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Taxonomic and functional turnover of Amazonian stream fish assemblages is determined by deforestation history and environmental variables at multiple scales

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High rates of deforestation, either in the past or the present, affect many of the ecological processes in streams. Integrating deforestation history and the current landscape structure enhances the evaluation of ecological effects of land-use change. This is especially true when contemporary landscape conditions are similar but the temporal path to those conditions differs. One approach that has shown promise for evaluating biodiversity responses over time and space is the β-diversity partitioning, which combines taxonomic and functional trait-based approaches. We tested hypotheses related to stream fish assemblages' turnover in watersheds with different environmental conditions and deforestation histories. We sampled fish from 75 watersheds in the Machado River basin, Brazil, and environmental factors were quantified at multiple scales. Taxonomic turnover was higher than expected by chance, whereas functional turnover was lower than expected by the observed taxonomic turnover, indicating that deterministic processes are structuring these assemblages. The turnover, and the environmental factors differed among watersheds with different deforestation histories. Besides being scale-dependent, turnover patterns are also likely dependent on land use dynamics and involve time-lags.

Keywords: β-diversity, Deterministic processes, Landscape, Madeira River basin, Scale-dependency.

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Altas taxas de desmatamento, seja no passado ou no presente, afetam muitos processos ecológicos em riachos. Integrar o histórico do desmatamento à estrutura atual da paisagem melhora a avaliação dos efeitos ecológicos da mudança do uso do solo. Isto é especialmente verdadeiro quando as condições da paisagem contemporânea são semelhantes, mas seguiram trajetórias distintas. Uma abordagem promissora para avaliar as respostas da biodiversidade ao longo do tempo e espaço é a partição da diversidade-β, que combina abordagens taxonômica e funcional. Testamos hipóteses relacionadas à substituição das assembleias de peixes de riachos em microbacias com diferentes condições ambientais e histórias de desmatamento. Amostramos 75 microbacias na bacia do rio Machado, fatores ambientais foram quantificados em múltiplas escalas. A substituição taxonômica foi maior do que esperada pelo acaso, enquanto a substituição funcional foi menor do que o esperado pela substituição taxonômica, indicando que as assembleias são estruturadas por processos determinísticos. As substituições e fatores ambientais diferiram entre microbacias com históricos de desmatamento distintos. Além de serem escala-dependentes, os padrões de substituição provavelmente são dependentes da dinâmica do uso do solo, envolvendo defasagem temporal.

Palavras-chave: Bacia do rio Madeira, Diversidade β, Escala-dependência, Paisagem, Processos determinísticos.

INTRODUCTION

Rivers and streams are characterized by elongated linear form at local scales and dendritic form at watershed scales, unidirectional flow (especially in headwaters and mid-reaches) and unstable substrates (Welcomme, 1985). The aforementioned characteristics entail an intimate connection with the surrounding terrestrial environment, and freshwater ecosystems tend to accumulate and concentrate impacts related to landscape modification or land use activities in the surrounding watershed (Hynes, 1975; Wear *et al*., 1998; Townsend *et al*., 2003). For example, high rates of deforestation in rainforests, either in the past or the present, affect many of the ecological processes occurring in the associated streams (Wright, Flecker, 2004; Paula *et al*., 2011; Brejão *et al*., 2018). Intact riparian zones or buffers may perform critical ecological functions in mitigating to some degree the impacts to freshwater systems caused by land cover change (Dwire, Lowrance, 2006). That said, the effects of land cover change are not fully understood, especially for highly diverse tropical systems that are currently experiencing high rates of impact (Bojsen, Barriga, 2002; Lorion, Kennedy, 2009; Leal *et al*., 2016). In particular, our understanding of how temporal and spatial dynamics of deforestation, not just the total area impacted, affect freshwater ecosystems is very limited.

Temporal aspects of the biodiversity response to deforestation can be separated into two interacting components: the timing or rate of land-use change and the rate of species responses to that change. Although many studies compare biodiversity among contemporary land-use categories (*e.g*., impacted and reference conditions), including details about deforestation history along with current landscape structure enhances the analytical power to evaluate ecological effects of land-use change (Ferraz *et al*., 2009). This is especially true when contemporary landscape conditions are similar but the temporal path to those conditions differs (Ferraz *et al*., 2009). Biodiversity responses to deforestation can vary greatly among species and over time scales ranging from coincident with deforestation to many decades after the deforestation event. For example, Brejão *et al*. (2018) found some stream fish species in the western Amazon exhibited strong negative threshold population responses with only minor deforestation in the watershed almost immediately after the impact, whereas others exhibited positive threshold responses almost two decades after deforestation occurred. Similarly, other studies have found legacy effects of land-use change on stream biodiversity such that historical land use is a better predictor of contemporary communities (Harding *et al*., 1998; Iwata *et al*., 2003; Zeni *et al*., 2017).

From the spatial context, deforestation typically occurs in a heterogeneous manner within watersheds and the heterogeneous distribution of land-use change can lead to heterogeneous or patchy species responses in space (Erős, Lowe, 2019). If connectivity is present among patches, movement of individuals can lead to source-sink metapopulation or metacommunity dynamics where immigrants from source populations in non-impacted sites support the persistence of sink populations in impacted sites (Schiesari *et al*., 2019). This rescue effect, if undetected, can lead to an underestimation of the effects of deforestation at the local scale. Alternatively, impacts of deforestation may be observed in seemingly unimpacted regions due to the flux of sediment, nutrients, and individuals from upstream to downstream or the severing of migration corridors. Together, these aspects indicate that the effects of deforestation may be distributed beyond the just local area impacted and also may be offset to some degree by the presence of source populations within the watershed (*e.g*., Montag *et al*., 2019).

Understanding the temporal and spatial dynamics of communities in response to temporal and spatial dynamics of land-use change is a challenging endeavor that requires integrating large temporal and spatial scales. One approach that has shown promise in this regard is β-diversity partitioning (*e.g*., Baselga *et al*., 2015; Zeni *et al*., 2020). As originally defined by Whittaker (1960), β-diversity is the change in species composition along a gradient or among sites in space. β-diversity can be partitioned into turnover and nestedness components where turnover represents species replacement among sites and nestedness represents a non-random loss or gain of species among sites (Baselga, 2010; Baeten *et al*., 2012). According to Socolar *et al.* (2016) the turnover occurs when the species present at one site are absent at another site, but are replaced by other species absent from the first, on the other hand, nestedness occurs when the species present at one site are absent at another, but are not replaced by additional species. In a conservation perspective across natural environments, the turnover implies that conservation must target multiple sites, while nestedness suggests that conservation might target the richest sites (Socolar *et al*., 2016).

Most β-diversity research has focused on spatial gradients, and findings from those studies demonstrate that habitat heterogeneity (including resulting from land-use change) is an important driver of β-diversity (Anderson *et al*., 2011; Siqueira *et al*., 2015). Regardless of the gradient of interest, analyses that quantify β-diversity and determine the environmental factors associated with β-diversity components can provide insight into the relative importance of deterministic (niche-based) and stochastic (neutral) processes in community assembly (Püttker *et al*., 2015; Mori *et al*., 2018; Roa-Fuentes *et al*., 2019).

Mechanistic interpretation of temporal and spatial dimensions of biodiversity responses to deforestation and effects on ecosystem processes can be informed by combining taxonomic and functional traits approaches (Petchey, Gaston, 2006; Hoeinghaus *et al*., 2007; Swenson *et al*., 2012). This is especially important in hyperdiverse tropical regions where functional redundancy may be high (Vitule *et al*., 2017), buffering the functional turnover. Taxonomic and functional β-diversity are expected to be positively correlated, but whether functional turnover is higher or lower than expected by species turnover has received less attention (Swenson, 2011).

In this study, we use a combined taxonomic and functional group approach to test whether (i) turnover is higher than expected by chance in streams from deforested watersheds and in comparison with streams from forested watersheds, according to Socolar *et al.* (2016), high intensity land use reduces the total abundance of many species across the assemblage regional pool, and the β-diversity can increase as species become rarer, (ii) timing of deforestation affects turnover due to different temporal responses of sensitive and tolerant species to time and extent of deforestation (Brejão *et al*., 2018), because the loss of sensitive species in deforested usually is faster than the processes of colonization and settling of tolerant species due to habitat homogenization process, (iii) both local (instream) and watershed (landscape) variables are associated with turnover in deforested streams, since these streams are located in heterogeneous landscapes, whereas only local variables are associated with turnover in forested streams, since these streams are located in homogeneous landscapes. Specifically, for river basins that were recently deforested, remnants of preserved areas could be of great value because they are still able to harbour subsets of satellite species that can play a role as source assemblages in the regional context (Pérez-Mayorga *et al*., 2017), and (iv) the above patterns differ between analyses using taxonomic and functional groups defined by ecomorphological traits, instead of β-diversity has usually being evaluated by species composition and abundance, (Swenson *et al*., 2012; Mori *et al*., 2018), where then are all treated as functionally equivalent (Swenson *et al*., 2012).

MATERIAL AND METHODS

Study area. Field research was conducted in the Machado River basin, Brazil (Fig. 1). The Machado River is a tributary of the Madeira River in the western Amazon, and drains the most populated region of Rondônia state, Brazil (Fernandes, Guimarães, 2002). The climate is tropical humid: temperatures range from 19 to 33 °C, and annual rainfall is 2,500 mm (Krusche *et al*., 2005). Native vegetation is open humid tropical forest (primary forest), and current land cover includes a matrix of primary forest, secondary forest (regrowth on previously deforested land), and pasture (Ferraz *et al*., 2009). This region has many *terra firme* streams, which are intermittent during most of the dry season. We surveyed 75 first- to third-order streams representing sub-basins dominated by intact primary forest or pasture with various deforestation histories. In general, sampled streams were shallow with low-velocity flow and warm temperatures.

Streambeds were predominantly comprised by sand, litter pack, and large woody debris, and stream banks usually provided submerged microhabitat structure derived from the riparian environment such as tree roots and grasses (Tab. 1).

Field and laboratory methods. Streams were sampled once in the dry season (August–October 2011 and June–July 2012). Field methods were standardized to allow for comparisons of environmental parameters and species abundances across sites. Each sampling reach was 80 m long and was isolated with block nets (5–mm mesh) prior to sampling. After reach delimitation, physical and chemical factors characterizing instream and riparian ecotone habitats were quantified using standard methods (Tab. 1). Next, fishes were sampled from all available microhabitats within the enclosed stream reach by two collectors using a seine (1.5 x 2 m, 2–mm mesh) and dip nets (0.5 x 0.8 m, 2–mm mesh) for 1 h. Fishes were collected under Instituto Chico Mendes de Conservação da Biodiversidade permits 4355–1/2012.

All collected individuals were identified with assistance from taxonomic specialists, and voucher specimens were deposited in the Coleção de Peixes do Departamento de Zoologia e Botânica (DZSJRP 14402–14552, 14626–14731, 14733–14753, 14755–14775, 14884–14958, 14960–14999, 15001–15141, 16538–17454, 18154) at the Universidade Estadual Paulista Júlio de Mesquita Filho, São José do Rio Preto, São Paulo State, Brazil. Following species identification, we quantified ten ecomorphological traits related to habitat use, foraging, and locomotion for each species (Brejão *et al*., 2018). Traits were calculated using 11 measurements from adult individuals (1–5 individuals per species, depending on availability of specimens). Measurements were linear distances (*e.g*., body width) or surface areas (*e.g*., area of the body and fins) measured to the nearest 0.01 mm with a stereomicroscope (Zeiss Discovery V12 SteREO) coupled with imaging software (Axio-Vision Zeiss) and a digital caliper.

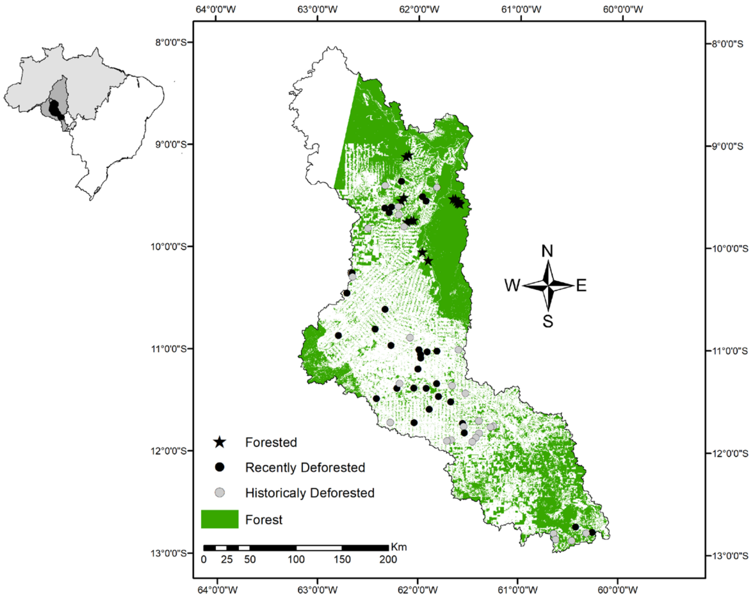

FIGURE 1 | Sampled sites and forest fragments in the Machado River basin, Brazil. The inset map of Brazil depicts the relative location of the study area (black) within the Madeira River basin (dark gray), inside the Amazon biome (light gray).

TABLE 1 | Summary of instream and riparian ecotone environmental variables, observed mean ± standard deviation, and explanation of how each variable was obtained.

Variables	Code	Mean ± SD	Explanation
Riparian ecotone variables (For this calculation, both stream sides were computed)			
Trees in stream banks (%)	TRE	13.23 ± 18.33	– Percentage of the reach bank extension that was covered by riparian trees.
Grasses in stream banks (%)	GRA	35.03 ± 38.01	– Percentage of the reach bank extension that was covered by marginal grasses derived from surrounding pasture entering the water.
Submerged roots in stream banks (%)	FRO	3.33 ± 7.63	– Percentage of the reach bank extension that presented roots derived from riparian trees entering the water.
Riparian litter (%)	RLI	10.79 ± 12.66	– Percentage of the reach bank extension that presented fallen leaves derived from riparian trees
Instream variables			
Sand substrate (%)	SAN	53.58 ± 29.17	– Percent of sand substrate in the stream reach
Consolidated substrate (%)	CSU	5.08 ± 9.94	– Percent of gravel and cobble (particle size 2–256 mm) substrate in the reach
Litter packs on stream bed (%)	LIT	14.34 ± 18.24	– Percent of fallen leaves on the streambed in the reach
Large woody debris on stream bed (%)	BAT	11.35 ± 10.78	– Percent of fallen branches and tree trunks on the streambed in the reach.
Depth (cm)	DEP	27.54 ± 13.68	– Average depth
Width (m)	WID	3.00 ± 1.41	– Average width
Water flow (m s^{-1})	CUR	0.38 ± 0.23	– Average water velocity
Dissolved oxygen (mg l^{-1})	DOX	6.63 ± 2.24	– Average dissolved oxygen concentration
Conductivity (µS)	CON	18.39 ± 21.09	– Average conductivity
Temperature (°C)	WTE	24.06 ± 2.26	– Average water temperature

Land-use classification and multimetric landscape index. Land use classification was based on Landsat 5 TM satellite images (30 x 30 m resolution) obtained and released by the National Institute for Space Research (INPE). The land use map consists of three categories: primary forest, secondary forest, and pasture. Classification was conducted using the supervised Maximum Likelihood Classification method (Jensen, 2007) and the software Erdas 9.2. Land-use change was analyzed from 1984 to 2011 at 4-year intervals and calculated using the Land-Use Change Analysis Tool (LUCAT; Ferraz *et al*., 2012) at the watershed and 100 m riparian buffer scales associated with each stream site. LUCAT calculates the area and proportion of the area occupied by each type of land use present in a unit of analysis. This tool also provides indices such as Forest Change Curve Profile (FCCP) and Land Use Intensity (LUI; Ferraz *et al*., 2009). FCCP represents temporal deforestation patterns, indicating when vegetation change processes occurred during the period of record. This index varies from -1 to 1, where values close to the extremes represent more significant transformations in the landscape during a short time and values close to zero represent gradual changes in land use. Positive values of FCCP indicate older changes and negative values indicate recent changes. Watersheds clustered in three groups based on FCCP values: 1) reference watersheds that were not deforested (ref; n = 18), recently deforested watersheds (new; n = 31), and historically deforested watersheds (old; n = 26). LUI complements FCCP and represents the average time since deforestation for the watershed and can be considered as an accumulated effect metric over time. Fluvial distance was quantified using the Network Analyst extension in ArcGIS, which produces a triangular matrix containing the stream distance among all sampled sites.

Following the methodology proposed by Ferraz *et al*. (2014), we calculated a multimetric landscape index to estimate forest quality ranking based on landscape attributes and forest remnants structure, which scores each 1 ha pixel (100 x 100m) with forest cover in the basin at the time of sampling according to the metrics shown in Tab. 2. These metrics take into account the landscape configuration relative to the location for each pixel throughout the Machado River basin and assign each forested pixel (non-forested pixels are not scored) a value based on the effect of the deforestation process on a regional scale. For each metric, we produced a thematic map, ranking each forested pixel according to the sum operation among all thematic maps. Sum values ranged between 5 and 16 (Fig. 2A), and we determined that pixels with the highest observed aggregate metric values (15 and 16) indicate forest areas with high quality, corresponding with ancient forest with high contiguity and proximity to forested pixels located far from the patch edge. Such high-quality forest has been called *effective forest*, because those patches are expected to perform their ecosystem functions at an adequate level (Fig. 2B). Mean and standard deviation of effective forest at the watershed and riparian buffer scales, along with other landscape variables are summarized in Tab. 3.

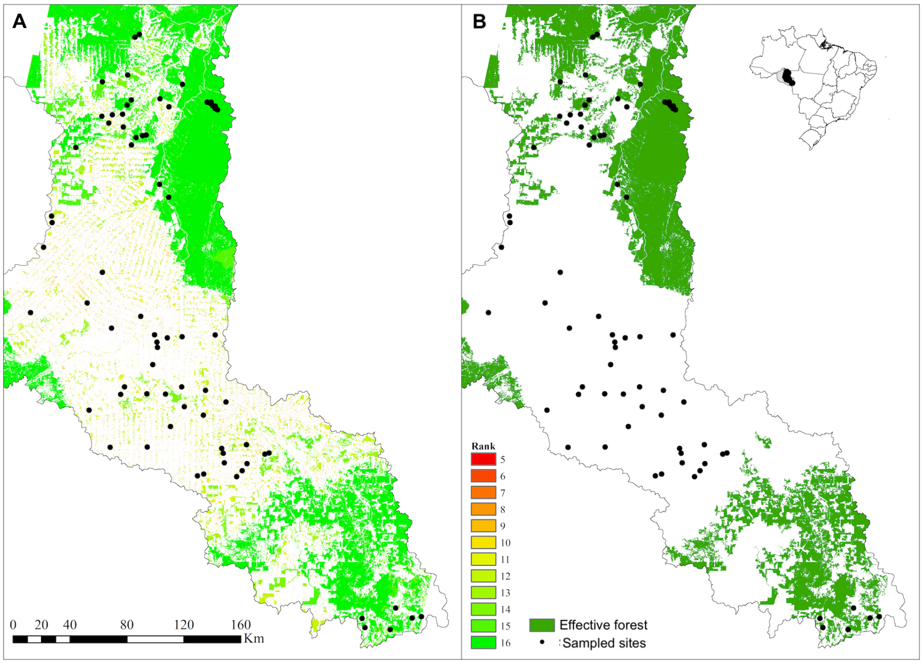

FIGURE 2 | Distribution of sampling sites with (**A**) forest patches ranked according to the forest quality multimetric index and (**B**) effective forest cover. Non-forested area is white and is not included in the multimetric index calculation (or legend).

TABLE 2 | Metrics used to estimate forest quality ranking based on landscape and forest patch structure (Ferraz *et al*., 2014).

Metrics	Weight	
Forest age (years)		
0–7 7.1–19 19.1–23 >23	1 2 3 4	Forest age is quantified by temporal overlaying of land cover maps, using the difference between the most recent date and the first year of forest occurrence in the past.
Local forest neighborhood dominance (%)		
0 0.1–0.33 0.34–0.66 0.67–1	1 2 3 4	Neighborhood dominance is calculated as the proportion of forest in the eight cells surrounding the focal cell. Weight increases with higher proportion of forest coverage considering that interior forest can perform better ecosystem services than forest edge.
Forest proximity (number of units)		
0–76 76.1–1200 1200.1–5000 >5000	1 2 3 4	Forest proximity is calculated as the mean proximity index of forest present in a 2 km buffer around the focal cell. Proximity is used as a surrogate for local habitat connectivity. Weight increases with proximity considering that more connected patches provide higher levels of some regulating ecosystem services than more isolated ones.
Forest contiguity (%)		
0 0.1–0.8 0.9–2.4 >2.4	1 2 3 4	Forest contiguity is quantified as the relative size of the forest patch in relation to the focal cell. Weight increases with contiguity considering that larger forest patches are able to provide higher levels of ecosystem services provisioning.

TABLE 3 | Summary of landscape variables at the watershed and riparian zone scales (mean ± standard deviation).

Landscape variables	Code	Mean ± SD
Watershed scale		
Mature forest proportion	MF_WSHD	0.36 ± 0.36
Effective forest proportion	EF_WSHD	0.27 ± 0.40
Land use intensity	LUI_WSHD	0.35 ± 0.25
Riparian zone scale		
Mature forest proportion	MF_BUFF	0.41 ± 0.38
Effective forest proportion	EF_BUFF	0.28 ± 0.42
Land use intensity	LUI_BUFF	0.34 ± 0.26

Quantifying turnover. Taxonomic turnover was estimated using a null-modeling approach and a modified Raup-Crick metric for abundance data (subsequently abbreviated as βRC; Raup, Crick, 1979; Püttker *et al*., 2015). The advantage of this metric combined with the null-modeling approach is that it permits discrimination of compositional variation among local communities independently from differences in local species richness, *i.e*., it measures β-diversity associated exclusively with species turnover, while controlling for differences in nestedness (Chase *et al*., 2011; Baeten *et al*., 2012; Püttker *et al*., 2015). The null-modeling approach measures the deviation from the expectation that the dissimilarity of the communities is stochastic (Raup, Crick, 1979;

Chase *et al*., 2011; Püttker *et al*., 2015), which allows for evaluation of the importance of deterministic (niche-based) and stochastic (neutral) processes in community assembly (Chase *et al*., 2011; Püttker *et al*., 2015).

Functional turnover was estimated using two distance metrics based on the functional traits matrix and species abundance data and compared with a null distribution that was generated by randomizing species identities across the community matrix (Swenson, 2011; Roa-Fuentes *et al*., 2019). The first metric calculates the mean pairwise distance (βMPD) for pairs of species functional traits sets between samples, and the second metric (βMNTD) calculates the average distance between species functional traits sets in the first sample and its nearest neighbor in the second sample. The two metrics are complementary (Swenson, 2011): βMPD evaluates the total dissimilarity between two communities and is sometimes considered a basal diversity metric (Swenson, 2014), whereas βMNTD is regarded as a terminal relatedness measure because it is more sensitive to variations near the tips of the phylogenetic or functional dendrogram (Webb, 2000). The standardized effect size was calculated for each metric. In this approach, positive values of functional turnover indicate higher traits turnover than expected by species turnover, whereas negative values of functional turnover indicate lower traits turnover than expected by species turnover (Swenson, 2011, 2014).

Data analyses. To test the hypothesis (i) and (ii), a series of one sample t-tests was used to test if the mean value of each turnover metric between sites was significantly different from the expected value for random data (Wang *et al*., 2013). A distance-based approach was used to assess variation in turnover metric values in relation to environmental and spatial distances among the sampled communities (Tuomisto, Ruokolainen, 2006). A bootstrap ANOVA test with 10,000 permutations, complemented with the *post hoc* test of Tuckey, using 'lmboot' (Heyman, 2019) and 'agricolae' (Mendiburu, 2020) packages, was used to test for differences in turnover rates between stream groups (*i.e*., reference, recently deforested, and historically deforested). For each stream group, we applied the 'bioenv' function from the 'vegan' package (Oksanen *et al*., 2018) to obtain the subsets of environmental variables best correlated with community turnover (Clarke, Ainsworth, 1993) (**S1**). The spatial distances were obtained measuring the fluvial distance between one sampling site to all the others for each group of streams, this procedure was made with the Network Analyst, from ArcGIS 9.3. Mantel and partial Mantel tests with 10,000 permutations were used to determine the significance of variation in turnover related to environmental and spatial distances (Legendre, Legendre, 2012).

To test the hypothesis (iii) and (iv), multiple regression on matrices (MRM) was used to assess the relative contributions of local, watershed and network distance factors on turnover (Legendre *et al*., 1994) using the 'MRM' function in the 'ecodist' package (Goslee, Urban, 2007). We also performed a commonality analysis, which allows for the partitioning of the coefficient of determination (R^2) into effects explained uniquely by each environmental predictor or environmental predictor subset – landscape or local – (*Unique*), and effects explained commonly by all possible combinations of environmental predictors or environmental predictor subsets (*Common*) (Sorice, Conner, 2010; Ray-Mukherjee *et al*., 2014). Commonality analysis was performed and structure coefficients estimated using the 'regr' function in the 'yhat' package (Nimon *et al*., 2017). All the analyses were performed using R (R Development Core Team, 2014).

RESULTS

In total for the 75 stream communities sampled, we collected 22,851 individuals belonging to 138 species, 30 families and six orders (**S1** and **S2**). In all cases, mean turnover differed from the expected value of zero ($P < 0.05$, Fig. 3, **S3**). Mean values for taxonomic turnover were greater than zero, indicating higher species turnover than expected by chance (Fig. 3). In contrast, functional turnover had mean values less than zero, indicating that functional turnover was lower than the expected given the observed values for taxonomic turnover (Fig. 3; **S4**).

Turnover increased with environmental distance for all turnover metrics for both taxonomic and functional datasets (Tab. 4). That is, there was a significant distance-decay relationship between community and environmental similarity. Even after controlling for stream network distance, all turnover standardized effect sizes remained significantly correlated with environmental distance (Tab. 4). On the other hand, distance-decay relationships between pairwise turnover and stream network distance were significant for all taxonomic turnover metrics but only for functional turnover in streams with recently deforested watersheds (ses.β.MNTD.new; Tab. 4). After controlling for environmental distance, stream network distance was correlated with taxonomic turnover metrics for all streams together, streams with recently deforested watersheds and streams with historically deforested watersheds, but not reference streams (ses.β.RC.all, ses.β.RC.new and ses.β.RC.old; Tab. 4).

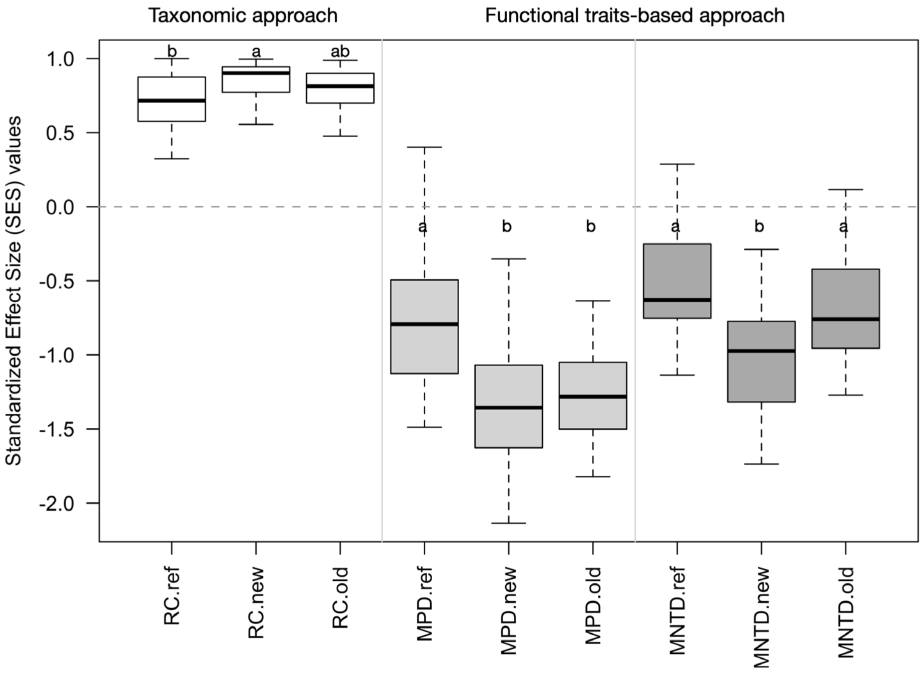

FIGURE 3 | Standardized effect sizes for each taxonomic and functional turnover metric (mean and 95% confidence intervals). RC = Raup-Crick; MPD = mean pairwise distance; MNTD = mean nearest taxon distance; ref = streams with forested watersheds; new = streams with recently deforested watersheds; old = streams with historically deforested watersheds.

TABLE 4 | Mantel and partial Mantel tests for the correlation between standardized effect size (ses) of turnover metrics and predictor distances (environment and network) using Pearson's correlation (ρ), with 10,000 permutations. Significant values in bold: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

Turnover facet	Effect of environment	Effect of network	Effect of environment controlling for network	Effect of network controlling for environment
Taxonomic				
ses.β.RC.all	**0.3584*** **	**0.2297*** **	**0.3132*** **	**0.1407*** **
ses.β.RC.ref	**0.6503*** **	**0.372*** **	**0.5867*** **	0.1445
ses.β.RC.new	**0.2596*** **	**0.2175** **	**0.1956** **	**0.1324* **
ses.β.RC.old	**0.2349** **	**0.2944*** **	**0.1423* **	**0.2300*** **
Functional				
ses.β.MPD.all	**0.2874*** **	0.0541	**0.2831*** **	-0.0167
ses.β.MPD.ref	**0.4095*** **	-0.2845	**0.4649*** **	-0.3668
ses.β.MPD.new	**0.4257*** **	0.1889	**0.3890*** **	0.0219
ses.β.MPD.old	**0.5171** **	0.1785	**0.4956** **	0.0559
ses.β.MNTD.all	**0.2949*** **	0.04031	**0.2932*** **	-0.0230
ses.β.MNTD.ref	**0.3418* **	-0.4219	**0.4087** **	-0.4740
ses.β.MNTD.new	**0.3277*** **	**0.2362*** **	**0.2386*** **	0.0497
ses.β.MNTD.old	**0.4277** **	0.0725	**0.4226** **	-0.0001

In comparisons among stream groups, taxonomic turnover (βRC) was different between streams with forested watersheds and streams with recently deforested watersheds (P = 0.021), but not for other comparisons (P > 0.05; Fig. 3). For functional turnover, we detected significant differences in βMPD between streams with forested watersheds and streams with recently deforested watersheds (P < 0.001) and also historically deforested watersheds (P = 0.005; Fig. 3). There was no difference in βMPD between streams with recently and historically deforested watersheds (P > 0.05; Fig. 3). For βMNTD, functional turnover was different between streams with forested watersheds and streams with recently deforested watersheds (P < 0.001; Fig. 3). In contrast with βMPD, βMNTD was different between streams with recently and historically deforested watersheds (P = 0.016), but not different between streams with forested watersheds and streams with historically deforested watersheds (P > 0.05; Fig. 3).

The results of MRM and commonality analysis indicate that variation in the environment-turnover relationship for streams with deforested watersheds was explained by both local- and watershed-scale variables, whereas only local scale variables explained variation in the environment-turnover relationship for streams with forested watersheds (**S5**; Fig. 4). That said, environment-turnover relationships were mostly weak, though significant, for all streams ($R^2 \leq 0.14$; $P < 0.001$; **S5**) and for streams with recently deforested watersheds ($R^2 \leq 0.20$; $P < 0.001$; **S5**). Streams with forested watersheds, on the other hand, had stronger environmental-turnover relationships than observed for other groups ($R^2 = 0.28$–0.44; $P < 0.001$; **S5**). Environment-turnover relationships varied across metrics for streams with historically deforested watersheds; taxonomic turnover was weakly correlated ($R^2 = 0.11$; $P < 0.001$; **S5**) and functional turnover was slightly more strongly related with environmental factors ($R^2 \geq 0.26$; $P < 0.001$; **S5**).

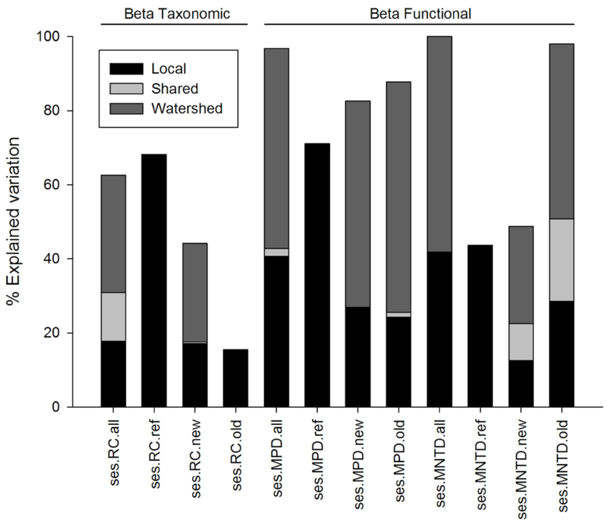

FIGURE 4 | Explained variation of environmental contribution in turnover metrics partitioned by MRM and associated commonality analysis into pure local, shared and pure catchment components. RC = Raup-Crick; MPD = mean pairwise distance; MNTD = mean nearest taxon distance; all = all sampled streams; ref = streams with forested watersheds; new = streams with recently deforested watersheds; old = streams with historically deforested watersheds.

DISCUSSION

For all comparisons in this study, mean turnover was different than expected by chance, indicating that deterministic processes are structuring these stream fish assemblages. That said, the pattern of turnover differed between analyses based on taxonomy and functional trait-based approaches. Specifically, turnover was higher than expected by chance in taxonomic analyses, whereas functional turnover was lower than expected given the values for taxonomic turnover. Thus, assemblages are taxonomically dissimilar but functionally similar, indicating that species turnover is occurring primarily among functionally equivalent species, which leads to infer to a functional redundancy concerning the use of habitat, foraging and locomotion.

We also observed meaningful differences among the three stream groups. Taxonomic turnover was different among streams with recently deforested watersheds compared with streams with forested watersheds. Functional turnover was different among streams with forested watersheds compared with either streams with recently deforested or historically deforested watersheds for βMPD. In comparison, functional turnover was different among streams with recently deforested watersheds than either streams with forested or historically deforested watersheds for βMNTD. As such, both our first and second hypotheses were partially supported, though the patterns in turnover were more complex than anticipated. Observed patterns of turnover among streams with forested watersheds was driven by local-scale environmental variables only, whereas turnover among streams with deforested watersheds, whether recently or historically deforested, was driven by a combination of local- and watershed-scale environmental variables, supporting our third hypothesis (**S3**). Finally, in most cases the above patterns differed between analyses using taxonomic and functional data, supporting our fourth hypothesis.

The observed pattern of taxonomic turnover exceeding the level expected by chance could indicate that this fish assemblage is being structured by the disturbance (Baselga, 2010), with the dominant species in local assemblages differing among deforested sites (Püttker *et al*., 2015; Siqueira *et al*., 2015), and localy rare species differing among forested sites (Pérez-Mayorga *et al*., 2017). If we consider that resource gradients or patch types generate differences in the local demography of species (Leibold *et al*., 2004), it is expected that each site had unique levels of species abundances (Janzen, Schoener, 1968; Tucker *et al*., 2016). Higher species turnover found in recently deforested sites may be associated with the emergence of novel niches, due to the initial consequences of deforestation (*i.e*., changes in flow complexity, depth, substrate composition, stream bank stability, and emergence of marginal grasses) while still retaining relict structures and microhabitats found in pristine streams with forested watersheds (*i.e*., fine roots, litter packs, branches, and trunks derived from the riparian forest) (Pérez-Mayorga *et al*., 2017). This novel environmental scenario could allow for the beginning of the colonization and establishment process of tolerant species while sensitive species are still occupying relict habitat structure from the previous condition (*i.e*., time lags). Applying an approach based on site occupancy by fish species to study the same stream system, Pérez-Mayorga *et al*. (2017) identified two processes structuring this metacommunity: while intermediate species are explained only by dispersal-based processes, the satellite species are explained mainly by niche-based but also by dispersal-based processes. It is interesting to observe that within these two groups we found species both sensitive to and tolerant to deforestation. Thus, the presence of a fish species in a site with a deforested watershed can be independent of its dispersal or colonization ability (*i.e*., could be a relict from the pre-deforestation condition); these findings reinforce the possibility of an ongoing colonization-establishment process occurring in streams with recently deforested watersheds. Likewise, our results reinforce the dispersal importance for the stream fish assemblages structuring. Specifically, the dispersal was very important for the taxonomic dimension but not so far for the functional dimension, probably indicating that taxonomically distinct species could be dispersing between sites but their set of functional traits are very similar.

In general, land use intensity reduces dissimilarity among local communities (*i.e*., reduces turnover); this process of biotic homogenization is driven by the loss of sensitive species and gradual increase in abundances of tolerant species (Brejão *et al*., 2018; Roa-Fuentes *et al*., 2019). Surprisingly, taxonomic turnover did not differ between groups of streams with forested and historically deforested watersheds, and turnover in both groups was lower than that found among streams with recently deforested watersheds. According to the landscape divergence hypothesis (Laurance *et al*., 2007), disturbed areas are likely to diverge in species composition because of differences in the effects of disturbance, or in how disturbances processes interact with underlying differences in environmental heterogeneity (Arroyo-Rodríguez *et al*., 2013). Land use intensity measures the trajectory of land use changes in a given area (Ferraz *et al*., 2009), while effective forest measures the quality of the forest remnants along the landscape (Ferraz *et al*., 2014). Interestingly, taxonomic turnover in recently deforested streams was associated with land use intensity in the basin, indicating that the assemblage structure of these sites is still under the influence of the trajectory of change, and that they are probably going through a moment of population reduction of sensitive species and increase in abundance of tolerant species. On the other hand, the taxonomic turnover in historically deforested watersheds associated with the amount of effective forest in the watershed indicates that the permanence of old-growth forest is important to prevent total homogenization of the local habitat, allowing species substitution to still occur between streams.

Usually, forested sites have higher differences in species abundances among sites (β-diversity) than agricultural landscapes (Karp *et al*., 2012; Siqueira *et al*., 2015; Solar *et al*., 2015), but agricultural intensification may lead to higher β-diversity in high-intensity agriculture patches than that found in forest and low-intensity agriculture patches (Karp *et al*., 2012). Each fish species response to the extent and time since deforestation is distinct, where sensitive species abundance decreases and tolerant species abundance increases over the time since the impact (Brejão *et al*., 2018). The abundance structure in streams with recently deforested watersheds is likely to be highly variable (see the abrupt increase in abundance of *Serrapinnus microdon* and *S. notomelas*, **S1**), driven by the dynamic filtering of changing environmental conditions (Connell, 1978; Leibold *et al*., 2004). High taxonomic turnover among streams with recently deforested watersheds could explain the weak relationship between species/traits and environmental conditions for this group. On the other hand, in streams with forested and historically deforested watersheds, the abundance structure and species turnover may be more stable when compared with streams from recently deforested watersheds, either due to the absence of disturbance or consolidation of disturbance. For example, see *Hyphessobrycon agulha* and *Gymnorhamphichthys rondoni* in streams with forested watersheds and *Bryconops caudomaculatus* and *Creagrutus petilus* in streams with historically deforested watersheds (**S1**).

Functional turnover was lower than expected by chance given the observed species turnover, indicating that variation between two communities occurs mainly within groups of functionally similar species (Swenson, 2011; Swenson, 2014). Large functional overlap could explain the low level of functional turnover, with frequent species replacements occurring mostly between functionally redundant species (Villéger *et al*., 2013). In our study system, two species with similar traits (*Farlowella* cf. *oxyrryncha* and *Gymnorhamphichthys rondoni*) are shared by the three groups of streams and are located in the extremes of the functional space, thus making a large contribution to functional diversity, especially in streams with deforested watersheds (**S6** and **S7**; Bordignon, 2017). The morphological aspects of these species allow them to explore specific niches and structures closely related to the riparian forest. Due to its thin and elongated body, together with its brown coloration, *Farlowella* resemble small tree branches (Covain, Fisch-Muller, 2007), and they are usually found foraging, grazing the periphyton, among similar structures (Brejão *et al*., 2013). *Gymnorhamphichthys rondoni* is a species with psammophilic habit, using its long snout and electric field to probe sand and leaf litter substrates, looking for small invertebrates during the night and burying itself in the sandy substrate during the day (Zuanon *et al*., 2006; Brejão *et al*., 2013). The presence of these species in all groups of streams is probably buffering the overlap of functional space between fish communities, explaining low rates of functional turnover when we have high rates of taxonomic turnover.

Although environment–turnover relationships were mostly weak, it is interesting that turnover metrics are mainly related to instream habitat complexity indicators (*i.e.*, litter packs, fine roots, and trees in the stream margin) and forest quality at the watershed and riparian buffer scales. Landscape modifications are known to influence the physical and chemical characteristics of streams (Gorman, Karr, 1978; Cruz *et al*., 2013; Siqueira *et al*., 2015; Leal *et al*., 2016), thereby indirectly affecting many of the ecological processes occurring in streams (Wright, Flecker, 2004; Paula *et al*., 2011). Maintaining pristine forest remnants associated with landscape complexity and connectivity may extend the prevalence of sensitive species with unique functional traits across the landscape, contributing to the taxonomic and functional integrity of these stream communities.

Although highly impacted by deforestation activities, the study region still retains a diverse regional fish species pool with a large proportion of rare species (see Bordignon, 2017). As described above, our analyses indicate that rare species turnover has only a minor contribution to functional turnover due to high functional redundancy in the species pool. In contrast, assemblages from agroecosystem streams with a long history of impact are characterized by a simplified regional species pool composed mostly by tolerant species with a common set of traits (*e.g*., Casatti *et al*., 2015; Zeni *et al*., 2017), and rare species with unique sets of traits contribute disproportionately to the functional turnover of these communities (Roa-Fuentes *et al*., 2019). Our results do not clearly indicate if the same outcome is expected over time for this region. However, our approach allowed us to assess effects of deforestation and time since deforestation on taxonomic and functional turnover among fish assemblages, and suggest that besides being scale-dependent (Karp *et al*., 2012), turnover patterns are also likely dependent on land use dynamics and involve time lags.

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COMPETING INTERESTS

The authors declare no competing interests.

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