Neotropical Ichthyology

Original article https://doi.org/10.1590/1982-0224-2022-0091

Fish functional responses to local habitat variation in streams within multiple land uses areas in the Amazon

Calebe Maia[1], Gilberto N. Salvador[2], Tiago O. Begot[2], Pâmela V. Freitas[2], Flávia A. S. Nonato[2], Naiara R. Torres[2], Leandro Juen[2] and Luciano F. A. Montag[2]

Correspondence:
Luciano F. A. Montag
lfamontag@gmail.com

In this study, we assessed the effects of multiple land uses and local habitat variables on the composition of fish functional trophic groups (FTG's) and on the ecomorphological traits of fish in Amazonian streams. We evaluated land use types and local habitat variables in 26 streams distributed within a land use gradient. Land use and habitat variables affected the composition of FTG's, as evidenced by the increased abundance of diurnal channel drift feeders in areas with high dissolved oxygen and deeper thalweg. At the same time, diurnal surface pickers, as well as diggers, and ambush and stalker predators were more abundant in streams with higher canopy density. Only habitat variables affected the ecomorphological characteristics of the species. Fish with higher values of relative caudal peduncle length were positively associated with high canopy density, while fish with greater relative mouth width were negatively associated with the variables impact in the riparian zone and cover of fish shelter. The stream fish functional structure was mainly affected by the impacts caused to the local habitat resulting from different land uses. Thus, preserving forest remnants, as well as recovering degraded areas, is essential for the maintenance of aquatic biodiversity in the region.

Keywords: Agriculture, Bauxite ore, Environmental variables, Human disturbance, Land uses.

Submitted February 16, 2022
Accepted November 4, 2022
by Caroline Arantes
Epub December 16, 2022

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

Neotrop. Ichthyol.
vol. 20, no. 4, Maringá 2022

1 Programa de Pós-graduação em Ecologia Aquática e Pesca, Universidade Federal do Pará, Rua Augusto Corrêa, 01, Guamá, 66075-110 Belém, PA, Brazil. (CM) calebe.maia@yahoo.com.br.

2 Laboratório de Ecologia e Conservação, Instituto de Ciências Biológicas, Rua Augusto Corrêa, 01, Guamá, 66075-110 Belém, PA, Brazil. (GNS) curimata_gilbert@hotmail.com, (TOB) tbegot@gmail.com, (PVF) pamelavirgolino@gmail.com, (FASN) flavisilva21@gmail.com, (NRT) naiararaiol@hotmail.com, (LJ) leandrojuen@ufpa.br, (LFAM) lfamontag@gmail.com (corresponding author).

Neste estudo, avaliamos os efeitos dos múltiplos usos da terra e de variáveis do habitat local sobre a composição de grupos tróficos funcionais (FTG's), e nos traços ecomorfológicos, de peixes em riachos amazônicos. Analisamos os tipos de uso da terra e variáveis da estrutura do habitat local em 26 riachos distribuídos dentro de um gradiente de uso da terra. O uso da terra e as variáveis de habitat afetaram a composição de FTG's, evidenciado pelo aumento na abundância de peixes diurnos que se alimentam de organismos em suspensão na água em áreas com maiores valores de oxigênio dissolvido e profundidade do talvegue. Ao passo que os peixes diurnos catadores de superfície, bem como os escavadores e predadores de emboscada foram mais abundantes em riachos com maior densidade florestal. Apenas as variáveis do habitat afetaram as características ecomorfológicas das espécies. Peixes com maiores valores de comprimento relativo do pedúnculo caudal foram associados positivamente com alta densidade do dossel, enquanto peixes que apresentam maior largura relativa da boca foram associados negativamente com as variáveis impacto na zona ripária e abrigo para peixes. A estrutura funcional da comunidade de peixes de riachos foi afetada principalmente pelos impactos causados ao habitat decorrentes de diferentes usos da terra. Portando, preservar os remanescentes florestais, bem como recuperar áreas já degradadas, é fundamental para a manutenção da biodiversidade aquática na região.

Palavras-chave: Agricultura, Minério de bauxita, Perturbação antropogênica, Usos da terra, Variáveis ambientais.

INTRODUCTION

The Amazon region is primarily covered by a dense tropical forest and encompasses several aquatic ecosystems, including streams, lakes, floodplains, and rivers (Sioli, 1991). The forest is strongly connected to the physical structure of streams and provides a large amount of allochthonous material (Sioli, 1991; Benone *et al*., 2017; Carvalho *et al*., 2018), which contributes to increasing fauna diversity, serving as a source of food and shelter (Junk *et al*., 2007; Benone *et al*., 2017). Moreover, the hierarchical classification of watersheds upholds that freshwater environments are nested subsystems, and the functions and structure of the lower levels are dependent on the characteristics of the upper levels (Frissell *et al*., 1986; Tonkin *et al*., 2018). Therefore, the watersheds of freshwater environments are structured and controlled by natural and anthropogenic variables at different spatial and temporal scales (Vannote *et al*., 1980; Frissell *et al*., 1986).

Multiple land uses in Amazonian catchments can affect the environmental heterogeneity and integrity of streams (Paiva *et al*., 2017; Ferreira *et al*., 2018; Leão *et al*., 2020). For example, implementing agriculture provides an increase in nutrient intake and fine sediments into the streams, changing channel morphology, and decreasing canopy cover, water flow, dissolved oxygen concentrations, and the number of woody debris found in the stream channel (Leal *et al*., 2016; Luiza-Andrade *et al*., 2017; Ferreira *et al*., 2018).

In pasture areas, there is an increase in water temperature, conductivity, and the cover of grasses and macrophytes on the streambank, given that losing the adjacent vegetation facilitates these processes, which changes the heterogeneity of the stream habitat (Paiva *et al*., 2017; Brejão *et al*., 2018; Leão *et al*., 2020; Fares *et al*., 2020). Mining activities have contributed to higher bank erosions, which increase stream siltation and water turbidity (Brosse *et al*., 2011; Allard *et al*., 2016).

Changes in local habitat characteristics caused by multiple land uses also influence the structure of aquatic communities (Siqueira *et al*., 2015; Carvalho *et al*., 2018; Leão *et al*., 2020). The homogenization of aquatic communities is one of the major consequences of land use changes (Petsch, 2016; Leitão *et al*., 2018). This homogenization occurs because many species require specific habitat conditions and change in these conditions leads to the simplification of communities with a loss of species diversity (Southwood, 1977; Soberón, 2007).

Fish are one of the most affected groups by changes in the landscape (Bojsen, Barriga, 2002; Dias *et al*., 2010; Leitão *et al*., 2018). Several approaches can be used to assess land use impacts on the fish community, functional ecology being one of them (Benone *et al*., 2020; Colares *et al*., 2022). Functional ecology approaches evaluate the diversity of functional traits, which are components of organisms' phenotypes, and which influence the ecological processes of the community, regardless of the phylogeny of the organisms (Petchey, Gaston, 2006). For example, fish have several strategies for acquiring food resources (Simberloff, Dayan, 1991). They are usually sorted into functional trophic groups (FTGs) related to differences or similarities in the species ability to capture food (Brejão *et al*., 2013). Land uses changes caused by the human impact may increase the abundance of some functional trophic groups, like grazers or diurnal pickers, and decline or cause loss of habitat specialists, such as benthic fishes (Bojsen, Barriga, 2002; Lorion, Kennedy, 2009; Ferreira *et al*., 2018; Leitão *et al*., 2018). Studies of ecomorphological traits report a loss of species with specialized traits in deforested areas, with a reduction or loss of species that are associated with the exploitation of complex habitats or allochthonous structures from the forest (Brejão *et al*., 2018; Zeni *et al*., 2019; Chua *et al*., 2020). For example, deforestation of a stream catchment negatively affects species that exploit the streambed or forest micro-habitats (Brejão *et al*., 2018; Leitão *et al*., 2018). The degradation of riparian zones, followed by the growth of grasses on the banks and reduction of woody debris in streams, increases the occurrence of fish with traits such as the upturned mouth and low body mass (Chua *et al*., 2020), driving the community with similar habits or tactics in the degraded areas (Dias *et al*., 2010; Zeni, Casatti, 2014; Ribeiro *et al*., 2016; Leitão *et al*., 2018).

In the Amazon, the relationship among land uses, local habitat, and community descriptors are not always clear, once the environmental factors do not contribute similarly to this structuring (Leal *et al*., 2016; Leitão *et al*., 2018; Montag *et al*., 2019). Therefore, measuring the relationship between biological and environmental variables is essential to understand the effects of environmental conditions on the structure of fish communities in Amazonian streams surrounded by different types of land uses (Leal *et al*., 2017). In this context, the present study investigated the relationships among land uses and local habitat variables, the composition of functional trophic groups, and the ecomorphological traits of fish in streams with multiple land uses in eastern Amazonia.

We assumed multiple land uses along stream catchments change the local habitat, changing environmental variables related to the structure of the riparian vegetation, canopy cover, fish shelter, and dissolved oxygen (Leal *et al*., 2016; Ferreira *et al*., 2018; Zeni *et al*., 2019). Minor changes in the local habitat structure and integrity may favor some fish functional groups, capable of tolerating a greater variation of environmental conditions. (Zeni, Casatti, 2014; Leal *et al*., 2016; Zeni *et al*., 2019). On the other hand, the local habitat is the major driver in structuring aquatic communities (Southwood, 1977). Therefore, we expect that (1) both land use variables and local habitat variables will influence the composition of fish functional groups, and (2) community structure based on the ecomorphological traits of fish will mainly be associated with local habitat variables and not with land use.

MATERIAL AND METHODS

Study area. We conducted the study in 26 first to third order streams (Strahler classification) at the middle Capim River basin (Fig. 1). The selected streams were distributed along a gradient of anthropogenic impact, from areas with a low percentage of forest (0.29% of the total catchment) to forested areas (92.91% of the total catchment, see Supplementary Material), always seeking to contemplate all the conditions and the existing environmental variability in the studied region. The Capim River basin drains nearly 37,000 km² (Lima, Pontes, 2012), and is classified as a tropical humid drainage basin, with two well-defined seasons: a rainy season, from December to May, and a dry season, from June to November (Alvares *et al*., 2013). The mean annual precipitation is 1,743 mm, relative humidity is 81%, and the mean temperature is 26.3 °C (Francez *et al*., 2009).

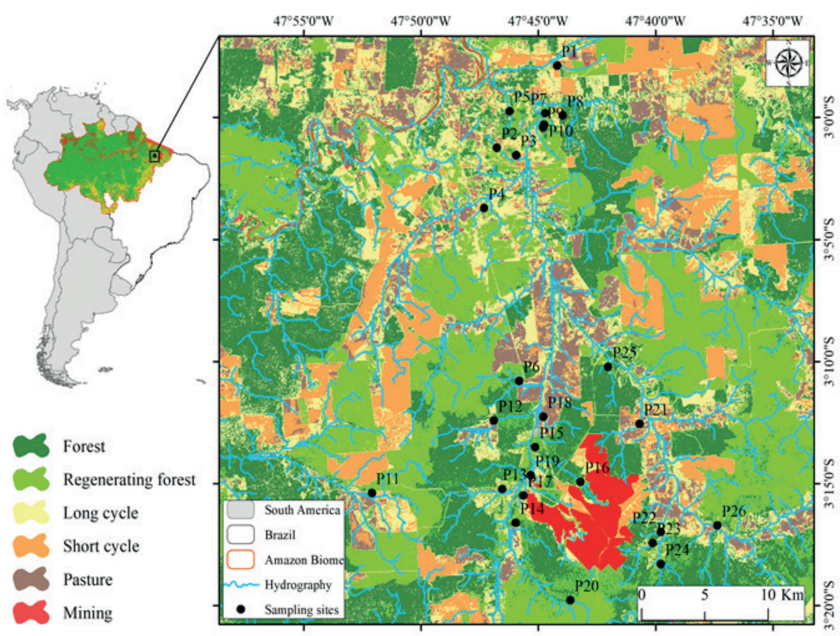

FIGURE 1 | Location of sampling streams (Middle Capim River basin, Pará State, Brazil). The characteristics of each land use class are described in the Material and Methods section.

The region of Paragominas is covered by tropical rainforests (Almeida *et al*., 2009). However, it has undergone an extensive land conversion from forest to farmland in the last 40 years (Loureiro, 2012), and much of the area has been converted to cattle ranching, mechanized farms, and areas of silviculture (*Eucalyptus* sp. and *Tectona grandis* L. f.) (IBGE, 2017). Besides these activities, the extraction of bauxite ore and logging is also relevant economic activity in the region (IBGE, 2017).

Land use characteristics. For the evaluation of land use, we first calculated the catchment area upstream from each site. Then, the catchment and hydrography were delimited using the topographic data present in the Shuttle Radar Topography Mission (SRTM) with TauDem 5.3 (Tarboton, 2005; QGIS Development Team, 2017).

We calculated land use for each catchment area through the supervised classification of Landsat 8 images, using the Semi-Automatic Classification plugin in QGis 2.18 (Macedo *et al*., 2014; Congedo, 2016). Images from 2014 to 2017 were obtained from the United States Geological Survey's (USGS) Earth Explorer project. These images provide information on the shape and texture of landscape elements, identifying different land use types within the stream catchments (Macedo *et al*., 2014). In addition, the image sets were submitted to atmospheric correction to reduce reflectance effects (Antunes *et al*., 2012).

We classified the images into six classes that represent the most common land use types in the studied region: (i) Forest: mature forest or forest at an advanced state of regeneration; (ii) Regeneration: forest in regeneration; (iii) Long-cycle agriculture: plantations of *Eucalyptus* sp. and *Tectona grandis* L. F.; (iv) Short-cycle agriculture: grain production; (v) Pasture, and (vi) Mining: areas including mining pits, industrial areas, tailing ponds, and spoil tips (Almeida *et al*., 2016). To avoid errors, after the use of semi-automatic classification, each category was validated using high-resolution Google Earth images (Macedo *et al*., 2014). Finally, we calculated the proportion of the land use types (in square meters) at each catchment area.

Local habitat assessment. The local habitat variables were measured in the 26 study streams in 2014 and 2017, invariably in the dry season. We apply the habitat assessment protocol developed by the United States Environmental Protection Agency (Kaufmann *et al*., 1999; Peck *et al*., 2006), adapted for the tropical region by Callisto *et al.* (2014). At each sampled stream, we delimited a stretch of 150 m, which was subdivided into ten equidistant longitudinal sections and 11 cross-sections (Peck *et al*., 2006).

We selected the variables used in the present study based on previous research in the Amazon basin (Bojsen, Barriga, 2002; Dias *et al*., 2010; Leal *et al*., 2017; Prudente *et al*., 2017; Ferreira *et al*., 2018; Montag *et al*., 2019). These variables were: dissolved oxygen concentration (mg/L), the density of canopy cover in the channel (%), impact index in the riparian zone, thalweg depth (cm), and cover of fish shelters (%). Dissolved oxygen concentration was measured on three equidistant transects using a multiparameter probe (Horiba U-50). At optimum concentrations, dissolved oxygen supports high species richness and abundance of individuals, whereas, under hypoxic conditions, only certain species with appropriate adaptations can tolerate and survive in these conditions (Dias *et al*., 2010; Prudente *et al*., 2017). The density of forest cover on the stream channel was measured with a densitometer, positioned upstream, downstream, center to the right, and center to the left, allowing for the analysis of the input of sunlight and organic matter, such as leaves and branches, into the stream (Bojsen, Barriga, 2002; Prudente *et al*., 2017). We compiled the Impact index in the riparian zone in each cross-section based on the presence and proximity of the site to human disturbance. It was visually assessed in both stream banks, quantifying the occurrence (presence or absence) of the different land use types or human disturbance (plantation, pasture, logging operations, mining activity, walls/dykes/canals/dams, buildings, pavement or cleared lot, roads/railroads, water or drainage pipes, landfill/trash, and parks/lawns). The observations were assigned to one of three classes of proximity: within the stream or on the banks, within the riparian plot, outside the riparian plot, as well as the fourth class of 0, when no disturbance was observed (Juen *et al*., 2016; Ferreira *et al*., 2018). The characterization of depth along the thalweg (the deepest portion of the channel) of each stream included 150 m longitudinal equidistant measures (Peck *et al*., 2006). The cover of fish shelters was estimated visually in a 5 m stretch downstream and upstream of each cross-section, resulting from the sum of the visual analysis for the presence of large woody debris, small woody debris, roots and trees, coarse litter, overhanging vegetation, undercut banks, and macrophytes or marginal grasses (Peck *et al*., 2006).

Fish sampling. The sampling of the ichthyofauna occurred at the same time as the sampling of the habitat variables took place (the dry season of 2014 and 2017). We used circular sieve nets to catch fishes (55 cm in diameter with a 3 mm metallic mesh), and a total sampling effort of six hours/collector was equally divided among the longitudinal sections (Prudente *et al*., 2017). The fish were euthanized with the anesthetic Eugenol, fixed in 10% formalin, and after 48 h, they were transferred to 70% alcohol. We identified the specimens using taxonomic keys (*e.g*., Géry, 1977; Kullander, 1986; Britski *et al*., 2007) and, whenever necessary, by consulting specialists in neotropical fish systematics. We deposited the material collected during this study in the ichthyology collection of the Museu de Zoologia da Universidade Federal do Pará, Belém, Pará State, Brazil.

The composition of Functional Trophic Group (FTG). The characterization of functional trophic groups (FTG) of fish was performed based on Brejão *et al*. (2013) for fish from Amazonian streams, which sorted the species into 18 FTGs, according to two main characteristics: (1) its most frequently observed feeding tactic; and (2) its spatial distribution in the stream environment, considering their horizontal (streambanks or main channel) and vertical (water column) dimensions. The study also considered the terms "where", "how" and "when" different species feed, framed into 15 pre-defined feeding tactics, to form the following FTGs: Surface pickers, drift feeders, roving predators, stalking predators, ambush predators, mud-eaters, diggers, browsers, grubbers, nibblers, sit-and-wait predators, crepuscular to nocturnal predators, grazers, parasites, and invertebrate pickers. Based on this, the authors identified and sorted the fish communities into functional trophic groups, which were: Diurnal channel drift feeders, diurnal backwater drift feeders, diurnal surface pickers, surface strikers, ambush and stalking predators, pursuit predators, mud-eaters, nibblers, browsers, sit-and-wait predators, grazers, grubbers, diggers, pickers and browsers, nocturnal invertebrate pickers, crepuscular to nocturnal drift feeders, crepuscular to nocturnal bottom predators, and parasites (Brejão *et al*., 2013).

Ecomorphological traits. We measured the morphological traits of five adult specimens with similar sizes representing each identified species. When fewer than five specimens were available for a given species, we measured all the specimens captured. When the species presented sexual dimorphism, only females were measured, as they have smaller size variations throughout the reproductive cycle when compared to males (Winemiller, 1992; Novakowski *et al*., 2004). The traits were measured following the protocols of Winemiller (1991) and Soares *et al*. (2013). We obtained all the morphological measurements on the left side of the individual, based on a straight line between points, using a digital caliper with a precision of 0.1 mm. The area of the fins was measured by drawing the contour of the structures on graph paper after they had been fixed and distended (Casatti, Castro, 2006). These drawings were scanned and measured in the ImageJ software (Schneider *et al*., 2012).

These measurements were later converted into five ecomorphological traits (Tab. 1): (i) the relative caudal peduncle length (RCPL), (ii) relative area of the pectoral fin (RAPF), (iii) relative height (RH), (iv) relative head length (RHL) and (v) relative mouth width (RMW). These traits provide useful insights into the relationship of the species with the environment, given that the understanding of its ecomorphology is vital for the interpretation of its capacity to survive the pressures imposed by different environments on the species in terms of its ability to feed, reproduce, and seek shelter (Winemiller, 1992; Casatti, Castro, 2006).

Data analysis. To guarantee spatial independence among the samples, we performed a Principal Coordinates of Neighbor Matrices (PCNM) analysis using the fluvial distance between each pair of streams. We used forward selection to identify the PCNM axes with the highest degree of association with the fish assemblages. The selected axes were used in the subsequent analyses to control the effects of space on the structure of fish communities (Dray *et al*., 2006).

The proportion of land use in the stream catchment was ordinate in a Principal Components Analysis (PCA), to describe the gradient of land use. The data was previously log-transformed to reduce the presence of outliers. We used the Broken-Stick criterion to select the axes (Legendre, Legendre, 2012). This method selects the axes with observed eigenvalues higher than values estimated randomly (Jackson, 1993).

TABLE 1 | Ecomorphological traits and their ecological implications related to body size, vertical (water column) and lateral (marginal and central) habitat, and resource use.

Ecomorphological traits	Ecological implications
Relative caudal peduncle length (RCPL)	Relatively long peduncles indicate fishes with good swimming abilities inhabiting turbulent waters (Gatz, 1979b; Watson, Balon, 1984).
Relative area of the pectoral fin (RAPF)	High values indicate slow swimmers that use pectoral fins to perform maneuvers and breakings or fish inhabiting fast waters, which use their pectoral fins as airfoils to deflect the water current upward and thereby maintain themselves firmly attached to the substrate (Mahon, 1984; Watson, Balon, 1984).
Relative height (RH)	Low values indicate fish that inhabit fast waters (Gatz, 1979).
Relative head length (RHL)	Directly related to prey size, high values of RHL suggests species that are able to feed on relatively large prey (Gatz, 1979b).
Relative width of the mouth (RWM)	High values indicate fishes that feed on larger prey (Winemiller, 1991).

The axis retained in the selection criterion of this analysis was used as a predictive variable, representing land use in the following analyses to test the relationship between the community descriptors and environmental variables.

We evaluated ecomorphological traits using the community-weighted mean index (CWM), based on the traits of each fish species weighted by their abundance (Lavorel *et al*., 2008). To calculate the CWM index, we compiled two matrices, one of species abundance and the other with the ecomorphological traits. The CWM is the mean value of the ecomorphological traits weighted by the relative abundance of each characteristic within the studied community (Violle *et al*., 2007). Composition data based on fish abundance were prepared for these analyzes using the Hellinger transformation (Legendre, Legendre, 2012).

To assess the relationships between land use and local habitat variables, and the functional trophic composition and ecomorphological traits, we performed two Redundancy Analysis (RDA), validated by Analysis of Variance (ANOVA). We performed one using the composition of fish FTG, and other using ecomorphological traits, weighted by species abundance in the CWM (Borcard, Legendre, 2002). In this analysis, we used the local habitat variables and land use, represented by the first axis of the Principal Components Analysis (PCA1). We chose this axis as a predictive variable, aiming to maintain the smallest number of variables as possible in the Redundancy Analysis (RDA) model (Legendre, Legendre, 2012).

The composition of FTG fish data was prepared for these analyses using the Hellinger transformation (Legendre, Legendre, 2012). We controlled the spatial effect using the PCNM axes in all the redundancy analyses. We ran all the analyses in the R software, version 3.4.1, using the 'vegan' and 'packfor' packages (R Development Core Team, 2015; Oksanen *et al*., 2018).

RESULTS

Land use and local habitat. The land use of the studied catchments showed a high proportion of forest (42.2 ± 30.2%, on average) and forest in regeneration (23.5 ± 21.2%) cover. Other land uses were long-cycle silviculture, covering nearly a fifth of the area (14.9 ± 13.1%), short-cycle croplands (7.4 ± 10.4%), mining (6.3 ± 12.3%) and pasture (5.3 ± 8.6%) (Tab. **S1**). Summarizing the land use gradient in a PCA retained only the first axis (PCA1), which explained 41.3% of the stream catchment's land use variation. All land use types associated with human activities (short and long cycle agriculture, pasture and mining) were grouped on the negative side of the PCA1. In contrast, the forested cover was grouped on the opposite side. (Fig. 2; Tab. **S1**).

Focusing on the local habitat variables, the proportion of the cover of fish shelters had an average of 90.3% (± 32.3%), the mean of the thalweg depth was 34.2 cm (± 16.4), the density of canopy cover in the channel was 33.8% (± 19.5%), dissolved oxygen concentration was 6.02 mg/l-1 (± 1.97), and impact index in the riparian zone had an average of 0.53 (± 0.44) (Tab. 2). In general, sites with greater forest cover (forest or in regeneration) have higher values of density of canopy in the channel, higher value oxygen concentration, high thalweg depth, a high cover of fish shelters, and low values of impact index in the riparian zone.

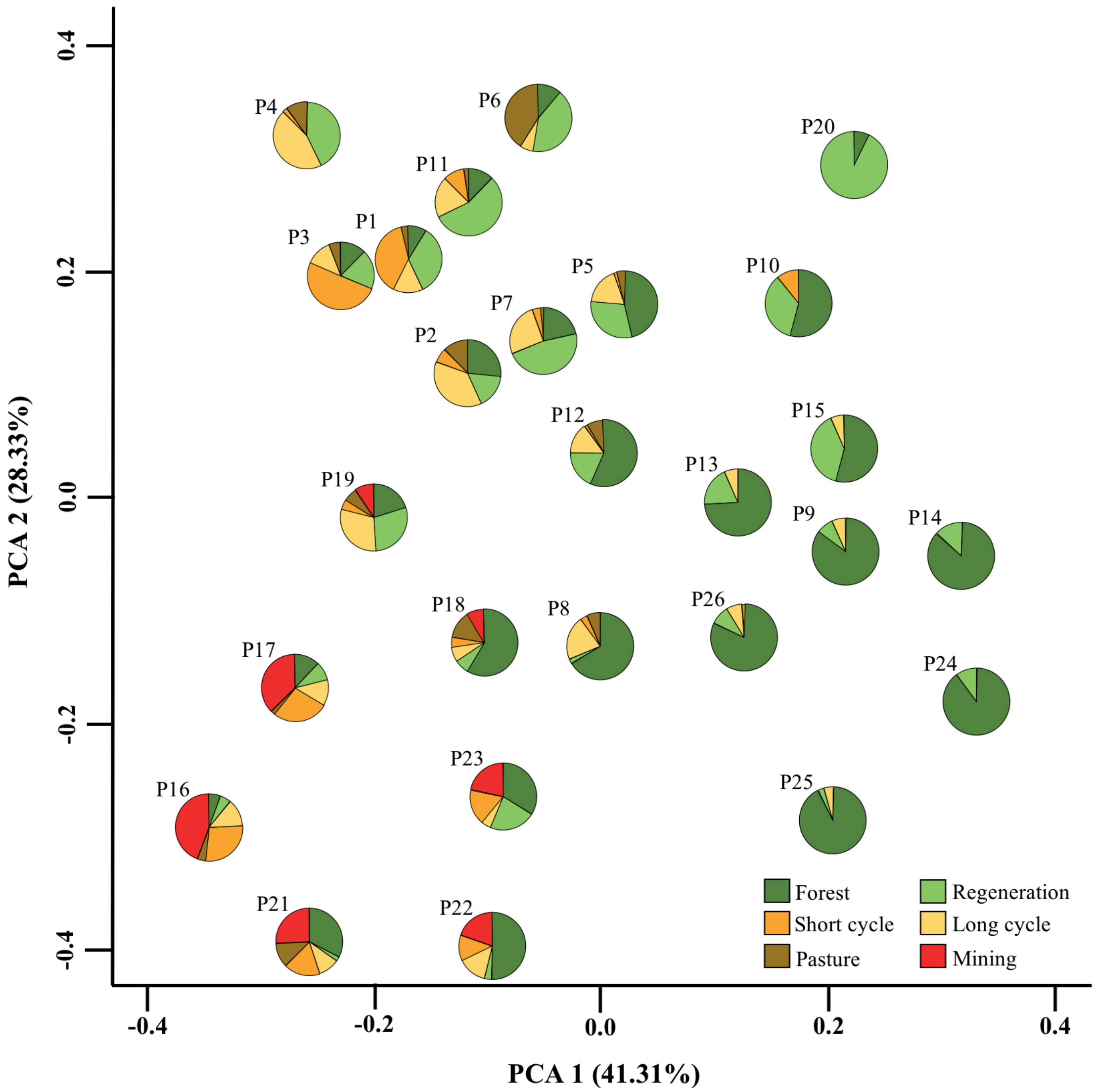

FIGURE 2 | Ordination of the types of land use in the catchment areas of the study streams at the Capim River basin, eastern Amazon.

TABLE 2 | Local habitat variables of streams sampled in this study (Capim River basin, Eastern Amazon, Brazil). The table columns represent: Label = habitat variable code; Max = Maximum value; Min = Minimum value; Mean = mean value; SD = standard deviation.

Local habitat variables	Label	Max	Min	Mean	SD
Cover of fish shelters (%)	Cover of fish shelters	157.73	34.55	90.25	32.34
Thalweg depth (cm)	Thalweg depth	69.96	13.90	34.16	16.40
Density of canopy cover in the channel (%)	Canopy density	65.34	6.82	33.76	19.51
Dissolved oxygen concentration (mg L^{-1})	Dissolved oxygen	9.12	2.87	6.02	1.97
Impact index in riparian zone	Impact in riparian zone	1.43	0.00	0.53	0.44

Fish assemblages and the influence of land use and local habitat variables. We collected 9,325 fish specimens belonging to 69 species, 20 families and six orders. There was a predominance of the Characiformes order, with 81.3% of the total number of individuals, followed by Cichliformes (8.2% of the total) and Gymnotiformes (4.4%). The most abundant characiform species were *Hyphessobrycon heterorhabdus* (Ulrey, 1894), with 3,188 individuals (33.2% of the total), and *Copella arnoldi* (Regan, 1912), with 1,279 individuals (13.6%). The most common cichliforms were *Apistogramma* gr. *regani* Kullander, 1980 (2.5% of the individuals) and *Apistogramma agassizii* (Steindachner, 1875) (2.4%), while the most numerous gymnotiforms were *Brachyhypopomus* sp. (1.1%) and *Brachyhypopomus brevirostris* (Steindachner, 1868), with 0.8% of the individuals (Tab. **S2**).

A total of 13 FTG's were registered. The group with the largest number of species were nocturnal invertebrate pickers, represented by 15 species, followed by diurnal backwater drift feeders with 10 species, diurnal channel drift feeders with 6 species, and diurnal surface pickers and crepuscular to nocturnal bottom predators, with 6 species each. The abundance of diurnal backwater drift feeders and diurnal surface pickers were the most representative, with 55.8% and 20.4%, respectively (Tab. **S3**).

The composition of the FTG's was affected by local habitat and land use variables ($F = 1.76$; $df = 6$; $p = 0.024$). The first axis, which explained 15% of the variance, was negatively associated with high canopy density and positively associated with high thalweg depth and high concentrations of dissolved oxygen. The second axis, which explained 14% of the variance, was positively affected by the cover of fish shelters and negatively affected by land use (Fig. 3; variables loadings >3). Diurnal channel drift feeders (FTG 3) were positively associated with high concentrations of dissolved oxygen and deeper thalweg, while diurnal backwater drift feeders (FTG 4) were positively associated with high cover of fish shelters and negatively associated with land use. On the other hand, diurnal surface pickers (FTG 7) and diggers (FTG 9) were negatively associated with thalweg depth and dissolved oxygen, while ambush and stalking predators (FTG 11) were positively associated with high canopy density (Fig. 3).

Functional structure based on ecomorphological traits of the fish community was affected more strongly by habitat variables than by land use ($F = 1.84$; $df = 6$; $p = 0.042$). The first axis, which explained 20% of the variance, was positively associated with deeper thalweg and high concentrations of dissolved oxygen, and negatively associated with high canopy density. The second axis, which explained 17% of the variance, was negatively associated with the cover of fish shelters and impact in riparian zone (Fig. 4). The trait relative caudal peduncle length (RCPL) was positively associated with high canopy density. While relative mouth width (RMW) was negatively associated with impact in riparian zone and cover of fish shelters. Furthermore, relative height (RH) and relative area of pectoral fin (RAPF) were positively associated with thalweg depth and dissolved oxygen concentrations (Fig. 4).

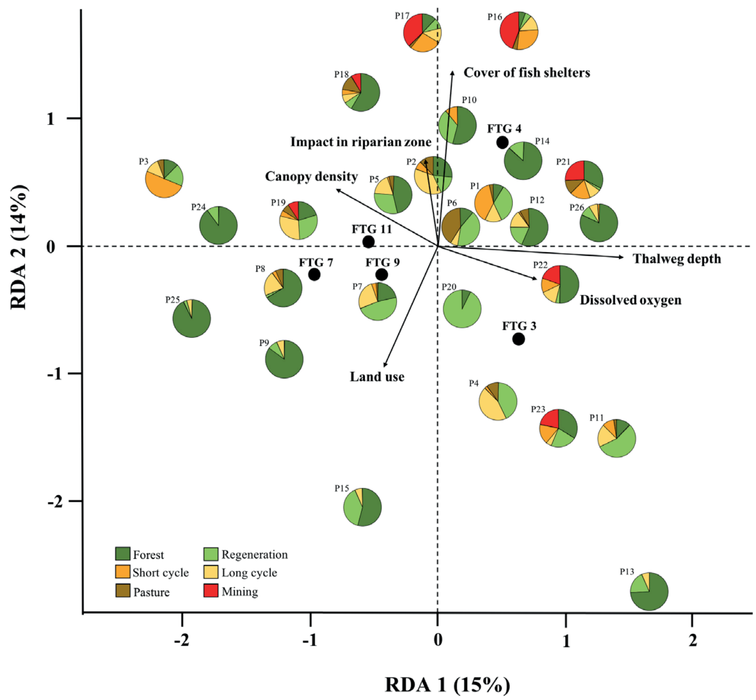

FIGURE 3 | Relationships between fish functional trophic groups and environmental variables (land use and local habitat) in the streams evaluated in this study. The groups are represented by the labels: Diurnal channel drift feeders (FTG 3), Diurnal backwater drift feeders (FTG 4), Diurnal surface pickers (FTG 7), Diggers (FTG 9) and Ambush and stalking predators (FTG 11). The FTG's with a correlation between 0.2 and -0.2 have been omitted for better visualization of the results.

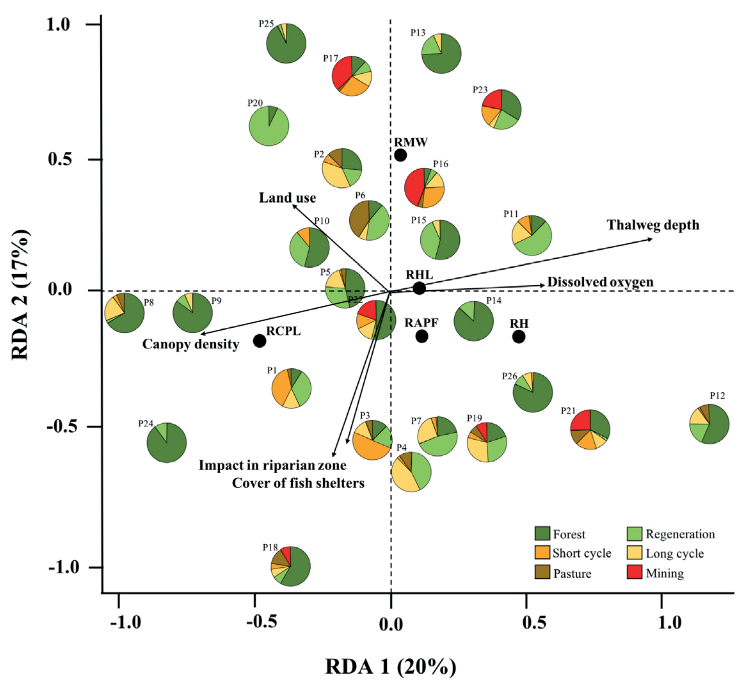

FIGURE 4 | Relationships between the ecomorphological traits of fish species and environmental variables (land use and local habitat) in the streams evaluated in this study. Traits are represented by labels: relative head length (RHL), relative mouth width (RMW), relative height (RH), relative area of pectoral fin (RAPF) and relative caudal peduncle length (RCPL).

DISCUSSION

The results of this study demonstrate that fish functional diversity was influenced by land uses and local habitat variables. Although, the functional trophic group (FTG) was more responsive to both.

In these terms, diurnal surface pickers (FTG 7) and diggers (FTG 9) were negatively associated with thalweg depth and dissolved oxygen. These variables were also positively associated with diurnal channel drift feeders (FTG 3). On the other hand, diurnal backwater drift feeders (FTG 4) were positively associated with high cover of fish shelters, while ambush and stalking predators were positively associated with high canopy density. Considering the ecomorphological traits, the local habitat was more important than land uses variables in the structuring of communities. High canopy density, shelter covering, and impact in riparian zone were associated with higher values of relative caudal peduncle length (RCPL).

Furthermore, stream catchments comprise different types of land uses. Some stream catchments have only two types of land uses, but other locations can have five types. Agricultural activities had high negative loadings on the first PCA axis, for both short-cycle and long-cycle agriculture, followed by pasture and mining. The positive side of the PCA axis was composed of forest and regenerating forest.

Agricultural activities, mining of bauxite and pasture have enormous potential to drastically reduce the natural forest within stream catchments (Mol, Ouboter, 2004; Sonter *et al*., 2017). This exposes the remaining vegetation to adverse conditions because of the additional number of clearings and access roads, which also decrease canopy cover and the remaining riparian vegetation and increase the Impact index in the riparian zone (Sonter *et al*., 2017; Apriadi *et al*., 2018). Changes in the structure of the riparian zone, canopy cover, channel morphology, and water quality affect the structure of fish communities by increasing the abundance of fish species that are more common in the streams located near areas under human disturbance, as observed at Amazonian streams (Dias *et al*., 2010; Leal *et al*., 2017).

This study shows that the high abundance of diurnal channel drift feeders (*Bryconops* sp., *Iguanodectes rachovii* Regan, 1912, *Melanorivulus* sp., *Moenkhausia collettii* (Steindachner, 1882), *M. comma* Eigenmann, 1908, and *M. oligolepis* (Günther, 1864)) was associated with high concentrations of dissolved oxygen and increased thalweg depth. The species in these groups collect food drifting on the water surface of the main channel, in streams with shifting flow conditions, or in high-current areas (Brejão *et al*., 2013). In comparison, the high cover of fish shelters was associated with a high abundance of diurnal backwater drift feeders (*Crenuchus spilurus* Günther, 1863, *Hemigrammus bellottii* (Steindachner, 1882), *H. levis* Durbin, 1908, *H. ocellifer* (Steindachner, 1882), *H. rodwayi* Durbin, 1909, and *Hyphessobrycon heterorhabdus*). The species representing this group feed on allochthonous items that drift in backwaters close to the streambanks, *e.g.*, small invertebrates. These preys are commonly associated with shelters, such as trunks and leaves (Paiva *et al*., 2021; Lima *et al*., 2022), showing how important the riparian vegetation is for this group (Zuanon *et al*., 2015).

The high abundance of diurnal surface pickers (FTG 7) and diggers (FTG 9) was negatively associated with thalweg depth and dissolved oxygen. Fish species from the Lebiasinidae family (FTG 7) were associated with catchments that had low proportions of natural forest cover (Montag *et al*., 2019). Due to the low proportion of natural forest cover, those catchments may have increased sediment input, which could decrease the thalweg depth, also reducing water flow or creating ponds, favoring species commonly inhabiting reentries and marginal ponds in anthropogenic conditions and with low oxygen concentrations (Casatti *et al*., 2009; Dias *et al*., 2010). The digger group (FTG 9) is mostly represented by Cichlids (*Apistogramma* spp. and *Satanoperca jurupari* (Heckel, 1840)). Many fishes of this functional group find shelter among leaves, branches, and roots at the banks, and in small reentrances in the banks in rather shallow areas or in-stream impoundments (Brejão *et al*., 2013; Zuanon *et al*., 2015). As the name means, the diggers group (FTG 9) dig in the substrate with their mouths, bite small portions of fine particulate organic matter, and shelter themselves between branches and leaves deposited at the bottom of the stream (Brejão *et al*., 2013). In Amazonian areas impacted by oil palm plantations, there was an increase in the abundance of diggers, especially cichlids, followed by an increase in the percentage of fine substrate and proportion of human impact (Ferreira *et al*., 2018). In addition, some diggers species can populate lateral pools or other lentic environments with low oxygen concentrations (Casatti *et al*., 2009; Zuanon *et al*., 2015). These findings indicate that diggers may be indicators of impacted environmental conditions, given their ability to withstand major variations in the environment, due to their trophic plasticity (Abelha *et al*., 2001; Casatti *et al*., 2009).

A high abundance of ambush and stalking predators (FTG 11) was associated with high canopy density. The representatives of this functional trophic group are *Gymnotus* spp., *Crenicichla* gr. *saxatilis* Linnaeus, 1758, *Crenicichla* sp., *Erythrinus erythrinus* (Bloch & Schneider, 1801), *Hoplerythrinus unitaeniatus* (Spix & Agassiz, 1829), and *Hoplias malabaricus* (Bloch, 1794). These fish species capture prey by ambushing them near the banks or at the bottom of the stream. Their strategy is to hide among leaves, branches, and roots and wait for the moment to attack the prey (Brejão *et al*., 2013). In Amazonian streams, some studies reported similar results, in which they observed that this functional group benefits from more forested environments because the allochthonous material provided by the forest, such as boughs, woods, leaves, and roots are used in foraging activities (Zuanon *et al*., 2015; Montag *et al*., 2019; Zeni *et al*., 2019).

Associations between species ecomorphological traits and local habitat characteristics were important drivers of the fish community structure. The highest values of the relative caudal peduncle length (RCPL) trait were positively associated with high canopy density. The species that had the highest values of this trait were *Hypopygus lepturus* Hoedeman, 1962 and *Steatogenys duidae* (LaMonte, 1929), which use their ability of electron localization to detect prey among leaflets, adjacent vegetation, and root clusters (Brejão *et al*., 2013; Zuanon *et al*., 2015). *Hypopygus lepturus* are predominant in pastures because species with relatively large caudal peduncles are morphologically adapted to inhabit environments with high water flow that are characteristics of these environments dominated by grasses (Cantanhêde *et al*., 2021). However, many species of Hypopomidae are associated with clumps of roots, marginal vegetation, and reeds from the forest, to increase the effectiveness of camouflage. In habitats with these characteristics thus make Hypopomidae are practically immobile, avoiding sight-oriented predators, which means these species benefit from both marginal grassroots and material from canopy forests (Zuanon *et al*., 2015).

We observed that the high impact rate in the riparian zone caused the opening of clearings in some stretches of streams. Even so, large trees (high canopy) still provide allochthonous material from the forest to the stream beds. Therefore, these clearings contribute to the entry of grasses, macrophytes (Fares *et al*., 2020), and fine roots on the streambanks (Casatti *et al*., 2009), adding to the allochthonous forest material and favoring fish species that swim through undulations in the posterior part of slow-flowing water. Fish species that swim slower and are more maneuverable, tend to occupy and move through complex structures, such as branches, roots and macrophytes. Furthermore, this environmental complexity provides shelter from predators and food resources for different organisms (Ribeiro *et al*., 2016; Zeni *et al*., 2019; Nonato *et al*., 2021).

Fish with a relatively long head (high RHL) were associated with high thalweg depth and high dissolved oxygen concentrations, such as *Satanoperca jurupari*, *Aequidens tetramerus* (Heckel, 1840), and *Trachelyopterus galeatus* (Linnaeus, 1766). These variables are also related to fish with a relatively wide mouth (RMW). The species that have these traits are: *Denticetopsis epa* Vari, Ferraris & de Pinna, 2005, *Helogenes marmoratus* Günther, 1863, *Mastiglanis asopos* Bockmann, 1994, *Gladioglanis conquistador* Lundberg, Bornbusch & Mago-Leccia, 1991. Some species swim actively at the main channel or explore the backwaters or areas close to the surface, others capture large food items that fall in the water and are drifted by the current (Brejão *et al*., 2013). Thus, oxygen can better benefit species that explore backwaters, close to stream surfaces or in areas of high current, capturing food items that fall and are dragged by the water (Brejão *et al*., 2013; Ribeiro *et al*., 2016). In addition, high thalweg depth may benefit species such as *Mastiglanis asopos* and *Gladioglanis conquistador*, who remain stationary at the bottom of the channel, waiting for food swept away by the current. When prey or particle touch their barbels or fin rays, they quickly attack in the direction of the prey or explore the environment with their barbels in search of prey (Zuanon *et al*., 2015). This suggests that rapids and concentration of oxygen in the water can be regulated by the conservation of the riparian zone in the streams that supplies allochthonous materials and retains the entry of sediments, causing the burial of substrates and consequent reduction of water flow and oxygen (Casatti *et al*., 2009). In addition, changes in the stream substrate can lead to losses of species with specialized habit such as benthic species that forage in diversified substrates and to increases in the predominance of surface water fishes (Casatti *et al*., 2015; Allard *et al*., 2016; Apriadi *et al*., 2018).

Species with high value relative to body height (RH) such as *Hemigrammus* spp., *Carnegiella strigata* (Günther, 1864), *Moenkhausia comma*, and fish with a relatively large pectoral fin (RAPF) such as *Rineloricaria* sp., and *Rhamdia muelleri* (Günther, 1864), were generally related positively with high thalweg depth and high dissolved oxygen concentrations. However, they were also negatively related to canopy density. These species explore the water surface, swim close to the banks, or explore complex environments with their barbels in search of prey, mainly larger benthic macroinvertebrates and small fish. One example of species with such habit is *Rhamdia muelleri*, that searches for preys with their barbels (Brejão *et al*., 2013). Environments with allochthonous material originating from the forest are more complex and provide micro-habitats for these species to forage, as well as for the species inhabiting the water column, and perhaps this is the reason behind this opposite relationship to land use (Casatti *et al*., 2015; Ribeiro *et al*., 2016).

Our results indicate that local habitat variables have a greater influence on the structure of fish communities than land uses. Furthermore, they reinforced the importance of local variables closely related to the marginal vegetation and the environmental integrity and structure of the ravine. Therefore, ensuring that local conditions are kept stable even in a modified matrix is a major challenge for fish conservation. One of the ways to achieve this goal will be through complying with the permanent protection area that must be established around all streams as stated in the Brazilian legislation (Dala-Corte *et al*., 2020; Leal *et al*., 2020). This effect has been observed in previous studies that assessed the influence of multiple land use on stream fish and found that the local habitat is the main predictor of the distribution of Neotropical fish species (Leal *et al*., 2017; Roa-Fuentes, Casatti, 2017; Montag *et al*., 2019). This may be associated with the paths that environmental change takes to affect the fish community structure (Leitão *et al*., 2018). In addition, aquatic communities present distinct responses to the thresholds of forest cover loss or do not respond similarly in areas highly impacted by human activities (Leitão *et al*., 2018; Arantes *et al*., 2019; Dala-Corte *et al*., 2020).

For some fish species, the effects of land use on the community structure may only become apparent when more than 40% of the forest cover has been lost (Brejão *et al*., 2018). In the present study, while the streams surveyed were located within areas with different land use types, a relatively high percentage of forest cover was still present in the stream catchment areas (Leal *et al*., 2016). The presence of riparian buffer zones at many sites may attenuate the impacts of land-use change on the local biota (Pusey, Arthington, 2003; Leal *et al*., 2016; Paiva *et al*., 2017; Arantes *et al*., 2019) because these effects might still be dependent on the scale or operate at different scales (Allan *et al*., 1997; Allan, 2004; Leal *et al*., 2016). We emphasize the importance of conducting assessments on multiple spatial scales to uncover the impacts of multiple land use on the structure of the aquatic biodiversity of Amazonian streams. The continuous assessment and monitoring of streams are paramount for evaluating and mitigating the effects of land use change on fish communities. In addition, conserving the still forested areas in the watershed is essential for the maintenance of the natural characteristics of the streams. Finally, recovering areas degraded by mining, cattle ranching, and farming will also be important for the maintenance of favorable environmental conditions for the conservation of fish diversity in the region.

ACKNOWLEDGMENTS

We thank the Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq for granting a masters scholarship to CM (process: 132128/2017-9), a post-doctoral scholarship to TOB (process: 154748/2018-8), research productivity scholarships to LJ (process 304710/2019-9), and LFAM (process 302406/2019-0), and a senior internship scholarship to LFAM for research at Texas A&M University (process 88881.119097/2016-1). We are also grateful to the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for granting CM a doctoral scholarship (process: 88882.445579/2019-01), and PROCAD-AMAZONIA/CAPES, for funding the senior internship scholarship for LJ for research at the University of Florida (process 88881.474457/2020-01). Financial support was provided by Norsk Hydro through the Brazil-Norway Biodiversity Research Consortium (BRC). We also thank CIKEL for logistic support during field sampling, and PROPESP/UFPA for supporting the translation of the manuscript. We thank A. L. Andrade, A. L. Fares, B. S. Prudente, C. Kaory, L. Calvão, T. S. Michelan, and T. A. P. Barbosa for collaborating during the field work, and M. B. Mendonça for support in fish species identification. This article is the BRC0045 in the publication series of the Biodiversity Research Consortium Brazil-Norway (BRC).

REFERENCES

- **Abelha MCF, Agostinho AA, Goulart E.** Plasticidade trófica em peixes de água doce. Acta Sci Biol Sci. 2001; 23:425–34. https://doi.org/10.4025/actascibiolsci.v23i0.2696
- **Allan JD.** Landscapes and riverscapes: The influence of land use on stream ecosystems. Annu Rev Ecol Evol Syst. 2004; 35:257–84. https://doi.org/10.1146/annurev.ecolsys.35.120202.110122
- **Allan JD, Erickson DL, Fay J.** The influence of catchment land use on stream integrity across multiple spatial scales. Freshw Biol. 1997; 37(1):149–61. https://doi.org/10.1046/j.1365-2427.1997.d01-546.x
- **Almeida CA, Coutinho AC, Esquerdo JCDM, Adami M, Venturieri A, Diniz CG *et al*.** High spatial resolution land use and land cover mapping of the Brazilian Legal Amazon in 2008 using Landsat-5/TM and MODIS data. Acta Amazon. 2016; 46(2):291–302. https://doi.org/10.1590/1809-4392201505504
- **Almeida SS, Silva ASL, Silva ICB.** Cobertura vegetal. In: Monteiro MA, Coelho MCN, Barbosa EJS, editors. Atlas socioambiental: Municípios de Tomé-Açu, Aurora do Pará, Ipixuna do Pará, Paragominas e Ulianópolis. Belém: NAEA; 2009. p.112–24.
- **Alvares CA, Stape JL, Sentelhas PC, Gonçalves JLM, Sparovek G.** Köppen's climate classification map for Brazil. Meteorologische Zeitschrift. 2013; 22(6):711–28. https://doi.org/10.1127/0941-2948/2013/0507
- **Allard L, Popée M, Vigouroux R, Brosse S.** Effect of reduced impact logging and small-scale mining disturbances on Neotropical stream fish assemblages. Aquat Sci. 2016; 78:315–25. http://dx.doi.org/10.1007/s00027-015-0433-4
- **Antunes MAH, Debiasi P, Costa AR, Gleriani JM.** Correção atmosférica de imagens Alos/Avnir-2 utilizando o modelo 6S. Rev Bras Cart. 2012; 64(4):531–39. Available from: https://seer.ufu.br/index.php/revistabrasileiracartografia/article/view/44818/23829
- **Apriadi T, Pratama G, Putra RD, Jaya YV.** Comparative study on the fish diversity from natural and bauxite post- mining in wetland system of Bintan Island, Indonesia. Biodiversitas. 2018; 19(3):967–73. https://doi.org/10.13057/biodiv/d190327
- **Arantes CC, Winemiller KO, Asher A, Castello L, Hess LL, Petrere M *et al*.** Floodplain land cover affects biomass distribution of fish functional diversity in the Amazon River. Sci Rep. 2019; 9(16684). https://doi.org/10.1038/s41598-019-52243-0
- **Benone NL, Esposito MC, Juen L, Pompeu PS, Montag LFA.** Regional controls on physical habitat structure of Amazon streams. River Res Appl. 2017; 33(5):766–76. http://dx.doi.org/10.1002/rra.3137
- **Benone NL, Soares BE, Lobato CMC, Seabra LB, Bauman D, Montag LFA.** How modified landscapes filter rare species and modulate the regional pool of ecological traits? Hydrobiologia. 2020; 849:4499–514. https://doi.org/10.1007/s10750-020-04405-9
- **Bojsen BH, Barriga R.** Effects of deflorestation on fish community structure in Ecuadorian Amazon streams. Freshw Biol. 2002; 47(11):2246–60. http://dx.doi.org/10.1046/j.1365-2427.2002.00956.x
- **Borcard D, Legendre P.** All scale spatial analysis of ecological data by means of principal coordinates of neighbor matrices. Ecol Modell. 2002; 153(1–2):51–68. https://doi.org/10.1016/S0304-3800(01)00501-4
- **Brejão GL, Gerhard P, Zuanon J.** Functional trophic composition of the ichthyofauna of forest streams in eastern Brazilian Amazon. Neotrop Ichthyol. 2013; 11(2):361–73. https://doi.org/10.1590/S1679-62252013005000006

- **Brejão GL, Hoeinghaus DJ, Pérez-Mayorga MA, Ferraz SFB, Casatti L.** Threshold responses of Amazonian stream fishes to timing and extent of deforestation. Conserv Biol. 2018; 32(4):860–71. https://doi.org/10.1111/cobi.13061
- **Britski HA, Silimon KZ, Silimon S, Lopes BS.** Peixes do Pantanal: Manual de identificação. Brasília: EMBRAPA-SPI; 2007.
- **Brosse S, Grenouillet G, Gevrey M, Khazraie K, Tudesque L.** Small-scale gold mining erodes fish assemblage structure in small neotropical streams. Biodivers Conserv. 2011; 20:1013–26. http://dx.doi.org/10.1007/s10531-011-0011-6
- **Cantanhêde LG, Luiza-Andrade A, Leão H, Montag LFA.** How does conversion from forest to pasture affect the taxonomic and functional structure of the fish assemblages in Amazonian streams? Ecol Freshw Fish. 2021; 30(3):334–46. https://doi.org/10.1111/eff.12589
- **Callisto M, Alves CBM, Lopes JM, Castro MA.** Condições ecológicas em bacias hidrográficas de empreendimentos hidrelétricos. Belo Horizonte: CEMIG; 2014.
- **Carvalho FG, Roque FO, Barbosa L, Montag LFA, Juen L.** Oil palm plantation is not a suitable environment for most forest specialist species of Odonata in Amazonia. Anim Conserv. 2018; 21(6):526–33. https://doi.org/10.1111/acv.12427
- **Casatti L, Castro RMC.** Testing the ecomorphological hypothesis in a headwater riffles fish assemblage of the Rio São Francisco, southeastern Brazil. Neotrop Ichthyol. 2006; 4(2):203–14. https://doi.org/10.1590/S1679-62252006000200006
- **Casatti L, Ferreira CP, Carvalho FR.** Grass-dominated stream sites exhibit low fish species diversity and dominance by guppies: An assessment of two tropical pasture river basins. Hydrobiologia. 2009; 632:273–83. http://dx.doi.org/10.1007/s10750-009-9849-y
- **Casatti L, Teresa FB, Zeni JO, Ribeiro MD, Brejão GL, Ceneviva-Bastos M.** More of the same: High functional redundancy in stream fish assemblages from Tropical Agroecosystems. Environ Manag. 2015; 55:1300–14. http://dx.doi.org/10.1007/s00267-015-0461-9
- **Colares LF, Lobato CMC, Montag LFA, Dunk B.** Extinction of rare fish predicts an abrupt loss of ecological function in the future of Amazonian streams. Freshw Biol. 2022; 67(2):263–74. https://doi.org/10.1111/fwb.13839
- **Congedo L.** Semi-automatic classification plugin documentation. 2016. http://dx.doi.org/10.13140/RG.2.2.29474.02242/1
- **Dala-Corte RB, Melo AS, Siqueira T, Bini LM, Martins RT, Cunico AM *et al*.** Thresholds of freshwater biodiversity in response to riparian vegetation loss in the Neotropical region. J Appl Ecol. 2020. 57(7):1391–402. https://doi.org/10.1111/1365-2664.13657
- **Dias MS, Magnusson WE, Zuanon J.** Effects of reduced-impact logging on fish assemblages in Central Amazonia. Conserv Biol. 2010; 24(1):278–86. http://dx.doi.org/10.1111/j.1523-1739.2009.01299.x
- **Dray S, Legendre P, Peres-Neto PR.** Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecol Modell. 2006; 196(3–4):483–93. https://doi.org/10.1016/j.ecolmodel.2006.02.015
- **Chua KWJ, Lim FKS, Ahmad AB, Tan HH, Yeo DCJ.** Morphological traits mediate fish occurrences in oil palm-impacted tropical streams. Freshw Biol. 2020; 65(6):1153–64. https://doi.org/10.1111/fwb.13500
- **Fares ALB, Calvão LB, Torres NR, Gurgel ESC, Michelan TS.** Environmental factors affect macrophyte diversity on Amazonian aquatic ecosystems inserted in an anthropogenic landscape. Ecol Indic. 2020; 113:106231. https://doi.org/10.1016/j.ecolind.2020.106231
- **Ferreira MC, Begot TO, Prudente BS, Juen L, Montag LFA.** Effects of oil palm plantations on habitat structure and fish assemblages in Amazon streams. Environ Biol Fish. 2018; 101:547–62. https://doi.org/10.1007/s10641-018-0716-4
- **Francez LMB, Carvalho JOP, Jardim FCS, Quanz B, Pinheiro KAO.** Efeito de duas intensidades de colheita de madeira na estrutura de uma floresta natural na região de Paragominas, Pará. Acta Amazon. 2009; 39(4):851–63. http://dx.doi.org/10.1590/S0044-59672009000400014

- **Frissell CA, Liss WJ, Warren CE, Hurley MD.** A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environ Manag. 1986; 10:199–214. http://dx.doi.org/10.1007/BF01867358
- **Géry J.** Characoids of the world. Neptune City: T.F.H. publications; 1977.
- **Instituto Brasileiro de Geografia e Estatística (IBGE).** 2017. Available from: https://cidades.ibge.gov.br/brasil/pa/paragominas/panorama
- **Jackson DA.** Stopping rules in principal components analysis: A comparison of heuristical and statistical approaches. Ecology. 1993; 74(8):2201–14. https://doi.org/10.2307/1939574
- **Juen L, Cunha EJ, Carvalho FG, Ferreira MC, Begot TO, Andrade AL *et al*.** Effects of oil palm plantations on the habitat structure and biota of streams in Eastern Amazon. River Res Appl. 2016; 32(10):2081–94. https://doi.org/10.1002/rra.3050
- **Junk WJ, Soares MGM, Bayley PB.** Freshwater fishes of the Amazon River basin: their biodiversity, fisheries, and habitats. Aquat Ecosyst Health Manag. 2007; 10(2):153–73. http://dx.doi.org/10.1080/14634980701351023
- **Kaufmann PR, Levine P, Robison EG, Seeliger C, Peck DV.** Quantifying physical habitat in wadeable streams. EPA/620/R-99/003. Washington: U.S. Environmental Protection Agency; 1999.
- **Kullander SO.** Cichlid fishes of the Amazon River drainage of Peru. Stockholm: Swedish Museum of Natural History; 1986.
- **Leão H, Siqueira T, Torres NR, Montag LFA.** Ecological uniqueness of fish communities from streams in modified landscapes of Eastern Amazonia. Ecol Indic. 2020; 111:106039. http://dx.doi.org/10.1016/j.ecolind.2019.106039
- **Leal CG, Lennox GD, Ferraz SFB, Ferreira J, Gardner TA, Thomson JR *et al*.** Integrated terrestrial-freshwater planning doubles conservation of tropical aquatic species. Science, 2020; 370(6512):117–21. https://doi.org/10.1126/science.aba7580
- **Leal CG, Barlow J, Gardner TA, Hughes RM, Leitão RP, Mac Nally R *et al*.** Is environmental legislation conserving tropical stream faunas? A large-scale assessment of local, riparian and catchment-scale influences on Amazonian fish. J Appl Ecol. 2017; 55(3):1312–26. https://doi.org/10.1111/1365-2664.13028
- **Leal CG, Pompeu PS, Gardner TA, Leitão RP, Hughes RM, Kaufmann PR *et al*.** Multi-scale assessment of human-induced changes to Amazonian instream habitats. Landsc Ecol. 2016; 31:1725–45. https://doi.org/10.1007/s10980-016-0358-x
- **Legendre P, Legendre L.** Numerical ecology. Oxford: Elsevier; 2012.
- **Lima AMM, Pontes MX.** Dinâmica da paisagem da bacia do rio Capim-PA. Rev Bras Geogr Fis. 2012; 1:127–42. http://dx.doi.org/10.26848/rbgf.v5i1.232779
- **Lima M, Firmino VC, Paiva CKS, Juen L, Brasil LS.** Land use changes disrupt streams and affect the functional feeding groups of aquatic insects in the Amazon. J Insect Conserv. 2022; 26:137–48. https://doi.org/10.1007/s10841-022-00375-6
- **Leitão RP, Zuanon J, Mouillot D, Leal CG, Hughes RM, Kaufmann PR *et al*.** Disentangling the pathways of land use impacts on the functional structure of fish assemblages in Amazon streams. Ecography. 2018; 41:219–32. http://dx.doi.org/10.1111/ecog.02845
- **Lorion CM, Kennedy BP.** Riparian Forest buffers mitigate the effects of deforestation on fish assemblages in tropical headwater streams. Ecol Appl. 2009; 19(2):468–79. http://dx.doi.org/10.1890/08-0050.1
- **Loureiro VR.** A Amazônia no século 21: novas formas de desenvolvimento. Rev Direit GV. 2012; 8(2):527–52. https://doi.org/10.1590/S1808-24322012000200006
- **Lavorel S, Grigulis K, Mclntryre S, Williams NSG, Garden D, Dorrough J *et al*.** Assessing functional diversity in the field methodology matters! Funct Ecol. 2008; 22(1):134–47. https://doi.org/10.1111/j.1365-2435.2007.01339.x
- **Luiza-Andrade A, Brasil LS, Benone NL, Shimano Y, Farias APJ, Montag LF *et al*.** Influence of oil palm monoculture on the taxonomic and functional composition of aquatic insect communities in eastern Brazilian Amazonia. Ecol Indic. 2017; 82:478–83. http://dx.doi.org/10.1016/j.ecolind.2017.07.006

- **Macedo DR, Hughes RM, Ligeiro R, Ferreira WR, Castro MA, Junqueira NT *et al.*** The relative influence of catchment and site variables on fish and macroinvertebrate richness in Cerrado biome streams. Lands Ecol. 2014; 29:1001–16. https://doi.org/10.1007/s10980-014-0036-9
- **Mol JH, Ouboter PE.** Downstream effects of erosion from small-scale gold mining on the instream habitat and fish community of a small neotropical rainforest stream. Conserv Biol. 2004; 18(1):201–14. http://dx.doi.org/10.1111/j.1523-1739.2004.00080.x
- **Montag LFA, Winemiller KO, Keppeler FW, Leão H, Benone NL, Torres NR *et al.*** Land cover, riparian zones and instream habitat influence stream fish assemblages in the eastern Amazon. Ecol Freshw Fish. 2019; 28(2):317–29. http://dx.doi.org/10.1111/eff.12455
- **Novakowski KI, Torres R, Gardner RL, Voulgaris G.** Geomorphic analysis of tidal creek networks. Water Resour Res. 2004; 40(5):1–13. https://doi.org/10.1029/2003WR002722
- **Nonato FAS, Michelan TS, Freitas PV, Maia C, Montag LFA.** Heterogeneity of macrophyte banks affects the structure of fish communities in flooded habitats of the Amazon Basin. Aquat Ecol. 2021; 55:215–26. https://doi.org/10.1007/s10452-020-09823-4
- **Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D *et al.*** Vegan: Community ecology. R package version 2.4-6; 2018.
- **Paiva CKS, Faria APJ, Calvão LB, Juen L.** Effect of oil palm on the Plecoptera and Trichoptera (Insecta) assemblages in streams of eastern Amazon. Environ Monit Assess. 2017; 189(8):393. https://doi.org/10.1007/s10661-017-6116-y
- **Paiva CKS, Faria APJ, Calvão LB, Juen L.** The anthropic gradient determines the taxonomic diversity of aquatic insects in Amazonian streams. Hydrobiologia. 2021; 848:1073–85. https://doi.org/10.1007/s10750-021-04515-y
- **Peck DV, Herlihy AT, Hill BH, Hughes RM, Kaufmann PR, Klemm DJ *et al.*** Environmental monitoring and assessment program - surface waters western pilot study: field operations manual for wadeable streams. EPA 600/R-06/003. Washington: US Environmental Protection Agency; 2006.
- **Petchey OL, Gaston KJ.** Functional diversity: Back to basics and looking forward. Ecol Lett. 2006; 9(6):741–58. https://doi.org/10.1111/j.1461-0248.2006.00924.x
- **Petsch DK.** Causes and consequences of biotic homogenization in freshwater ecosystems. Int Rev Hydrobiologia. 2016; 101:113–22. http://dx.doi.org/10.1002/iroh.201601850
- **Prudente BS, Pompeu PS, Juen L, Montag LFA.** Effects of reduced-impact logging on physical habitat and fish assemblages in streams of Eastern Amazonia. Fresh Biol. 2017; 62(2):303–16. http://dx.doi.org/10.1111/fwb.12868
- **Pusey BJ, Arthington AH.** Importance of the riparian zone to the conservation and management of freshwater fish: A review. Mar Freshw Res. 2003; 54(1):1–16. http://dx.doi.org/10.1071/MF02041
- **QGIS Development Team.** QGIS geographic information system. open-source geospatial foundation project, 2017. Available from: https://qgis.org/en/site/
- **Ribeiro MD, Teresa FB, Casatti L.** Use of functional traits to assess changes in stream fish assemblages across a habitat gradient. Neotrop Ichthyol. 2016; 14(1):e140185. https://doi.org/10.1590/1982-0224-20140185
- **R Development Core Team.** R: A language and environment for statistical computing. R Foundation for statistical computing. Vienna. 2015. Available from: https://www.R-project. org/
- **Roa-Fuentes CA, Casatti L.** Influence of environmental features at multiple scales and spatial structure on stream fish communities in a tropical agricultural region. J Freshw Ecol. 2017; 32(1):273–87. https://doi.org/10.1080/02705060.2017.1287129

- **Schneider CA, Rasband WS, Eliceiri KW.** NIH image to ImageJ: 25 years of image analysis. Nat Methods. 2012; 9:1–12. https://doi.org/10.1038/nmeth.2089
- **Simberloff D, Dayan T.** The guild concept and the structure of ecological communities. Annu Rev Ecol Syst. 1991; 22:115–43. http://dx.doi.org/10.1146/annurev.es.22.110191.000555
- **Siqueira T, Lacerda CGLT, Saito VS.** How does landscape modification induce biological homogenization in Tropical stream metacommunities? Biotropica. 2015; 47(4):509–16. https://doi.org/10.1111/btp.12224
- **Sioli H.** Amazônia: Fundamentos da ecologia da maior região de florestas tropicais. Petrópolis: Editora Vozes; 1991.
- **Soares BE, Ruffeil TOB, Montag LFA.** Ecomorphological patterns of the fishes inhabiting the tide pools of the amazonian coastal zone, Brazil. Neotrop Ichthyol. 2013; 11(4):845–58. https://doi.org/10.1590/S1679-62252013000400013
- **Soberón J.** Grinnellian and Eltonian niches and geographic distributions of species. Ecol Lett. 2007; 10(12):1115–23. http://dx.doi.org/10.1111/j.1461-0248.2007.01107.x
- **Southwood TRE.** Habitat, the templet for ecological strategies? J Anim Ecol. 1977; 46(2):337–65. https://doi.org/10.2307/3817
- **Sonter LJ, Herrera D, Barrett DJ, Galford GL, Moran CJ, Soares-Filho BS.** Mining drives extensive deforestation in the Brazilian Amazon. Nat Commun. 2017; 8:1013. https://www.nature.com/articles/s41467-017-00557-w
- **Tarboton DG.** Terrain analysis using digital elevation models (TauDEM). Utah State University, Logan. 2005.
- **Tonkin JD, Heino J, Altermatt F.** Metacommunities in river networks: The importance of network structure and connectivity on patterns and processes. Freshwater Biol. 2018; 63(1):1–05. https://doi.org/10.1111/fwb.13045
- **Vannote RL, Minshall GW, Cummins KW, Sedell JR, Gushing CE.** The river continuum concept. Can J Fish Aquat Sci. 1980; 37:130–37. https://doi.org/10.1139/f80-017
- **Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I *et al*.** Let the concept of trait be functional. Oikos. 2007; 116(5):882–92. https://doi.org/10.1111/j.0030-1299.2007.15559.x
- **Winemiller KO.** Ecomorphological diversification of freshwater fish assemblages from five biotic regions. Ecol Monogr. 1991; 61(4):343–65. https://doi.org/10.2307/2937046
- **Winemiller KO.** Life history strategies and the effectiveness of sexual selection. Oikos. 1992; 63(2):318–27. https://doi.org/10.2307/3545395
- **Zeni JO, Casatti L.** The influence of habitat homogenization on the trophic structure of fish fauna in tropical streams. Hydrobiologia. 2014; 726:259–70. https://doi.org/10.1007/s10750-013-1772-6
- **Zeni JO, Pérez-Mayorga MA, Roa-Fuentes CA, Brejão GL, Casatti L.** How deforestation drives stream habitat changes and the functional structure of fish assemblages in different tropical regions. Aquat Conserv. 2019; 29(8):1238–52. https://doi.org/10.1002/aqc.3128
- **Zuanon J, Mendonça FP, Espírito-Santo HMV, Dias MS, Galuch AV, Akama A.** Guia de peixes da reserva Ducke - Amazônia Central. Manaus: Editora INPA; 2015.

AUTHORS' CONTRIBUTION

Calebe Maia: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Validation, Visualization, Writing-original draft, Writing-review and editing.

Gilberto N. Salvador: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Validation, Visualization, Writing-original draft, Writing-review and editing.

Tiago O. Begot: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Validation, Visualization, Writing-original draft, Writing-review and editing.

Pâmela V. Freitas: Conceptualization, Visualization, Writing-original draft.

Flávia A. S. Nonato: Visualization, Writing-original draft,
Naiara R. Torres: Methodology, Visualization, Writing-original draft,
Leandro Juen: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing-original draft, Writing-review and editing.
Luciano F. A. Montag: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Validation, Visualization, Writing-original draft, Writing-review and editing.

ETHICAL STATEMENT

The field expedition was conducted under license number 4681–1 granted by the Sistema de Autorização e Informação em Biodiversidade (SISBIO) and was approved by the Ethics Committee of the Universidade Federal do Pará (CEUA nº 8293020418).

COMPETING INTERESTS

The authors declare no competing interests.

HOW TO CITE THIS ARTICLE

- **Maia C, Salvador GN, Begot TO, Freitas PV, Nonato FAS, Torres NR, Juen L, Montag LFA.** Fish functional responses to local habitat variation in streams within multiple land uses areas in the Amazon. Neotrop Ichthyol. 2022; 20(4):e220091. https://doi.org/10.1590/1982-0224-2022-0091

Neotropical Ichthyology

OPEN ACCESS

SBI
Official Journal of the Sociedade Brasileira de Ictiologia