



Fish community turnover in a dammed Andean River over time

Correspondence:
Luz Jiménez-Segura
luz.jimenez@udea.edu.com

Daniel Valencia-Rodríguez¹, Juliana Herrera-Pérez¹,
 Daniel Restrepo-Santamaría¹, Andrés Galeano²,
 R. Scott Winton^{3,4} and Luz Jiménez-Segura¹

We describe the change in the fish community of the Porce River in Magdalena River Basin, Colombia, following the construction of the Porce III hydropower reservoir based on 13 years of monitoring data. The results show a clear reduction of the number of native species, which have been supplanted by colonizing non-native species, especially in the reservoir. Four native species detected prior to dam construction have apparently disappeared, but 12 new species were registered post-construction. We analyzed spatial changes in beta diversity in the aquatic environments surrounding the dam. The new environment generated by the reservoir presents a unique species composition and contributes significantly to the total beta diversity of the system. Altogether three distinct new fish assemblages emerged following reservoir formation and there are now six assemblages where there had previously been three. This dramatic change, already visible within a decade of construction, highlights just how strong of an impact dam construction has on habitats and how rapidly fish communities react in this hotspot for endemic fish diversity. Our findings demonstrate the importance of monitoring fish communities for revealing the impact of damming on river ecosystems and informs potential complementary fish diversity inventories elsewhere in the Magdalena River basin.

Keywords: Beta diversity, Freshwater ichthyofauna, Hydropower, Long-term monitoring, Magdalena River.

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¹ Grupo de Ictiología, Departamento de Biología, Universidad de Antioquia, Calle 67, No 53 - 108, Laboratorio 7-308, Medellín, Colombia. (DVR) davarod@gmail.com, (JHP) juliana.herrerap@udea.edu.com, (DRS) dasanta24@gmail.com, (LJS) luz.jimenez@udea.edu.com (corresponding author).

² Empresas Públicas de Medellín, Carrera 58, No 42 - 125, Medellín, Colombia. ANDRES.GALEANO@epm.com.

³ Institute of Biogeochemistry and Pollutant Dynamics, ETH Zurich, 8092, Zurich, Switzerland. scott.winton@gmail.com.

⁴ Eawag, Swiss Federal Institute of Aquatic Science and Technology, 6047 Kastanienbaum, Switzerland.

Describimos el cambio en la comunidad de peces del río Porce en la cuenca del río Magdalena en Colombia luego de la construcción del embalse hidroeléctrico Porce III con base en 13 años de datos de monitoreo. Los resultados mostraron una reducción de especies nativas y, el embalse ha sido colonizado por especies no nativas. A lo largo del monitoreo cuatro especies desaparecieron de las capturas, y se registró la aparición de 12 especies nuevas después de la construcción del embalse. Analizamos los cambios espaciales en la diversidad beta en los ambientes acuáticos que rodean la presa. El nuevo entorno generado por el embalse presenta una composición de especies única; en total, surgieron tres nuevos ensamblajes de peces distintos después de la formación del embalse y ahora hay seis ensamblajes. Este cambio, ya visible a una década de la construcción, resalta cuán fuerte es el impacto que tiene la construcción de presas en los hábitats y cuán rápido reaccionan las comunidades de peces. Nuestros hallazgos demuestran la importancia de monitorear las comunidades de peces para revelar el impacto de las represas en los ecosistemas fluviales, además permite complementar los inventarios de diversidad en la cuenca del río Magdalena.

Palabras clave: Diversidad beta, Energía hidroeléctrica, Ictiofauna de agua dulce, Monitoreo a largo plazo, Río Magdalena.

INTRODUCTION

Colombia is one of the most diverse countries in the world in terms of freshwater fish species (Cala-Cala, 2019; Dagosta *et al.*, 2020). Its ecosystems provide habitat to 1,572 species of fish, with the Orinoco and Amazon River basins being the most diverse with approximately 1,469 species (DoNascimento *et al.*, 2020). In contrast, the diversity of fish in the Magdalena River basin, sandwiched between three Andean cordilleras, is not so high, supporting just ~233 species fish (DoNascimento *et al.*, 2020). However, 68% of Magdalena fish species are endemic (García-Alzate *et al.*, 2020), making it one of the few basins in the world with such high freshwater fish endemism and a region with acute needs for freshwater biodiversity conservation (Abell *et al.*, 2008).

A major threat to freshwater biodiversity in many parts of the world, including the Magdalena basin, is hydropower development. Hydropower provides a renewable source of electricity for Colombia and other Neotropical countries (Finer, Jenkins, 2012). Although little is known about the response of aquatic biota in Andean aquatic systems to dams, in other regions of the world, particularly in Brazil, changes have been identified in the basin, both downstream and upstream of dam sites (Agostinho *et al.*, 2016; Dias *et al.*, 2020). The most conspicuous changes are the disruption in the river longitudinal connectivity with a formation of a new environments (an artificial lake, a river sector upstream the reservoir and another river sector, downstream of it), the change in the natural flow seasonality, and exotic fish invasion in the reservoir (Winemiller *et al.*, 2016). Petts (1980) describes the effects of reservoir formation as hierarchical responses. First-order effects are related to changes in river hydrology, beginning with the filling of the reservoir, retention of sediments and nutrients in the

reservoir, and the change in the downstream flow regime. The second-order changes (on a larger scale of time) are related to the change in the geomorphology of the river channel and the influence of the river on its floodplains below the dam. The third-order changes occur in aquatic biota due to the interaction of the first two categories of effects. The resilience of aquatic biota to habitat modification is a major focus of research on the impacts of human activities on the environment (Borgwardt *et al.*, 2019) and such studies are possible if the scientist has a standardized data set spanning before and after the impact event in the unnaturally modified areas.

In the case of native fish, most of them do not have the physiological, morphological and behavioral characteristics to persist in modified aquatic systems (Agostinho *et al.*, 2008; Carvajal-Quintero *et al.*, 2017). Therefore, modification often leads to a decline in native species abundance and richness and favors the establishment of non-native species especially when the latter are introduced to promote fishing (Jiménez-Segura *et al.*, 2014). It has been documented that the introduction of non-native fish species in the Magdalena basin is an increasingly important contributor to the threat of species extinction and degradation of aquatic ecosystems (Lasso *et al.*, 2020), and yet within this basin there is little or no investigation on its effect on ecosystems (Barletta *et al.*, 2010). Native and non-native species compete for habitat space (Gozlan *et al.*, 2010; Cucherousset, Olden, 2011) and it is of great conservation interest to know the degree to which native species persist or are supplanted by non-natives in the vicinity of hydroelectric plants built in the Colombian Andean region, potentially allowing for the generation of recommendations and opportunities for the conservation management of native species in dammed Andean aquatic systems.

This work reveals the changes in aquatic environments and their organisms through time and space that arise from energy generation projects in the Magdalena basin. This type of infrastructure can influence the patterns of diversity and assembly of fish on small scales. It's important to bear in mind that this area has already been intervened by the construction of other hydroelectric plants, and that other types of economic activities such as informal mining and livestock are developed in the basin that directly affects the bodies of water. In this study, we leverage 13 years of monitoring data to explore the trends in the ichthyofauna present within the Porce River and assess the legacy of construction of Porce III reservoir. We address the following questions: How would this community change, considering the local environmental context, during and after the dam? How is the community change related to environment types and species characteristics? Does the richness and abundance of non-native species change over time and in different environments? Since the monitoring data set spans from construction to present day, answering these questions places into focus the impact of dam construction and reservoir formation on Andean fish communities. Although the effects of dams on fish have been investigated in other regions, in Tropical Andes, the response of ichthyofauna to reservoirs is unknown.

MATERIAL AND METHODS

Study area. The Porce River is located in the northwestern region of South America. It is born at 2,660 m above sea level (masl) and after flowing 247 km northward, it

joins the Nechi River at 170 masl, which eventually joins the Cauca River and then the Magdalena before emptying into the Caribbean Sea. With an average annual rainfall of 2,458 mm, a range of temperature 19 to 24°C, an average relative humidity greater than 80%, the basin has 5,227 km², two rainy seasons (May–June, October–November) and two dry seasons (January–March, July–September) within the annual cycle. Before the Porce II Dam, the Porce River basin drains landscapes highly transformed by agriculture and livestock and urban, suburban and exurban housing expansion. It also receives the wastewater discharge from Medellín, a city with six million inhabitants (Silva-Arroyave, 2008; Álvarez-Bustamante *et al.*, 2018).

The Porce River Basin has been heavily exploited for hydropower. Two power stations were constructed by Empresas Públicas de Medellín (EPM), generating 1,105 MW for the Colombian power grids, nearly 1% of the total hydropower installed capacity of Colombia. This study is focused on the Porce III reservoir and adjacent waters, formed in 2011 at 544 m elevation and producing 700 MW. The Porce III reservoir receives an average flow of 171.3 m³.s⁻¹, coming partly from the turbinated waters from Porce II and partly from the Guadalupe River. The Porce III reservoir has a volume of 176.9 Mm³, an average depth of 37.6 m, a flooded area of 4,704 km², 14 km length, an average width of 500 m. A network of small tributaries provide water year-round (Fig. 1). The water level of the Porce III reservoir fluctuates widely, frequently and rapidly. Its hydrologic residence time does not exceed eight days (Silva-Arroyave, 2008). Hourly power generation is determined by the Unidad de Planeación Minero Energética (UPME), an agency of the Colombian government that plans the hydropower generation from the power plants with the demand in the country. As a result, downstream the discharge tunnel (310 m elevation), the Porce River experiences extreme hydropeaking at the hourly timescale. Between the Porce III dam and of the discharge tunnel, the river channel is 13 km long and maintains a minimum environmental flow of 12 m³.s⁻¹, roughly 7% of the mean discharge.

Sampling design for ichthyofauna monitoring. Field campaigns were conducted twice a year (dry and rainy period) by students and scientists from the Universidad de Antioquia. We use data from campaigns made between 2008 and 2020. During these 13 years, there were two time periods relative to the dam construction: 2008–2011 (construction), and 2012–2020 (post-construction). Fish samples were taken in eighteen sites which were grouped into six environments: RPM – Isolated Porce River between the dams Porce II and Porce III (one sample site), RG – Rivers flowing to the isolated Porce River (*i.e.*, Guadalupe River; one sample site), RSV – Porce III reservoir (four samples sites), CRF – Creeks flowing to the reservoir (five samples sites), CFD – Creeks flowing to the Porce River below the dam (four samples sites), and RPD – Porce River downstream of the dam (three sample sites); RSV and RPD environments were only sampling after dam construction (see Fig. 1; Tab. S1). Due to the selectivity of the catch method to each fish species and size, we standardize the catch effort for each environment (flowing channels and the reservoir). We use the same catch effort for each environment along the monitoring time. In flowing channels (streams, river channel and creeks), the catch effort was 30 sets with each of the three cast nets (different mesh sizes 0.5, 1.5, and 3.5 cm), plus 60 min of sweeps with portable electric fishing equipment with an amp of pulsating current (340 V, 1–2 A, dc) along 100 m of the

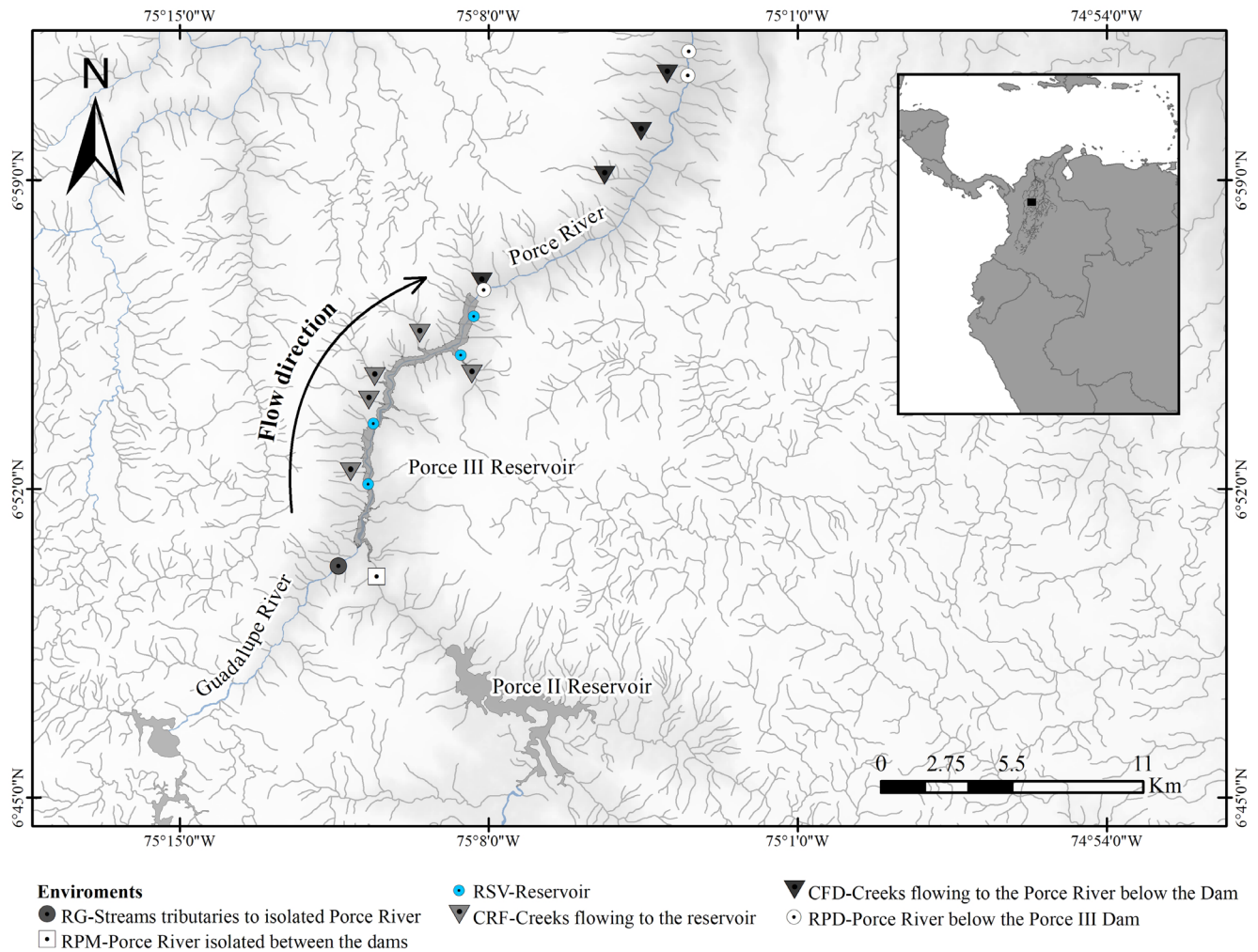


FIGURE 1 | Sampling sites in Porcine III reservoir. The digital elevation model (SRTM, 1 arc-second) was obtained from USGS Earth Explorer (<https://earthexplorer.usgs.gov>) and shape file of dams was obtained from IGAC (<https://geoportal.igac.gov.co/>). All other products were produced by the authors and are copyright-free.

flowing channel. In the reservoir the catch effort was three gill nets (each one 100 m long and 3 m high) in the littoral zone. Exposure time was four hours (due to the access security regulations to the reservoirs: 6:00–8:00h and 12:00 and 14:00h); two nets at the surface and the third one, at three meters deep. Each net had ten types of mesh size (1–10 cm between opposite knots) to increase the probability of catching fish of different species and sizes.

Fish data. Caught fish were anesthetized with eugenol solution to reduce stress during handling (Javahery *et al.*, 2012). For fish belonging to complex taxonomic groups, a sample of ten specimens was taken to the laboratory. These specimens were included in the Colección de Ictiología del Instituto de Biología de la Universidad de Antioquia, Medellín, and the list of registered species and number of collected specimens are in Tab. S2. Classification of species follows Fricke *et al.* (2021) and the Colombia

checklist according to DoNascimento *et al.* (2020). Species determination followed several taxonomic keys for specific groups (Rosen, Bailey, 1963; Dahl, 1971; Harold, Vari, 1994; Skelton, 2001; Armbruster, 2005; Maldonado-Ocampo *et al.*, 2005; Román-Valencia, Arcila-Mesa, 2010; Londoño-Burbano *et al.*, 2011; Ortega-Lara, 2012; Román-Valencia *et al.*, 2013; Hernández *et al.*, 2015; Lujan *et al.*, 2015).

Data analyses. All catches were analyzed for defined number of species and their abundances in each place and system for each year from 2008 to 2020. Species frequency was estimated as the number of times each fish species was captured in each environment versus the total number of sampling units in that environment.

Alpha-diversity analysis. To address the question—how would community change, considering the local environmental context, during and after the dam? —we evaluated the temporal variation (year as an explanatory variable) and species richness (response variable) using generalized linear models (GLM) to separately assess native and non-native species, additionally we performed a GLM using the entire community (Fig. S3). Also, we tested for differences in the richness of the species number of native and non-native species for each sampling time between the six aquatic environments. The difference in richness among environment was assessed by applying a Kruskal–Wallis test, if a significant difference was detected (level of significance $\alpha = 0.05$), we use post hoc pairwise comparisons using the Wilcoxon rank-sum test, with P-value adjustment according to Holm’s procedure (Holm, 1979). Holm’s procedure is considered a more powerful correction (*i.e.*, more likely to detect an effect if it exists) than is Bonferroni for multiple comparisons, providing better protection against Type I error (Wright, 1992).

Spatio-temporal variation of fish communities: contribution of sites and species. To assess differences in fish assemblages stemming from reservoir creation we used non-parametric multivariate methods. Resemblance matrices were generated using the Jaccard similarity index (presence / absence) that were compiled into a matrix of distances of fish species. Differences in the spatial and temporal distribution of similarities among environments were assessed with a permutational multivariate ANOVA (PERMANOVA) using the *adonis* function in the *vegan* package (Oksanen *et al.*, 2015). To evaluate the differences between the assemblies of fish we calculated the p-values corrected by Bonferroni with the *pairwise.adonis* function in the *pairwise Adonis* package in R (Martinez-Arbizu, 2020). The results were displayed on a non-metric multidimensional scale graph (nMDS) in two four-year periods before filling the reservoir from 2008 to 2011 and after filling the reservoir from 2017 to 2020, considering the stress of 0.20 as an acceptable goodness of fit (Clarke *et al.*, 2014). Similarity-profile analysis was performed, and the results were overlaid on the nMDS plots, so as to demonstrate structure among samples (Clarke *et al.*, 2008).

Beta-diversity analysis. To address whether the fish species community change related to different environment and species characteristics, we calculate the spatio-temporal variation of fish communities following a beta diversity contribution approach (Legendre, Cáceres, 2013). We computed the total variance in beta diversity (BDTotal) for each year and then partitioned this measure into Local Contribution to Beta Diversity (LCBD) for each aquatic environment and calculated Species Contributions to Beta-Diversity (SCBD) using Hellinger-transformed abundance data and function *beta.div* available in the package *adespatial* (Dray *et al.*, 2018). The Local Contribution to Beta Diversity represents community composition’s uniqueness in sampling sites across the sampling region and indicates how much each site contributes to beta diversity. This

approach identifies stations with significantly different community composition. Thus, a site with average and common species composition is expected to have zero value, whereas large values indicate sites with different communities. In this particular study we used this metric to compare each aquatic environment contribution. The Species Contributions to Beta-Diversity indicates the contribution of a species to the overall beta diversity in the data set. All statistical analyses and graphics were performed in software R (R version 3.6.3; R Development Core Team, 2020).

RESULTS

From 2008 to 2020, a total of 14,353 fish were captured (3,919 individuals captured during construction and 10,434 individuals captured after dam construction; see Tab. S2), representing five orders, 14 families and 45 species. During the construction of the dam (years between 2008 to 2011), 23 species of fish were caught. The species of Siluriformes and Characiformes together represented 56% of the total. Cichlidae was the family with more species (22%), followed by Characidae (17%). Families with a unique species were Callichthyidae (*Hoplosternum magdalenae* Eigenmann, 1913), Apterodontidae (*Apterodontus eschmeyeri* de Santana, Maldonado-Ocampo, Severi & Mendes, 2004) and Bryconidae (*Brycon henni* Eigenmann, 1913). After dam construction and filling of the reservoir (years between 2012 to 2020), 44 species of fish were caught in different aquatic environments, including 15 ones not previously detected, both species native and non-native. Characiformes represented 43.1% of post-construction fish species, followed by Siluriformes with 27.2%. Characidae and Cichlidae families were the richest with 18% each.

Relative abundance of fish changed between pre- and post-impoundment periods. The species with the highest number of captured during construction were *Astrobalepus* spp. (27.3%), *B. henni* (21.6%), and *Poecilia caucana* (Steindachner, 1880) (11.7%). After the construction, the species with the highest catch rates were *Astyanax microlepis* Eigenmann, 1913 (26.7 %), *Astrobalepus* spp. (16.1%) and *Hemibrycon* spp. (11.8 %). Some species abundance decreased after the construction of the dam, while the catches of other species increased, particularly non-native fish species *Oreochromis niloticus* (Linnaeus, 1758), *Coptodon rendalli* (Boulenger, 1897), and *Parachromis friedrichsthalii* (Heckel, 1840) (Tab. S2).

Abundance of each family changed during the monitoring period within each environment (Fig. 2; Tab. S2). In creeks (CFD, CFR), the most abundant family was Astrobalepidae, and it was found only in these environments. The isolated Porco River (RPM) had three dominant families (Poeciliidae, Characidae, Parodontidae) but in the last three years, Characidae has become less abundant. The Guadalupe River (RG) had a diverse family composition dominated by Bryconidae, Loricariidae, and Parodontidae, and the abundance of each of these families fluctuated over time. In 2010, the family Bryconidae had the greatest abundance in this ecosystem, after impoundment it reduced its abundance, and in the last six years this family increased gradually in RG. After the reservoir formation in 2011, the abundance of species such as *B. henni* (Bryconidae), *P. caucana* (Poeciliidae), *Roeboides dayi* (Steindachner, 1878) (Characidae), and *Lasiancistrus caucanus* Eigenmann, 1912 (Loricariidae) declined in CRF and RSV. In the newly formed reservoir (RSV) Cichlidae (mostly non-native) and Characidae, became abundant. In the

Porce River downstream of the dam (RPD) after the construction of the dam a stability of the environment is observed in terms of abundance, where it is mainly dominated by the Characidae family.

The number of fish species in each environment was between 1 to 16 species (mean \pm sd: 6.5 ± 0.2 species) during the years 2008 to 2020, and the maximum number of species collected in a year ranged from 14 to 28 (mean \pm sd: 3.3 ± 0.8 species). Over the study period, the number of native fish species increased in some environments, but declined in others, and non-native species increased over the study period (Fig. 3).

Spatial patterns of total species richness showed that the number of non-native species and the number of native species was different among the environments ($X^2 = 17.02$, $p = 0.004$; Fig. 4), with the Porce River channel below the dam being the richest (RPD). Compared to other environments, the number of native species was lower in the reservoir, and non-native species richness was higher ($X^2 = 60.59$, $p < 0.001$; Fig. 4). The highest contribution of non-native species was mainly detected in the reservoir (RSV) and in the Porce isolated River (RPM) (Fig. 4).

The nMDS and PERMANOVA analysis showed differences in temporal and spatial significance in fish assemblage among aquatic environments in the reservoir area Porce III (Fig. 5). During filling the dam (years between 2008 to 2011), fish

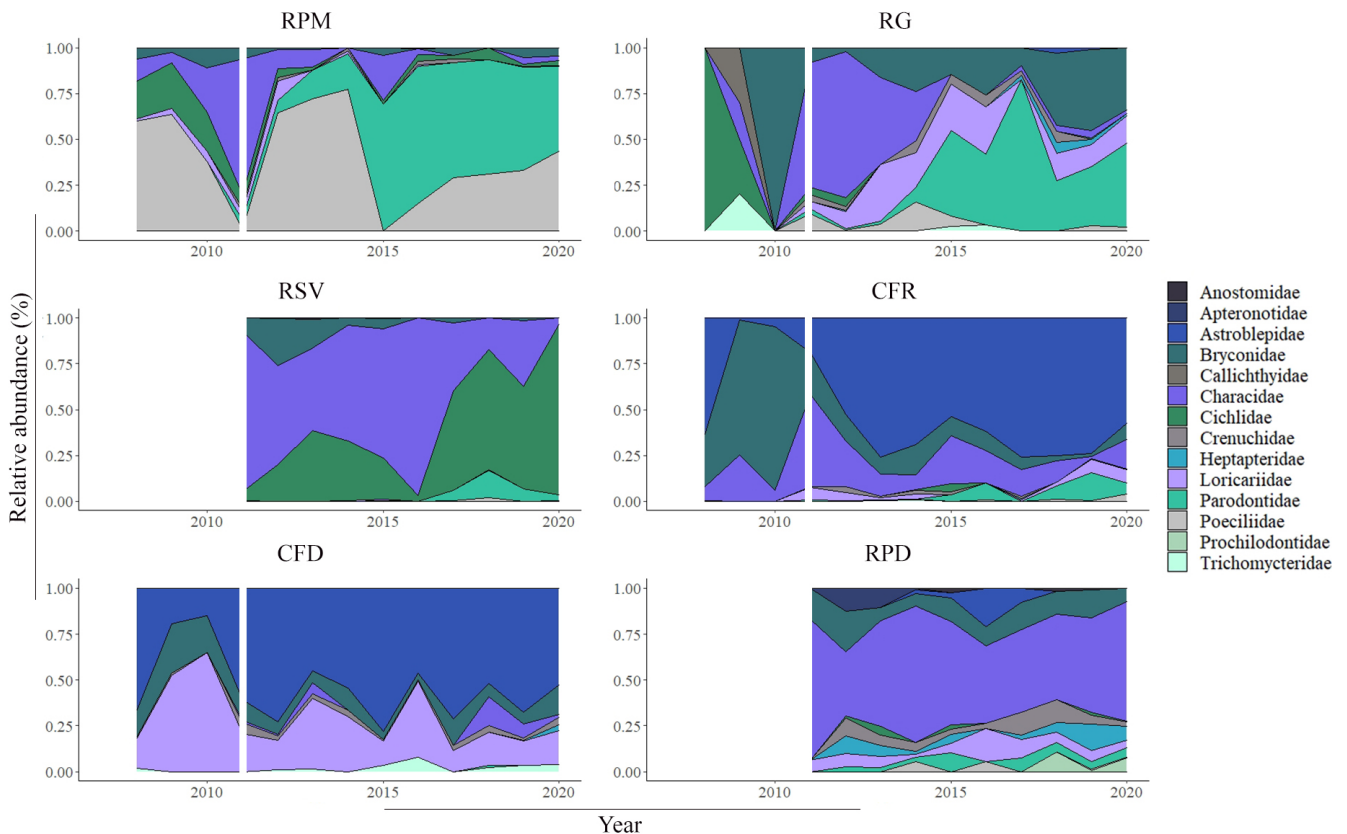


FIGURE 2 | Changes in relative abundance over time in each aquatic environment (RPM) Porce River isolated between the dams, (RG) Guadalupe River, (RSV) Reservoir, (CFR) Creeks flowing to the reservoir, (CFD) Creeks flowing to the Porce River below the dam, and (RPD) Porce River below the Porce III dam. White vertical line represents the year of filling and separates the years of pre-construction and post-filling of the reservoir.

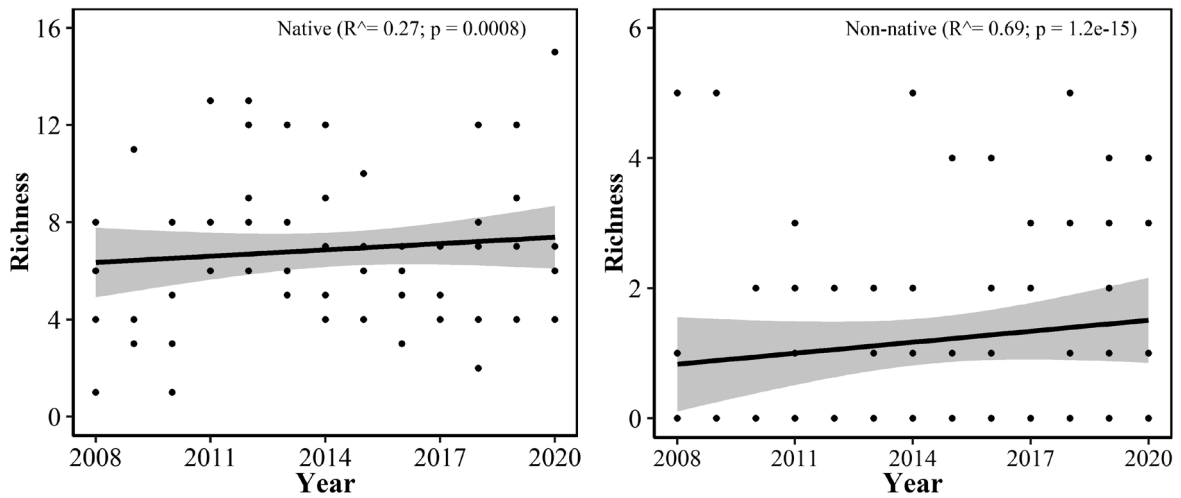


FIGURE 3 | Observed fish-species richness vs. time. Observed fish-species richness native (left) and non-native (right) by sampling year in the area of influence of the Porce III reservoir. The generalized linear models and their confidence interval have been added. Each point represents an environment.

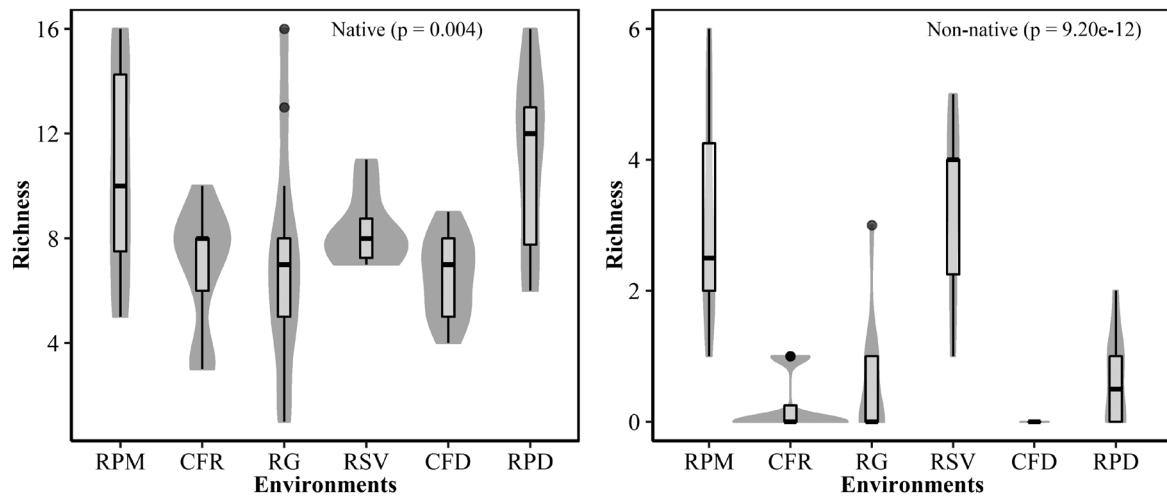


FIGURE 4 | Observed fish-species richness vs. environments. Violin plot comparing the median, interquartile range, and 95% confidence interval on the distribution pattern of richness among environments (left: native fish, right: non-native fish). The shape of the violin plot represents data distribution by kernel-density estimation, meaning that wider sections represent a higher probability of that given value of richness in that environment; the skinnier sections represent a lower probability. P-values from Kruskal–Wallis test for richness among environment is displayed. The environments were identified from upstream to downstream direction, as follows: (RPM) Porce River isolated between the dams, (RG) Guadalupe River, (RSV) Reservoir, (CFR) Creeks flowing to the reservoir, (CFD) Creeks flowing to the Porce River below the dam and (RPD) Porce River below the Porce III dam.

assemblages were different between most aquatic environments. However, the Porce River environment shared fish species with the other assemblages, reflecting the existing connection of the river, stream, and creeks (Fig. 5A). After filling the reservoir, the connection between environments were broken and fish assemblages

diverged to three new fish species assemblages (Fig. 5B). Fish-assemblage ordination shows a similarity between creek environments (CFD and CFR); this is because some CFR localities, such as Santa Ana, Plan de Pérez, Bramadora (as shown in the Tab. S1), and the localities of the CFD environment share the presence of species of the genera *Astroblepus* Humboldt, 1805. The river and stream environments that remained connected following reservoir formation (RG and RPM) showed more similarity. The assemblages in the reservoir and the river below the dam were the most different.

The beta diversity (BD) for the whole riverine area in the two first years is ranged between 0.60 and 0.70 after this time the BD reduces to 0.55 and it starts to recover in the next four years (2011 to 2014), keeping constant in the following years. Before the impoundment, the isolated Porce River channel and creeks flowing to the future reservoir area were environments with the higher contribution to beta diversity. After impoundment, the reservoir (RSV) has been the environment with a higher and significant contribution ($p < 0.05$) to beta diversity because of new non-native fish species in its fish assemblages and their abundance (Fig. 6). The Porce River downstream of the dam contributed the least to beta diversity. In the SCBD results, *Astroblepus* spp. was the species that contributed to changes in beta diversity in the most of the years, followed by *A. microlepis*.

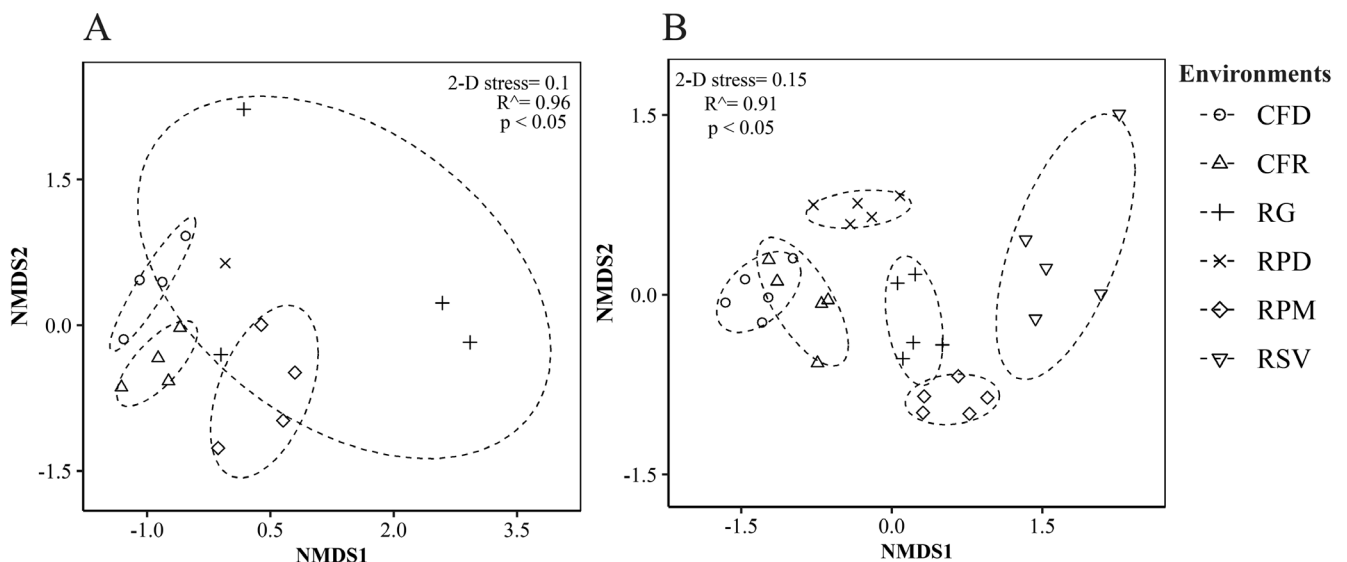


FIGURE 5 | Fish-assemblage ordination in the aquatic environments of Porce III by non-metric multidimensional scaling (nMDS) using Jaccard similarity index. **A.** Before filling the reservoir from 2008 to 2011 and **B.** After filling the reservoir from 2017 to 2020. Environments are identified by symbols, and assemblage groups are identified by lines (70% of similarity). (RPM) Porce River isolated between the dams, (RG) Guadalupe River, (RSV) Reservoir, (CFR) Creeks flowing to the reservoir, (CFD) Creeks flowing to the Porce River below the dam, and (RPD) Porce River below the Porce III dam.

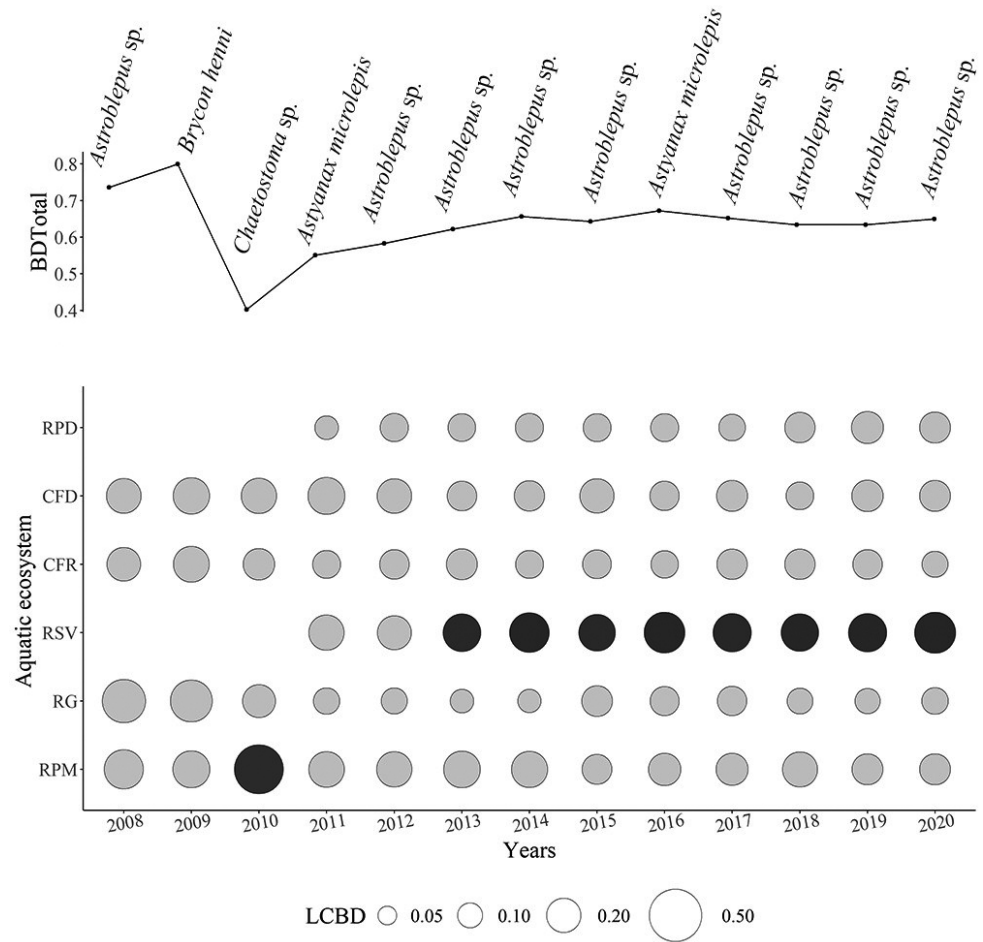


FIGURE 6 | Total variance in beta diversity (BDTotal) in each year and first Species Contributions to Beta-Diversity (SCBD) by year. Local contribution to beta-diversity (LCBD) per aquatic environment and year (black circles represents significant values $p < 0.05$).

DISCUSSION

We recorded fewer species before impoundment than at the time of filling and operation, which may be due to differences in the number of years of sampling. Further, in this particular case, the sector of the riverbed of the Porce River that was dammed was poor in species records (Tab. S2). Jiménez-Segura *et al.* (2014) estimated that within this altitudinal range (680 to 924 masl), it is expected to find approximately 81 species. On the other hand, it is known that during the first days of filling individuals of several species occupied the entire reservoir and water column independently of the type of habitat and during this time the experimental fisheries usually registered high catches. In the same way, this initial diversity tends to decrease over time since only a few species can survive this new type of system (Agostinho *et al.*, 1999).

The increase in non-native species and the decrease in abundance of native species following the formation of the Porce III reservoir is striking. This is a pattern in Neotropical dammed rivers previously described by several authors (Bunn, Arthington,

2002; Orsi, Britton, 2014; Agostinho *et al.*, 2016; Lima *et al.*, 2016). This phenomenon could be a result of environmental filters of the modified fluvial environment and the response of the fish species populations (Gomes, Miranda, 2001). Cichlids such as *Oreochromis* spp. and *Coptodon* spp. are typical of lakes in Africa (Nelson *et al.*, 2016) and, because they build nests and care for their fry (Goodwin *et al.*, 1998), the environmental conditions of the South American reservoirs favor the proliferation of these species (Agostinho *et al.*, 2016).

Distribution of fish richness by family in the Porcè River is similar to the general trend of the richness of these fish species in the ecosystems of the Magdalena River basin (Jiménez-Segura *et al.*, 2016). Characiformes and Siluriformes are the richest fish Orders in South America (Albert *et al.*, 2011) and their species are widespread in the South American basins including in the wide variety of Andean aquatic habitats (Anderson, Maldonado-Ocampo, 2011); for the study area has been captured 19.3% of the Magdalena-Cauca total species richness (DoNascimento *et al.*, 2020). Presence of four species of potamodromous fish *Brycon rubricauda* Steindachner, 1879, *Megaleporinus muyscorum* (Steindachner, 1900), *Ichthyoelephas longirostris* (Steindachner, 1879), and *Prochilodus magdalenae* Steindachner, 1879 next to the Porcè III dam is evidence that Porcè River was a migratory route for these species before the dam blocked migration, and it continues to be a spawning area as migratory species have been detected downstream the of Porcè III dam (Rivera-Coley, 2020). Changes in species richness may be being influenced by changes in the characteristics of new habitats, for example, Hamp (2019) found that water depth and velocity, substrate composition and the abundance of organic matter are most important drivers for the distribution of Andean fish species in non-regulated rivers. Magdalena species are adapted to specific ecological niches (Castellanos-Mejía *et al.*, 2021; Valencia-Rodríguez *et al.*, 2021) and as dam construction eliminates some of these environments and creates new ones, it is not such a surprise that fish assemblages are changing in response to these modifications.

Human modifications to ecosystems, such as dams and reservoirs, precipitate changes in the physical and chemical conditions of water bodies (Borgwardt *et al.*, 2019). These alterations lead to ecological changes that undoubtedly affect the diversity of organisms and their interspecific interactions (Agostinho *et al.*, 1992; Winemiller *et al.*, 2016). It follows that the persistence of any fish species in such a modified aquatic habitat will depend on its adaptive strategies and capacity to explore the newly available habitat resources and fill new ecological niches. Changes in species abundance and occurrence led to each aquatic environment in the dammed reach of the Porcè River to develop a unique fish assemblage (Álvarez-Bustamante *et al.*, 2018). Streams (RG), creeks (CRF and CFD) and the river channel in the modified river section (RPM and RPD) had the greatest number of species. In these environments, species of the genus *Hemibrycon* Günther, 1864, *Parodon* Valenciennes, 1850, and *Astroblepus* were the most abundant. In the Porcè III reservoir (RSV), the fish assemblage was the poorest, however, a high abundance of Cichlidae was observed (most of them non-native fish species). This finding reflects the reality that each aquatic environment within this river waterscape offers different habitats for fish species (Jiménez-Segura *et al.*, 2014; Álvarez-Bustamante *et al.*, 2018) and populations of the fish species respond to this spatial heterogeneity.

In the modified section of the Porcè River, populations of fish species changed because of these new conditions offered by the Porcè III reservoir. With the filling

of the reservoir, in the Porce River channel there was a loss of riverine microhabitats but, at the same time, lentic microhabitats were formed; these new environments are favorable to the Cichlid species (Agostinho *et al.*, 2016), since their reproductive strategy in equilibrium (*i.e.*, comparatively large oocytes, broods protection and acyclic spawning) is favor by slow-flow environments that guaranteeing a greater survival of their offspring (Winemiller, 1989). The increase of non-natives species richness over time was not surprising, since the introduction of non-native fish species in the Magdalena-Cauca basin is increasingly recognized as an important contributor to the threat of species extinction and ecosystem degradation (Lasso *et al.*, 2020). In the Porce III reservoir ten non-natives species are present. Cichlids species are abundant in the reservoir and they are fisheries resources (López-Sánchez *et al.*, 2018). In the Porce River and Guadalupe River, the non-native species were Poecilids. Globally, the effect of the introduction and invasion of these species is poorly known (Gutiérrez, 2010). Hypotheses of their interaction with native species have been proposed, for example, Cichlids may compete for space (reproduction and/or refuge) with native species (van Breukelen, 2015; Hert, 1995). Non-native fish species in aquatic systems can trigger a series of effects, such as the displacement of native species, hybridization, modification of the interaction between species and possible alterations of the native ecosystem conditions (Gozlan *et al.*, 2010; Cucherousset, Olden, 2011).

Fish community in the areas of influence of a reservoir reflects a restructuring of the original fish community of the unmodified river (Agostinho *et al.*, 1999; Jiménez-Segura *et al.*, 2014). The new composition of fishes will depend on the time of formation of the reservoir, as well as its characteristics, shape, depth, perimeter, retention time, water surface area, streams and tributary rivers (Agostinho *et al.*, 1999, 2008). Before the Porce III reservoir filling, the Porce River channel was a path for fish dispersion between the creeks flowing to Porce River and similarities in the fish assemblages between the creeks were high. The new reservoir is a semi-permeable barrier to this fish dispersion. Within the isolated creeks flowing to the reservoir, some fish species changed their abundances and new assemblages formed. So, the turnover of the fish community in the Porce River represents a change because of the formation of the dam. After nine years, we observe that there are six fish assemblages, three of which are new forming after the creation of the, in addition to the three previously existing ones in the isolated river channel, isolated creeks and isolated streams. This is a relatively rapid response (less than a decade) of the fish assemblage to damming, indicating that in the Andes, fish communities may react more quickly than has been observed in Brazilian reservoirs, (*e.g.*, Paraná River) where the researchers detected reductions in the relative abundances of local species, and a good colonization process occurred for species with low longevity and high reproductive potential 15 years post dam construction (Agostinho *et al.*, 2008).

We detect that before the completion of the reservoir in the Porce River there was a diverse fish community and in the year 2010 after the reservoir filling started, there was initial homogenization in species composition, noticeable in the decrease of total beta diversity (BD_{total}). Once the communities began to establish, the BD_{total} became an almost constant value. In terms of local contribution to beta diversity (LCBD), we obtained a characteristic pattern where the reservoir is the ecosystem that significantly contributes to the regional species turnover over the last eight years. This pattern begins to become evident once the dominant community in the reservoir is established

(apparently two years after the reservoir). In the Porce III reservoir the assemblage is mainly composed of non-native species that survive in the new environmental conditions. In this case, high LCBD values indicate sites with a unique composition that includes a very low number of species, most of them non-natives species. The reservoir fish assemblage instead of being a product of a single evolutionary history merges from a unique anthropogenic action, and as a result, a pool of non-natives fishes in a reservoir in the Andes fluvial network is established. On the other hand, in species contributions to beta diversity the native species that most contribute to beta diversity are the species of the complex *Astroblepus* spp., which is the most abundant at regional scale and is usually restricted to tributary streams.

In this study, we implicitly assume that the first-order effects of habitat fragmentation and severe alteration of hydrologic regimes brought about by dam construction are the forces driving the changes in fish community structure we observe. We should note that changes in physic-chemical habitat conditions, especially temperature and dissolved oxygen, stemming from dam construction and management (or even other processes, such as catchment land-use change, which may be relevant over the 13-year time horizon of the study), might also be important (Jiménez-Segura *et al.*, 2016). An analysis of how physic-chemical conditions of Porce River surface waters have changed pre- and post- dam construction and whether such changes could serve as plausible alternative or synergistic mechanisms driving fish community response is beyond the scope of this paper, but would be a worthy topic for further research. Our work demonstrates that dam construction is associated with major changes in fish community structure, but we cannot provide a full mechanistic accounting of the processes driving those changes without considering physic-chemical changes to water quality.

Finally, it is evident that hydropower projects alter the biological diversity of the fish species. Damming modifies the ecosystem and transforms the physic-chemical character of adjacent surface waters (Winton *et al.*, 2019), thus indirectly affecting the ecology of the system. Porce III reservoir is only one of the reservoirs in the Porce River basin. The influence of the position of a reservoir along a river demonstrates the importance of a larger-scale spatial analysis, that is, across river basins considering possible effects of tributaries and the lotic section. Because of migratory fish downstream the Porce III dam, it would be important to include sampling sites in different rivers in the Magdalena basin in monitoring. Changes in fish assemblages are easily detected over long time periods. It is important to maintain long-term monitoring schemes to evaluate if the effects of the reservoir on the genetic diversity of native fish as the new reservoir ages and the species assemblages adjust to the novel environments. Future monitoring schemes could include complementary methods, such as metabarcoding of eDNA, for discovering cryptic fish species that are difficult to detect using the conventional methods (Valentini *et al.*, 2016).

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AUTHORS' CONTRIBUTION

Daniel Valencia-Rodríguez: Conceptualization, Data curation, Formal analysis, Methodology, Writing-review and editing.

Juliana Herrera-Pérez: Conceptualization, Formal analysis, Methodology, Writing-review and editing.

Daniel Restrepo-Santamaría: Data curation, Methodology, Writing-review and editing.

Andrés Galeano: Methodology, Resources, Writing-review and editing.

R. Scott Winton: Conceptualization, Writing-review and editing.

Luz Jiménez-Segura: Conceptualization, Methodology, Writing-review and editing.



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ETHICAL STATEMENT

This study was carried out with recommendations and approval of the Ethics Committee for Animal Experimentation from the Universidad de Antioquia (CEEAA). Protocol was reviewed and approved in November 14 of 2017 by CEEAA and the investigation was approved in December 7 of 2017. The specimens were collected under collection license number 0524 of May 27, 2014.

COMPETING INTERESTS

The authors declare no competing interests.

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