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RESEARCH ARTICLE

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How do rivers, geographic distance, and dispersal behavior influence genetic structure in two sympatric New World monkeys?

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Dispersal, one of the major factors affecting the gene flow between populations, shapes the spatial distribution of genetic diversity within species. *Alouatta macconnelli* and *Saguinus midas* are two Neotropical monkey species that sympatrically inhabit the Guiana shield in northern Amazonia and are likely to differ in their dispersal behavior and vagility. We took advantage of their sympatry to investigate, over a fine geographical scale (~50 km long), the relationship between spatial genetic structure, on the one hand, and geographical features and the species' dispersal behavior on the other. A total of 84 *A. macconnelli* individuals from 25 social units and 76 *S. midas* individuals from 19 social units were genotyped for nine microsatellite markers. Both species displayed high genetic diversity and allelic richness. However, patterns of genetic structure differed between the two species. In *A. macconnelli*, no genetic substructuring was observed, while in *S. midas* we detected significant structuring, but this structuring was not correlated with geographical features, such as the location of individuals relative to the river and/or the distance between them. Instead, the geographical distribution of genetic variation observed for each species is predominantly explained by each species' dispersal pattern. We identified bisexual dispersal for both species, but with significant differences, either in the distance or in the rate of dispersal, between species and sexes. Genetic relatedness within social units was higher in *S. midas* than in *A. macconnelli*: gene flow between social units seems limited in *S. midas*, especially for females, while high dispersal characterizes *A. macconnelli*, where females seem to disperse at lower rate but at a longer distance than males.

KEYWORDS
Alouatta macconnelli, dispersal, genetic structure, *Saguinus midas*, sex-bias, social organization

1 | INTRODUCTION

Several aspects of primate social organization, including mating behavior, group composition and dynamics (fission, fusion, etc.), and patterns of dispersal influence how genetic variation is partitioned among populations and between and within social groups (Di Fiore, 2012; Melnick, 1987). In primate species, several types of dispersal patterns (e.g., bisexual versus sex-biased) are observed (Di Fiore, 2012; Goldizen, 1988). Such diversity, commonly observed between species, may also be observed between populations of the same species (Di Fiore, 2012; Goldizen, 1988). Dispersal patterns are one component of a species' social organization and, at the same time, are potentially impacted by landscape features that can prevent or limit gene flow, thereby promoting divergence via genetic drift. Therefore, dispersal is one of the principal factors that influence how genetic variation is distributed across social and physical landscape.

A major current focus of population genetic studies is to disentangle the relative influences on a species' genetic structure that are due to biological properties of the species (such as behavior or social organization) versus those linked to the habitat features

(such as the physical landscape or environmental factors). One way is to compare patterns of genetic variation in sympatric species that experience the same environmental influences. Indeed, environmental factors, shared by sympatric taxa, could be at the origin of similar patterns of population genetic structure among different taxa (Avise, 2004; Gaither, Toonen, Robertson, Planes, & Bowen, 2010; Hewitt, 2000, 2004), while factors such as differences in dispersal behavior could contribute to diverse patterns of population structure for different species living in the same environment (e.g., Kyle & Boulding, 2000; Russo, Solé-Cava, & Thorpe, 1994; Zhang et al., 2012). Most comparative studies of population genetic structure have examined co-distributed taxa across broad spatial scales (e.g., Castoe, Spencer, & Parkinson, 2007; Chen et al., 2010; Haring, Gamauf, & Kryukov, 2007; Newton, Nassar, & Fleming, 2003). Geographic factors (e.g., major barriers to dispersal) are likely to impact dispersal at both broad and fine spatial scales and may influence different species in similar ways, whereas the differences between sympatric species in dispersal behavior are likely to act mainly at a finer scale (e.g., over the scale of several home-ranges). To date, limited attention has been paid to comparative examination of the population genetic structure of related vertebrate species, sampled at a fine scale in the same habitat, to evaluate consequences of physical barriers to gene flow (but see fishes [Dawson, Louie, Barlow, Jacobs, & Swift, 2002; Whiteley, Spruell, & Allendorf, 2004], frogs [Brede & Beebee, 2004; Pabijan, Wollenberg, & Vences, 2012], mammals [Kraaijeveld-Smit, Lindenmayer, Taylor, MacGregor, & Wertheim, 2007; Di Fiore, Link, Schmitt, & Spehar; Rossiter et al., 2012]). However, a recent review pointed the importance of quantifying environmental gradients and incorporating ecology in the analysis of population genetics (Orsini, Vanoverbeke, Swillen, Mergeay, & De Meester, 2013).

To evaluate the extent to which species' dispersal patterns, geographical distances, and landscape features, such as rivers, that may act as physical barriers to gene flow together influence the genetic characteristics of sympatric taxa, we studied two species of Neotropical primates: *Alouatta macconnelli* (Atelidae), the Guianan red howler monkey, and *Saguinus midas* (Cebidae), the golden-handed tamarin. These species differ in body size, and, although knowledge about their social systems is still limited and based mainly on inferences from related species, they likely differ in multiple aspects of social organization, including group size, group composition, and dispersal behavior. Howler monkey species live in multi-male/multi-female groups of variable size (Brockett, Horwich, & Jones, 2000; Clarke & Glander 2008; Horwich, Brockett, & Jones, 2000; Pope 1992; Van Belle, Estrada, Strier, & Di Fiore, 2012). They are characterized by bisexual dispersal with variation in the direction and degree of sex bias across species and environmental conditions (e.g., Clarke & Glander, 2008; Glander, 1992; Nidiffer & Cortes-Ortiz, 2015; Oklander, Kowalewski, & Corach, 2010; Pope, 1992, 2000; Van Belle et al., 2012). Tamarins, by contrast, tend to live in familial social groups, that consist of several breeding-age males and females within a functionally polyandrous single female-breeding system (French, Inglett, & Dethlefs, 1989; Goldizen, 1988; Goldizen, Mendelson, vanVlaardingen, & Terborgh, 1996; Huck, Lottker, Bohle, & Heymann, 2005; S. F. Ferrari & Ferrari, 1989; Sussman & Garber, 1987). Animals of both sexes may disperse (Goldizen & Terborgh, 1989; Goldizen et al., 1996; Lottker, Huck, & Heymann, 2004), and dispersal distances are, overall, relatively short, at least in *S. mystax* and *S. geoffroyi* (Diaz-Munoz & Ribeiro, 2014; Huck, Roos, & Heymann, 2007), although sometimes animals remain in their natal groups into adolescence or early adulthood and may breed or attempt to breed in their natal groups. Thus, although dispersal in both *Alouatta* and *Saguinus* is characterized as bisexual, dispersal distances seem to be more limited in *Saguinus* than in *Alouatta* species. This conclusion, however, is based only on a handful of studies of different species from those studied here (tamarins: *S. fuscicollis* [Goldizen et al., 1996] and *S. mystax* [Huck et al., 2007]; howler monkeys: *Alouatta seniculus* [Pope 1992]).

Along the Sinnamary River in French Guiana, these arboreal species live in the same forest (Gond et al., 2011) and in the same geomorphological landscape units (Guitet, Pélissier, Brunaux, Jaouen, & Sabatier, 2015), with no detectable environmental variation at this scale. This situation provides an opportunity to study the role of natural barriers to gene flow by controlling for the possible association of genetic differentiation with environmental variables. The role of rivers as barriers to gene flow in the Neotropics has been extensively debated. Ayres and Clutton-Brock (1992) first suggested that Amazonian rivers are effective barriers to primate species dispersal. They also found that the impact of those rivers is largely related to their width, seasonal and annual stability, rate of flow, and the ability of species to cross these ecological barriers. According to this framework, the rivers of the Guiana shield could potentially act as barriers to gene flow and have a significant effect on the structuring of genetic variation, possibly leading, to high genetic differentiation between individuals from opposite riverbank.

In this paper, we describe genetic variation and how it is patterned within and among groups of two sympatric neotropical primates, *A. macconnelli* and *S. midas*, from French Guiana that were sampled along and on each side of the Sinnamary River (~50 km long) and two of its tributaries. Using multi-locus microsatellite genotypes, we compared the fine-scale population genetic structures of these two species living in a common physical landscape. Specifically, we examined the relation between genetic structure and geographical distances and the impact of potential barriers to dispersal (a 60–300 m wide river and its tributaries) on the genetic structure of both species.

If individual dispersal distances are long, as may be the case for *Alouatta* species, we would expect to see little evidence of geographic structuring for this species. On the contrary, we predicted that the more limited dispersal distances of tamarins would be reflected by greater evidence of geographical structuring and a clear pattern of isolation by distance (IBD) (Avise, 2004; Di Fiore, 2012; Melnick, 1987).

We also tested the degree to which dispersal is sex-biased in both taxa and consider our findings in light of likely differences in dispersal behavior for males versus females in both taxa. In case of sex-biased dispersal, that is, strong male or female philopatry, in which individuals remain in their natal groups and reside as adults with same-sex kin, gene flow is expected to be highly restricted for the more philopatric sex, resulting in a greater degree of genetic variation and

differentiation across the landscape than that seen in the dispersing sex (Avise, 2004; Di Fiore, 2012; Goudet, Perrin, & Waser, 2002; Lawson Handley & Perrin, 2007; Melnick, 1987). For *A. macconnelli*, given the bisexual dispersal pattern and somewhat female biased dispersal behavior reported in other species of howler monkeys, we expected to find evidence of high levels of gene flow, potentially sex-biased, between social units, and little geographic substructuring. For *S. midas*, we expected to see evidence of more limited dispersal between social units and evidence of close genetic relationships among animals of both sexes within units and a significant geographical structuring. Finally, we expected that the river might make a more effective barrier to dispersal for the smaller, less vagile tamarins than for the howler monkeys.

2 | METHODS

2.1 | Biological material

A total of 114 red howler monkey individuals (*A. macconnelli*) and 90 golden-handed tamarin individuals (*S. midas*) were sampled in French Guiana on the Sinnamary River and its two main tributaries, Crique Tigre (CT, 20–50 m wide) and Crique Courcibo (CC, 30–70 m wide) (Figures 1 and 2). The width of the Sinnamary River, prior to the construction of the "Petit Saut" hydroelectric dam, varied from approximately 60–300 m (at the dam location), in the region surveyed. Our sampling occurred in 1994 and 1995 during a capture and translocation operation (Vié, 1999) during the filling of a dam reservoir that flooded ~400 km^2 of primary forest with water up to 35 m deep. As much as possible, we attempted to follow the recommendations of the IUCN Guidelines for reintroduction (IUCN, 1998) and translocations projects (Caldecott, & Kavanagh, 1988). The translocation operation included permanent surveys of the lake during the water rising period to identify the most critical areas and most highly threatened animals. Once isolated on immersed trees or branches, trapped monkeys were caught manually under the supervision of a biologist and/or a veterinarian. After an entire group was captured, the animals were transferred by boat to a veterinary facility, and each trip lasted 2 h or less.

The samples correspond to both solitary animals and to entire social groups comprising, for both species, from two to eight individuals. A total of 25 groups and 2 solitaries were sampled for *A. macconnelli*, and 19 groups and 2 solitaries were sampled for *S. midas* (Table S1). Due to the imprecision of the available maps and the unavailability of efficient personal GPS systems at the time of sampling, the capture locations were recorded on a 500 m grid associated with kilometric points departing from the dam and following the Sinnamary River course, up to 54 km upriver from the dam reservoir. The indication of the side of the river bank was also recorded (Table S1, Figures 1 and 2). For this study, we a posteriori assigned the coordinates of each social group on a geo-referenced map of the river, using ArcGis v. 10.2, superimposed on the grid, the location of capture being assigned at the centroid of the projected cells. The monkeys were captured in the flooded forest and anesthetized before being relocated to a nearby non-flooded site. Various minor clinical procedures were conducted, including a clinical examination, sampling of blood and external parasites, collection of body measurements, and skin biopsies from the ear (de Thoisy et al., 2001). The skin biopsies were kept in 90% alcohol, and the DNA was extracted using either with a Phenol-Chloroform procedure or the DNeasy Blood & Tissue Kit from Qiagen (Qiagen Inc., Valencia, CA), according to the manufacturer's instructions.

2.2 | Microsatellite genotyping

To avoid some of the confounding effects of family structure, we excluded juveniles and sub-adults from our analyses. We selected microsatellite markers that were identified in other New World monkey species *Sapajus* (formerly *Cebus*) *capucinus*, *Sapajus apella*, *Ateles belzebuth*, *Alouatta palliata*, *Alouatta caraya*, *Saguinus bicolor*, and *Lagothrix lagotricha* (see the references in Table S2). We initially screened 23 markers, 13 of which were subsequently chosen based on their polymorphism and genotyping peak quality: seven of them are tetranucleotide repeats and six are dinucleotides (Table S2). The markers were co-amplified in 10 µl of a mixture containing 5 µl of Qiagen Multiplex PCR Master Mix (Qiagen, Valencia, CA), 0.2 µM of each primer (the forward primers were 5′ labeled with a fluorescing molecule, 6-FAM or HEX), and 10 ng of template DNA in an Eppendorf Mastercycler programmed for 15 min of denaturing at 95°C, 35 cycles of 30 s at 94°C, 90 s at 50 or 60°C, and 60 s at 72°C, and a final extension at 72°C for 30 min. Alleles were scored on an ABI 3130 XL at Genopole (Toulouse-Midi-Pyrenees) using GeneMapper (v. 3.7) for verification and correction. We reamplified, at least three times, damaged samples by optimizing their PCR conditions, such as the annealing temperature, DNA concentration, and number of cycles. Because the microsatellites were developed from related species, we sequenced one allele of each locus from the individuals genotyped as homozygotes. The PCR products were directly sequenced on both strands.

2.3 | Population genetic analyses

The raw data were checked for potential scoring errors such as stutter bands, null alleles (NA), and large allele dropout using Micro-Checker 2.2.3 (Van Oosterhout et al., 2004). Possible linkage disequilibrium (LD) among pairs of loci were evaluated using Fstat v. 2.9 (Goudet, 2001), with the corresponding p values (p) adjusted for multiple comparisons with a Bonferroni procedure ($\alpha = 0.05$). The level of genetic variation at the population level was measured as the mean number of alleles per locus (MNA) and the observed (Ho) and expected (He) heterozygosities. To avoid biased estimates of genetic diversity due to sample size differences, we estimated the allelic richness (AR) per locus and per sample using the rarefaction approach in Fstat (Goudet, 2001). The standard sample size consisted of the smallest species sample with a complete genotype at all loci ($N = 65$ individuals). For each population and locus, tests for deviation from Hardy–Weinberg equilibrium (HWE) were conducted in Genepop (Rousset, 2008). The significance levels of the tests were obtained using a Markov chain of 100,000 steps.

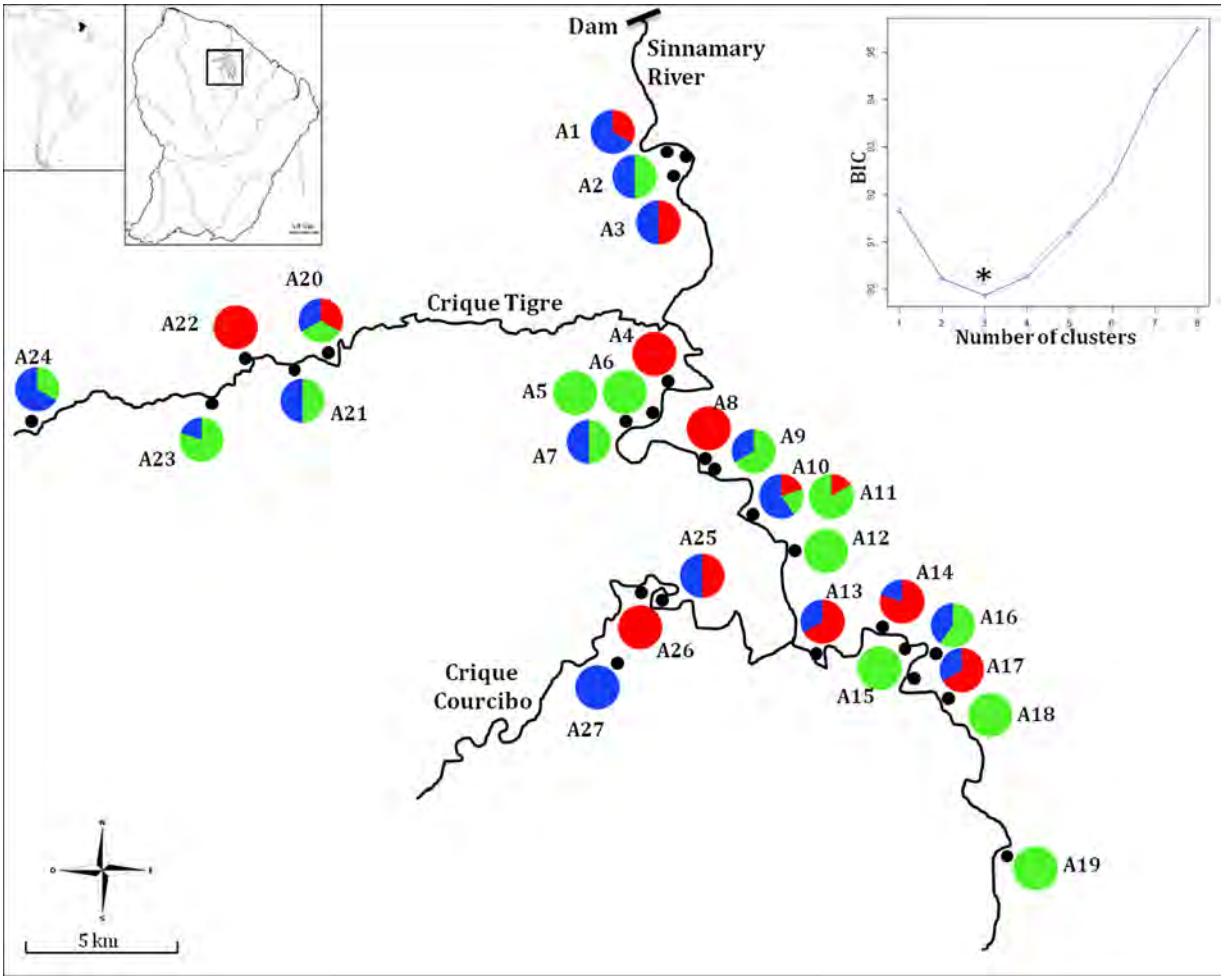

FIGURE 1 Map of French Guiana showing the geographic distribution of the *A. macconnelli* social units sampled along the Sinnamary River and its tributaries. The numbers refer to Table SI. The pie charts refer to the variance distribution for $K = 3$ (DAPC analysis)

To investigate the level of genetic differentiation among social groups, we estimated pairwise F_{ST} values between social units, and their significance, using Genetix v. 4.05.2 (Belkhir, Borsa, Chikhi, Raufaste, & Bonhomme, 2004). To avoid the bias of small effective groups, we used data only from social units with greater than three adult individuals; genotypes from solitary individuals as well as those animals with three or more untyped loci were excluded from the analysis (Table S1). We also estimated pairwise F_{ST} between individuals located on different rivers (i.e., the Sinnamary and its tributaries) and riverbanks (left versus right) to test the effect of the river on genetic differentiation. Hierarchical analysis of molecular variance (AMOVA) was computed using Arlequin v3.5 (Excoffier, Laval, & Schneider) and the significance of the genetic structure was tested using 10,000 permutations. Variance components were extracted for three hierarchical levels: (1) among individuals within social groups; (2) among social groups within geographical clusters; and (3) among geographical clusters. The geographical clusters were partitioned according two different structures: the riverbanks (separating social groups from the left and right banks of the Sinnamary River) and the water course (separating social groups along the Sinnamary river versus the tributaries).

We estimated isolation by distance (IBD), analyzing the correlation between the genetic differentiation (represented by individual-by-individual genetic distance for codominant data) and geographical distance (represented by $\log_{10}$ [Distance in km]) between social groups. Pairwise inter-individual genetic distances (codominant genotypic distances; Smouse & Peakall, 1999) were calculated in GeneAIEx v. 6.2 (Peakall & Smouse, 2006) and the linear Euclidian distances between individuals were estimated using ArcGIS v. 10.2 (ESRI, Redlands, CA) from the estimated geographic coordinates assigned to the individuals' social groups. Mantel tests were conducted at the population level with the ade4 package (Chessel, Dufour, & Thioulouse, 2004) for R 3.1.0 (R Development Core Team, 2012), with males and females examined separately. We tested the difference in the correlation coefficient between genetic differentiation and geographical distance for males versus females using 10,000 randomizations: we tested whether the observed difference exceeded the 95% confidence intervals (CI) of a null distribution obtained by randomly assigning sex to individuals, according to observed proportions of males and females in the dataset.

The spatial autocorrelation analysis was conducted with GeneAIEx (Peakall & Smouse, 2006). The spatial autocorrelation coefficient r was generated using the geographic distance between

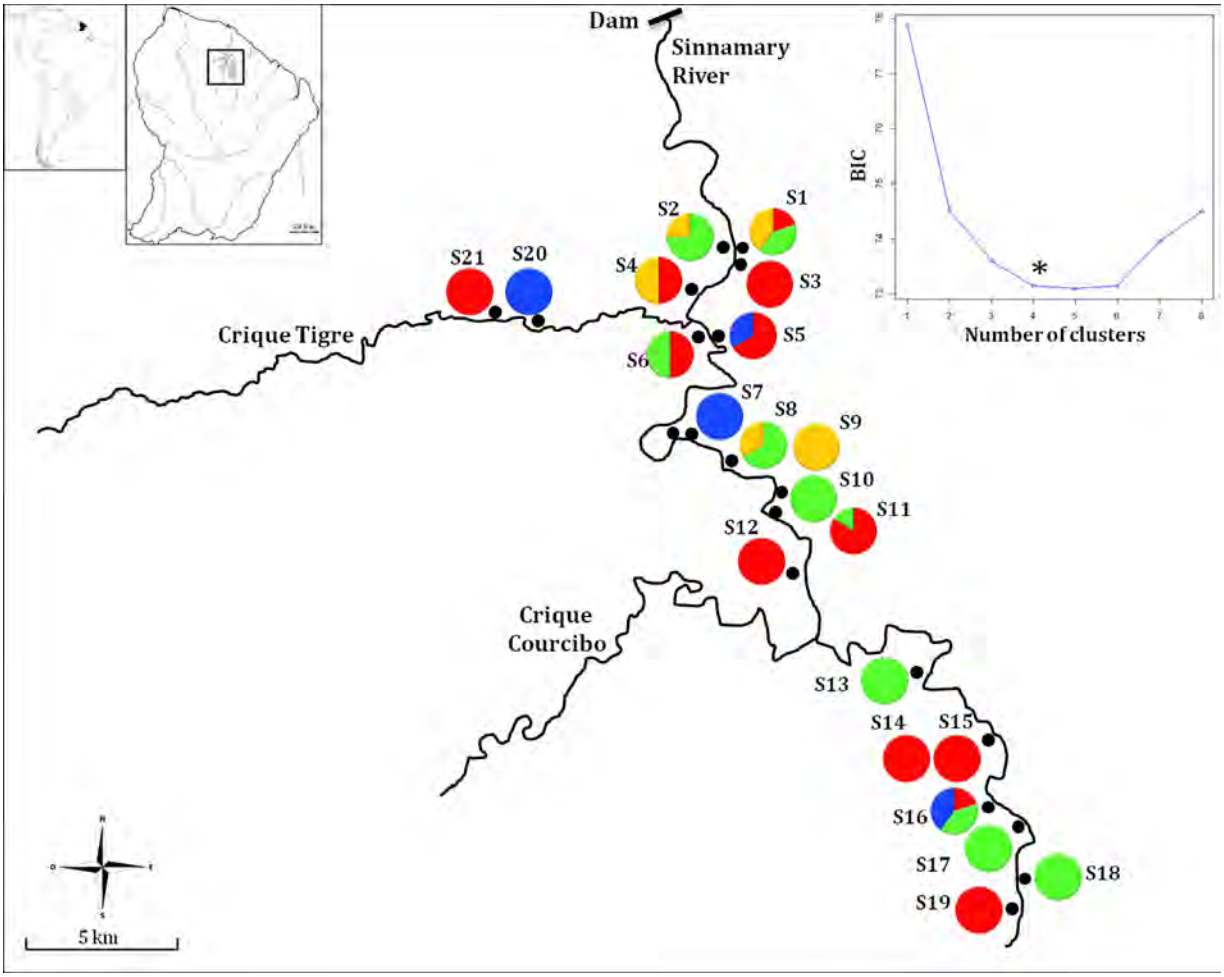

FIGURE 2 Map of French Guiana showing the geographic distribution of the *S. midas* social units sampled along the Sinnamary River and its tributaries. The numbers refer to Table SI. The pie charts refer to the variance distribution for $K = 4$ (DAPC analysis)

social groups, determined as explained above, and the genetic distances from multi-locus genotypes, which were calculated following Smouse and Peakall (1999). Values of *r* allow determination of the geographic scale at which individuals are genetically related; the distance between the samples for which *r* does not significantly differ from zero provides an approximation of the distance where population structure can be detected (Peakall, Ruibal, & Lindenmayer, 2003). Statistical significance tests were performed using random permutations: each test was based on 10,000 permutations and 10,000 bootstraps to define the upper and lower bounds of the 95% CI of *r*. The distance-class bounds were based on the distribution of the pairwise geographic distances between social groups. We tested several distance class sizes and used a distance class size of 500 m because it allowed for distinguishing the relationships within groups as well as those between neighbor groups and distant groups. Moreover, these classes are suitable for testing sex-biased dispersal (Banks & Peakall, 2012).

To infer possible population structure from the microsatellite data set, we used two model-based approaches, Structure (Pritchard, Stephens, & Donnelly, 2000) and Geneland (Guillot, Mortier, & Estoup, 2005), as well as an exploratory method, Discriminant Analysis of Principal Components (DAPC). Individual-based Bayesian assignment tests implemented in Structure v2.3.4 (Pritchard, Stephens, & Donnelly, 2000) were used to infer population structure from the microsatellite data set. To determine the most likely number of genetic clusters (*K*), 15 independent replicates were run for values of *K* ranging from 1 to 13. For each replicate, tests were run with 50,000 burn-in steps followed by 200,000 Markov Chain Monte Carlo replications. All the tests were run under an admixture model assuming correlated allele frequencies. The most likely *K* was determined using the method of Evanno, Regnaut, and Goudet (2005). Geneland v.4.0.2 (Guillot et al., 2005) uses spatial coordinates and genotypes to map the range of genetic clusters in the space and assign individuals to each subpopulation. We evaluated the optimal *K* from 1 to 10, with 10,000 MCMC iterations.

One of the shortcomings of these Bayesian clustering methods concerns their assumptions, that is, HWE and linkage equilibrium. Both of our studied populations comprise social groups with inbreeding potential, so model assumptions may not always be verifiable, which restricts the applicability of such approaches to our data. We thus applied DAPC, a multi-variate method designed to identify and describe clusters of genetically related individuals with principal components analysis (PCA), as a prior step to discriminant analysis (DA), using the adegenet (Jombart, 2008) and ade4 packages (Chessel et al., 2004) for *R*. The variables submitted to DA are perfectly

uncorrelated, and their number is less than that of the analyzed individuals (Jombart, Devillard, & Balloux, 2010).

3 | RESULTS

Five common microsatellite loci were successfully amplified in both species (Ceb10, Ceb121, Ceb128, Sb38, and PEPC8), and eight additional loci differed between the species (4 per species). Each individual was thus genotyped at a total of nine polymorphic microsatellites (Table S1). The poor quality of certain samples (presumably due to bad conservation conditions), induced a partial failure of the genotyping (≤3 markers) for ~20% of the *A. macconnelli* and 7% of the *S. midas* individuals. A total of 84 *A. macconnelli* from 25 social groups and 2 solitaries (35 males, 48 females, plus 1 unsexed) and 76 *S. midas* from 19 groups and 2 solitaries (48 males and 28 females) were successfully genotyped, for at least six loci, by the multiplexing of two to three markers (Table S2). Because the primers were designed from different New World monkeys (see references in Table S2), the repeat motif and surrounding sequences were verified by sequencing specific alleles for each species. No linkage disequilibrium was detected between any pair of markers ($p < 0.05$ after Bonferroni correction) for either *A. macconnelli* or *S. midas*.

3.1 | Genetic diversity in *A. macconnelli and S. midas*

The genetic diversity of *A. macconnelli* and *S. midas* was high, as can be seen in Table 1. The parameter comparisons between the two species might have been biased since the markers genotyped differed between the two species, but the average observed genetic diversity of these species, using only the five common markers, (Ceb10, Ceb121, Ceb128, SB38, and PEPC8) is comparable to that obtained with all the markers (Table 1, Ho values of 0.717 versus 0.748 and 0.747 versus 0.737, for *A. macconnelli* and *S. midas*, respectively). The number of alleles per locus ranged from 7 to 14 for *A. macconnelli* and from 6 to 12 for *S. midas*. The allelic richness, standardized for 65 individuals based on the common loci, was 8.0 (±SD 0.73) for *A. macconnelli* and 8.65 (±SD 2.82) for *S. midas* (Table 1). A significant departure from HWE was detected for two out of the nine markers ($p < 0.001$) for each species. This heterozygote deficiency suggests that significant null allele frequencies exist for these markers (estimated to be 8% and 23%, respectively, for *A. macconnelli* Ceb121 and PEPC8; estimated to be ~15% for *S. midas* Ceb121 and Ab16). The F_{IS} fixation indexes, although weak for the two species, were significant and positive ($F_{IS} = 0.070$ for *A. macconnelli* and $F_{IS} = 0.066$ for *S. midas*, on average), but did not significantly differ from 0 if the two loci with a high estimated frequency of null alleles were discarded.

In *A. macconnelli*, the distributions of the inter-individual genetic distances observed within (13.42 ± SD 3.7) and between social groups (16.20 ± SD 3.1) were quite similar. In contrast, these distributions were different for *S. midas*, with a mean intra-group distance of 9.8 (±SD 3.5), much lower than the mean distance calculated between social groups (16.3 ± SD 3.1).

3.2 | Population structuring and isolation by distance

Two data sets were analyzed: the first set included all the genotyped samples, and the second set excluded samples with three or more missing genotyping data points. As no significant difference between the two data sets was observed, only the results for the first set (76 individuals for *S. midas* and 84 for *A. macconnelli*) are presented and discussed.

The genetic differentiation between *A. macconnelli* social groups ($N = 9$), estimated using F_{ST} indexes, showed globally low values (mean $F_{ST} = 0.09 \pm$ SD 0.05), ranging from 0.00 to 0.18, although significantly different from 0 for 24 of the 36 pairwise comparisons (Table S3). Significant genetic differentiation was even observed between geographically close groups on the same river bank (e.g., $F_{ST} = 0.11$, $p = 0.016$ for A14 versus A16, which are separated by only 2 km), while no significant genetic differentiation was observed between some groups located on opposite banks (for A6 and A16, separated by 10 km, $F_{ST} = 0.02$, $p > 0.05$). Moreover, the two groups sampled in the tributaries (CT: A23 and CC: A27) significantly differed from all the other groups along the Sinnamary. We identified no significant genetic differentiation between individuals from the opposite riverbanks of either the Sinnamary or the Crique Courcibo ($F_{ST} = 0.002$ to 0.004, $p > 0.05$), but we did find significant differentiation between samples from different rivers ($F_{ST} = 0.03$ to 0.11, $p < 0.05$), as well as between opposite riverbanks of the Crique Tigre ($F_{ST} = 0.08$, $p < 0.01$) (Table S4). The hierarchical analyses of molecular variance revealed no significant partitioning among geographical clusters (opposite Sinnamary riverbanks or "Sinnamary river" vs. "tributaries") explaining a very low percentage of the genetic variance (<0.5%). However, a significant partitioning of genetic variation was revealed among the social groups within geographical clusters, explaining in the two structures tested ~7.5% of the genetic variance ($p < 0.001$) with ~92% of the genetic variance within social groups (Table S5).

For *S. midas*, a noteworthy genetic differentiation was observed between social groups ($N = 9$, mean $F_{ST} = 0.22 \pm$ SD 0.09, from 0 to 0.37, $p < 0.01$), with significant F_{ST} values for 35 pairwise comparisons out of 36 (Table S3). This significant differentiation can be observed between physically proximal social groups, both on the same bank of the river (e.g., S15 vs. S16, 3 km apart, $F_{ST} = 0.13$, $p < 0.01$) and on the opposite banks (S1 vs. S2, $F_{ST} = 0.12$, $p < 0.01$). However, this genetic differentiation, surprisingly high between social groups, should be considered cautiously because our data set does not completely adhere to the models of population genetics upon which the estimator is based (model of panmictic population with unrelated individuals) (Pearse & Crandall, 2004). We identified a significant differentiation that is higher between rivers ($F_{ST} = 0.07$–0.09, $p < 0.01$), than opposite river banks ($F_{ST} = 0.03$, $p < 0.01$, Table S4). These results are congruent with the hierarchical analyses of molecular variance (AMOVA), which revealed significant partitioning between the Sinnamary river and its tributaries, explaining 5.5% of the overall genetic variance ($p < 0.05$), whereas less than 1% of the genetic variance is distributed among the opposite Sinnamary riverbanks (Table S5). We also observed a significant partitioning among social groups within geographical clusters (opposite Sinnamary riverbanks or "Sinnamary river" vs.

TABLE 1 Summary statistics by locus and species based on nine microsatellite loci (5 in common)

Alouatta macconnelli							*Saguinus midas*						
Locus	***N***	**NA**	**AR**	**He**	**Ho**	F_{IS}	**Locus**	***N***	**NA**	**AR**	**He**	**Ho**	F_{IS}
Ceb128	83	7	7.00	0.784	0.795	−0.008	Ceb128	65	7	7.00	0.773	0.692	0.112
Sb38	84	8	7.61	0.740	0.750	−0.007	Sb38	75	12	11.83	0.833	0.827	0.014
PEPC8	71	8	8.00	0.854	0.690	0.198*	PEPC8	76	12	11.57	0.865	0.882	−0.012
Ceb121	80	9	8.60	0.786	0.663	0.163*	Ceb121	73	7	7.00	0.768	0.534	0.311*
Ceb10	83	9	8.80	0.684	0.687	0.002	Ceb10	76	6	5.86	0.751	0.803	−0.062
Mean 5 loci	80	8.20	8.00	0.770	0.717		Mean 5 loci	73	8.80	8.65	0.798	0.747	
D8S165	83	11	10.66	0.805	0.759	0.063	Ceb120	75	6	5.98	0.702	0.760	−0.076
AC45	84	14	13.63	0.860	0.810	0.065	Ceb11	76	12	11.96	0.846	0.895	−0.051
L1118	84	13	12.47	0.857	0.845	0.019	Ab16	71	10	9.75	0.823	0.563	0.322*
AP68	84	9	8.83	0.806	0.738	0.090	Sb7	75	7	6.87	0.708	0.680	0.047
Mean	81.8	9.78	9.51	0.797	0.748		Mean	73.6	8.78	8.64	0.786	0.737	

N, number of genotyped individuals; NA, number of alleles; AR, allelic richness based on 65 individuals; He, unbiased expected heterozygosity; H_0, observed heterozygosity; F_{IS}, fixation index per locus.
*Significant values, $p < 0.01$.

"tributaries"), explaining ~15.5% of the total genetic variance ($p < 0.001$), while ~80% of the genetic variance was observed within social groups (Table S5).

We found a weak but significant correlation between the genetic and geographical distances among samples of both species *A. macconnelli* and *S. midas* (coefficient of correlation $r = 0.104$ and $r = 0.173$, $p < 0.05$, respectively, data not shown); however, only a small fraction of the genetic variance is explained by IBD. When males and females are examined separately, we found a significant correlation for both sexes in *S. midas* ($r = 0.285$ vs. $r = 0.162$, $p < 0.001$, for the females and males, respectively), but only for females of *A. macconnelli* ($r = 0.129$, $p < 0.001$ vs. $r = 0.059$, $p > 0.05$). Interestingly, in both species, we observed a significant higher IBD for females than males (randomization test, $p < 0.05$).

3.3 | Spatial autocorrelation

As illustrated in Figure 3, the spatial autocorrelation analysis revealed for both species significant positive spatial genetic structure ($p < 0.001$) for the first distance class representing within-unit comparisons. However, the level of autocorrelation r was higher for *S. midas* than for *A. macconnelli* ($r = 0.38$ vs. 0.15, respectively; Figure 3). Moreover, for *S. midas* only, an extension of this phenomenon to the less than or equal to 500 m distance class, which included close neighbor social units, was observed ($r = 0.15$). The spatial autocorrelation analyses that were run separately for males and females revealed results that differed according to sex and species, and none of them completely matched the outcomes obtained using the total data set (males and females together). Within *S. midas*, similar r values were observed in females and males for the within-unit comparisons (Figure 3). However, a higher r value between close neighbor units was observed in females ($r = 0.388$) compared with males ($r = 0.107$, Figure 3). The opposite pattern was observed in *A. macconnelli*, with higher autocorrelation values noted in females ($r = 0.254$) compared with males ($r = 0.164$, Figure 3) for the within-unit comparisons. The pattern differed for the comparisons between close neighbor units, with males showing significantly stronger genetic structure than females (significant positive values up to the 2nd class for males, but not for females), as well as a higher autocorrelation value for males ($r = 0.160$) than for females ($r = 0.025$, Figure 3).

3.4 | Identification of population units

Our analyses based on F_{ST} genetic differentiation between social groups may be biased due to small sample size (between 4 and 6 or 7 specimens, according to the species) and individual relatedness. Thus, we conducted a clustering analysis that does not require prior population information or spatial data (Structure). Calculations of deltaK produced a modal value of the statistic at $K = 1$. The resulting clustering revealed no substructuring for *A. macconnelli* (one genetic cluster) and an optimal number of genetic clusters of five ($K = 5$) for *S. midas*. Ignoring the markers with deviation from HWE, the optimal number of *S. midas* genetic clusters was two ($K = 2$) (supplementary Figure S1). For *S. midas*, two points can be highlighted. The two genetic clusters did not globally follow the geographic localization of the social units, and, even if individuals in the same social unit were globally assigned to the same cluster, approximately half of the units displayed individuals with mixed assignation (<80% assignation to a single cluster). With increasing K, a more fine-grained population structure was revealed. For $K = 3$, individuals from the two neighbor social units S14 and S15 differed from all the others, with the exception of the closest unit (S13), which had an assignation of only 50%.

Using Geneland, which applies Bayesian model-based spatial clustering and provides information on the area of the sampling probabilities for the individuals in space, no genetic structuring was inferred between the *A. macconnelli* social units. However, the *S. midas* social groups were assigned to six genetic clusters unlinked to the spatial geographic distribution (data not shown). Although minor differences were apparent in the assignment of single individuals, the results obtained by Geneland were globally consistent with the results obtained by Structure. The populations being structured in social groups, the

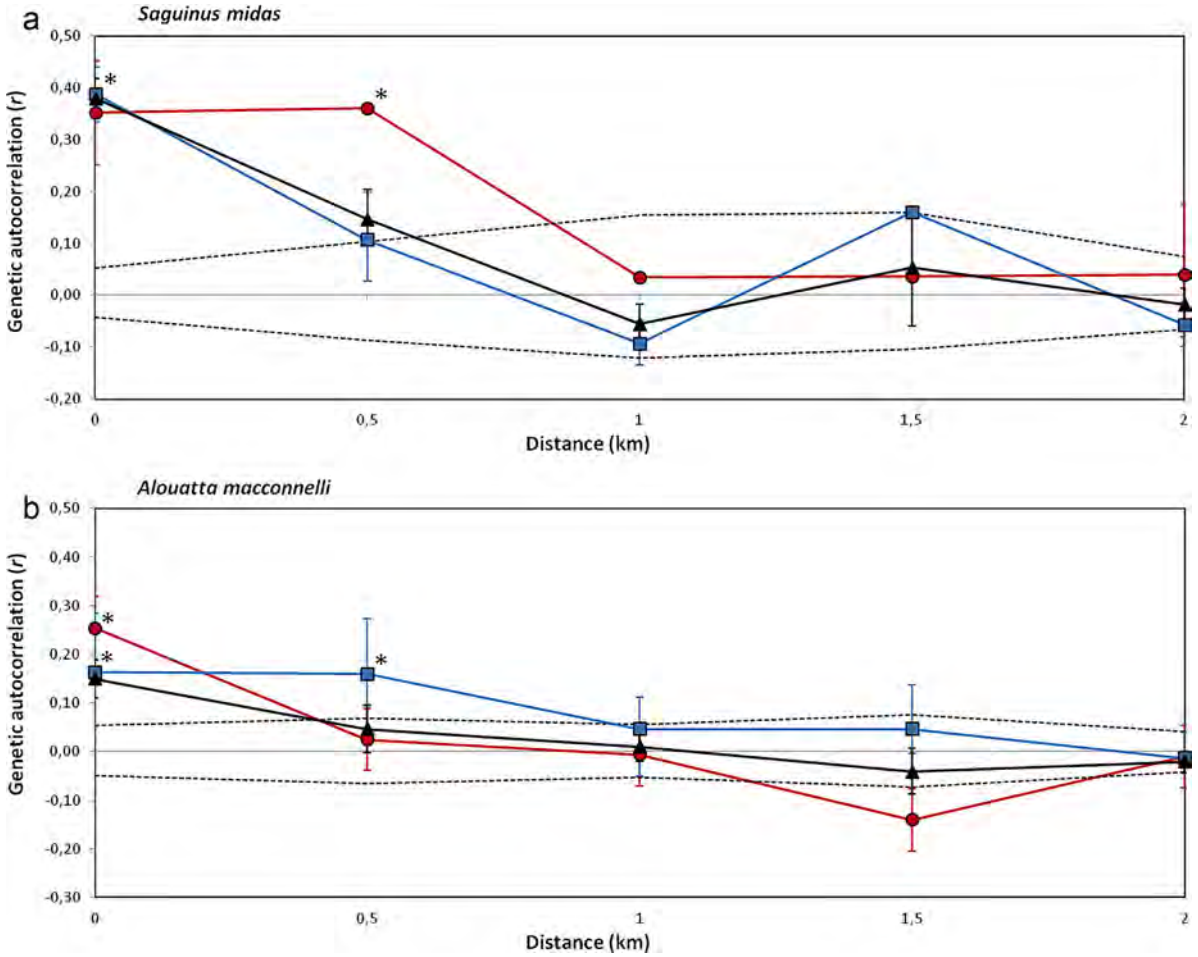

FIGURE 3 Correlogram plots of the genetic correlation coefficient (*r*) as a function of the geographic distance between (A) *S. midas*, with all mature individuals ($n = 76$) in black, adult females only ($n = 28$) in red, and adult males only ($n = 48$) in blue; (B) *A. macconnelli*, with all mature individuals ($n = 84$) in black, adult females only ($n = 48$) in red, and adult males only ($n = 35$) in blue. The 95% confidence interval with reference to the null hypothesis of a random distribution of genotypes (dashed lines) and bootstrapped 95% confidence error bars are shown. The asterisks denote significantly positive *r* values at $\alpha = 0.05$. All the individuals of the same group fall within the 0 km distance class

HWE and linkage equilibrium were not always verified, restricting the applicability of Bayesian clustering methods to our samples.

DAPC, a multi-variate method designed to identify and describe clusters of genetically related individuals, revealed a low degree of inferred structuring at $K = 3$ (59% of the variance, Figure 1) for *A. macconnelli*; indeed, the different clustering solutions show low variation when they are compared using the Bayesian Information Criterion (BIC). For *S. midas*, four genetic clusters were identified ($K = 4$; 48% of the variance), and the assignation of an entire social group to one cluster was higher than that in Structure (Figures 2 and S1). As observed with our Structure analyses, no geographical pattern, linked either to distance or localization on the banks of the river, emerged.

4 | DISCUSSION

A. macconnelli (Atelidae) and *S. midas* (Callithrichidae), New World monkeys of the Northern Amazonian region, were sampled along the Sinnamary river, upstream of the dam and prior to its modification by the dam reservoir. We took advantage of their sympatry and variation in social organization to test, on a fine scale, hypotheses about the factors involved in their genetic diversity patterns and population genetic structuring.

The genetic diversity found in our two studied species was surprisingly high (He ~ 80%, AR ~ 9) given the restricted sampling area surveyed, and including social units comprising individuals not completely unrelated. Although a few population genetic studies with equally fine scale sampling have shown similar heterozygosity values (He = 0.71 to He = 0.81: *Lagothrix lagotricha*, *Saguinus mystax*, *Saguinus weddelli*, and *Saimiri oerstedii* (Blair & Melnick, 2012; Di Fiore & Fleischer 2004, 2005; Garber, Porter, Spross, & Di Fiore, 2015; Huck et al., 2007), the published genetic diversity has been relatively lower (He = 0.56 to He = 0.64) in the majority of the New World monkeys studied, including other *Saguinus* and *Alouatta* species (e.g., Diaz-Munoz, 2012; Hagell, Whipple, & Chambers, 2013; Milton, Lozier, & Lacey, 2009; Nidiffer and Cortes-Ortiz 2015; Ruiz-Garcia et al., 2014; Van Belle et al., 2012).

On the Guiana shield, the rivers in their current courses originated in the Pleistocene, after the last marine introgression (Lujan, Armbruster, Albert, & Reis, 2011). Since then, the geological evidence

suggests that they remained more channeled over years and seasons, contrary to many white-water watercourses of the Amazonia basin (Bates, Haffer, & Grismer, 2004). Despite the long-term stability of the Sinnamary watercourse, we found no evidence that it acts as barrier to gene flow. Also, in the region surveyed, we found no evidence for genetic substructuring in *A. macconnelli*, while genetic differentiation and structuring were observed in *S. midas*. These contrasted patterns are probably not related to their generation times since they are quite similar (5 years for *Alouatta* [cited in Milton et al., 2009] versus three years for *Saguinus* [Farias, Santos, Gordo, & Hrbek, 2015 for *Saguinus bicolor*]). The genetic diversity patterns observed in both species are not consistent with the role of the Sinnamary River as a potential barrier to gene flow, or with the geographical distances between social units. Indeed, for each species, the location on riverbanks explained only a minor part of the genetic variation (<1%) with no effect on the differentiation between social units from opposite river bank. Moreover, we detected only a weak isolation-by-distance (IBD) pattern, as IBD explains a minor part of the variation (R^2 ~1% and 3% for *A. macconnelli* and *S. midas*, respectively). This suggests that both of these systems are characterized by extensive gene flow across the geographical scale sampled in the present study. Previous fine-scale genetic studies also detected little or no evidence of IBD in *A. seniculus* or *A. caraya* (Oklander et al., 2010; Pope, 1992). A similar fine geographical IBD pattern was previously reported in gorilla populations of mature individuals (Roy, Gray, Stoinski, Robbins, & Vigilant, 2014). However, some limitations with our samples are worth noting. Although our data are supported statistically, our sample is linearly distributed along the river, and we likely under-estimated the association between genetic and geographic distances. IBD might become highly significant if the sampling were to include social units farther away from the river, that is, on a larger geographical scale. We note, for both species, that the social units located on tributaries appeared clearly differentiated from those located along the Sinnamary, and this was especially true for *S. midas*, for which ~5% of the genetic variation was explained by the partitioning between the Sinnamary and its tributary. The genetic diversity patterns are rather linked to the life-traits of the two species than to geographical features.

In *A. macconnelli*, the low genetic autocorrelation signal between all the mature individuals within social group, as well as the distribution of the inter-individual genetic distances between and within social groups, suggest dispersal by both sexes. This is consistent with the social organization observed in other *Alouatta* species wherein adults can disperse across large distances and form or join other groups to reproduce (although certain members of either sex can remain in their natal social groups as adults) (e.g., Brockett et al., 2000; Clarke & Glander, 2008; Pope, 1992; Van Belle et al., 2012). We found evidence that *A. macconnelli* adults, living in adjacent groups, were on average more closely related to each other genetically than those living in more remote groups. Moreover, females had higher spatial autocorrelation coefficients within units than males that suggest, together with the significant IBD pattern in females only, a propensity for the females to disperse at a lower rate than the males. In males only, the level of autocorrelation was both significant and similar within units and between neighbor units (second distance class), suggesting a lower dispersal distance than in females. These results are consistent with previous reports of dispersal distance in different howler species (Crockett, 1998; Glander, 1992; Pope, 1992). Although dispersal in *Alouatta* species is characterized as bisexual, dispersal pattern variations have been reported, particularly concerning the proportion of females and males that remain in their natal group versus those that disperse and the occurrence of transient or secondary dispersal (e.g., Clarke and Glander, 2008; Nidiffer & Cortes-Ortiz, 2015; Pope 1992, 2000; Van Belle et al., 2012). Dispersal has been described to be female-biased in *A. palliata* (Glander, 1992) but male-biased in *A. seniculus* (Crockett & Pope, 1993) and *A. caraya* (Oklander et al., 2010), as seems to be the case for *A. macconnelli* in French Guiana.

In contrast, *S. midas* individuals are more highly related within groups than those of *A. macconnelli*, as shown by the distribution of the genetic distances across social groups and the high level of spatial autocorrelation. The limited gene flow between *S. midas* social groups is consistent with the social organization of tamarins that consist of several breeding-age males and females within a functionally polyandrous breeding system (Goldizen, 1988; French et al., 1989; Goldizen et al., 1996; Huck et al., 2005; S. F. Ferrari & Ferrari, 1989; Sussman & Garber, 1987). Interestingly, cooperative polyandry and limited individual dispersal distance have been observed to limit gene flow in other *Saguinus* species (Diaz-Munoz & Ribeiro, 2014; Goldizen et al., 1996; Huck et al., 2007). Moreover, we found evidence that the level of spatial autocorrelation within social groups was similar and high for both sexes. This close genetic relationship within social group suggests either that the individuals remain in their natal group (philopatry) or that same-sexed relatives emigrate into the same social group. Our results are consistent with patterns identified in other *Saguinus* species. Actually, both observational and genetic studies have found dispersal by both sexes (Garber, On, Moya, & Pruetz, 1993; Goldizen & Terborgh, 1989; Goldizen et al., 1996; Lottker et al., 2004). Although sometimes animals remain in their natal groups where they may breed or attempt to breed, males may more commonly leave their natal group and sometimes disperse in pairs (fraternal cooperative polyandry) (Diaz-Munoz, 2011; Garber et al., 1993, 2015; Huck et al., 2005). Moreover, genetic data from *S. mystax* suggests that females may disperse over longer distances than males, that is, into the adjacent and over-next home-ranges, perhaps due to limited reproductive opportunities in a polyandrous social mating system (Huck et al., 2007). Conversely, in *S. midas* adult females living in adjacent groups were, on average, genetically more closely related to each other than males, which is consistent with the observed IBD patterns, suggesting a more restricted or a shorter distance dispersal by females.

Although we found that the patterning of genetic variation observed in both species does not seem to be tied to geographic features, we cannot completely eliminate confounding factors due to the habitat, defined here as "geographical" and not based on ecological features. Indeed, even in the same biogeographic area, dispersal patterns may also vary between species with the presence of competing species, and with the distribution and phenology of food resources (Henzi, Lycett, & Piper, 1997; Koenig, Beise, Chalise, & Ganzhorn, 1998;

Sinha, Mukhopadhyay, Datta-Roy, & Ram, 2005): population dynamics of different species will likely react differently to mid and short term oscillations of phenology (Peres, 1994; Silva et al., 2013).

5 | CONCLUSIONS

The primary objectives of this study were to characterize and compare the genetic diversity in howler monkey and golden-handed tamarin populations, located along the Sinnamary River upstream of a dam before it was filled. Our study provides a framework for future studies. First, elucidating the genetic diversity of these wild primate populations, which were sampled two decades ago, is a useful foundation for comparative studies of genetic structure before and after the dam construction, as well as for the development of conservation strategies aimed at protecting these primate species. Second, this genetic diversity study provides a useful base to better understand the social organization of these species, which are difficult to follow in the field, particularly as regards their within and inter-group relatedness.

At the scale observed, the genetic structuring of both species was more highly impacted by their social organization than by distance or geographical features. Multiplication of dams in Amazonia will isolate genetically populations, with long-term loss of diversity in the future (Benchimol & Peres, 2015). Although we did not identify the river in its original course as a barrier to dispersal, the ensuing reservoir created as a function of damming is currently a much more tangible dispersal barrier for both species. Our data, derived from samples gathered prior to this large scale disturbance, could provide baselines to assess how their genetic diversities have been impacted by the fragmentation due to anthropogenic factors, such as the construction of the current reservoir.

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