



Single-Species Co-management Improves Fish Assemblage Structure and Composition in a Tropical River

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Co-management is increasingly recognized as an effective model for managing fisheries, but little information exists on whether co-management can produce effects in species other than the target species. Fishery co-management in the tropics, where fish diversity is high and fish catches tend to be multispecies, is prone to produce assemblage-wide effects via alterations in the food web and changes in the overall capture of non-target species. Here, we assessed the effects of co-management for the species *Arapaima* sp. in relation to the structure and composition of the overall fish assemblage in floodplain lakes of the central Amazon Basin. These floodplain lakes are managed under a system of zoning of fishing activities. We used data from surveys of six floodplain lakes, including two lakes of each of three categories (lakes where fishing is prohibited, limited-access lakes, and open fishing lakes). The surveys were carried out before and after implementation of co-management, through gillnet fishing. The study area was the lower Solimões River, in the Amazon Basin, Brazil. Statistical models showed significant changes in the composition and structure of the fish assemblages after the implementation of the co-management, regardless of the zoning category. Through regulation of gear use and fishing practices, co-management allowed the colonization of species that had not been present before, which lead to higher richness and consequently increased fish sizes, abundance and biomass. Species of sedentary habits, migrants of short and medium distances, with commercial importance benefited the most from co-management. In the results presented in temporal scale, it was possible to observe a potential spillover effect being provided by the lakes where fishing is prohibited (no-take zones) and those of limited access that benefited those open to fishing. Thus, co-management had positive effects in the structure and composition of fish assemblages in all lakes, regardless of zoning category.

Keywords: biodiversity, fish diversity, fishing agreements, fishery management based on communities, amazonia

Abbreviations: ADAPTA, adaptations of aquatic biota of the amazon; AM, after management; ANOVA, analysis of variance; BM, before management; CAPES, co-ordination for the improvement of higher education personnel; CNPq, Brazilian National Research Council; CPUEn, capture per unit of effort (in number); CPUew, capture per unit of effort (in weight); FAPEAM, Amazonas State Research Foundation; H', shannon's diversity index; MPAs, marine protected areas; N, numerical abundance; PAPAC, publication of scientific articles support program; PERMANOVA, multivariate analysis of permutational variance; SDS, secretariat for sustainable development; S, species richness; UFAM, Universidade Federal do Amazonas.

INTRODUCTION

Since the 1990s, the discussion of co-management in fisheries has intensified. According to Symes (2006), co-management can be defined as systems in which responsibility for management is shared between the state and user groups, usually at the local level. It is important to note that co-management differs from community-based resource management with purely local approaches of self-management by users (Linke and Bruckmeier, 2015). Thus, co-management is being increasingly recognized as an effective model for managing fisheries (Carlsson and Berkes, 2005; Berkes, 2009). Many studies have shown that co-management tends to increase levels of stakeholder engagement, decrease non-compliance with management rules, and promote sustainable use of target fish resources (Chuenpagdee and Jentoft, 2007; Linke and Bruckmeier, 2015). In biologically diverse environments, due to co-management in terms of the amount of catch, fishing seasons, and gear used in fishing, changes in fisher's behavior can be expected to produce indirect effects on the fish assemblage which hosts the target species. However, little information exists on whether co-management can produce effects in species other than the target species, either in freshwater environments (Silvano et al., 2009; Campos-Silva et al., 2018; Medeiros-Leal et al., 2018) or marine (Gelcich et al., 2008).

For fisheries in tropical environments, where fish diversity is high, the fish catches tend to be multispecies (Mahon, 1997; Welcomme et al., 2010). In these environments, fisheries often exploit as much as 100 or more fish species, and catches of any one species often are accompanied by several more (McClanahan and Mangi, 2004). However, this pattern does not hold in the Amazon Basin due to moderate selectivity of fisheries, where the five preferred species can correspond to more than 50% (up to 84%) of the total catch (Hallwass and Silvano, 2016). This moderate selectivity suggests that fisheries in the Amazon are prime candidates for single-species management initiatives with assemblage-wide effects. However, previous studies have emphasized the difficulties of promoting sustainable fisheries in these tropical environments, due to the high diversity of species. That is, the collection of data sufficient for stock assessments become a difficult task and assessment and management approaches need to be fundamentally different to those of large-scale commercial fisheries (Andrew et al., 2007; Lorenzen et al., 2016).

The multispecies nature of these fisheries has been shown to produce adverse effects in species that are historically vulnerable to heavy exploitation and may also affect the structure, composition and functioning of the fish assemblages (Bellwood et al., 2003; Gasparini et al., 2005; Silvano et al., 2009, 2017). Besides that, the fishing down process predicts that increases in fishing effort in these fisheries gradually decrease the average body size of the exploited assemblage and cause a replacement of larger species, which typically have slow growth and low reproductive outputs (e.g., K-strategists), by small, fast-growing species with high reproductive outputs (e.g., r-strategists) (Welcomme, 1999), as observed in some Amazonian rivers (Hallwass et al., 2020). This is different from the fishing down

marine food web phenomenon which predicts decreases in trophic levels (Pauly and Christensen, 1993).

A less appreciated aspect of fisheries management in tropical environments, however, is that management efforts targeted at one or more species may improve the status of not only the targeted taxa, but also the status of other species in the exploited fish assemblage. This process can occur via changes in the overall capture of less-target or non-preferred species and trophic cascades. Changes in the amount of fishing effort and catch, restrictions of non-selective fishing gear, seasonal restrictions on fishing, or even the implementation of no-take reserves could decrease harvests of sensitive taxa groups or under-sized specimens, even if they are less-targeted or non-preferred. Such plausible effects could in turn lead to changes in the overall diversity of species available in these systems, at least locally (Silvano et al., 2009; Soares et al., 2014; Morales et al., 2019). Trophic cascade effects can occur since the abundance of targeted, predatory taxa are maintained at higher levels, thereby affecting the abundance of prey taxa via predation, as has been shown in marine environments (Baum and Worm, 2009). This process can be expected to have a pronounced effect in tropical inland environments where piscivores fish exert the greatest control of the structure and composition of fish communities (Rodríguez and Lewis, 1997). There is, therefore, a likelihood that co-management aimed at single species or groups of target species can produce effects on entire fish assemblages, promoting conservation of fish diversity in the world's most biologically diverse aquatic environments.

The definition of zoning systems with total or partial restriction to fishing, models which have been implemented in the Brazilian Amazon, have been shown in other studies to be an effective way of protecting the biodiversity in marine and continental environments (Russ et al., 2004; Gerber et al., 2005; Castejón and Charles, 2013; Azevedo-Santos et al., 2019). In the Amazon, the implementation of protected areas, through fishing agreements among users of fishing resources, which establish distinct fishing regimes in floodplain lake systems, have been achieving success in the recovery of stocks of the target species in several areas of the Amazon (Almeida et al., 2009; Sánchez-Botero et al., 2010; Arantes and Freitas, 2016; Campos-Silva and Peres, 2016; Petersen et al., 2016; Keppeler et al., 2017). According to Castro (2000) the *Arapaima* sp. is the main species that has presented a positive response to these co-management (fishing agreements) systems and since 1999, the fishing agreements have paved the way as a promising single-species co-management tool focused on the sustainable *Arapaima* sp. exploitation in the Brazilian Amazon (Campos-Silva and Peres, 2016).

Herein, we assessed the effects of co-management when targeted at one fish taxon in relation to the structure and composition of the overall fish assemblage. Our case study analyses the *Arapaima* sp. co-management scheme implemented in the central Amazon Basin. We assessed fish assemblage data for a group of floodplain lakes during the periods before and after the implementation of the *Arapaima* sp. co-management policies and under different management regimes, from no-take to open to fishing, to answer two research questions: (i) does the implementation of co-management for the *Arapaima* sp. affect

the structure and composition of the fish assemblage? and (ii) do the effects on the fish assemblage vary in floodplain lakes under different management regimes?

MATERIALS AND METHODS

Case Study and Area

Our study area was the Paciência Island (approximately 68 km² of area), located in the lower Solimões River, in Amazonas State, Brazil, which hosts a system of floodplain lakes (**Figure 1**). The ecosystem in the Paciência Island includes whitewater *varzea* floodplains, which are key habitats for aquatic biodiversity, including fish (Freitas et al., 2010, 2018; Arantes et al., 2019; Morales et al., 2019) and other groups, such as river turtles of the genus *Podocnemis* (*Podocnemis expansa*, *Podocnemis unifilis*, and *Podocnemis sextuberculata*) (Campos-Silva et al., 2017). In the whitewater rivers, such as the Solimões River, the floodplains are highly productive and determine the existence of abundant stocks that have been intensively exploited for over four decades (Batista et al., 1998; Isaac et al., 2016), which has even caused over-exploitation of some stocks (Sant'anna et al., 2014; Campos et al., 2015).

The *Arapaima* sp. co-management scheme studied here follows a system whereby fishers perform direct counts of *Arapaima* sp. at the moment of their obligate aerial breathing using a standardized and scientifically validated method (Castello, 2004). In this co-management scheme, locally known as a fishing agreement, the fishers, who are supported by local governmental and non-governmental organizations, use the counts to get conservative fishing quotas (Castello et al., 2009), which are set under the condition that fishers comply with minimum size (>1.5 m total length) and closed season (December–May) rules of harvesting. Fishers seeking a harvest quota must also adhere to a community-wide co-management plan, which in our study sites included a zoning plan regulating use of floodplain resources and the establishment of distinct levels of fishery restrictions in the lakes.

Since 2011, fisheries in Paciência Island are managed by a fishing agreement established by the Ruling Decree N° 02/2011 (SDS, 2011) that encompasses 32 lakes distributed in three categories of fishing restrictions: no-take lakes, limited access lakes, and open fishing lakes. Since then, the population density of *Arapaima* sp. has increased over the years (**Figure 2**). The following six floodplain lakes, which belong to three zoning categories of the island's zoning plan, are listed in detail here:

- No-take lakes: Lakes Cacao (03°18'32.9"S and 60°12'54.1"W) and Baixo (03°18'09.0"S and 60°13'35.4"W) are lakes intended for the reproduction and development of species, where fishing activities in all modalities are prohibited in order to ensure the preservation of species;
- Limited access lakes: Lakes Sacambu (03°18'46.0"S and 60°13'19.0"W) and Preto (03°18'33.0"S and 60°13'09.5"W) are reserved for subsistence fishing, in addition to the managed fishing of *Arapaima* sp. and

other species, while always complying with the current legislation;

- Open fishing lakes: Lakes Caído (03°17'35.1"S and 60°12'35.0"W) and Piranha (03°17'57.3"S and 60°13'20.0"W) where commercial fishing is permitted when it complies with current legislation and where *Arapaima* sp. and other species may be farmed (**Figure 1**).

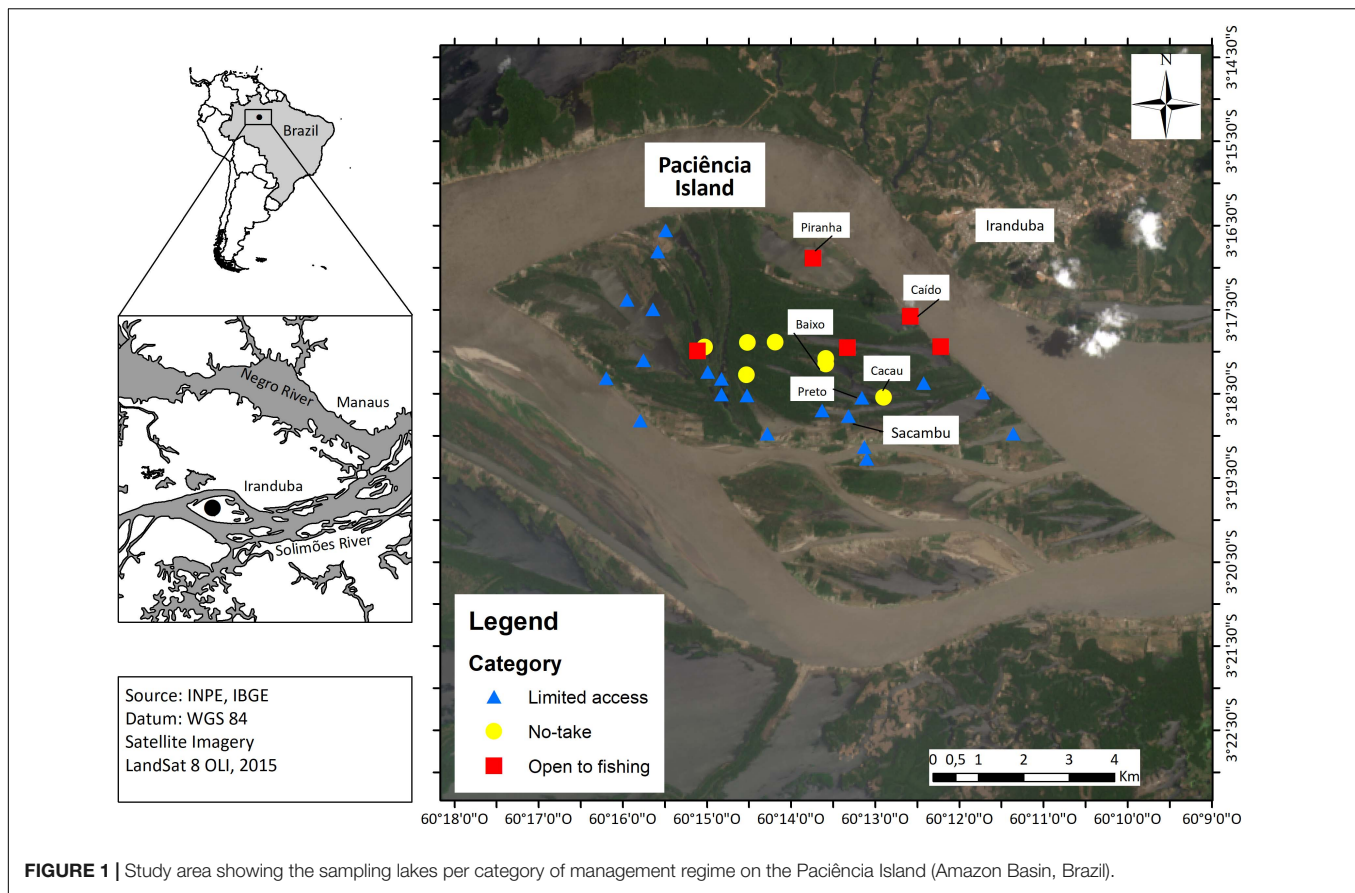
Data Collection

Fish assemblage samples were taken before and after the implementation of the *Arapaima* sp. management plan, always during the rising and receding water periods of the hydrological cycle. These two moments are when the water level is the same, but they occur before the connection among lakes that happens during the high water season (**Supplementary Appendix I**). A total of 48 sampling events were carried out, 24 before implementation of co-management (BM; in 2004, 2005, and 2006) and 24 after implementation of co-management (AM; in 2016 and 2017), a table with the sample design is available in **Supplementary Appendix II** to better understanding the sampling. The sampling was carried out with standardized fishing effort, using gill nets of 15 m in length × 2 m height, with mesh sizes ranging from 30, 40, 50, 60, 70, 80, 90, 100, 110, and 120 mm between opposite knots, which establishes a battery of ten nets. Two batteries of nets were used, which were located near the shore and in the center of the lake, in order to sample species of the aquatic environment. The daily sampling period was of 8 h, which was divided into 4 h in the early morning (04:00–08:00) and 4 h in the late afternoon (16:00–20:00), in order to reduce the damage caused by predators attracted to the fish in the nets and sample the hours of principal activity of the fish. These samples were grouped to use in analysis described in the next section.

The fish were identified with the help of systematic keys (Géry, 1977; Ferreira et al., 1998; Santos et al., 2006; Soares et al., 2007) and individual standard length (cm) and total weight (g.) were measured. The specimens that were unable to be identified were preserved in 10% formalin and taken to the Laboratory of Fisheries Ecology at the Federal University of Amazonas (UFAM) for subsequent identification with the help of specialized professionals. Fish sampling for this study was carried out under license No. 50662-1 (Instituto Chico Mendes de Conservação da Biodiversidade-ICMBio/Brazil). Along with fish samples, we measured the environmental parameters: temperature, pH, and dissolved oxygen, depth and transparency levels at each lake, at the same spots where we set gillnets. We measured these environmental variables in the early morning and late afternoon, near to the water surface and bottom, and averaged these data in a single daily measure for each variable. The free software QGIS, version 2.8.5 (OSGEO, 2015) was used to measure the distance between the lakes shown in **Figure 1**.

Data Analyses

The composition and structure of the fish assemblages were described through estimates of richness (S), Shannon's diversity (H'), numerical abundance (N), and catch per unit of effort (CPUE_n = number of fish/m²/h and CPUE_w = weight of fish/m²/h). To test the effect of co-management time



(before and after co-management) and among the categories of fishing restriction (No-take, limited access and open fishing) in the lakes on the diversity of fish assemblage and environmental parameters, we applied a two-way analysis of variance (ANOVAs), where the response variables were S , H' , N , capture per unit of effort (in number) (CPUE_n), capture per unit of effort (in weight) (CPUE_w), and environmental parameters (temperature, pH, oxygen, depth, and transparency). Pearson's linear correlation was also applied to verify relationships among the structure of the fish assemblages and environmental parameters. Assumptions of normality, linearity, and homoscedasticity were inspected employing the residuals before running these ANOVAs and we log-transformed the data to ensure these assumptions were met.

To evaluate the existence of statistical differences in the species composition of fish assemblages, a two-way multivariate analysis of permutational variance was performed (PERMANOVA: factor 1 = management time; factor 2 = categories of fishing restriction). Beforehand, the numerical abundance data were transformed using the Hellinger distance, and a Bray-Curtis dissimilarity matrix (Anderson, 2008) was used as the basis for the PERMANOVA. Then, the percentage similarity routine (SIMPER) was applied to the Bray-Curtis dissimilarity matrix, identifying the species that most contributed to the formation of the groups, assuming $p \leq 0.05$ as the limit of significant contribution of each species. A non-metric dimensional scaling

(nMDS) (Borcard et al., 2018) was performed to show the patterns detected by PERMANOVA and SIMPER analysis. Differences in length composition for groups of species identified in SIMPER analysis, by co-management time was tested using a two-sample Kolmogorov–Smirnov test and among the categories of fishing restriction, we applied a Kruskal–Wallis test, both with a significance level of $p \leq 0.05$.

Finally, a Mantel test (Mantel, 1967) was used to test the effect of the distance between lakes on the fish assemblage and evaluate the existence of correlations among the ecological distances (alpha diversity) and the geographical distances between the lakes. This was assumed because the Euclidean distances were estimated from the numerical abundance data of the species in each lake. All statistical analyses were performed using the software R-4.0.1 (R Core Team, 2020), using the packages *Vegan* (Oksanen et al., 2007) and *ggplot2* (Wickham, 2016).

RESULTS

Fish Abundance and Species Composition

A total of 7,647 fish were collected, corresponding to 547.19 kg, which were distributed among 112 species, 24 families, and six orders (Supplementary Appendix III). Of this total, 2,105 fish with a biomass of 152.74 kg were collected before co-management

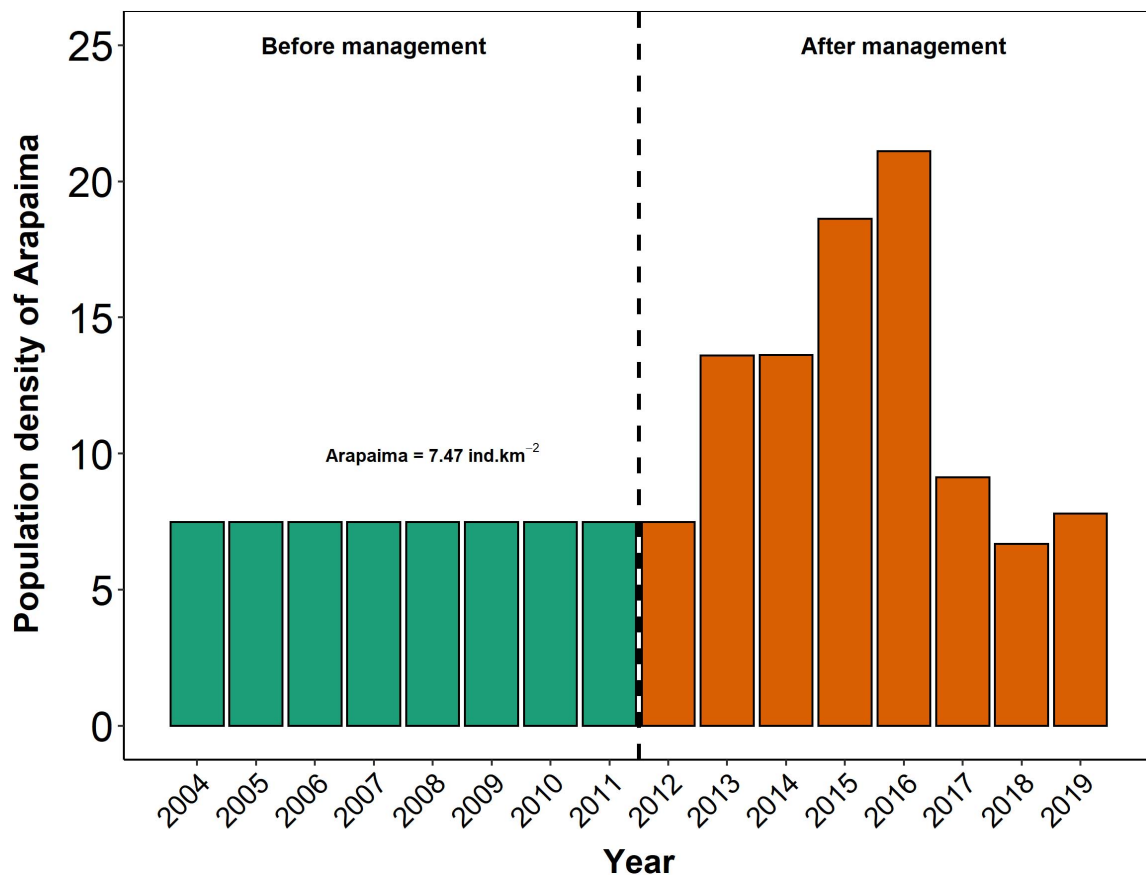


FIGURE 2 | Time-series data on population density of *Arapaima* sp. based by counts (> 1 m total length) in Paciência Island. Density data shown for 2004–2011 are estimated based on the assumption that they are identical to that for 2012, first year with annual counts.

(BM), and were distributed in 78 species, 22 families, and six orders. After the co-management was implemented (AM), 5,542 fish with a biomass of 394.45 kg were caught, and these were distributed in 98 species, 24 families, and six orders.

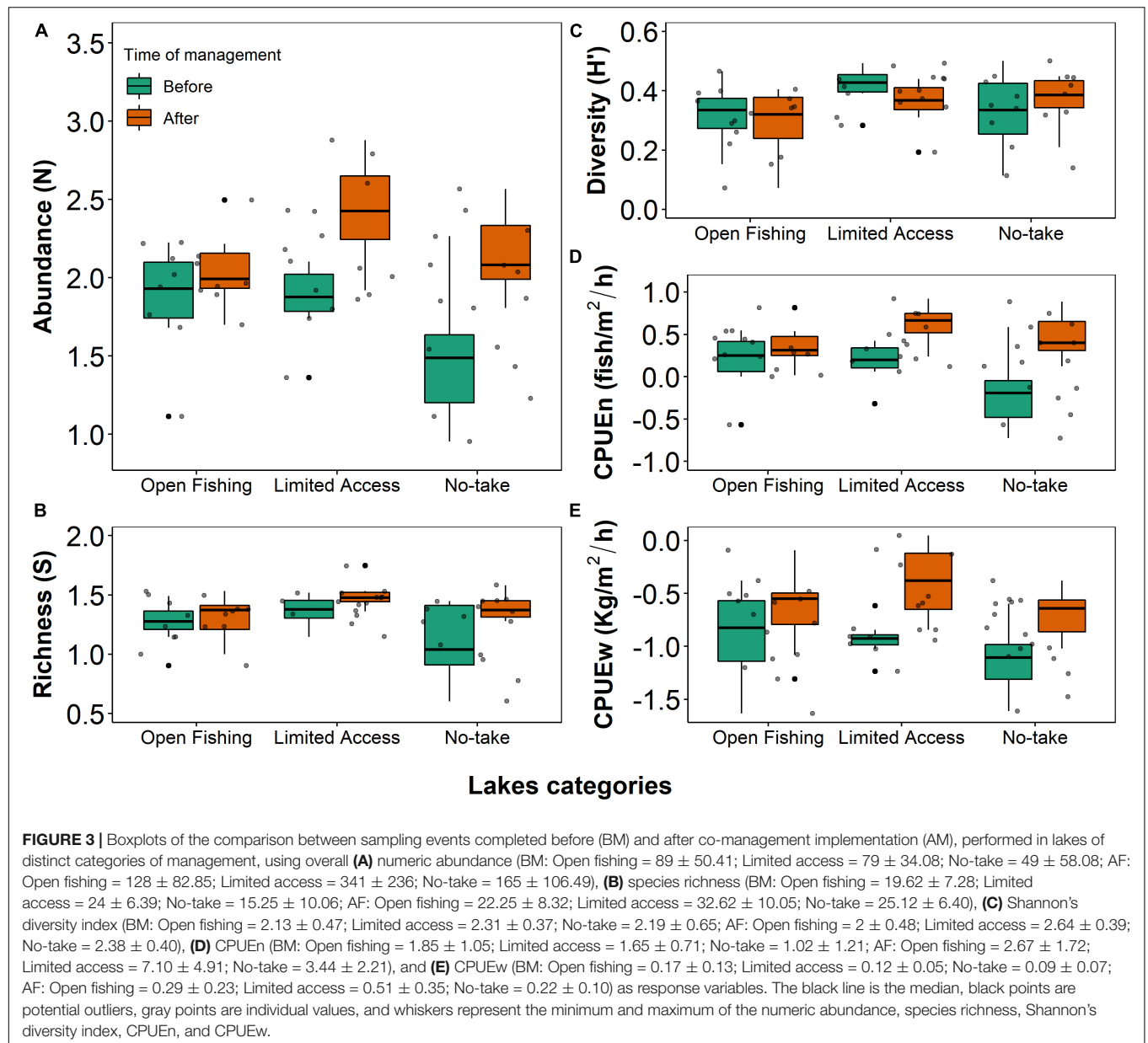
Our findings reveal that the implementation of co-management for *Arapaima* sp. affected the structure and composition of the fish assemblage. The two-way ANOVAs showed significant differences for numeric abundance ($F = 27.42$; $df = 1, 42$; $p < 0.001$), species richness ($F = 9.24$; $df = 1, 42$; $p = 0.004$), CPUEn ($F = 27.42$; $df = 1, 42$; $p < 0.001$), and CPUew ($F = 18.486$; $df = 1, 42$; $p < 0.001$) which indicates that the implementation of the co-management system resulted in greater abundance, biomass and diversity throughout the lake system of the Paciência Island (Figures 3A–E). We also found that the fish assemblage varied, not only with respect to the implementation of co-management, but also across floodplain lakes under different management regimes. The two-way ANOVAs indicated significant differences of numeric abundance ($F = 4.36$; $df = 2, 42$; $p = 0.019$), species richness ($F = 4.67$; $df = 2, 42$; $p = 0.014$), and CPUEn ($F = 4.36$; $df = 2, 42$; $p = 0.019$) among lakes under distinct management regimes. There were no detectable effects of co-management time among the categories of fishing restriction with Shannon's diversity index measured

and no interaction effect was detected between the factors and all response variables: S, H', N, CPUEn, and CPUew (Table 1). Lakes of limited access, where a quota of *Arapaima* sp. is fished annually, showed the highest values of numeric abundance, species richness, CPUEn, and CPUew (Figures 3A,B,D,E).

The PERMANOVA identified differences in the structure of the assemblages sampled both before and after the implementation of the co-management (pseudo- $F = 5.69$, $df = 1.42$, $R^2 = 0.105$, $p = 0.001$), and indicated differences in the structure and composition of the assemblages of fish in the lakes, according to the categories of restriction on the fishery (pseudo- $F = 1.96$, $df = 2.42$, $R^2 = 0.072$, $p < 0.001$). No interaction effect was detected between the factors of management implementation period and type of lake according to the level of fishing restriction (pseudo- $F = 1.28$, $df = 2.42$, $R^2 = 0.047$, $p = 0.122$). The nMDS (stress value: 0.212) helped to better explore the results of the PERMANOVA, which indicated a clear distinction between the assemblages sampled before (to the right), and after (to the left) the implementation of the co-management scheme in the lake system of the Paciência Island. *Brycon amazonicus* (BRA), *Psectrogaster rutiloides* (PSR), and *Mesonauta festivum* (MFE) were the dominant

TABLE 1 | Summary of results of two-way ANOVAs employing numerical abundance (N), catch per unit effort (CPUE_N = number of fish/m²/h and CPUE_W = weight of fish/m²/h), richness (S) and Shannon's index (H') as response variables.

	df	N		CPUE _N		CPUE _W		S		H'	
		F	p	F	p	F	p	F	p	F	p
Time	1	27.429	<0.001	27.429	<0.001	18.486	<0.001	9.24	0.004	0.237	0.629
Categories	2	4.251	0.019	4.251	0.019	2.467	0.097	4.676	0.014	2.765	0.074
Time × Categories	2	2.513	0.093	2.513	0.093	0.919	0.406	1.828	0.173	1.302	0.282
Residuals	42										



species in the assemblages before the implementation of co-management, however *Ageneiosus ucayalensis* (AGU), *Triportheus albus* (TRA), *Tetragopterus argenteus* (TAR), *Calophrys macropterus* (CMA), and *Curimata ocellata* (COC)

dominated the assemblages after the implementation of co-management (Figure 4).

The SIMPER analysis identified eleven fish species that contributed most to the observed differences among the

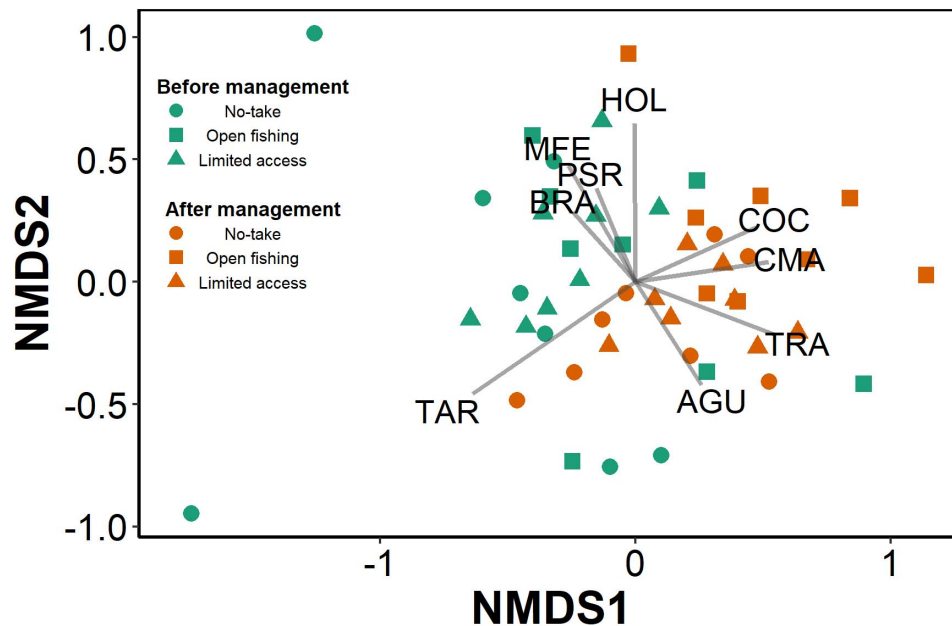


FIGURE 4 | Non-metric multidimensional scaling (axes nMDS1 vs. nMDS2) plot where the green points represent the sampling events completed performed before co-management implementation and orange represent the sampling events completed after co-management implementation. Circles represent samplings in no-take lakes, triangles represent samplings in limited access lakes, and squares in open to fishing lakes. BRA, *Brycon amazonicus*; PSR, *Psectrogaster rutiloides*; MFE, *Mesonauta festivum*; AGU, *Ageneiosus ucyalensis*; TRA, *Triportheus albus*; TAR, *Tetragopterus argenteus*; CMA, *Calophysus macropterus*; COC, *Curimata ocellata*.

co-management time and categories of fishing restriction: *Potamorhina altamazonica* (PAL) was more abundant in open fishing and limited access and *Triportheus angulatus* (TAN) in no-take lakes before the co-management (Figures 5A–C). After co-management, TRA and TAN were more abundant in three categories (Figures 5D–F). The lengths of these species were different over time (Kolmogorov–Smirnov: $D = 0.138$; $p < 0.001$; Figure 6A) and among the categories of fishing restriction (Kruskal–Wallis: $\chi^2 = 51.16$; $p < 0.001$), showing a subtle increase in fish sizes after the implementation of co-management (Figure 6B).

Environmental Variables

The means values of temperature ($^{\circ}\text{C}$; $F = 5.51$; $\text{df} = 1, 42$; $p = 0.02$), pH ($F = 35.42$; $\text{df} = 1, 42$; $p < 0.001$), and dissolved oxygen (mg. l^{-1} ; $F = 8.02$; $\text{df} = 1, 36$; $p = 0.03$), differ over time (before and after co-management). Transparency (cm ; $F = 6.07$; $\text{df} = 2, 27$; $p < 0.003$) differed only according to the categories of restriction on fishing. The environmental parameters dissolved oxygen, temperature, and pH did not differ between lakes categories or depth. Considering all sampling events (total 48), only pH showed a correlation to numeric abundance ($R^2 = 0.38$; $\text{df} = 46$; $p = 0.008$), CPUE ($R^2 = 0.37$; $\text{df} = 46$; $p = 0.008$), CPUEw ($R^2 = 0.37$; $\text{df} = 46$; $p = 0.009$), and species richness ($R^2 = 0.37$; $\text{df} = 46$; $p < 0.009$). All mean and standard deviations values of these environmental parameters are presented in Table 2.

The Mantel test indicated a low correlation ($R^2 = 0.227$; $p = 0.177$) among the ecological distances and the geographical distances among the lakes, indicating that the differences observed among the assemblage estimates obtained in the lakes,

according to the type of co-management, are not related to the geographical distances among the lakes.

DISCUSSION

Our results indicate that co-management focused on one single taxa and implemented within a framework of zoning of fishing activities improved the structure and composition of the fish assemblages in floodplain lakes of the Amazon Basin. Several new fish species were sampled in the Paciência Island after the co-management was implemented, such as *Acestrorhynchus falcatus*, *Sternarchella schotti*, *Parapteronotus hasemani*, *Pristigaster cayana*, *Hemiodus unimaculatus*, *Metynnis hypsauchen*, etc., and two new families: *Apterontidae* and *Sternopygidae*. Our results show that the implementation of *Arapaima* sp. co-management induced beneficial changes for the fish assemblages of the lakes of the Paciência Island, with increases in the abundance (Numerical and CPUE), biomass (CPUEw), size (S_L , cm), and richness of species. These increases in biodiversity provide greater buffering effects against disturbances, helping to ensure ecosystem stability (McCann, 2000; Nagelkerken et al., 2017). Similarly, previous studies have shown that areas under some type of management have higher values of species richness when compared to areas open to fishing and without management (Lubchenco et al., 2003; Sweke et al., 2013). The greatest increases in total abundance, when summed across all lakes, after the implementation of the fishing agreement were observed in small species, such as TRA, TAN, *Potamorhina latior*, and PAL, medium size species, such as *Mylossoma*

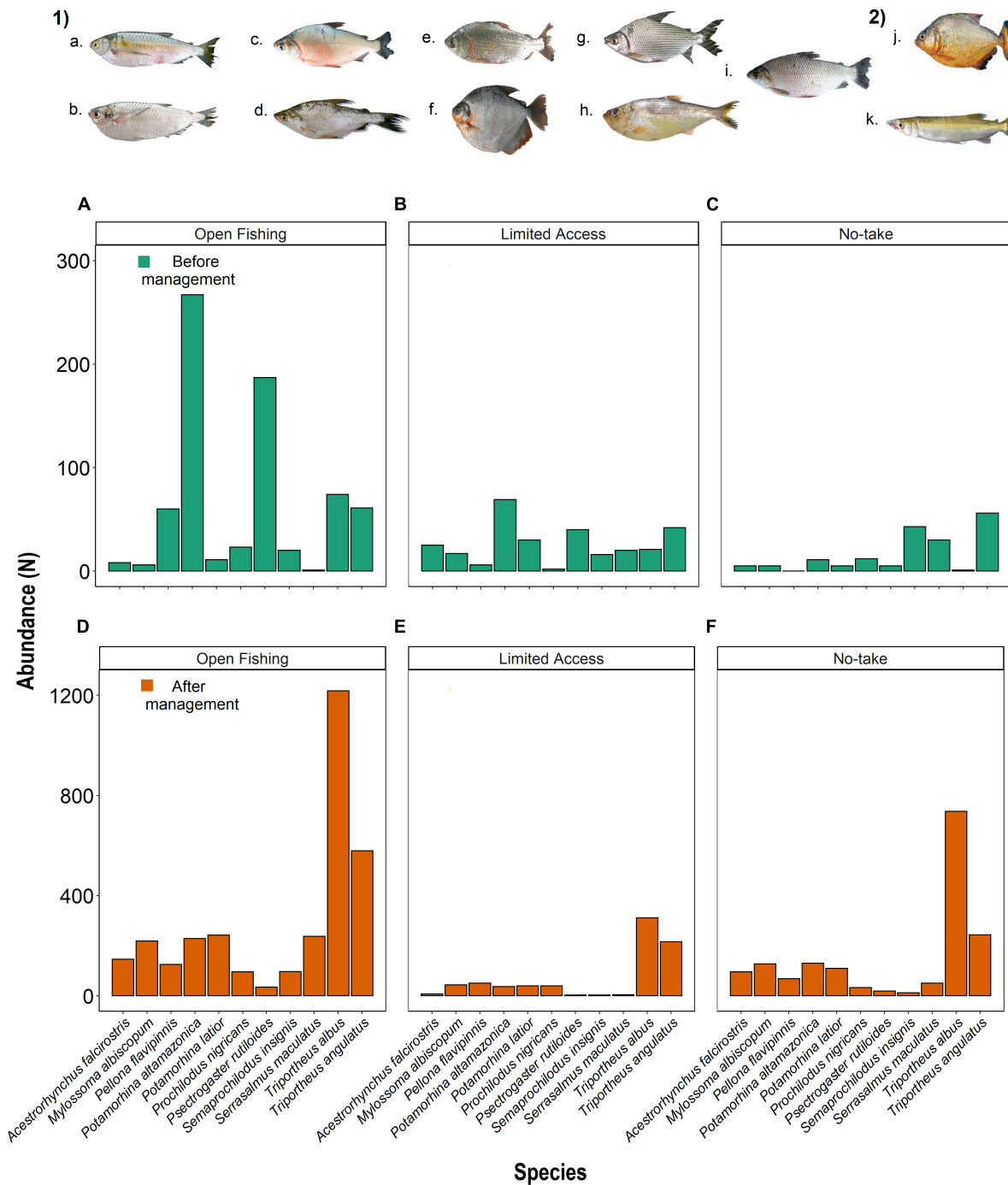
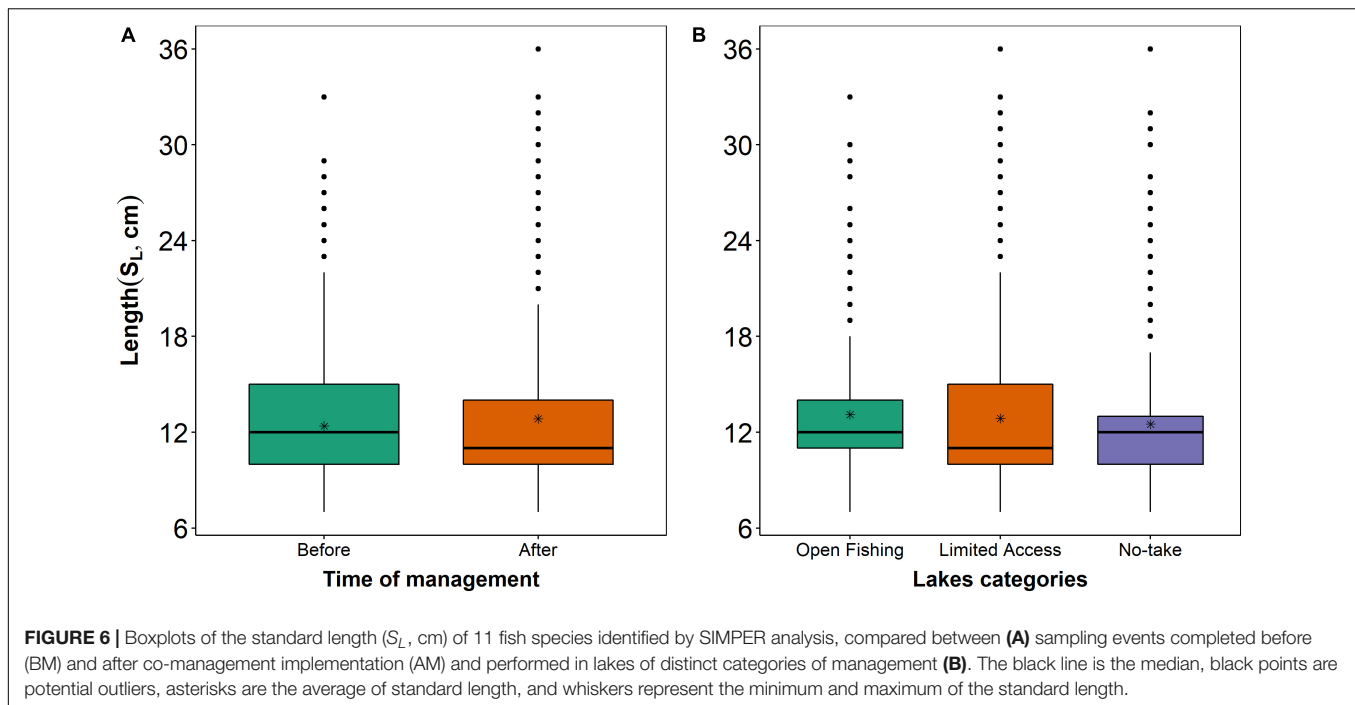


FIGURE 5 | Numerical abundance of fish species that contributed most to the observed similarities, according to SIMPER analysis among lakes of distinct categories of management: Before co-management (A) Open fishing, (B) Limited access, (C) No-take and after co-management (D) Open fishing, (E) Limited access, (F) No-take. (1) Short and medium distances migrants: (a) *Triportheus albus*, (b) *Triportheus angulatus*, (c) *Potamorhina altamazonica*, (d) *Potamorhina latior*, (e) *Psectrogaster rutiloides*, (f) *Mylossoma albiglacium*, (g) *Semaprochilodus insignis*, (h) *Pellona flavipinnis*, (i) *Prochilodus nigricans*; (2) Sedentary species: (j) *Acestrorhynchus falcirostris*, (k) *Serrasalmus maculatus*. Photos: Soares et al. (2007).

albiglacium, *Semaprochilodus insignis*, and *Prochilodus nigricans*, and larger sized species, such as *Pellona flavipinnis*, which are typical shoal-forming and short- and medium-distance migrants (Figures 5D–F; Taphorn, 1992; Villacorta-Correa and Saint-Paul,

1999; Lima and Araujo-Lima, 2004; Malabarba, 2004; Granado-Lorencio et al., 2005). Some medium and large sedentary species (Neves, 2000; Ruffino and Issac, 2000; Granado-Lorencio et al., 2005) also showed an increase in abundance, such as *Serrasalmus*



maculatus and *Acestrorhynchus falcirostris* (Figures 5D–F). In the Paciência Island, most of these species have a commercial importance for local fishers (Souza et al., 2015). A similar pattern also was observed in floodplain lakes with co-managed measures in the eastern Amazon for some species, such as *P. nigricans* and *A. falcirostris* (Silvano et al., 2014).

The positive effects of the co-management, evidenced by the comparison between sampling done before and after the implementation of the fishing agreement for the Paciência Island lakes, could be due the homogenization process promoted annually by the flooding. The flooding season creates connections between the floodplain habitats (lakes and rivers), allowing fish to move and migrate between habitats, resulting in a homogenization of fish communities (Freitas et al., 2010; Gomes et al., 2012; Hurd et al., 2016). The homogenization that occurs in the flood, when there is an expansion of aquatic environments, can also minimize the effects of biotic interactions (Gomes et al., 2012), including the potential increase in predation levels that result from the increase in population density of *Arapaima* sp. (Figure 2).

The results also indicated that the effects are distinct among lakes with distinct levels of fishing restriction, with higher abundances both in number of individuals, CPUEn, biomass (CPUew), richness, and sizes (S_L , cm) in limited access lakes. The effects of predation on the structures of aquatic communities have been observed in several types of aquatic environments, including small lakes (Tonn et al., 1992), streams in temperate environments (Giam and Olden, 2016), coral reefs (Boaden and Kingsford, 2015), and floodplain lakes (Rodríguez and Lewis, 1997), without intervention of management actions. In addition, in most freshwater tropical environments, predation is a driving force in fish community structure, affecting the species composition, abundance, biomass, and can mediate

species coexistence in the short term (Freitas et al., 2010; Petry et al., 2010). Our results indicate that managed fishing in these lakes, with the annual harvesting of a pre-established number of *Arapaima* sp. (one of the top predators in the food chain) presents the most positive effects for the fish assemblages of the Amazon floodplain lakes. This annual harvesting of part of the predators can modulate the top down effects that act in the structuring of fish assemblages (Borer et al., 2005).

Similar studies, previously conducted by Silvano et al. (2009); Soares et al. (2014), and Morales et al. (2019), in different managed areas of the Brazilian Amazon, did not observe differences in the composition and structure of fish assemblages among lakes of different categories of fishing restrictions. According to these studies, the absence or non-detection of the effects of the type of management can be explained by factors such as the distance from the lakes to the river, short periods of effective management, and the existence of high intensity ecological factors, such as the flood pulse, which overlaps with the lower intensity effects that result from management. Our study provides new insights into co-management effects in freshwater ecosystems, as we compare data collected over an interval of more than 10 years (before and after-co-management), which may have allowed us to demonstrate the consolidation of the effects of management and potential spillover effects. Such a process can be defined as the net movement of fish across the boundary of a reserve into the fished ground, which would be expected to occur on the basis of fundamental physical principles of random movement (Buxton et al., 2014). The spillover effect provides an increase in fishing yields, abundance, and biomass, as well as helping to protect biodiversity in environments near to no-take zones (Russ et al., 2004). This effect has been observed mainly in marine protected areas (MPAs) (Buxton et al., 2014), community-managed marine reserves (Silva et al., 2015) and also suggested

TABLE 2 | The mean (with standard deviation values) of the environmental variables of Paciência Island in the lower Solimões River.

Environmental variables	Before management (BM)			After management (AM)		
	Open to Fishing	Limited Access	No-take Zones	Open to Fishing	Limited Access	No-take Zones
Dissolved oxygen	2.49 ± 1.48	3.41 ± 1.36	2.64 ± 1.32	1.8 ± 1.43	2.26 ± 1.14	1.14 ± 0.52
pH	6.82 ± 0.49	6.91 ± 0.43	6.82 ± 0.26	7.56 ± 0.34	7.63 ± 0.28	7.83 ± 0.80
Temperature (°C)	30.09 ± 1.83	30.55 ± 2.21	30.64 ± 0.26	29.25 ± 0.89	29.55 ± 1.66	27.92 ± 3.41
Depth (m)	4.20 ± 1.61	4.08 ± 6.39	4.73 ± 1.72	4.21 ± 3.37	4.42 ± 2.33	3.2 ± 2.58
Transparency (cm)	59 ± 15.14	71.83 ± 8.18	87.83 ± 31.65	58.33 ± 16.93	76.5 ± 23.21	95 ± 27.01

in floodplain lakes in the Amazon (Silvano et al., 2009; Arantes and Freitas, 2016). However, more ecosystem-based approaches should be considered using food-web models, assessing the ability of fisheries agreements to reduce fishing effort and to supply biomass to a near no-take zone.

It is known there are a complex relationship between environmental variables and fish assemblages in the Amazon (Rodríguez and Lewis, 1997; Tejerina-Garro et al., 1998; Petry et al., 2003; Keppeler et al., 2017). Most environmental parameters measured in our study showed significant differences before and after co-management implementation, but did not differ according to the categories of fishing restriction (except transparency). Furthermore, just pH was found to have a positive correlation with the fish assemblage descriptors. Floodplain lakes in the Amazon are dynamic environments and the environmental parameters change along a hydrological cycle (rising, high, receding, and dry waters, see **Supplementary Appendix I**). However, we believe the effects of the co-management to be more important than the effects of the environmental variables, which can experience natural variations. Previous studies have also shown that piscivory is one of the factors driving the structure of fish assemblages in tropical floodplain lakes (Rodríguez and Lewis, 1997). Piscivory is influenced by transparency, which is controlled by depth and area, and which emphasizes the random contribution to assemblage variation in these environments (Rodríguez and Lewis, 1997; Freitas et al., 2014). All of the lakes sampled in this study are in the lower stretch of the Solimões River, one of the largest white water rivers in the Amazon, and the differences in pH, oxygen, and temperature can be random. Therefore, we need to better understand how environmental variables do influence fish assemblage in tropical rivers, so that they can be accounted for in management proposals for fish conservation and fisheries sustainability (Keppeler et al., 2017).

Although it is not the primary objective of this article, it is important to mention the social and economic benefits of fishing agreements that have been implemented in the Amazonian floodplains, and which have been proven by several studies (Castello et al., 2009, 2011; Campos-Silva and Peres, 2016; Campos-Silva et al., 2017). In the system of lakes of the Paciência Island, in addition to the increments in the income of the riverine population, as a result of the annual fishing of *Arapaima* sp., it was observed an increase of the abundance of other species, which can contribute to food security of the riverine people who fish for subsistence in these lakes.

CONCLUSION

The co-management strategy known as the Fisheries Agreement, which is implemented in the floodplain lakes of the Paciência Island, although aimed at the recovery of stocks and the maintenance of sustainable fishing of *Arapaima* sp. had positive effects on the entire fish assemblage, with increases in abundance, biomass, richness, and sizes. The results also indicate that managed fishing of this species (a top predator in the food chain of the Amazonian floodplains) may be contributing to the maintenance of the abundance and diversity of the lakes where fishing restricted by annual quotas occurs. The continuity and improvement of this fishery management strategy will depend directly on the expansion of knowledge of the biology of the species exploited, the environmental characteristics of the lakes where they live and the biological interactions in the assemblage.

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/s.

ETHICS STATEMENT

The animal study was reviewed and approved by License No. 50662-1 153 (Instituto Chico Mendes de Conservação da Biodiversidade-ICMBio/Brazil).

AUTHOR CONTRIBUTIONS

FS-S and WM-L designed the study. WM-L performed the sampling, collected the data, and analyzed and drafted the original version of the manuscript. LC and CF reviewed the manuscript. FS-S supervised this research, obtained financial support, and discussed and revised the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2021.604170/full#supplementary-material>

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