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The influence of landscape at multiple spatial scales of the river basins at the Eastern Amazon fish assemblage

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The Amazon River basins present distinct natural and anthropogenic characteristics that influence the structure of stream habitats and their associated biota. The influence of these characteristics can be evaluated through different spatial scales. We aimed to assess the influence (with and without the effect of spatial-geographical factors) of local, macroscale, and land-use variables in the structure of stream fish assemblages of Amazonian catchments with different deforestation levels. A partial redundancy analysis and a reduced metrics model were used to assess these influences. With geographic-spatial effects, we verified that the macroscale and local variables explained the variation in fish composition, and, without the effects, land use also explained the variation in this composition. In the forested catchments, the biota was associated with streams with natural characteristics (*e.g.*, leaf banks). In the deforested catchments, it was associated with land use, sandy catchments with higher soil density (higher capacity of degradation), and less complex streams (fewer leaf banks, more sand). The associated fish have life features linked to these characteristics (*e.g.*, *Gymnorhamphichthys rondoni* associated with sand). This configuration seems to be a result of both the impact of land use in the catchment (*i.e.*, increased erosion, increased sedimentation) and the naturally sandy constitution of the catchment as well, reflecting the sandy substrate.

Keywords: Conservation, Degradation, Land use, Soil density and spatial scale.

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A Amazônia apresenta bacias hidrográficas com características naturais e antrópicas que estão presentes em distintas escalas espaciais da paisagem e que influenciam a estrutura do habitat de riachos e sua biota associada. Nosso objetivo foi verificar a influência (com e sem o efeito de fatores espaciais e geográficos) de variáveis locais, de macroescala e uso da terra na estrutura de assembleias de peixes de riachos de microbacias amazônicas com diferentes níveis de desmatamento. A análise de redundância parcial e modelo reduzido de métricas foram realizadas para verificar essas influências. Com os efeitos geográfico-espaciais, verificou-se que as variáveis de macroescala e locais explicavam a variação da composição dos peixes, e sem os efeitos, os usos da terra também explicaram. Nas microbacias florestadas, a biota foi associada a riachos com características naturais (*e.g.*, bancos de folhas). Nas microbacias desmatadas, foi associada a usos da terra, a microbacias arenosas com maior densidade do solo (maior capacidade de degradação) e a riachos menos complexos (menos bancos de folhas e mais areia). Os peixes associados a essas microbacias desmatadas possuem aspectos de vida atrelados a essas características (*e.g.*, *Gymnorhamphichthys rondoni* associado a areia). Essa configuração parece ser um reflexo tanto do impacto do uso da terra na microbacia (*i.e.*, maior erosão, maior sedimentação) quanto da própria constituição natural arenosa da microbacia, refletindo o substrato arenoso.

Palavras-chave: Conservação, Degradação, Densidade do solo, Escala espacial e Uso da terra.

INTRODUCTION

Stream ecosystems are structured by dynamic and hierarchical factors that vary at different spatio-temporal scales (Allan, Johnson, 1997; Ward, 1998; Yu *et al*., 2016). In general, these environments are controlled by landscape structures throughout the drainage basin, which in turn reflects the heterogeneity of stream habitat structure (Hynes, 1975), and tend to shape the structure of biotic communities (Frissell *et al*., 1986; Hawkins *et al*., 1993; Cunico *et al*., 2012). This is because streams are hierarchically organized systems (Frissell *et al*., 1986) in which large-scale processes such as land-use changes and geology control local-scale conditions (Frissell *et al*., 1986; Hawkins *et al*., 1993; Cunico *et al*., 2012).

Through the natural hierarchical organization, environmental variables in large scale control habitat features (Frissell *et al*., 1986). However, measuring the influence of land use at different spatial scales on the stream ecosystem has become a challenge in landscape ecology as its distribution in the basin is uneven (Allan, Johnson, 1997). Under these conditions, it is difficult to distinguish which scale gives rise to the influence of a given environmental variable. It has been seen that landscape features of different scales (*e.g.*, larger scale and smaller scale) can be interconnected, influencing stream biota (Richards *et al*., 1996; Lorenz, Feld, 2013). For example, the structure of aquatic biota is influenced by physicochemical variables (Allan, 2004), which are influenced by geology and climate (natural scale of the basin). However, these variables are also affected by land use on small and large scales (Steel *et al*., 2010).

In general, it is known that land use can modify the stream landscape by suppressing native vegetation (Larson *et al*., 2019). Thus, the implementation of agro-industrial activities in the basins, especially those that result in large-scale changes in land use, has been considered a threat to environmental heterogeneity, biological diversity and, consequently, ecosystem services provided by streams, when performed without proper planning (Leal *et al*., 2016). Thus, it has been identified that large-scale agriculture interferes within the stream, such as water quality change (Mori *et al*., 2015; Yadav *et al*., 2019), nutrient and sediment input increase (De Mello *et al*., 2020) and interference in the trophic structure of the community (Loomer *et al*., 2022). At small scales (local scale) close to streams, loss of riparian cover reduces wood and litter debris and increases sedimentation (Hyatt, Naiman, 2001; Carvalho *et al*., 2018) and solar radiation, therefore increasing the primary production (Turunen *et al*., 2021). Similarly, large-scale grazing activity also interferes with water quality (*e.g*., phosphate input) (Mori *et al*., 2015). Large-scale urbanization, by waterproofing the drainage basin, interferes with infiltration and surface runoff (Poff *et al*., 1997; Nath *et al*., 2021). For fish, this may be reflected in the degradation of their habitat, such as the reduction of pools and backwaters microhabitat (Schlosser, 1991; Paredes del Puerto *et al*., 2021), as well as removal or covering of the substrate by sediment, may interfere with feeding, prevent foraging and facilitate predation (Nerbonne, Vondracek, 2001; Osmundson *et al*., 2002). This can result in loss and even replacement of species (Marzin *et al*., 2013; Paredes del Puerto *et al*., 2021).

As seen above, there is a challenge in identifying the contribution of the effects of factors at different scales on the stream ecosystem and thus defining a better conservation strategy. Although the common practice is to maintain a strip of riparian vegetation throughout the drainage, this may not be enough to maintain habitat complexity and ichthyofauna structure, especially in greatly altered basins (Dala-Corte *et al*., 2020). Therefore, it is necessary to evaluate the conditions of the basin as a whole, including processes that act on different spatial scales, to obtain a detailed picture of the possible factors affecting ichthyofauna (Wang *et al*., 2002; Leal *et al*., 2016; Nava-López *et al*., 2016; Effert-Fanta *et al*., 2019; Seabra *et al*., 2021). This is within the Challenge 2 proposed by Erös (2017), where the role of local and regional processes in metacommunity organization should be evaluated.

Several factors can influence species distributions in a region and a combination of some methods has been used to assess this influence (Vélez-Martin, 2012). These distributions may be the result of adaptations to environmental conditions and interactions with other species along the gradient (Quinn, Dunham, 1983; Orlóci, 1993). These spatial patterns are a consequence of multiple causal factors, whose relative contributions depend on each environmental context (Borcard *et al*., 1992). To provide answers about these influences, variance partitioning has been used to evaluate the isolated and shared influence of environmental and spatial factors on species composition (Borcard *et al*., 1992; Legendre *et al*., 2005). According to Legendre *et al*. (2009), variations associated with environmental factors can be attributed to niche factors, and spatial variation has been associated with spatial autocorrelation in species distribution. In this case, space is not an isolated variable, but an expression of neutral processes on the composition of the community that were not directly evaluated, unlike environmental factors (Vélez-Martin, 2012). Spatial variables are expected to be of major importance at large spatial scales (Dray *et al*., 2006). Due to their dendritic nature, stream systems have a marked spatial structure that can enhance dispersal limitation to fishes (Heino *et al*., 2015; Benone *et al*., 2020). This aligns with spatial autocorrelation, since streams separated by larger distances should present more dissimilar fish assemblages than closer streams as a result that can be associated with increasing dispersal limitation and/or increasing environmental dissimilarity (Blanchet *et al*., 2014; Heino *et al*., 2015).

To narrow this knowledge gap, in this paper we evaluated: What is the influence of local variables (characteristics of the instream habitat), macroscale variables (*e.g*., soil variables, slope), and land-use variables (pasture, agriculture, and urbanization from drainage network buffers and catchment area) on the fish assemblage structure, with and without the effect of spatial-geographical factors? Removing these effects, we also sought to answer: Which spatial scales (drainage network buffers and catchment area) and associated environmental variables influence these assemblages the most at different levels of deforestation? We hypothesized that there is an influence of environmental variables present at different spatial scales on fish assemblages from streams of four catchments with different levels of deforestation. We believe that, in less deforested catchments, macroscale variables together with local variables are structuring fish assemblages, favored by the greater complexity of the habitat (*e.g*., more leaf banks). On the other hand, we believe that, in deforested catchments, land use, together with macroscale variables and local variables, are structuring fish assemblages related to less complex habitats (for example, fewer leaf banks and greater amount of sand in the channel).

MATERIAL AND METHODS

Study area. We sampled 76 streams, not flooded, of first to third order, located in four watersheds of the Eastern Amazon. Seven streams are in the Tapajós River basin, 18 in the Anapu River basin, 14 in the Acará River basin and 37 in the Capim River basin (Fig. 1). Streams have been defined in Catchments with different landscape features. These regions present differences in geomorphological (Benone *et al*., 2017), hydrogeological (Ribeiro, 2006), and land use history processes (Silva *et al*., 2005).

The Tapajós River basin has a humid tropical climate of the *Ami* type (Köppen), with an average temperature of 25.5 °C, an average rainfall of 1.920 mm, with a predominance of Dystrophic Yellow Latosol, and relief with altitudes ranging from 30 to 200 m (average: 175 m). The studied streams are located within the Tapajós National Forest created in 1974 (Federal Decree 73.684) and are all from conserved micro basins (Veloso *et al*., 1991; Parrotta *et al*., 1995). The Anapu River basin has a hot and humid Am (Köppen) climate, with an average temperature of 26.7 °C and an average rainfall of 2000 mm (Lisboa, 2002). It has lake-like limnological characteristics resulting from valley drowning during the Holocene (Behling, da Costa, 2000). This region of the Anapu River basin is covered by “solid ground”, “floodplain” and “flooded” forests, which are exposed to daily and seasonal periodic flooding of rivers (Ferreira, 1997). Water has little suspended material and a lot of organic debris (Costa *et al*., 2002). Its streams are shallow and can reach approximately 10 m in width by floodplain influence (Montag *et al*., 2008).

In the region of Acará and Capim river basins, the climate is tropical humid, of the type Af (Köppen), according to adaptation by Peel *et al*. (2007), with an average temperature of 26 °C (Oliveira *et al*., 2002) and average precipitation of 2,344 mm (Albuquerque *et al*., 2010). In the region of Acará River, the vegetation is of the subperenolia type with several species of economic value. The geology is made up of clay with sand beds and ferruginous concretions, within the lowered Amazon Plateau, which presents the relief with varied, intensely drained slope; and within the floodplain, with flooded areas accompanied by watercourses, consisting of recent unconsolidated sediments (Schobbenhaus *et al*., 1984; Embrapa, 2005). The Capim River basin is an area of great economic circulation in the Eastern Amazon that was directed along the Belém-Brasília Highway (BR-010), where it concentrates infrastructure for industrial, mining, logging and agricultural projects. It is separated by two sectors, upper and lower-middle Capim River, which are differentiated by relief and downstream slope (Lima, Ponte, 2012).

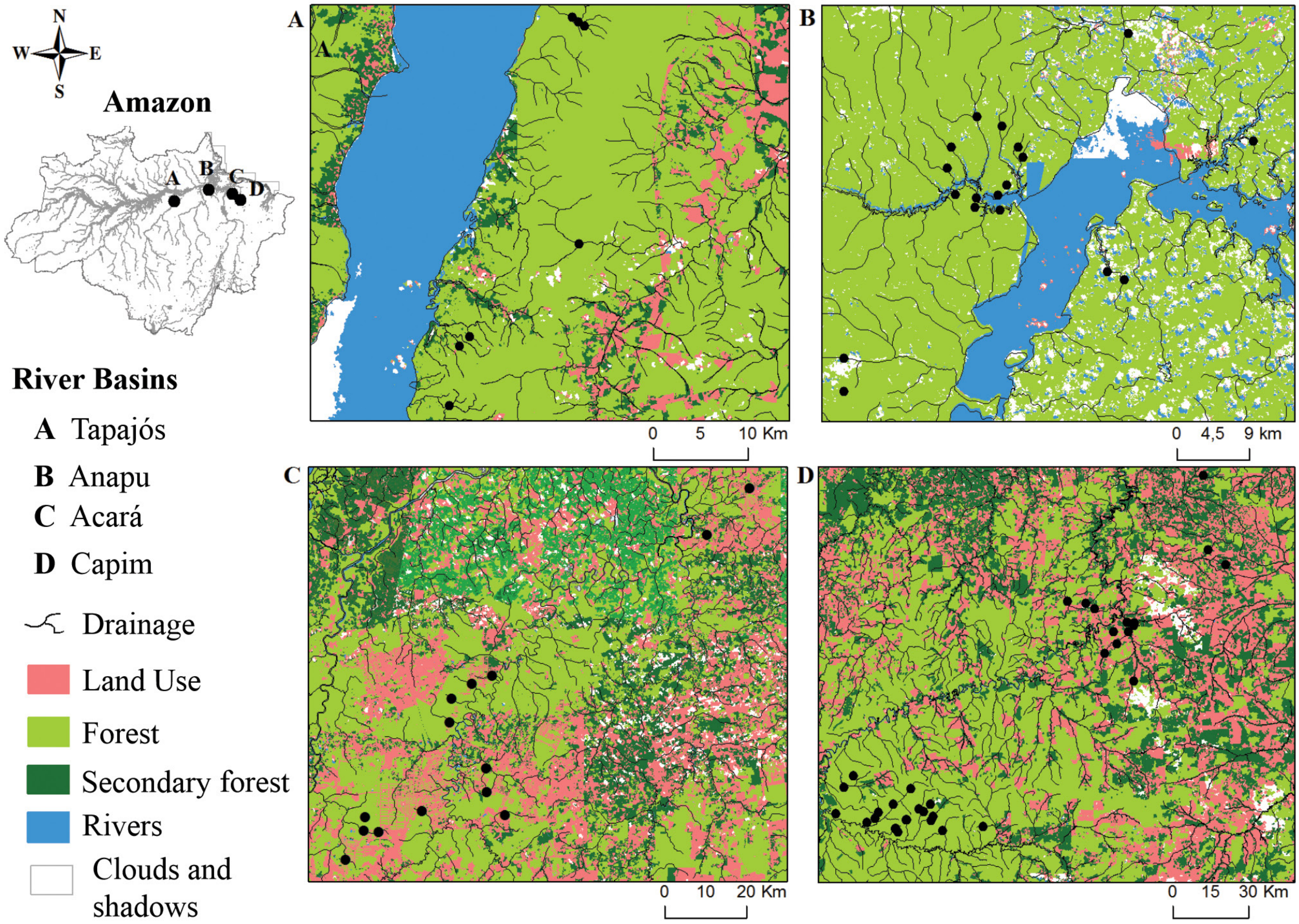

FIGURE 1 | Study area containing 76 streams distributed in four Eastern Amazon basins and land use distribution. Land use: represents all uses (*e.g*., pasture, agriculture, and urbanization).

Sampling design and fish rating. In each stream, we sampled a 150 m stretch to collect the fish assemblages, which made up the response matrix, and characteristic variables of the instream habitat, hereafter called local variables. In each catchment, we measured variables such as soil type, soil density, and slope to represent the environmental heterogeneity on this scale, hereafter called macroscale variables. The variables of land use were obtained throughout the catchment and in 30, 60, and 90 m buffers along the stream network, upstream of the stream, and are hereafter called land-use variables (Tab. 1).

Sampling took place once in each stream during the dry season between 2014 and 2016. In each stream, the 150 m stretch was divided into ten 15 m longitudinal sections through 11 transections. For fish sampling, we used 55 mm diameter and 2 mm mesh circular sieve nets. The sampling effort was 18 minutes with two collectors for each longitudinal section, totaling 3 h for each stream (Jacob *et al*., 2021). Collected fish were anesthetized using Eugenol's solution according to the guidelines of the National Council for Animal Experimentation Control (CONCEA, 2015). The specimens were fixed in 10% formaldehyde solution and, after 48 h, transferred to 70% ethanol. In the laboratory, fish were identified to the lowest possible taxonomic level and deposited in the collection of the Museu de Zoologia da Universidade Federal do Pará, Belém, Pará, Brazil (MZUFPA). Taxonomic classification (at species level and above) followed the Eschmeyer's Catalog of Fisches (Fricke *et al*., 2023).

Environmental variables. *Local variables*. Local variables are characteristic of the instream physical habitat. The habitat of each stream was characterized according to the adapted version (Callisto *et al*., 2014) of the stream assessment protocol of the US Environmental Protection Agency (Kaufmann *et al*., 1999; Peck *et al*., 2006). Local variables related to channel morphology (*e.g*., width and depth), substrate (*e.g*., rock and sand), flow types (*e.g*., rapids and pools), riparian vegetation cover (*e.g*., canopy cover and riparian estimates), fish shelter (*e.g*., leaf and litter banks), sinuosity and water chemistry (pH and Dissolved oxygen) were obtained (Tab. 1; Tab. **S1**).

Land use variables. The percentage of land use was obtained through satellite images of a 5-m resolution RapidEye sensor, made available by the Brazilian Ministry of Environment (MMA, 2016) from 2014 to 2016. Images were processed using PCI v. 10.2 and Geomatics v. 10 (PCI Geomatics, 2009) and rated by eCognition v. 9.0 software (Trimble Geospatial, 2014) to get the percentage of land use classes. Images were classified by summarizing similar and representative dominant categories of land cover and land use in the region.

Land use metrics were quantified in four spatial areas (scales) in the catchment and in drainage buffers in the stream network upstream: 1) Small (S), limited by a 30-m buffer (counted from the edge to a width of 30 m – coincident with the width determined as protection area by the Brazilian Forest Code for streams up to 10 m wide); 2) Medium (M), 60 m buffer (counted from the bank to a width of 60 m), 3) Large (L), 90 m buffer (counted from the bank to a width of 90 m) and 4) Catchment (T), total area upstream 150 m of sampling (Tab. 1; Fig. 2). These methods were based on similar studies conducted in drainage basins worldwide (Richards *et al*., 1996; Wang *et al*., 1997, 2001b; Lammert, Allan, 1999).

Macroscale variables. Macroscale variables were obtained in the catchment and consisted of the slope average, and the soil types and density. The slope was obtained from each raster cell on the 30 m resolution SRTM image surface (Shuttle Radar Topography Mission-GLCF, 2017). Soil types were obtained from SoilGrids250m (https://soilgrids.org/#!/?layer=TAXNWRB_250m&vector=1) website, which calculates from Earth's surface (0.00 depth): clay percentage, rock fragments (% volume), silt percentage (2–50 µm), sand percentage (50–2000 µm) and soil density (kg/m^3). The latter indicates that the higher the density, the less clayey and less porous the soil and, consequently, the greater will be the restrictions on root system growth and plant development and its degradation if subjected to environmental change (Tormena *et al*., 1998; Cunha *et al*., 2001) (Tab. 1).

Statistical analysis. The local variables (instream habitat) were selected previously to obtain those most representative of the natural heterogeneity of the catchments. In the first stage, we removed the metrics (i) with little variation (coefficients of variation < 10%), (ii) that have values equal to zero in > 80% of the samples, and (iii) that have similar information through Spearman correlations ($r \geq |0.7|$). This resulted in 23 instream habitat variables remaining (Fig. 3). In a second stage, we conducted a Principal Component Analysis (PCA) with these remaining local variables, which were previously standardized because they were not dimensionally homogeneous (Tab. **S2**) (Legendre, Legendre, 2012). In the following analysis, the first three axes containing the representative scores of the local variables were used. Up to the third axis, they contained 48% of the accumulated variation (Fig. 3; Tab. **S3**).

To obtain the variables that represented the influence of land use on the fish assemblage, we performed four PCAs of the previously standardized land-use variables (*i.e*., pasture, agriculture, and urban use) present in the four spatial scales (*i.e*., 30, 60, and 90 m buffers and catchment) (Fig. 3). These variables were then represented by the scores of the first three PC axes (% of the accumulated variation of the variables in the four scales, respectively: 97.2%, 97.4%, 97.8%, and 96.9%) (Fig. 3; Tab. **S3**).

The macroscale variables were previously standardized to conduct a PCA. The resulting scores were used up to the third axis (accumulated variation: 84.1%) (Tab. **S3**) and, together with other geographic factors (consisting of identity of the catchments), made up the macroscale variables (Fig. 3).

We also used spatial variables represented by spatial filters calculated by the Neighbor Matrix Principal Coordinate Analysis (PCNM) (Borcard *et al*., 2004) of data of latitude and longitude of each stream to respond to spatial influence using spatial coordinate data (latitude and longitude). By this method the eigenvectors (*i.e*., spatial predictors known as "spatial filters" – Griffith; Peres-Neto *et al*., 2006) are extracted from a matrix of connectivity or distance between the sampling units and describe the spatial structure of the data at different scales (Diniz-Filho, Bini, 2005). The filters were chosen by the forward method (Legendre *et al*., 1997; Borcard *et al*., 2004; Dray *et al*., 2006; Legendre, Legendre, 2012) (Fig. 3).

These two last factor groups (*i.e*., geographic factors and spatial filters) were inserted to assess previously the effects of the macroscale variables on the distribution of fish assemblages. This distribution depends on biogeographic processes that determine, together with other factors, the regional pool from which the local communities are formed, in which species abundance would be shaped (MacArthur, Wilson, 1963; Hubbell, 2001). The Amazon's extension has conditions that generate the species

TABLE 1 | Local variables (instream habitat characteristics), macroscale variables obtained in the catchment, and land-use variables obtained from four spatial scales collected in 76 streams of four catchments of Eastern Amazon. *1The most succinct descriptions and sampling methodology of the local variables were described in the supplementary material (Tab. **S1**). *2Abbreviations for upstream scales of streams: in the drainage network (S: Small; M: Medium); in every catchment area (T: Catchment).

Scales	Variables unabbreviated	Codes
	Local variables*1	
Instream habitat	**Channel morphology**	
	Distance excavated margins average (m)	EM
	Average of thalweg depth (cm)	TD
	Margins angle average (degrees)	MA
	Ratio width & depth section	L/P
	Substrate	
	Thin gravel (%)	CF
	Substrate > 16mm Diameter (%)	SUB>16mm
	Sand (%)	SSA
	Fine sediments (%)	FN
	Roots (%)	RF
	Thin Burlap (%)	SF
	Leaf Bank (%)	LB
	Wood (%)	WO
	Immersion Average (%)	IM
	Organic Matter (%)	OM
	Flow Types	
	Rapids (%)	RA
	Glides (%) - Smooth flow	SF
	Any Type of Pool	PI
	Riparian vegetation cover	
	Ground Cover Average	CR
	Canopy estimate and coverage	
	Canal Canopy Average (%)	DO
	Fish Shelter	
	Shelter - Leaf Bank Average	AB-BF
	Sinuosity	
	Sinuosity Stretch	SIN
	Water chemistry	
	pH	pH
	Dissolved oxygen (mg/L)	OD
	Macroscale variables	
Catchment	**Inclination**	
	Catchment slope average	CSL
	Soil	
	Clay average (%)	CLY
	Rock fragments average (%)	FRO
	Silt average (%)	SIT
	Sand average (%)	CSA
	Soil density average (Kg/m^3)	SDY
	Land use variables	
Stream network upstream*2 (buffers 30 - S, 60 -M, 90m - L) and catchment (T)	Urban use (%)	UR
	Pasture use (%)	PAS
	Agricultural use (%)	AGR

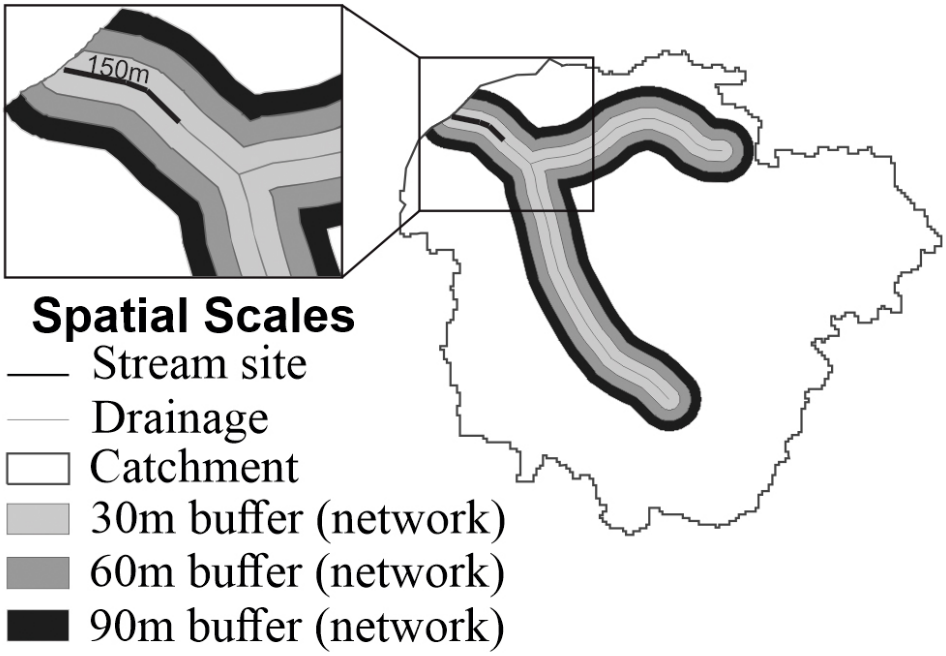

FIGURE 2 | Scheme showing different spatial scales from which land use types were quantified in four catchments of the Eastern Amazon.

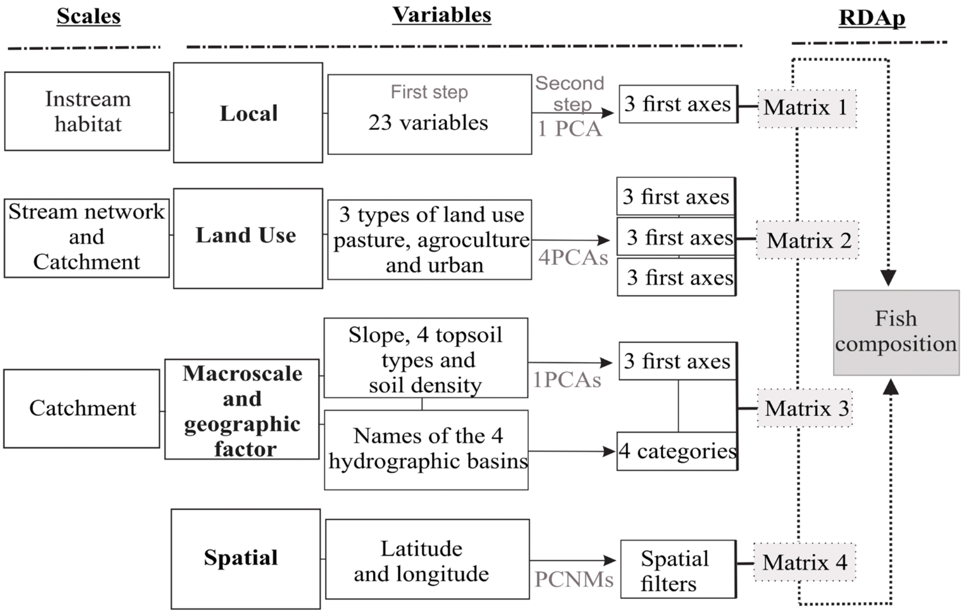

FIGURE 3 | Graphic model showing the environmental and spatial variables that composed the four matrices used in the RDAp.

pool by geographic and spatial interference. For example, fish community variations have been found along the Amazon extension associated with characteristics of the local environment and the heterogeneity of the landscape (Benone *et al*., 2022). The characteristics of the local environment and the heterogeneity of the landscape are factors that influence the allocation of potentially colonizing species from the regional pool in local communities in the geographic space.

With these four variable sets, we conducted a variance partitioning (RDAp) to try to identify what is the influence of the matrix of local variables, land use, and macroscale variables on the structure of fish assemblages considering the effect of spatial and geographic variation as well (Fig. 3). The RDAp was used to test whether there were differentiated effects (separate and shared) of each environmental and spatial matrix on the variations of the fish assemblage described through an adjusted R^2 (Peres-Neto *et al*., 2006). In summary, the RDAp consisted of four environmental matrices: the first of local explanatory variables represented by the first three PC axes; the second of land-use variables represented by the first three PC axes; the third of macroscale variables (first three PC axis) together with geographic factors (*i.e*., name of the catchments - consisting of identity of the catchments); and the fourth of space, representing environmental filters (Fig. 3). To test the significance levels of the components of the model, we applied analyses of variance (ANOVA) with 999 permutations. PC axes were chosen as matrices because they remove the collinearity of the variables (an assumption of the RDAp) and still being able to represent the data patterns of the raw data.

For the following analysis, we removed the residues of the effect of space and geographic categories from the composition matrix of fish species to assess the restricted influence of the effects of environmental variables (local, macroscale, and land use) on the structure of fish assemblages. We conducted an ANOVA to know whether environmental filters and macroscale variables, together with geographic factors, show spatial autocorrelation. As the result was significant, the associated residues were removed and only a biotic matrix remained, which only responds to the desired environmental variables.

We conducted a multiple regression through the DistLM (Distance-based linear model) routine, which produces a model displayed in a dbRDA (Distance-based redundancy analysis) (Anderson *et al*., 2008) to answer: 1) What is the influence of local, macroscale, and land-use variables on the structure of fish assemblages without the effects of spatial and geographic factors? 2) Which spatial scales and associated environmental variables influence these assemblages the most at the different levels of deforestation?

This routine tested the null hypothesis of the absence of a relationship between the data of species composition and the combined environmental variables installed in the model (local, macroscale, and land use). We used a similarity matrix with the Bray-Curtis coefficient of transformed data (log X + 1) of the new biotic matrix. The environmental matrix consisted of the union of the standardized variables of the three spatial scales (Legendre, Legendre, 2012), *i.e*.: 1) 15 local variables obtained up to the third axis of the PCA in the second stage of selection of local metrics with loadings > 0.25 (Tabs. **S2**, **S3**); 2) 12 land-use variables of the drainage and catchment network; and 3) 6 macroscale variables (slope, four types of surface soil and soil density). From these variables, we obtained a model that included the environmental variables with the greater explanatory power for the variation in assemblage composition using the forward selection method

(Blanchet *et al*., 2008) and the selection criteria of AIC models (Akaike, 1973).

The DistLM routine presents the sequential test in which the result indicates which variable, and in which order, has the power to explain the variation in the composition of the data set when added to the set of predictor variables ($p < 0.05$). The dbRDA is the ordination in which the figure presents the reduced model described in DistLM showing axes that are directly, linearly, and significantly related to predictor variables (Anderson *et al*., 2008). Only the predictor variables of the sequential test were shown in the graph. The fish species most correlated ($r > |0.5|$) to the ordinated data set were also displayed. The analyses were performed in PRIMER 6 with the PERMANOVA + add-on program package (Anderson *et al*., 2008).

To assess the influence of deforestation on the structure of stream-fish assemblages, we suggested three levels of catchment deforestation within the interval from 0 to 100%. They were displayed in the dbRDA as "forested", "intermediate" and "deforested" catchments. Catchments between 80 and 100% of forest in the total area were considered "forested"; catchments between 50 and 80% of forest were considered "intermediate"; and catchments between 0 and 50% of forest were considered "deforested".

RESULTS

Ichthyofauna. All 76 streams of the four catchments presented a total of 125 fish species (29,262 specimens), distributed into seven orders, with greater richness for Characiformes (29), Siluriformes (27), and Gymnotiformes (22); and 29 families, with greater richness for Characidae (22), Cichlidae (15), and Hypopomidae (13) (Tab. **S4**).

Local variables, basin, land use, and biota structure. Variance partitioning showed that the predictor variables explained 39% of the variation in fish composition (Fig. 4). The macroscale variables were the ones that explained this variation the most (Macroscale = 0.07, $p = 0.001$), followed by the local variables (Local = 0.02, $p = 0.001$), and space (PCNMs = 0.02, $p = 0.001$). Land use did not provide a significant explanation for the structuring of fish assemblages (Land use = 0.01, $p > 0.05$). Space and macroscale variables together explained the structure of fish assemblages the most (Space = 0.14). The combination of these variables with the variables of land use did not explain the structure of fish assemblages (Fig. 4).

The DistLM model selected 18 variables with greater power to explain the variation in fish composition data. These variables explain half of the data variation ($R^2 = 0.50$ of the adjusted model) (Tab. 2). Of these, five are land uses at different scales (*e.g*., PAS_S: 30 m buffer pasture, PAS_L: 60 m buffer pasture, UR_S: 30 m buffer urbanization, and AGR_T: agriculture from catchment); four are macroscale (CLY: clay average, SDY: average of catchment soil density, CSA: average of catchment sand percentage, CSL: catchment slope average) and 10 are local (EM: average distance from excavated margins; OM: organic matter (%); SIN: stretch sinuosity; TD: average of thalweg depth (cm); SSA: stream sand (%); SF: smooth flow (%); LB: leaf bank (%); MA: average margin angle; RF: rapid flow, and pH) (Tab. 2).

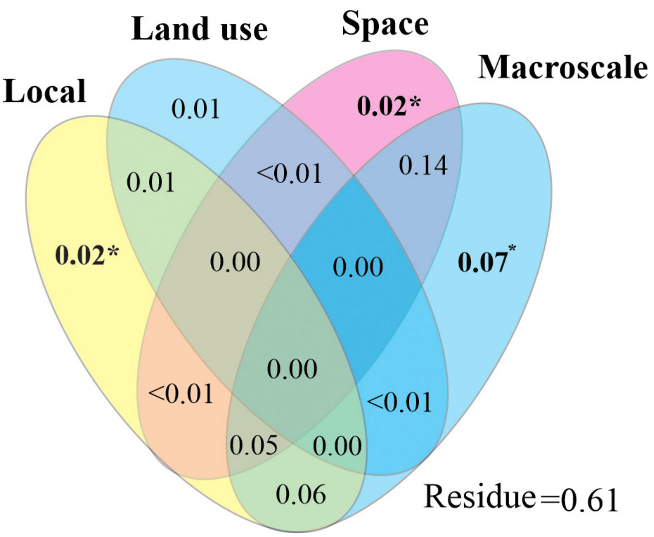

FIGURE 4 | Venn's diagram showing the exclusive and shared explanation of environmental variables (local, land use, and macroscale) and space in structuring fish assemblages in four catchments of the Eastern Amazon. Local = variation explained by the local matrix (variables of instream habitat); land use = variation explained by the land-use matrix (agriculture, pasture, and urbanization of drainage-network buffers and catchment); space = variation explained by the space matrix (environmental filters); macroscale = variation explained by the matrix of macroscale variables (soil characteristics and geographic factor); and residue = variation not explained. * $p < 0.05$.

TABLE 2 | Sequential test of the DistLM adjusted model to obtain variables with the greater predictive power of explanation in the structure of fish assemblages of catchments from four Eastern Amazon catchments. AIC = 574 and $R^2 = 0.50$; Prop = proportion of individual explanation of variable; Cumul = cumulative explanation ratio. Scales = Local: instream habitat variables, Macroscale: macroscale variables and Land use: land-use variables; Significant predictor variables * $p < 0.05$.

Group	Variables	AIC	SS (trace)	Pseudo-F	p	Prop.	Cumul.
Local	EM	586	13551	6.2	0.001*	0.08	0.08
Local	OM	583	11302	5.5	0.001*	0.06	0.14
Macroscale	CLY	581	6520	3.3	0.001*	0.04	0.18
Local	SIN	580	5777	3.0	0.002*	0.03	0.21
Local	TD	579	5012	2.7	0.002*	0.03	0.24
Macroscale	SDY	579	4382	2.4	0.004*	0.03	0.27
Land use	PAS_L	578	4679	2.6	0.001*	0.03	0.29
Local	SSA	577	4337	2.4	0.006*	0.02	0.32
Macroscale	CSA	577	3891	2.2	0.007*	0.02	0.34
Local	SF	576	3177	1.8	0.03*	0.02	0.36
Macroscale	CSL	576	3468	2.0	0.012*	0.02	0.38
Local	LB	576	3201	1.9	0.029*	0.02	0.40
Land use	PAS_S	575	3096	1.9	0.036*	0.02	0.41
Local	MA	575	2918	1.8	0.045*	0.02	0.43
Land use	AGR_T	575	2782	1.7	0.047*	0.02	0.45
Local	RF	575	2740	1.7	0.044*	0.02	0.46
Land use	UR_S	575	2512	1.6	0.091	0.01	0.48
Local	pH	575	2496	1.6	0.07	0.01	0.49

The two dbRDA axes explained 41.1% of the variation of the adjusted model and 20.3% of the total variation in the fish composition of the streams in the four catchments. The first axis presented the greatest explanation of the model (24.7% of the adjusted model and 12.2% of the total variation), followed by the second axis (16.4% of the model explanation and 8.1% of the total variation) (Fig. 5).

The streams of the lower right quadrant of the dbRDA graph have their catchments more forested and with lower soil density (SDY). They are more configured for a habitat structure of a more sinuous (SIN) channel with more angular (MA) and excavated margins (EM). These streams were more related to the species *Denticetopsis epa* (Dent) (Fig. 5).

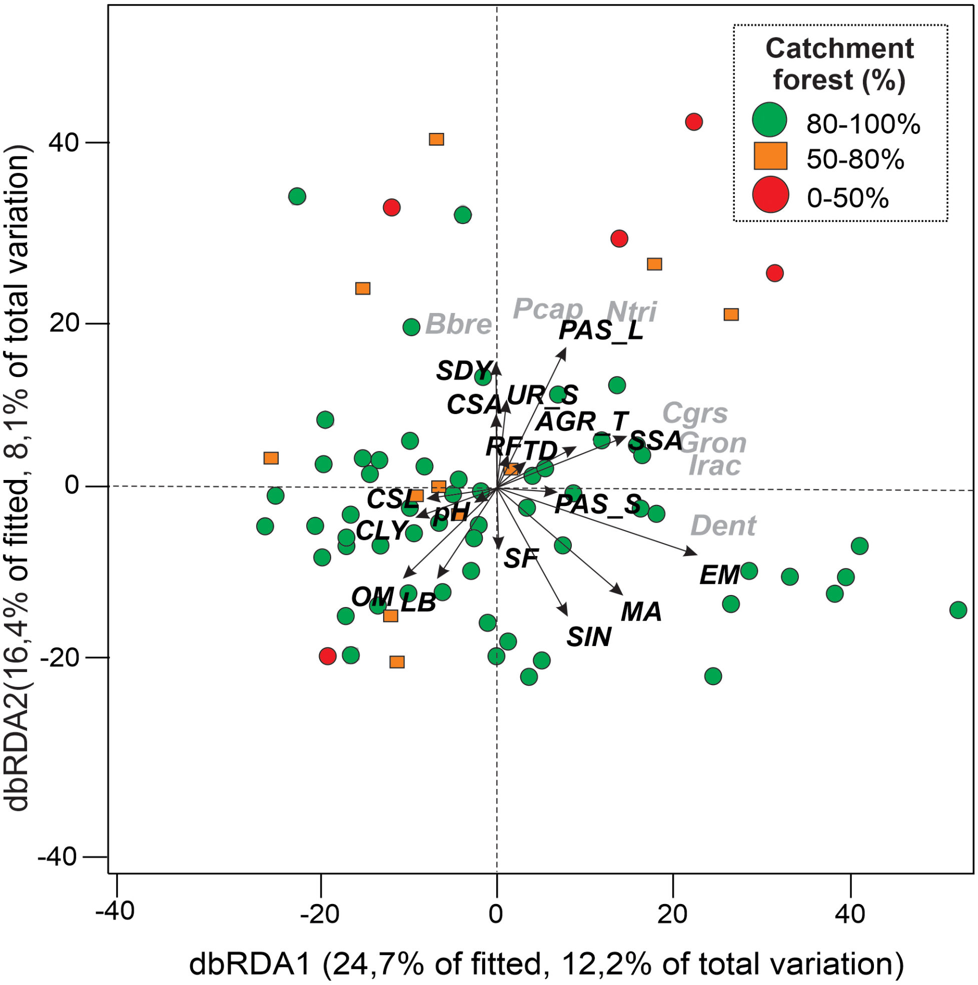

FIGURE 5 | The dbRDA graph displays the distribution of fish data according to the most explanatory (local, macroscale, and land use) variables selected in the distLM model. Environmental variables were chosen by Forward and best model by AIC. Species code: *Brachyhypopomus brevirostris* (*Pbre*), *Pyrrhulina capim* (*Pcap*), *Nannostomus trifasciatus* (*Ntri*), *Gymnorhamphichthys rondoni* (*Gron*), *Iguanodectes rachovii* (*Irac*), *Denticetopsis epa* (*Dent*). Abbreviations: Local variables: EM: Average distance from excavated margins, MA: Average margin angle, SIN: Stretch sinuosity, SF: Smooth flow, LB: Substrate leaf bank, OM: Substrate organic matter, pH, RF: Rapids flow; TD: Average of thalweg depth; SSA: Stream sand. Macroscale variables: CLY: Catchment clay average, CSL: Catchment slope average, SDY: Catchment soil density, CSA: Catchment substrate sand; Land use: UR_S: Urbanization in 30m buffer, PAS_L: Pasture in 60m buffer, AGR_T: agriculture on catchment, PAS_S: Pasture in 30m buffer.

Streams of the lower-left quadrant also had, in general, more forested catchments. They present more clayey catchments (CLY) with lower soil density (SDY). The streams were configured by a less sinuous (SIN) channel structure, with less angular (MA) and less excavated margins (EM) and substrate with more leaf banks (LB) and organic matter (OM). This group was in opposition to the presence of land use of the distinct spatial scales (Fig. 5).

Streams of the upper right quadrant presented, in general, more deforested catchments and smaller habitat complexity (fewer leaf banks and less excavated margins). They are more associated with higher soil density (SDY) consisting mainly of sand (CSA) and more sandy channels (SSA). These channels are less sinuous (SIN), deeper in the thalweg (TD), and with faster flow (RF). They were negatively associated with leaf banks (LB). These streams were associated with land use at different spatial scales of the catchment. In order of greater influence, they were more associated with pastures in the 90-m buffer, urbanization in the 30-m buffer, and agriculture in the catchment. Environmental characteristics were correlated with species such as *Brachyhypopomus brevirostris* (*Pbre*), *Nannostomus trifasciatus* (*Ntri*), *Gymnorhamphichthys rondoni* (*Gron*), *Pyrrhulina capim* (*Pcap*), and *Iguanodectes rachovii* (*Irac*) (Fig. 5).

DISCUSSION

Local variables, catchment, land-use and biota structure. By considering the effect of space and the geographic characteristics (*e.g.*, macroscale variables and different basin types), we observed that the effect of land use lacks the strength to interfere in the structure of the assemblages. The significant effect of the geographic characteristics on this biota reflects the influence of the Amazon's extension and the difference of the river basins. This demonstrates that the distribution of these species is affected more by geographic dispersal barriers and different natural environmental conditions, which increases turnover (Dambros *et al*., 2017), than by the magnitude of land use in these catchments. Because of this, in general, this fish biota is more influenced by macroscale characteristics than by anthropogenic ones.

However, after removing the geographic and spatial effects from the model plotted in the dbRDA, that, besides the influence of some macroscale and local characteristics, land use was also associated with the biota of streams with deforested catchments. Therefore, without the spatial-geographic effects, we confirmed our hypothesis that fish assemblages are structured in association with both natural and anthropogenic variables that are present at different spatial scales of the catchments with different deforestation levels.

The stream ecosystem can be influenced by the interaction of different environmental factors of distinct spatial scales, either natural or anthropogenic. This association can influence the structure of the stream biota. For example, other studies, in conserved river basins of the Amazon, were identified the influence of macroscale characteristics (*e.g.*, altitude and slope) on the local variables of the streams (*e.g.*, water speed, sediments, and channel morphology) (Benone *et al*., 2017). These variables are responsible for structuring fish assemblages (Parsapour-Moghaddam *et al*., 2019). In altered catchments, we identified the influence of land use at different spatial scales on the local variables (*e.g.*, channel morphology) and fish functional structure and richness (Leitão *et al*., 2018). The fish assemblage structure from streams in less deforested catchments, which were presented in the lower quadrants of the dbRDA, showed to be related mainly to local or macroscale natural variables as discussed below.

In the lower right quadrant, *Denticetopsis epa* was the species most correlated to streams with local variables typical of a catchment with higher topography and lower soil density. In general, higher topographies are more sinuous, with more angular margins and excavated by the natural action of the hydrodynamics in the stream (Galloway, Hobday, 1996; Allan, Castillo, 2007). Indeed, sinuosity is influenced by topography, soil and vegetation characteristics (Lazarus, Constantine, 2013). In low-density soils, porosity is increased, and this condition facilitates infiltration and aeration, which results in better conditions for vegetation development (Brady, Weil, 2008; Jankauskas *et al*., 2008). A well-developed reticular system in the channels of angular margins probably propitiates the formation of the excavated margins in these streams of higher topography. *Denticetopsis epa* has already been related to forested streams in other studies in the Amazon (Ferreira *et al*., 2018).

In the lower-left quadrant, the fish assemblage structure was mainly associated with both local and macroscale variables (more clayey catchments with lower soil density). Among the local characteristics for conserved streams, we can cite the leaf banks that results from allochthonous input and, consequently, improve the local habitat complexity. Leaf banks serve as microhabitats for shelter, feeding, and reproduction of individuals from several stream-dwelling species (Muotka, Laasonen, 2002). Another effect of leaf banks is the retention of woody material in the channel, which dissipates the energy of the flow, stabilizes the margins, forms pools, and keeps the habitat complexity that supports great biodiversity (Benson, Magnuson, 1992; Junqueira *et al*., 2016).

At least partially, this local structure results from the geomorphological influence of forested catchments, where the lower slope and channel sinuosity is related to the lower elevation of the basins which, usually, has lower energy of the water flow (Sullivan *et al*., 2006), favoring the increase of input and accumulation of leaves and wood in the streams. Additionally, a lower soil density in the catchment is directly related to more clayey and less porous soils and, as we have seen, can favor a more vegetated environment by having better reticular systems (Jankauskas *et al*., 2008).

The structure of the assemblages from streams of more deforested catchments, presented in the upper right quadrant of the dbRDA, showed to be more related to anthropogenic variables of distinct spatial scales of the catchment, higher soil density, and sand in the catchment and streams. These streams were more associated, in order, with pasture, urbanization, and agriculture. Studies in other Brazilian basins indicate that, without adequate management, these activities remove the riparian cover of the drainage network and the upstream forest in the catchment, which can affect the local habitat structure (Leal *et al*., 2016) and, consequently, the different fish assemblages (Junqueira *et al*., 2016).

Deforestation decreases the input of wood and leaves into the channel (Paula *et al*., 2011) and can increase the frequency of flash floods along the basin, destabilize and erode the margins and increase sedimentation, which homogenizes the structure of the stream (Wang *et al*., 2001a,b; Allan, Castillo, 2007; Haygarth *et al*., 2012; Hughes *et al*., 2014; Leitão *et al*., 2018). Sedimentation is a process that alters the structure of fish assemblages and can even threaten functional groups (Bryce *et al*., 2010; Leitão *et al*., 2018). For example, it was identified that fish groups with functional traits associated with the benthic part of the streambed were more affected by the reduction of bed stability in altered Amazonian streams. The predominant process of this alteration was related to the destabilization of the banks, and the erosion of the exposed soil with consequent flow of high amounts of fine sediments in the channel (Leitão *et al*., 2018).

The constitution of the sandy catchment with high soil density may be contributing to this degradation since this soil is susceptible to erosion when exposed to use (Jankauskas *et al*., 2008), which may explain the sand in the channel. It is worth highlighting that many studies conducted in the Brazilian Amazon reported lower values of soil density in areas of native forest, while others described an increase in density in surface layers in areas of direct planting, in the subsurface in conventional preparation, as well as in pasture areas due to cattle trampling (Silva, 2021). Therefore, the increased density in the streams herein evaluated is a natural aspect of the soil in these catchments, but it may also be increasing due to the intensity of land use in this region. Roberts *et al*. (2016) state that, as river basins have different soil characteristics that promote different movement and transportation of sediments and nutrients, different practices of land use must consider different measures of land management.

Our results indicate that the greater influence of land uses in these catchments may be contributing to change the habitat structure (*e.g*., more sand in the channel, low habitat heterogeneity), and may be favoring the species found. Other studies found *Nannostomus trifasciatus* (*Ntri*) to be more abundant in streams bordered by palm cultivation than in forested streams (Ferreira *et al*., 2018). Widely distributed in South America, *Gymnorhamphichthys rondoni* (*Gron*) is associated with a sandy substrate, similar to others of the same genus, where it forages for prey (Zuanon *et al*., 2006) and, therefore, is highly dependent on a sandy substrate to obtain food (Tesk *et al*., 2014). *Iguanodectes rachovii* (*Irac*) presented higher constancy (50% of the samples) in streams of microhabitats dominated by agriculture in the Amazon (Corrêa *et al*., 2012). *Pyrrhulina capim* (*Pcap*) is a generalist species (Silva *et al*., 2016), *i.e*., in conditions of change, it can take the maximum advantage of the available natural resources and have a broad ecological niche. Therefore, the environmental condition of the deforested streams, combined with the living conditions of these species and where they are typically found, suggests that the evaluated species may be associated with a less complex habitat that may be favored by two conditions: a) by land use in the catchment area; b) and the characteristics of lower soil density that may be due to natural conditions of the catchment basin and/or the influence of land use.

Spatial scales and land use. We found evidence of the effect of land use in different parts of the catchment on the structure of the fish assemblage, as found in other studies as well (Dala-Corte *et al*., 2016; Bierschenk *et al*., 2019; Alvarenga *et al*., 2021; Almeida *et al*., 2022). Thus, we believe that only delimiting the areas along the drainage networks and the total area of the catchments seems to be insufficient to protect the ecosystems of these Amazon streams. In this way, it is important to develop “legal environmental strategies”, both state and federal, supported by conservation policies that align the promotion of land use, better environmental management practices and the conservation of the catchment as a whole. Thus, focus, for example, on increasing research to assess these influences on biota to respond to the impacts of these land uses.

Frimpong *et al*. (2005) evaluated the influence of land use at different widths and lengths of drainage-network buffers on fish assemblages and identified that, in streams of the region of Indiana, USA, land use in buffers measuring 30 m × 600 m predicted this biota the best. Sickle, Johnson (2008) identified, in the Willamette River basin (Oregon, USA), that land use along the drainage network influenced fish assemblages up to 10 km from the drainage, reducing to almost zero when near 30 m from the channel. Therefore, as our more altered catchments are part of a highly deforested region of the Amazon, the so-called "Deforestation Arc" (Santos *et al*., 2021), it is necessary to adopt appropriate laws, inspection and control of the distribution and magnitude of the impact of use and consequent changes on streams and their fauna.

Leal *et al*. (2018) suggested a reevaluation of the Brazilian legislation on the protection of streams and their fauna by considering the influence of land use on the biota of streams not only in the riparian zone but in the entire basin. They found a high turnover rate between basins that was influenced by land use. They observed that catchment-scale pressures had an importance that was compatible with pressures in the drainage scale on fish assemblages of Amazonian River basins.

In our study, among the most frequent uses, agriculture and urbanization showed to have a greater influence when distributed across the whole catchment, and pasture when present in 60 m buffers. This suggests that the criteria for the delimitation of protected areas of Amazonian streams must consider the differentiated influence of the types of land use along the catchment for the protection of streams and their biota.

The structure of the stream assemblages in less deforested catchments showed to be related to more natural variables, either local (*e.g*., more leaves) or macroscale (lower density associated with a larger reticular system). These characteristics seem to contribute to keeping the habitat complexity of the streams (more leaves and woody debris). On the other hand, assemblages that are in streams of more deforested catchments were associated, mainly with more anthropogenic variables, such as different land uses present in distinct areas of the catchment. These uses, together with macroscale characteristics (*i.e*., soil density, catchment consisting of sand) seem to increase the erosion capacity of the stream, favoring the local structure of a less complex habitat. That is, the joint influence of these characteristics may be making the streams more prone to erosion.

The Amazon has intensely deforested river basins that are influencing the local and biotic structure of streams with a long history of land use. In our work, we suggest that, to protect the habitat and fish of small streams in catchments of the eastern Amazon, one must evaluate the influence of distinct land uses in different parts of the catchment, not only in 30-m drainage stretches as determined by Brazilian Forest Code (CFB – law 12.651, May 25, 2012). Moreover, we suggest a better assessment of the natural weaknesses and peculiarities of streams, and the impacts of land uses on their environment and their biota. Among the peculiarities that deserve attention, we suggest the evaluation of the different soil characteristics of watersheds in land use areas, as our work presents evidence that a higher soil density favors stream degradation.

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ETHICAL STATEMENT

The Ethics Committee of the Universidade Federal do Pará approved the collection and conservation of fish (CEUA n° 8293020418).

COMPETING INTERESTS

The author declares no competing interests.

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