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ORIGINAL ARTICLE

French Guiana Amerindian demographic history as revealed by autosomal and Y-chromosome STRs

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Abstract

Background: Previous investigations of French Guiana Amerindians performed by this group included blood group and protein genetic markers, mitochondrial DNA and Y-chromosome investigations. Molecular autosomal data and more extensive Y-chromosome determinations were lacking.

Subjects and methods: The genetic variability of 15 autosome (ASTRs) and 17 Y-chromosome (YSTRs) microsatellite loci was studied in four French Guiana (Emerillon, Palikur, Wayampi, Kali'na) and one Brazilian (Apalai) Amerindian populations. A sixth group, the Peruvian Matsiguenga of the Maipurean linguistic family, was included in the data analysis since they could provide information about the past migration of people from that linguistic stock into northeastern Amazonia.

Results: Marked ASTR and YSTR variability was found, with 96% of the YSTR haplotypes being found in one population only. There was excellent agreement between the present and previous autosomal or uniparental results. Multidimensional scaling based on F_{ST} genetic distances and population structure analysis revealed heterogeneity in gene distribution, with a clear difference between the Matsiguenga and Emerillon and the other groups. In the latter, Wilcoxon sign-rank test between observed and expected heterozygosity and the mode of allele frequency distribution revealed clues of a significant past genetic bottleneck. The Wayampi stand genetically closer to the Apalai, Palikur and Kali'na when examined for the autosome but not the Y-chromosome panel of markers, suggesting preferential female gene flow.

Conclusion: The new data provided additional important information about the biological history of people from a remote South American region, indicating how gene diversity analyses can be used to increase understanding of human microevolutionary processes.

Keywords: French Guiana, Amerindians, microsatellites, bottleneck events

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Introduction

French Guiana is located in South America approximately between latitudes 2° and 5°50' North and longitudes 51°30' and 54°40' West, on the eastern part of the vast Guiana Plateau that straddles Venezuela, northern Brazil and the three Guianas, which consist of the former Dutch and British colonies and the present French department. The French Guianan region is made up of a Precambrian insular shelf mostly covered by Amazonian rainforest bordered by littoral sandy savannah and mangrove swamps.

The coastal part of this apparently harsh environment was settled as early as 100 AD by members of the Maipurean branch of the Arawak linguistic family, followed by Karib-speaking populations circa 900 AD (Grenand and Grenand 1985; Rostain 1994). The Maipure originated from northern Peru, the Karib from either Venezuela, the Guiana Plateau or even the upper Xingu (Urban 1992; Campbell 1997). Later, between the 15th and 19th centuries, populations of the Tupi-Guarani linguistic family moved into the French Guiana hinterland from the south, completing the radial diffusion of the Tupi linguistic stock which may have started at the southern rim of the Amazon river (Campbell 1997; Marrero et al. 2007).

Historical observations of the coastal groups by Europeans date from the turn of the 17th century (1606), but it took a century for them to meet the hinterland populations (1720). At the time of contact, no less than 20 Amerindian 'nations' were identified (Hurault 1965). Currently, six Amerindian populations of three linguistic stocks live in French Guiana: Palikur and Arawak-Lokono (Maipurean), Kali'na and Wayana (Karib), Emerillon and Wayampi (Tupi-Guarani) (Nimuendajú 1926; Grenand and Grenand 1985; 1987). These populations are geographically close to the Brazilian Apalai, another Karib-speaking group that merged with a portion of the French Guianan Wayana during the 19th century (Salzano et al. 1988). Today the Palikur and Arawak-Lokono represent the most eastern Maipurean-speaking tribes of South America, deriving from people of the Arawak linguistic phylum that may have spread into the northern part of South America from the Peruvian Andean foothills ~3000 years ago (Campbell 1997).

Previous genetic studies of French Guiana and related Amerindian populations have shown interesting features. The Karib tribes present lower inter-population genetic distances than the Tupi-Guarani, probably due to the fact that their higher effective population sizes would have prevented genetic drift (Callegari-Jacques and Salzano 1989). Among the Tupi-Guarani, the Emerillon seem to have suffered genetic drift effects due to small population size (Mazières et al. 2009). Additionally, data from previous genetic systems (i.e. red cell and serum proteins, the first region of the hypervariable segment of mitochondrial DNA and eight Y-chromosome SNPs) have suggested a two-stage peopling of French Guiana, starting in the littoral and then moving into the hinterland (Mazières et al. 2007; 2008; 2009).

STR data have proved to be very informative for studies of Amazonian Native populations (Dos Santos et al. 2009). On the other hand, little genetic information has been obtained for the specific male fraction in the area of our interest, besides the knowledge that Amerindians display few polymorphisms for the major Y-chromosome lineages (Ruiz-Linares et al. 1999; Bortolini et al. 2003).

To scrutinize the patterns of Amerindian peopling in the northeastern corner of Amazonia we investigated 15 autosomal and 17 Y-chromosome short tandem repeat polymorphisms (ASTRs, YSTRs) in four French Guianan (Emerillon, Palikur, Wayampi and Kali'na) and two related (Brazilian Apalai and Peruvian Maipurean-speaking Matsiguenga) Amerindian populations. The results were compared with previously obtained uni- and biparental data from the same populations, and the following questions were addressed: (a) Are the data

215 consistent regardless of their mode of inheritance? (b) To what extent is the population
 216 structure compatible with geographical, linguistic or historical data? and (c) Can we infer the
 217 main patterns of Amerindian peopling in that Amazonian region?
 218

219 **Subjects and methods**

220 *Population sampling and pedigree recording*

221 The present study includes samples of the Emerillon from the margins of the Camopi and
 222 Tampock tributaries (median point: 3°N, 53°10W), the Wayampi from the margins of the
 223 mid and lower Oyapock river (3°10'N, 52°20'W), the Palikur from a place near the Oyapock
 224 estuary (4°N, 51°45'W) and the Kali'na who live in a region between the Mana and Maroni
 225 mouths (5°44'N, 53°55'W). Additional Brazilian (Apalai: 1°10'N, 54°50'W) and Peruvian
 226 (Matsiguenga: 12°S, 72°30'W) populations complete our population data set. All samples
 227 were collected during the 1964–1985 missions, led by three of us (G.L., E.B. and F.M.S),
 228 under the auspices of the Centre National de la Recherche Scientifique (Centre
 229 d'Hemotypologie, Toulouse, France), Institut National de la Santé et de la Recherche
 230 Médicale, Universidade Federal do Rio Grande do Sul, and Fundação Nacional do Índio
 231 (FUNAI) who gave permission to contact the Brazilian Apalai. All blood samples were
 232 collected into vacutainers containing EDTA or ACD anti-coagulants and conserved in
 233 isothermal boxes at 4°C. Simultaneously with the sample collections, individuals were
 234 questioned about their pedigree and clan membership. Genealogical trees were then
 235 sketched so that relatives could be traced as far back as three generations on average.
 236
 237

238 *Laboratory determinations*

239 Using pedigree records, unrelated family founders were preferentially analysed because they
 240 would provide a more representative sample of the population studied. Additionally the
 241 researcher who performed most of the determinations (S.M.) was typed for the studied
 242 genetic markers to detect possible sample contamination.
 243

244 A total of 30 Emerillon, 30 Palikur, 29 Wayampi and 23 Kali'na from French Guiana, 26
 245 Apalai from northern Brazil and 29 Matsiguenga from southern Peru were screened for the
 246 15 (CSF1PO, D2S1338, D3S1358, D5S818, D7S820, D8S1179, D13S317, D16S539,
 247 D18S51, D19S433, D21S11, TH01, FGA, TPOX and vWA) autosomal STR loci identified
 248 by the commercial AmpF ℓ STR[®] Identifier[®] PCR Amplification kit (Applied Biosystems,
 249 Darmstadt, Germany). Population descriptions and geographic locations have been
 250 presented in Mazières et al. (2007; 2008). All DNA amplifications and genotyping were
 251 performed at the Departamento de Genética of the Universidade Federal do Rio Grande do
 252 Sul (Porto Alegre, Brazil) following the kit user manual instructions. Length fragments were
 253 amplified in single reactions for all 15 loci using fluorescently labelled primers in a
 254 GeneAmp PCR System 9600 thermocycler (Applied Biosystems). Electrophoresis of the
 255 amplified fragments, mixed with formamide and GS500 LIZ Size Standard was carried out
 256 in an ABI PRISM 310 Genetic Analyser using the separation medium performance
 257 optimized polymer (POP) 4 and 47 cm capillaries (Applied Biosystems). The 3.2.1 version
 258 of GENESCANTM was used to track lanes and measure fragment sizes, while the
 259 GENOTYPERTM version 2.5.2 software was used to automatically designate alleles in
 260 comparison with locus-specific allelic ladders.

261 DNA from male subjects of the six studied populations (13 Emerillon, 28 Palikur, 30
 262 Wayampi, 17 Kali'na, 28 Apalai and 13 Matsiguenga) were genotyped at the Laboratoire
 263 AMIS (Toulouse, France) for 17 Y-chromosomal STR loci (DYS19, DYS389I, DYS389II,

322 DYS390, DYS391, DYS392, DYS393, DYS385a, DYS385b, DYS437, DYS438, DYS439,
323 DYS448, DYS456, DYS458, DYS635 and GATA H4) using the AmpF ℓ STR[®] YFiler[®]
324 PCR Amplification kit (Applied Biosystems). Previous SNPs screening ensured that no
325 non-Amerindian admixture occurred in the selected samples (Mazières et al. 2008). DNA
326 amplification was carried out in a GeneAmp 2700 Thermal cycler (Applied Biosystems)
327 following the manufacturer's instructions. The target length fragment, mixed with
328 formamide and GS600 LIZ Size Standard was then separated by electrophoresis in a ABI
329 PRISM 3100 Genetic Analyser using the separation medium performance optimized
330 polymer (POP) 6. Runs were performed at the Sequencing and Genotyping Service, IFR30,
331 UMR 5165 CNRS-UPS III, Purpan University Hospital, Toulouse, France. The version 3.2
332 GENEMAPPER[®] analysis software was used to assign allele sizes in comparison with locus
333 specific allelic ladders.

335 *Statistical analyses*

336
337 Allele frequencies were calculated using the GENEPOP web utility (Raymond and Rousset
338 1995). Mean number of alleles, estimates of gene diversity over YSTR loci and mean
339 expected heterozygosity H were obtained with the ARLEQUIN v3.1 package (Excoffier et al.
340 2005). Levels of gene diversity for the YSTR loci were estimated through the
341 POWERMARKER v3.25 package (Liu and Muse 2005). The F_{ST} -based distances
342 (Weir and Cockerham 1984) were calculated from the autosomal and Y-chromosomal STR
343 genotypes assuming the stepwise mutation model using ARLEQUIN v3.1. Genetic
344 relationships were finally displayed through a metric multidimensional scaling (MDS) plot
345 using XLSTAT-Pro 7.5.2[®].

346 To evaluate total patterns of genetic diversity in the French Guiana area, ASTRs and
347 YSTRs genetic diversities were also compared to those previously obtained for the blood
348 group and protein systems, mtDNA haplogroup frequencies and HVS-I variation (Mazières
349 et al. 2007; 2008). Pairwise and general correlation between ranks of genetic diversities
350 calculated with different markers were measured with Spearman's correlation coefficient and
351 Kendall's coefficient of concordance (Siegel 1956), respectively. Friedman's and Nemenyi's
352 tests were used to compare the populations for the ranked diversities (Zar 1999), using the
353 SPSS[®] v.13 for Windows[™] program.

354 Estimation of a putative genetic bottleneck (i.e. reduction of the population effective size
355 N_e) from allele frequencies is possible using the BOTTLENECK package (Cornuet and
356 Luikart 1996). This program contrasts recently bottlenecked from non-bottlenecked
357 populations, whose N_e remained stationary for more than the past dozen generations, testing
358 two genetic peculiarities: the mode of distribution of allele frequencies and the difference
359 between observed and expected gene diversities. Briefly, it assumes that in stationary
360 populations alleles at low frequencies are expected to be more abundant than alleles at
361 intermediate frequencies, the allele frequencies distribution being L-shaped (Luikart et al.
362 1998a). During a reduction of the effective population size rare alleles tend to be lost rapidly,
363 shifting the allele frequency distribution toward the intermediate allele frequency class
364 (Luikart et al. 1998a). Also, in recently reduced populations, allele numbers decrease faster
365 than gene diversity (Allendorf 1986), conditioning the observed gene diversity to be
366 significantly higher than the expected one, since the latter is computed from the observed
367 number of alleles under the assumption of a constant-size population (Luikart et al. 1998b).
368 The ASTRs distribution was tested with the mode-shift indicator and the Wilcoxon sign-
369 rank test furnished by BOTTLENECK (Cornuet and Luikart 1996). One thousand
370 iterations per locus were performed and the loci were assumed to fit both the stepwise

(SMM) and the two-phased (TPM) mutation models, which are both likely to be realistic mutation models for microsatellite loci in human populations (Valdes et al. 1993; Di Rienzo et al. 1994). Three markers (D19S433, D21S11 and TH01) accounting for 20% of the 15 ASTR loci studied present intermediate allelic forms (e.g. D21S11*32.2) and thus could evolve following a multistep mutation model (namely the Infinite Allele Model or IAM). Therefore, 20% of multistep mutations were assumed together with lower proportions (10% and 5%) for TPM, as recommended by the BOTTLENECK manual. A variance σ^2 of 28 was used since σ is roughly equal to the typical step size (Di Rienzo et al. 1994), which amounts to 5.3 allele repeats in the total sample investigated.

Our sampled populations were investigated to verify if they constituted different genetic entities, by clustering individuals as a function of their genotypes using STRUCTURE 2.2 (Pritchard et al. 2000; Falush et al. 2003). The autosomal set of markers was used, since the method requires non-linked markers only. For each number of clusters ($K = 2-11$), 10 runs were performed with a burn-in period of 20 000 iterations followed by 10 000 Monte Carlo Markov Chain replications. All runs were based on the admixture model, in which each individual is assumed to have ancestry in multiple genetic clusters. The Greedy CLUMPP 1.1.1 algorithm (Jakobsson and Rosenberg 2007) was used to find the optimal cluster membership.

Finally, the allele frequencies for 11 ASTRs (CSF1PO, D3S1358, D5S818, D7S820, D8S1179, D13S317, D16S539, D18S51, D21S11, TH01 and TPOX) were compared to those from 21 other populations available in the literature (Hutz et al. 2002; Kohlrausch et al. 2005; Crossetti et al. 2008; González-Andrade et al. 2008; Dos-Santos et al. 2009). The D_a genetic distances were then computed using DISPAN[®] (Ota 1993) and the genetic relationships were estimated through a neighbour joining tree with 1000 bootstrap replications to test the reliability of the branches. Using the Mantel test furnished by XLSTAT-Pro 7.5.2[®], the D_a matrix was then compared to the geographic distances calculated with the Google Earth 5.0.1 ruler tool. Geographic coordinates of the populations (Table S1) were gathered from the authors' works or estimated according to the linguistic maps available at www.ird.fr and www.ethnologue.com websites.

Results

Supplementary Material Table S2 provides the allele frequency distribution for the 15 ASTRs investigated in our six sampled populations from the French Guiana area and the Peruvian Matsigenka. After Bonferroni correction for multiple comparisons (Bonferroni 1936) no deviations from Hardy-Weinberg equilibrium were observed with the exception of the D21S11 and FGA loci in the Palikur sample. Considering the five populations from northern Amazonia as one group, 107 alleles were detected, 111 if the Peruvian Matsigenka are included, ranging from three (TH01) to 13 (D18S51). The most frequent allele shared by the six groups is the same at only one locus: D3S1358 (*15). This allele was also found to be the most frequent in 11 out of 14 populations from Paraguay, northern Argentina (Chaco) and Brazil (Hutz et al. 2002; Kohlrausch et al. 2005; Crossetti et al. 2008).

YSTRs haplotypes detected in the male fraction of the studied populations are presented in Supplementary Material Table S3. A total of 55 different arrangements were found in the 129 males. Only two haplotypes (3.6%) were detected in more than one population: H5 was observed in one Wayampi and five Emerillon lineages while H9 is shared by two Apalai and two Kali'na men. No variation was observed in 11 YSTRs, DYS389I, DYS393, DYS438, DYS439, DYS448, DYS459 and GATAH4 in the Emerillon; DYS19 in Emerillon and Wayampi; DYS391 in Emerillon and Palikur; DYS392 in Apalai, Emerillon and Matsigenka; and DYS437 in Apalai, Kali'na and Matsigenka.

Table I. Gene diversity estimates and number of alleles for 15 ASTRs and 17 YSTRs in six South Amerindian populations.

		Level of gene diversity ^a				Number of alleles ^a			
		ASTRs		YSTRs ^b		ASTRs		YSTRs	
		Het.	SE	Gene diversity	SE	Average	SE	Average	SE
543	Emerillon	0.63	0.14	0.22 (0.10)	0.13 (0.10)	4.3	1.6	1.5	0.6
544	Palikur	0.64	0.17	0.47 (0.38)	0.25 (0.25)	5.3	2.0	3.2	1.2
545	Wayampi	0.69	0.11	0.24 (0.25)	0.14 (0.18)	5.3	1.8	2.9	1.2
546	Kali'na	0.72	0.09	0.54 (0.49)	0.29 (0.31)	5.9	2.0	2.9	0.9
546	Apalai	0.72	0.11	0.47 (0.36)	0.25 (0.24)	6.1	1.9	3.2	1.2
547	Matsiguenga	0.66	0.14	0.31 (0.22)	0.18 (0.17)	5.0	1.7	2.4	0.8
548	South America ^c								
	lowest	0.58		0.00					
549	Mean	0.68		0.33					
550	highest	0.78		0.56					

^aHeterogeneity assessment with Friedman's non-parametric test using exact the Monte Carlo method: (1) ASTR average heterozygosity: $\chi^2 = 15.191$; $df = 5$; $p < 0.01$; Y STR average diversity: $\chi^2 = 26.906$; $df = 5$; $p < 0.01$. (2) number of alleles: ASTRs: $\chi^2 = 26.671$; $df = 5$; $p < 0.001$; YSTRs: $\chi^2 = 32.682$; $df = 5$; $p < 0.001$.

^bValues in parentheses were obtained for the commonly analysed DYS19, DYS390, DYS391, DYS392 and DYS393 microsatellites.

^cData from 472 and 418 individuals examined for 15 ASTRs and five YSTRs, respectively (Bianchi et al. 1998; Hutz et al. 2002; Bortolini et al. 2003; Kohlrausch et al. 2005; Crossetti et al. 2008; González-Andrade et al. 2008; Tirado et al. 2009).

Gene diversity estimates across loci are listed in Table I. Values vary from 0.63 (Emerillon) to 0.72 (Apalai and Kali'na) for the ASTRs and from 0.22 (Emerillon) to 0.54 (Kali'na) for the YSTRs. When comparing the same 15 ASTRs and five YSTRs (DYS19, DYS390, DYS391, DYS392 and DYS393) in other South Amerindians, the six populations under study fall within the observed range for the continent (Table I). The average number of alleles per locus vary from 4.3 (Emerillon) to 6.1 (Apalai) for the ASTRs and from 1.5 (Emerillon) to 3.2 (Apalai) for the YSTRs.

The French Guianan populations plus the related Apalai and Matsiguenga were compared using the F_{ST} -based genetic distance for the ASTRs genotypes and YSTRs haplotypes (Tables S4 and S5). All pairwise comparisons were statistically significant ($p < 0.05$) and the genetic relationships are displayed in Figure 1. To ensure the reliability of the F_{ST} distances calculated for the ASTRs, the D_a genetic distance (Table S6; Nei et al. 1983), which was found to perform comparatively well in estimation of population trees from autosomal microsatellite allele frequency data (Takezaki and Nei 1996), has been estimated with POWERMARKER (Liu and Muse 2005) and the matrices compared through a Mantel test. A highly significant correlation ($r^{F_{ST}-D_a} = 0.919$, $p = 0.001$) links the two distance methods, highlighting the accuracy of all results with the F_{ST} distance estimator in our ASTRs data set. In Figure 1, general agreement between bi- (Figure 1(a)) and uniparental (Figure 1(b)) genetic markers can be observed, with a central core clustering the coastal Palikur and Kali'na together with the Apalai, while the Emerillon and Matsiguenga occupy peripheral positions. The Wayampi stand differently depending on the genetic markers considered; they are placed closer to the Apalai-Palikur-Kali'na cluster for the autosomal dataset, but not for the YSTRs.

The STRUCTURE analysis, based on the 167 ASTR genotyped individuals, indicated a number of clusters equal to the number of populations tested as the best adjustment. Table II presents the average membership scores. High mean scores were obtained in cluster 1 by the Matsiguenga (0.89), in cluster 3 by the Emerillon (0.92) and in cluster 5 by the Wayampi

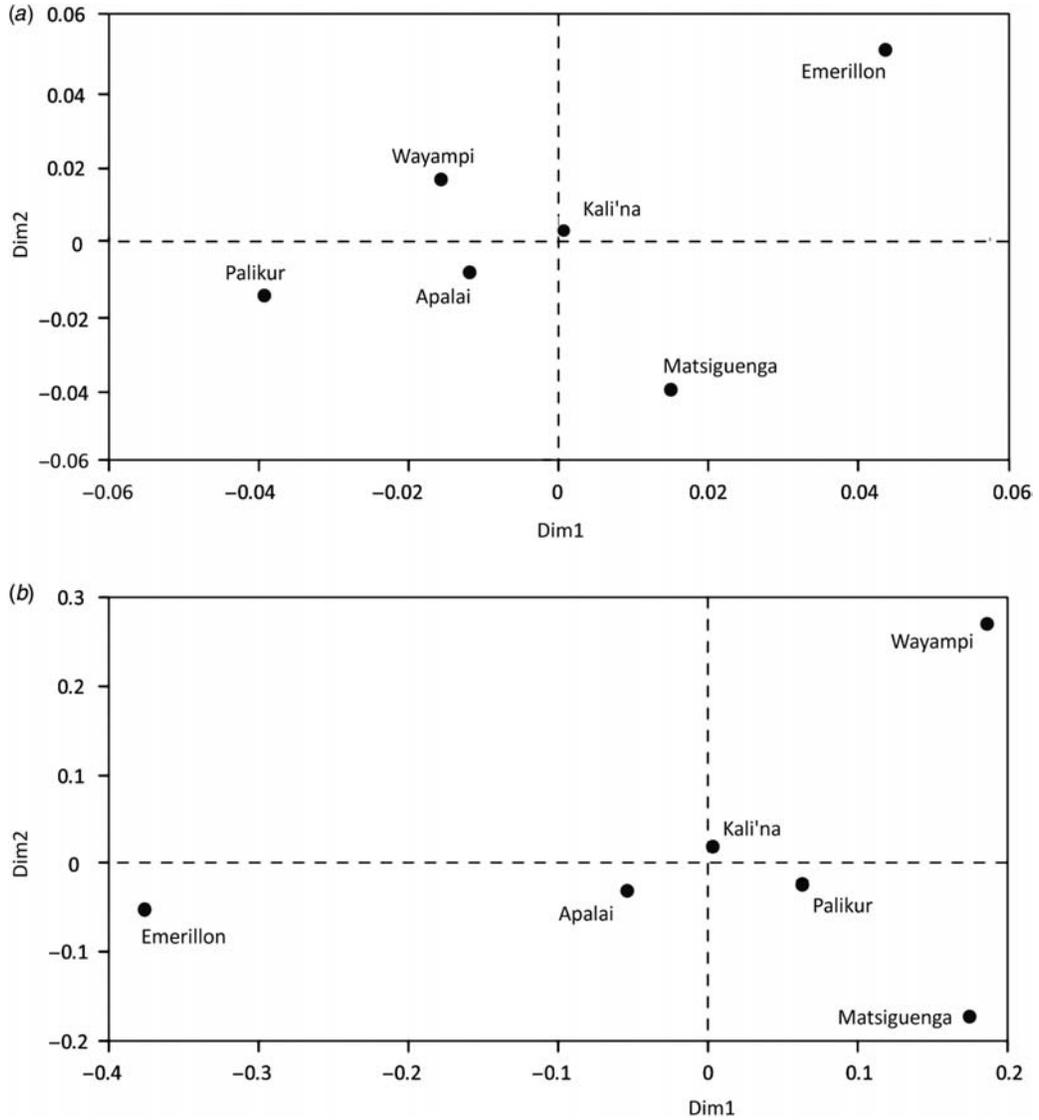


Figure 1. Metric multidimensional scaling plots of F_{ST} based distances between five northern Amazonian and one related Peruvian Amerindian populations considering (a) 15 ASTRs (stress: 0.011) and (b) 17 YSTRs (stress: 0.003).

(0.74). Clusters 2 and 6 show composite affiliations (2: Apalai 0.46/Kali'na 0.62; 6: Palikur 0.54/Apalai 0.41). Although no clear main affiliation can be distinguished for cluster 4, in this inferred group the highest scores were observed for Palikur and Kali'na. These results basically confirm those observed in the MDS plot: Apalai, Kali'na and Palikur have higher genetic similarities while Matsiguenga, Emerillon and Wayampi each have a more particular ASTR profile.

The five French Guianan and Northern Brazilian populations were sorted according to level of genetic variability and the ranks compared with previously published data for bi- and uniparental genetic systems (Table III). Kendall's concordance coefficient among the four markers ($r = 0.863$; $p < 0.01$), as well as Spearman's correlation coefficients between the

Table II. Average membership scores in the six inferred clusters obtained by the STRUCTURE analysis of 167 individuals from four French Guiana and two related Amerindian populations.

Population	N° of individuals	Average membership in the inferred cluster					
		1	2	3	4	5	6
Emerillon	30	0.014	0.022	0.916	0.017	0.017	0.013
Palikur	30	0.050	0.058	0.011	0.319	0.020	0.524
Wayampi	29	0.042	0.091	0.059	0.010	0.744	0.053
Kali'na	23	0.076	0.617	0.048	0.159	0.043	0.056
Apalai	26	0.041	0.456	0.044	0.012	0.038	0.410
Matsiguenga	29	0.890	0.021	0.037	0.012	0.023	0.017

two biparental or uniparental markers ($r=0.900$, $p < 0.05$) suggest that the STR pattern of gene diversity agrees with protein and mtDNA data in our set of populations. It is especially important for uniparental markers (mtDNA and Y-chromosome) to match the biparental protein and ASTR systems, since genetic diversity can be altered by their lower effective size N_e .

When tribes were compared for the level of variability at the four sets of markers, significant differences were found (Friedman's test: 13.8, $p < 0.001$). The Emerillon showed the lowest level followed by the Palikur and Wayampi, while the Apalai and Kali'na had the highest values. Multiple comparisons using the Nemenyi method revealed that the Emerillon significantly differed from both the Apalai and the Kali'na (Table III).

The diploid loci were then analysed to test whether their distribution suggested stationary or recently bottlenecked populations (Table IV). Excess of observed heterozygosity with significant p -values were found for the Emerillon ($p^{80\%SMM} = 0.002$, $p^{90\%SMM} = 0.013$), Wayampi ($p^{80\%SMM} = 0.001$, $p^{90\%SMM} = 0.006$) and Matsiguenga ($p^{80\%SMM} = 0.001$, $p^{90\%SMM} = 0.009$) when the markers were assumed to fit the two-phase (TPM) allowing for 80% and 90% of the stepwise (SMM) models. Although the p -values increased along with the SMM proportion, the Emerillon and the Wayampi still showed a significant excess of observed heterozygosity ($p^{95\%SMM} = 0.028$ and 0.047, respectively) at 95% of SMM. As far as the allele frequency distributions are concerned, L-shaped modes, expected in non-recently bottlenecked populations, were observed in all studied tribes with the exception of the Emerillon.

Discussion

The autosomal and Y-chromosome STRs tested proved to be highly variable, as has been observed in other populations, and the intervals of variation found were within the range previously observed in Amerindians. However, there is clear inter-tribal heterogeneity, with the Emerillon showing a more restricted variability and the Apalai (a hinterland) and Kali'na (a coastal) Karib populations presenting the highest amount of variation.

The distinctiveness between the two Maipurean-speaking groups, Matsiguenga and Palikur, had been previously found (Mazières et al. 2008), suggesting that people of this language are genetically heterogeneous. This heterogeneity could have predated their postulated southwest–northeastern movement (suggested on linguistic grounds; Urban 1992; Campbell 1997) or may have developed during this migration process. Analyses of a more representative number of Maipurean tribes are necessary to clarify this issue.

The population clustering between the Palikur, Kali'na and Apalai in Figure 1 agree first with an independent settlement of the littoral (Rostain 1994) and second with lower

Table III. Ascending ranks of five Amerindian populations from the French Guiana area according to four gene diversity parameters obtained with bi- and uniparental genetic markers.^a

	Autosomal		Uniparental		Average	Nemenyi's test for pairwise comparisons ^c
	Protein	ASTRs	MtDNA ^b	YSTRs		
Emerillon	2	1	1	1	1.3	A
Palikur	1	2	2	3	2	A,B
Wayampi	3	3	3	2	2.8	A,B
Kaliña	4	4	5	5	4.5	B
Apalai	5	5	4	4	4.5	B
Spearman's correlation coefficient	0.90 ($p = 0.037$)		0.90 ($p = 0.037$)			

^a Protein and mtDNA data from Mazières et al. (2007; 2008).^b Based on mtDNA haplogroup frequencies.^c Same capital letter indicates statistically non-significant pairwise differences ($p > 0.05$).

Table IV. *P*-values of the Wilcoxon sign-rank test for excess of observed heterozygosity and mode distribution of the allele frequencies assuming the stepwise (SMM) and two-phase (TPM) mutation models.

Populations	TPM with 80% of SMM	TPM with 90% of SMM	TPM with 95% of SMM	SMM	Mode
Emerillon	0.002*	0.013*	0.028*	0.104	Shifted
Palikur	0.300	0.445	0.598	0.805	L-shaped
Wayampi	0.001*	0.006*	0.047*	0.360	L-shaped
Kali'na	0.054	0.227	0.360	0.700	L-shaped
Apalai	0.068	0.151	0.227	0.360	L-shaped
Matsiguenga	0.001*	0.009*	0.054	0.339	L-shaped

*Significant *p*-values.

inter-population variation among the northern Amazonian Karib populations (Callegari-Jacques and Salzano 1989). To better examine this pattern in the French Guiana area, we performed additional analyses of variance (AMOVA) considering groups based on geographic location or linguistic affiliations. Geographic groups were 'littoral' (Palikur, Kali'na) and 'interior' (Emerillon, Wayampi, Apalai), whereas language groups were 'Karib' (Kali'na, Apalai), 'Maipure' (Palikur, Matsiguenga) and 'Tupi' (Emerillon, Wayampi). An interesting feature is the lower amount of inter-population variation in the littoral ($\Phi_{ST}^{ASTRs} = 0.044$; $\Phi_{ST}^{YSTRs} = 0.097$) than in the interior groups ($\Phi_{ST}^{ASTRs} = 0.057$; $\Phi_{ST}^{YSTRs} = 0.448$). When comparing groups according to linguistic stock, more homogeneity is found within the Karib ($\Phi_{ST}^{ASTRs} = 0.014$; $\Phi_{ST}^{YSTRs} = 0.104$) than in the other linguistic clusters, namely 'Maipure' ($\Phi_{ST}^{ASTRs} = 0.061$; $\Phi_{ST}^{YSTRs} = 0.221$) and 'Tupi' ($\Phi_{ST}^{ASTRs} = 0.061$; $\Phi_{ST}^{YSTRs} = 0.651$), all in agreement with the inferences cited above.

To accurately estimate the level of sex differences in gene flow, the YSTR AMOVA results were compared with those from the mtDNA HVS-I nucleotide results (Mazieres et al. 2008). A slightly less pronounced population similarity was observed for the mtDNA in the littoral and Karib populations (littoral: $\Phi_{ST}^{mtDNA} = 0.126$; $\Phi_{ST}^{YSTRs} = 0.097$; Karib: $\Phi_{ST}^{mtDNA} = 0.210$; $\Phi_{ST}^{YSTRs} = 0.104$), whereas the opposite pattern could be observed in all the other geographic or linguistic groups (interior: $\Phi_{ST}^{mtDNA} = 0.198$; $\Phi_{ST}^{YSTRs} = 0.448$; Maipure: $\Phi_{ST}^{mtDNA} = 0.200$; $\Phi_{ST}^{YSTRs} = 0.221$; and Tupi: $\Phi_{ST}^{mtDNA} = 0.177$; $\Phi_{ST}^{YSTRs} = 0.651$). In this context, the clustering of the Tupi-speaking and hinterland Wayampi with the Palikur, Kali'na and Apalai when the ASTRs (Figure 1) or other systems were considered (Mazieres et al. 2007; 2008), but not when the YSTRs were taken into consideration, suggests that directional sex-biased gene flow occurred in this ethnic group. This is historically confirmed by reports of capture of women as the Wayampi settled along the Oyapock river (Hurault 1965).

When the genetic distances observed for the ASTRs and YSTRs were compared to those of protein systems and mtDNA (Mazieres et al. 2007; 2008), positive correlations for all pair-wise comparisons of genetic distances for markers with partially or fully maternal inheritance (Mantel's test: $r^{ASTRs-protein} = 0.850$, $r^{mtDNA-protein} = 0.195$, $r^{ASTRs-mtDNA} = 0.045$) and a negative association between YSTRs and mtDNA genetic distances ($r = -0.150$) were found. These results, together with the high F_{ST} values among interior and Tupi groups for the YSTRs, are in accordance with the historical event we have just mentioned for the Wayampi.

Comparison of the allele frequencies for 11 ASTRs examined in the six populations under study and 21 other South Amerindian groups through a neighbour joining tree did not yield a clear separation either by geography or language, with very low bootstrap values and a Multidimensional Scale (MDS) analysis did not improve the pattern (data not shown), in accordance with Dos Santos et al. (2009) who, using the same 11 genetic markers, could not

1071 find clear geographic or linguistic patterns among Amazonian Amerindians. Indeed, no
 1072 correlation has been detected in our data between the D_a and geographic distances (Table S7)
 1073 (Mantel test, $r = -0.012$; $p = 0.48$).

1074 The result indicating a recent genetic bottleneck in the Emerillon agrees with our previous
 1075 findings (Mazières et al. 2007) and is undoubtedly related to the demographic decrease that
 1076 occurred among Amerindians during the last century (Hurault 1965; Mazières et al. 2009).
 1077 Genetic and demographic bottlenecks (i.e. reduction of the effective and census sizes of the
 1078 population, respectively) are not automatically linked (Luikart et al. 1998b). The former can
 1079 occur without reduction of the total population size if the next generation descends from a
 1080 few mating pairs or a few breeders of one sex (Low 1988; Kittles et al. 1999; Wilder et al.
 1081 2004; Hammer et al. 2008). Conversely, a demographic reduction does not always lead to a
 1082 severe loss of genetic diversity (Allendorf 1986). Central African Pygmies present an
 1083 enlightening illustration of these phenomena. These hunter-gatherers show more variability
 1084 for the HV S-I mtDNA (haplotype diversity above 0.80, Destro-Bisol et al. 2004), ASTRs
 1085 (mean heterozygosity = 0.76, Destro-Bisol et al. 2000) and YSTRs (gene diversity = 0.56,
 1086 Coia et al. 2004) than South Amerindians (mean values for HV S-I = 0.77, Mazières et al.
 1087 2008; ASTRs = 0.68; YSTRs = 0.34, Table I), but no signs of population expansion
 1088 (Excoffier and Schneider 1999) or substantial population decrease (Patin et al. 2009).
 1089

1090 **Conclusions**

1091
 1092 Answers to the questions posed in the introduction are as follows: First, agreement of
 1093 patterns found across the genetic markers was observed, and our multiple comparison
 1094 analysis revealed a meaningful pattern of genetic diversity and relationships in the area.
 1095 Second, geography seems to be more important than language in shaping the relationships
 1096 found, and our data largely agree with historical records. Special note should be made of the
 1097 Emerillon results; their population decline was clearly reflected in the genetic parameters
 1098 considered. Lastly, the clustering of all groups besides the Matsiguenga and Emerillon on a
 1099 single nucleus prevents inferences about early colonization patterns. However, different
 1100 histories may have existed between Wayampi males and females.
 1101

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1103
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 1114

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