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When roads cross streams: fish assemblage responses to fluvial fragmentation in lowland Amazonian streams

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Roads affect biodiversity by increasing mortality rates, habitat loss, and natural landscape fragmentation. Poorly installed culverts can impound streams, changing the environmental conditions, and affecting aquatic communities. We evaluated the effects of road crossings on the taxonomic composition and functional structure of fish assemblages in lowland eastern Amazonian streams, Brazil. We tested the hypothesis that the presence of road-derived impoundments affects assemblage taxonomic and functional composition and structure. Two predictions were addressed: (1) Species and functional group composition will differ in impounded reaches in relation to lotic reaches; (2) Assemblages in downstream lotic reaches will be richer in species and functional groups in relation to upstream lotic and impoundment reaches. We sampled five streams crossed by roads presenting impoundment formation, conducted by visual census (day, dusk, and night) in 200 m line transects. Assemblage composition from lentic reaches was different from lotic reaches, and Shannon diversity from downstream reaches was different from upstream and impoundment, however, beta diversity partitioning between lotic reaches showed higher nestedness contribution, reinforcing the role of impoundment in limiting fish dispersal between lotic reaches. These results suggest that impoundments impose environmental and dispersal constraints to fish, affecting their longitudinal distribution in streams fragmented by roads.

Keywords: Deforestation arc, Dispersal-based process, Niche-based process, NMDS, Snorkeling

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Estradas afetam a biodiversidade aumentando as taxas de mortalidade, perda de hábitat e fragmentação. Cruzamentos mal instalados represam riachos, alterando as condições ambientais e afetando as comunidades aquáticas. Avaliamos os efeitos deste impacto sobre a estrutura taxonômica e funcional das assembleias de peixes em riachos da Amazônia Oriental, Brasil. Testamos a hipótese de que a presença dos alagados derivados de estradas afeta a composição e estrutura taxonômica e funcional das assembleias. Nossas predições foram: (1) A composição de espécies e grupos funcionais é diferente entre trechos alagados e lóticos; (2) Assembleias nos trechos à jusante serão mais ricas em espécies e grupos funcionais que os trechos à montante e alagados. Amostramos cinco riachos cruzados por estradas com formação de alagamentos por censo visual (dia, crepúsculo e noite) em transectos lineares de 200 m. A composição das assembleias dos trechos lênticos diferiu dos lóticos, e a diversidade de Shannon à jusante diferiu dos trechos montante e alagados, entretanto, nos lóticos, houve maior contribuição do aninhamento na partição da diversidade beta, reforçando o papel do represamento na limitação da dispersão de peixes entre estes. Sugerimos que os represamentos impõem restrições ambientais e de dispersão aos peixes, afetando sua distribuição longitudinal em riachos fragmentados por estradas.

Palavras-chave: Arco do desmatamento, Mergulho-livre, NMDS, Processos baseados em dispersão, Processos baseados em nicho.

INTRODUCTION

Despite many benefits that roads bring to human populations, they affect negatively biodiversity by increasing rates of mortality, habitat loss, and fragmentation of natural landscapes (Forman, Alexander, 1998; Spellerberg, 1998; Laurance *et al*., 2009). Given the importance of this issue, biological impacts of roads have been widely assessed for several taxonomic groups (Vos, Chardon, 1998; Haskell, 2000; Benítez-López *et al*., 2010). However, the evaluation of the extent by which roads affect biodiversity is still a challenge, especially in biodiversity-rich regions where there is knowledge shortfall on different facets of biodiversity (Hortal *et al*., 2015). Worst, this condition contrasts with the rapid human occupation that is accomplished by unplanned infrastructure development (Develey, Stouffer, 2001).

In streams crossed by roads, if crossing structures are poorly installed, they may alter flow and occasionally block fish passage. In such cases, water will tend to flood the stream reach upstream the road, with undersized culverts acting as damming structures. These impoundments will develop into deep habitats, with slow water flows and a silty substrate, conditions that are very distinct if compared to the natural course of the stream (Wellman *et al*., 2000). As a consequence, the fluvial habitat continuum becomes fragmented. These alterations result in habitat loss and fragmentation, which in turn influence species persistence and assemblage structure (Lake, 2000; Makrakis *et al*., 2012; Mariano *et al*., 2012).

Species functional traits influence their responses to habitat alterations (Violle *et al*., 2007; 2012), so that changes in community composition would occur in a non-random way (Keck *et al*., 2014). In the context of stream fragmentation caused by crossing structures, rheophilic and intolerant species may be negatively influenced (Rolls *et al*., 2014), as conditions in the impoundment would represent a barrier. Otherwise, limnophilic species can benefit and successfully explore these new environments (Warren Jr., Pardew, 1998). Therefore, one could expect that variations in species composition in streams fragmented by roads would be predictable into a trait-based approach (Leitão *et al*., 2018).

Headwater reaches isolated by impoundments in road-stream crossings could be compared to an isolated island, where persistence of populations tends to be dependent on species suitability to local conditions, being more influenced by random extinctions (Schlosser, 1995, 1998; Fagan, 2002). Differently, downstream lotic reaches could still be influenced by immigrants from the mainstream, so that assemblages could still sustain a higher number of species (Osborne, Wiley, 1992). Therefore, these hypotheses suggest that road-stream crossing could influence both niche- and dispersal-based processes, generating different patterns of assemblage composition and structure along the watercourse.

Land-use changes at watershed level facilitate the expansion of secondary and unofficial unpaved roads (Pocewicz, Garcia, 2016), which results in wide-spread ecological fragmentation of aquatic environment (Warren Jr., Pardew, 1998; Trombulak, Frissell, 2000; Freeman *et al*., 2007; Leitão *et al*., 2018). Based on this context, we hypothesized that the presence of anthropogenic impoundments raised from road-stream crossings, affect fish assemblages. We tested this hypothesis by evaluating the response of fish assemblages in relation to the position (upstream, impoundment and downstream) and flow characteristics (lotic or lentic) of stream reaches in fragmented streams in Eastern Amazon region. We used a multifaceted approach by considering the taxonomic and functional aspects of fish assemblages and addressed the following predictions: (1) Species and functional composition will differ in impoundments reaches in comparison to lotic reaches due to the differential influence of environmental conditions between these habitats; (2) Assemblages in downstream lotic reaches will be more diverse in species and functional groups in relation to upstream lotic and impoundment reaches, due to the relatively unmodified conditions in this habitat, associated with the connection downstream with mainstream, which, in turn, could act as a source of immigrants.

MATERIAL AND METHODS

Study Area. The study was accomplished in the northeast region of Pará State, which is one of the oldest occupation areas of eastern Amazon, where smallholder properties predominate (Watrin *et al*., 2009). The streams drain a flat terrain region and show sinuous unconfined channels, with high structural complexity, with habitats sequence alternating between runs, pools, and shallow water rapids. The main channel overflows in the rainy season, flooding the forested surroundings for a few months. The substrate is predominantly unconsolidated, with the accumulation of litter banks on the margins and in depositional sections (pools); roots from riparian vegetation and submerged trunks and logs compose important habitat units and are largely responsible for the channel structural complexity. The sampled stream segments (n = 5) are located at Maracanã and Marapanim river basins encompassed in the Igarapé-Açu, Marapanim and São Francisco do Pará municipalities (Fig. 1).

Sampling method. Ichthyofauna was sampled by visual census through line transect method (Sutherland, 2006). In each of the five sampled streams, three 200 m long transects were placed at the downstream, impounded and upstream reaches. To avoid sampling direct effects posed by roads onto the aquatic environment, the downstream and the impounded reaches line transects started at least 25 meters from the road crossing. Upstream reaches were placed in free-flowing sections, distancing 350 m to 820 m from the end of impounded sampled section (570 m ± 220 m), where the influence of the impounded area was not clearly observed. Fishes were quantified along each line transect, considering its length of 200 m and a 2 m wide visual field. While snorkeling, the observer moved slowly to upstream (*ca.* 4.2 m.min^{-1}), and collected information about richness and abundance from the observed specimens. The information about species presence and abundance gathered *in situ* was written on polystyrene plates during the snorkeling sessions. Between June and September 2010, 45 observation sessions were performed in the 15 stream reaches, totaling 37 hours of observations in three daily periods: 1) diurnal (between 11:00 and 14:00); 2) dusk (between 17:00 and 18:30) and 3) nocturnal (between 19:00 and 21:00).

Measurements of stream width were collected every ten meters along the transect line, depth and substrate characterization were measured at regular intervals along the

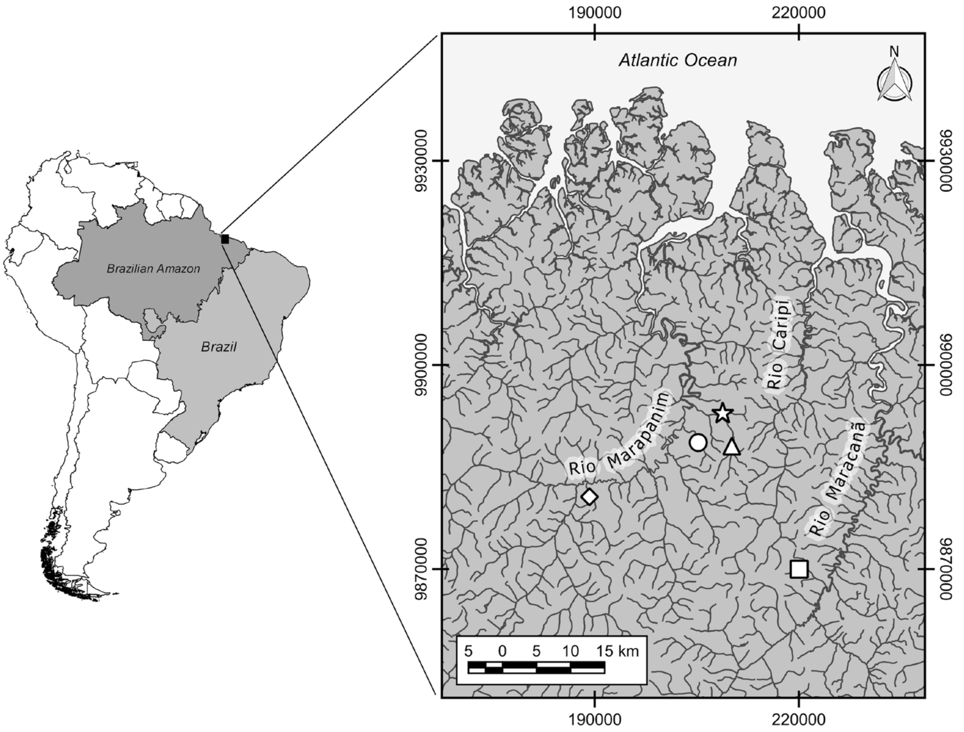

FIGURE 1 | Sampled streams location in northeastern Pará, Brazil. **Circle**: Igarapé Buiuna; **Diamond**: Igarapé Laranjal; **Square**: Igarapé São João; **Star**: Igarapé Pirapema; **Triangle**: Igarapé Timboteua.

width measures. At each depth measuring point, the substrate was categorized into nine categories: (1) gravel; (2) sand; (3) clay; (4) tree trunks (large wood with diameter > 10 cm); (5) coarse litter (leaves and small branches); (6) fine litter (shredded leaves); (7) roots (fine and coarse roots, from riparian vegetation); (8) macrophytes; and (9) FPOM (finely particulate organic matter). The reach area was obtained by multiplying the average width of wet channel by the length of the sampled section (Tab. 1). Since the high density of road-stream crossings in that region, we did not find five impact-free streams to use as reference sites.

Water flow was obtained by timing a semi-floating rubber ball running a defined distance. On each sampling reach, three segments (20 m) were selected in which the rubber ball was timed three times. After that, the average water flow at the sampling reach was obtained. The visibility was estimated as the visible extension of the transect guideline, marked meter by meter, before the beginning of each session.

Voucher specimens. Specimens of observed fish species were collected, preserved in 10% formalin, later washed in running water and maintained in 70% ethanol. The specimens were identified using identification keys (*e.g.*, Géry, 1977; Planquette *et al.*, 1996; Keith *et al.*, 2000 a,b; Sarmento-Soares, Martins-Ribeiro, 2008) and deposited at a reference collection maintained by one of the authors (PG). A representative set of the collected material was deposited at the Ichthyological Collection of the Museu Paraense Emílio Goeldi (MPEG 21370 to MPEG 21454).

Taxonomic and functional structure of assemblages. Species were grouped into functional groups according to the most frequently feeding tactic used by each species, combined with their swimming ability, spatial distribution (vertical and horizontal positions) and activity period (*see* table 1 in Brejão *et al.*, 2013). These information were gathered by *ad libitum* snorkeling sessions (Lehner, 1996). Body size for each observed species was obtained from FishBase database (Froese, Pauly, 2019) to the functional matrix, which were categorized in three classes: 1. Small body size (SL < 50 mm); 2. Medium body size (50 mm < SL < 100 mm); and 3. Big body size (SL > 100 mm). This information was included as the abundance of each class in each sampled reach. Species richness, Shannon diversity (H'), Simpson dominance (D), and Pielou evenness (e) were obtained from a matrix containing species abundance and functional group abundance, in order to describe the taxonomic and functional structure of fish assemblages, respectively. Non-Metric Multidimensional Scaling (NMDS) ordination analysis was used to access the taxonomic and functional assemblage composition.

In order to explore the way at which species and functional composition change across stream reaches, the beta diversity was decomposed into two additive components: turnover (replacement of species or functional groups) and nestedness (dissimilarity due to differences in species or functional groups richness) based on the Sørensen dissimilarity index (Baselga, 2010). Decomposition of beta diversity was calculated between reaches of the same stream.

Data Analysis. The environmental variables and fish assemblage structure differences between the three-stream reach groups (downstream, impoundment, upstream) were tested by ANOVA, recognizing the assumption of normality and equality of variance.

TABLE 1 | Environmental variables obtained for each one of 15 sampled stream reaches (200 m), the significant differences among reaches groups were highlighted in bold. Bui: Igarapé Buiuna, Lar: Igarapé Laranjal; Pir: Igarapé Pirapema; SJo: Igarapé São João; Tim: Igarapé Timboteua.

	Upstream						Impoundment						Downstream					
	Bui	Lar	Pir	SJo	Tim	Mean±SD	Bui	Lar	Pir	SJo	Tim	Mean±SD	Bui	Lar	Pir	SJo	Tim	Mean±SD
Width (m)	4.3	1.9	3.4	3.4	5.2	3.6±1.2	4.8	40.0	3.3	5.0	6.9	12.0 ±15.7	2.9	2.2	3.3	2.8	6.0	3.4±1.5
Depth (cm)*	**37.0**	**15.5**	**51.0**	**29.0**	**58.5**	**38.2±17.2**	**78.0**	**60.0**	**49.5**	**97.0**	**106.3**	**78.2±24.0**	**36.0**	**32.0**	**38.0**	**47.3**	**54.0**	**41.6±9.0**
Area (m^2)	74.0	31.0	102.0	58.0	117.0	76.4±34.3	148.2	8000.0	99.0	116.4	212.5	1715.2±3513.2	72.0	48.0	76.0	94.5	108.0	79.7±22.9
Volume (m^3)	27.4	4.8	52.0	16.8	68.4	33.9±26.0	115.6	2400.0	49.0	112.9	225.8	580.7±1019.0	25.9	15.4	28.9	44.7	58.3	34.6±16.9
Water flow ($m\ s^{-1}$)*	**0.2**	**0.1**	**0.2**	**0.3**	**0.4**	**0.2±0.1**	**0.1**	**0.0**	**0.2**	**0.0**	**0.2**	**0.1±0.1**	**0.4**	**0.2**	**0.3**	**0.4**	**0.4**	**0.3±0.1**
Gravel (%)	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0	0.0	7.4	0.9	1.7±3.2	3.4	0.0	0.0	0.0	17.1	4.1±7.4
Sand (%)	17.3	6.5	26.6	73.8	53.7	35.6±27.6	4.0	0.0	2.9	25.9	18.5	10.3±11.3	44.4	4.4	50.5	40.8	65.8	41.2±22.7
Clay (%)	0.9	0.0	0.0	0.0	0.0	0.2±0.4	0.0	0.0	2.9	0.0	0.9	0.8±1.3	0.9	1.1	0.0	0.0	0.9	0.6±0.5
Tree trunks or branches (%)	10.0	3.7	2.7	1.9	7.4	5.1±3.5	11.1	30.0	11.5	7.4	5.6	13.1±9.8	7.7	4.4	13.8	9.7	11.1	9.3±3.5
Coarse litter (%)	57.3	62.0	41.6	16.8	13.9	38.3±22.3	42.4	0.0	44.2	0.0	41.7	25.7±24.3	27.4	47.3	18.4	34.0	13.7	28.1±13.3
Fine litter (%)	7.3	22.2	16.8	3.7	16.7	13.3±7.6	30.3	0.0	14.4	44.4	19.4	21.7±16.7	0.0	22.0	6.4	6.8	2.6	7.6±8.5
Roots (%)	5.5	0.9	4.4	0.9	27.8	7.9±11.3	5.1	0.0	2.9	1.9	9.3	3.8±3.6	14.5	17.6	7.3	3.9	4.3	9.5±6.2
Macophytes (%)	0.0	0.0	0.0	0.9	5.6	1.30±2.4	5.1	10.0	2.9	13.0	3.7	6.9±4.4	1.7	3.3	0.0	0.0	0.0	1.0±1.5
FPOM (%)	1.8	4.6	8.0	1.9	0.0	3.3±3.1	2.0	60.0	18.3	0.0	0.0	16.1±25.7	0.0	0.0	3.7	4.9	0.0	1.7±2.4
Substrate diversity (H’)	1.3	1.1	1.5	0.9	1.5	1.3±0.3	1.5	0.9	1.6	1.5	1.6	1.4±0.3	1.4	1.4	1.4	1.4	1.3	1.4±0.0
Minimum temperature (°C)	26.0	25.5	25.0	25.5	25.0	25.4±0.4	26.0	30.0	25.0	26.0	25.5	26.5±2.0	26.0	27.0	25.0	26.0	25.0	25.8±0.8
Maximum temperature (°C)	26.0	25.5	26.0	26.0	26.0	25.9±0.2	27.5	31.5	26.0	27.0	26.0	27.6±2.3	27.0	27.0	26.0	26.5	25.0	26.3±0.8
Visibility (m)	2.0	3.0	1.5	5.0	1.2	2.5±1.5	1.6	3.0	2.0	3.0	1.0	2.1±0.9	2.0	1.5	1.3	2.0	1.2	1.6±0.4

To describe and evaluate the impoundment effect on the taxonomic and functional composition, the data of species abundance and functional group abundance across the three groups of reaches were analyzed by using a Non-Metric Multidimensional Scaling (NMDS) based on Bray-Curtis similarity index (Clarke, Warwick, 2001), complemented with an Analysis of Similarity (ANOSIM), with a 5% significance level. The significant environmental variables ($p < 0.05$) related to taxonomic and functional composition were identified and plotted by using the *envfit* function. All statistical analyses were performed in R (R Core Team, 2019) using Vegan (Oksanen *et al*., 2019) and MASS (Venables, Ripley, 2002) packages.

RESULTS

Stream reaches differed only in stream depth ($p = 0.006$, Fig. 2A) and water flow ($p = 0.01$, Fig. 2B). Upstream and downstream reaches were shallower than impounded reaches ($p = 0.01$); downstream reaches have faster water current than impounded reaches ($p = 0.01$), no significant differences were found between upstream and downstream reaches. No differences related to the others environmental descriptors among the three reach groups (upstream, impoundment and downstream) were found.

A total of 7,834 specimens from 65 species (Tab. **S1**) was sampled in the 15 stream reaches. These species were grouped in 18 functional trophic groups, according to their feeding tactics, water column occupation and period of activity.

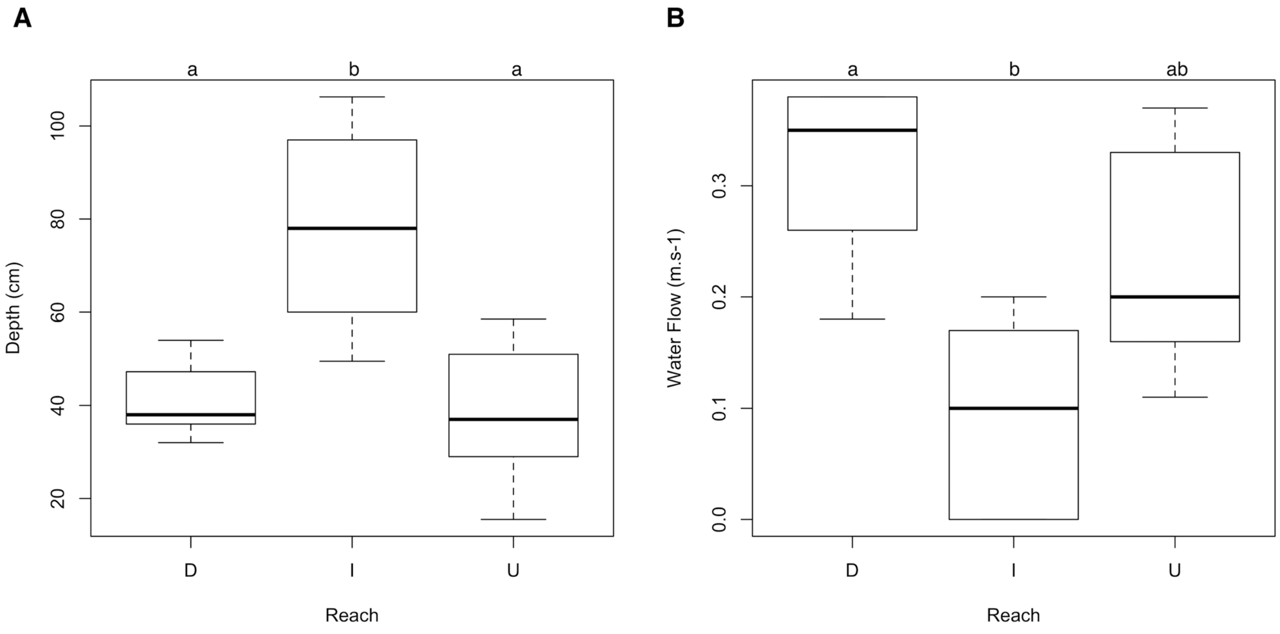

FIGURE 2 | ANOVA results for environmental significant differences among stream reach groups. **A.** Depth; **B.** Water flow. **D**: Downstream reaches from impoundments; **I**: Impounded reaches; **U**: Upstream reaches from impoundments.

The taxonomic and functional composition at impounded reaches differed from lotic reaches, but there was no difference between the lotic reaches (ANOSIM Taxonomic Composition: upstream *vs.* impoundment, p = 0.022; upstream *vs.* downstream, p = 0.312; impoundment *vs.* downstream, p = 0.007; ANOSIM Functional Composition: upstream *vs*. impoundment, p = 0.032; upstream *vs.* downstream, p = 0.243; impoundment *vs.* downstream, p = 0.006) (Figs. 3A–B). The functional composition differences were mainly related to the functional trophic groups, the body size was not important in this separation of the groups.

The changes in taxonomic and functional composition among stream reaches (*i.e.*, beta diversity) were associated with both turnover and nestedness. The turnover had a higher contribution for the total beta diversity between stream reaches, except between upstream and downstream reaches in relation to functional composition (Fig. 4). In addition, the nestedness component had a lower contribution for beta diversity of species and functional groups between upstream-impoundment reaches relative to impoundment-downstream and upstream-downstream (Fig. 4).

Diurnal species and functional groups associated with slower and deeper environments were grouped at impounded reaches, especially Cichlidae (*e.g.*, *Heros efasciatus* and *Satanoperca jurupari*), small species of Curimatidae (*e.g.*, *Curimatopsis* cf. *cryptica*), Lebiasinidae (*e.g.*, *Nannostomus eques*), and large pelagic predators (*e.g.*, *Acestrorhynchus* cf. *falcatus*), belonging to diggers, picker and browsers, mud-eaters, diurnal surface pickers, and pursuit predators functional groups (Figs. 3A–B). Differently, species and functional groups presenting twilight-night habits were grouped at lotic reaches, linked to shallow environments with high water flow, belonging mainly to Siluriformes (*e.g.*, *Mastiglanis asopos*, *Helogenes marmoratus*, *Denticetopsis epa*, *Tatia gyrina*, *Rineloricaria heteroptera*, and *Farlowella amazonum*), Gymnotiformes (*e.g.*, *Hypopygus lepturus* and *Gymnorhamphichthys rondoni*), Crenuchidae (*Characidium fasciatus*) and larger species of Characidae (*e.g.*, *Bryconops melanurus* and *Moenkhausia comma*), belonging to sit-and-wait predators, crepuscular to nocturnal drift feeders, grazers, invertebrate pickers and diurnal channel drift feeders functional groups (Figs. 3A–B).

Nine species were exclusively observed in downstream lotic reaches (*e.g.*, *Bryconamericus* cf. *diaphanus*, *Charax* cf. *metae*, *Bunocephalus coracoideus*, *Corydoras* cf. *acutus*, *Gymnotus coropinae*, *Hypopygus lepturus*, *Microsternarchus bilineatus*, and *Apteronotus albifrons*), and eight species, which were exclusively observed in lotic reaches, presented higher abundance in downstream, when compared to upstream lotic reaches (*Hoplias* cf. *malabaricus*, *Denticetopsis* cf. *epa*, *Helogenes marmorauts*, *Potamoglanis hasemani*, *Farlowella* cf. *amazonum*, *Pimelodella* sp., *Sternopygus macrurus*, and *Steatogenys duidae*) (Tab. **S1**). Regarding functional groups, grazers, sit-and-wait predators and crepuscular to nocturnal bottom predators and crepuscular to nocturnal drift feeders presented higher abundance in downstream lotic reaches (Tab. **S1**).

Regarding the assemblage structure, downstream reaches have higher taxonomic and functional diversity, in relation to upstream and impounded reaches (p = 0.01, Figs. 5A–B), which, in turn, have similar patterns. No differences were found for the other assemblage descriptors (Simpson dominance and Pielou evenness) (p > 0.148).

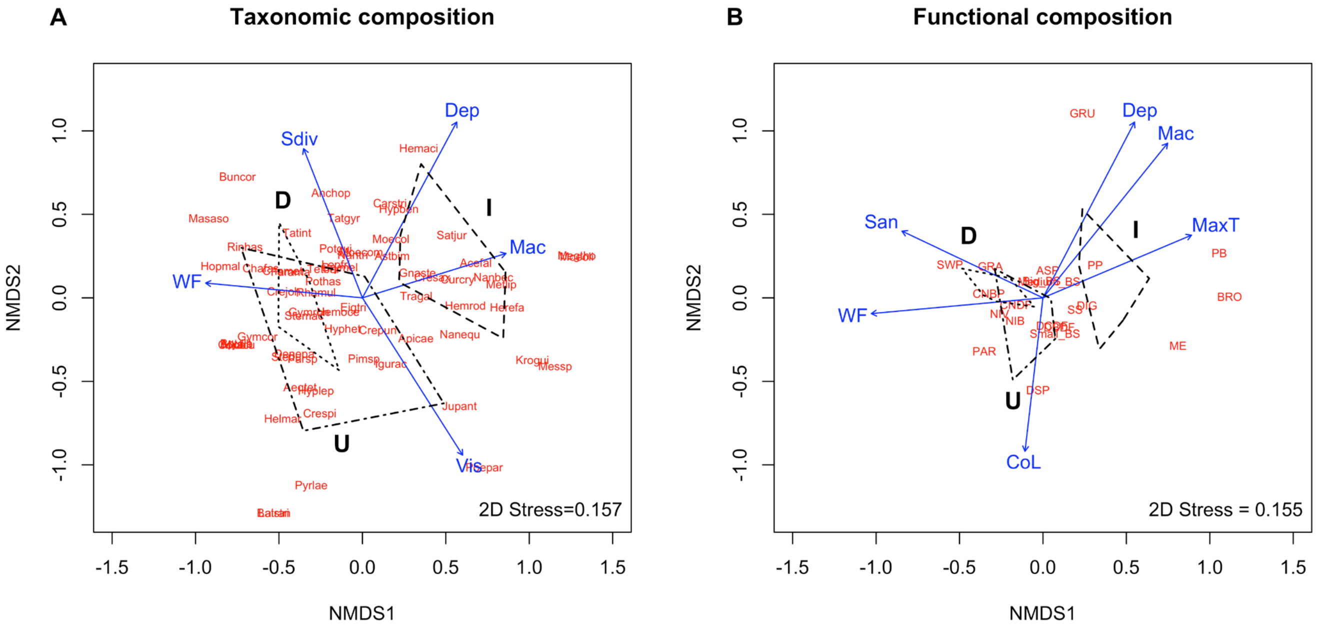

FIGURE 3 | NMDS results for fish assemblage composition in northeastern Amazonian streams. **A.** Taxonomic composition. Fitted variables: **Dep**: average depth; **Mac**: macrophytes; **Sdiv**: substrate diversity; **Vis**: visibility; **WF:** average water flow. **B.** Functional composition. **Fitted variables**: **CoL**: coarse litter; **Dep**: average depth; **Mac**: macrophytes; **MaxT**: maximum temperature; **San**: sand; **WF**: average water flow. Dot-dashed polygon: Upstream reaches (**U**); Dotted polygon: Downstream reaches (**D**); Dashed polygon: Impounded reaches (**I**). For species and functional groups codes, see Tab. **S1**.

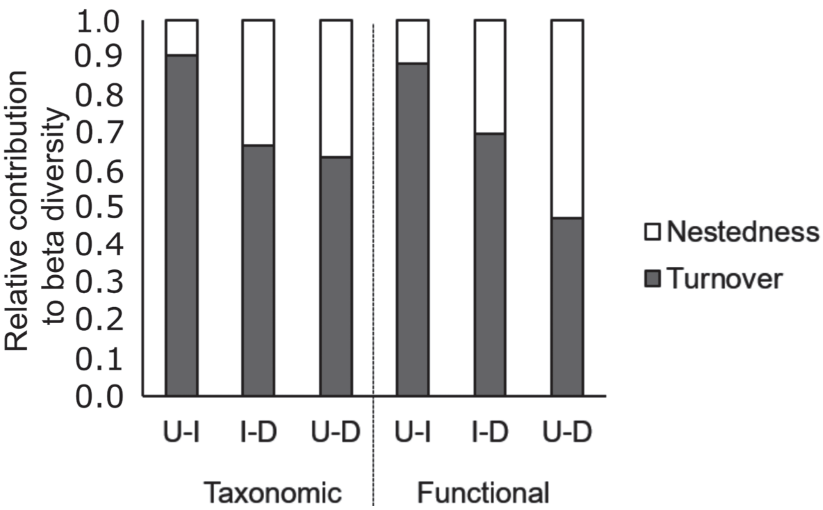

FIGURE 4 | Relative contribution of turnover and nestedness component to total beta diversity obtained after averaging pairwise dissimilarities (Sørensen index) between stream reaches at each stream. **D**: Downstream reaches from impoundments; **I**: Impounded reaches; **U**: Upstream reaches from impoundments.

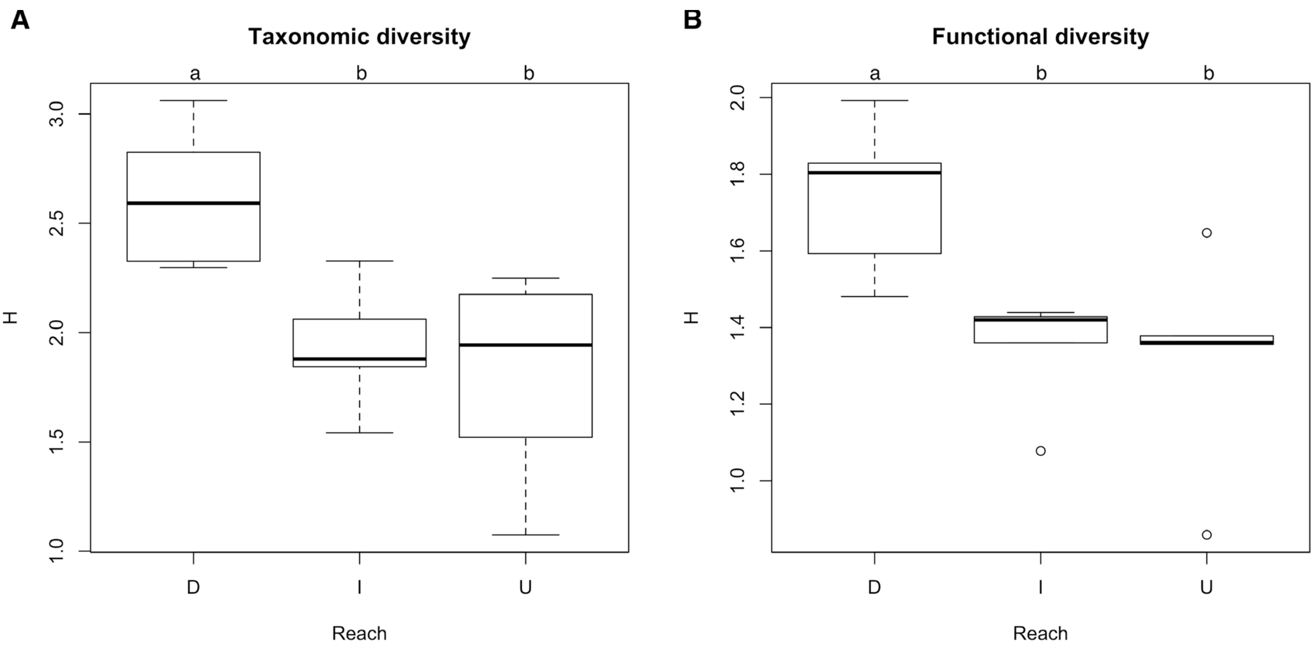

FIGURE 5 | ANOVA results for assemblage structure in northeastern Amazonian streams among stream reach groups. **A.** Taxonomic structure; **B.** Functional structure. **D**: Downstream reaches from impoundments; **I**: Impounded reaches; **U**: Upstream reaches from impoundments.

DISCUSSION

We tested the hypothesis that the presence of anthropogenic impoundments raised from road-stream crossings should affect fish assemblages. Our data show that impoundments are environmentally different from lotic reaches influencing the taxonomic and functional structure of fish assemblages. Upstream and downstream lotic reaches showed similar species/functional composition while they were different from impounded reaches, evidencing the influence of differential habitat constraints between lentic and lotic habitats. Furthermore, the damming effects seem to reverberate to the lotic reaches upstream from impoundments, which presented lower diversity than the lotic reaches downstream from impoundments, probably due to dispersal limitation from lower land species. These results suggest that poorly installed structures in road stream crossing influence aquatic assemblage structure mediated by their influences in habitat structure and connectivity. Despite the streams from this region being under a seasonal flooding regime (*Igapó*), the road-stream crossing embankment *per se* also constitute a barrier to the continuity of this natural process, interrupting the connection between the downstream lotic and the impounded reaches above the road, affecting fish movement (Fullerton *et al.*, 2010).

The increased width and volume of impoundment reaches is followed by the development of pelagic and benthic areas in these newly formed lotic habitats. This change, coupled with the water flow reduction and canopy opening caused by the death of riparian zone trees allows the proliferation of macrophytes, especially *Nymphaea* spp. and *Eleocharis* spp. In natural conditions, the streams from the studied region have weakly confined channels and their beds present complex conformation with intense lateral interactions with the floodplain (Brejão *et al*., 2013). Our field observations, confirmed on Google Earth imagery, indicate that these impoundments, with rather low heads (< 3 meters), can flood at least 1 km upstream from the road crossing, which represents from 25 to 500 times the mean width of the studied environments.

The stream impounding alters the system base level, promoting the raising of water level associated with the reduction of water flow, drowning the riparian forest permanently. Hence, this permanent root drowning leads the trees to languish and die (White, 2007), opening the riparian canopy, allowing the light input. The reduction of water flow increase the organic matter residence time, which, associated with the light intake increasing could support an autotrophic chain, interfering on the fluvial *continuum* (Vannote *et al*., 1980) and the spatial and environmental dynamics of the aquatic ecosystem upstream the crossing (Ward, Stanford, 1983) by permanently flooding a large portion of streams floodplains.

The species that are most successful in colonization after the formation of a reservoir are those adapted to the new environments created, such as submerged logs, macrophyte banks and extensive pelagic areas (Fernando, Holčík, 1982). In addition, species that do not migrate (sedentary species) tend to be more successful in colonizing the reservoirs as they generally have fewer demands on the complex spatial dynamics of their life cycle (Schlosser, 1995; Agostinho *et al*., 1999; Agostinho *et al*., 2008). In small-head dams, which the dimensions are more comparable with this study, the assemblages from impounded environments are characterized by species related to deeper and slow-flowing water habitats, while at the lotic downstream reaches, species related to shallow and swift-flowing habitats are, usually, more common (Gillette *et al*., 2005). In fact, the replacement of species was the main mechanism driving species and functional group differentiation between impoundment reaches and lotic reaches. Our results support these expectations, as the taxonomic and functional composition of impounded reaches differed from lotic ones in a predictable way.

In a recent review about the impacts of hydroelectric dams on fishes and fisheries in tropical rivers, Arantes *et al.* (2019) pointed out that shifts in assemblage composition and structure as one of the patterns frequently observed due to river damming, and they also identified that the most vulnerable species have functional traits associated with flowing water, flow pulses, and habitat complexity and connectivity. In our study we also observed these shifts comparing lotic and lentic reaches, since Cichlidae species that forage by digging the streambed (*Satanoperca jurupari*) or by browsing portions of periphyton adhered on macrophytes and logs, and picking suspended particles (*Heros efasciatus*); Curimatidae foraging organic matter on streambed; Lebiasinidae species, that are picking particles at surface and adhered macrophytes; and large bodied and visual oriented predators, like *Acestrorhynchus* cf. *falcatus*, were favored in impoundments, probably due the higher availability of these food items and the expansion of some habitat compartments in this novel environments. Otherwise, nocturnal, sensorial oriented species like invertebrate pickers (Gymnotiformes), probing their preys using their electric fields at night; Siluriformes species, picking food items drifting at streamflow (Auchenipteridae and Cetopsidae), actively hunting on streambed (Heptapteridae) or by sitting and wait (*Mastiglanis asopos*); and visual orientated diurnal species that forages by picking food items drifting at streamflow (*e.g.*, *Bryconops melanurus* and *Moenkhausia* *comma*) or by sitting-and-wait (*Characidium fasciatus*) were strongly associated with the lotic environments.

Despite similarities between upstream and downstream reaches in relation to species and functional composition, downstream reaches were more diverse than impoundment and upstream reaches, as evidenced by Shannon diversity results. As upstream lotic reaches show lower diversity than downstream lotic reaches, despite their environmental similarity, we could suggest that the environment does not explain these differences. While downstream reaches would be more influenced by mass effect due to the proximity from a mainstream source, dispersal from downstream to upstream reaches would be interrupted by the impoundment. As a consequence, downstream reaches would receive more immigrants and consequently maintain higher diversity via dispersal, suggesting that these road-stream crossings are barriers to fish movement, restricting their capacity to access the upstream habitats (Morita, Yamamoto, 2002). These interpretations are consistent with the higher contribution of nestedness component (*i.e.*, richness differences) for the beta diversity that we found between upstream and downstream reaches mainly in relation to functional groups. In fact, we found higher abundance of functional groups composed by benthic and nektobenthic species (grazers, sit-and-wait predators, and crepuscular to nocturnal bottom) in downstream reaches when compared to impounded and upstream reaches, the species into these groups probably did not have the ability to transpose the road crossing barrier. Moreover, upstream assemblages would also be more exposed to extinction, as limited immigration could not avoid extinction of declining populations via rescue effect (Brown, Kodric-Brown, 1977) and depending on the time since isolation (Morita, Yamamoto, 2002).

In the studied region, road-stream crossings are commonly made adding a sub-dimensioned culvert with diameter ranging from 0.4 m to 1.1 m, placed in stream valleys with width ranging from 70 m to 150 m, over the streambed and barred soil to prepare the embankment for the road. These poorly designed and installed culverts create a height gap, rise the water flow inside the structure, modify the substrate, alter the light input into the culverts and its surroundings, and, as observed in studied region, creates unsuitable habitats close to the downstream culvert outlet, like plunge pools (Powers, Orsborn, 1985; Warren Jr., Pardew, 1998; Wellman *et al*., 2000; Bouska, Paukert, 2010; Nislow *et al*., 2011; MacPherson *et al*., 2012; Mariano *et al*., 2012; Makrakis *et al*., 2012). These features act as a barrier isolating the downstream lotic reaches from impounded reaches and hindering fish dispersion to the upstream lotic environment. These environmental perturbations can be compared to low-head dams and beaver ponds from temperate systems, where higher species richness in lotic reaches is commonly documented, mostly in reaches downstream from impounded areas (Schlosser, Kallemeyn, 2000; Helms *et al*., 2011). In summary, we showed that the responses of fish assemblages to impoundment raised from road-stream crossing are predictable. Species composition varies according to lentic/lotic conditions, which can be explained by differential performance of species mediated by their traits. Moreover, impoundments can also act as a barrier, affecting immigration and extinction at upstream reaches. Therefore, our study provides evidence that niche- and dispersal-based processes drive community assembly in streams disturbed by impoundments in road-stream crossings.

The hydrological network fragmentation and lentification, which consist in transformation of the habitat characteristic of streams and rivers in the direction from lotic to lentic (Sabater, 2008), of water courses, when considered in larger scales, could drive an important beta diversity loss. Since stream lentification standardizes the stream environmental conditions, leading to the selection and predominance of a restrict set of species/functional groups adapted to those novel habitats, and interrupt the immigration processes to upstream lotic reaches. In an applied perspective, our results suggest that the simple placement of culverts on the streambed, although cheaper, is not ecologically functional. Therefore, it is important to establish standards and define best practices for constructing, installing and managing culverts in the Brazilian Amazon, in order to allow the free flow of water bodies, respecting the regional hydrological dynamics and reduce the inevitable impacts over fish assemblages.

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AUTHOR’S CONTRIBUTION

Gabriel L. Brejão: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration.

Fabricio B. Teresa: Conceptualization, Data curation, Formal analysis.

Pedro Gerhard: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration.

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COMPETING INTERESTS

The authors declare no competing interests.

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