PRIMARY RESEARCH PAPER

Temporal-scale assessment of population genetics of the freshwater fish *Prochilodus magdalenae* in an area impacted by construction of a dam

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Abstract Habitat fragmentation is among the main threats to freshwater fish biodiversity, with expected effects including genetic impacts due to disturbance of migration and declining population size. Major concern falls on highly exploited species such as *Prochilodus magdalenae*, a migratory characiform fish endemic to the Magdalena River basin supporting much of the Colombian artisanal fishery, whose migration route was interrupted by the Ituango hydroelectric project in the Cauca River. To determine the potential effects of fragmentation, this study evaluated the population genetics of this species on both geographical (upstream and downstream of the dam) and temporal (before and after the construction) scales by using 11 species-specific microsatellite markers. Contrary to expectation, genetic diversity and structure remained relatively stable. This study provided no evidence of genetic impacts on *P. magdalenae* associated with fragmentation over the short term (4–10 years, 5–12 generations) despite persisting threats, genetic evidence of bottleneck, and a high degree of inbreeding, showing the ability of this species to withstand disturbance of its habitat.

Keywords Microsatellite · Migratory fish · Habitat fragmentation · Genetic diversity · Gene flow · Effective population size

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Introduction

The global abundance of freshwater faunal stocks decreased by 84% between 1970 and 2016 (WWF, 2020), mainly due to overexploitation, water pollution, habitat degradation, water-flow modification, and species invasion (Dudgeon et al., 2006), in addition to climate change and the increase in emerging pollutants (Arthington et al., 2016; Reid et al., 2019). One of the most important disturbances in freshwater systems is the construction of dams, including disruption of the life cycle of migratory species (Liermann et al., 2012; Reis et al., 2016; Barbarossa et al., 2020; Herrera-Pérez et al., 2019; Reid et al., 2019). It is estimated that more than 76% of migratory river fish populations have been reduced since 1970 (Deinet et al., 2020), while construction of dams has accelerated and could affect almost 93% of the rivers around the planet by 2030 (Grill et al., 2015, 2019).

The Magdalena-Cauca basin, located in the northern Andes Mountains, concentrates most of the

Colombian human population and is a key area for the economy of the country (Restrepo et al., 2020). It has high aquatic biodiversity, with more than 235 fish species, and supports a large part of the Colombian artisanal fishery, with more than 14,300 tons landed in 2019 (García-Alzate et al., 2020; Valderrama et al., 2020). However, the biodiversity of this basin is threatened, including 54 of said species classified with some degree of vulnerability in the local red list (Mojica et al., 2012). These species are impacted by various anthropogenic activities related to water pollution, mining, livestock production, resource overexploitation, and habitat modification, including construction of dams (López-Casas et al., 2020).

One of these species is the characiform fish bocachico *Prochilodus magdalenae* Steindachner 1879, the most important fishery resource, with roughly 40% of total landings of the Magdalena-Cauca River basin in 2019 (Duarte et al., 2019; Valderrama et al., 2020), albeit with an estimated reduction of 76% of their fishery production since 1975 (Barreto, 2017). This species was classified as Critically Endangered in 2002 and has been listed as Vulnerable since 2012, in the Colombian red list of threatened freshwater fishes (Mojica et al., 2012). The national authorities have established a minimum landing size of 25 cm for this detritivorous fish, which inhabits the Magdalena, Atrato, and Sinú basins. This fish reaches sexual maturity at an average size of 20–25 cm and between 1 and 1.5 years of age, and can attain a maximum standard length of nearly 50 cm (Lasso et al., 2011). This species is iteroparous, meaning that it reproduces multiple times throughout its lifespan, and is known for its massive spawning events (Jiménez-Segura et al., 2010). This fish undergoes long longitudinal migrations, with reports of distances of up to 1,223 km (López-Casas et al., 2016), and exhibits two migration peaks per year that coincide with the flood cycles of the Cauca and Magdalena rivers (Barletta et al., 2015; Jiménez-Segura et al., 2010, 2016).

The population genetics of *P. magdalenae* has been more studied than for other fish species of the Magdalena-Cauca River basin (Márquez et al., 2020). The use of microsatellite DNA markers demonstrated the presence of populations with high genetic diversity, a significant degree of inbreeding, and the coexistence of two main genetic groups (stocks) in the Magdalena basin, as well as genetic differentiation among populations from the Magdalena, Atrato

and Sinú basins (Márquez et al., 2020). Additionally, despite the river connectivity and the wide native distribution of this species, the unexpected findings of spatial genetic structure within the Magdalena Basin may be explained by hybridization with related species and anthropogenic effects on its habitat such as restocking and fish translocation (Fontalvo et al., 2018; Orozco-Berdugo & Narváez-Barandica, 2014; Landínez-García et al., 2020). Although national and regional entities have made attempts to restock wild populations of this species in the last 20 years (see discussion in Landínez-García et al., 2020), detailed information of such practices remains unavailable.

The increasing environmental threats to freshwater fish species demand genetic evaluation of wild populations to assess microevolutionary processes that reflect landscape changes, infer the adaptive evolutionary risks and inform management and conservation planning (Manel et al., 2003; Schwartz et al., 2007; Laikre et al., 2010; Epps & Keyghobadi, 2015). While empirical studies about anthropogenic impacts on freshwater fish genetics are limited, impacts of isolation by dams on migratory fish populations at different geographic scales are documented (e.g.,Yamamoto et al., 2004; Van Leeuwen et al., 2018; Klütsch et al., 2019; Ruzich et al., 2019; Liu et al., 2020; Pimentel et al., 2020; Vega-Retter et al., 2020). In the Neotropics, studies of migratory fish populations fragmented by dams reported differences in genetic diversity and structure between upstream and downstream sections for species such as *Pseudoplatystoma corruscans* (Spix & Agassiz 1829) (Paraná River, Brazil; Prado et al., 2018), *Prochilodus magdalenae* (Magdalena River, Colombia; Fontalvo et al., 2018), *Prochilodus costatus* Valenciennes 1850 (San Francisco River, Brazil; Pimentel et al., 2020), *Trichomycterus areolatus* (Valenciennes 1846), and *Basilichthys microlepidotus* (Jenyns 1841) (Choapa River, Chile; Vega-Retter et al., 2020). This last study found significant changes on a temporal scale in the short term (5 years) after dam construction, whereas species such as *Pimelodus maculatus* Lacepède 1803 in the Upper Uruguay River basin (Ribolli et al., 2012) and *Prochilodus lineatus* (Valenciennes 1837) in the Paraná River (Ferreira et al., 2017) showed gene flow and high genetic diversity after similar (2–10 years) and even longer (15–30 years) periods of fragmentation, respectively. Indeed, the detection of genetic differences resulting from the

fragmentation of rivers and the level of impact seem to depend upon complex interactions of factors that include the degree of fragmentation and time elapsed since the disturbance (Ruzich et al., 2019; Liu et al., 2020; Vega-Retter et al., 2020), presence, or absence of fishways that facilitate migration (Ferreira et al., 2017) or translocation and restocking of fish (Klütsch et al., 2019; Pimentel et al., 2020), generation interval of each species (Epps & Keyghobadi, 2015; Ruzich et al., 2019), and pre-existing genetic diversity and structure (Epps & Keyghobadi, 2015; Landguth et al., 2010; Coleman et al., 2018).

The Cauca River is 1,350 km long and runs from south to north between the western and central Andes Mountains, from Laguna del Buey (Cauca Department) to Pinillos (Bolívar Department) in the Colombian Caribbean basin (Rodríguez-Olarte et al., 2011). The upper part of the river predominantly meanders, descending to about 900 m above sea level, while the middle and lower parts flow through a steep, narrow valley over the last 500 km, from the confluence with the Risaralda River to its mouth in the Magdalena River. This stretch of the river is known for the rapids and waterfalls that function as natural barriers to several migratory fish species (Galvis & Mojica, 2007; Rodríguez-Olarte et al., 2011), and it is where the Ituango Dam is located. The Ituango Dam is the largest in Colombia, standing 225 m high with a crest that is 550 m long and has no fishways. Its construction began in 2010, and it is expected to produce 2400 MW of power per year.

Given the recent fragmentation of populations of *P. magdalenae* by the Ituango hydroelectric project dam since 2014, persisting threats to its habitat, and the knowledge gap about short-term effects of these factors on fishes in the Cauca River, this study evaluated the population genetics of *P. magdalenae* collected between 2019 and 2021 in eight sections of the middle and lower Cauca River after the fragmentation (Ex-post sample). Thus, this study evaluates the hypotheses of both spatial (upstream–downstream of the dam) and temporal genetic differences (before–after dam construction) in *P. magdalenae* of the Cauca River over a period of 4–10 years. These hypotheses are based on (i) the genetic vulnerability of populations of this species in the Cauca River, showing genetic evidence of inbreeding and genetic bottleneck before the fragmentation (Landínez-García et al., 2020), (ii) the potential disruption of gene flow,

(iii) likely effective population size changes between upstream and downstream populations due to the fragmentation as has occurred in other species (Pavlova et al., 2017), (iv) the passage of several generations after the fragmentation event, allowing the detection of potential changes (Tallmon et al., 2010; Epps & Keyghobadi, 2015), and (v) the likelihood that the genetic diversity of high-dispersal species may reduce the time lag required to detect the potential impacts of habitat perturbations (Landguth et al., 2010; Fluker et al., 2014; Epps & Keyghobadi, 2015). Therefore, this study can contribute to understanding the dynamic relation between population genetics of the freshwater fish fauna and habitat disturbances.

Materials and methods

Sampling and genotyping

A total of 384 muscle or fin tissue samples from *Prochilodus magdalenae* were collected between 2019 and 2021 (Ex-post sample) from sections of the middle and lower parts of the Cauca River upstream (S1, PHI) and downstream (S2, S3, S4, S5, S6, and S7/S8) of the Ituango Dam (Fig. 1). The sections referred to in this study were previously sampled by Landínez-García and Márquez (2016) and Landínez-García et al. (2020) and were used for comparison with historical sample data (Ex-ante sample). PHI, a stretch of the river known for the presence of rapids and waterfalls, is the section where the Ituango Dam was constructed. Samples preserved in 70% ethanol were supplied by the Grupo de Ictiología from the Universidad de Antioquia (GIUA), Fundación Humedales, and Grupo de Biotecnología Animal from Universidad Nacional de Colombia, Sede Medellín. The sample sizes collected Ex-ante (Landínez-García et al., 2020) and Ex-post (this study) analyzed in this research were as follows: S1: 33|37, PHI: 0|25, S2: 30|18, S3: 28|13, S4: 38|141, S5: 40|28, S6: 94|36, S7/S8: 45|52.

DNA extraction and PCR amplification of 11 species-specific microsatellite loci (*Pma01*, *Pma02, Pma13, Pma14, Pma18, Pma25, Pma35, Pma36, Pma39, Pma40,* and *Pma46*) were performed according to Landínez-García et al. (2020). The amplified fragments were separated by capillary electrophoresis in an ABI 3730 XL automated DNA sequencer
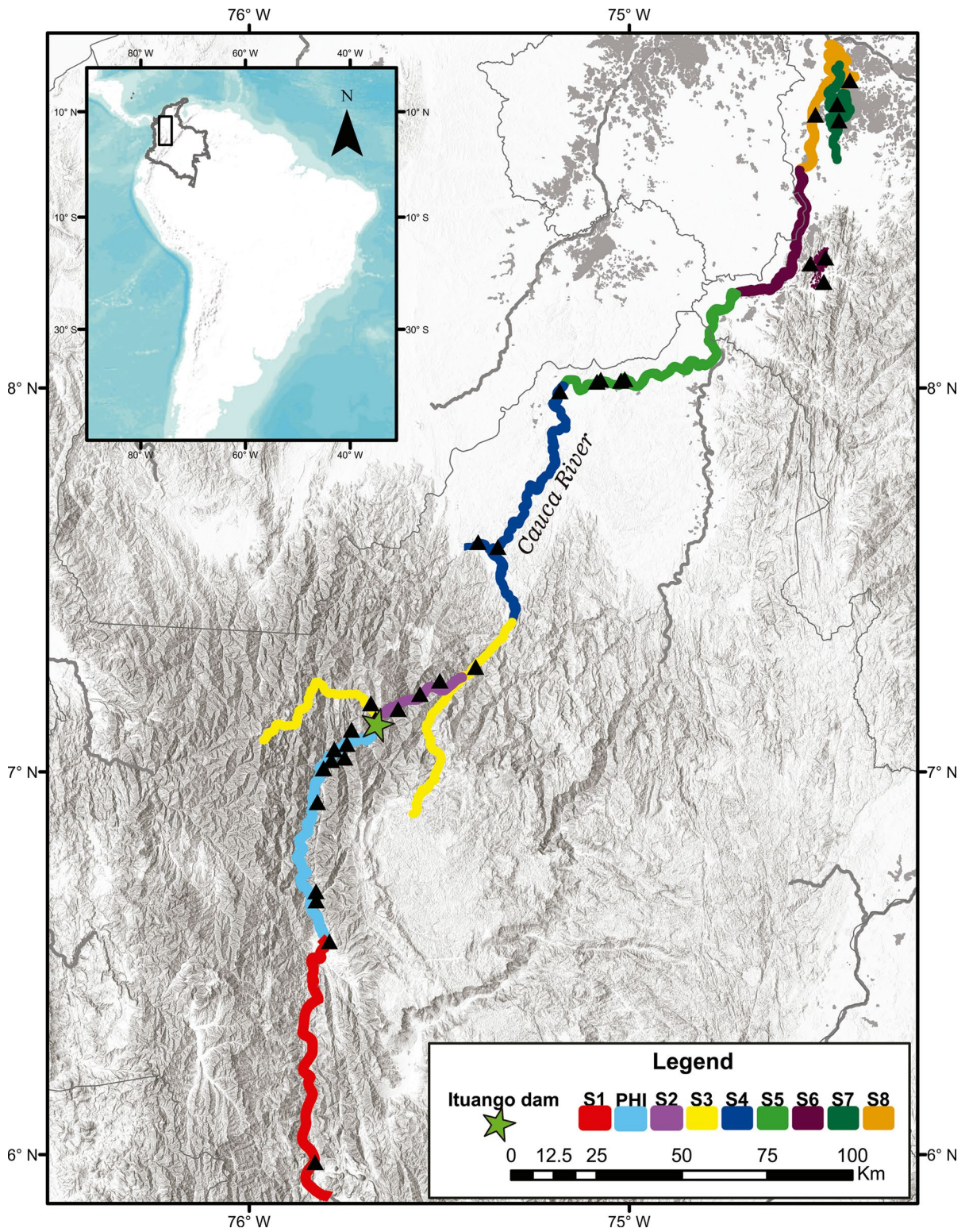
◄**Fig. 1** Sampling points (triangles) for *Prochilodus magdalenae* after the construction (Ex-post sample) of the Ituango Dam grouped into eight sections of the Cauca River, Colombia. *S1* Bolombolo, Puente Real, *PHI* Barbacoas, Brugo, Orobajo, La Pená, San Cristóbal Pená, Peque, Santa María, Sardinas, Llano Grande, *S2* El Aro, Gurimán, La Guamera, *S3* Ituango River mouth, Espíritu Santo River mouth, *S4* Cáceres, Caucasia, Tarazá, *S5* Barrio Chino, Palanca, floodplains La Ilusión and Palomar, *S6* floodplains Grande, La Caimanera and La Raya, *S7/S8* Tres Cruces, floodplains El Floral, Nueva and La Panela

(Applied Biosystems), using LIZ600 (Applied Biosystems) as an internal molecular size marker. Alleles were scored in GeneMarker software v.3.0.0, and amplification, scoring, and genotyping errors were evaluated using Micro-Checker v.2.2.3 (Van Oosterhout et al., 2004).

Genetic diversity and outlier loci screening

To quantify the genetic diversity of *P. magdalenae* in eight sections of the Cauca River from the Ex-post sample, the average value per locus of the number of alleles (N_a), allelic size range (R_a), and expected (H_E) and observed (H_O) heterozygosities were calculated using GenAlEx v6.51b2 (Peakall & Smouse, 2006, 2012). The allelic richness (A_r), for comparison of the number of alleles accounting for differing sample sizes, was calculated in FSTAT v.2.9.4 (Goudet, 2003). Inbreeding coefficients (F_{IS}) and deviations from Hardy–Weinberg (HWE) and linkage (LD) equilibria were evaluated in Arlequin v3.5.2.2 (Excoffier & Lischer, 2010). Fisher's Exact Test, implemented in the web version of Genepop v4.7.5 (Raymond & Rousset, 1995; Rousset, 2008), allowed calculation of the multilocus statistical significance of departures from HWE for collections from each river section or population. Bar plots were used for descriptive comparison among the genetic diversity metrics (N_a, A_r, R_a, H_E, H_O, and F_{IS}) with those reported by Landínez-García et al. (2020) in the Ex-ante sample (308 individuals, years 2010–2014). Additionally, the *G*-test (modified Fisher's exact probability test) implemented in the web version of Genepop v4.7.5 (Raymond & Rousset, 1995; Rousset, 2008) was used to evaluate the null hypothesis that the alleles from the Ex-ante and Ex-post samples were taken from the same distribution.

To identify candidate loci under natural selection (outlier loci) in the Ex-post sample, the BayeScan v2.1 software (Foll & Gaggiotti, 2008) was used setting 10:1 as the prior odds for the neutral model with respect to the model with selection, with 20 pilot runs and 5,000 iterations each, and a total of 250,000 subsequent iterations with 50,000 as the burn-in period. Loci with a posterior probability (PP) > 0.75 were considered significant. Samples with outlier loci were excluded from subsequent population genetic analyses, and the genetic diversity estimators were recalculated.

Demographic estimations

Two methods were applied to detect drastic reduction in population size or recent bottlenecks in the population. The first method involved calculating the standardized *M* index of Garza & Williamson (2001) using Arlequin v3.5.2.2 (Excoffier & Lischer, 2010). A reduction in the number of alleles with respect to the allelic size range of a population may indicate recent bottleneck events. The second method evaluated excess heterozygosity using the software BOTTLENECK v1.2.02 (Piry et al., 1999) with default settings and three mutation models of microsatellites in the coalescent simulation (Infinite Alleles Model—IAM, Two-Phase Model—TPM, Stepwise Mutation Model—SMM; Cornuet & Luikart, 1996; Luikart & Cornuet, 1998). The Bonferroni correction was applied in cases of multiple comparisons.

Estimation of the effective population size (N_e) was performed in NeEstimator v2.1 (Do et al., 2014) implementing the linkage disequilibrium (LD) method, which used a point estimation in each Ex-ante and Ex-post sample, ignoring allelic frequencies ≤ 0.02 that could overestimate N_e (Waples & Do, 2010; Do et al., 2014). A second approach included the temporal method, which estimates a single value of N_e from two or more sets of samples separated by *n* generations (Do et al., 2014). A rough calculation of n for *P. magdalenae* between the Ex-ante and Ex-post samples was based on a generation length of *1/mortality + age of first reproduction—1* (IUCN Standards and Petitions Committee, 2019), considering a total mortality of 3.45 individuals per year in the Cauca River (Zárate, Valderrama & Atencio, Fundación Humedales, personal communication), an average age of first maturity at 1.5 years (Lasso et al., 2011), and

an average time between samples of seven years. The other parameters considered in the temporal method were the estimator Fs, which shows less bias than its analogs F_c and F_k when evaluating the change in allele frequencies (Jorde & Ryman, 2007), jackknife confidence intervals (CIs), and sampling method Plan II, which does not require knowing the population size (N) to perform the estimation (Do et al., 2014). When N_e estimates yielded infinite values, this was interpreted as insufficient evidence of a finite population size, as the larger sampling variance compared to genetic drift signals suggests that the data cannot reliably support estimation of a finite N_e (Waples & Do, 2010).

The Geneclass2 software (Piry et al., 2004) was used to assess interpopulation migration events for the Ex-post sample, for which, based on the sampled sections, each of the individuals was assigned to its most probable section of origin. This approach used a Bayesian criterion using the maximum likelihood estimator L_home/L_max (relationship between the maximum likelihood of the individual of having originated from the sampled section and the maximum likelihood among all sections) and the statistical Monte Carlo resampling method proposed by Paetkau et al. (2004), with 10,000 individuals simulated and an error probability of 0.01.

Genetic structure

Analysis of molecular variance (AMOVA; Meirmans, 2006) and calculation of standardized pairwise indices of genetic distance F'_{ST} (Meirmans, 2006; Meirmans & Hedrick, 2011) and D_{EST} (Jost, 2008; Meirmans & Hedrick, 2011) using the GenAlEx v6.51b2 (Peakall & Smouse, 2006, 2012), applying the Bonferroni correction for multiple comparisons, were used to explore the genetic structure of the Ex-post sample of *P. magdalenae* in the Cauca River. Discriminant analysis of principal components (DAPC) implemented in the R package Adegenet (Jombart, 2008) was also employed and allowed visualizing spatial genetic structure by maximizing the differences in multilocus genotypes among collections. Bayesian clustering analysis using Structure v2.3.4 (Pritchard et al., 2000) was further utilized implementing the genetic mixture and correlated alleles models, with 600,000 Monte Carlo Markov chains with 100,000 regarded as the burn-in period. This

study evaluated $1 \leq K \leq m + 3$, where m is the number of a priori populations (Evanno et al., 2005), with 20 repetitions each. The most likely number of populations (K) was determined after comparing five different statistics (*MedMeaK, MaxMeaK, MedMedK* and *MaxMedK*: see Puechmaille, 2016; and ΔK: see Evanno et al., 2005) in addition to the histogram of the co-ancestry probabilities to each genetic stock, obtained in the StructureSelector online software (Li & Liu, 2018). A co-ancestry threshold value of 0.5 and 0.7 was applied to cluster the samples to each genetic stock in the Ex-ante and Ex-post samples, respectively. These methods were replicated for comparing the Ex-ante and Ex-post temporal samples for each genetic stock, considering both samples as different populations. Additionally, each temporal sample was divided into upstream and downstream subsamples, performing pairwise comparisons of F'_{ST} and D_{EST} indices to infer genetic differences by fragmentation.

Results

Outlier screening and genetic diversity

A set of 34 samples from the Grande floodplain in section S6 were excluded from the population genetic analysis as they exhibited four outlier loci (Online Resource 1). The eight sections of the Ex-post sample showed similar indices of genetic diversity (Table 1), with average number of alleles per locus in the range of 11.45 (S3)–19.62 (S4), allelic richness of 10.32 (PHI)–11.00 (S5) and expected heterozygosities of 0.885 (PHI)–0.908 (S5). There was no evidence of LD among loci, and each section showed significant departures from HWE and significant inbreeding values (17.4–23.3%; Table 1). In the overall sample, null alleles were detected at 7 loci (*Pma18*, *Pma14*, *Pma01*, *Pma36*, *Pma40*, *Pma39*, and *Pma35*), with frequencies ranging from 0.10 to 0.18. Two genetic stocks were suggested by some of the genetic structure analyses (stocks are described below in Genetic structure) with differences in genetic diversity indices, and showing similar and significant inbreeding values (Table 2).

All indices of genetic diversity for the Ex-post sample (2019–2021) were comparable to those for the Ex-ante sample (2010–2014; Fig. 2). However,

Table 1 Average per-locus genetic diversity metrics for *Prochilodus magdalenae* collected between 2019–2021 (Ex-post sample) in sections of the Cauca River

Deme	N	N_a	A_r	R_a	H_O	H_E	F_{IS}	P
S1*	37	15.27	10.62	63.36	0.686	0.893	**0.205**	**0.000**
PHI*	25	14.00	10.32	64.46	0.707	0.885	**0.225**	**0.000**
S2	18	12.73	10.59	62.55	0.708	0.904	**0.226**	**0.000**
S3	13	11.46	10.88	62.18	0.755	0.904	**0.186**	**0.000**
S4	141	19.64	10.94	78.27	0.729	0.900	**0.174**	**0.000**
S5	28	15.09	11.01	72.46	0.690	0.908	**0.233**	**0.000**
S6	36	16.55	10.84	72.09	0.723	0.894	**0.194**	**0.000**
S7/S8	52	17.27	10.65	77.73	0.688	0.898	**0.207**	**0.000**
Stock 1	125	18.09	17.72	76.00	0.716	0.894	**0.183**	**0.000**
Stock 2	117	19.46	19.24	81.46	0.698	0.895	**0.197**	**0.000**
Overall	350	22.91	22.74	89.82	0.713	0.902	**0.197**	**0.000**

Values in bold font denote statistical significance

*Sectors upstream of the Ituango dam

N sample size, N_a number of alleles, A_r allelic richness, R_a allelic range, H_E expected heterozygosity, H_O observed heterozygosity, F_{IS}: inbreeding coefficient, P P value of the test for deviation from Hardy–Weinberg equilibrium

Table 2 Genetic diversity metrics for *Prochilodus magdalenae* discriminated by genetic stocks, temporal samples (Ex-ante and Ex-post), and fragmented sections affected by the Ituango Dam (Upstream and Downstream)

Estimator	Stock 1						Stock 2					
	Global		Upstream		Downstream		Global		Upstream		Downstream	
	Ex-ante	Ex-post	Ex-ante	Ex-post	Ex-ante	Ex-post	Ex-ante	Ex-post	Ex-ante	Ex-post	Ex-ante	Ex-post
N	152	125	17	22	135	103	156	117	16	24	140	93
Na	20.64	18.09	11.64	12.46	20.18	17.64	19.09	19.46	11.00	13.46	18.82	19.09
A_r	19.42	17.72	11.38	11.34	12.49	12.08	17.87	19.24	11.00	12.02	11.74	12.41
R_a	82.73	76.00	61.18	56.91	82.73	74.64	79.73	81.46	56.55	65.09	78.64	80.73
H_O	0.720	0.716	0.663	0.680	0.727	0.724	0.730	0.698	0.670	0.679	0.736	0.703
H_E	0.895	0.894	0.880	0.878	0.896	0.897	0.892	0.895	0.886	0.878	0.892	0.897
F_{IS}	0.197	0.183	0.252	0.220	0.190	0.176	0.183	0.197	0.250	0.204	0.175	0.195
P_{FIS}	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**

Values in bold font denote statistical significance

N sample size, Na number of alleles, A_r allelic richness, R_a allelic range, H_O observed heterozygosity, H_E expected heterozygosity, F_{IS} inbreeding coefficient, P P value of the inbreeding coefficient

the G-test showed that seven of the 11 loci (*Pma18*, *Pma13*, *Pma14*, *Pma40*, *Pma39*, *Pma02*, *Pma25*) had temporal changes in the distribution of allele frequencies ($P < 0.05$).

Demographic estimations

Results of test to detect recent bottleneck showed M indices in the range of 0.15–0.23 for the nine sections and an overall value of 0.26 (Table 3); all were smaller than the reference value of 0.68 (Garza & Williamson, 2001). Additionally, the heterozygosity excess test results were significant ($P < 0.006$) under the IAM (all sections and overall). These results present genetic evidence of a recent bottleneck for *P. magdalenae* of the Cauca River.

The estimated effective population size using the linkage disequilibrium method (LD) was higher in the
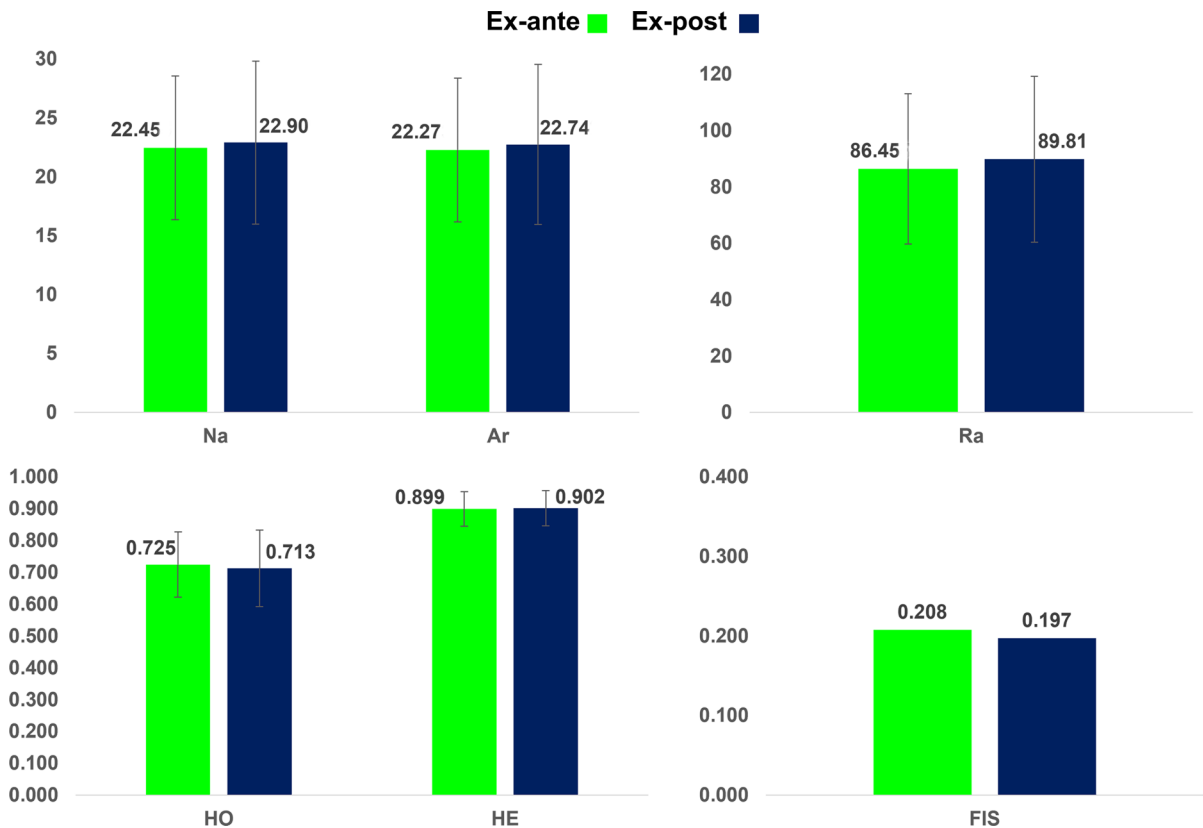
Fig. 2 Mean per-locus genetic diversity metrics for *Prochilodus magdalenae* collected from eight sections of the Cauca River before (Ex-ante: 2010–2014) and after (Ex-post: 2019–2021) the construction of the Ituango Dam. N_a number of alleles, A_r allelic richness, R_a allelic range, H_E expected heterozygosity, H_O observed heterozygosity, and F_{IS} inbreeding coefficient

Ex-post sample ($N_e = 7000.8$; CI 1,875.7-∞) than in the Ex-ante sample (2875.8, CI 1226.7-∞). In turn, these both values were higher than that obtained in the temporal method (755.3, CI: 423.8–3461.1), which was estimated using an average of $n = 7$ generations for *P. magdalenae* between the years 2010 and 2021. Additionally, it was not possible to estimate N_e in each genetic stock as estimations yielded infinite values ($N_e = ∞$; Table 3).

Finally, in the Ex-post sample, eight individuals were identified as likely migrants ($P < 0.01$) among fragmented river sections according to the results of the first-generation migrant detection test. Specifically, seven individuals collected downstream of the Ituango dam were detected as likely immigrants from upstream sections, while one individual collected upstream was identified as likely immigrant from downstream sections.

Genetic structure

No significant pairwise genetic differences were detected within the Ex-post sample (350 individuals, years 2019–2021) by the F'_{ST} and Jost's D_{EST} indices (Table 4). The geographic pattern of genetic variation was quantified as variance within individuals (77%), among individuals (23%), and among Sects. (0%), although the overall structure index calculated using the AMOVA was significant ($F'_{ST\ (7699)} = 0.045$, $P = 0.001$). Moreover, the absence of spatial genetic differentiation was graphically evident by observation of overlapping of points representing the respective sections in DAPC (Fig. 3a) and by the mixture of genetic stocks along the sampled area according to the distribution of the co-ancestry probabilities of the Bayesian analysis (Fig. 3b), since $K = 2$ was the most likely number of populations based on the

Table 3 Detection of recent bottleneck and effective population size estimation for collections of *Prochilodus magdalenae* from the Cauca River, Colombia

Site	M	IAM	TPM	SMM	N_e (CI)
PHI	0.15	**0.000**	0.051	0.517	1,515.4 (134.4−∞)
S1	0.17	**0.000**	**0.001**	0.260	2,541.4 (185.1−∞)
S2	0.14	**0.000**	**0.005**	0.483	4,027.7 (79.4−∞)
S3	0.13	**0.000**	0.103	0.483	∞ (126.3−∞)
S4	0.21	**0.000**	**0.002**	0.319	4,261.9 (816.1−∞)
S5	0.17	**0.001**	**0.002**	0.416	∞ (135.6−∞)
S6	0.23	**0.001**	0.027	0.681	∞ (1,029.5−∞)
S7/S8	0.19	**0.008**	0.027	0.551	∞ (629.1−∞)
Stock1	0.26	**0.000**	0.027	0.926	∞ (2,454.2−∞)
Stock1 upstream	0.23	**0.000**	0.740	0.010	∞ (313.1−∞)
Stock1 downstream	0.24	**0.000**	0.260	**0.002**	1,147.3 (375.2−∞)
Stock2	0.25	**0.000**	**0.001**	0.350	∞ (515.3−∞)
Stock2 upstream	0.21	**0.000**	0.958	0.289	357.1 (123.1−∞)
Stock2 downstream	0.24	**0.000**	0.973	**0.005**	∞ (1,331.4−∞)
Overall (Stock1 + Stock2)	0.26	**0.000**	0.034	0.880	7,000.8 (1,875.7−∞)
Stock1 ex-ante	0.21	**0.000**	0.027	0.861	∞ (786.8−∞)
Stock1 ex-ante upstream	0.20	**0.000**	0.483	0.008	∞ (8,732.5−∞)
Stock1 ex-ante downstream	0.24	**0.000**	**0.001**	0.681	1544.2 (567.5−∞)
Stock2 ex-ante upstream	0.20	**0.000**	0.120	**0.005**	∞ (172.1−∞)
Stock2 ex-ante downstream	0.24	**0.000**	0.992	**0.003**	2716.9 (640.0−∞)
Overall ex-ante (stock1 + stock2)	0.23	**0.000**	0.027	0.958	2875.8 (1226.7−∞)

M standardized index of Garza-Williamson (2001), *IAM* infinite alleles model, *TPM* two-phase model, *SMM* stepwise mutation model, *P* values of the excess of heterozygosity test implemented in BOTTLENECK v1.2.02 (Piry et al., 1999) depending on the assumed mutational model (values in bold denoting statistical significance). N_e effective population size estimated with the linkage disequilibrium method, *CI* Jackknife confidence interval

Table 4 Pairwise comparisons of the standardized indices of genetic structure F'_{ST} (below diagonal) and Jost´s D_{EST} (above diagonal) for *Prochilodus magdalenae* of the Ex-post sample (collected between 2019 and 2021) in the Cauca River, Colombia

|	PHI	S1	S2	S3	S4	S5	S6	S7/S8
PHI	–	0.064	0.053	0.015	0.012	− 0.005	0.025	0.008
S1	0.129	–	0.037	0.000	0.021	0.016	0.015	0.030
S2	0.070	0.064	–	− 0.029	0.023	− 0.012	0.049	0.002
S3	0.029	0.007	− 0.041	–	0.003	− 0.054	0.053	− 0.008
S4	0.016	0.061	0.025	0.001	–	0.014	0.046	0.010
S5	0.083	0.046	0.060	− 0.039	0.083	–	0.004	− 0.017
S6	0.025	0.070	0.067	0.069	0.053	0.079	–	0.024
S7/S8	0.005	0.102	0.020	0.002	0.018	0.070	0.023	–

No statistical significance was obtained after Bonferroni correction

five statistics calculated: *MedMeaK*, *MaxMeaK*, *MedMedK*, *MaxMedK,* and Δ*K*.

At the temporal scale, comparisons between Ex-ante and Ex-post samples in both stocks showed differences in the AMOVA results and standardized pairwise indices of genetic distances. For stock 1, the results were as follows: F'_{ST} (1, 553) = 0.080, $P = 0.001$, and DEST = 0.083, $P = 0.001$. For stock 2, the results were F'_{ST} (1, 545) = 0.106, $P = 0.001$ and DEST = 0.067, $P = 0.001$. However, the genetic variation was mostly explained by the variance within individuals (stock 1: 79%, stock 2: 78%) and among individuals (stock 1: 20%, stock 2: 21%), rather than between periods (only 1% in both stocks). Additionally, the temporal samples were not clearly discriminated by the DAPC (Fig. 4a). On the other hand, the fragmented sections affected by the dam showed

Fig. 3 **a** Results of discriminant analysis of principal components (DAPC; 90 principal components retained, explaining 85% of the variance), and **b** co-ancestry probabilities based on the Bayesian analysis of 350 individuals of *Prochilodus magdalenae* in the Ex-post sample (2019–2021, sections S1, PHI, S2, S3, S4, S5, S6, and S7/S8 of the Cauca River)
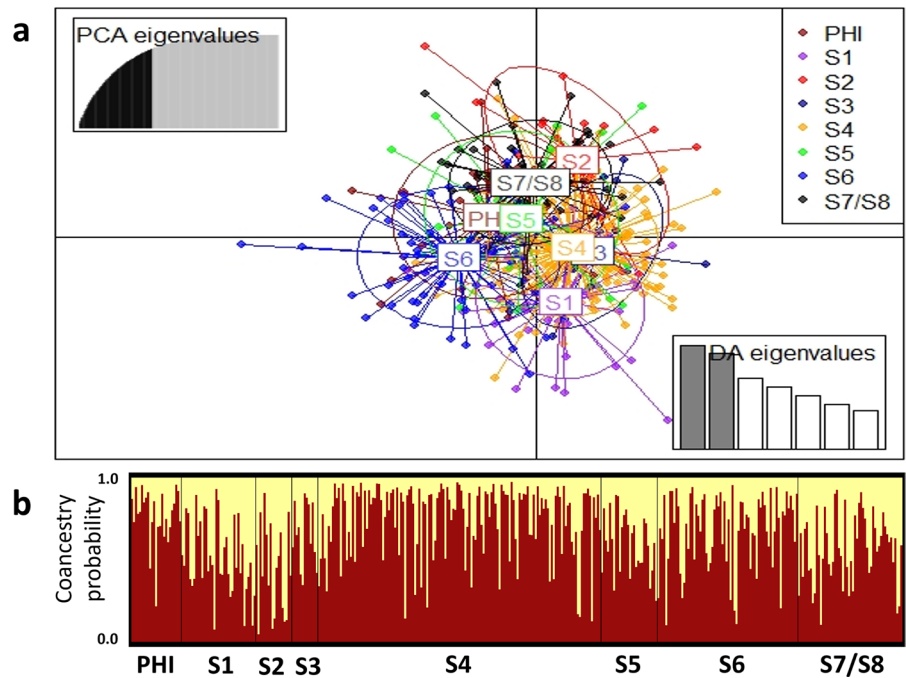
Fig. 4 Comparisons between Ex-ante and Ex-post samples of *Prochilodus magdalenae* from the Cauca River. **a** Results of discriminant analysis of principal components, DAPC; **b** co-ancestry probabilities based on the Bayesian analysis of 658 individuals: 308 Ex-ante (2010–2014), 350 Ex-post (2019–2021)
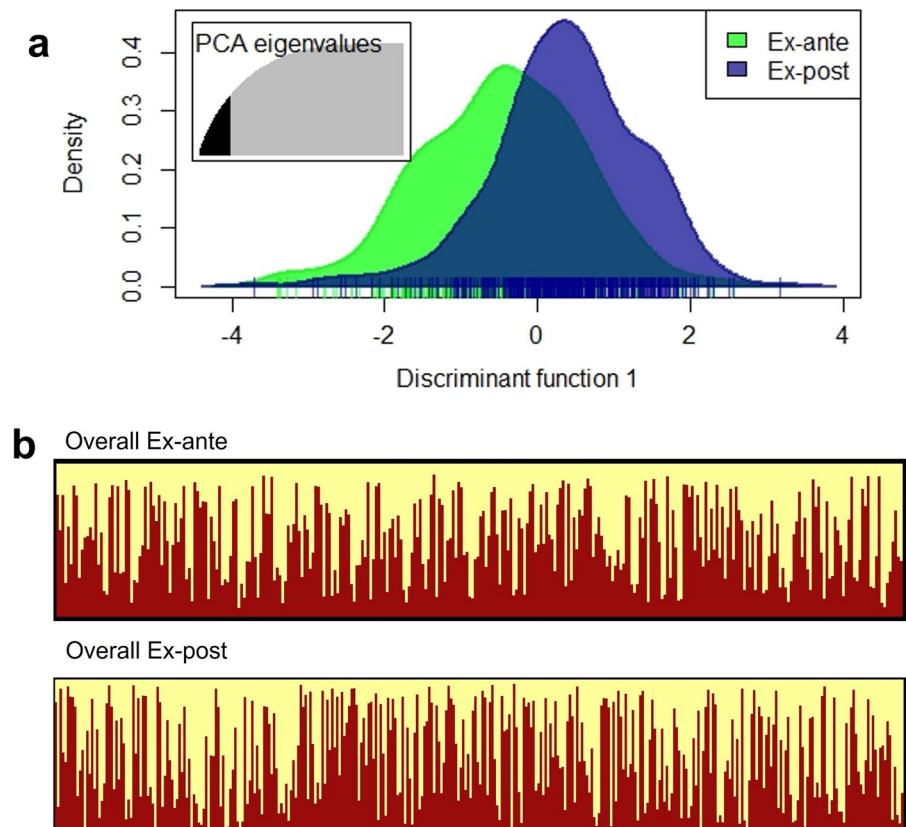
Table 5 Pairwise comparisons of the standardized indices of genetic structure F'_{ST} and Jost´s D_{EST} and their respective P values of temporal samples of *Prochilodus magdalenae* among upstream and downstream sections before (Ex-ante: 2010–2014) and after (Ex-post: 2019–2021) the construction of the Ituango Dam in the Cauca River, Colombia

Population	Period	Upstream vs Downstream			
		F'_{ST}	$P_{F'st}$	D_{EST}	P_{DEST}
Stock1	Ex-ante	0.037	0.082	0.031	0.104
	Ex-post	− 0.011	0.674	− 0.010	0.680
Stock2	Ex-ante	0.035	0.093	0.028	0.124
	Ex-post	0.056	0.047	0.032	0.058

no genetic differences either over space or time (Table 5).

In the Bayesian analysis, the most likely number of populations was estimated as $K=2$ for the *MedMeaK*, *MaxMeaK*, *MedMedK*, and *MaxMedK* estimators, and $K=4$ for ΔK. The histogram of $K=2$ showed the presence of a genetic stock mixture throughout the studied sections in the Cauca River (Fig. 4b).

Discussion

This study used temporal samples to compare population genetics of *Prochilodus magdalenae* before and after construction of a dam in the Cauca River in Colombia to assess genetic impacts attributable to habitat fragmentation. Dam construction often involves water-flow pattern modification and disruption of the dispersal and migration patterns of freshwater fishes, which in turn may impact spatial genetic structure by interruption of gene flow as well as changes in the amount and patterning of genetic variability (Baggio et al., 2018; Tamario et al., 2019). Suitable evaluation of those hypotheses may require temporal approaches that are difficult to achieve in practice, using empirical genetic data to deal with confounding factors related to other habitat disturbances (Schwartz et al., 2007; Epps & Keyghobadi, 2015). Indeed, such studies are few, and results often cannot be generalized due to differing life-history traits of the species or particular habitat conditions (see Beneteau, et al., 2008; Ruzich et al., 2019; Yamamoto et al., 2019; Liu et al., 2020; Vega-Retter et al., 2020).

This study showed no differences in the genetic diversity of *P. magdalenae* in the Cauca River between fragmented sections of the Ex-post sample (period 2019–2021). Moreover, H_E values remained higher than the average for Neotropical characiforms using species-specific microsatellites ($H_E = 0.675$; see Hilsdorf & Hallerman, 2017) and those reported in its congeners *Prochilodus argenteus* Spix & Agassiz 1829 (H_E: 0.690—0.827; Sanches et al., 2012; Melo et al., 2013; Coimbra et al., 2017), *P. costatus* (H_E: 0.490–0.867; Carvalho-Costa et al., 2008; Melo et al., 2013; Pimentel et al., 2020) and *P. lineatus* (H_E: 0.607—0.858; Rueda et al., 2013; Ferreira et al., 2017; Iwersen et al., 2019; Lopera-Barrero et al., 2016, 2019). Such stability in genetic diversity between fragmented sections may be explained not only by large effective population sizes, but also by the small number of generations produced within the short time that elapsed since the fragmentation of the river (Epps & Keyghobadi, 2015; Ruzich et al., 2019). Additionally, no changes were detected with respect to the Ex-ante sample (period 2010–2014), even though most indices in the Ex-post sample are slightly higher. Since the temporal comparisons of genetic diversity of this study are clearly descriptive and depend upon differences in the sample size as well as demographic variation (Landguth et al., 2010; Tallmon et al., 2010), slight temporal differences may be attributed to stochastic effects rather than real genetic changes in the sampled population (Epps & Keyghobadi, 2015). Therefore, *P. magdalenae* has conserved high genetic diversity in the middle and lower parts of the Cauca River, with no obvious changes detected over the short-term.

Despite the high genetic diversity, this species exhibited high heterozygosity deficit in the Ex-post, the same as in the Ex-ante sample from the Cauca River (Landínez-García et al., 2020) and populations from the Magdalena, Atrato, and Sinú rivers (Fontalvo et al., 2018; Landínez-García et al., 2020; Orozco-Berdugo & Narváez-Barandica, 2014). Possible causes of such deficit include the presence of null alleles, Wahlund effect, and endogamy (Waples, 2015). In contrast, factors less likely to contribute involve assortative mating, as *P. magdalenae* exhibits external fertilization and follows a seasonal reproductive strategy that involves group spawning in open areas without parental care (Jiménez-Segura et al., 2010; López-Casas et al., 2016), suggesting a

high likelihood of random fertilization among the co-migrating individuals.

The presence of null alleles is more likely when using amplification of heterologous markers compared to amplification of species-specific markers (Bhargava & Fuentes, 2010; Guichoux et al., 2011). In the case of *P. magdalenae*, both species-specific and heterologous markers have been assessed. Specifically, Landínez-García et al. (2020) and the present study found a lower degree of heterozygote deficit when using species-specific markers compared to heterologous microsatellites designed for *P. lineatus* (Fontalvo et al., 2018; Orozco-Berdugo & Narváez-Barandica, 2014). However, null alleles alone do not explain the significant deficits as they have been observed with both markers. Additionally, some authors have reported minor impacts on genetic differentiation and parentage analyses when using loci with frequencies of null alleles lower than 20% (Chapuis & Estoup, 2007; Huang et al., 2016; Rico et al., 2017).

Alternatively, the heterozygosity deficit may be explained by Wahlund effect due to the coexistence of two genetically distinct populations of *P. magdalenae* in the Cauca River evidenced by some results of genetic structure. However, the persistence of this deficit when analyzing each group separately indicates that inbreeding may explain the high heterozygosity deficit found in this species, as previously reported for this species (Orozco-Berdugo & Narváez-Barandica, 2014; Fontalvo et al., 2018; Landínez-García et al., 2020) and for such other fishes of the Cauca River as *Pimelodus yuma* Villa-Navarro & Acero P. 2017 (Joya et al., 2021) and *Pimelodus grosskopfii* Steindachner 1879 (Restrepo-Escobar et al., 2021). The stocking of highly related individuals is a non-excluding explanation, considering that this species has been a target of restocking efforts in this basin (De La Rosa et al., 2020; Landínez-García et al., 2020; Márquez et al., 2020). Such a high degree of inbreeding is of concern since, according to Franklin (1980) and Soulé (1980), inbreeding values higher than 10% in wild populations may result in adverse fitness and evolutionary effects on the species.

Considering the generalized concept of neutral evolution of microsatellites markers (Oliveira et al., 2006; Putman & Carbone, 2014), the detection of five candidate loci under natural selection for *P. magdalenae* in the floodplain Grande suggests either hitchhiking or background selection (Cutter & Payseur, 2013; Stephan, 2010). Landínez-García et al. (2020) argued that unidirectional gene flow from hatcheries to the wild populations, among other potential anthropogenic factors, could explain the selection signals and the unexpected genetic structure found in *P. magdalenae* in the Magdalena River. Candidate loci under natural selection have also been detected in the characid fish *Curimata mivartii* Steindachner 1878 in Las Culebras, a large floodplain close to Grande, which could be explained by isolation of this site with the Cauca River due to droughts produced by recent ENSO phenomena (Landínez-García & Marquez, 2018). Both unidirectional gene flow and temporal disconnections between floodplain and river could possibly explain the putative selection signals found in the Ex-post sample of *P. magdalenae* of the Cauca River. Although floodplains are essential habitats within the life cycle of fishes of the Magdalena-Cauca basin (Jiménez-Segura et al., 2020), their ecology and human impacts are largely unexplored, limiting the interpretation of these findings.

Demographic estimates showed that the effective population size (N_e) in the Ex-post sample substantially increased in the short-term using the LD method. Given that N_e is often positively correlated with population size, this result may seem contradictory considering the decreasing annual catches of *P. magdalenae* reported over the last 40 years in the Magdalena basin (Mojica et al., 2012; Barreto, 2017) and the genetic evidence of recent bottlenecks (Landínez-García et al., 2020; this study). Although the demographic recovery of this population is likely, an alternative explanation also includes the overestimation of N_e. Since the sampled area belongs to a wider geographic range of the Magdalena-Cauca River basin where this species occurs, the studied population is not a closed system, so N_e can be upwardly biased due to a high and constant rate of migration according to Waples & England (2011), who showed that under a total pool of parents larger than the local size, the estimation can converge on a value that represents the metapopulation effective size. Additionally, the coexistence of two mildly differentiated stocks may also explain such overestimation of the overall N_e, as its estimation assumes absence of genetic structure (Waples & Do, 2010; Waples & England, 2011). However, beyond the likely biased estimation, a higher N_e using the LD

method is expected to reflect a lower inbreeding rate in the wild population (Ryman et al., 2019). Therefore, the large N_e estimated herein would be concordant with the stable inbreeding indices found in the Cauca River over the short term (Martinez et al., 2018).

In contrast, the relatively small N_e estimate obtained using the temporal method may be downwardly biased because of unexpectedly large variance of the allele frequency changes. Likely biasing factors for the temporal method include high gene flow (Ryman et al., 2014), age-structured population (overlapping generations; Waples & Yokota, 2007), and fluctuating population size or non-severe bottleneck, this latter causing allele frequency changes by drift before some alleles are lost (Freeland, 2020). Given the relevance of the N_e for assessing the evolutionary risks of the species in the conservation context, the lower confidence intervals are a useful and more prudent metric to consider in this case (Waples & Do, 2010). Therefore, the lower confidence value estimated in the temporal method close to 500 may suggest long-term risks for maintenance of the evolutionary potential of *P. magdalenae* in the Cauca River (Frankham et al., 2014).

Results of the genetic structure analysis suggested high gene flow throughout the studied length of the Cauca River and the absence of spatial genetic structure even between sections upstream and downstream of the dam. This outcome is partly unexpected, as fragmented populations are subjected to some degree of isolation (Liermann et al., 2012; Epps & Keyghobadi, 2015; Barbarossa et al., 2020), causing differences in allele frequencies between fragmented sections due to genetic drift and bottlenecks, especially upstream of dams (Coleman et al., 2018; Vega-Retter et al., 2020; Yamamoto et al., 2004). Similar findings for gene flow in populations of migratory fishes fragmented by dams have been attributed to factors such as fishways or restocking between fragmented sections, permanence of barrier-free tributaries as alternative routes for migration and short-time periods elapsed since the habitat disturbance (Ribolli et al., 2012; Cheng et al., 2013; Ferreira et al., 2017; Prado et al., 2018; Pimentel et al., 2020). In this case, since the Ituango Dam has no fishways, such structures cannot explain the current gene flow of *P. magdalenae*. However, the recent occurrence of a disturbance on the population might require a number of

generations to manifest (a time lag), which limits the likelihood of detecting genetic changes over the short term (Epps & Keyghobadi, 2015). Additionally, this species has a preexistent high gene flow (Landínez-García et al., 2020) and a wide distribution due to the absence of other geographical barriers in most reaches of the Magdalena basin (López-Casas et al., 2016; Zapata & Usma, 2013), factors that can contribute to the maintenance of its genetic variability (Díez-del-Molino et al., 2013; Epps & Keyghobadi, 2015; Thomaz et al., 2016). Furthermore, dispersal or movement through the dam by translocation can also support gene flow. For instance, the detection of seven individuals collected downstream as likely migrants from upstream sections according to the Bayesian analysis of Geneclass2 (Piry et al., 2004) may indicate movement of individuals through the spillway or discharge tunnel of the dam, sampled individuals that migrated before fragmentation (considering a life cycle > 6 years for *P. magdalenae* in the Cauca River; unpublished data) and drift of larvae from upstream sections, although this last explanation seems unlikely due to the reservoir´s lentic environment (Agostinho et al., 2008). On the other hand, the assignment of one individual collected upstream to downstream sections as its most likely origin place suggests restocking or fish translocation, since such practices might be common in the Magdalena basin (Márquez et al., 2020).

Despite the absence of spatial genetic structure, the coexistence of two genetic stocks of *P. magdalenae*, an outcome common to both temporal samples, may respond to isolation over time (Hendry & Day, 2005) due to the migratory behavior of this species, wherein distinct groups of individuals may migrate during each of the two flood periods of the Cauca River (Jiménez-Segura et al., 2010, 2016; López-Casas et al., 2016). This pattern was also detected in the congener *P. lineatus*, showing three genetic stocks that migrate within the lower basin of the Uruguay River according to three seasonal periods (Rueda et al., 2013). Likewise, two stocks were detected in *P. costatus* within the same reproductive season with high gene flow (Braga-Silva & Galetti, 2016). However, the samples evaluated in this study constitute individuals collected in different years and periods of drought and flood, so this hypothesis must be assessed in further genetic studies that include sampling designs based on the migratory behavior of *P.*

magdalenae. Further, although both stocks showed genetic structure differences over time (as indicated by AMOVA and pairwise genetic indices between temporal samples), no genetic differences were found between fragmented sections (Table 5). Therefore, considering the uncertain biological reasons behind these genetic stocks and the potential impacts of restocking on the analysis of causality performed, this study did not find any apparent short-term effects of population fragmentation.

In conclusion, despite its disrupted migratory route in the Cauca River, *P. magdalenae* retained high genetic diversity in temporal samples, with stable inbreeding values and high gene flow both upstream and downstream of the Ituango Dam. Likely explanations for these outcomes include large effective population size and insufficient time elapsed since fragmentation to give rise to potential changes. Moreover, the slight variations in the frequencies of the stocks, which may result from restocking effects, are not attributable to the dam or any other habitat disturbances, and require further studies to determine the origin and dynamics of the genetic stocks that coexist in the river.

Data availability The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

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