

How does conversion from forest to pasture affect the taxonomic and functional structure of the fish assemblages in Amazonian streams?

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Abstract

Clearing land for the establishment of pasture is the principal cause of deforestation in the Amazon basin. We investigated how stream habitats and the taxonomic and functional structure of the fish fauna respond to the effects of the conversion of forest to pasture in the eastern Brazilian Amazon. We sampled 13 streams located in areas of forest and 13 streams within a pasture matrix. The structure of the stream habitats, and the taxonomic and functional structure of the fish assemblages were compared between forest and pasture, using univariate and multivariate analyses. Species richness did not vary between environments, although abundance was greater in forest streams. Functional divergence was lower in the pasture streams, indicating a reduced degree of niche differentiation. The pasture streams presented a higher percentage of artificial shelters, such as pipes and plastic containers, and riffles, while the forest streams had greater canopy cover formed by large trees, and a denser substrate formed by leaf litter. Environmental variables influenced the distribution of species based on their functional traits. The greater canopy cover in forest streams benefitted benthic species. The ongoing increase in the area of pasture in the Amazon region is causing changes in stream habitats, and in the taxonomic and functional structure of the local fish assemblages. The impacted streams did not favour the occurrence of species with parental care or piscivorous, invertivorous, and benthic habits. Overall, protecting forests and the stream margins will promote adequate conditions to maintain the equilibrium of Amazonian stream ecosystems.

KEYWORDS

environmental changes, functional traits, land use, riparian forest

1 | INTRODUCTION

In recent years, increasing economic development has resulted in high rates of change in land use which have a negative impact on both terrestrial and aquatic habitats (Newbold et al., 2018). In the Amazon region, many studies have demonstrated that these changes in land use

have resulted in a decrease in the basal area of the forest, changes in the physical–chemical characteristics of the water, such as its temperature and pH, the loss of riparian vegetation and impacts on the associated fauna (Luiza-Andrade et al., 2017; Mendes-Oliveira et al., 2017; Prudente et al., 2017). Nepstad et al. (2008) found that approximately 20% of the forest in the Amazon region has already been transformed

into open areas and predicted that, without changes in land-use practices, this percentage will increase to 50% by 2030.

Monocultures (Cunha & Juen, 2017; Nepstad et al., 2006), logging (Prudente et al., 2017) and ranching (Teresa & Casatti, 2012) have caused environmental changes such as an increased sediment input into watercourses, changes in the physical and chemical characteristics of the water, a decrease in the availability of natural shelters, and ultimately, a reduction in species diversity. Clearing land to establish areas of pasture has been identified as the principal cause of deforestation in the Amazon, with cattle ranches currently occupying a total area of approximately 480,000 km², which represents 60% of the area of the biome impacted so far (INPE, 2014). **These data reinforce the urgent need to understand the impact that the conversion of forest to pasture has on the environment and the associated biodiversity,** given that the ongoing trend is for more areas to be converted to pasture in the near future.

The transformation of the native vegetation into pasture involves a reduction in the heterogeneity of riparian habitats through the substitution of forest with grasses. While Brazilian environmental legislation (the Forestry Code, federal law 12.651/2012) mandates the preservation of a buffer of native riparian forest on agricultural properties, the legal parameters—a 30-metre buffer of forest on each margin of watercourses of up to 10 m in width—are ineffective for the maintenance of adequate environmental conditions for the survival and persistence of many of the less tolerant species found in the region's aquatic ecosystems (Pusey & Arthington, 2003). This is a preoccupying scenario, given that the Amazon is one of the world's most biologically diverse regions.

Despite the efforts of scientists to devise strategies for species conservation, most environmental assessments, worldwide, have focused solely on the taxonomic component of local biodiversity (Gaston, 2000), which is insufficient to determine the negative impact of deforestation on ecological functions, given that it considers only the number of taxa found in an assemblage. From a practical standpoint, very limited inferences can be made on the loss of ecosystem services when only measures of species diversity are available for an ecosystem (Toussaint et al., 2016). Given this, complementary measures of functional diversity, combined with indices of taxonomic diversity, can provide a valuable tool for the evaluation of the role of biodiversity in the maintenance of ecosystem services (Cardinale et al., 2012; Mouillot et al., 2011). The integration of these two measures of diversity also permits the assessment of the effects of anthropogenic impacts on biodiversity, given their complementarity, and provides a systematic overview of the loss of biodiversity and ecological function.

Recent research has demonstrated the negative effects of human activities on the taxonomic structure of aquatic assemblages, in particular, shift in species composition and a decrease in species richness (Roa-Fuentes & Casatti, 2017). Studies of the impacts of conversion from forested and riparian areas to pasture have demonstrated changes in the structure of riparian habitat (Stephens et al., 2016) and physical-chemical parameters (Nusslé et al., 2015), as well as the modification of the substrate, with a predominance of sand or silt (Casatti et al., 2006), and the speed of the water flow (Pusey & Arthington, 2003). The

effects of land use can influence different aspects of functional diversity, as functional richness (FRic), functional evenness (FEve), functional divergence, FDiv (Villéger et al., 2010), or even, on which functional traits are most representative in anthropogenic environments (e.g. tolerance of hypoxia, detritivory, algivory and swimming efficiency) (Bojsen & Barriga, 2002; Lorion & Kennedy, 2009; Teresa et al., 2015).

However, we still do not fully understand the influence of conversion from forest to pasture on the streams habitat, or even, on functional attributes of the fish, mainly on Amazonian streams (Teresa & Casatti, 2017; Villéger et al., 2008). Given this, our principal focus was to understand whether the environmental characteristics of pasture impede the occurrence of species with certain functional traits, and which traits are affected. The results of this study should provide important insights for the formulation of mitigatory measures related to a given specific metric, rather than a type of land use, which would thus be applicable to a range of scenarios of degradation, contributing to the mitigation of the loss of both taxonomic and functional diversity.

We investigated the taxonomic and functional structure of the fish assemblages of streams located in areas of forest and pasture to evaluate three main questions: (a) How do the environmental changes caused by the conversion of forest to pasture affect the species richness, abundance and composition of the local fish assemblages?; (b) How do the environmental changes caused by the conversion to pasture affect the functional diversity of the fish assemblages? and (c) How does conversion to pasture affect stream habitats, and which specific functional traits are related to the habitat variables that characterise the streams located within areas of forest and pasture? Our operational hypothesis is that streams located in pasture will be characterised by a loss of riparian forest and an increase in water temperature and the input of fine sediments, resulting in shifts in the composition of the fish fauna and their functional traits. The conversion of forest to pasture is also expected to have a negative impact on species with specific functional traits, such as parental care, benthic habits, and invertivorous or piscivorous diets (Casatti et al., 2012). Parental care, for example, may depend on the availability of allochthonous debris to provide shelter and is typical of species with a reduced dispersal capacity (Gutiérrez et al., 2018). The reduced heterogeneity in the substrate of the streambed may also be unfavourable to benthic species (Teresa et al., 2015), while many insect and fish prey may disappear due to the absence of riparian vegetation (Woodward & Hildrew, 2002). Following the loss of fishes with specific functional traits, we would also expect the pasture streams to have less functional richness, evenness and divergence.

2 | MATERIAL AND METHODS

2.1 | Study area

The study streams are located in the Capim River basin, in the municipalities of Paragominas, Ipixuna do Pará and Aurora do Pará, in

the state of Pará, Brazil (Figure 1). Together, these three municipalities cover a total area of 26,365.65 km², of which, 4,310.53 km² (approximately 16%) is covered with pasture (INPE, 2014). The region is dominated by dense submontane rainforest with a tropical rainy climate, classified as Af in the Köppen classification system (Peel et al., 2007). This region has a mean annual temperature of approximately 26°C and mean annual rainfall of 1,800 mm. The dry season lasts 6 months and peaks in intensity between August and October (Watrin & Rocha, 1992).

2.2 | Data collection

2.2.1 | Sample design

A total of 26 streams were selected randomly from a set of potential candidates. These sites were first- and second-order streams (*sensu* Strahler, 1957), and were selected based on their viability of access. These streams were divided into two treatments: 13 forested sites and 13 sites within areas of pasture on cattle ranches (for details of the study sites, see Table S1). The streams were sampled during the dry season to avoid the potential influence of seasonal variation on habitat structure and the composition of the fish assemblages (Espírito-Santo et al., 2009), as well as to facilitate sampling, which can be hampered by high water conditions.

The streams were classified as “forest” or “pasture” based on the percentage of land cover, determined by the Digital Image Processing (DIP) of RapidEye satellite images (RapidEye, 2015). The images were selected from the same years in which the fauna and habitat were sampled at each site. To define the percentage of forest cover at each stream, a 30 m buffer was created along the drainage network upstream from the sample point, using QGIS 2.18 (QGIS Development Team, 2018). The estimated percentage of deforestation was used to establish a colour gradient of the sample units. The pasture streams presented a relatively high percentage of deforestation in comparison with the forest streams (Table 1). Different types of land use were found within the buffers in the pasture streams, including farmland (mean = 1.78%), urban development (mean = 0.97%) and forest remnants (mean = 20.74%), although the predominant land use was pasture (mean = 61.12%). In the case of the forest streams, forest (mean = 95.68%) and secondary vegetation (mean = 3.40%) predominated.

To avoid spatial autocorrelation, a minimum distance of 1 km was established between each pair of sample points and each sample point was located on a separate stream. Due to the spatial arrangement of the sample units, we performed a redundancy analysis (RDA) based on the PCNM's (Principal Coordinates of Neighbour Matrices) of the response variables to test for potential spatial autocorrelation of the response variables. The results indicated that the spatial distribution of the points had no influence on the response variables, and thus that the analyses applied below reflected only

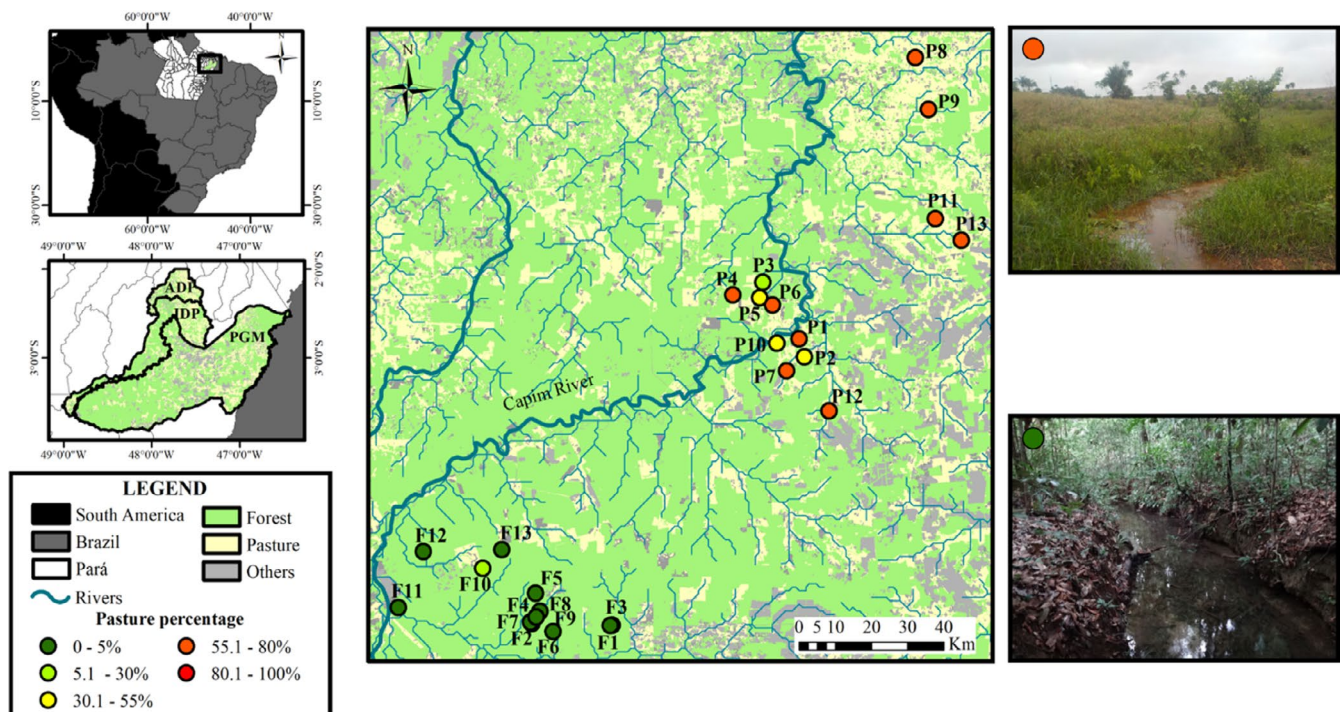


FIGURE 1 Location of the 26 streams sampled in areas of forest (preceded by an F) and pasture (preceded by a P) in the Capim River basin, in the eastern Brazilian Amazon basin. The sample sites are arranged in a gradient ranging from dark green (0%–5% pasture) to red (80.1%–100% pasture). ADP, Aurora do Pará; IDP, Ipiçuna do Pará; PGM, Paragominas

TABLE 1 Mean (\pm SD) for the environmental and landscape variables measured in the forest ($n = 13$) and pasture ($n = 13$) streams in the Capim River basin, eastern Brazilian Amazon

Stream habitat	Forest	Pasture
	Mean \pm SD	Mean \pm SD
%Mean canopy cover of large trees (Can_Tre)	24.28 \pm 7.89	8.36 \pm 8.14
% Substrate formed by leaf litter (Sub_Lit)	11.63 \pm 9.98	6.36 \pm 5.85
Quantity of artificial shelters (Art_She)	0.71 \pm 2.10	12.62 \pm 22.55
% Riffles (Per_Rif)	0.18 \pm 0.16	33.90 \pm 28.06
Landscape		
% Deforestation	0.67 \pm 2.19	64.02 \pm 18.04

the influence of the environmental factors (see Table S2). A 150 m reach was established at each stream and subdivided by 11 transects designated with the letters A (downstream) to K (upstream), resulting in 10 longitudinal segments of 15 m.

2.2.2 | Fish sampling

The fish assemblages were sampled by two collectors using two circular dip-nets 55 cm in diameter with a 2 mm mesh. We actively sampled the bottom, surface and margins of the streams. The margins are important because they provide access to most of the microhabitats observed in the streams. A standard sampling effort of three hours was established per section, with an interval of 18 min for the sampling of each segment, a schedule that has been used extensively in similar studies in the Amazon region (Leal et al., 2017; Prudente et al., 2017). The fish collected from each stream were euthanised with a lethal dose of anaesthetic (Eugenol; American Veterinary Medical Association, 2013), fixed in 10% formalin and, after 48 hr, transferred to 70% alcohol for storage. The specimens were identified to the lowest possible level using taxonomic keys and consultation with specialists. The surveys were conducted under licence number 4681-1 issued by the Chico Mendes Institute of Biodiversity Conservation of the Brazilian Ministry of the Environment. The voucher specimens were deposited in the Zoology Museum of the Institute of Biological Sciences (ICB) at the Federal University of Pará (UFPA) and the Goeldi Museum (MPEG), both in Belém, Pará (Brazil).

2.2.3 | Stream habitats

The environmental variables were measured using the protocol of the US Environmental Protection Agency (EMAP/US-EPA; Peck et al., 2006 and Kaufmann et al., 1999), as adapted by Callisto et al. (2014) for tropical streams. This protocol evaluates features including the stream morphology, water flow, substrate,

forest cover, fish shelters, woody debris and anthropogenic pressures. The specific variables used in the present study were selected based on previous research in the Amazon basin (Cunha & Juen, 2017; Prudente et al., 2017), in accordance with their capacity to predict the structure of fish assemblages: (a) Mean canopy cover formed by large trees (Diameter at breast height > 0.3 m, height > 5 m) [Can_Tre]; (b) The quantity of artificial shelters (any artificial structure derived from human activity found in the stream) [Art_She]; (c) The percentage of the substrate formed by the leaf litter (substrate formed by the accumulation of leaf litter) [Sub_Lit], and (d) the percentage of riffles (stream flow of increased water velocity and turbulence) [Per_Rif] (see Table S3 for details on the measurement methods).

2.2.4 | Functional traits

We used 14 qualitative and quantitative functional traits to evaluate the functional structure of the fish assemblages. The quantitative traits consisted of the mean values of the ecomorphological characteristics of the fish, which were obtained from the measurement of five individuals of each species. In order to avoid potential allometric effects on the analyses, we chose adult individuals (Winemiller, 1991). In the case of sexually dimorphic species, the females were selected for analysis, given that they present less variation in body dimensions, whereas males typically invest in larger and more ornate fins which can interfere with the morphological configuration of the individual (Py-Daniel & Fernandes, 2005). A total of 16 morphometric measurements were obtained from each specimen (Table S4). All measurements were taken in a straight line between the reference points with a digital caliper (0.1 mm precision). To measure areas, the outline of the target region was traced onto graph paper and the area was calculated using ImageJ 1.48 (Rasband, 2006). These measurements were converted into 12 ecomorphological traits that made up the matrix of functional traits (Table S5), each with its respective ecological interpretation (Table S6).

We also included a qualitative assessment of functional traits based primarily on existing scientific literature. We considered trophic guilds (algivore, omnivore, piscivore, detritivore, allochthonous invertivore, autochthonous invertivore, and parasite) and parental care. We conducted our review in the FishBase database (Froese & Pauly, 2017), articles (see Table S7) and also supplemented our results with the stomach contents of some species. To find the articles, we used the keywords "feeding ecology" or "diet" followed by the species name on Google Scholar. When no data were found for a given species, those available for the genus or the family were used (Carvalho & Tejerina-Garro, 2015). The "parental care" trait was transformed into a binary format, that is, "1" (present) or "2" (absent), while the "trophic guild" data were transformed through fuzzy logic (Chevenet et al., 1994). This approach is based on an affinity index, in which a proportion is generated for each guild based in the index of food importance. Each

trophic guild was assigned one of four values (0, 1, 2 or 3), where zero indicates no affinity with the trophic guild and 3 indicates the highest degree of affinity. These values were assigned according to the relative importance index of each item consumed, thus covering not only the principal feeding habit of the species, but also items consumed secondarily (Table S8).

2.3 | Data analysis

2.3.1 | Species richness, abundance and composition

We applied three methods to determine how the environmental changes caused by the conversion of the forest to pasture affect the species richness, abundance and composition of the fish assemblages. We used rarefaction curves to determine species richness, due to the differences in abundance among the species. The number of samples was diluted statistically in the results of the rarefaction analysis (Gotelli & Colwell, 2001), which enabled the comparison of areas surveyed with varying sampling effort by standardising the expected species richness to samples of the same size.

We evaluated the differences in the abundance of all species between habitats (forest vs. pasture). We additionally tested for differences in abundance of those species unique of each habitat (i.e. excluding species registered in the two habitats; hereafter "exclusive species"). Assessing exclusive species is important because they play an ecological role only in the habitats in which they occur, as opposed to shared species (Büchi & Vuilleumier, 2016). For this, we used Student's *t* test ($p < .05$), through *t.test* function of the *stats* package (the assumptions of normality and homoscedasticity were met in all cases) in the R software, version 3.3.1 (R Development Core Team, 2016).

To evaluate species composition, we used a Principal Coordinates Analysis (PCoA) of the Bray–Curtis matrix, to determine whether clusters of species were formed by habitat. We used a Permutational Multivariate Analysis of Variance (PERMANOVA) to verify the variation found in the PCoA matrices. The probability of the PERMANOVA was obtained using the Monte Carlo method, based on 9,999 permutations, considering a significance of $p < .05$ (Anderson & Walsh, 2013). These analyses were run in the *cmdscale* and *adonis* functions of the *stats* and *vegan* packages, respectively, in the R software.

2.3.2 | Functional diversity indices

We used three multivariate indices of functional diversity (see Villéger et al., 2008) to determine how the environmental changes caused by the conversion of the forest to pasture affect the functional diversity of the fish assemblages. The indices included: (a) Functional richness (FRic), which indicates the amount of functional space filled by the fish assemblage; (b) Functional evenness (FEve), which measures the regularity of the spacing between species and how their abundance is distributed in functional space to permit the balanced and efficient

exploitation of the available resources, and (c) Functional divergence (FDiv), which defines how far the abundance of each species is from the centre of the functional space, providing a means of evaluating whether more abundant species are closer to the limits of the functional space. The functional trait data included ecomorphological attributes (quantitative, Table S5), parental care (qualitative/binary, 0 or 1, Table S8) and trophic guild data (qualitative/categorical through fuzzy logic, Table S8). These data were analysed using the *data.frame*, *prep.binary* and *prep.fuzzy* functions, respectively. The data were standardised using the *decostand* function with the *normalise* argument, which makes the sum of squares equal to one. The indices were calculated in the *dbFD* function of the *FD* package (Laliberté et al., 2014). Each index was compared between treatments (forest vs. pasture) using Student's *t* test ($p < .05$) run in the *t.test* function of the *stats* package (the assumptions of normality and homoscedasticity were met in all cases) of the R software.

2.3.3 | Functional traits–environmental variables relationship

We used an RLQ ordination analysis (Dolédéc et al., 1996) to determine how the conversion of forest to pasture affects stream habitats and which functional traits are related specifically to the habitat variables that characterise the streams located in the two habitats. This analysis is based on three matrices: R, a stream habitat matrix; L, a species abundance matrix, and Q, a functional traits matrix, and conducts a double inertia analysis, because takes into account simultaneous use of two sets of data (R and Q matrices), combining the data sets and identifying the co-relationships between them, with the link being expressed by the species abundance matrix (L).

The rows of the L matrix correspond to those of the R matrix, while the L columns correspond to the rows of the Q matrix. The R matrix (environmental data) was ordinated using a Principal Components Analysis (PCA), while the species abundance matrix (L) was ordinated using a Correspondence Analysis (CA; Dolédéc et al., 1996), which provided a combined species and sample ordination (Dray et al., 2014). The Q matrix (functional traits) was ordinated by the Hill–Smith method (Hill & Smith, 1976) using Gower's distance matrix, given that it contained both qualitative and quantitative variables.

In addition to the RLQ analysis, we applied the fourth-corner method (Legendre et al., 1997), as proposed by Dray et al. (2014), which combines these three matrices into a single matrix. To control for type I errors, Dray and Legendre (2008) proposed an alternative approach, which combines two permutation models: Model 2, to test the null hypothesis that the distribution of the species with fixed traits is not influenced by the environmental conditions, and Model 4, to test the null hypothesis that the species composition of the samples with fixed environmental conditions is not influenced by the species traits. As the two models were significant, we evaluated the peer-to-peer relationship between each trait and the environmental variables to verify whether there was a significant correlation, either positive or negative.

These analyses were run in the *ade4* (Dray & Dufour, 2007) and *vegan* packages (Oksanen et al., 2017), in the R software.

3 | RESULTS

3.1 | Species richness, abundance and composition

Using rarefaction curves (Figure 2) to compare the estimated richness, we verified that the forest ($S_{\text{est}} = 37.88 \pm 2.79$) and pasture ($S_{\text{est}} = 43 \pm 2.52$) did not differ significantly from each other considering the same subsample size (approximately 3,000 individuals). The forest streams had 18 exclusive species and the pasture streams, 16 exclusive species, while the two habitats shared 27 species.

The abundance of fish was significantly greater in the forest streams ($t = 2.49$; $df = 24$; $p = .02$), with a total of 5,043 individuals, in comparison with 3,032 individuals in the pasture streams. When only the species exclusive to one of the two habitats were considered, however, abundance was significantly greater ($t = -2.15$; $df = 32$; $p = .03$) in the pasture streams (852 individuals) in comparison with the forest streams (178 individuals). On the other hand, when only the 27 shared species were considered, there were no significant differences between pasture (2,180 individuals) and forest streams (4,865 individuals), in terms of abundance ($t = 1.10$; $df = 52$; $p = .27$).

Species composition varied significantly between forest and pasture streams (pseudo- $F = 6.364$; $df = 1$; $p = .001$; Figure 3). We collected a total of 8,075 individuals belonging to six orders, 21 families

and 61 species of fish (Table S9). *Hyphessobrycon heterorhabdus* (Ulrey, 1894) was the most abundant species in both forest ($n = 2,315$ individuals) and pasture streams ($n = 673$). The most common exclusive species in the forest streams were *Brachyhypopomus* sp. ($n = 86$ individuals), *Gymnotus* gr. *pantherinus* (Steindachner, 1908) ($n = 85$) and *Characidium* cf. *etheostoma* Cope, 1872 ($n = 13$). In the pasture streams, the most common exclusive species were *Hemigrammus rodwayi* (Durbin, 1909) ($n = 290$ individuals), *Nannostomus nitidus* Weitzman, 1978 ($n = 142$) and *Satanoperca jurupari* (Heckel, 1840) ($n = 135$).

3.2 | Functional diversity indices

The functional divergence of the fish was significantly higher in the forest streams in comparison with the pasture streams ($t = 2.32$; $df = 24$; $p = .02$). However, no significant variation was found between habitats in either functional evenness ($t = -0.32$; $df = 24$; $p = .75$) or richness ($t = 1.83$; $df = 24$; $p = .07$).

3.3 | Functional traits–environmental variables relationship

The results of the RLQ analysis revealed considerable variability between the functional traits of the fish and the environmental variables. The first axis explained 88.05% of the variation, while the second axis explained 5.20% (for more details, see Table S10). Gradients were observed in the data (Figure 4a), in which the streams with the greatest amount of forest presented higher mean canopy cover formed by large trees (Can_Tre) and leaf litter substrate (Sub_Lit), while the streams with the greatest amount of pasture presented higher values for artificial shelters (Art_She) and the percentage of riffles (Per_Rif). The environmental characteristics of the forest and pasture habitats are summarised in Table 1.

In the analysis of the functional structure, two main groups were formed by the ordination of the functional traits (Figure 4b). Our results indicated forest streams having a larger number of species with parental care, piscivores and invertivores, as well as certain ecomorphological traits, including reduced swimming ability (Caudal peduncle compression index/CPCI and Coefficient of fineness/CF) and benthic habits (Relative eye position/REP). The pasture streams had more species with no parental care, detritivores, algivores, and omnivores, and ecomorphological traits such as a greater frequency of swimming (Pectoral fin aspect ratio/PFAR) and consumption of large prey (Relative head length/RHL).

The fourth-corner analysis of the relationship between environmental variables and functional traits indicated that the stream habitat affected the distribution of species (model 2: $p < .001$) and correlated with the functional traits (model 4: $p = .036$). Greater canopy cover of large trees benefited species with higher values for the ecomorphological attribute "relative eye position" (REP) ($r = .214$; $p = .033$).

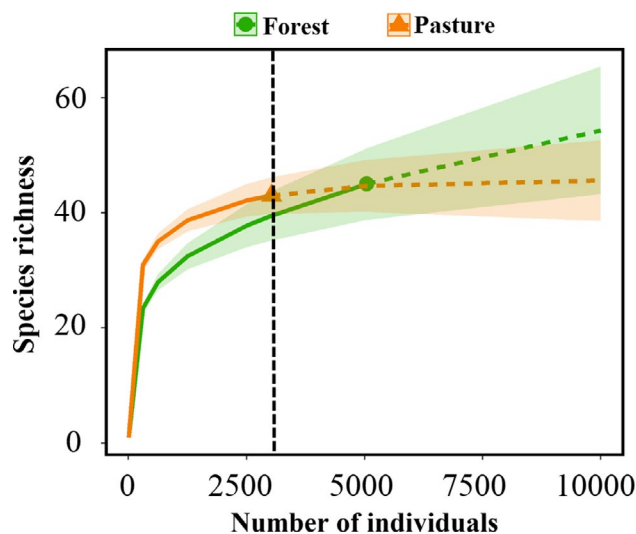


FIGURE 2 Rarefaction curves of the species in relation to the number of registered individuals (continuous line) and the shaded regions represent the 95% confidence intervals (error bars), recorded in the forest and pasture streams, sampled in the Capim River basin, eastern Brazilian Amazon basin. The green and orange solid lines indicate interpolation and dashed lines indicate extrapolation. The black dashed line indicates the maximum number of individuals collected in the smallest sample (Pasture = 3,032 individuals)

FIGURE 3 Plot of the results of the Principal Coordinates Analysis (PCoA) of the fish assemblages recorded in the forest and pasture streams sampled in the Capim River basin, in the eastern Brazilian Amazon. The fish silhouettes represent examples of species recorded in each environment and were provided by Gilberto Salvador; Douglas Bastos; Prólgarapés; Pierres Yves and FishBase.

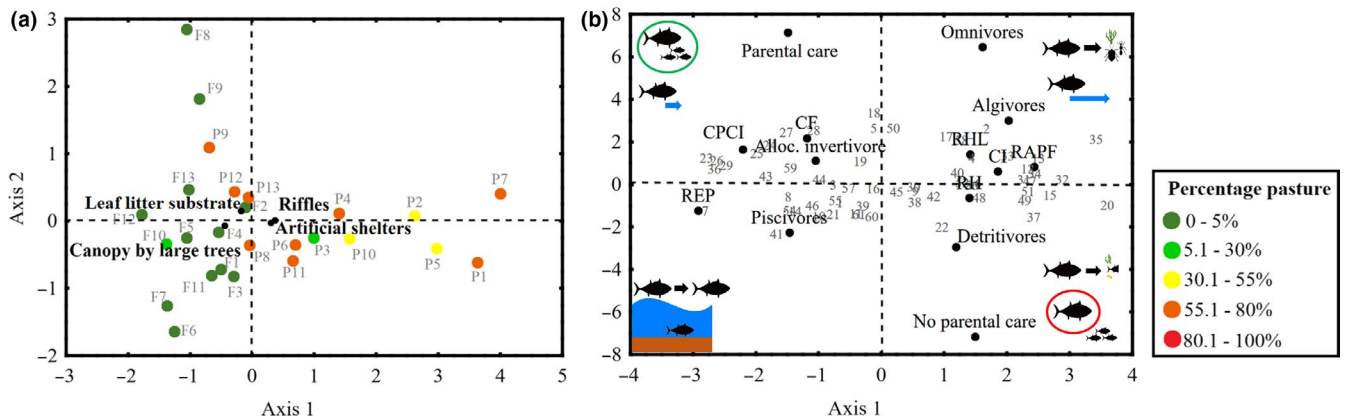
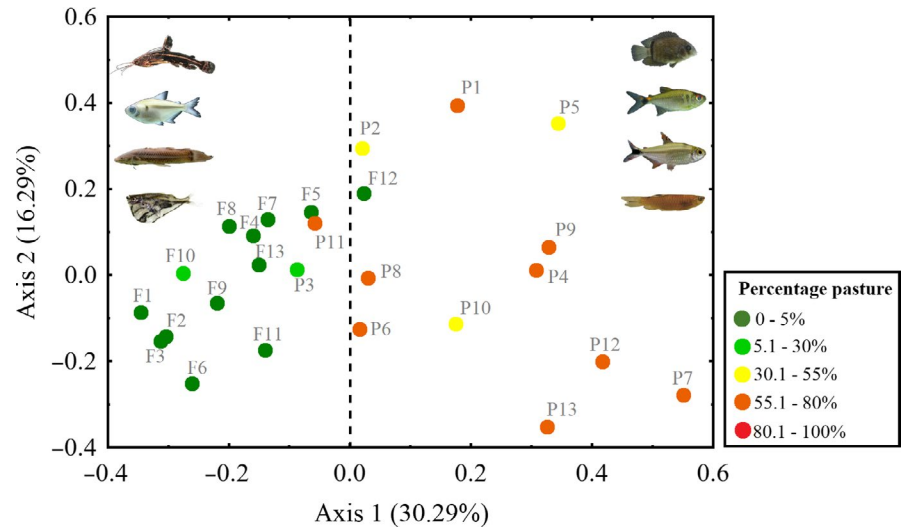


FIGURE 4 Results of the RLQ analysis of the fish assemblages recorded in the forest and pasture streams sampled in the Capim River basin, in the eastern Brazilian Amazon basin: (a) Ordination of the sample sites and environmental variables (PCA/weighted by the CA scores); (b) Ordination of species and functional traits (Hill-Smith/ weighted by the CA scores). The first axis of the RLQ analysis accounts for 88.05% of the total variation in the data, while the second axis accounts for 5.20%. In (a), F indicates a forest stream and P indicates a pasture stream. The sample sites are arranged in a gradient ranging from dark green (0%–5% pasture in the surrounding environment) to red (80.1%–100% pasture). In (b), blue arrows indicate swimming ability, black arrows indicate type of food consumed, green circle indicates presence of parental care, while red indicates absence of parental care. The species identification numbers and the abbreviations of the functional traits are provided in Tables S5 and S8

4 | DISCUSSION

The Amazon region is the world's principal focus of tropical deforestation, and intervention is urgently needed to prevent a large-scale, irreversible ecological disaster. As Brazil is responsible for more than half of the deforestation in the Amazon, the present study provides important insights into how changes in land use affect riparian forests and, in turn, stream habitats and the taxonomic and functional diversity of their fish assemblages in the Brazilian Amazon. Our findings should contribute to the development of viable solutions for the impacts of deforestation.

The rarefaction curves showed that the species richness of pasture streams was greater than that of forest streams, as the sampling effort, in terms of individuals, was increasing. This pattern may have been caused by the invasion of opportunistic and generalist species, which benefit from environmental conditions in human-impacted

streams (Teresa et al., 2015). However, when we compare richness, mediated by the lower abundance between habitats (3,000 individuals in pasture), we saw that the deforestation does not affect species richness. Ilha et al. (2019) did find that the number of fish species decreased with deforestation, although a considerable amount of evidence indicates that deforestation may not affect the species richness of stream fish (Bojsen & Barriga, 2002; Sutherland et al., 2002). It is important to note, however, that the land conversion in the study region has occurred within the past 50 years, which means that species richness patterns may not have stabilised. In this case, species loss may have been masked by extinction debt, given that species are often slow to respond to the effects of environmental change, with extinction occurring only after decades or even centuries, in some cases (e.g. Brejão et al., 2018; Hylander & Ehrlén, 2013; Ilha et al., 2019).

Our findings indicate that abundance varied between habitats, being significantly higher, on average, in the forest streams. However, it is important to note that, when the shared species were excluded from the analysis, the abundance of fish was greater in the pasture streams, reflecting their dominance in this habitat. We found no significant differences between pasture and forest when only shared species were considered. Therefore, because they are species that occur both in pastures and in forests, the ecological functions exercised by them are, until then, guaranteed in both environments. In fact, most studies indicate that deforestation provokes an increase in total fish abundance due to the proliferation of generalist species (e.g. Casatti et al., 2009; Lorion & Kennedy, 2009), which are able to adapt to local conditions, and thus increase in abundance due to the lack of competition for resources, given the absence of less tolerant species.

Generalist and specialist species can be defined in terms of the range of the types of prey they exploit or by the amplitude of the environmental conditions in which they are able to thrive (Richmond et al., 2005). While generalist species may occupy environments with sub-optimal conditions and feed on an enormous variety of prey, specialist species are more sensitive to environmental conditions and tend to feed on specific types of prey. *Hyphessybron heterorhabdus* is one generalist species known to occupy a wide range of habitats (Agostinho et al., 2007), which may account for its relatively similar abundance in both pasture and forest streams. The most abundant species in pasture streams, *Hemigrammus rodwayi* (Characidae), *Nannostomus nitidus* (Lebiasinidae) and *Satanoperca jurupari* (Cichlidae), are members of families that are composed of fish with high trophic plasticity able to tolerate extreme conditions (Ilha et al., 2019; Silva et al., 2016; Winemiller, 1989). Specialist species, such as *Brachyhypopomus* sp. and *Gymnotus* gr. *pantherinus* (order Gymnotiformes), were more abundant in forest streams. These fish are nocturnal and typically take refuge in deeper waters during the day (Brejão et al., 2013). They also have an electrosensory system, which makes them particularly sensitive to changes in water quality, so they are also good bioindicators (Montag et al., 2019). The Characiform fishes of the genera *Characidium* are mostly benthic and diurnal, and usually inhabit leaf beds, branches and other complex microhabitats from which they ambush their prey (Brejão et al., 2013; Montag et al., 2019), which explains the representativeness of *Characidium* cf. *etheostoma* in forested streams.

In addition to these changes in the taxonomic structure of the fish assemblages, there were also shifts in their functional diversity. Functional divergence (FDiv) was the parameter most sensitive to the effects of deforestation in comparison with either evenness (FEve) or richness, FRic (Mouchet et al., 2010; Villéger et al., 2008). The functional richness was constant, in fact, and reflected the similarity of species richness between the two habitats. However, although the number of functional traits was similar, the composition was not. This variation in the composition of functional attributes is probably associated to forest cover, and consequently the greater contribution of allochthonous material, in addition to the type of substrate and available shelters may all benefit species with varying ecological

requirements (Lorion & Kennedy, 2009; Pusey & Arthington, 2003; Teresa et al., 2015) and influence the types of functional trait found in the assemblage, rather than the quantity of traits. Functional evenness was also similar between the two habitats, which indicates that the functional space was fully occupied. Teresa and Casatti (2012) found a similar pattern between forested and deforested streams in southeastern Brazil, and concluded that, in the absence of more sensitive species, opportunists filled vacant ecological roles in the deforested streams, leading to the more uniform use of resources. For example, the decrease in forest cover in deforested streams favours the entry of light and, consequently, increases primary productivity (Lorion & Kennedy, 2009). Therefore, as an indirect effect of deforestation, there is an increase in the occurrence of species that have an algivorous diet, such as *Bryconops caudomaculatus* and *Hemigrammus* sp., registered only in pasture streams. The increase in niche space in deforested streams may thus be determined by the appearance of novel ecological opportunities, which favour the occurrence of opportunistic species (Teresa & Casatti, 2012).

However, functional divergence was higher in the forest streams, which indicates that the dominant species have distinct ecological characteristics, reflecting a high degree of niche differentiation. In the pasture streams, generally the most tolerant species with high trophic plasticity are those that manage to survive, resulting in a high degree of functional redundancy in this habitat (Córdova-Tapia et al., 2017). Villéger et al. (2010) obtained similar results in a study of habitats that have degraded over time, with greater functional divergence being found in non-impacted environments, and divergence decreasing with increasing anthropogenic pressure. These authors related this pattern specifically to a decrease in the relative abundance of specialist foragers, and an increase in the abundance of more generalist species, which led to a significant decrease in both functional divergence and community-level specialization. In the present study, the reduced functional divergence of the pasture streams is related to the reduction in the dominance of more specialised species, such as *Gymnotus* gr. *coropinae* and *Helogenes marmoratus* (both of which feed exclusively on invertebrates), and the increase in the abundance of more generalist species, such as *Copella arnoldi* and *Satanoperca jurupari*, which have a high degree of trophic plasticity. Both these species have omnivorous diets, with that of *C. arnoldi* being based on allochthonous insects and crustaceans (Abelha et al., 2001), while *S. jurupari* feeds mainly on fish and aquatic insects (Zuanon et al., 2015). Forested habitats can result in a greater variety of habitat and food resources, and thus support a larger number of ecologically divergent species. The environmental characteristics of the pasture streams may act as filters, limiting either the occurrence or the abundance of certain species. The most abundant species would thus be expected to have similar niches, which would allow them to tolerate the conditions imposed by the environmental filters (Mason et al., 2008; Mouillot et al., 2007).

The clearing of the riparian forest exposes a stream to adverse conditions, resulting in structural changes in this environment (Clapcott et al., 2012; Prudente et al., 2017). In particular, the pasture streams had a more homogeneous forest, when present, dominated

by young trees of intermediate size, and were characterised by an abundance of artificial shelters, such as pipes and plastic containers discarded by local residents, as well as many areas of riffle. The forest streams were characterised by their extensive canopy cover and a substrate formed by leaf litter. The changes observed in the stream habitats are consistent with those of Casatti et al. (2009) who studied tropical streams with and without the presence of pasture. These authors found that streams with riparian vegetation had a greater diversification of substrates, comprising allochthonous material from the surrounding riparian forest, which reinforces the link between canopy cover and the presence of organic matter in the stream.

In the streams at which the forest has been cleared, the supply of allochthonous material, such as woody debris, which acts as a natural mechanism of flow retention (Dias & Thomaz, 2011), is greatly reduced, while sedimentation increases due to the input of eroded soils, which reduces stream depth progressively (Casatti et al., 2006). The reduction in the depth of the impacted streams, and the decrease in forest cover, and consequently, allochthonous material result in an increase in current velocity because the grasses present in pasture streams, alone, are inadequate to resist the erosional forces of flowing water. On the other hand, vegetation with woody root systems provides a physical barrier to high velocities and turbulence, increasing surface (Baillie & Davies, 2002; Beschta & Platts, 1986). These conditions favours species adapted morphologically for life in faster-flowing streams. One example of this type of morphological adaptation is the relatively elongated anal fin of species such as *Hypopygus lepturus* Hoedeman, 1962 and *Microsternarchus aff. bilineatus* Fernández-Yépez, 1968, which were more abundant in the pasture streams. This trait is found in actively swimming fish and facilitates their occupation of environments with turbulent flow patterns (Gatz-Jr, 1979).

Anthropogenic disturbances can have a variety of effects on freshwater habitats, their fauna and ecological functions. For example, Ilha et al. (2019) recorded a decrease in fish body size due to an increase in the temperature of deforested streams. Casotti et al. (2015) reported that the level of conservation of the riparian zone influenced the decomposition of leaves by shredding invertebrates, which probably reflects the sensitivity of these shredders to changes in the availability of food resources and habitats. Our results also revealed the effects of anthropogenic disturbance on the fish assemblages, including a greater abundance of fish and functional divergence in forested streams, and the predominance of generalists in pasture streams.

Our findings indicate that environmental variables influence the distribution of species based on their functional traits. For streams located within the forest, the greater canopy cover favoured the occurrence of benthic species, which have more dorsally oriented eyes, and spend much of their time on the stream bed in search of certain types of substrate for shelter or food. As forests provide the input of a range of allochthonous materials, including leaves, branches, and sediments (Juen et al., 2016), the forested environment favours the occurrence of species that have a strong association with the stream

bed. The organic matter derived from the riparian forest provides a substrate for the development of microorganisms, which are a source of food for both invertebrates and fish (e.g. Angermeier & Karr, 1983; Pusey & Arthington, 2003), as well as providing refuges (Angermeier & Karr, 1983) and also a reference for the visual orientation of the fish (Brooks et al., 2004). In addition, the high levels of sedimentation and silting of the streams that drain agricultural areas further reduce the availability of microhabitats at the bottom of water courses, resulting in a reduction in the occurrence of benthic species (Brejão et al., 2013; Montag et al., 2019). High levels of fine sediment likely influence species such as *Helogenes marmoratus*, a fish that uses submerged litter as a daytime refuge (Sabino & Zuanon, 1998), and *Ituglanis amazonicus*, which tends to keep to well-sheltered locations, such as submerged roots and cracks in logs, and buries itself in the substrate when it feels threatened (Zuanon et al., 2015).

We highlight the need to preserve the riparian forest of streams to maintain their aquatic biota, although it is still unclear what an adequate buffer would be. Many studies have emphasised the importance of riparian forests for the conservation of aquatic biodiversity (Chua et al., 2020; Ding et al., 2013; Leal et al., 2017), but the conversion of forests to pasture and cropland is advancing progressively across the whole of Brazil. A number of studies (e.g. Leal et al., 2017; Luke et al., 2018; Montag et al., 2019) have shown that the 30 m buffer of riparian forest mandated by the Brazilian environmental legislation (the Forest Code - federal law number 12,651/2012) is insufficient to guarantee the biological integrity of the streams that it is designed to protect. Our results also indicated that the streams located within a pasture matrix, in which the 30-m riparian buffer is respected, presented significant shifts in habitat characteristics and the composition of the aquatic community, in relation to forests, showing the insufficiency of this riparian zone size.

Finally, our results further reinforce the need for a review of the current conservation strategies for streams and adjacent habitats. Irrespective of any such review, we would recommend greater controls on the use of riparian environments, given that the access of cattle to watercourses also contributes the degradation of riparian habitats (Costa & Voltolini, 2013), and the trampling of the stream margin results in the compaction of the soil and the destruction of potential refuges for many fish species (Parente & Maia, 2011). It is also important to guarantee the preservation of the original, native vegetation, rather than allowing it to be replaced with plantations of exotic tree species, given that many studies have highlighted the importance of the heterogeneity of the natural forest habitats for the maintenance of the species diversity of Amazonian streams (Luiza-Andrade et al., 2017; Prudente et al., 2017). Overall, protecting forests and stream margins through the improvement and enforcement of the environmental legislation should help to guarantee the taxonomic and functional diversity of these environments, which will, in turn, ensure conditions for the adequate functioning of the ecosystem, which generates essential environmental services for local human populations.

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CONFLICT OF INTEREST

The authors declare that they have no conflicts of interests.

AUTHORS' CONTRIBUTION

LGC and LFAM conceived and designed the investigation. HL and ALA conducted the field and/or laboratory work. LGC and ALA analysed the data. LFAM and HL contributed materials, reagents and/or analysis tools. LGC, ALA, HL and LFAM wrote the paper.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the attached supporting material.

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SUPPORTING INFORMATION

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