



# Patterns of Pelagic Fish Diversity in Floodplain Lakes of Whitewater and Blackwater Drainage Systems Within the Central Amazon River Basin of Brazil

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The Amazon River Basin, one of the world's most threatened ecosystems, has an enormous diversity of fish species, a result of temporally and spatially complex habitat containing biogeochemically different river systems. The annual hydrologic cycle results in floodplain lakes during low water and inundates forests during high water, exposing fish to different resources and environmental conditions. The two principal river systems in the central Brazilian Amazon are blackwater, with nutrient-poor acidic water, and nutrient-rich whitewater. Although species-rich, the Amazon Basin is data-poor in terms of comparative studies on a regional scale. We analyzed data sets from independent sampling studies of pelagic fish in 16 floodplain lakes, nine whitewater (Rio Solimões) and seven blackwater (Rio Negro), in the central Amazon Basin of Brazil. Our findings suggest striking similarities in pelagic fish diversity patterns. Species richness was virtually equal (165 in whitewater and 168 in blackwater). Both species richness, and number of migratory species, per lake increased toward the confluence of the rivers in both systems in our study. The proportion of unique species was also similar in whitewater lakes and blackwater (41 and 43%, respectively), boosting total regional richness to 237 species. However, species composition in whitewater lakes was more homogenous (lower  $\beta$  diversity), and species composition was associated with conductivity and pH in whitewater, but with dissolved oxygen and transparency in blackwater. Therefore, regional fish diversity cannot be represented by sampling one lake or even one drainage system, but must include multiple lakes from both systems. These two systems may differ in sensitivity to anthropogenic stressors such as damming and deforestation.

**Keywords:** Amazon Basin, fish conservation, fish species diversity, floodplain lakes, tropical biodiversity

## INTRODUCTION

The Amazon River Basin is the world's largest freshwater ecosystem, with an aquatic surface area of 93,000 km<sup>2</sup> (Allen and Pavelsky, 2018). This enormous ecosystem is home to an extraordinary diversity of fish. At least 2,716 fish species, including 1,696 of which are endemic to the basin, have been identified so far (Reis et al., 2016; Dagosta and Pinna, 2019). It is also one of the earth's most endangered ecosystems, largely from ongoing anthropogenic stressors to its hydrology and biodiversity such as dam building that reduces connectivity among habitats (Kahn et al., 2014; Hurd et al., 2016; Santos et al., 2018), oil and gas development (Finer et al., 2008), overfishing of both food species and ornamental fish (Campos et al., 2015; Costa-Pereira and Galetti, 2017; Castanho et al., 2019), invasive alien species (Latini and Petrere, 2004), deforestation (Lobón-Cervía et al., 2015), urbanization (Tregidgo et al., 2017), and droughts caused by deforestation and global warming (Castello et al., 2013; Freitas et al., 2013; Nazareno and Laurance, 2015). These problems have caused growing concern over the question of how to preserve fish species richness and also conserve fishery stocks, which are the most important sources of protein for human communities in the region (Castello et al., 2013). We therefore need to understand patterns of species distribution within this basin well enough to design ways to preserve aquatic biodiversity. Our aim is to discern how pelagic fish species diversity, which includes many species harvested for human consumption, is distributed between physically different drainage systems that flow through the central portion of the Amazon River Basin in Brazil.

The putative evolutionary causes that generated the enormous diversity of fish species in this basin, such as geologic age, productivity, adaptive radiation, and extensive allopatry have been discussed and conjectured by many authors. Recently, Albert et al. (2020) concluded that historical geologic processes periodically interrupted aquatic connectivity and created isolated areas that set the stage for habitat specialization and allopatric speciation, which was more important than adaptive radiation within habitats in explaining the development of high overall diversity. The present-day physical environment includes an annual hydrologic cycle that alternates between complete inundation of floodplain forests at high water, and formation of floodplain lakes with varying degrees of connection (or isolation) from river channels at low water. This "flood pulse" (Junk et al., 1989), in which water depth can vary 15 m or more depending on specific location along the rivers, is considered to be the dominant feature of the physical environment for fish species in this region (Junk et al., 1997; Silva et al., 2020). Floodplains occupy 73,500 km<sup>2</sup> (Hess et al., 2015), providing important habitat for Amazonian fish, some of which remain on the floodplain all their lives, dispersing into the flooded forests to feed at high water and then returning to open water of the lakes as the water recedes. Others migrate out of the lakes to spawn in rivers when the boundaries between lakes and the river channels are erased during high water season (Fernandes, 1997).

There are two different aquatic systems in the central Amazon Basin of Brazil, based on biogeochemistry: whitewater and blackwater. Many smaller tributaries contribute flow to each of

these systems, but the main blackwater artery in this region is the Rio Negro, with floodplains known as *igapós*, and the principle whitewater river is the Rio Solimões (Rio Amazonas west of the border with Columbia), with *várzeas*. The confluence of these two rivers occurs at the city of Manaus, and downriver from that point is known in Brazil as the Rio Amazonas.

Rivers in the whitewater system carry a high load of suspended nutrient-rich sediments to the floodplain during the flood season, causing the water to be the color of heavily creamed coffee and supporting highly productive terrestrial and aquatic plant communities, including floodplain forests (Furch, 1984; Junk and Piedade, 1997; Junk et al., 2011). In contrast, blackwater rivers (the color of strong tea) are very poor in nutrients and more acidic than whitewater, and thus very low in net primary productivity (Bogotá-Gregory et al., 2020). Most of the productivity in the blackwater system is in the form of allochthonous input from the adjacent forests, especially when high water floods them and allows fish close access to such forest products as vegetation, insects, and fruits (Furch, 1984; Loebens et al., 2019). In fact, it is very likely that fish were the first frugivorous vertebrates to disperse terrestrial plant seeds (ichthyochory), beginning in the Paleozoic (Horn et al., 2011).

Much of the literature reporting comparative fish species richness between these two drainage systems tends to show higher richness in whitewater than in blackwater area, although this finding is not uniform. For instance, in a survey of published comparisons of fish diversity between these two systems Crampton (2011) found that the western whitewater habitats tended to have more species than the blackwater drainage, but Saint-Paul et al. (2000) reported that blackwater fish assemblages were 10% more diverse than those in whitewater. The failure to agree on this is probably largely due to differences in how and where different studies were conducted.

Most of the published studies comparing fish diversity between systems have been limited in terms of landscape area or number of lakes, comparisons of unequal areas between blackwater and whitewater, types of habitat sampled within lakes, and sampling methodology. Much of the difficulty in making comparisons of this kind is rooted in scale dependence. Differences in species composition among lakes of the same drainage system result in high  $\beta$ -diversity (Freitas et al., 2014), so representation of species richness must be based on multiple lakes. Within each lake there are different habitats (e.g., open water, shoreline, and macrophyte meadows in whitewater lakes) that fragment the within-lake distribution of resident species so that all of these must be sampled (Siqueira-Souza et al., 2016). There is also a temporal scale: since fish assemblages vary in species composition among the hydrologic seasons, it is necessary to sample during both high and low water periods in order to obtain representative fish species diversity (Merona et al., 1993; Scarabotti et al., 2011; Siqueira-Souza et al., 2016). Finally, sampling methodology of many studies were inadequate to capture fish that are too small for the gill nets employed, or have behaviors that did not bring them into contact with the collection gear. Thus, the number of species sampled do not constitute total fish diversity in these studies, but are still useful for assessing species richness of selected groups.

The most common sampling strategy for fish in the basin has involved deployment of gill nets with varying mesh sizes (Saint-Paul et al., 2000), which are adequate for medium-large body size pelagic fish but not for smaller fish, or for benthic species during high water season when nets don't reach the bottom of the lakes. A notable exception to this sampling limitation is Bogotá-Gregory et al. (2020), who used a variety of sampling gear to get a more accurate picture of total fish diversity, and arrived at the conclusion that whitewater fish had higher fish diversity than blackwater (and also than clearwater, which does not occur in our part of the Amazon Basin).

We examined patterns in the species richness of moderate-to-large size pelagic fish inhabiting floodplain lakes of the Rio Negro and Rio Solimões in the Central Amazon River Basin of Brazil, specifically located upstream from the merging of the two rivers at Manaus. Specifically, we assessed pelagic species richness in individual lakes ( $\alpha$ -diversity), comparison of richness among lakes within each system ( $\beta$ -diversity), comparison of numbers of shared and unshared species between the systems, physical properties of the water associated with diversity in each system, and geographic distance of lakes from the confluence of the two rivers. We also noted those species with known migratory behavior. We were able to compare multiple unpublished data sets from several independent studies, carried out by different research teams working on local censuses, for different reasons, in either the blackwater or whitewater system, but that employed the same sampling protocol to census fish species in floodplain lakes. Further, these comparisons are from lakes in relatively close regional proximity, which reduces the potentially confounding factor of wider geographical variability within the basin (Bogotá-Gregory et al., 2020).

## MATERIALS AND METHODS

### Study Sites

Fish sampling was conducted by independent teams of researchers at 16 lakes along the middle and lower reaches of the Rio Negro (seven lakes) and Rio Solimões (nine lakes) upstream from the confluence of these two rivers that forms the main channel of the Rio Amazonas (Figure 1). The lakes varied substantially in area and depth over the seasons of the hydrologic cycle, and except at low water include flooded forests at their margins, but the range of sizes (surface areas) of the whitewater and blackwater lakes we sampled did not differ between systems (Appendix 1).

### Fish Sampling

The fish assemblages of 16 Amazonian floodplain lakes were sampled by independent research groups from the Federal University of Amazonas (UFAM) and the National Institute of Amazonian Research (INPA) between 2005 and 2013 (Appendix 1). Nine of these were whitewater lakes located on the floodplain of the middle and lower reaches of the Rio Solimões, and seven were blackwater lakes along the Rio Negro (Figure 1).

All lakes in this combination of studies were typical of Amazonian floodplain lakes, and were sampled during both high and low water seasons of the hydrologic cycle for between 1 and 8 years (Appendix 1). The sampling gear consisted of floating

gillnets of standardized dimensions: 20 m long by 2 m high (deep), with mesh sizes of 30, 40, 50, 60, 70, 80, 90, 100, 110, and 120 mm between opposite knots of the stretched mesh. Although samplings were carried out by independent groups, all sampling events proceeded according to the same protocol: gillnets were deployed at 0600 (daybreak) and left for 48 h at each collection site, and fish were collected from them every 6 h to minimize the predation effect (mainly foraging by piranha) on entangled fishes. Floodplain lake habitats have consistent sub-habitats: open water, floating macrophyte meadows (in whitewater; they do not occur in blackwater), and the flooded forest at the margins of the lakes except at low water (Siqueira-Souza et al., 2016). Therefore, gillnets were set at each of these sub-habitats during every sampling period. Fish collecting for all these studies was done under licenses 16889-2, 30052-1, 34446-3, and 50662-1 (Instituto Chico Mendes de Conservação da Biodiversidade-ICMBio/Brazil).

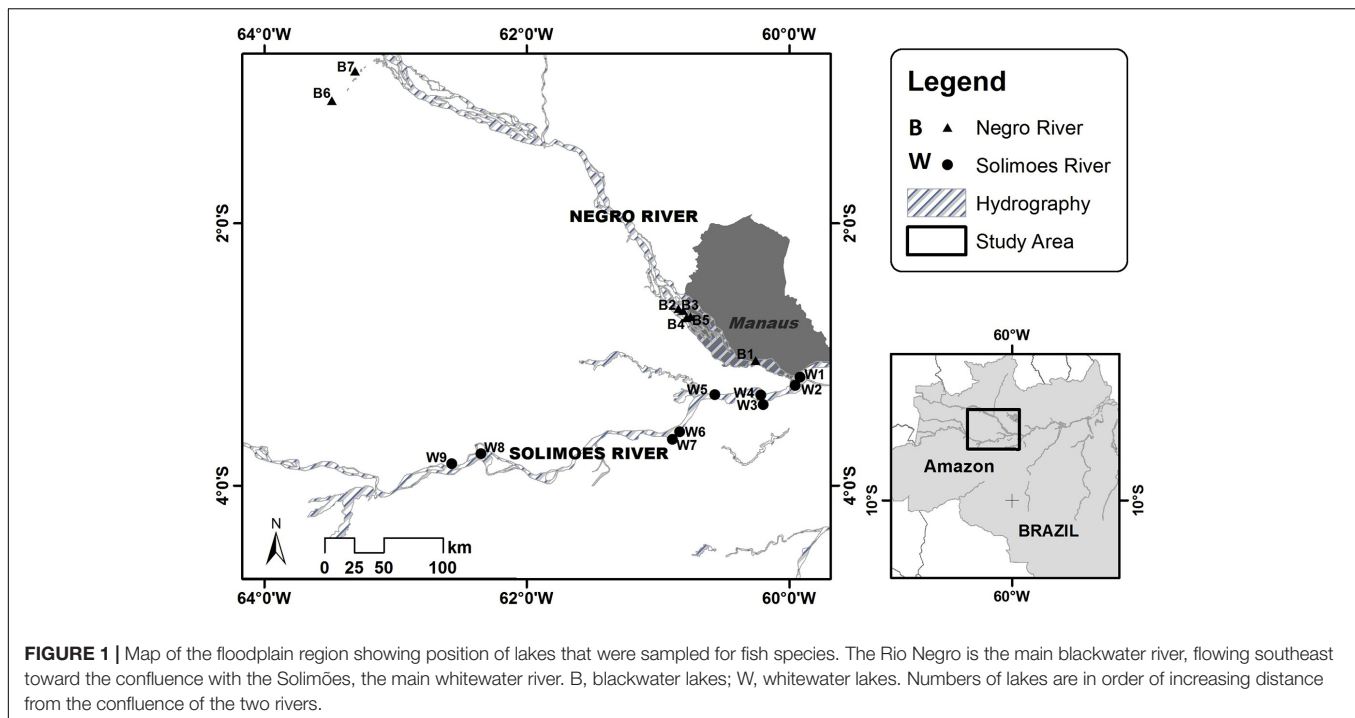
Because the lakes in our combined data set were not all sampled for the same number of years, owing to having come from different local studies that were not initially related to each other, the question arises of whether the data are biased because of potential variability in species composition between successive years. We saw no indication of this in any of our multiple-year data sets. In fact, although fish are free to move in and out of lakes during high water, which could result in random assortment among lakes, other researchers, e.g., Petry et al. (2003); Arrington and Winemiller (2006), and Fernandes et al. (2014) have noted non-random species composition, indicating affinity for a specific habitat that may qualify some regional species distributions as metapopulations (Hurd et al., 2016). Stability of species assemblages is even true for small temporary pools, and the variation in species composition declines with increasing volume of water (Espírito-Santo and Zuanon, 2017).

### Data Analysis

We constructed a rarefaction curve for each lake. Rarefaction gives us an expected number of species from a small sample drawn at random from a larger pool of individuals (Gotelli and Colwell, 2001), so the curve generated by plotting accumulated numbers of species against number of individuals sampled tells us how close we have come to representing most of the species actually present in the lake (i.e.,  $\alpha$ -diversity). Since we were specifically interested in species richness rather than relative abundance, it was important not to exclude rare species from our analyses.

We investigated the potential importance of lake size, distance between each lake and the confluence of Rios Negro and Solimões and environmental variables such as conductivity, dissolved oxygen, pH, temperature, and transparency on the taxonomic structure of local fish assemblages using Redundancy Analysis (RDA) (Ter Braak and Verdonschot, 1995). The number of fish belonging to each taxon was Hellinger-transformed prior to RDA. We tested for significance using a Monte-Carlo permutation test with 999 random permutations under the null model of no effect.

We used Moran's I statistic (Fortin et al., 1989) to test the spatial correlation between species richness and the geographical distance between sampling sites and the confluence of Solimões



and Negro River for both systems. This procedure was repeated using known migratory species richness and the same geographical distances. To test the null hypothesis that there is no influence of the geographic distance on the fish diversity we performed generalized linear models based on Poisson probability distribution (Zuur et al., 2009) using the number of species as response variable ( $Y_i$ ) and geographic distance between the sampled lake and the confluence of the two rivers as predictor variable ( $X_i$ ). This procedure was carried out for the lakes of both systems separately.

Given the possibility that migratory species might be able to move between the two drainage systems, thus complicating the assignment of “home” habitat, we also performed generalized linear models based on Poisson probability distribution (Zuur et al., 2009) using the number of known migratory species (Appendix 2) as response variable ( $Y_i$ ) and geographic distance between the sampled lake and the confluence of the two rivers as predictor variable ( $X_i$ ). This procedure was carried out for the lakes of both systems separately.

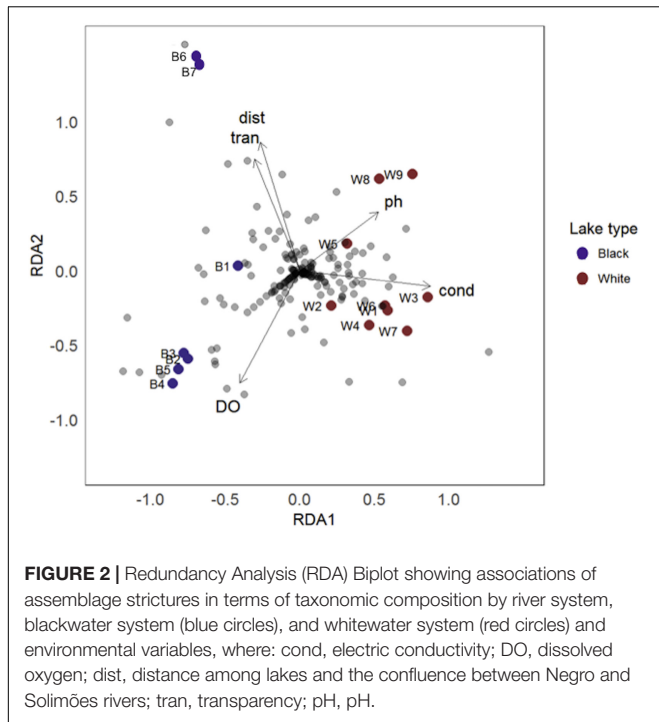
All statistical analyses were carried out using R Statistical Software (R Development Core Team, 2012). RDA were done with Vegan package (Oksanen et al., 2010), GLMs were fitted using the CAR (Fox and Weisberg, 2011) and MASS packages (Ripley et al., 2013) and Moran’s I estimates were calculated using the APE package (Paradis et al., 2004).

## RESULTS

Rarefaction curves were asymptotic, showing that the sampling effort was adequate to represent the bulk of pelagic fish species

richness (Appendix 3). Fish community composition (Appendix 4) revealed that pelagic species richness was nearly identical between blackwater lakes (total  $S = 160$ ) and whitewater lakes ( $S = 161$ ) although there were substantial differences in species composition between the systems. Mean overall abundance of fish in blackwater lakes (1,487.28) also was not significantly different than of whitewater lakes (1,890.11) ( $t_{14} = -0.314$ ,  $P = 0.723$ ). Almost the same number of species were unique (unshared between systems) to each system: 74 or 31.6% in whitewater lakes; 73 or 31.2% in blackwater, which is reasonably consistent with overall endemism for the region (Reis et al., 2016). Thus, there were more unshared (147) than shared (87) species between these two systems, so that combined (regional) species richness was 234, substantially higher than if all species had been found in both systems (Appendix 4).

The RDA resulted in  $R^2 = 0.666$  with two significant axes [RDA1:  $F = 7.132$ ,  $\text{Pr}(>F) = 0.01$  and RDA2:  $F = 3.811$ ,  $\text{Pr}(>F) = 0.005$ ]. A gradient was strongly associated with axis RDA1 and indicates that species composition of lakes differed between the two systems, with blackwater lakes to the left of whitewater lakes in **Figure 2**. Blackwater lakes appear less homogeneous (greater  $\beta$ -diversity) than whitewater lakes on axis RDA2, and showed a pattern where lakes nearer the confluence of the two systems are on the lower side of the graph, and the lakes located more distant are on the upper side (see **Figure 1** for position of lakes). This pattern is not as evident in whitewater lakes, although the lakes W8 and W9, located more distant of the confluence, also are on the upper side of the RDA plot. The key environmental variables that ordered the type of each lake by its fish species richness were conductivity, dissolved oxygen and pH, whereas transparency and distance from the confluence



**FIGURE 2 |** Redundancy Analysis (RDA) Biplot showing associations of assemblage structures in terms of taxonomic composition by river system, blackwater system (blue circles), and whitewater system (red circles) and environmental variables, where: cond, electric conductivity; DO, dissolved oxygen; dist, distance among lakes and the confluence between Negro and Solimões rivers; tran, transparency; pH, pH.

**TABLE 1 |** Results of Redundancy Analyses (RDA) for species richness and environmental variables representative of lakes in both the Negro and Solimões River drainage systems.

Variable	Variance	Pseudo-F	Pr(>F)
pH	0.101	3.875	0.02
Conductivity	0.127	4.878	0.01
Dissolved oxygen	0.072	2.782	0.01
Temperature	0.015	0.567	0.80
Transparency	0.046	1.780	0.06
Lake area	0.012	0.454	0.93
Distance from the lake to the confluence between Negro and Solimões Rivers	0.042	1.607	0.08
Residual	0.208		

between Negro and Solimões rivers showed only a slight effect and temperature and lake area showed no effect (Table 1). Conductivity and pH were directly associated with whitewater lakes while dissolved oxygen, transparency and distance from the confluence between Negro and Solimões rivers clustered the blackwater lakes (Figure 2).

The null hypothesis that there is no spatial correlation between the total number of fish species and the geographic distance between the sampling sites and the confluence of Negro and Solimões rivers was rejected for the blackwater Negro River ( $P = 0.013$ ) and for the whitewater Solimões River lakes ( $P = 0.014$ ). Fish species richness within lakes ( $\alpha$  diversity) declined as a function of geographic distance from the confluence of the rivers in both whitewater and blackwater (Table 2 and Figure 3).

The total number of known migratory fish species among our collections was 40 in whitewater and 38 in blackwater,

**TABLE 2 |** Results of generalized linear models between total species richness and geographic distance to the confluence of the Negro and Solimões River drainage systems.

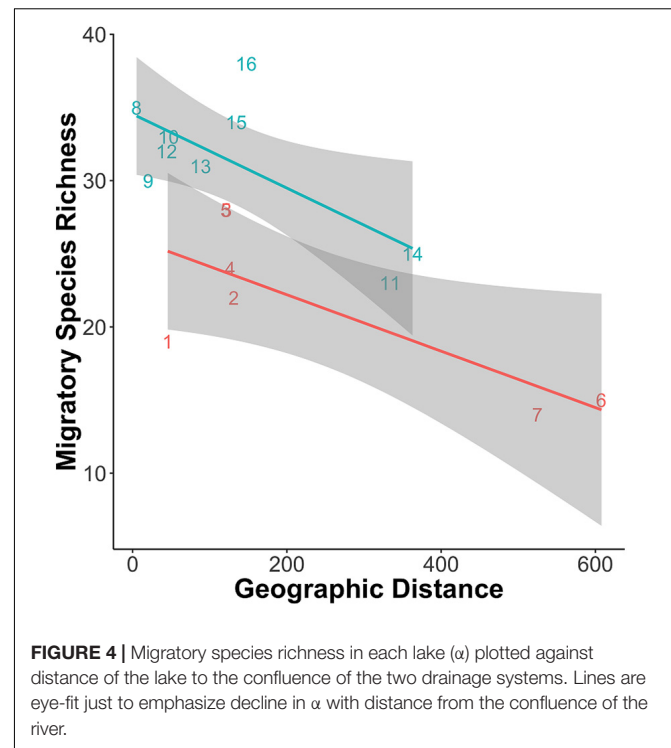
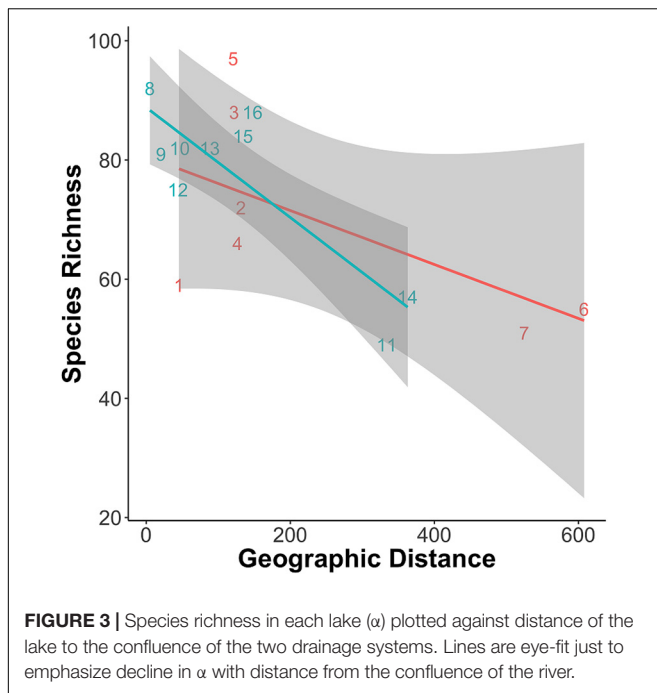
Negro	Estimate	Z-value	P-value
Intercept	4.4018	65.721	<0.001
Geographic Distance	-0.00069	-2.992	0.003
Explained Deviance	38.07%		
<b>Solimões</b>			
Intercept	4.4983	84.247	<0.001
Geographic Distance	-0.0013	-3.926	<0.001
Explained Deviance	70.61%		

with 11.6% of migrating species unique to whitewater and 7.0% unique to blackwater (Appendix 2). As with total richness, the null hypothesis that there is no spatial correlation between the number of migratory species and the geographic distance between the sampling sites and the confluence of Negro and Solimões rivers was rejected for the blackwater Negro River lakes ( $P = 0.004$ ) and for the white water Solimões River ( $P = 0.036$ ). As with total richness, the number of migratory species within lakes declined as a function of geographical distance from the confluence (Table 3 and Figure 4).

## DISCUSSION

Pelagic fish species diversity of these floodplain lakes, measured as total species richness and as mean richness/lake, was essentially equivalent. This was also true of mean fish abundance per lake between systems. The proportion of species unique to either system was close to the estimated percentage of endemic species for the entire Amazon Basin, and also considerably boosted regional species richness higher than was found in either system separately.

The pattern of diversity increasing toward the confluence of the rivers in both systems, is consistent with most earlier reports, e.g., Vannote et al. (1980) and Fernandes et al. (2004), but see Oberdorff et al. (2019) for the opposite result on a larger scale. Initially, we wondered if migratory species would move between systems and thus be counted in both systems. However, the general trend for migrants is to move from the lakes of either system to the rivers of the same system to breed as the water recedes from the floodplains, and then to return to the lakes to feed in the flooded forest during high water, while their juveniles drift from the river to the floodplain (Fernandes, 1997; Araújo-Lima and Ruffino, 2003). The many present-day migratory fish of the Amazon River Basin have some of the longest migratory routes of any freshwater fish. For instance, the catfish *Brachyplatystoma rousseauxii* migrates approximately 5,500 km from the Atlantic estuary of the Amazon westward to the Andean headwaters to breed (Vásquez et al., 2009; Duponchelle et al., 2016, 2021; Barthem et al., 2017; Hauser et al., 2020). Thus, migratory species should be good candidates for dispersal among different river systems. However, there are many Amazonian fish species for which migratory behavior is not yet known (Appendix 2), and the many variables associated with



**TABLE 3** | Results of generalized linear models between migratory species richness and geographic distance to the confluence of the Negro and Solimões River drainage systems.

Negro	Estimate	Z-value	P-value
Intercept	3.2846	27.403	<0.001
Geographic Distance	-0.001	-2.289	0.022
Explained Deviance	60.90%		
Solimões			
Intercept	3.5478	41.942	<0.001
Geographic Distance	-0.0008	-1.991	0.034
Explained Deviance	49.94%		

migratory behavior are just beginning to be analyzed (Alò et al., 2020). Further, there is still the question of how non-migratory species, many of which are shared between the two systems, got from one to the other.

The fact that different physical environmental variables were associated in RDA with species assemblages in lakes of the two systems (conductivity and pH in whitewater; transparency and dissolved oxygen in blackwater) lacks a mechanistic explanation at present, and probably requires physiological investigation, especially of species that occur in only one of the two drainage systems. Floodplain lakes situated where the two river systems meet are open to species from both blackwater and whitewater rivers, and exhibit high variation in physical conditions (Röpke et al., 2016) that might be good transitional zones for cross colonization. This could result in higher species diversity close to the confluence. However, it also has been suggested that the substantial differences in water chemistry, such as pH and conductivity, are barriers to cross migration between systems due to chemical intolerance, particularly from the

whitewater to more acid blackwater (Farias and Hrbek, 2008; Lima and Ribeiro, 2011).

Components of the floodplain landscape, including terrestrial wetland shrubs that are rooted vegetation and more permanent than floating macrophyte meadows, also have been proposed as important to maintenance of floodplain fish diversity (Freitas et al., 2018). Other studies have demonstrated that the forest cover bordering Amazonian floodplain lakes is a determinant of both the taxonomic and functional diversity of fish assemblages (Arantes et al., 2017, 2019), which indicates that the overall floodplain landscape exerts an important influence on fish diversity (Lobón-Cerviá et al., 2015; Freitas et al., 2018). Another factor is connectivity among habitats, which can stabilize regional populations and preserve diversity by inter-habitat migration and metapopulation dynamics (Arrington and Winemiller, 2006; Miyazono et al., 2010; Hurd et al., 2016).

We hope that our results will stimulate more studies on regional spatial scales, including a comparison among lakes between lakes upstream from the merging of the Solimões and Negro rivers with those downstream lakes bordering the main Amazon channel after they merge. This will require teams of researchers using the same sampling techniques concurrently in widely separated portions of the Basin. DNA analysis should allow us to compare rates and trends in speciation (Pyron and Burbrink, 2013) between the two systems. Molecular genetics has already given us fresh insight on phylogenetic trends and biogeography of some important Amazonian fishes (Farias and Hrbek, 2008; Lovejoy et al., 2010; López-Fernández et al., 2010; Lima and Ribeiro, 2011). We also need much more

basic biological information for many species, such as well-defined trophic niche positions that would allow us to calculate functional diversity, and more complete information on life cycles, migratory behavior, physiological responses to water chemistry, and biogeographic distribution.

## CONCLUSION

We identified several patterns in our data that reveal both similarities and differences between pelagic fish assemblages of whitewater and blackwater floodplains in the sampled region of the central Amazon River Basin of Brazil. Overall, there were surprisingly more similarities than differences.

Similarities: total number of species caught, number of shared, and unshared species (more shared than unshared between systems), number of migrating species, abundance of fish, and the decline in both  $\alpha$ -diversity and number of migrating species with upstream distance from the confluence of the Rios Negro and Solomões.

Differences: heterogeneity of fish assemblages ( $\beta$ -diversity) was lower among whitewater lakes, and fish diversity was associated with different physical factors in the two systems: conductivity and pH in whitewater, and dissolved oxygen and transparency in blackwater.

Information from comparative sampling of fish in different areas and drainage systems can be important to efforts at conservation. Designing intelligent strategies for conserving dwindling fishery stocks and preserving the remaining biodiversity of the Amazon Basin may depend in part on recognition that the different systems and spatially separated areas within them have different vulnerabilities. For instance, deforestation will reduce allochthonous sources of food that are crucial to blackwater fish, depressing  $\beta$  diversity among lakes (Arantes et al., 2017, 2019), but may be less important to species living in productive whitewater. On the other hand, upriver damming will fragment migratory routes of some species in both systems (Barthem et al., 1991). Damming also may negatively affect whitewater floodplains more than in blackwater because in addition to reducing migration it will reduce sediment flow and prevent nutrients that support both aquatic and terrestrial productivity from reaching the lowland wetlands of the Central Amazon (Forsberg et al., 2017).

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## DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

## ETHICS STATEMENT

Ethical review and approval was not required for the animal study because the license to the samplings included a description of the fish catches to support the ethical requests.

## AUTHOR CONTRIBUTIONS

FS-S, KY, and MS collected the data. FS-S, CF, LH, GC, and JK designed the study and methodology. CF and LH performed statistical analysis. All authors contributed to writing of the manuscript and approved the submitted.

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## SUPPLEMENTARY MATERIAL

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