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ARTICLE

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Contrasts in riverscape patterns of intraspecific genetic variation in a diverse Neotropical fish community of high conservation value

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Spatial patterns of genetic variation compared across species provide information about the predictability of genetic diversity in natural populations, and areas requiring conservation measures. Due to their remarkable fish diversity, rivers in Neotropical regions are ideal systems to confront theory with observations and would benefit greatly from such approaches given their increasing vulnerability to anthropogenic pressures. We used SNP data from 18 fish species with contrasting life-history traits, co-sampled across 12 sites in the Maroni– a major river system from the Guiana Shield –, to compare patterns of intraspecific genetic variation and identify their underlying drivers. Analyses of covariance revealed a decrease in genetic diversity as distance from the river outlet increased for 5 of the 18 species, illustrating a pattern commonly observed in riverscapes for species with low-to-medium dispersal abilities. However, the mean within-site genetic diversity was lowest in the two easternmost tributaries of the Upper Maroni and around an urbanized location downstream, indicating the need to address the potential influence of local pressures in these areas, such as gold mining or fishing. Finally, the relative influence of isolation by stream distance, isolation by discontinuous river flow, and isolation by spatial heterogeneity in effective size on pairwise genetic differentiation varied across species. Species with similar dispersal and reproductive guilds did not necessarily display shared patterns of population structure. Increasing the knowledge of specific life history traits and ecological requirements of fish species in these remote areas should help further understand factors that influence their current patterns of genetic variation.

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INTRODUCTION

Genetic diversity has long been acknowledged as an essential aspect of biodiversity (Pereira et al. 2013) and a critical support to the resilience of individuals (Dobzhansky 1965), populations (Frankham 1995), and communities (Crutsinger 2016). A loss of genetic diversity could have irreversible impacts on populations (Allendorf et al. 2008) and genetic monitoring is crucial for managing them. Despite analytical and technical issues challenging the integration of genetic information into conservation practices (Hoban et al. 2021), researchers are pursuing efforts to understand the evolution of molecular data for a variety of taxa. Collecting genetic information at several levels of organization (populations, species, communities) can help to understand evolutionary processes that occur in the wild (Vellend and Geber 2005). Multispecies databases are increasingly developed to georeference new molecular markers or samples collected at various spatio-temporal scales (Deck et al. 2017). Comparative population genetics is an emerging field with promising applications for conservation (Pauls et al. 2014; Leigh et al. 2021).

Comparing the evolutionary trajectories between species (comparative phylogeography) can reveal long-term processes that influenced their current patterns of genetic variation (Jenkins et al. 2018). Similarly, comparing patterns of genetic variation across species that live in sympatry (or share landscape features) has provided insights into the landscape-related factors that influence them (DeWoody and Avise 2000; Paz-Vinas et al. 2015; Selkoe et al. 2016). For instance, riverscape topography is known to influence patterns of genetic diversity strongly in fish populations (Prunier et al. 2017a). Indeed, river networks typically display a fractal, "dendritic" structure (*dendritic ecological network* DEN; Campbell Grant et al. 2007) where primary streams and confluences show higher connectivity within the network than peripheral areas like headwaters. This causes a heterogeneous spatial repartition of genetic diversity in relation to the network complexity because genetic diversity tends to accumulate within highly-connected areas at migration-drift equilibrium (Paz-Vinas and Blanchet 2015; Thomaz et al. 2016). Furthermore, empirical observations from strictly freshwater species frequently reported higher local genetic diversity in downstream, highly-connected

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areas than in upstream headwaters (Chaput-Bardy et al. 2009; Paz-Vinas et al. 2015).

Subsidiarily to the network properties per se, downstream-biased migration, greater downstream habitat availability, or upstream-directed colonization with successive founder effects were suggested as potential evolutionary processes generating such pattern of a *downstream increase in genetic diversity* (DIGD) (Paz-Vinas et al. 2015). Species with low-to-medium dispersal abilities are also more likely to be influenced by network properties and to show DIGD (Paz-Vinas and Blanchet 2015), since gene flow is restricted further by the topography of the river network.

However, many biological or environmental factors can also modify this general, expected pattern of genetic variability, leading to idiosyncratic patterns that challenge the predictability of spatial genetic variation in natural populations. Notably, particular non-equilibrium processes, specific colonization routes, or environmental constraints that decrease effective population size (N_e) locally can alter expected spatial patterns such as DIGD (Salisbury et al. 2016; Pilger et al. 2017; Richmond et al. 2018). Interactions among local (e.g., water quality) or regional (e.g., DEN properties) riverscape features, species' life history traits and their evolutionary trajectories are complex (Pilger et al. 2017; Paz-Vinas et al. 2018). Their relative influence on patterns of genetic variation is not completely understood (Ruzzante et al. 2019; Blanchet et al. 2020), and it remains unclear how diverse these patterns might actually be across a range of co-distributed species belonging to the same clade.

Several meta-analysis studies have compared patterns of spatial genetic variation between species at large geographical scales, aggregating previously published datasets (e.g., DeWoody and Avise 2000; Paz-Vinas et al. 2015; Lino et al. 2018). These approaches provide a dense multi-taxa overview of drivers of genetic variability in the wild (Leigh et al. 2021). Another more-recently widening approach is based on the simultaneous sampling of several co-distributed species. This co-sampling can be used to directly compare species with a variety of ecological characteristics (Selkoe et al. 2014; Leigh et al. 2021) from a common environment. Overall, comparative approaches can identify common patterns of genetic variation shared by most species or, conversely, reveal species showing atypical patterns. Comparing patterns of genetic variation among co-distributed species can also reveal spatial hot- or coldspots of genetic diversity (Paz-Vinas et al. 2018) and provide information about species' vulnerabilities to localized anthropogenic pressures (Blanchet et al. 2010), with direct applications for management policies. However, because sampling multiple species simultaneously is often logistically and technically burdensome, most co-sampling studies to-date have included a limited number of species (<10). The lack of available molecular markers also hinders collection of multi-species datasets (Horne 2014).

Neotropical freshwater habitats harbor a high specific and functional ichthyodiversity (Abell et al. 2008), with more than 5600 species described to-date. Coastal rivers in the Guiana Shield are smaller than in other Neotropical regions, yet contain similar habitats and exceptional ichthyodiversity. The Maroni is one of its most speciose basins, with 264 strictly freshwater fish species, of which 16.9% are considered endemic (Le Bail et al. 2012; see also Papa et al. 2021 suggesting 25 additional cryptic species using molecular data). This unique biodiversity heritage provides cultural and commercial resources for an expanding community of native people (Longin et al. 2021a;b). However, its intraspecific facet remains poorly documented (Hilsdorf and Hallerman 2017) and genetic diversity and conservation status of most species remain unknown, even though these ecosystems are experiencing increasing anthropogenic pressures (Reis et al. 2016; Longin et al. 2021b).

Here we used genotypic data obtained for 18 native, co-distributed fish species in the Upper Maroni (French Guiana) during a conservation program led by the Parc Amazonien de Guyane in collaboration with local fishermen. We aimed at examining and comparing spatial patterns of genetic variation across species in order to reveal areas of potential conservation interest (i.e., hot- or coldspots of genetic diversity) across the Upper Maroni, to evaluate if genetic structure could be explained by factors such as riverscape distance, to identify common or idiosyncratic patterns of spatial genetic variation across species in relationship with their known biological characteristics and, overall, to provide a reference snapshot for local conservation practitioners. We focused on species with a variety of biological characteristics and contrasting dispersal abilities, sampled across the main river network of the Upper Maroni. Firstly, we examined how local genetic diversity varied across our study zone. We tested whether a repeatable pattern of DIGD exists among the species sampled. We considered that a species displayed DIGD when local genetic diversity was higher (and local genetic isolation lower) in downstream areas than in headwaters, and we expected this pattern to be more distinct for brood hider or guarder species with little active or passive dispersal of eggs (both of which suggest low dispersal ability). We also examined how genetic diversity varied spatially on average, i.e., using species as independent observations within each site. Secondly, we examined the relative influence of isolation by stream distance, isolation by discontinuous river flow and isolation by spatial heterogeneity in effective size on genetic structure across species. We evaluated whether species with similar life history traits displayed comparable patterns of spatial genetic variation. We also unfolded a preliminary outline of evolutionary processes that may generate DIGD for the species concerned.

METHODS

Notation and definitions for statistical indices used in this study are provided in Table 1.

Study zone and model species

The Maroni is the largest river in French Guiana (>68,700 km^2). With the river Mana sharing the same outlet, this biogeographical subunit of the Guianas ecoregion harbors a particular ichthyofauna which marks a transition between an extended Proto-Berbice ecoregion (Lujan and Armbruster 2011), with strong influence from the Amazon, in the west, and other coastal rivers in French Guiana in the east (Lemopoulos and Covain 2019). Our study zone comprises a portion of the main channel (Lawa) flowing above the Abattis Cottica, and extends upstream towards four main tributaries, from west to east: the Litani, Marouini, Tampok, and Waki (Fig. 1). Sampling sites (Fig. 1, Table 2) were located in large and open river channels with Strahler index > 4. Five sites were located near the Lawa and the urbanized area of Maripasoula (La.0, La.1a, La.1b, Li.1, and Ta.1), while seven sites were located in more remote regions along secondary streams (Li.2, Li.3, Ma.2, Ma.3, Ta.2, Ta.3, and Wa.3). Although sites La.1b and Li.1 lay close to each other in Euclidian distance, they are relatively isolated from each other by steep rapids. Nevertheless, there exist no natural nor artificial barriers across our study zone and flowing is considered continuous, even though all river sections may be subject to seasonal variations in depth and width.

The 18 focal fish species are ubiquitous across the study zone and were selected because they could potentially be found across all sites. They have different life history traits according to their reproductive guild and their migratory behavior as adults (Table S1.1 from Appendix 1). Six species are broadcast spawners and long-distance migrants; they release a large number of eggs into the water column; they can move and reproduce across the entire study zone during the rainy season. Seven species are brood hiders and short-distance migrants; they fertilize and lay their eggs on the substrate; they usually only migrate along secondary streams to reproduce, mostly in the early rainy season. Finally, five species are brood guarders that provide parental care to their progeny; they are usually linked to particular and restricted habitats and display very limited dispersal compared to the other species. All species have overlapping

Table 1. Definitions and notations used in this study.

Notation	Definition
Statistics calculated within each site and for each species (185 observations per statistic):	
P_{95}	Local polymorphism rate for a species within a site, computed as the proportion of loci with minor allele frequency ≥ 0.05.
H_S	Local expected heterozygosity for a species within a site.
$F_{ST.P}$	Local genetic isolation for a species within a site, as provided by the averaged pairwise F_{ST} value between this site and the others.
$S_TF_{ST.P}$	Standardized $F_{ST.P}$ values so that the lowest value for the species is zero and the highest value is unity.
I_D	Internal diversity for a species within a site, provided as a measure of how much and in which sense overall genetic diversity would change if the site was not included in the dataset. Smallest (i.e., negative) values indicate high local contributions to overall genetic diversity, i.e., high local genetic diversity.
N_e	Estimate of local effective size for a species within a site, as provided by the linkage-disequilibrium method implemented in the software NeEstimator2.
Statistics calculated for each species (18 observations per statistic)	
COR_P	Indicates if local polymorphism rate is higher (positive COR_P) or lower (negative COR_P) in upstream than in downstream sites for a species.
COR_{HS}	Indicates if local expected heterozygosity is higher (positive COR_{HS}) or lower (negative COR_{HS}) in upstream than in downstream sites for a species.
$COR_{FST.P}$	Indicates if local genetic isolation is higher (positive $COR_{FST.P}$) or lower (negative $COR_{FST.P}$) in upstream than in downstream sites for a species.
COR_{IBD} / $COR_{IBD\text{-}PAZ}$	Informs about the influence of pairwise riverscape distance between sites on genetic differentiation as provided by pairwise F_{ST} for a species.
COR_{IBF} / $COR_{IBF\text{-}PAZ}$	Informs about the influence of pairwise connectivity by river flow (i.e., with or without continuous, unidirectional water flowing between two sites) on genetic differentiation as provided by pairwise F_{ST} for a species.
COR_{NE}	Informs about the influence of spatial heterogeneity in effective size N_e between sites on genetic differentiation as provided by pairwise F_{ST} for a species.
Abbreviations	
ABCRF	Approximate Bayesian Computation with random-forest
ASYM	Asymmetrical, downstream-biased migration as a potential process underlying DIGD.
COLON	Upstream-directed colonization as a potential process underlying DIGD.
DIFFNE	Higher downstream habitat availability as a potential process underlying DIGD.
DEN	Dendritic Ecological Network
DIGD	Downstream Increase in Genetic Diversity
EMM	Estimated Marginal Means obtained from an analysis of covariance between upstream distance and P_{95}, H_S, or $F_{ST.P}$ as the response variable, accounting for the influence of the Species as a categorical factor. Provides the predicted trend of the response variable with upstream distance for each species.
MRM	Analysis of Multiple Regression on distance Matrices, assessing the relative influence of isolation by stream distance, isolation by discontinuous river flow and isolation by spatial heterogeneity in effective size on pairwise genetic differentiation for each species.

generations and a generation time longer than 1 year. Beyond these categories, five of the 18 species are endemic to the Maroni River and its two nearest adjacent basins (Le Bail et al. 2012).

Genetic data and analyses

We used the genotypic data of Delord et al. (2018) for all 18 species. Here, we summarize essential information about field sampling and the development of molecular markers. Additional details are provided in the Supplementary note associated to Table S1.1 and Fig. S1.1. Fish were sampled from late 2013 to early 2016 during a program led by the Parc Amazonien de Guyane, using mainly trammel and cast nets and mostly during the dry season (July–December). SNP markers were developed for each species independently, using the protocol described by Delord et al. (2018): for each species, a subsample of ~20 individuals was selected across all sampling sites to build a SNP-discovery set. Their DNA extracts were mixed into a single library for pooled-RAD sequencing. Next, sequencing reads were analyzed using a custom bioinformatics pipeline (RAD4SNPs) designed to select polymorphic sites without individual nor population information, but mainly on the basis of depth coverage and the quality of flanking sequences to enable the design of amplification primers for future individual genotyping. Finally, 111 to 157 neutral, biallelic, nuclear SNP markers were scored for each species (full marker data available from the Dryad repository: https://doi.org/10.5061/dryad.2b6b43k). For one species (*Cynodon meionactis*), the dataset was supplemented with 31 SNPs available from the same protocol. During sample collection, the ideal sample size was set at 20 specimens per species and per site, which was sometimes missed due to a variety of field constraints. Ultimately, 145–283 individuals were retained per species, with each species sampled from at least 9 sites (Table S1.1), and each site represented by at least 12 species in the final dataset (Table 2). Sample sizes per species and site in this study are provided in Table 3.

Describing DIGD and riverscape patterns of genetic variation across species

We based our statistical analyses on the twelve sampling sites with species representing independent replicates of these sites, irrespective of their overall genetic structure. For each species and each site, we first computed several indices of local genetic diversity: the polymorphism rate (P_{95}) (proportion of loci with minor allele frequency ≥ 0.05) using a modified *rarefactor* function from the R package DIVERSITY (Keenan et al. 2013) with R version 4.0.4 (Core Team 2021); expected (H_S) and observed (H_O) heterozygosity using the R package HIERFSTAT (Goudet and Jombart 2017). For each species, we assessed the overall genetic structure using the fixation index F_{ST} (Weir and Cockerham 1984) and its significance using the G-test in HIERFSTAT. We also calculated pairwise F_{ST} values between sites and computed their confidence intervals using 999 bootstraps. Then, we calculated a site-specific F_{ST} ($F_{ST.P}$) for each sampling site by averaging its pairwise F_{ST} values with all other sampling sites to assess local genetic

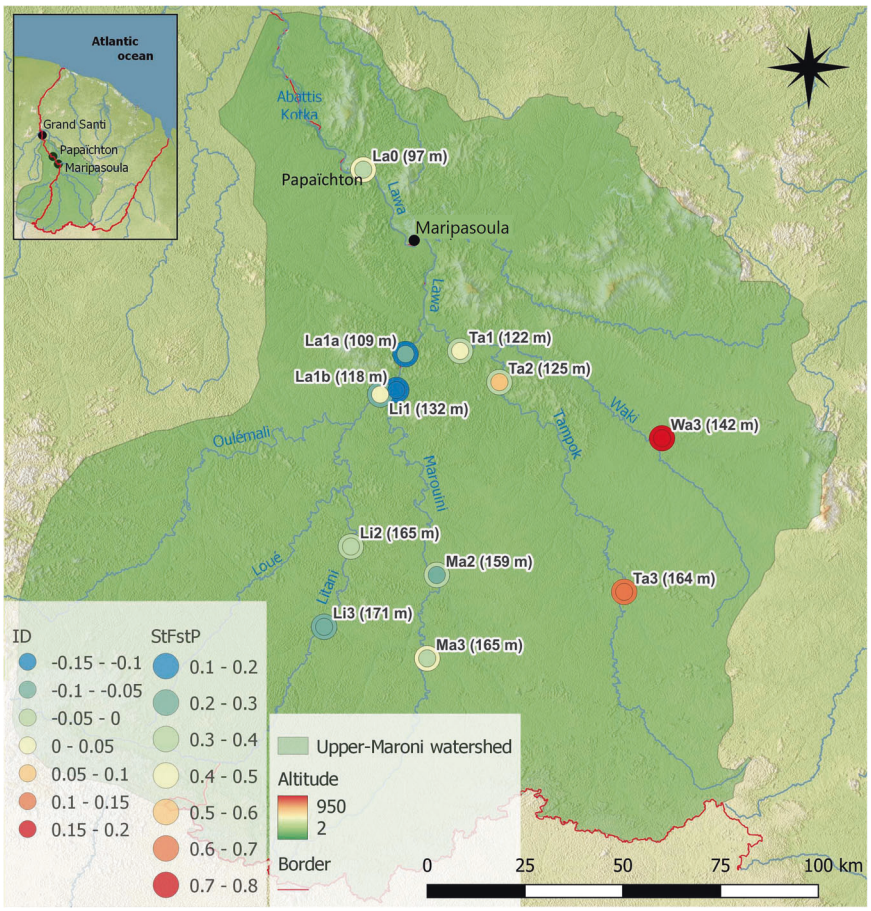

Fig. 1 Map of French Guiana (inset) and the Upper Maroni River with the 12 sampling locations and their elevation (i.e., altitude, in meters). Each sampling site is inner-colored according to the mean (i.e., across species) of internal diversity (I_D, which increases as local genetic diversity decreases) and outer-colored according to the mean of the standardized local genetic isolation ($S_TF_{ST.P}$). The blue-to-red gradient indicates low to high values of I_D and $S_TF_{ST.P}$, i.e., decreasing local genetic diversity and increasing local genetic isolation.

Table 2. Information about each site sampled on the Upper Maroni River for this study.

Site	Local name	Latitude	Longitude	Year(s)[a]	River	Upstream distance[b]	No. species
La.0	Papaïchton	3.8083	−54.1491	2013–2016	Lawa	72	13
La.1a	Twenke/Taluen	3.3813	−54.0504	2013–2015	Lawa	141	15
La.1b	Antecume-Pata	3.2980	−54.0713	2013–2015	Lawa	148	15
Li.1	Pidima/Pilima-Pata	3.2875	−54.1085	2014–2015	Litani	151	12
Li.2	Apsik Icholi	2.9358	−54.1748	2014–2016	Litani	212	16
Li.3	Eléüéletpe icholi	2.7496	−54.2359	2014–2016	Litani	244	17
Ma.2	Langa Soula	2.8704	−53.9770	2014–2016	Marouini	241	18
Ma.3	Wayo Gaan Soula	2.6771	−53.9985	2014–2016	Marouini	277	17
Ta.1	Kayodé/Wempi	3.3890	−53.9246	2013–2015	Tampok	144	14
Ta.2	Saut Tampok	3.3169	−53.8340	2015–2016	Tampok	177	18
Ta.3	Saut Pierkourou	2.8323	−53.5455	2015	Tampok	274	17
Wa.3	Saut l'Inspecteur	3.1879	−53.4592	2015–2016	Waki	218	13

[a]Year(s) corresponds to the sampling period.
[b]Upstream distance corresponds to the riverscape distance (in km) between each site and the town of Grand Santi.

isolation, or "uniqueness" (Pflüger and Balkenhol 2014; Paz-Vinas et al. 2015). Because none of the species displayed locally private alleles (i.e., present at only one site), indices developed for them were not considered.

To observe the upstream reduction in local genetic diversity expected for species under the DIGD pattern, we calculated (for each species) the Pearson coefficient of correlation between the location of each site along the downstream-to-upstream gradient (upstream distance) and each of the three site-specific genetic indices computed previously (P_{95}, H_S, and $F_{ST.P}$). Those coefficients will be hereafter referred as COR_P, COR_{HS}, and $COR_{FST.P}$, respectively. For species that display DIGD, we expected that P_{95} and H_S (local genetic diversity) would decrease (leading to negative coefficients COR_P and COR_{HS}), but $F_{ST.P}$ (local genetic isolation) would

Table 3. Number of individual samples collected per site for each species. Hyphens indicate sites where the species could not be sampled.

Species	La.0	La.1a	La.1b	Li.1	Li.2	Li.3	Ma.2	Ma.3	Ta.1	Ta.2	Ta.3	Wa.3
Brycon falcatus	14	–	18	–	20	23	22	21	–	24	19	13
Cynodon meionactis	–	15	–	–	20	21	21	20	25	20	20	22
Triportheus brachypomus	–	12	–	–	15	20	20	17	23	19	19	29
Hoplias aimara	33	13	16	12	25	20	20	20	11	20	19	20
Leporinus friderici	20	21	20	13	10	21	25	15	19	21	12	11
Leporinus lebaili	13	–	16	–	10	18	19	21	–	12	16	20
Acnodon oligacanthus	21	22	27	25	20	20	20	23	–	20	20	–
Myloplus rhomboidalis	24	20	26	42	29	17	20	19	13	18	14	–
Myloplus rubripinnis	–	19	32	19	19	24	20	15	27	23	20	–
Tometes lebaili	17	19	33	37	–	15	6	15	–	16	13	–
Serrasalmus eigenmanni	–	11	–	–	20	21	23	19	19	20	20	25
Serrasalmus rhombeus	24	22	20	21	21	22	18	22	26	22	18	17
Ageneiosus inermis	18	–	23	29	20	22	20	21	21	20	20	18
Doras micropoeus	18	28	15	20	20	16	15	20	21	12	–	–
Harttia guianensis	–	20	28	–	22	21	18	20	20	22	20	21
Hypostomus gymnorhynchus	20	26	17	10	–	19	18	20	25	23	19	20
Pseudancistrus barbatus	30	21	23	30	21	20	22	22	31	22	20	21
Geophagus harreri	21	23	21	15	10	–	15	–	10	13	19	17

increase (leading to positive coefficient $COR_{FST.P}$), as upstream distance increased. We defined the upstream distance of each site as the distance to the town of Grand Santi (in km; Fig. 1, Table 2), which lays at the downstream edge of our study zone. All riverscape distances were obtained from the national GIS database *IGN BD TOPO® Hydrographic Network*, version 2.2. We also performed three linear regression models with P_{95}, H_S, and $F_{ST.P}$ as response variables, respectively, to see how the relationship between local genetic diversity (or isolation) and upstream distance varied across species and to test for generalization of the DIGD pattern. To this end, we set species as a categorical fixed-effect factor and upstream distance as a continuous fixed-effect factor in each linear regression model (analyses of covariance performed using the R function *lm*). From each model, we extracted the estimated marginal mean (EMM) per species using the R package EMMEANS (Lenth 2018). EMM, along with their confidence intervals, enable to compare the trend (and associated uncertainty) of the relationship between the response variable (P_{95}, H_S, or $F_{ST.P}$) and upstream distance between species.

To provide an overall, multispecies vision of genetic variation across the study zone, we calculated two additional genetic diversity indices for each species at each site. Our objective was to assess whether certain sites displayed remarkable patterns of diversity or isolation and to reveal hot- and coldspots of diversity. First, for each species, we calculated the local contribution of each site to the species overall genetic variation across the study zone. For that, we used an estimate of local "internal diversity" (hereafter referred as I_D, Caballero and Toro 2002) calculated using MOLKIN software, version 2.0 (Gutiérrez et al. 2005). I_D, calculated for a given site, illustrates the direction and magnitude of the change in overall genetic diversity if this site was excluded from the full species dataset. If negative, I_D indicates that overall diversity would decrease if this site was absent from the full species dataset, implying it has a high contribution to overall diversity. Conversely, if positive, I_D indicates that overall diversity would increase if this site was absent from the full species dataset, implying it has a low contribution to overall genetic diversity. In addition, the absolute value of I_D indicates its magnitude. Expressed as percentages, I_D values were used to compare each site's contribution to overall diversity, across species. Second, for each species, we standardized all $F_{ST.P}$ values (hereafter referred as $S_TF_{ST.P}$) between 0 (lowest $F_{ST.P}$) and 1 (highest $F_{ST.P}$) to identify sites frequently associated to species lowest or highest value of local genetic isolation.

Comparing patterns of spatial genetic variation across species

To better understand drivers of spatial structure across species, we assessed the relative influence of stream distance (in km), connectivity by river flow, and spatial heterogeneity in effective size on pairwise genetic differentiation (linearized pairwise $F_{ST} = F_{ST}/(1\text{-}F_{ST})$) using multiple linear regression on distance matrices (MRM) (Paz-Vinas et al. 2015; Pilger et al. 2017).

For each species, the response matrix contained linearized pairwise F_{ST} values, while three independent matrices were used as explanatory factors. The first matrix contained riverscape distances (in km) between each pair of sites to test for isolation by stream distance. The second matrix described whether each pair of sites was connected by continuous, unidirectional water flowing (value of 0) or not (value of 1) (Paz-Vinas et al. 2015) to test for isolation by discontinuous river flow.

The third matrix contained the difference in local effective population size (N_e) between each pair of sites. Spatial heterogeneity in effective size was identified as a potential driver of between-site genetic structure even in the presence of gene flow (Prunier et al. 2017b). Thus, for each species, we calculated the matrix of pairwise N_e values as the harmonic mean of local N_e point estimates for all pairs of sites (Eq. (3) of Prunier et al. 2017b). The harmonic mean weights smaller values more heavily, and highlights the contribution of local genetic drift on pairwise genetic variation that is expected when one or both local N_e estimates are small. We estimated current local N_e for each species at each site independently, using the linkage-disequilibrium method implemented within the NEESTIMATOR software version 2.1 (Do et al. 2014), setting the minimum allele frequency to 0.05. Estimates from this method need to be interpreted with caution when it is applied on samples drawn from populations with overlapping generations or potential admixture with immigrant individuals over recent generations, as both could influence patterns of linkage-disequilibrium (Waples and England 2011; Waples et al. 2014). Biases may also occur when sample size is low, in which case estimates may be arbitrarily high, infinite and associated to wide confidence intervals. Thus, we did not focus on the quantitative estimates of N_e except when these were strikingly small and associated to finite confidence intervals (see Results section). Instead, we were interested in whether pairwise genetic variation could be explained by steepness of N_e variations between sites. When actual N_e point estimates were higher than 500 (or infinite), we arbitrarily set them to 500 before building our matrix of pairwise N_e values for the MRM analyses. 500 was chosen as a fairly typical value, commonly considered as a relatively large effective size (Franklin 1980). This enabled to avoid statistical artifacts introduced by punctually very high and possibly unreliable N_e estimates, and rather focus the MRM on differences between smaller N_e estimates. We also ran MRM analyses using the lower bound of the confidence intervals of N_e instead of point estimates, and we also ran MRM analyses while keeping all "outlier" (i.e., larger than 500) N_e estimates and replacing infinite estimates by the mean N_e calculated across all sites for the species.

From each of the 18 MRM analyses, we extracted standardized beta-coefficients, which described the effect of each explanatory factor on pairwise genetic differentiation: isolation by stream distance (COR_{IBD}), isolation by discontinuous river flow (COR_{IBF}), and isolation by spatial heterogeneity in effective size (COR_{NE}).

We performed a multivariate approach, including all 18 species and the previously computed indices of spatial genetic variation, to visualize potential clusters of species displaying similar patterns and evaluate how species with similar life history traits would position one from each other (Selkoe et al. 2014). We used estimates of overall genetic structure (F_{ST}), descriptors of DIGD (COR_P, COR_{HS}, and COR_{FSTP}) and factors explaining pairwise genetic variation (COR_{IBD}, COR_{IBF}, and COR_{NE}) as continuous variables within a principal component analysis (PCA) with species as statistical individuals, using the R package FACTOMINER (Lê et al. 2008).

Inferring evolutionary processes that influence DIGD across species

For species that displayed DIGD (negative COR_P and/or COR_{HS}, positive $COR_{FST.P}$ and relatively high overall F_{ST}), we used the simulation-based results obtained by Paz-Vinas et al. (2015) to obtain preliminary information about which of several evolutionary processes (or combination of processes) might generate it. Paz-Vinas et al. (2015) simulated genotypic data for subpopulations evenly distributed across a dendritic ecological network (DEN). These data were generated under seven evolutionary scenarios all likely to generate DIGD, but with distinct genetic signatures as provided by a small set of easily computable summary statistics. Those seven scenarios are asymmetrical, downstream-biased migration (ASYM), upstream-biased colonization (COLON), higher downstream habitat availability (DIFFNE) or any combinations of two or all processes. Paz-Vinas et al. (2015) also generated data under a null model (NULL) in which none of the three processes applied, indicating that global genetic variation results only from the dendritic structure of the river network itself. Data were simulated under a wide range of local effective sizes (50 to 10,000), migration rates (0.001 to 0.30) and other demographic parameters for each scenario. The summary statistics obtained from those simulations could be used under an ABC model-choice procedure (*Approximate bayesian computation*, Csilléry et al. 2010), in order to determine which evolutionary scenario would most likely explain the DIGD pattern observed from an empirical dataset. Paz-Vinas et al. (2015) applied this framework to several previously published datasets in order to outline which processes might most frequently underlie DIGD in riverine species. This approach has to be led very cautiously, as it relies on a generic set of genotype data simulated under a DEN with "generic" properties (symmetric fixed branching, fixed number of sampled subpopulations) and compared to empirical datasets, which do not necessarily fully match those properties. Nevertheless, this framework provides a valuable baseline to understand the various processes that may exist in riverscapes along with their specific genetic signatures (Blanchet et al. 2020). More importantly, it may be of particular interest when applied on a set of co-sampled and co-distributed species, where direct comparisons might be even more informative because of the common sampling scheme.

Thus, we applied the approach developed by Paz-Vinas et al. (2015) to the five species that displayed DIGD (see Results), using the ABCRF method (Pudlo et al. 2016) from the eponymous R package, which performs model selection based on a random forest of classification and regression trees (Breiman 2001) instead of classical ABC algorithms. As a reference table, we used values of eight summary statistics, provided from the generic simulated data from Paz-Vinas et al. (2015) under all evolutionary processes (https://doi.org/10.5061/dryad.38c1g). Those summary statistics were overall fixation indices F_{IS}, F_{ST}, and F_{IT}; COR_{AR} (analogous to our COR_P), COR_{HS}, $COR_{FST.P}$, COR_{IBD}, and COR_{IBF}. Thus, for the species that displayed DIGD, we used overall F_{IS}, F_{ST}, and F_{IT}, COR_P, COR_{HS}, $COR_{FST.P}$, $COR_{IBD\text{-}PAZ}$, and $COR_{IBF\text{-}PAZ}$ computed from our own data as observed summary statistics (Table S1.4) for model selection using the ABCRF method. $COR_{IBD\text{-}PAZ}$ and $COR_{IBF\text{-}PAZ}$ were calculated in the same way as COR_{IBD} and COR_{IBF} from our original MRM analysis, but this time without including our matrix of spatial heterogeneity in effective size, since Paz-Vinas et al. (2015) did not consider this factor or pairwise genetic differentiation within their model selection framework.

Using their full set of 10 summary statistics, Paz-Vinas et al. (2015) obtained an "out-of-bag" error rate (percentage of sets of simulated summary statistics that were not correctly assigned to the evolutionary scenario under which they were generated) of 11.9%. In our case, we obtained an "out-of-bag" error rate of 14.3% using eight summary statistics and generating 500 classification trees. Albeit this value may seem fairly high, it remains comparable to figures reported from other ABCRF applications (e.g., Rougemont et al. 2016; Fraimout et al. 2017) and so was considered acceptable to apply the method, albeit with caution. The ABCRF model-choice procedure enabled us to identify which evolutionary scenario might best fit the set of summary statistics observed for each species that displayed DIGD, with the associated posterior probabilities. Additional information about the ABCRF framework, its application and potential limitations to discriminate between processes underlying DIGD in our case is provided in the Supplementary note associated to Table S1.4.

RESULTS

All genetic indices calculated for each species and sampling site are available in Appendix 2. P_{95} and H_S varied among sites and species, from 0.697 to 0.999 and from 0.257 to 0.436, respectively. Local $F_{ST.P}$ ranged from −0.001 to 0.072. Overall F_{ST}, calculated for each species, ranged from 0.000 to 0.038; they were significant for eleven species (Table 4). Pairwise F_{ST} ranged from 0.000 to 0.099 across all 18 species (Tables S1.2.1–S1.2.18). Significant values often revealed stronger genetic differentiation between the eastern (Tampok and Waki rivers) and the rest of our study zone, converging with results from individual-based genetic clustering methods such as DAPC (Jombart et al. 2010) or STRUCTURE (Pritchard et al. 2000) (not shown). Additionally, significant values often (but not always) involved sites located in upstream reaches of the Upper Maroni.

DIGD and spatial contrasts in local genetic diversity

COR_P, calculated for each species, ranged from −0.447 to 0.584 (Table 4). COR_{HS} ranged from −0.485 to 0.557, while $COR_{FST.P}$ had more and greater positive values that ranged from −0.326 to 0.752, indicating that local genetic isolation ($F_{ST.P}$) showed a stronger relationship with upstream distance across species. Analyses of covariance showed large and significant differences in local values of P_{95}, H_S, and $F_{ST.P}$ across species. For P_{95} and H_S, the interaction between upstream distance and species was non-significant, and species explained 88 and 96% of overall variation, respectively (Table S1.3). Upstream distance had no significant effect overall on P_{95} or H_S across the 18 species. In contrast, for $F_{ST.P}$, the interaction between upstream distance and species was significant and explained 5.0% of overall variation in $F_{ST.P}$ (Table S1.3). EMM values (mean and confidence intervals) illustrated the contrasting covariation of upstream distance with P_{95}, H_S, and $F_{ST.P}$ values across species (Fig. 2). For four species (*Tometes lebaili*, *Serrasalmus eigenmanni, Pseudancistrus barbatus* and *Geophagus harreri*) P_{95} and H_S both tended to decrease, and $F_{ST.P}$ to increase as upstream distance increased, with substantial genetic structure (overall $F_{ST} > 0.010$). In addition, *Myloplus rhomboidalis* showed no trend with upstream distance for H_S, but a decreasing P_{95}, increasing $F_{ST.P}$ and overall $F_{ST} = 0.008$. We considered that these five species displayed DIGD.

I_D, calculated for each sampling site for each species, ranged from −0.690 to 0.750 (Fig. S1.2 from Appendix 1). Mean I_D and $S_TF_{ST.P}$ values (i.e., averaged across species for each sampling site) revealed a distinct difference between the eastern and western areas of the study zone (Fig. 1). Sites in the Tampok and the Waki tributaries (Ta.1, Ta.2, Ta.3, and Wa.3) in the eastern area displayed higher mean I_D and $S_TF_{ST.P}$ (lower local genetic diversity and higher local genetic isolation) compared with sites in the Litani and Marouini tributaries (Li.1, Li.2, Li.3, Ma.2, and Ma.3) in the western area (Fig. 1 and S1.2). In both eastern and western areas, however, mean I_D and $S_TF_{ST.P}$ were lower (higher local genetic diversity and lower local genetic isolation) near confluences with the Lawa than within upstream sites. On the Lawa, two sites (La.1a and La.1b) with intermediate position had the lowest mean I_D and $S_TF_{ST.P}$ while the most downstream site of our study zone (La.0) had a higher mean I_D and lower mean $S_TF_{ST.P}$.

Shared and idiosyncratic patterns of genetic structure across species

Estimates of N_e for each species and sampling site ranged from 7 to infinite (Table S1.5). Ninety-eight N_e estimates (of 185) were set to 500 for the MRM analyses (Appendix 2), comprising 41 N_e

Table 4. Indices of overall spatial genetic variation obtained for each species[a].

Species	Family	No. sites	No. samples	No. loci	F_{IS}	F_{ST}[b]	F_{IT}	COR_P	COR_{HS}	$COR_{FST.P}$	Results of MRM analyses			
											COR_{IBD}	COR_{IBF}	COR_{NE}	R^2
Brycon falcatus	Characidae	9	174	155	0.015	0.001	0.016	−0.282	−0.478	−0.217	0.130	−0.123	0.358	0.115
Cynodon meionactis	Characidae	9	184	188	0.007	0.002	0.009	0.119	0.224	0.323	0.383	−0.106	0.028	0.033
Triportheus brachypomus	Characidae	9	174	148	0.009	0.001	0.010	0.102	0.269	−0.263	0.214	−0.081	0.261	0.000
Hoplias aimara	Erythrinidae	12	229	154	0.001	0.005	0.006	0.584	−0.135	−0.127	**0.414**	−0.078	**0.616**	**0.547**
Leporinus friderici	Anostomidae	12	208	141	−0.004	0.002	−0.002	0.059	0.078	−0.326	−0.060	−0.081	−0.023	0.000
Leporinus lebaili	Anostomidae	9	145	150	0.024	0.000	0.023	0.317	0.557	−0.146	0.227	**−0.470**	0.152	0.069
Acnodon oligacanthus	Serrasalmidae	10	218	138	0.024	0.000	0.024	0.197	−0.091	−0.046	0.066	**0.469**	0.220	**0.154**
Myloplus rhomboidalis	Serrasalmidae	11	242	137	0.021	**0.008**	0.029	−0.379	0.023	0.467	**0.652**	**0.236**	0.000	**0.581**
Myloplus rubripinnis	Serrasalmidae	10	218	118	0.020	**0.001**	0.021	0.199	−0.258	0.300	**0.404**	0.033	−0.003	0.118
Tometes lebaili	Serrasalmidae	9	171	156	0.015	**0.012**	0.027	−0.413	−0.328	0.706	**0.345**	**0.374**	**0.378**	**0.710**
Serrasalmus eigenmanni	Serrasalmidae	9	178	150	0.008	**0.029**	0.036	−0.289	−0.485	0.209	0.202	**0.545**	−0.057	**0.416**
Serrasalmus rhombeus	Serrasalmidae	12	253	154	0.029	**0.006**	0.035	−0.094	0.077	0.164	0.114	**0.308**	**0.365**	**0.210**
Ageneiosus inermis	Ageneiosidae	11	232	111	0.001	**0.004**	0.005	−0.352	0.280	0.674	**0.419**	0.221	0.113	0.251
Doras micropoeus	Doradidae	10	185	150	−0.001	0.001	0.001	0.251	0.159	0.092	0.059	−0.242	0.319	0.093
Harttia guianensis	Loricariidae	10	212	154	0.018	**0.013**	0.030	−0.027	0.165	0.197	0.102	**0.370**	−0.200	**0.150**
Hypostomus gymnorhynchus	Loricariidae	11	217	153	0.027	**0.007**	0.034	0.284	−0.100	0.752	**0.826**	0.011	−0.060	**0.691**
Pseudancistrus barbatus	Loricariidae	12	283	151	0.013	**0.020**	0.033	−0.234	−0.142	0.600	**0.649**	0.136	−0.079	**0.524**
Geophagus harreri	Cichlidae	10	164	150	0.022	**0.038**	0.059	−0.447	−0.477	0.599	0.240	**0.370**	**0.398**	**0.482**

[a]COR_P, COR_{HS} and $COR_{FST.P}$ correspond to Pearson correlation coefficients between upstream distance and local polymorphism rate (P_{95}), expected heterozygosity (H_S), and local genetic isolation ($F_{ST.P}$), respectively. COR_{IBD}, COR_{IBF}, and COR_{NE} are standardized beta-coefficients extracted from analyses of multiple linear regression on distance matrices (MRM) that tested the pairwise relationship between riverscape distance, flow connectivity, or effective population size (N_e), respectively, and linearized pairwise F_{ST}. R^2 is the adjusted r-squared from each MRM. Bold values are significant.
[b]Bold values are significant according to a Goudet G-test with 9999 permutations for overall F_{ST}.

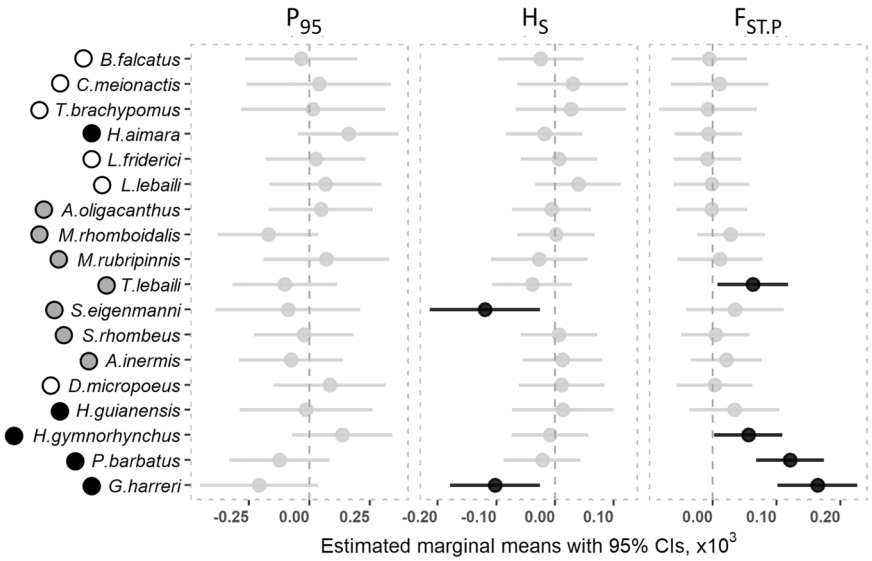

Fig. 2 Estimated marginal means (EMM), with 95% confidence intervals (CIs, horizontal bars), for each fish species from the three analyses of covariance showing the relationship between upstream distance (explanatory factor) and the local polymorphism rate (P_{95}), expected heterozygosity (H_S), and local genetic isolation ($F_{ST.P}$) as response variables. Significant EMM (i.e., CIs not including zero) are shown in black. All values on the x-axis were multiplied by 10^3 to increase intelligibility. Species labels indicate their class of life history traits with broadcast spawners, long-distance migrants in white, brood hiders, short-distance migrants in gray and guarders, sedentary species in black.

estimates higher than 500 and 57 infinite estimates. Expectedly, MRM analyses revealed no significant isolation by stream distance, discontinuous river flow (i.e., positive COR_{IBF}) or spatial heterogeneity in effective size for any broadcast spawner, long-distance migrant species. By contrast, seven short-distance migrant or sedentary species showed significant isolation by stream distance with COR_{IBD} ranging from 0.345 to 0.826 and seven short-distance migrant or sedentary species showed significant isolation by discontinuous river flow with COR_{IBF} ranging from 0.236 to 0.545 (Table 4). Only two species (*M. rhomboidalis* and *T. lebaili*) displayed both significant COR_{IBD} and COR_{IBF}. *S. eigenmanni* displayed the highest COR_{IBF} (=0.545) in accordance with a particularly strong genetic break (according to pairwise F_{ST} values, Table S1.2.11) between the eastern tributaries (Tampok and Waki) and the rest of the study zone. Finally, spatial heterogeneity in effective size had a significant influence on pairwise genetic differentiation for four species, along with isolation by stream distance (*Hoplias aimara*; $COR_{NE} = 0.616$), isolation by discontinuous river flow (*G. harreri* and *Serrasalmus rhombeus*; $COR_{NE} =$ 0.398 and 0.365, respectively), or both (*T. lebaili*; $COR_{NE} = 0.378$). MRM results for alternative handling of outlier and infinite N_e estimates are provided in Table S1.6 and did not show any striking difference with the current analyses (See also Fig. S1.4).

The first two components of the PCA explained more than 66% of the between-species variability (Fig. 3). The first PCA axis opposed all broadcast spawners, long-distance migrant (but also a few short-distance migrant and one sedentary) species with lower overall F_{ST} and higher COR_P and COR_{HS} (left half of the PCA biplot) to other short-distance migrant and sedentary species displaying higher overall F_{ST}, higher COR_{IBF}, and lower (including negative) COR_P and COR_{HS} (right half of the biplot), such as the five species that displayed DIGD. The second PCA axis opposed species with higher COR_{IBD} to species with higher COR_{NE}.

Outline of the evolutionary processes influencing DIGD

For four of the five species that displayed DIGD, COLONDIFFNE (i.e., a combination of upstream-biased colonization and higher downstream habitat availability) was the most frequently assigned evolutionary scenario according to the ABCRF model-choice procedure (Table 5), indicating that DIGD may result from a combination of higher downstream habitat availability (DIFFNE) and upstream-directed colonization (COLON). For one species (*P. barbatus*), COLON was the most frequently assigned process, indicating that DIGD may result from upstream-directed colonization only. However, posterior probabilities associated with each selected model were low, ranging from 0.554 to 0.779 (Table 5). Indeed, for all five species, a non-negligible number of regression trees assigned the empirical statistics to other evolutionary scenarios, usually COLON or DIFFNE alone, or a combination of both for *P. barbatus*. For one species (*S. eigenmanni*), the selected model (COLONDIFFNE) was closely followed by one that combined all three evolutionary processes: DIFFNE, COLON, and ASYM (asymmetrical, downstream-biased migration).

DISCUSSION

Comparative approaches are increasingly contributing to the field of conservation genetics. Studying a large number of species should be possible through close collaborations with biodiversity managers in the field and the development of efficient collecting and genotyping tools (Hoban et al. 2013), including the use of high-throughput-sequencing to develop molecular resources for non-model species (Lepais et al. 2020). Here, we used SNP data from 18 co-sampled Neotropical fish species at 12 sites in the Upper Maroni to describe riverscape genetic variability across species in this remote (but increasingly inhabited by people) area of high ichthyodiversity. Currently, few studies focus on comparative multispecies population genetics, especially in Neotropical areas (Leigh et al. 2021) and, to our knowledge, few comparative studies have included as many species and samples collected in the same area (but see Selkoe et al. 2016 for an example of combining meta-analysis and co-sampling; and Zbinden et al. 2022 for a recent, extensive co-sampling application).

We observed DIGD for a few species displaying moderate or low dispersal abilities. This pattern, previously documented in temperate freshwater habitats (Blanchet et al. 2020), may result from increasing habitat availability downstream and upstream-directed colonization, according to the ABCRF analysis. Nonetheless, spatial comparison of local genetic indices (per species and averaged across all species) also highlighted contrasts among

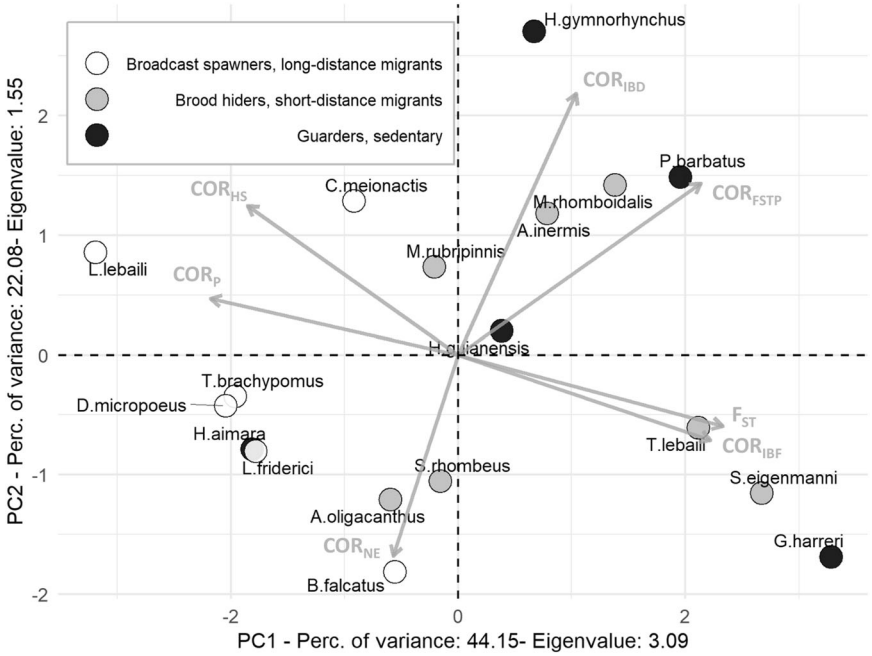

Fig. 3 Biplot of the principal component analysis used to describe the relative position of all species according to their patterns of overall genetic variation. Variables are global FST values, the strength of isolation by stream distance (CORIBD), by discontinuous river flow (CORIBF), by spatial heterogeneity in effective size (CORNE) extracted from multiple linear regression on distance matrices (MRM) analyses, and values of CORP, CORHS, and CORFST.P which correspond to Pearson correlation coefficients between upstream distance and local polymorphism rate (P95), expected heterozygosity (HS), and local genetic isolation (FST.P), respectively.

sites, some of which were genetic hot- or coldspots regardless of their upstream/downstream position along the main channel or tributaries of the Upper Maroni. Moreover, riverscape patterns of genetic variation and the influencing factors varied across species. Some species had contrasting patterns of genetic structure despite having similar ecological characteristics and life history traits. This coexistence of shared and idiosyncratic patterns of genetic variation will constitute the basis of the discussion.

Occurrences of DIGD in the Upper Maroni and their underlying processes

For all six species documented as long-distance migrants and broadcast spawners, we were not able to reject panmixia based on our dataset nor to detect any presence of DIGD. In contrast, we identified significant genetic structure and DIGD in five species, which were all short-distance migrants or sedentary species with medium-to-low fecundity. This supports previous observations that the dendritic structure of river networks has more influence on genetic variation for species with low dispersal ability and/or small N_e (Chaput-Bardy et al. 2009; Paz-Vinas and Blanchet 2015; Zbinden et al. 2022). Nevertheless, the other seven short-distance migrant, sedentary, brood-hider, or guarder species did not display this particular riverscape pattern, which ended up underrepresented in our dataset (i.e., DIGD being detected in only 5 of 18 species). Based on our results, DIGD thus did not seem to be a prevalent pattern of genetic variation in the Upper Maroni -although we must recall that, in spite of the consequent number of species studied here, it still represents an infinitesimal proportion of the significant ichthyodiversity of the region. Instead, there seem to exist constrated patterns of genetic variation across species, as discussed later.

The ABCRF approach usually identified a combination of higher downstream habitat availability (DIFFNE) and upstream-directed colonization (COLON) as the processes most likely to influence the DIGD for the species concerned, albeit with low posterior probability. This could have been because the approach cannot distinguish between these processes in our case, or because they both influenced genetic diversity of the species in the study zone. In their review of riverscape genetics, Blanchet et al. (2020) highlighted that upstream-directed colonization was the process that most frequently influenced DIGD in rivers. In the Maroni though, diversification and past colonization routes of most fish taxa were documented as resulting from the formation of a Pleistocene refuge and relatively ancient stream-capture events between headwaters of the Maroni and neighboring watersheds (e.g., between the Litani and the river Jari in the Tucumaque mountains, Fisch-Muller et al. 2018) and less likely from exchanges of fish with other coastal rivers through estuaries (Lemopoulos and Covain 2019). In addition, current patterns of landscape genetic variation are considered to result mainly from environmental heterogeneity (Borstein et al. 2022) and species life history traits (Papa et al. 2021), although specific reconstructions of past demography and evolutionary trajectories are missing. Thus, upstream-directed colonization from the river outlet to the headwaters seems less likely to have occurred in our study zone, unless it relies on contemporary non-equilibrium processes such as extinction-recolonization of upstream reaches due to local environment constraints. This would support the parallel implication of higher downstream habitat availability to explain DIGD there, as suggested by the ABCRF results. However, low posterior probabilities and the relatively high out-of-bag score of the ABCRF in our case (14.3%) hampers a greater understanding of the relative influence of these two processes at this stage. The power of the ABCRF analysis to further distinguish between them may be limited by our small number of sites, the use of biallelic SNP markers (See supplementary note from Table S1.4) or by relatively important gene flow or local effective size. Ultimately, we tested only three evolutionary processes (and combinations thereof), although other processes may potentially generate DIGD in the wild (Blanchet et al. 2020).

Hot- and coldspots of local genetic diversity in the Upper Maroni

The DIGD pattern, when it existed, was often weak. COR_P, COR_{HS}, and $COR_{FST.P}$ never exceeded 0.584, 0.557, and 0.752, respectively,

Table 5. Results of the ABCRF (*approximate Bayesian computation with random-forest*) model-choice procedure performed to determine which evolutionary process (or combination of processes) best explained the downstream increase in genetic diversity (DIGD) observed for five species with a decreasing polymorphism rate (P_{95}) and/or expected heterozygosity (H_S), and increasing local genetic isolation ($F_{ST.P}$), as upstream distance increased[a].

Species	Number of votes attributed to each process (or combination thereof)							Process(es) selected	RF posterior probability
	ASYM	COLON	DIFFNE	ASYM COLON	ASYM DIFFNE	COLON DIFFNE	ASYMCOLONDIFFNE	NULL		
Geophagus harreri	6	62	90	11	4	**268**	55	4	COLONDIFFNE	0.746
Myloplus rhomboidalis	26	117	137	0	0	**172**	1	47	COLONDIFFNE	0.554
Pseudancistrus barbatus	2	**222**	67	2	0	196	0	11	COLON	0.595
Serrasalmus eigenmanni	11	53	53	14	3	**191**	170	5	COLONDIFFNE	0.779
Tometes lebaili	1	17	187	1	1	**285**	8	3	COLONDIFFNE	0.630

[a]The processes examined were downstream-biased migration (ASYM), upstream-directed colonization (COLON), and higher downstream habitat availability (DIFFNE). A combination of these labels indicates a combination of processes. In the NULL model, only the dendritic hydrographic structure influenced the pattern of genetic structure. The out-of-bag error rate in the analysis was of 14.3%. ABCRF analyses were performed by running 500 random-forest (RF) trees in which the eight possible processes received votes. Bold values indicate the process selected.

and the EMM from the analyses of covariance had large confidence intervals that often included zero. Most DIGD studies of fish rarely consider more than ~15 sampling sites (e.g., Salisbury et al. 2016; Pilger et al. 2017; Richmond et al. 2018); however, the Upper Maroni is a dense watershed, and our 12 sampling sites may lack the resolution required to reveal stronger DIGD patterns (but see Alther et al. 2021, who also highlighted complex patterns of DIGD in *Gammarus fossarum* even though 95 sampling sites were sampled). In particular, a sampling design biased against the most upstream sites (which are usually more isolated, especially within a network with complex branching, Thomaz et al. 2016) may underestimate the strength of DIGD. A weak DIGD pattern may also result from analyzing too few molecular markers. However, we used an average ~150 SNP per species, which, for most applications, is consistent with the genetic information provided by 10–15 microsatellites (Morin et al. 2004), a fairly common design used in other DIGD studies (Pilger et al. 2017; Ruzzante et al. 2019; Alther et al. 2021). Moreover, these SNP markers were developed from a discovery panel drawn from the same place and time as the current study, in order to capture the main patterns of spatial genetic variation in the Upper Maroni (Delord et al. 2018).

The weak DIGD pattern for the five species could ultimately have resulted from the contrasting local genetic diversity between the eastern and western areas of the study zone, as revealed by local I_D and $F_{ST.P}$ values. We observed lower mean genetic diversity in the Tampok and the Waki tributaries than in the Marouini and Litani, regardless of the upstream distance. This trend was also observed for certain species with low genetic structure, such as *C. meionactis* and *S. rhombeus* (Figs. S1.3.2, S1.3.12). This diverging trend suggests that the dendritic structure of the river network is not the only feature that influences spatial patterns of genetic diversity along the upstream gradient. At a larger geographical scale, Papa et al. (2021) identified significant global genetic divergence between western (i.e., Suriname) and eastern (i.e., our study zone) regions of the Maroni River using multispecies genetic landscapes based on the mitochondrial gene COI. This may result from current expansion of population ranges from the Maroni toward adjacent watersheds. They also highlighted divergence between the Marouini and the Tampok to a lesser extent, a finding strengthened by our results, and suggested to arise mainly from species dispersal abilities or intra- and interspecific competition. Here, we further hypothesize that lower habitat availability, accessibility, or quality may explain the lower local genetic diversity detected in association with higher local genetic isolation in the eastern area of our study zone. The Waki is narrower than the other tributaries sampled, which implies lower habitat availability. The Tampok is a narrow valley, with large variations in seasonal water levels but little river overflow, which may decrease access to certain habitats. In addition, local practitioners have observed that the Tampok and Waki were more influenced by local, small-scale gold mining activities in the past decade than the Marouini or Litani, which may have polluted the water, increased water turbidity, or degraded riverbanks, thus reducing habitat quality for fish. In conclusion, local genetic diversity was generally lower, and the DIGD more pronounced, in the eastern area (including the Tampok and Waki) than in the western area (including the Litani, Marouini, and sites La.1a and La.1b of the Upper Lawa).

In the main channel (Lawa), local genetic diversity was slightly lower (and local genetic isolation slightly higher) at site La.0 than at La.1a or La.1b for several species (Fig. 1 and S1.2). La.0 harbors the highest human density in the study zone, surrounding the downstream village of Papaïchton and the city of Maripasoula, and where fishing pressure is higher than that at other locations (Longin et al. 2021b). For instance, *H. aimara*, one of the species most targeted by fishermen in this location, had a low polymorphism rate, high local genetic isolation, and small N_e

(Table S1.5), similar to other species such as *Leporinus friderici* and *Brycon falcatus*. This may indicate that their populations experience substantial fishing pressure in these areas (Allendorf et al. 2008; Longin et al. 2021b).

In conclusion, the expected overall DIGD pattern in the Upper Maroni is likely to be influenced by local habitat characteristics along a west-to-east gradient of decreasing habitat quality or availability, in addition to the dendritic structure and upstream distance. Moreover, anthropogenic pressures at certain sites, such as gold mining or fishing, may influence patterns of local genetic variation in areas with increasing human presence. Collecting local physico-chemical data at high spatial resolution across the study zone (e.g., turbidity, dissolved oxygen or mercury concentration, diversity and availability of fish habitats) may enable to better understand the influence of environmental features on spatial genetic variation in the Upper Maroni, e.g., through the application of complementary riverscape genetic frameworks (Davis et al. 2018). Anthropogenic influences on spatial genetic variation may be much less predictable than the influence of the river network, and perhaps weaker (Prunier et al. 2017a). However, it could be a non-negligible predictor of riverscape genetic variation, and quantifying it will require additional studies to address multicollinearity among environmental and anthropogenic variables (Blanchet et al. 2020).

Contrasting patterns and factors affecting genetic structure across species

The infrequent occurrence of DIGD in our results, and its interference with potentially independent local constraints also lead to consider the various patterns of genetic structure observed across the 18 focal species. As mentioned earlier, all species documented as long-distance migrants and broadcast spawners displayed seemingly negligible genetic structure. However, the other species displayed contrasting patterns, as revealed by MRM and multivariate analyses where species sharing similar life history traits were not necessarily grouped together. Endemic species did not associate to any particular structuring pattern either. All of them were evenly distributed along both axes of the PCA biplot, with, for instance, a distinct contrast between species displaying high isolation by stream distance, as revealed by COR_{IBD} (e.g., *H. gymnorhynchus*), and species whose genetic structure depended more on riverscape topography or spatial heterogeneity in effective size, as revealed by COR_{IBF} and COR_{NE} (e.g., *G. harreri*). The six Serrasalmidae species, all of which are documented as brood-hiders and short-distance migrants (Table 4 and Supplementary Table S1.1), had highly contrasting patterns of genetic variation. Conversely, *H. aimara*, a species considered to be sedentary and a guarder, had surprisingly low genetic structure (Table 4, Fig. 3), except at site La.0, as mentioned. Such idiosyncratic patterns were identified in other studies as well (Paz-Vinas et al. 2018), whereas other work suggest more consistent patterns with a strongly predominant influence of stream hierarchy across a number of co-distributed species sharing similar traits (Zbinden et al. 2022). Several hypotheses can be discussed to explain the idiosyncratic patterns observed in our case.

Body size, although usually considered to be positively associated with higher dispersal abilities (Radinger and Wolter 2014), did not complement the differences observed across species. For instance, small-bodied herbivorous Serrasalmidae species had lower genetic structure than larger-bodied herbivorous Serrasalmidae (e.g., *Myloplus rubripinnis*, with non-significant overall $F_{ST} = 0.001$, compared with larger-bodied *M. rhomboidalis* and *T. lebaili*, with $F_{ST} \geq 0.008$). A more restricted ecological niche or reproduction timing might better explain these observations. For instance, *T. lebaili* and *M. rhomboidalis* depend completely on flowing water of large streams, including during the breeding period (Planquette et al. 1996; Jégu and Keith 2005), which may limit gene flow at larger spatial scales. *T. lebaili* also has considerable foraging specialization (Planquette et al. 1996; Jégu and Keith 2005), since it feeds almost exclusively on Podostemaceae plants that bloom in shallow rapids. *S. eigenmanni*, another Serrasalmidae species with high genetic structure, is found only in densely vegetated riverbanks (fisherman Janakale Makiloewala, pers. comm.). Results for *H. aimara* could be explained by its high fecundity (Planquette et al. 1996), if early dispersal compensates for adult territoriality.

Neotropical rivers host high species richness, and tremendous efforts were deployed to inventory it. However, information about the ecological optima, reproductive cycles, vital rates, and vulnerability of these species to environmental constraints is still lacking. In such cases, comparative population genetic approaches help by providing a holistic overview of intraspecific patterns, but biological interpretation of spatial genetic signatures appear limited by current knowledge. For instance, it would be useful to assess whether the higher genetic structure observed for large-bodied herbivorous Serrasalmidae results solely from a narrower spatial ecological niche that limits genetic connectivity, or also from naturally low abundance or local pressures (e.g., habitat degradation, fishing) resulting in smaller reproductive output and smaller N_e (which is more difficult to assess).

Similarly, collecting additional information about life history traits and the ecology of the focal species, in parallel to considering physico-chemical parameters from the environment, may enable us to better understand in which case we might observe a particular pattern of genetic structure across riverine species -and in which way it may, or not, be associated to DIGD. Subsidiarily, we may recall that all species studied here remain relatively ubiquitous across the study zone. It is possible that studying more sedentary, guarder species with narrower niche would provide additional illustrations of DIGD in the Upper Maroni.

An initial snapshot of genetic variation in fish in the Upper Maroni: conclusions and perspectives

Our study provides useful information for identifying geographic areas and species in the Upper Maroni that could be of conservation interest. Additional environmental data could ease our understanding of the patterns observed, especially with regard to habitat quality. The information provided at the intraspecific level could be combined with traditional biodiversity surveys at the interspecific level by local professionals and managers, to propose relevant actions that maximize the conservation of both aspects of biodiversity. Our comparative approach could also serve as a baseline for future similar studies, for instance, with higher sampling coverage and/or high-density genomic datasets for species of particular interest in the Upper Maroni. The genetic approach is a useful conservation tool in the Neotropics, where data collection to apply conventional tools for population monitoring (such as mark-recapture, catch-per-unit-effort standardization, or telemetry) is infeasible or technically challenging in such diverse and remote areas (Meunier et al. 1994).

Our genetic approach highlighted species that may be more vulnerable to certain local anthropogenic pressures. For instance, *T. lebaili* and *M. rhomboidalis* have high cultural and commercial importance to local human communities in the Upper Maroni. We observed significant spatial genetic variation for both species. In *T. lebaili*, linearized pairwise F_{ST} values were significantly influenced by stream distance, discontinuous river flow and spatial heterogeneity in effective size. This indicates potentially higher susceptibility to local pressures such as habitat degradation or fishing, which could lead to local losses of genetic diversity. Similarly, the significant genetic isolation and lower polymorphism of the economically important *H. aimara* around an area of high fishing pressure should be considered in future management

policies. Once available, integrating more detailed information about species' life history traits and ecological requirements in a comparative population genetics framework, in addition to riverscape features, will be crucial to further identify the relative influence (and potential predictability) of riverscape and biological factors on genetic diversity in fish species in the Upper Maroni and at a larger scale.

The increasing anthropogenic pressures on Upper Maroni fish populations (e.g., water pollution, habitat degradation, fishing) raises questions about their vulnerability and threatens the prosperity of subsistence fishing in southern French Guiana. Their potential influence on life history traits (e.g., mean body size; Longin et al. 2021b) may also influence patterns of genetic variation and community dynamics at a larger scale (Evangelista et al. 2021). Although we observed no direct evidence of local anthropogenic genetic erosion in the study zone, these pressures can occur even if they are currently compensated by large N_e or gene flow. For instance, local anthropogenic genetic drift in downstream areas might be compensated by DIGD, thus making it difficult to identify these pervasive impacts. Thus, long-term patterns of genetic variation in the riverscape depend on the spatial variation in N_e, the intensity of anthropogenic pressure, and the strength and direction of inter-site gene flow. Methods to finely quantify the strength and direction of gene flow had too low power to provide reliable results with our low-density data (results not shown) and we were unable to identify any of the sampling sites as a source or sink of genetic variation. A less descriptive, more mechanistic study of processes that influence patterns of genetic variation in fishes in the Upper Maroni (e.g., combining high-density genomic tools with past and current demography inference) could provide important insights into the potential influence of anthropogenic pressures on fish populations. To develop sustainable management policies for fish stocks, it could help to use a simulation-based framework that explicitly incorporates all spatial features of the Upper Maroni and focuses specifically on distinguishing between natural evolutionary scenarios that generate DIGD, and scenarios that also include the influence of anthropogenic factors, like harvesting. This was considered beyond the scope of the current study, but identified as a priority focus for future work to illustrate long-term patterns of riverscape genetic variation under anthropogenic pressures in the Upper Maroni. In addition, long-term genetic monitoring could be a promising approach to follow patterns of genetic variation over time, identify a gradual loss of local or global riverscape genetic diversity (Mathieu-Bégné et al. 2018), and determine the influence of local pressures on intraspecific dynamics of an entire metapopulation (Palstra and Ruzzante 2011).

DATA AVAILABILITY

Supplementary notes, figures, and tables for this article are provided in MARONI_Appendix1.pdf. Individual genotypes and genetic diversity data used in the current study are accessible through the Dryad repository https://doi.org/10.5061/dryad.dbrv15f5n, as well as sequence information about the 31 additional SNPs used for species *C. meionactis*. The R command lines used to analyze those data are provided and commented in MARONI_Appendix2.pdf. There are no financial benefits to report.

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AUTHOR CONTRIBUTIONS

CD contributed to specimen and molecular data collection, designed and ran the analyses, and wrote the manuscript. EJP and SB contributed to the design of analyses and reviewed the manuscript. GL, RR, and RV organized fieldwork, contributed to specimen collection and reviewed the manuscript. J-MR, P-YLB, and SL conceptualized and supervised the research, contributed to specimen collection, contributed to the design of analyses and reviewed the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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COMPETING INTERESTS

The authors declare no competing interests.

ADDITIONAL INFORMATION

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