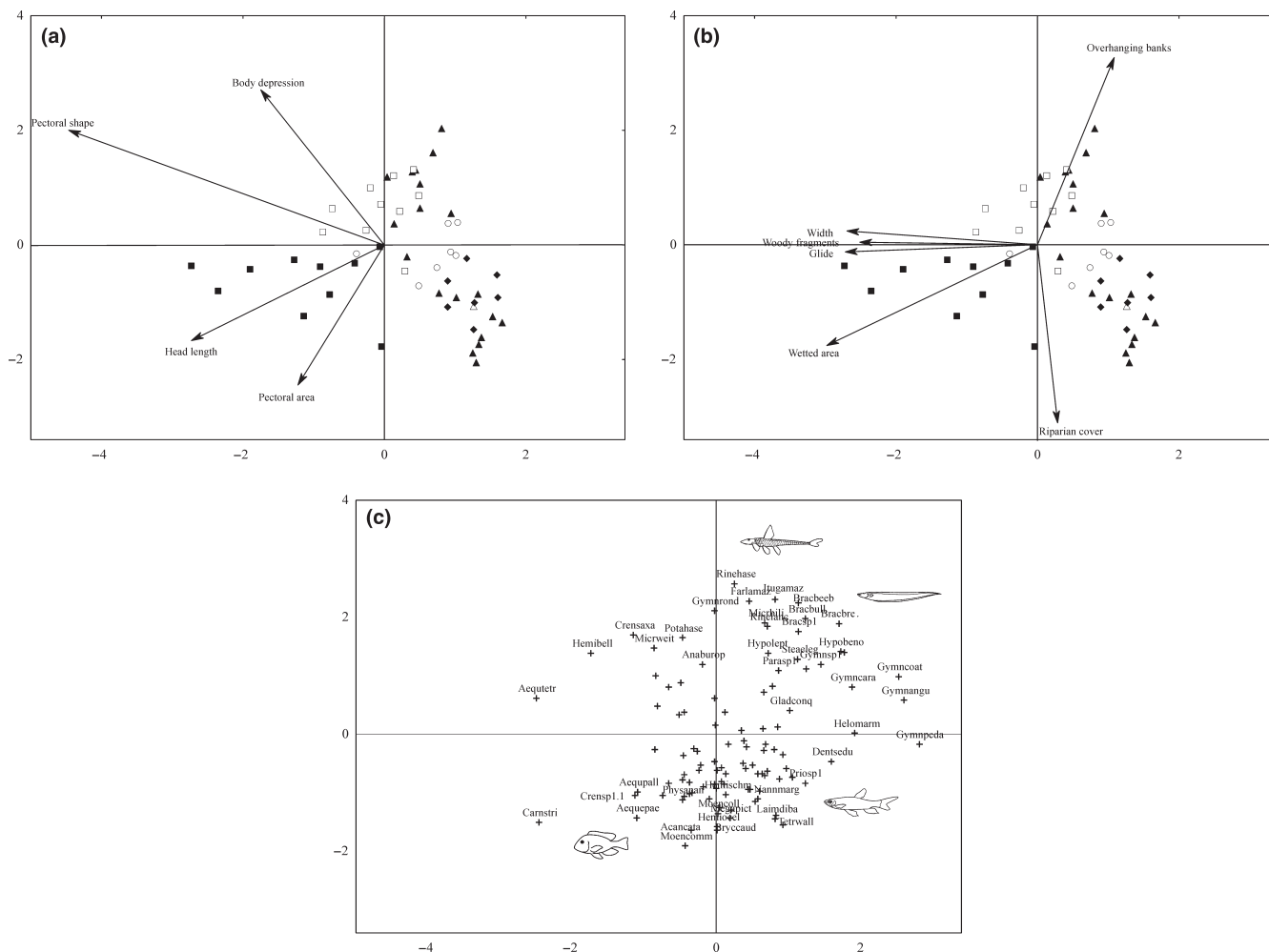
FIGURE 2 Ordination of the traits (a), environmental variables (b) and fish species (c) recorded in the 54 streams surveyed in the Brazilian Amazon region. The symbols representing each stream correspond to the respective drainage basin (□ = Acará, ■ = Anapu, ▲ = Capim, ○ = Juruena, △ = Negro, ◆ = Tapajós). The species codes are provided in Supporting Information Table S4. Fish drawings from FishBase (www.fishbase.org)

The fish species with relatively long heads, such as *Carnegiella strigata* and *Crenicara* sp., were associated with broad, deep and slowly flowing streams. This head configuration is related to the exploitation of relatively large prey. The species that consume large prey identified in this study feed mostly on aquatic invertebrates and small fishes, and the streams with which they were associated (in the Anapu basin) contain large amounts of habitat suitable for macroinvertebrates and small fishes, such as leaf litter and woody fragments, which accumulate on the bottom (Benone, Ligeiro, Juen, & Montag, 2018; Brejão, Gerhard, & Zuanon, 2013; Pilotto, Bertoncin, Harvey, Wharton, & Pusch, 2014; Zuanon et al., 2015). These types of microhabitat may thus favour a high abundance of macroinvertebrate and small fishes (Carvalho & Tejerina-Garro, 2018).

By contrast, narrow, shady streams with few woody fragments are typical of the Juruena, Negro and Tapajós basins. These basins are located at higher altitudes, with steeper terrain, which contributes to higher flow velocities that restrict the width of the channel and prevent the deposition of woody fragments (Benone et al., 2017). As these streams are relatively shady, the resident species tend to feed on items obtained from the riparian vegetation, as observed in the invertivorous *Laimosemion* cf. *dibaphus* and *Nannostomus marginatus*, which exploit autochthonous and allochthonous resources respectively (Kemenes & Forsberg, 2014). The allochthonous insectivores forage near the surface while the autochthonous insectivores feed on submerged leaves and branches (Brejão et al., 2013; Kemenes & Forsberg, 2014). The consumption of allochthonous resources tends to increase in streams with greater riparian cover (Collins, Kohler, Thomas, Fetzer, & Flecker, 2016), given that the vegetation restricts the incidence of sunlight onto the streams, and thus limits the primary productivity of these bodies of water, forcing the fish to depend more on terrestrial prey (Kraus et al., 2016). In addition to feeding resources, the riparian vegetation also contributes to the complexity of the stream environment (Andrade et al., 2017).

In the present study, the fish associated with shadier streams (e.g., *Laimosemion* cf. *dibaphus*) had more rounded pectoral fins and elongated bodies, traits typical of species found in structurally complex habitats such as stream margins, given that these morphological features confer greater manoeuvrability, and the ability to move rapidly between obstacles (Dala-Corte et al., 2016; Wainwright, Bellwood, & Westneat, 2002). However, the majority of the species associated with shady streams in the present study presented generalist body shapes. This indicates a weak association between these species and specific niches. As fish body forms determine their capacity to exploit specific feeding resources (Winemiller, 1991), these generalist shapes may be favourable to the fish assemblages in shady streams, by allowing the species to exploit a range of different resources (Ramírez et al., 2015).

By contrast, fish with morphologically specialised bodies can exploit specific niches. These species include the gymnotiforms and loricariids, which were associated with the narrow, fast-flowing streams with overhanging banks of the Acará and Capim basins. These species have relatively small pectoral fins for their body size, although the pectoral fins have different functions in these two groups. The elongated body of the gymnotiforms is poorly adapted for long-distance movements, and these fish typically seek refuge in substrates, such as banks of leaf litter, vegetation or roots, where they are protected from predators as they detect their own prey by electrolocation (Babineau, Lewis, & Longtin, 2007). In the gymnotiforms, the anal fin is the principal propellant, while the pectoral fins are used to direct the movement of the fish (Youngerman, Flammang, & Lauder, 2014).

In the benthic loricariids, rounded pectoral fins are used to stabilise the fish on bottom substrates (Drucker & Lauder, 2000; Oliveira et al., 2010). The depressed body of the loricariids is also an adaptation for a benthic lifestyle in the fast-flowing streams in which they were collected. This is because fish with depressed bodies, such as *Rineloricaria* cf. *hasemani* and *Farlowella amazonum*, offer less resistance to stronger flows (Gordon, McMahon, & Finlayson, 2004), resisting the forces that tend to raise their bodies from the substrate (Webb, 1975), with the depressed body shape being reinforced by the relatively broad pectoral and pelvic fins, which create a large surface that the pressure of the flow forces against the substrate (Winemiller, Agostinho, & Caramaschi, 2011).

The morphology of *Farlowella amazonum* and *Brachyhypopomus brevirostris* is typical of the species associated with streams that have a relatively high proportion of overhanging banks. These species with relatively small fins and depressed or elongated bodies were associated strongly with streams that have overhanging bank microhabitats. The fish assemblages of streams are closely related to the characteristics of the margins of these bodies of water due to the availability of feeding resources, and the protection provided by this environment (Brejão et al., 2013; Wolff, Taylor, Heske, & Schooley, 2016). Overhanging banks are the result of erosive processes in relatively fast-flowing streams (Benone et al., 2017). This microhabitat can be an important refuge for many stream fish species during spawning or periods of inactivity (Akbaripasand & Closs, 2018; DeFilippo et al., 2018).

The results of the present study indicated that many species were associated with streams with a greater abundance of overhanging banks. The presence of *Gymnorhamphichthys rondoni* in these streams is an example of an association between the environment and feeding habits. This species forages for fish and aquatic invertebrates in these environments during the night (Sazima, Carvalho, Mendonça, & Zuanon, 2006). The margins of the stream may also represent an important refuge from the intense flow of the main channel for fish such as the gymnotiforms, which are poorly adapted, morphologically, to cope with strong flows. The streams of the Acará basin had a high proportion of overhanging banks and low riparian cover, as observed in Figure 2b and Table S1. Periphytivore species, such as *Rineloricaria* cf. *hasemani* and *Farlowella amazonum*, can be found in these streams due to the exposure of the channel to sunlight, which favours the production of algae (Carvalho & Tejerina-Garro, 2018; Collins, Thomas et al., 2016b; Zuanon et al., 2015).

The findings of the present study provide an important contribution to the understanding of the functional structure of fish assemblages in relation to the variation in local environmental variables in Amazonian streams. Factors such as the riparian vegetation cover,

the availability of refuges and stream flow velocities, which are often referred to as determinants of community structure (Benone et al., 2018; Mendonça, Magnusson, & Zuanon, 2005; Roa-Fuentes & Casatti, 2017), also have a functional effect on the fish assemblages. Given the scarcity of data on the functional structure of fish assemblages in Amazonian streams, our study provides important insights for the better understanding of the trait–environment associations found in aquatic ecosystems.

ACKNOWLEDGEMENTS

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHORS' CONTRIBUTION

L.L.S. and N.L.B. conceived and designed the investigation, performed field and laboratory work; L.L.S., N.L.B. and B.E.S. analysed the data; L.F.A.M., R.B.B., B.E.S. and N.L.B.revised and contributed with the manuscript writing; L.L.S. wrote the paper.

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