Population genetics of three threatened catfish species in heterogeneous environments of the Cauca River, Colombia

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Neotropical catfishes *Ageneiosus pardalis*, *Pimelodus grosskopfii* and *Sorubim cuspicaudus* are migratory fishes of commercial importance that exhibit decreasing populations due to overfishing and other anthropic interventions. This study used species-specific microsatellite loci to test the hypothesis that threatened fish populations show genetic vulnerability signs and are genetically structured in the middle and lower sections of the Cauca River. The studied species exhibit genetic diversity levels higher than the average values reported for Neotropical Siluriformes; however, they seem to have suffered recent bottlenecks and they present significant endogamy levels that are higher for the critically endangered catfish *P. grosskopfii*. Furthermore, both *Ageneiosus pardalis* and *S. cuspicaudus* are each formed by one genetic group, while *Pimelodus grosskopfii* comprises two coexisting genetic groups. The information obtained in this study is useful for the decision making in management plans that are appropriate for the sustainability of these three species populations within the proposal for the expansion of the hydroelectric development and other anthropic activities.

**Keywords:** Freshwater fish, Genetic diversity, Genetic structure, Microsatellites, Siluriformes.

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Los bagres Neotropicales *Ageneiosus pardalis*, *Pimelodus grosskopfii* y *Sorubim cuspicaudus*, son peces migratorios de importancia comercial cuyas poblaciones han disminuido debido a la sobrepesca y otras intervenciones antrópicas. En este trabajo, se utilizaron loci microsatélites especie-específicos para contrastar la hipótesis de que las poblaciones de peces amenazadas muestran señales de vulnerabilidad genética y están genéticamente estructuradas en los sectores medio y bajo del río Cauca. Las especies estudiadas exhiben niveles de diversidad genética superiores a los promedios reportados para Siluriformes Neotropicales; sin embargo, parecen haber sufrido cuellos de botella recientes y presentan niveles significativos de endogamia que son más altos para el bagre en peligro crítico, *P. grosskopfii*. Además, *Ageneiosus pardalis* y *S. cuspicaudus* están conformados cada uno por un solo grupo genético, mientras que *Pimelodus grosskopfii* comprende dos grupos genéticos que coexisten. La información obtenida en este estudio es útil para la toma de decisiones en planes de manejo que sean adecuados para la sostenibilidad de las poblaciones de estas tres especies de bagre dentro de las propuestas para la expansión de desarrollo hidroeléctrico y otras actividades antrópicas.

**Palabras clave:** Diversidad genética, Estructura genética, Microsatélites, Pez dulceacuícola, Siluriformes.

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**INTRODUCTION**

The Siluriformes order comprises 38 families, 15 of which are exclusively in Central and South America (Ferraris, 2007; Fricke et al., 2020). Six of these families encompass the 86% of the 2347 catfish valid species of Neotropical distribution (Ferraris, 2007; Fricke et al., 2020): Auchenipteridae (125), Callichthyidae (221), Heptapteridae (226), Loricariidae (1000), Pimelodidae (114), and Trichomycteridae (327). These species, known as catfishes, have commercial importance in different regions as nourish source, ornamental fishes or even sport fishing (Usma-Oviedo et al., 2009; Nelson et al., 2016).

Population genetic studies in Neotropical catfishes are centered in members of commercial interest of Pimelodidae (17) family, and in lower proportion, of Loricariidae (6), Trichomycteridae (1), and Heptateridae (2) families. To the date, evidences for gene flow have been found in species that perform medium and large distance migrations during their lifecycle, such as *Brachyplatystoma flavicans* (Coronel et al., 2004), *Brachyplatystoma rousseauxii* (Barista, Alves-Gomes, 2006), *Pimelodus maculatus* (Almeida et al., 2001, 2003; Ramella et al., 2006; Ribolli et al., 2012), *Pseudoplatystoma fasciatum* (Coronel et al., 2004), *Pseudoplatystoma magdalenatium* (Gallo, Diaz-Sarmiento, 2003), *Pseudoplatystoma corruscans* (Dantas et al., 2013; Vaini et al., 2016; Prado et al., 2018), and *Pseudoplatystoma reticulatum* (Vaini et al., 2016; Prado et al., 2018).

Nevertheless, genetic structure of populations of some species has been found and it seems to be explained by various types of behaviors: (1) sedentarism and short-distance migration range in *Steindachneridion parahybae* (Fonseca et al., 2017), *Trichogaster longipinnis* (Zamudio et al., 2009), *Iheringichthys labrosus*, and *Pimelodus cf. absconditus*...
(Almeida et al., 2001); (2) fidelity to breeding or spawning sites (homing) in \textit{P. corruscans} (Pereira et al., 2009), \textit{P. reticulatum} (Abreu et al., 2009), and \textit{Rhamdia quelen} (Rios et al., 2019), and (3) presence of natural or artificial geographical barriers in \textit{P. maculatus} in Paranapanema River (Almeida et al., 2003), \textit{P. corruscans} in Paraná River (Sekine et al., 2002), and between Paraná and São Francisco rivers (Carvalho et al., 2012), and \textit{P. corruscans} and \textit{P. reticulatum} in Paraná and Paraguay rivers (Prado et al., 2018).

Contrary to the majority of population genetics studies in Amazonas and Paraná basins, very few have been performed in Colombian basins, most of which are found in grey literature (see Mancera-Rodríguez et al., 2013; Márquez et al., 2020). For the remaining freshwater catfishes in northwestern South America, there is still unawareness of genetic diversity, demography and population structure which limits the implementation of effective rules for their management and protection.

The latter is important since populations of these species have been affected by overfishing and other indirect effects of anthropogenic activities like mining, dam construction, gravel sand extraction, basins contamination and continuous water extraction for agricultural and livestock purposes, which have led to the decay and decrease of the populations of said species in all Colombian basins (Galvis, Mojica, 2007; Usma-Oviedo et al., 2009; Barletta et al., 2010; Jiménez-Segura et al., 2016).

To contrast the hypothesis that threatened fish populations show genetic vulnerability signs in Cauca River sections exposed to anthropic activities, three catfish species were chosen, with differences in their standard length, migration range and reproductive strategies. \textit{Ageneiosus pardalis} Lütken, 1874, is a medium size species (standard length between 12.83–42.98 cm; Ribeiro et al., 2017), with short-distance migration range (< 100 km), marked sexual dimorphism (Dahl, 1971; Mojica et al., 2012a), elaborated courtship and copulation (Galvis et al., 1997) and distribution from south Panamá to north Venezuela; \textit{Pimelodus grosskopfii} Steindachner, 1879, is a small size species (standard length between 10.17–32.12 cm; Villa-Navarro et al., 2017), with medium migration range (100–500 km), external reproduction, endemic of the Magdalena-Cauca Colombian basin (Mojica et al., 2006; Ortega-Lara et al., 2006), and \textit{Sorubim cuspicanus} Littmann, Burr & Nass, 2000, a medium size species (can reach lengths greater than 80 cm; Littmann et al., 2000), with medium–distance migration range (100–500 km), external reproduction and distribution in the rivers Catatumbo (Ortega-Lara et al., 2012), Magdalena (Mojica et al., 2006; Villa-Navarro et al., 2006), Sinú and Cauca (Littmann et al., 2000) in northwestern South America.

The appointed species are a good model for population genetics analysis since they are exposed to anthropic interventions such as loss of habitats, deforestation, river-course fragmentation, introduction of exotic fish species, contamination and overfishing (Barletta et al., 2010; FAO, 2015; Jiménez-Segura et al., 2016; AUNAP, 2020). The decreasing population density of the three species led to their classification as vulnerable in the Colombian red list of freshwater fishes (Mojica et al., 2012b). Additionally, due to this decline in populations, \textit{P. grosskopfii} was included as a critically endangered threatened species in the red list of threatened species of the International Union for Conservation of Nature – IUCN (Villa-Navarro et al., 2016). Thus, the \textit{a priori} expectation was that the species showed high values of inbreeding and recent bottlenecks, as they are exposed to different anthropic interventions that might affect the density of their populations.
Moreover, the studied area comprises the middle and lower sections of the Cauca River, which includes near 500 km of the main channel of the river, 110 km of torrents and 40,000 ha of swamps. This area also includes the Cauca River canyon, the steepest margin of the Antioqueño Plateau in the northern portion of the Central Cordillera (Restrepo-Moreno et al., 2009), which has been considered a geographic barrier for many fish species (Dahl, 1971). Additionally, this area presents differences in habitats, water speeds, temperatures and it constitutes the influence zone of the Ituango hydroelectric project. In this context, this study also tested the hypothesis that populations of these species, collected before the beginning of the construction of the hydroelectric, were genetically structured. The a priori expectation was that the environmental heterogeneity of the zone caused genetic structuration. The answer to these queries generates information of interest to propose rules of management and conservation, suitable for the preservation of natural populations of these fish species.

MATERIAL AND METHODS

A total of 492 preserved in alcohol muscle tissues of *A. pardalis* (193), *P. grosskopfii* (170), and *S. cuspicaudus* (129) were analyzed. Said tissues were provided by Integral S.A through the scientific cooperation agreement CT–2013–002443, framed in the environmental license of Ministerio de Ambiente, Vivienda y Desarrollo Territorial # 0155 of January 30th, 2009. Samples were collected between 2011–2014 in the middle (sections S1–S4) and lower (sections S5–S8) sections of the Cauca River, located upstream (S1) and downstream (S2–S8) of the construction zone of Ituango hydroelectric project (Fig. 1; Tab. 1). The middle section of the Cauca River encompasses the Cauca River canyon, characterized by a steep topography with the presence of rapid zones (S1–S3) followed by a vast alluvial plain surrounded by mountains, with swamp ecosystems connected with the main river channel (S4). The section S5 includes the mouth of the Nechí River, a hydrologically monomodal river prone to flooding and scouring, and the remaining lower section (S6–S8) shows soft topography with flat and wavy surfaces wherein several swamps connected to rivers through canals are formed, conforming complex swampy systems (Mejía-Rivera et al., 2007; Betancur-Vargas et al., 2009).

DNA extraction was performed with the commercial kit PureLink® Genomic DNA (ThermoFisher Scientific), following the instructions of the manufacturer. PCR conditions previously described by Landínez-García, Marquez (2016, 2018) were employed to amplify between 13 and 20 microsatellite loci for *A. pardalis* (Apar03, Apar04, Apar05, Apar11, Apar12, Apar14, Apar18, Apar19, Apar20, Apar21, Apar22, Apar23, Apar25, Apar27, Apar28, Apar30, Apar32, Apar34, Apar35, Apar36); *P. grosskopfii* (Pgrk01, Pgrk02, Pgrk03, Pgrk08, Pgrk10, Pgrk14, Pgrk15, Pgrk19, Pgrk24, Pgrk27, Pgrk28, Pgrk31, Pgrk40), and *S. cuspicaudus* (Scus03, Scus10, Scus12, Scus15, Scus16, Scus17, Scus18, Scus20, Scus21, Scus22, Scus23, Scus24, Scus25, Scus28, Scus32, Scus35, Scus39, Scus40, Scus41; Restrepo-Escobar, Marquez, 2020). PCR products were separated in an automatic sequencer ABI 3130 (Applied Biosystems, USA) using GeneScan–500 LIZ dye size standard (Applied Biosystems, USA) as internal marker and the allelic fragments were denoted according to their molecular size and scored using GeneMapper (Applied Biosystems, USA). Before the statistical analysis, the Micro-
FIGURE 1 | Location of sampling sites of *Pimelodus grosskopfii*, *Sorubim cuspicaudus*, and *Ageneiosus pardalis* in the middle and lower sections of the Cauca River.

TABLE 1 | Number of individuals of *Pimelodus grosskopfii*, *Sorubim cuspicaudus*, and *Ageneiosus pardalis* analyzed in the middle and lower basin of the Cauca River. S1–S4: Middle section of the Cauca River, S1 and S2–S4 are located upstream and downstream of the construction zone of the dam, respectively. S5–S8: Lower section of the Cauca River.

| Sections | *P. grosskopfii* | *S. cuspicaudus* | *A. pardalis* |
|----------|-----------------|-----------------|--------------|
| S1       | 44              | –               | –            |
| S2/S3    | 25              | 19              | –            |
| S4       | 18              | 22              | –            |
| S5       | 26              | 43              | 45           |
| S6       | 35              | 25              | 84           |
| S7/S8    | 22              | 20              | 64           |
| Total    | 170             | 129             | 193          |
Checker v2.2.1 software (Van Oosterhout et al., 2004) was used to detect possible genotyping errors. For samples of each studied section and genetic group, it was determined the genetic diversity calculating the expected and observed heterozygosities and the average number of alleles per locus with GenAlex v6.502 software (Peakall, Smouse, 2012). Additionally, the Arlequin v3.5.2.2 software (Excoffier, Lischer, 2010) was employed to test departures of the Hardy–Weinberg equilibrium, linkage equilibrium and calculate the inbreeding coefficient ($F_{IS}$) by population. In multiple comparisons, the statistical significance was adjusted by the Bonferroni sequential correction (Rice, 1989). Finally, two tests were used to determine whether the populations of these species have suffered a recent genetic bottleneck, the one-tailed test of Wilcoxon (Luikart, Cornuet, 1998), and M ratio of Garza, Williamson (2001) calculated respectively in Bottleneck v1.2.02 software (Piry et al., 1999) and the Arlequin v3.5.2.2. program (Excoffier, Lischer, 2010).

To determine the number of possible genetic groups for *A. pardalis*, *P. grosskopfii*, and *S. cuspicaudus* in the middle and lower basins of the Cauca River, it was used different complementary approaches. The Bayesian clustering method with STRUCTURE v2.3.4 software (Pritchard et al., 2000) used the following conditions: 100000 MCMC, 10000 burn-in, admixture model, correlated allele frequency, and LOCPRIOR option. Simulations were repeated 20 times per each number of evaluated probable populations: 1–6 for *A. pardalis*, 1–8 for *S. cuspicaudus*, and 1–9 for *P. grosskopfii*. The most probable number of population was calculated using the ΔK method (Evanno et al., 2005) and the estimators MedMedK, MedMeaK, MaxMedK, and MaxMeaK (Puechmaille, 2016) with the web-based software STRUCTURESELECTOR (Li, Liu, 2018). The STRUCTURE results were summarized using the integrated software CLUMPAK (Kopelman et al., 2015) to generate a graphical representation of the results. Wherein STRUCTURE detected different genetic groups, the allocation of each individual to each group was determined by the coancestry coefficient from the Q-matrix generated by CLUMPAK (Kopelman et al., 2015) from the 20 simulations produced by STRUCTURE. Moreover, the genetic differentiation of each of the species among sectors of the Cauca River was calculated with the Analysis of Molecular Variance AMOVA and the standardized estimators $F_{ST}$ (Meirmans, 2006) and Jost’s Dest (Meirmans, Hedrick, 2011) using the GenAlex v6.502 software (Peakall, Smouse, 2012), and a Discriminant Analysis of Principal Components (DAPC) was performed using the package adegenet (Jombart, 2008) for R v3.4.0 program (R Development Core Team, 2017).

RESULTS

The sampling performed by Integral S.A. between 2011–2014 revealed that *A. pardalis*, *P. grosskopfii*, and *S. cuspicaudus* were differentially distributed in the middle and lower sections of the Cauca River. Namely, and despite having the same migration range, *P. grosskopfii* was found in all sampled sites, including upstream of the Cauca River canyon, whereas *S. cuspicaudus* was found in the downstream area of Cauca River canyon and the construction zone of the dam (S3–S8). In contrast, short-distance migration range *A. pardalis* was only captured in the lower basin of the river (S5–S8; Tab. 1).
Genetic diversity and population demographics. *Pimelodus grosskopfii* showed similar or nearly similar genetic diversity values in all evaluated sections (Na=10.308–13.308; He=0.849–0.866; Ho=0.607–0.682) and in the genetic groups proposed by the genetic structure analysis described below (Na=12.846–16.615; He=0.858–0.866; Ho=0.614–0.664; Tab. 2), further to statistical significance in heterozygosity deficit and inbreeding coefficients (F<sub>IS</sub>=0.108–0.218; P<0.000; Tab. 2).

Likewise, *S. cuspicaudus* exhibited similar values of genetic diversity within the analyzed sections (Na=8.105–9.368; He=0.771–0.785; Ho=0.745–0.795; Tab. 2); however, in this case the genotypic frequencies behaved according to Hardy-Weinberg equilibrium except from S5 wherein the heterozygosity deficit was significant. Moreover, the inbreeding coefficient was significant in S5 (F<sub>IS</sub>=0.045; P=0.026) and S8 (F<sub>IS</sub>=0.058; P=0.032; Tab. 2).

In accordance with the other two species, *A. pardalis* showed similar genetic diversity values (Na=10.850–12.550; He=0.832–0.839; Ho=0.791–0.822; Tab. 2); statistical significance in heterozygosity deficits and coefficients of inbreeding in all the evaluated samples (F<sub>IS</sub>=0.026–0.086; P<0.007) although in lesser magnitude than in *P. grosskopfii* (Tab. 2).

| TABLE 2 | Genetic diversity, M-ratio estimator and bottleneck for populations and genetic groups of *Pimelodus grosskopfii*, *Sorubim cuspicaudus*, and *Ageneiosus pardalis* in the middle and lower sections of the Cauca River. N: Number of analyzed individuals, Na: Average number of alleles/locus, Ho: Observed heterozygosity, He: Expected heterozygosity, P: statistical significance of Hardy-Weinberg equilibrium; F<sub>IS</sub>: inbreeding coefficient, M-ratio: M estimator of Garza, Williamson (2001), IAM: infinite alleles model, TPM: two phase model, SMM: stepwise model. Values in bold denote statistical significance. |
| N  | Na | Ho     | He     | P     | F<sub>IS</sub> | M-ratio | IAM   | TPM   | SMM   |
|----|----|--------|--------|-------|-------------|---------|-------|-------|-------|
| **Pimelodus grosskopfii** | | | | | | | | | |
| S1 | 44 | 13.308±1.184 | 0.682±0.020 | 0.863±0.015 | 0.000 | 0.147 | 0.217±0.049 | 0.000 | 0.003 | 0.342 |
| S2/S3 | 25 | 11.615±0.675 | 0.679±0.062 | 0.870±0.012 | 0.000 | 0.157 | 0.224±0.057 | 0.000 | 0.000 | 0.317 |
| S4 | 18 | 10.308±0.728 | 0.660±0.068 | 0.823±0.013 | 0.000 | 0.178 | 0.197±0.054 | 0.000 | 0.000 | 0.064 |
| S5 | 26 | 12.462±0.991 | 0.618±0.061 | 0.866±0.011 | 0.000 | 0.177 | 0.201±0.058 | 0.000 | 0.001 | 0.527 |
| S6 | 35 | 12.385±0.984 | 0.607±0.051 | 0.835±0.014 | 0.000 | 0.186 | 0.215±0.045 | 0.000 | 0.000 | 0.847 |
| S7/S8 | 22 | 11.538±1.029 | 0.666±0.055 | 0.849±0.017 | 0.000 | 0.199 | 0.227±0.048 | 0.000 | 0.040 | 0.526 |
| Genetic group 1 | 64 | 12.846±1.061 | 0.614±0.050 | 0.858±0.017 | 0.000 | 0.218 | 0.225±0.061 | 0.000 | 0.000 | 0.987 |
| Genetic group 2 | 106 | 16.615±1.583 | 0.664±0.050 | 0.866±0.011 | 0.000 | 0.108 | 0.212±0.046 | 0.000 | 0.000 | 0.936 |
| **Sorubim cuspicaudus** | | | | | | | | | |
| S3 | 19 | 8.105±0.501 | 0.767±0.029 | 0.774±0.020 | 0.814 | 0.018 | 0.229±0.053 | 0.000 | 0.000 | 0.928 |
| S4 | 22 | 8.316±0.536 | 0.788±0.023 | 0.771±0.024 | 0.352 | -0.065 | 0.248±0.068 | 0.000 | 0.176 | 0.922 |
| S5 | 43 | 9.368±0.613 | 0.745±0.028 | 0.783±0.020 | 0.000 | 0.045 | 0.258±0.049 | 0.000 | 0.020 | 0.973 |
| S6 | 25 | 8.684±0.484 | 0.795±0.024 | 0.783±0.019 | 0.412 | -0.045 | 0.253±0.063 | 0.000 | 0.129 | 0.916 |
| S7/S8 | 20 | 8.263±0.561 | 0.745±0.028 | 0.785±0.017 | 0.124 | 0.058 | 0.257±0.055 | 0.001 | 0.078 | 0.675 |
| **Ageneiosus pardalis** | | | | | | | | | |
| S5 | 45 | 10.850±0.559 | 0.772±0.039 | 0.832±0.017 | 0.000 | 0.086 | 0.242±0.046 | 0.000 | 0.007 | 0.249 |
| S6 | 84 | 12.550±0.755 | 0.791±0.027 | 0.839±0.015 | 0.000 | 0.060 | 0.240±0.042 | 0.000 | 0.002 | 0.607 |
| S7/S8 | 64 | 11.950±0.630 | 0.822±0.021 | 0.839±0.014 | 0.000 | 0.026 | 0.245±0.043 | 0.000 | 0.000 | 0.892 |
The analysis for detecting bottleneck showed significant values for all the species in the evaluated sections under the IAM, while no significance was found under the SMM and the TPM showed significance in all or almost all of the evaluated sections in *A. pardalis*, *P. grosskopfii* (except S8), and *S. cusicaudus* (except S4, S6, and S7/8). Additionally, the three species showed values of the M ratio of Garza, Williamson, (2001) lower than 0.680 (*P. grosskopfii*: 0.197–0.227; *S. cusicaudus*: 0.229–0.258; *A. pardalis*: 0.242–0.245; Tab. 2), which has been proposed as limit value for inferring that the population has suffered a recent decline in population (Garza, Williamson, 2001).

**Genetic structure analysis.** In the distribution range of the evaluated samples in middle and lower sections of the Cauca River, the Bayesian analysis of STRUCTURE showed the homogeneous distribution of two coexisting genetic groups in *P. grosskopfii* (K=2; MedMedK=2; MedMeanK=2; MaxMedK=2; MaxMeanK=2; Fig. 2A), one genetic group in *S. cusicaudus*, wherein each individual exhibits a similar genetic admixture of two biological groups (K=2; MedMedK=1; MedMeanK=1; MaxMedK=2; MaxMeanK=2; Fig. 2B), and one main genetic group with some genetic admixture in *A. pardalis* (ΔK=2; MedMedK=1; MedMeanK=1; MaxMedK=1; MaxMeanK=1; Fig. 2C).

The homogeneous distribution of the genetic groups of *P. grosskopfii* (FST: 0.004, P: 0.075), *S. cusicaudus* (FST: 0.003, P: 0.084) and *A. pardalis* (FST: 0.001, P: 0.066) in the middle and lower sections of the Cauca River was corroborated by AMOVA, the pairwise comparisons with standardized estimators F’ST and Dest (Tab. 3), and DAPC (Figs. 2D–F).

**FIGURE 2** | Population structure suggested by STRUCTURE (A–C) and the Discriminant Analysis of the Principal Components (D–F) for *Pimelodus grosskopfii* (A, D), *Sorubim cusicaudus* (B, E), and *Ageneiosus pardalis* (C, F).
**TABLE 3** | Statistical values $F_{ST}$ and Dest by pairs of the *Pimelodus grosskopfii*, *Sorubim cuspicaudus*, and *Ageneiosus pardalis* populations in middle and lower sections of the Cauca River.

|                  | $F_{ST}$ (P) | Dest (P) |
|------------------|-------------|----------|
| **Pimelodus grosskopfii** |
| S1–S2/S3         | 0.010 (0.502) | -0.004 (0.543) |
| S1–S4            | 0.013 (0.432) | -0.002 (0.504) |
| S1–S5            | 0.012 (0.095) | 0.027 (0.098) |
| S1–S6            | 0.009 (0.276) | 0.008 (0.284) |
| S1–S7/S8         | 0.013 (0.123) | 0.027 (0.123) |
| S2/S3–S4         | 0.018 (0.332) | 0.010 (0.332) |
| S2/S3–S5         | 0.012 (0.831) | -0.028 (0.829) |
| S2/S3–S6         | 0.013 (0.215) | 0.019 (0.219) |
| S2/S3–S7/S8      | 0.018 (0.041) | 0.055 (0.014) |
| S4–S5            | 0.015 (0.649) | -0.018 (0.666) |
| S4–S6            | 0.014 (0.635) | -0.013 (0.656) |
| S4–S7/S8         | 0.019 (0.169) | 0.033 (0.177) |
| S5–S6            | 0.012 (0.361) | 0.007 (0.352) |
| S5–S7/S8         | 0.017 (0.037) | 0.052 (0.037) |
| S6–S7/S8         | 0.016 (0.037) | 0.050 (0.036) |
| **Sorubim cuspicaudus** |
| S3–S4            | 0.015 (0.180) | 0.014 (0.186) |
| S3–S5            | 0.010 (0.531) | -0.003 (0.555) |
| S3–S6            | 0.014 (0.208) | 0.010 (0.217) |
| S3–S7/S8         | 0.012 (0.837) | -0.017 (0.838) |
| S4–S5            | 0.009 (0.562) | -0.002 (0.546) |
| S4–S6            | 0.012 (0.298) | 0.007 (0.298) |
| S4–S7/S8         | 0.015 (0.146) | 0.017 (0.150) |
| S5–S6            | 0.010 (0.159) | 0.010 (0.159) |
| S5–S7/S8         | 0.009 (0.665) | -0.006 (0.679) |
| S6–S7/S8         | 0.011 (0.774) | -0.011 (0.785) |
| **Ageneiosus pardalis** |
| S5–S6            | 0.005 (0.615) | -0.003 (0.624) |
| S5–S7/S8         | 0.007 (0.120) | 0.008 (0.127) |
| S6–S7/S8         | 0.005 (0.029) | 0.011 (0.029) |

**DISCUSSION**

This study employed species-specific microsatellite *loci* to acknowledge the level of genetic diversity, demographic status and genetic structure degree of three species of Colombian endemic Neotropical catfishes that coexist in the middle and lower sections of the Cauca River basin. The *a priori* expectation was that the species showed high values of inbreeding and recent bottlenecks as they are subject of different anthropic interventions that might affect the density of their populations. Furthermore, it was expected a population genetic structure concordant with some heterogeneous features of the basin.
Genetic diversity and population demography. The three studied species showed higher levels of genetic diversity than the average values reported for Neotropical catfishes (Na=7.470, He=0.609; revision of Hilsdorf, Hallerman, 2017) although *S. cuspicaudus* showed lower diversity (Na=8.547, He=0.779) than *A. pardalis* (Na=11.783, He=0.835) and *P. grosskopfii* (Na=11.143, He=0.847).

The average expected heterozygosity values in the three species were higher than in other Neotropical catfishes such as *T. longipinnis* (He=0.393, Zamudio et al., 2009), *S. parahybae* (He=0.470, Fonseca et al., 2017), *P. reticulatum* (He=0.498–0.751, Abreu et al., 2009; Vaini et al., 2016), and *P. corruscans* (He=0.709–0.760, Pereira et al., 2009; Dantas et al., 2013; Vaini et al., 2016). Nonetheless, the genetic diversity observed in this study was lower than those found in *R. quelen* (He=0.614–0.909, Ríos et al., 2017; 2019), *P. punctifer* (He=0.783, Telles et al., 2014), *P. corruscans* (He=0.862, Prado et al., 2017), and *P. maculatus* (He=0.871, Ribolli et al., 2012).

In *S. cuspicaudus*, genotypic frequencies were distributed according to Hardy-Weinberg equilibrium and the inbreeding values were not significant save for sections S5 and S8 in which values lower than 10% suggest a careful management to prevent adverse effects regarding fitness (Frankham et al., 2014). On the contrary, and despite their high genetic diversity, *A. pardalis* and *P. grosskopfii* exhibited a heterozygosity deficit that cannot be explained by the Wahlund effect in the only genetic group formed by *A. pardalis* nor in each of the two genetic groups of *P. grosskopfii* that co-migrate in the studied area, wherein the heterozygosity deficit stayed significant.

Unlike *P. grosskopfii*, which has external reproduction (Loir et al., 1989), the assortative mating can explain the heterozygosity deficit in *A. pardalis* since it has internal insemination and elaborated courtships (Galvis et al., 1997) and the females store spermatozoa inside their ovaries (Contreras et al., 2012). However, to verify this hypothesis, it remains necessary to further research the reproductive behavior of these species.

Alternatively, the heterozygosity deficit could be explained by inbreeding as *A. pardalis* (2.600–8.600%) and *P. grosskopfii* (10.800–21.800%) showed significant $F_{IS}$ values. This effect may result from different anthropic activities like overfishing due to diminishments in captures since 1994 (Jiménez-Segura, Villa-Navarro, 2011) and their presence in the first 10 species captured for the Magdalena-Cauca basin (AUNAP, 2020). Other factor that could negatively contribute to the studied catfish species is the contamination in basins caused by mining as in the studied zone there is gold, silver, and platinum extraction (UPME, 2019), and there is evidence of mercury bioaccumulation, a residual contaminant of this activity, in several species that cohabit in the zone (Marrugo-Negrete et al., 2008; Álvarez et al., 2012).

All those factors above mentioned may explain the recent decline in populations suggested by bottlenecks in the three studied species, supporting the hypothesis of genetic vulnerability of fishes due to anthropic interventions. A non-excluding alternative considers the climate factor as an additional influence of the demographic aspects of the populations of these species. Extreme changes in the Cauca River flow as consequences of the climatic phenomenon *El niño-Southern Oscillation* (ENSO) presented in the region in the prior years, wherein since 2007 there has been extreme NIÑA (2007–2008 and 2010–2011) and NIÑO (2009–2010, Hoyos et al., 2013) phenomena, could have caused bottlenecks as described in the same region for *Curimata mivartii* (Landínez-
This climate factor could contribute to bottlenecks phenomena associated to overfishing, which has been described for other Neotropical catfishes as *P. corruscans*, *P. reticulatum*, and *B. flavigans* (Coronel et al., 2004; Prado et al., 2018).

**Genetic structure analysis.** This study did not find significant differences among individuals of middle and lower sections of the Cauca River, which indicates that the environmental heterogeneity of the basin and, in particular, the steep slope of the Cauca River canyon is not a barrier for the gene flow of *P. grosskopfii*. However, such slope seems to limit of dispersion of *S. cuspicaudus* and *A. pardalis* in the middle section of the Cauca River since no individuals of these species were captured in the higher sections of the studied area in the sampled period (2011–2014). This result is not surprising for a short migrator like *A. pardalis*; nonetheless, the spatial distribution differed in the middle range migrators *S. cuspicaudus* and *P. grosskopfii*, suggesting that besides from their migration range, other factors as body conformation, habitat preferences and behavior, can play an important role in the observed spatial distribution, which is an important approach for future researches. A strong limitation to spatial distribution by the Cauca River canyon is also observed in *Pseudopimelodus atricaudus*, a new species described in the lower section of the Cauca River that diverged about 16 mya from its congener *P. magnus* distributed upstream the Cauca River canyon (Rangel-Medrano et al., 2020; Restrepo-Gómez et al., 2020).

In the spatial distribution analyzed for each species, the Bayesian analysis of STRUCTURE, the DAPC, the AMOVA and the pairwise distances showed absence of geographic population structure in the studied species. These results concord with the ones described for other Neotropical catfishes that perform medium and large distance migrations as *P. maculatus* (Almeida et al., 2001, 2003; Ribolli et al., 2012), *B. flavigans* (Coronel et al., 2004), *B. rousseauxii* (Batista, Alves–Gomes, 2006), *P. corruscans* and *P. reticulatum* (Vaini et al., 2016; Prado et al., 2018). Nevertheless, our results with *A. pardalis* and *S. cuspicaudus* contrast with the results for *P. corruscans* in the basin of rivers Paraguay and Paraná wherein the authors hypothesize a possible homing behavior for the species (Pereira et al., 2009; Dantas et al., 2013).

Distinct from *A. pardalis* and *S. cuspicaudus*, each formed by one genetic group, *P. grosskopfii* represented two coexisting genetic groups in the evaluated sections of the Cauca River. This result in *P. grosskopfii* could reflect a possible spatial reproductive isolation, considering the preference for reproductive sites (homing) described for other species of Pimelodidae family as *B. rousseauxii* (Batista, Alves–Gomes, 2006), *P. corruscans* (Pereira et al., 2009; Dantas et al., 2013), and *P. reticulatum* (Abreu et al., 2009). Another non-excluding alternative is that *P. grosskopfii* experiences temporary reproductive isolation as the Cauca River presents two hydrological periods of shallow and deep waters that could benefit two reproductive periods of the fish species that habit this basin (Jiménez-Segura et al., 2010; López-Casas et al., 2016). This explanation is supported in the observation of a greater number of individuals of *P. grosskopfii* participating in the migration during the first period compared to the second hydrological period of the Magdalena River (López–Casas et al., 2016). Despite the latter, to the date, there is no detailed information as per the reproductive periods and behaviors of *P. grosskopfii* that allows to elucidate the origin of the genetic groups.

Under this context, it is recommended that the information obtained in this study
regarding the structure and diversity of three coexisting species of catfishes in the middle and lower sections of the Cauca River is considered within the expansion proposals of the hydroelectric development for Colombia (Angarita et al., 2018) and of other anthropic activities. The higher values of the inbreeding coefficient were found for *P. grosskopfii*, included in 2016 as a critical danger species in the red list of the International Union for Conservation of Nature – IUCN (Villa-Navarro et al., 2016), for which it is necessary to enforce the proposed measures for the recovery and conservation of natural populations of the species. Despite the inbreeding values found for *S. cuspicaudus* and *A. pardalis* are lower than 10%, which is the suggested limit to avoid substantial losses in the reproductive features (Soulé, 1980), it is advisable to continue monitoring these populations to evaluate the changes of the species over time since it has been indicated that inbreeding values higher than zero ($F_{IS} > 0$) can cause negative effects in the fitness of natural populations (Frankham et al., 2014).

In conclusion, employing species-specific microsatellite loci, this study determined the diversity and possible genetic structure in the middle and lower sections of the Cauca River for the Neotropical catfishes *A. pardalis*, *P. grosskopfii* and *S. cuspicaudus*. The genetic diversity levels of the three species (expected heterozygosity and number of alleles/locus) are high; however, all the studied species seem to have suffered recent bottlenecks and exhibit significant inbreeding values, which are greater for *P. grosskopfii*, currently in a higher risk category. Furthermore, *P. grosskopfii* shows the coexistence of two genetic groups while *A. pardalis* and *S. cuspicaudus* are mainly represented by a genetic group. Contrary to the expectations, none of the evaluated species showed population structure related to some heterogeneous features of the basin. It was also evidenced that the cannon of the Cauca River in this zone does not represent a barrier to the gene flow of *P. grosskopfii* but it seems to limit the dispersion of *A. pardalis* and *S. cuspicaudus*.

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**AUTHOR’S CONTRIBUTION**

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**ETHICAL STATEMENT**

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COMPETING INTERESTS
The authors declare no competing interests.

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