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Land cover, riparian zones and instream habitat influence stream fish assemblages in the eastern Amazon

Luciano F. A. Montag[1,2] | **Kirk O. Winemiller**[2] | **Friedrich W. Keppeler**[2] | **Híngara Leão**[3] | **Naraiana L. Benone**[1,4] | **Naiara R. Torres**[5] | **Bruno S. Prudente**[6] | **Tiago O. Begot**[3] | **Luke M. Bower**[2] | **David E. Saenz**[2] | **Edwin O. Lopez-Delgado**[2] | **Yasmin Quintana**[2] | **David J. Hoeinghaus**[7] | **Leandro Juen**[1]

[1]Laboratório de Ecologia e Conservação, Instituto de Ciências Biológicas, Universidade Federal do Pará, Belém, Brazil
[2]Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas, USA
[3]Programa de Pós-graduação em Zoologia, Museu Paraense Emílio Goeldi/Universidade Federal do Pará, Belém, Brazil
[4]Programa de Pós-graduação em Ecologia, Instituto de Ciências Biológicas, Universidade Federal do Pará, Belém, Brazil
[5]Programa de Pós-graduação em Ecologia Aquática e Pesca, Instituto de Ciências Biológicas, Universidade Federal do Pará, Belém, Brazil
[6]Universidade Federal Rural da Amazônia, Capitão Poço, Brazil
[7]Department of Biological Sciences, Advanced Environmental Research Institute, University of North Texas, Denton, Texas, USA

Correspondence
Luciano F. A. Montag, Laboratório de Ecologia e Conservação, Instituto de Ciências Biológicas, Universidade Federal do Pará, Belém, Brazil.
Email: lfamontag@gmail.com

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Abstract

The Amazon rainforest has experienced rapid land-use changes over the last few decades, including extensive deforestation that can affect riparian habitats and streams. The aim of this study was to assess responses of stream fish assemblages to deforestation and land cover change in the eastern Amazon. We expected that percentage of forest in the catchment is correlated with local habitat complexity, which in turn determines fish assemblage composition and structure. We sampled 71 streams in areas with different land uses and tested for relationships between stream fish assemblages and local habitat and landscape variables while controlling for the effect of intersite distance. Fish assemblage composition and structure were correlated with forest coverage, but local habitat variables explained more of the variation in both assemblage composition and structure than landscape variables. Intersite distance contributed to variance explained by local habitat and landscape variables, and the percentage of variance explained by the unique contribution of local habitat was approximately equivalent to the shared variance explained by all three factors in the model. In these streams of the eastern Amazon, fish assemblages were most strongly influenced by features of instream and riparian habitats, yet indirect effects of deforestation on fish assemblage composition and structure were observed even though intact riparian zones were present at most sites. Long-term monitoring of the hydrographic basin, instream habitat and aquatic fauna is needed to test for potential legacy effects and time lags, as well as assess species responses to continuing deforestation and land-use changes in the Amazon.

KEYWORDS
aquatic biodiversity, forest cover, human impact, landscape, local habitat, ordination, variance partitioning

1 | INTRODUCTION

Land-use change is an important driver of biodiversity change in freshwater ecosystems (Allan, 2004). Small streams are particularly sensitive to landscape alteration due to the importance of catchment inputs for maintenance of instream habitat and food web dynamics (e.g., Brejão, Hoeinghaus, Pérez-Mayorga, Ferraz, & Casatti, 2018; Leal et al., 2017; Sweeney et al., 2004). For example, deforestation can increase sedimentation and reduce woody debris inputs, resulting in simplified and homogenised habitats and altered hydrology and water chemistry (Cardinale, Palmer, Swan, Brooks, & Poff, 2002). Intact riparian zones can decrease some negative effects of catchment deforestation on streams (Chen et al., 2017; Pusey & Arthington, 2003). Removal of riparian vegetation destabilises stream banks, disrupts fluxes between terrestrial and aquatic food webs, increases solar radiation and water temperature and alters ecosystem metabolism and nutrient dynamics (Nakano & Murakami, 2001; Teresa, Casatti, & Cianciaruso, 2015; Zeni, Hoeinghaus, & Casatti, 2017).

Stream diversity often responds strongly to changes in instream conditions caused by catchment and riparian deforestation (e.g., Brejão et al., 2018; Leal et al., 2017; Teresa & Casatti, 2012). For example, as instream habitats are simplified and homogenised, populations of specialist species often decline or are extirpated, whereas generalist species tend to increase in abundance (Brejão et al., 2018; Zeni et al., 2017). Furthermore, stream longitudinal connectivity may be affected by anthropogenic disturbance occurring at different spatial scales, and disturbance at one location may impact the condition and biodiversity of a connected stream reach (Allan, 2004; Benone, Esposito, Juen, Pompeu, & Montag, 2017; Winemiller, Flecker, & Hoeinghaus, 2010). Alternatively, an impacted stream may act as a sink habitat that is repeatedly recolonised by species from an unimpacted location (Noss, 1990). From a metacommunity perspective, the aforementioned processes would represent a balance between environmental filtering and dispersal, leading to a combination of species sorting and mass effects across a heterogeneous landscape (Leibold et al., 2004; reviewed for lotic systems by Winemiller et al., 2010). However, some studies have found that stream fish assemblages appeared to be minimally affected by deforestation, and in some cases, richness and density increased in impacted areas (Bojsen & Barriga, 2002; Burcham, 1988; Toham & Teugels, 1999). These findings suggest that the effect of forest cover may be context dependent, vary according to scale, or be influenced by other factors (e.g., temperature, habitat complexity), any of which could hinder discovery of general relationships.

Effects of deforestation on biodiversity are especially concerning in megadiverse tropical regions (Laurance, Sayer, & Cassman, 2014). At the global scale, approximately 13 million hectares of forests were cleared annually between 2000 and 2010, with most of that deforestation occurring in developing countries of the tropics, especially in South America (Blaser, Sarre, Poore, & Johnson, 2011). This is unsurprising given that accelerated land-use change is driven by growth of human populations; economic activities; and/or demand for food, timber products and energy (Laurance & Balmford, 2013; Lobón-Cerviá, Mazzoni, & Rezende, 2016). For example, the Amazon region has the world's largest remaining tropical forest but also high rates of deforestation due to a rapidly growing population (currently >30 million people) that is largely supported by natural resource extraction and land conversion for agriculture (Gardner et al., 2013). Despite the fact that deforestation rates are highest in tropical regions, impacts of deforestation on aquatic biodiversity are poorly documented in the tropics compared with temperate regions. Given considerable differences in climate, land cover, biodiversity and other aspects between tropical and temperate regions, it is unclear whether generalisations from temperate research directly apply to tropical settings. Thus, research on effects of deforestation on tropical systems is urgently needed.

Herein, we report findings from an extensive survey of 71 streams in the eastern Amazon basin that share the same regional species pool and similar climate, native vegetation, topography and geology but differ in the type and intensity of catchment land cover change. We hypothesised that the regional fish metacommunity is structured by a combination of species sorting and mass effects (Leibold et al., 2004; Winemiller et al., 2010). Specifically, we expected that local habitat (primarily habitat complexity, which we predict is associated with percentage of forest in the catchment) is the primary driver of fish assemblage structure (i.e., species sorting), and that distance between sites may account for some additional variation due to potential movement among sites (i.e., mass effects). Local habitat features previously reported to influence stream fish assemblages were measured (i.e., instream and riparian zone), and analyses included factors at different landscape scales (i.e., immediate and total catchments) while controlling for spatial autocorrelation. Variance partitioning was used to assess the relative importance of unique and shared contributions of local and landscape factors to fish assemblage composition and structure.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area lies within a region of the eastern Amazon (Pará State, Brazil) that historically was covered by dense ombrophilous (tolerant of wet conditions) forest. The climate is classified as equatorial "Af" in the Köppen system (Peel, Finlayson, & McMahon, 2007). Mean annual temperature is 27.2°C, and the mean annual precipitation is 1,800 mm, with rainfall well-distributed throughout the year and exceeding 50 mm even in the driest months (i.e., August through October; Watrin & Rocha, 1992). In recent decades, the region has experienced increased deforestation for timber harvest (Pereira, Zweede, Asner, & Keller, 2002) and clearing for pastures and crops. Presently, oil palm production is the main crop, but interest in sugarcane is increasing. Most of the remaining forests are subjected to reduced-impact logging that aims to minimise damage to soil and forest, or conventional logging that involves minimal consideration of forest resilience (Prudente, Pompeu, Juen, & Montag, 2017). Within our study region, conventional logging started in the 1970s, oil palm has been cultivated since the 1980s, and reduced-impact logging was established in 2000 under guidelines proposed by the mandatory forest management plan of the Brazilian Forest Code (Law 4.771/65; Brasil, 1965). Some of the sites sampled in this study were surveyed in previous studies (Benone et al., 2017; Ferreira, Begot, Prudente, Juen, & Montag, 2018; Juen et al., 2016; Prudente, Pompeu, & Montag, 2018; Prudente et al., 2017). Related studies from the project Sustainable Amazon Network (Rede Amazônia Sustentável) by Leitão et al. (2018), Gardner et al. (2013) and Leal et al. (2016, 2017) are from the same basin, but different sampling sites.

2.2 | Study design

We sampled the fish assemblages at 71 sites in 1st- to 3rd-order streams in areas with different land-use patterns within the Acará and Capim catchments (Figure 1). We selected each stream based on land cover (logging, crops, pasture and forest), accessibility and relative independence of sites across subdrainages (i.e., a minimum fluvial distance of 2 km between sampling sites was used to avoid pseudoreplication). The drainage network was constructed from a SRTM Digital Elevation Model with a spatial resolution of 30 metres (https://earthexplorer.usgs.gov/). We avoided sampling streams near roads or bridges; in situations where it was not possible to avoid these built structures, we sampled fish at least 500 m upstream of these structures. We measured or estimated local and landscape variables (defined below) at each site, and fluvial distance was measured between all pairs of sites using 1:100,000 scale images. Fishes were surveyed, and local environmental data were collected during the dry season (August–October, between 2012 and 2015)

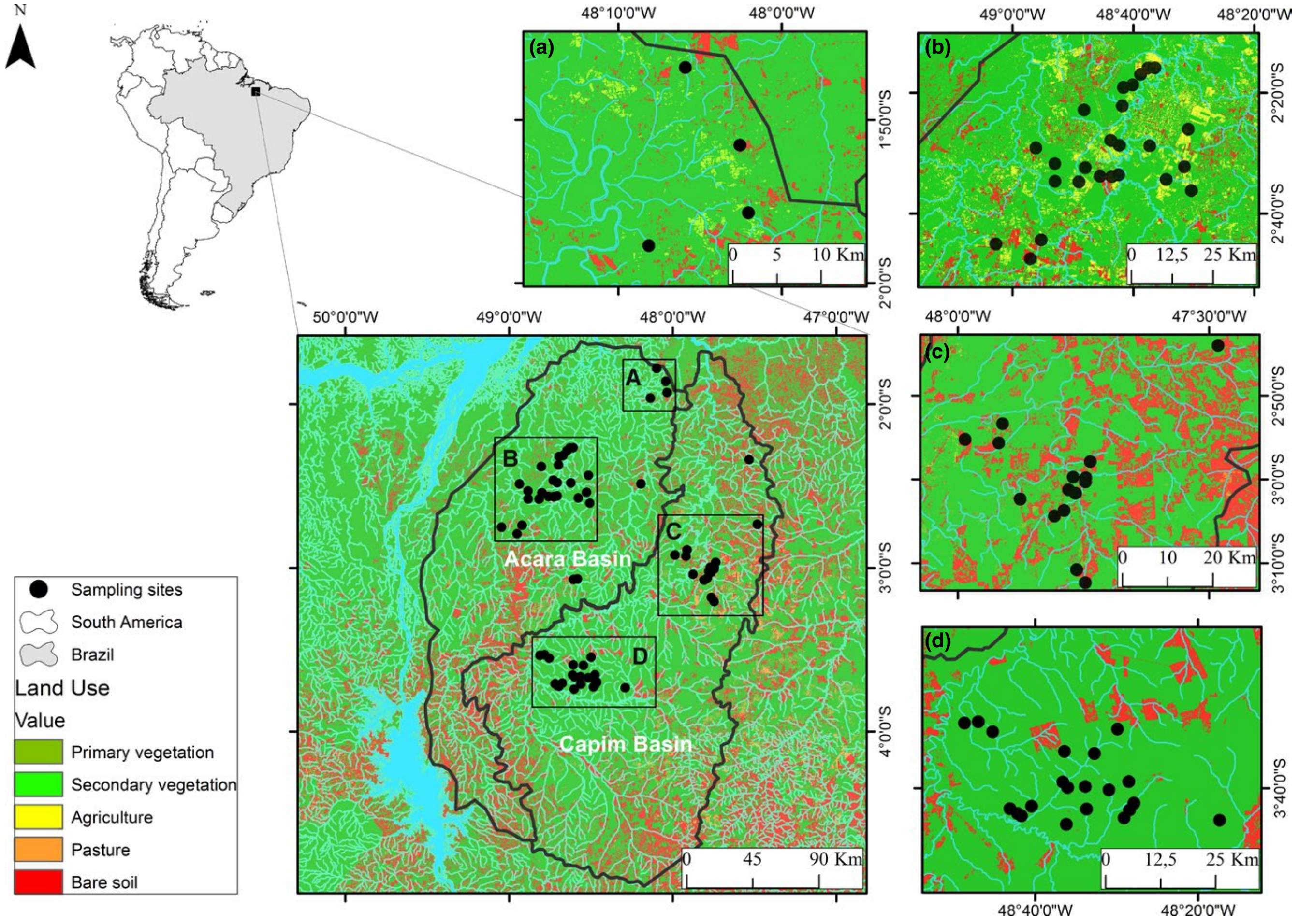

FIGURE 1 Study area in the Acará–Capim basin (eastern Amazon, Brazil). Survey sites (n = 71) are denoted by black circles, and land-use categories (i.e., primary forest, secondary forest, agriculture, pasture and bare soil) are denoted by colours within each catchment (solid black lines)

when discharge is lowest and sampling efficiency is greatest, and to avoid influence from seasonal variation (Espírito-Santo, Magnusson, Zuanon, Mendonça, & Landeiro, 2009). According to historical data (Meteorological station Belém—PA—OMM: 82191; INMET, 2018), there were no abnormal periods of precipitation and temperature in the study area during 2012–2015. We observed no significant human disturbance in the study area during the study period, and interannual differences are not expected to influence results and conclusions.

2.3 | Fish assemblage structure

We sampled the fish assemblages with two circular 55-cm-diameter dip nets with 2-mm mesh. This active sampling method was used along stream channel banks and substrates and enabled efficient sampling of most microhabitats within these small streams (Uieda & Castro, 1999). The sampling unit for this study was a 150-m stretch of each stream, subdivided into 10 subsections of 15 m each. During each stream survey, total sampling effort was 18 min for each subsection, totalling 3 hr of effort per site (Ferreira et al., 2018; Prudente et al., 2017). Collected fishes were euthanised with lethal doses of the anaesthetic Eugenol, fixed in a 10% formalin solution and transferred to 70% ethanol after 48 hr. In the laboratory, specimens were identified to the lowest feasible taxonomic level using published keys (e.g., Albert, 2001; Reis, Kullander, & Ferraris, 2003; Van der Seen & Albert, 2018) and, in some cases, examinations by specialists. Specimens were deposited in the ichthyological collection of the Museu Paraense Emílio Goeldi (MPEG) in Belém, Brazil. Surveys were conducted under permit #4681–1 from the Instituto Chico Mendes de Conservação da Biodiversidade of the Ministério do Meio Ambiente (Brazilian Ministry of the Environment).

2.4 | Environmental variables

Instream habitat and riparian zone variables (hereafter cited as “local variables”) were measured following the method proposed by Peck et al. (2006), with data reduction and metric calculations following Kaufmann, Levine, Robison, Seeliger, and Peck (1999). We collected data for environmental variables that have shown significant associations with stream fish assemblages in the eastern Amazon (e.g., Ferreira et al., 2018; Juen et al., 2016; Prudente et al., 2017). We measured 26 physical (e.g., substrate, discharge and flow regime) and chemical (e.g., pH and dissolved oxygen) variables that comprise seven general categories: channel morphology, substrate, flow, large woody debris, fish cover, riparian vegetation cover and human impact (Table 1). Human impact was estimated as the proportion of the stream reach directly affected by the presence of channelisation, dams, buildings, roads, pipelines, rubble and rubbish. This was calculated by dividing the number of human-influenced subsections by the total number of subsections (10 per stream reach). Thus, the variable ranged from 0, in stream reaches without any human influence, to 1 in completely modified stream reaches (human influence present along the entire stream stretch studied; for details, see Kaufmann et al. (1999)).

We quantified land cover variables for the entire drainage network upstream of the sampling site (hereafter “total catchment”) and within a 30-m buffer extending 300 m upstream and downstream from the sampling site (hereafter “immediate catchment”; see Supporting Information Figure S1) to capture potential landscape influences on stream fish assemblages (Frimpong et al., 2005; Molina, Roa-Fuentes, Zeni, & Casatti, 2017). Buffer zones at the immediate catchment scale are comparable to the way riparian buffers are measured according to Brazilian law. Land cover classifications followed Zhu, Li, Wang, Chu, and Yan (2017) and included the following: (a) primary vegetation, characterised by areas with dense ombrophilous forest; (b) secondary vegetation, with vegetation resulting from natural succession processes after total or partial suppression of primary vegetation by anthropogenic actions or natural causes; (c) agricultural areas, with areas occupied by agricultural activities, including both monocultures and polycultures; (d) pasture, with areas occupied by intensive and/or extensive livestock farming; and (e) bare soil, with areas of unprotected soil, mainly containing road networks, such as dirt roads and highways.

Land cover was classified through digital image processing of the RapidEye Earth Imaging System (REIS) optical sensor. REIS sensor images cover an area 77 km wide by 1,500 km long with a 5-m spatial resolution and 5-band spectral resolution, which allows for greater precision in the classification of land use and ground cover. Images were selected from the same year that the field surveys were conducted. All images were grained and orthorectified and then subjected to atmospheric correction to attenuate the effects of the atmosphere on the spectral response of the targets in the scenes and convert the digital number pixel values to reflectance (Richards & Jia, 1999). This image processing was performed with PCI Geomatics 2015 software using the ATCOR Ground Reflectance module. After atmospheric correction of the images, a mosaic of REIS scenes was compiled using the OrthoEngine module and the REIS mosaic was submitted to object-oriented classification using eCognition 9 software. Validation of the classification was performed with TerraClass 2014 images provided by the Instituto Nacional de Pesquisas Espaciais (Almeida et al., 2016).

2.5 | Data analysis

Analytical procedures to assess the unique and shared contributions of local habitat, landscape and intersite hydrographic distance on stream fish assemblages generally followed the method described by Borcard and Legendre (2002), which is based on redundancy analyses (RDA; Legendre, Oksanen, & ter Braak, 2011). Abundance data were transformed using a Hellinger transformation in order to avoid biases caused by the species abundance paradox (Legendre & Gallagher, 2001). A principal coordinates of neighbor matrices (PCNM) analysis was conducted using the matrix of intersite fluvial distances to generate variables that represent distance components (Landeiro, Magnusson, Melo, Espírito-Santo, & Bini, 2011). Two

TABLE 1 Summary of among-stream variation in local habitat and landscape variables (*SD* = standard deviation)

Factor	Variable	Abbreviation	RDA	Mean	*SD*	Min.	Max.
Local habitat	*Channel morphology*						
	Mean depth of thalweg (cm)	**DEPTH**	**C, S**	**30.5**	**7.16**	**18.53**	**44.43**
	_SD_ depth of thalweg (cm)	**SD_DEPT**	**S**	**12.03**	**3.53**	**5.75**	**24.34**
	_SD_ incision height (m)	**SD_INC**	**C, S**	**1.34**	**1.08**	**0**	**3.98**
	Mean longitudinal section width × depth ratio (m/m)	**WD_RAT**	**C**	**9.12**	**2.38**	**4.59**	**16.32**
	Substrate						
	Silt/muck/clay (%)	SILT		10.95	8.93	0	30.67
	Total organic matter (litter, wood, roots and algae) (%)	ORGAN		58.72	16.42	28	100
	Wood (%)	WOOD		8.52	7.27	0	40
	Roots (%)	ROOTS		9.41	9.11	0	48.57
	Coarse litter (%)	LITTE		26.2	15.66	0	61.54
	Mean residual pools (m^2/150 m of channel)	POOLS		1.62	0.72	0.5	5.35
	Flow						
	Riffle (%)	RIFFL		1.25	3.04	0	18.67
	Fast channel habitats (%)	FAST		26.49	24.84	0	94
	Sequence fast flow, slow flow and pools (index)	SEQ_FLW		0.12	0.06	0.01	0.31
	Riparian vegetation cover						
	_SD_ canopy density banks (%)	**SD_BANK**	**S**	**6.77**	**6.18**	**0.89**	**37.2**
	Mean area covered by herbaceous vegetation layer >0.5 cm	**HERB**	**S**	**2.7**	**5.71**	**0**	**27.84**
	Mean woody cover	**WOODY_C**	**C, S**	**111.81**	**55.82**	**17.27**	**236.25**
	SD woody cover	SD_WD_C		26.32	8.33	10.13	49.77
	Large woody debris						
	Number LWD inside bankfull channel/m^2 – size class 1	LWD1		0.12	0.09	0	0.37
	Number LWD inside + above/m^2 – size class 3	LWD3		0.15	1.18	0	10.05
	Fish cover						
	Mean large woody debris areal cover	WD_DB_C		13.04	11.08	0.46	51.14
	Proportion of trees and roots	TREE_ROO		0.92	0.13	0.46	1
	Proportion of undercut banks	**UND_BAN**	**C, S**	**0.33**	**0.34**	**0**	**1**
	Human impact						
	Proportion of human impact	**IMPAC**	**S**	**0.34**	**0.35**	**0**	**1**
	Water quality						
	pH	PH		4.85	0.53	3.45	6.92
	Electrical conductivity (μS/cm)	**COND**		**0.02**	**0.01**	**0.01**	**0.04**
	Dissolved oxygen mg/L	**DO**	**C**	**7.6**	**3.24**	**2.98**	**14.9**
Landscape	*Total catchment (%)*						
	Primary forest	PRI_T		64.26	39.57	0	100
	Secondary forest	**SEC_T**	[a]	**9.83**	**20.03**	**0**	**99.05**
	Agriculture	AGR_T	[a]	12.78	29.39	0	100
	Pasture	PAS_T	[a]	4.76	14.62	0	93.99
	Bare soil	BAR_T	[a]	7.21	16.82	0	93.78
	Immediate catchment (%)						
	Primary forest	**PRI_I**	[a]	**60.35**	**43.65**	**0**	**100**
	Secondary forest	**SEC_I**	[a]	**9.34**	**19.86**	**0**	**95.04**
	Agriculture	AGR_I	[a]	15.69	31.56	0	100
	Pasture	PAS_I	[a]	3.9	13.2	0	69.79
	Bare soil	BAR_I	[a]	10.72	24.03	0	97.1

Notes. Bold print denotes variables retained after forward selection in RDAs for fish assemblage composition and structure, and C and S in the "RDA" column denote which analyses (composition and structure respectively) the variable was included in.

[a] Landscape variables were reduced in PCAs before being included in the RDA analysis (see Table 2).

TABLE 2 Results of the principal component analysis for landscape variables. Loadings indicate the contribution of each variable to the first and second principal components. Superscript "C" indicates axes that were important for fish composition data and superscript "S" for fish structure

		Loading	
Landscape variables	**Abbreviation**	**PC1_T**	**PC2_T^{C}**
Total catchment			
Primary forest	**PRI_T**	**0.85**	−0.25
Secondary forest	**SEC_T**	−0.16	**0.49**
Agriculture	**AGR_T**	**−0.47**	**−0.75**
Pasture	PAS_T	−0.08	0.23
Bare soil	BAR_T	−0.12	0.26
% explained		62.6%	20.5%
Eigenvalues		2121.5	696.6
		PC1_I^{CS}	**PC2_I^{C}**
Immediate catchment			
Primary forest	**PRI_I**	**0.84**	0.20
Secondary forest	SEC_I	−0.14	−0.24
Agriculture	**AGR_I**	**−0.46**	**0.72**
Pasture	PAS_I	−0.02	−0.06
Bare soil	BAR_I	−0.21	**−0.61**
% explained		64.1%	19.4%
Eigenvalues		2631.7	798.3

Notes. Variables in bold are important for principal component interpretation.

PCNM eigenvectors were extracted and used as conditional (i.e., to control for effects of intersite distance) or predictor variables in subsequent analyses. The significance of the PCNM axes was tested by Moran's I statistic (Landeiro et al., 2011).

Independent RDAs were conducted using each of the three environmental datasets (i.e., local habitat, landscape, distance) to explain variation in fish assemblage composition (i.e., species presence–absence) and structure (i.e., species relative abundances). Variance inflation factors (VIF) were assessed to identify potential multicollinearity among environmental variables within total catchment and immediate catchment scales. Values >10 (Curto & Pinto, 2010) indicated that landscape variables for both total catchment and immediate catchment were highly autocorrelated. Therefore, principal components analysis (PCA) was used to generate composite gradients (i.e., PC1 and PC2) representing landscape attributes for both catchment scales that could be included in subsequent RDAs. To simplify the RDA models generated, we used forward selection based on permutation tests (9,999 randomisations) to include only those variables that significantly contributed to variance explained. The adjusted coefficient of multiple determination (adjusted-R^2) for each global model was calculated and used as a secondary stopping criterion for forward selection (Borcard & Legendre, 2002).

To visualise the relationships between fish assemblages and local habitat and landscape variables selected in the RDA models, a combined RDA was conducted with PCNM axes included as conditional factors to control for effects of intersite distance. Next, variance partitioning was conducted using partial RDA (i.e., pRDA) to identify the unique and shared contributions of local habitat, landscape and distance for explaining fish assemblage composition and structure (Peres-Neto, Legendre, Dray, & Borcard, 2006). Only variables selected in the independent RDA analyses were included, significant variables with loadings >|0.6| were considered important, and significance of unique contributions of local habitat, landscape and distance variables was assessed using permutation tests.

All analyses were performed using R (R Core Team, 2013). PCNM, RDA and pRDA were implemented using the *vegan* (Oksanen et al., 2018) and *packfor* packages (Dray, Legendre, & Blanchet, 2011), and the *faraway* package was used to calculate VIF (Faraway, 2016). Significance was assessed as $p \le 0.05$.

3 | RESULTS

3.1 | Fish assemblages and significant environmental variables

Ninety-one fish species represented by 27,733 specimens were collected during surveys. Approximately half of the species were considered rare (i.e., 46 species with <15 individuals collected; Supporting Information Table S1). Six species represented approximately 70% of the total sample abundance. Those six species were *Hyphessobrycon heterorhabdus* (8,460 specimens, captured from 70 sites), *Microcharacidium weitzmani* (4,372 specimens, 56 sites), *Apistogramma* gr. *regani* (2,405 specimens, 59 sites), *Copella arnoldi* (1,975 specimens, 50 sites), *Iguanodectes rachovii* (1,170 specimens, 49 sites) and *Pyrrhulina* aff. *brevis* (1,034 specimens, 67 sites).

Only 6 of the 26 local habitat variables were selected for inclusion in the assemblage composition RDA, and eight local habitat variables were selected for the assemblage structure RDA (Table 1). Surprisingly, none of the variables associated with substrate, flow or woody debris were included in either RDA. All channel morphology variables were selected in either the final model for assemblage composition or structure (Table 1). Other variables included in either model were three variables associated with riparian vegetation (standard deviation of canopy density, mean area covered by herbaceous vegetation layer >0.5 cm and mean area of woody cover), one fish cover variable (proportion of undercut banks), human impact and dissolved oxygen concentration (Table 1).

All landscape variables had high among-site variation (Table 1), and PCA yielded similar patterns for the total (T) and immediate (I) catchment scales. At the total catchment scale, the first two principal components explained 83.1% of the variation in landscape features (Table 2). PC1_T (62.6% variance explained) was positively associated with primary vegetation cover and negatively associated with agriculture, whereas PC2_T (20.5%) was positively associated with secondary vegetation and negatively associated with agriculture. For the immediate catchment scale, PC1_I and PC2_I explained 83.5% of the total variation (Table 2). PC1_I (64.1%) was positively associated with primary vegetation and negatively associated with agriculture, and PC2_I (19.4%) was positively associated with agriculture and negatively associated with secondary vegetation. Forward selection included both PC axes from the immediate catchment scale (PC1_I and PC2_I) and PC2_T from the total catchment scale in the RDA for assemblage composition; only PC1_I from the immediate catchment was selected in the RDA for assemblage structure.

Both PCNM axes were significant (Moran's I, *p*-value <0.001) and explained 65.9% of the variation in the intersite distance matrix (PCNM1: 38.7% variance explained, Moran's *I* = 0.83; PCNM2: 27.2%, Moran's *I* = 0.72). Only PCNM1 was selected for inclusion in the final model for the RDA for assemblage composition, whereas both PCNM axes were included in the RDA for assemblage structure (Supporting Information Table S2).

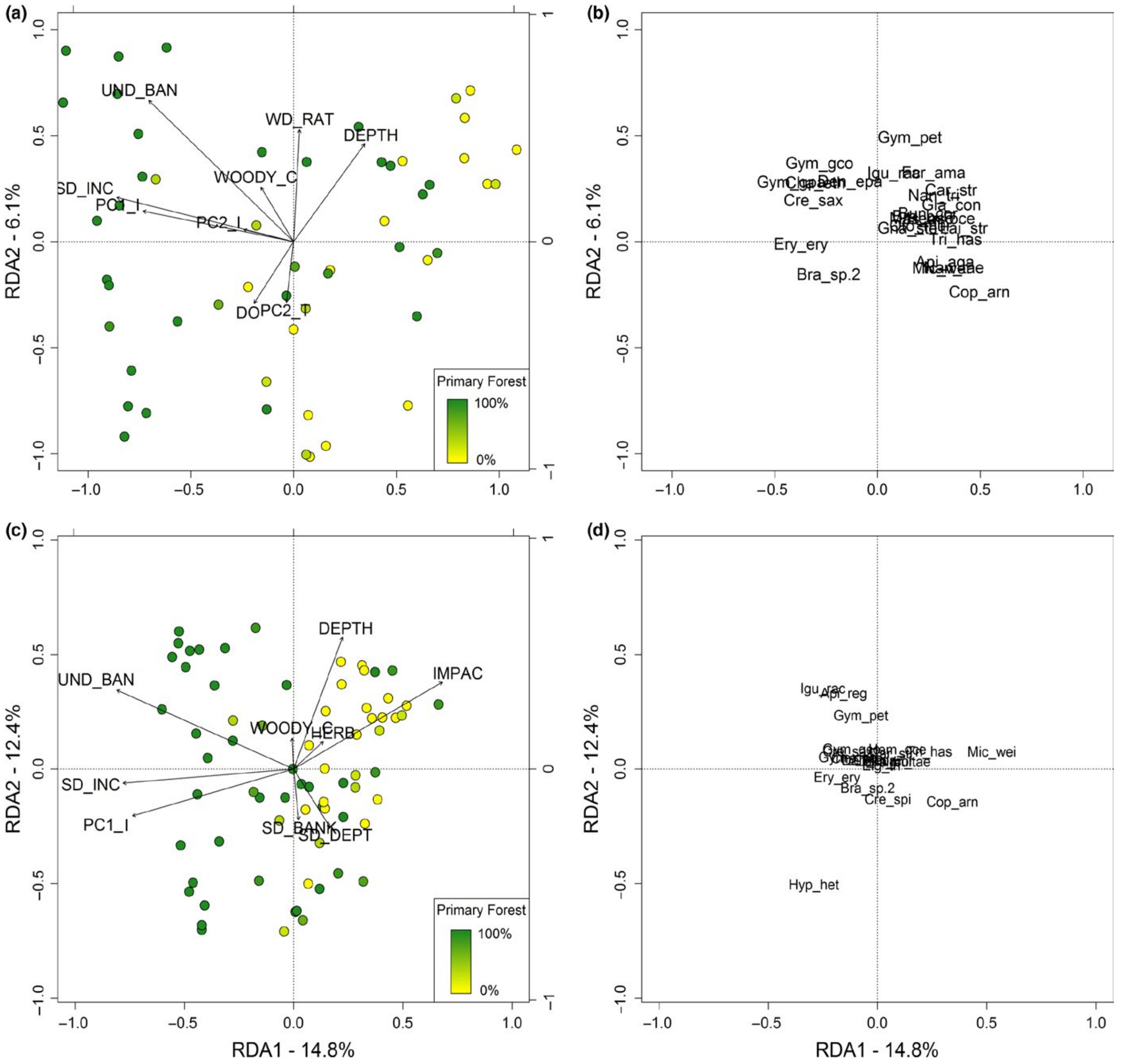

FIGURE 2 Redundancy analysis biplots for fish assemblage composition (a and b) and structure (c and d). PCNM axes were used as conditioning variables to control for spatial relationships prior to explaining variation attributed to instream habitat and landscape variables. Biplots show RDA scores for 71 streams spanning a gradient of forest cover that ranges from yellow, representing nonforest, to green, representing a densely forested in watershed. Species with goodness of fit lower than 0.2 were omitted from the plot for ease of interpretation. Some species abbreviations in plots (b) and (d) were removed to improve legibility; see Supporting Information Table S1 for species RDA axis loadings. Codes for environmental variables and species are given in Tables 1 and 2, respectively

3.2 | Fish assemblage–environment relationships and variance partitioning

The first two RDA axes ($F = 2.84$; $df = 9$; $p < 0.001$), constrained by local and landscape variables and conditioned by distance, accounted for 16.9% of the total variation in fish assemblage composition among sites. Axis 1 explained 10.8% of the variation and was associated with *SD* of incision height, PC1_I and proportion of undercut banks (Figure 2a; Supporting Information Table S3). Axis 1 was correlated with a gradient of forest cover (Pearson correlation = −0.68) with high forest cover sites associated with negative scores and low forest cover sites with positive scores (Figure 2a). Axis 2 explained 6.06% of the variation and was associated with proportion of undercut banks, width-to-depth ratio and depth (Figure 2a). The primary fish species associated with forested sites and greater variation in bank incision height and greater proportion of undercut banks were *Denticetopsis epa*, *Brachyhypopomus* sp. 2, *Characidium* cf. *etheostoma*, *Crenicichla* gr. *saxatilis*, *Erythrinus erythrinus*, *Gymnotus* gr. *coropinae* and *G.* gr. *pantherinus* (Figure 2b; Supporting Information Table S4).

For assemblage structure (species relative abundances), the first two RDA axes ($F = 4.36$; $df = 9$; $p < 0.001$) explained 27.2% of the variation. The first axis accounted for 14.8% of the variation explained and, similar to the assemblage composition analysis, was negatively correlated with forest cover (Pearson correlation = −0.73; Figure 2b). Incision height *SD*, proportion of undercut banks and PC1_I were associated with negative values on Axis 1 and high forest cover, whereas human impact loaded positively on the first axis and is associated with low forest cover (Figure 2c; Supporting Information Table S3). Depth was positively associated with Axis 2. Species distinguishing assemblage structure of forested sites include *Crenicichla* gr. *saxatilis*, *Characidium* cf. *etheostoma*, *Erythrinus erythrinus*, *Gymnorhamphichthys petiti*, *Gymnotus gr. coropinae*, *G. gr. pantherinus*, and *Crenicichla* gr. *saxatilis*, whereas species distinguishing assemblage structure of nonforested sites with human impacts were *Hemigrammus ocellifer*, *Potamoglanis hasemani*, *Nannacara* cf. *taenia*, *Carnegiella strigata* and *Bunocephalus coracoideus* (Figure 2d; Supporting Information Table S4).

Local habitat variables explained greater proportions of unique variation in assemblage composition and structure than either landscape variables or fluvial distance (Figure 3). Specifically, local habitat factors alone explained 8% of the variation in assemblage composition ($F = 2.11$; $p < 0.001$) and 14% of the variation in assemblage structure ($F = 2.76$; $p < 0.001$). Variance explained by landscape and distance variables alone never exceed 3%, whereas the shared components of variance explained were similar to that of local habitat alone (Figure 3; Supporting Information Table S5). Variation explained by local habitat and fluvial distance together was 4% and 8% for assemblage composition and structure, respectively, and the shared variation explained by all three predictor categories together was an additional 4% for assemblage composition and 7% for structure (Figure 3).

4 | DISCUSSION

As expected, fish assemblages of eastern Amazonian streams were significantly associated with both landscape, represented mainly by per cent forest cover, and local habitat variables. However, fish assemblages were more strongly related to local habitat than landscape features. Similarly, Terra, Hughes, and Araújo (2016) and Roa-Fuentes and Casatti (2017) found that fish assemblage structure was more influenced by local variables than catchment and spatial variables. In a separate study involving different sites within our study basin, Leal et al. (2017) also found that fish assemblages were more strongly associated with local habitat variables than landscape features. In contrast to reports of strong associations between catchment characteristics, instream habitat and fish assemblages in other regions (e.g., Lorion & Kennedy, 2009), we found relatively weak relationships between landscape and local habitat variables with fish assemblage composition and structure (<15% of variation in assemblage composition or structure was explained by each set of variables). Inclusion of the variable "intersite distance" in the model nearly doubled the percentage of variation explained by sets of landscape or local habitat variables (Figure 3). Similar findings were reported from other stream fish studies (e.g., Grenouillet, Pont, & Hérissé, 2004; Magalhães, Batalha, & Collares-Pereira, 2002). Furthermore, approximately half of the variance explained for assemblage composition and structure is shared among the combination of instream habitat and distance plus all three predictor-variable categories (distance, local habitat and landscape).

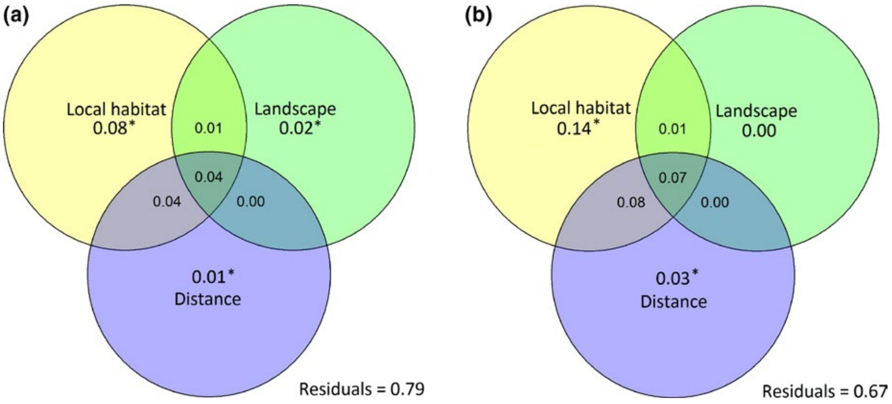

FIGURE 3 Venn diagram summarising variance partitioning (pRDA) among local habitat, landscape and distance variables for fish assemblage composition (a) and structure (b). *indicates $p < 0.05$ for the testable components (unique contributions of local habitat, landscape and distance)

Based on previous research, we hypothesised that landscape factors would indirectly affect fish assemblages through influences on local habitat. Land cover varied along a gradient ranging from 100% primary vegetation to deforested agricultural areas. Terrestrial landscapes influence processes such as rainwater retention and inputs of sediments and allochthonous food resources in small streams, such as those in this study (Leal et al., 2017). Rainwater retention depends on humidity, temperature and soil porosity, all of which are strongly influenced by vegetation cover. Many energy sources supporting tropical stream food webs (e.g., terrestrial arthropods, leaves, seeds, fruits) originate from riparian vegetation (Brejão, Gerhard, & Zuanon, 2013). Land cover was only weakly (though significantly) correlated with assemblage composition and structure, and standard deviation of incision height and proportion of undercut banks exhibited similar relationships in the RDAs, but with greater variation explained in partitioning analyses. These results support our expectation that the relationship between land cover and fish assemblage composition and structure is probably derived from indirect effects of landscape on local habitat (including the shared variance explained by landscape and local factors).

The strength of the relationship between land cover and fish assemblages is highly variable among regions (e.g., Tiburcio, Carvalho, Ferreira, Goitein, & Ribeiro, 2016). Over the last few decades, the Amazon region has undergone changes in forest cover with impacts to both terrestrial and aquatic ecosystems (Juen et al., 2016; Laurance et al., 2014). In the eastern Amazon, there is some evidence that certain features of stream ecology appear to be maintained despite impacts from deforestation (Ferreira et al., 2018). In our study, most fish species were not strongly associated with landscape variables, initially suggesting some degree of resilience to land-use impacts at the catchment scale (Uieda & Pinto, 2011). For example, stream network connectivity could allow species with high dispersal capacity to persist in degraded habitats via mass effects (Perkin & Gido, 2012). The contribution of distance to the shared variance explained by local habitat and all three predictor categories together provides some support for this interpretation, but there was no shared variation explained by distance and landscape together (i.e., without inclusion of local instream habitat), and therefore, habitat filtering is presumed to play a dominant role in structuring the fish assemblages. One plausible explanation for the limited relationship between landscape variables and fish assemblages is the presence of primary and secondary forest within local catchments or riparian zones. Forest cover in the riparian zone could minimise the impacts of reduced forest cover in the catchment on instream habitat and fish assemblages (Terra et al., 2016). A minimum width of riparian buffer, as required by Brazilian law, was present at most of our survey sites, which may have mitigated the negative effects of land-use changes on local catchments. However, the primary axis in RDA analyses was essentially a gradient of primary forest cover, and the local habitat variables selected in the RDA are likely affected by catchment land use and human impact. Thus, deforestation appears to be indirectly affecting stream fish assemblages through alteration of instream habitat *even though* riparian zones are mostly intact. This interpretation corroborates findings by a recent study conducted by Leal et al. (2017), which concluded that the minimum riparian buffer established by Brazilian law was not sufficient to protect stream fish biodiversity.

The habitat variables with the strongest correlations with patterns of species composition and assemblage structure in forested sites were undercut banks and the standard deviation of incision height. In contrast, sites with mostly deforested catchments tended to be deeper (with low variation in incision height) and have greater per cent of human impact. Riparian vegetation promotes steeper and more stable banks with undercuts that provide cover for aquatic organisms (Florsheim, Mount, & Chin, 2008). Incision height variance is an important metric of channel morphology as well as an indicator of streambed degradation. High incision height variance can result from natural erosion processes (Duncan, Goodloe, Meyer, & Prowell, 2011), but could also reflect recent erosion in response to human impacts (e.g., discharge of urban storm water or rapid run-off from a degraded catchment) (Rogger et al., 2017). Low incision height variance has been associated with stream channel simplification and low habitat complexity (Roni, Pess, Beechie, & Hanson, 2014). In our study, higher values of the standard deviation of incision height were associated with greater forest cover, suggesting that these forested areas may support natural processes of erosion and deposition that promote stream channel complexity (e.g., caused by a high frequency of small-scale disturbances such as individual tree falls). Low incision height variation and greater depth in deforested sites suggest that deforestation affects stream fish assemblages through loss of geomorphic complexity due to erosion and down-cutting.

The fish species that were strongly associated with undercut banks and forested areas were those that inhabit structurally complex microhabitats (e.g., *Characidium* cf. *etheostoma*, *Erythrinus erythrinus*, *Gymnotus* gr. *coropinae*, *G.* gr. *pantherinus* and *Brachyhypopomus* sp. 2). Gymnotiformes are nocturnal fishes that often take refuge in undercut banks during daytime (Brejão et al., 2013; Maxime & Albert, 2009). Because they are strongly reliant on their electrosensory system, gymnotiformes are particularly sensitive to changes in water quality and have been promoted for use as bioindicators (Thomas, Flroion, & Chretien, 1998). Characiform fishes of the genera *Characidium* and *Erythrinus* are diurnal benthic species that generally inhabit leaf packs, twigs and other structurally complex microhabitats from where they ambush prey (Brejão et al., 2013). Consequently, these species benefit from accumulation of debris from riparian forests in stream channels. Fishes positively associated with non-forested areas were mostly diurnal omnivorous species. Some of these species are benthic (e.g., *Bunocephalus coracoideus* and *Microcharacidium weitzmani*), and others swim actively within the water column (e.g., *Carnegiella strigata*, *Copella arnoldi*, *Hemigrammus ocellifer*, *Laimosemion* cf. *strigatus* and *Nannacara* cf. *taenia*; Brejão et al., 2013).

Direct human influence on local habitat affected fish assemblage structure and was negatively associated with forest cover. Expansion of road networks directly increases stream channel erosion and sedimentation, promotes further expansion of agriculture and access to streams and disrupts connectivity (Leal et al., 2016; Leitão et al., 2018; Wantzen & Mol, 2013). Disrupted connectivity likely affects the potential for dispersal and the importance of intersite distance on assemblage composition and structure. Within our study area, non-forested areas usually were associated with dirt roads. In addition to run-off, vehicles and wind suspend dust from the dirt road network, and deposition of sediment in streams modifies habitat and ecological dynamics (Croke & Mockler, 2001). For example, excessive sedimentation and silting reduce the availability of structurally complex habitat for benthic fishes, resulting in local assemblages dominated by habitat generalists (Brejão et al., 2013).

A recent study by Brejão et al. (2018) in the western Amazon found that many stream fishes exhibited significant negative threshold responses to low levels of catchment deforestation within just a few years of the impact, whereas positive responses by generalist species occurred many years after deforestation. In addition, past land-use change could have a legacy effect on contemporary biodiversity; thus, there may be time lags for observable responses to impacts (Iwata, Nakano, & Inoue, 2003; Zeni et al., 2017). Thus, an important consideration is the temporal sequence of anthropogenic impacts. For example, the lack of strong relationships between catchment land use and fish assemblage composition and structure in this study could be partly due to a time lag in response of instream habitat to changes in land use and/or a lag in assemblage response to instream habitat change. Such time lags could mask impacts of land-use change on stream fish assemblages such that interpretations of analyses using contemporary landscape features (e.g., deforested catchments) suggest resilience of fish assemblages to landscape change when in fact the timescale was too short to detect a response (Brejão et al., 2018; Iwata et al., 2003; Zeni et al., 2017). Thus, longer-term studies may be required to elucidate effects of land-use gradients on assemblage structure, especially if catchments are subjected to variable periods and types of land uses, and if specialist taxa have already been extirpated (Zeni et al., 2017).

Given the strong interrelationships between terrestrial and aquatic habitats (Tambosi, Vidal, Ferraz, & Metzger, 2015), management of riparian vegetation has become the main strategy to maintain the ecological quality and integrity of stream ecosystems (White & Greer, 2006). For this reason, Brazil's forest code designated riparian zones throughout the country as Permanent Preservation Areas. However, in areas such as the Amazon, where agro-industry activities are rapidly expanding, the legally established limits for riparian zones are often disrespected (Baraka & Katz, 2015). Our results indicate that although most streams in the study area present relatively intact riparian zones, even across different levels of deforestation in the basin, focusing solely on the conservation of riparian vegetation may be insufficient for maintaining the biotic components of streams (Leal et al., 2017). It is also important to consider the dendritic nature of stream systems and fluvial connectivity (i.e., intersite distance contributed to shared variance explained by local habitat and landscape variables in our study) as well as the catchment landscape. For example, deforestation increases the vulnerability of riparian zones to edge effects, compromising the integrity of the stream as a whole (Heartsill-Scalley & Aide, 2003).

Although the Acará and Capim river catchments have experienced moderate deforestation, there are still many streams with intact riparian vegetation, several large intact forest fragments and high-quality habitat supporting diverse freshwater fish assemblages. However, this finding does not consider potential time lags or legacy effects (Harding, Benfield, Bolstad, Helfman, & Jones, 1998; Leitão et al., 2018; Zeni et al., 2017) and land cover change in the basin is rapid and evolving (e.g., secondary forest and new agricultural crops, such as sugarcane, likely will expand over the coming years). This highlights a challenge and an opportunity for understanding effects of deforestation and land cover change on the integrity of Amazonian stream systems. The challenge is the need for long-term monitoring of landscape attributes, instream conditions essential for maintaining biodiversity and species distributions and abundances to address time lags and legacy effects. For relatively unimpacted areas, initiating long-term monitoring now should be viewed as an opportunity to generate data on the relationships between landscape, instream conditions and stream diversity to serve as baseline data for continuing research. Baseline data that represent relatively "pristine" conditions are lacking in most instances, which can undermine the ability of studies to interpret ecological dynamics in response to land cover change (Zeni et al., 2017). Long-term monitoring studies should incorporate key indicator variables for habitat evaluation (e.g., undercut bank and *SD* incision height from this study, wood volume as proposed by Leal et al. (2017) and Leitão et al. (2018)). Other physical habitat variables (channel morphology, substrate, water velocity, submerged wood structure, riparian vegetation cover and human influence) should also be monitored because they have been shown to influence aquatic biota in various ways depending on the region and associated environmental conditions (Kaufmann et al., 1999; Peck et al., 2006). Lastly, long-term monitoring studies should also incorporate data on spatial relationships (e.g., this study) as well as the history (e.g., Zeni et al., 2017) and rate (e.g., Brejão et al., 2018) of land cover change.

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CONFLICT OF INTEREST

The authors have no conflict of interests to declare.

AUTHORS' CONTRIBUTION

LFAM, KOW and LJ conceived and designed the investigation. HL, BSP and TOB performed field and/or laboratory work. FWK, NLB, NRT and LMB analysed the data. DES, EOL and YQM contributed materials, reagents and/or analysis tools. LFAM, KOW, FWK and DJH wrote the paper.

ORCID

Luciano F. A. Montag http://orcid.org/0000-0001-9370-6747
Kirk O. Winemiller http://orcid.org/0000-0003-0236-5129
Friedrich W. Keppeler http://orcid.org/0000-0002-5165-1298
Híngara Leão http://orcid.org/0000-0002-9938-7967
Naraiana L. Benone http://orcid.org/0000-0003-4155-9938
Naiara R. Torres http://orcid.org/0000-0003-1446-6760
Bruno S. Prudente http://orcid.org/0000-0003-4226-2431
Tiago O. Begot http://orcid.org/0000-0002-4879-3869
Luke M. Bower http://orcid.org/0000-0002-0739-858X
David E. Saenz http://orcid.org/0000-0003-0238-0919
Edwin O. Lopez-Delgado http://orcid.org/0000-0002-4010-1880
Yasmin Quintana http://orcid.org/0000-0002-1051-0202
David J. Hoeinghaus http://orcid.org/0000-0003-0363-8723
Leandro Juen http://orcid.org/0000-0002-6188-4386

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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