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https://researchonline.ljmu.ac.uk/id/eprint/27144/

Article

Citation (please note it is advisable to refer to the publisher's version if you intend to cite from this work)

Torres, JB, Martucci, V, Aldrich, MC, Vilar, MG, MacKinney, T, Tariq, M ORCID logoORCID: https://orcid.org/0000-0002-8239-9339, Gaieski, JB, Hernandez, RB, Browne, ZE, Stevenson, M, Walters, W, Schurr, TG, Adhikarla, S, Adler, CJ, Balanovska, E, Balanovsky, O, Bertranpetit, J

Published in final edited form as:

Am J Phys Anthropol. 2019 July ; 169(3): 482–497. doi:10.1002/ajpa.23859.

Analysis of biogeographic ancestry reveals complex genetic histories for indigenous communities of St. Vincent and Trinidad

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Abstract

Objectives: From a genetic perspective, relatively little is known about how mass emigrations of African, European, and Asian peoples beginning in the 16th century affected Indigenous Caribbean populations. Therefore, we explored the impact of serial colonization on the genetic variation of the first Caribbean islanders.

Materials and methods: Sixty-four members of St. Vincent's Garifuna Community and 36 members of Trinidad's Santa Rosa First People's Community (FPC) of Arima were characterized for mitochondrial DNA and Y-chromosome diversity via direct sequencing and targeted SNP and STR genotyping. A subset of 32 Garifuna and 18 FPC participants were genotyped using the

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CONFLICT OF INTEREST
The authors declare no potential conflict of interest.

DATA AVAILABILITY STATEMENT
The mtDNA and Y-chromosome data for all individuals are available in anonymized form in Tables S3–S6, and will be submitted to GenBank (or another database) for public access upon publication of this article. The data that support the findings of this study, specifically the autosomal SNP data, are available upon reasonable request from the corresponding author.

SUPPORTING INFORMATION
Additional supporting information may be found online in the Supporting Information section at the end of this article.

GenoChip 2.0 microarray. The resulting data were used to examine genetic diversity, admixture, and sex biased gene flow in the study communities.

Results: The Garifuna were most genetically comparable to African descendant populations, whereas the FPC were more similar to admixed American groups. Both communities also exhibited moderate frequencies of Indigenous American matrilines and patrilines. Autosomal SNP analysis indicated modest Indigenous American ancestry in these populations, while both showed varying degrees of African, European, South Asian, and East Asian ancestry, with patterns of sex-biased gene flow differing between the island communities.

Discussion: These patterns of genetic variation are consistent with historical records of migration, forced, or voluntary, and suggest that different migration events shaped the genetic make-up of each island community. This genomic study is the highest resolution analysis yet conducted with these communities, and provides a fuller understanding of the complex bio-histories of Indigenous Caribbean peoples in the Lesser Antilles.

Keywords

admixture; autosomal DNA; Caribbean; mtDNA; Y-chromosome

1 | INTRODUCTION

The Caribbean region comprises 700 islands that constitute a land mass of approximately 235,700 km^2 (91,000 mi^2) in size, and is inhabited by over 44 million people (Palmié & Scarano, 2013; United Nations, 2017). Many of the islands (although not all) can be placed into one of three broad groupings: (a) the Greater Antilles, which include Cuba, Hispaniola, Jamaica, Puerto Rico; (b) the Lesser Antilles, which stretch from Grenada to the Virgin Islands; and (c) the Bahamian Archipelago, which, while not part of the Antillean chain per se, was settled by Indigenous Americans and, thus, is grouped culturally with the Antilles (Figure 1). The earliest evidence for human presence into the Caribbean dates to 7,800 years before present (YBP) in Trinidad. However, the initial dispersal into Trinidad likely did not require crossing water as the island was coextensive with the South American continent throughout the early Holocene (Fitzpatrick, 2015). Aside from this date, the strongest evidence for human presence within the islands dates to 6,000 YBP in Hispaniola and Cuba. There are also early or Archaic settlements on Puerto Rico, Anguilla, Antigua, Barbuda, Nevis, Saba, St. Kitts, St. Maarten, and St. Thomas. These dispersals are thought to have emerged from northern South America, although evidence from sites on Hispaniola and Cuba also suggest that Mesoamerica may have been a point of origin for early expansions into the Caribbean (Fitzpatrick & Keegan, 2007).

After these initial dispersals into the Caribbean, many of the Lesser Antillean islands became populated in a series of migrations from South America beginning around 2,500 YBP, and other islands such as Puerto Rico that were already inhabited, gained new migrants. Around 1,400 YBP, beginning in Puerto Rico, there was a population expansion west and northward into Cuba, Hispaniola, Jamaica, and the Bahamas. The diversification of material culture concurrent with this expansion suggests the development of a more complex social organization relative to the initial Caribbean migrant groups (Fitzpatrick, 2015).

The descendants of these autochthonous expansions later encountered the first Europeans to arrive in the Caribbean at the end of the 15th century. Estimates of the number of people inhabiting the Caribbean at the time of European contact vary widely, with some estimates as high as 6 million people and others as low as 200,000 (Weeks, 2001). Ethnohistorical data also suggests that, at the time of European contact, more than eight different ethnic groups resided in the Caribbean (Granberry, 2013; Mol, 2007). Regardless of the number of inhabitants, Indigenous Caribbean populations experienced dramatic demographic shifts after the arrival of European and African peoples. Disease, genocide, and systemic institutionalized marginalization contributed to declining numbers of Indigenous people throughout the region (Allaire, 2003; Sued-Badillo, 2003; Weeks, 2001). The effects of marginalization were wide-ranging across the Caribbean region, and these effects have been documented in a variety of studies (Beckles, 2008; Fraser, 2014; Lenik, 2012; Palmer, 2014).

Contrary to common narratives about the post-contact Caribbean, Indigenous Caribbean communities were not entirely extinguished. Most of the information recorded about Indigenous Caribbean peoples at European contact was first chronicled by missionaries and then later by travel writers and anthropologists (Hulme, 2000; Hulme & Whitehead, 1992). Although somewhat fragmented and biased, these accounts indicate that Indigenous peoples survived and forged communities in response to the challenges of European colonization and African slavery. In particular, some communities persisted in more localized regions throughout the Caribbean, notably in Cuba, Puerto Rico, Hispaniola, Dominica, St. Vincent, St. Lucia, Martinique, and Trinidad (Barreiro, 2006; Castanha, 2010; Forte, 2006; González, 1988; Hulme, 2000; Simmons, 1960; Yaremko, 2009).

In addition to the changes that European colonization brought to Indigenous communities throughout the Lesser Antilles, the importation of enslaved African peoples also had dramatic impacts on the demography of each island community. Between the 16th and 18th centuries, an estimated 8 million Africans were enslaved and transported to the Americas. Roughly half were brought to the Caribbean and, an estimated 1.5 million Africans were enslaved in the British Caribbean islands alone (Knight, 1990). The importation of enslaved African peoples varied across time and by island, but was most intense in the decades just prior to the 1807 abolition of the slave trade throughout the British Caribbean (Knight & Laurence, 2011).

Subsequent to the influx of African people into the Caribbean, the 1834 Slavery Abolition Act resulted in mass redistributions of African-descended people out of and throughout the Caribbean region. These movements, in addition to a series of other social and economic factors, resulted in an agricultural labor void throughout many Caribbean islands (Moreno & Cateau, 2011). For the British islands, this meant a redistribution of nearly free labor within its empire, with ~430,000 laborers being moved from colonial India to British colonial possessions in the Caribbean between 1838 and 1917 (Bolland, 1981; Kale, 1998). These laborers were contracted to work, usually in the agricultural sector, between 3 and 10 years as repayment for the costs of migration (Roopnarine, 2003). Although there was migration of indentured laborers from other regions of the world, it was much more limited in scale (Engerman, 1984). For example, approximately 2,800 Chinese laborers migrated to Trinidad during this period (Look Lai, 1993). Throughout the remainder of the 19th and 20th centuries, Chinese communities in Trinidad became more established, migrated from rural to urban areas, and developed businesses in retail and importation, as well as within the petroleum industry (Ho, 1990). Although intermarriage with other local groups occurred, due to social strictures, this practice was limited, resulting in a somewhat insular community (Ho, 1989, 1990).

It was these complicated histories of St. Vincent and Trinidad that first led us to begin a population genetics study of the islands' Indigenous communities (Benn Torres et al., 2015). In this initial work, we detected maternal Indigenous ancestry in 42% of the participants, with the remainder exhibiting African and South Asian maternal ancestry. Analysis of Y-chromosome variation revealed paternal Indigenous American ancestry indicated by the presence of haplogroup Q-M3 in 28% of the male participants from both communities, with the remainder possessing either African or European haplogroups. Overall, this study illustrated the role of the region's first peoples in shaping the genetic diversity seen in contemporary Caribbean populations, while also affirming genetic contributions from people of Europe, Africa, and South Asia.

Our previous study worked to address questions about the initial migrations into Caribbean and illuminate the genetic relationships between circum-Caribbean groups. However, there are still many gaps in our knowledge about the pre- and post-European colonial experiences of Indigenous Caribbean communities. In the current study, we use high-resolution autosomal data and additional samples yielding novel uniparental data to illuminate the impact of colonization and subsequent migrations on the genetic diversity of two contemporary Indigenous Caribbean communities in Trinidad and in St. Vincent.

2 | MATERIALS AND METHODS

2.1 | Ethics statement

Ethics review and approval for the current study was obtained from the University of Pennsylvania IRB #8, the University of Notre Dame IRB, Vanderbilt University's IRB, and the Ministries of Health in both Trinidad and St. Vincent. In addition, representative community organizations, such as the First Peoples' Community (FPC) of Arima in Trinidad, and the Garifuna Heritage Foundation in St. Vincent and the Grenadines, reviewed and supported of the project. Finally, each participant provided written informed consent prior to study enrollment.

2.2 | Sample and data collection

We conducted fieldwork in St. Vincent and Trinidad in 2014–2015 to re-engage with the study communities and expand the sample size for genomic analysis. Following the informed consent process, we collected buccal swabs from a total of 100 Trinidadian and Vincentian residents who self-identified as belonging to each island's Indigenous population. All participants were visibly healthy and over the age of 18, and had at least three grandparents from the respective communities. Of these 100 individuals, 36 belonged to the FPC in Arima and Lopinot, while the remaining 64 individuals claimed membership in the Garifuna community of St. Vincent, based in the Kingstown area and three North windward communities (Owia, Fancy, and Sandy Bay) (Figure 1). Twenty-eight of these persons had participated in the previous study, including 13 FPC and 15 Garifuna members (Benn Torres et al., 2015). These samples were combined with previously collected samples for all subsequent genetic analyses (see below). In addition to collecting genetic samples, we conducted a genealogical interview with each participant. During these interviews, information about family surnames, birthplaces, and languages spoken for three generations were recorded.

2.3 | Demographic information

The current Indigenous populations on both Trinidad and St. Vincent are demographically small communities. The most recent available data from the 2011 Trinidadian census lists 1,397 self-defined Indigenous persons, while the Vincentian 2001 census lists 3,813 individuals with this status (National Statistical Office & C. C. (CARICOM) S, 2001, 2014). According to the same census information, Trinidad has a population size of 1,240,300 people, making the Indigenous population only 0.11% of the total. St. Vincent has a smaller population size of only 106,253 people, making self-identified Indigenous persons 3.6% of the total population. For this reason, the ability to obtain representative samples in such small communities is limited by the number of eligible and unrelated people who consent to participate in a study.

Although small sample sizes can potentially lower the robustness of statistical and phylogenetic analyses of genetic data (Bacchetti, 2013; Halsey, Curran-Everett, Vowler, & Drummond, 2015; Krzywinski & Altman, 2013; Subramanian, 2016), those from the current study provide a novel perspective that might otherwise be overlooked in addressing questions about the pre- and post-European history of these communities. In particular, we can learn more about the genetic diversity within and between each Indigenous community which provides some idea about the genetic complexity of the peoples of the Caribbean. In addition, we can gain greater detail on the impact of European colonization, the importation of enslaved Africans, and South Asian indenture on each island’s native population.

2.4 | Genotyping and quality control methods

Genomic DNA was extracted from buccal swabs with Qiagen PureGene kits following manufacturer’s instructions, and DNA extracts were then quantified using a NanoDrop 2000 Spectrophotometer.

All Vincentian and Trinidadian DNAs obtained during fieldwork in 2014–2015 were prepared for GenoChip analysis, including 36 FPC and 64 Garifuna. Based on genealogical information, three Trinidadians were identified as being close relatives, while another 13 of the samples did not yield sufficient quality DNA for microarray analysis. For St. Vincent, 22 Garifuna samples failed to yield sufficient quality DNA for microarray analysis with the Genochip. The loss of these samples could be methodologically related, possibly due to a chemical incompatibility with our downstream genotyping analyses, or possibly related to the extensive use of the extracted DNAs for different analyses prior to GenoChip analysis. These exclusions left 20 Trinidadian and 42 Vincentian samples available for autosomal

SNP analysis. The selected samples were then sent to Family Tree DNA in Houston, Texas, for analysis with the Illumina Genochip 2.0 microarray, which provides data for 135,000 autosomal SNPs, 12,000 SNPs from the nonrecombining portion of the Y-chromosome (NRY), and 3,000 SNPs for the mitochondrial DNA for each sample (Elhaik et al., 2013).

A subsequent review of participants' genealogical information and preliminary autosomal admixture results led us to remove another seven Vincentian individuals from further analysis, as they did not have clear familial ties to the Garifuna community. These exclusions resulted in data from a total of 35 Vincentian samples being used in subsequent analyses. All of the abovementioned familial relationships were later assessed with additional quality control (QC) meaures using the autosomal SNP data generated in the study (see below).

After genotyping and prior to statistical analysis, a number of QC measures were employed. These included checking for inconsistencies between recorded sex and genetic sex, removing individual samples for which <98% of the genotyped markers failed to type, checking for relatedness (IBD cut-off = 0.2), removing markers that had a minor allele frequency ≤5% and evaluating markers for deviations from Hardy Weinburg ($p \leq 10^{-5}$) (Figure S1). All QC steps were conducted using the appropriate functions in PLINK, v. 1.9 (Purcell et al., 2007). The QC and validation measures yielded a total of 118,042 SNPs in 18 individuals from FPC/Lopinot and 117,498 SNPs in 32 Garifuna individuals, yielding the final data set that was used in the statistical analyses.

2.5 | Uniparental marker analysis

In addition to GenoChip analysis, all of the recently collected samples were subjected to mtDNA and Y-chromosome analysis to characterize their haploid genetic variation, as previously described (Benn Torres et al., 2015; Schurr, Dulik, Owings, et al., 2012). The resulting data were combined with those previously obtained for the Garfiuna and FPC (Benn Torres et al., 2015) to evaluate the distribution of haploid genetic lineages in these populations.

To trace the maternal ancestry of these individuals, the entire mtDNA control region (CR) (np 16024–576) for 49 Garifuna and 23 FPC participants was sequenced, and the resulting sequences aligned, edited, and compared to the rCRS (Andrews et al., 1999) in Sequencher, v.4.9 (Gene Codes). Haplogrep (Weissensteiner et al., 2016), an automated online web application based on Phylotree, Build 17 (van Oven & Kayser, 2009), was used to identify mtDNA haplogroups based on hypervariable segment 1 and 2 (HVS2 and HVS2) polymorphisms. This analysis was undertaken because CR variants are somewhat underrepresented relative to the coding regions in the SNP design of the GenoChip, due the presence of recurrent mutations and small indels in the CR (Elhaik et al., 2013), and also to obtain mtDNA data for all participants that could be used to identify their haplogroup status, as not all of their samples were amenable to SNP genotyping with the GenoChip.

To compliment the Y-chromosome SNP data from the GenoChip, paternal haplotypes for 15 Vincentian and 12 Trinidadian male participants were defined through the analysis of 17 Y-chromosome short tandem repeats (Y-STRs) that are part of the AmpFℓSTR Y-filer

Amplification Kit (ABI), and a set of eight diagnostic SNPs defining major branches of the Y-chromosome phylogeny, as previously described (Benn Torres et al., 2015; Schurr, Dulik, Vilar, Owings, & Gaieski, 2012). Haplogroup status was reckoned with Y-STR data using Athey's Haplogroup Predictor (Athey, 2006) and Nevgen Y-DNA Haplogroup Predictor (http://www.nevgen.org/).

2.6 | Global ancestry estimation

The FPC/Lopinot and Garifuna genotyping data were merged with those from reference populations from the 1000 Genomes Project (The 1000 Genomes Consortium, 2015) and the African (Mbuti and Biaka Pygmy, Bantu, Madenka, Mozabite, and San) and American (Colombian, Karitiana, Maya, Pima, and Surui) populations from the Human Genome Diversity Project (Cann et al., 2002) (Table S1). When performing the merging procedures, we applied the same QC for individual missingness (98% call rate), which did not remove any individuals. We also applied the genotyping call rate filter (98%) to the 1000 Genomes populations. This filter was not applied to the HGDP dataset to maximize the number of consensus SNPs available for merging. In addition, we did not apply the minor allele frequency or Hardy–Weinberg equilibrium filters due to the heterogeneity between subpopulations in the 1000 Genomes and HGDP datasets. Before pruning, there were 82,924 variants. After QC filtering, the genotyping data were pruned in PLINK using a window size of 50, step size of 5, and variance inflation factor threshold of 2 such that variants were in linkage equilibrium, leaving 54,251 SNPs for estimation of global ancestry. Principal components analysis (PCA) was implemented using EIGENSTRAT (Price et al., 2006) to visualize population substructure in the data. Global ancestry was estimated for $K = 2$ to $K = 12$ clusters using a maximum likelihood method, as implemented in ADMIXTURE 1.3.0 (Alexander, Novembre, & Lange, 2009). We confirmed global ancestry estimates using the Bayesian program fastSTRUCTURE (Raj, Stephens, & Pritchard, 2014). We also estimated global ancestry on the X chromosome and compared this value with estimates of global ancestry on the autosomes. The haploid function in ADMIXTURE was used to account for male hemizygosity on the X chromosome, which adjusts the calculated log-likelihood based on the individual's sex (Shringarpure, Bustamante, Lange, & Alexander, 2016). Statistically significant differences in X-chromosome versus autosomal mean global ancestry were assessed using a paired t test.

2.7 | Descriptive statistics

Pairwise F_{ST} estimates between populations was calculated using Arlequin 3.5 (Excoffier & Lischer, 2010), which uses the Weir and Cockerham method (Weir & Cockerham, 1984). Statistical significance was calculated by Arlequin based on 100 permutations. Representative subpopulations for this analysis were chosen based on the population with the highest ancestry of a particular component, as indicated by the analysis completed using ADMIXTURE 1.3.0. Accordingly, the representative populations were Han Chinese (CHB), European-Americans (CEPH), Yorubans (YRI), Surui from Brazil (SUR), and Sri Lankan Tamil (STU) (Table S2).

3 | RESULTS

3.1 | Haploid marker genotyping

In St. Vincent, the current analysis of Garifuna individuals yielded approximately the same pattern of genetic diversity as seen in our previous study. As indicated by CR polymorphisms, a number of individuals had Indigenous mtDNAs belonging to haplogroups A2 and C1, with C1 being the more common lineage (Table 1a and Table S3). The CR sequences for these samples were also similar to those previously observed in Garifuna communities (Benn Torres et al., 2015). Aside from several individuals with West Eurasian mtDNAs from haplogroups H and U5, the remaining individuals had mtDNAs from African haplogroups L0–L3. The CR sequences in these African mtDNAs were quite diverse, indicating that individuals with widely varying maternal genetic backgrounds contributed to the contemporary Garifuna population.

Regarding the Y-chromosome, in addition to confirming the haplogroup status of previously sampled individuals (Benn Torres et al., 2015), haplogroup prediction based on STR and SNP genotyping revealed most Garifuna men to have African E1b1a haplotypes (Table 1b and Table S4). In addition, several men had Y-chromosomes belonging to West Eurasian haplogroups I1, R1a and R1b, and one had an Indigenous Y-chromosome belonging to haplogroup Q-M3. The overall pattern of Y-chromosome diversity in Garifuna participants was consistent between our earlier and the current study.

In Trinidad, the analysis of haploid markers revealed new details about FPC/Lopinot genetic diversity (Table 1a and Table S5). The expanded analysis detected frequencies of Indigenous mtDNAs similar to our previous study, with A2 being much more common, but also revealed haplogroups B2 and D1 in the new samples, which had not been observed in the previous study. African mtDNAs belonging to haplogroups L1, L2, and L3 were also detected, as well as two individuals having West Eurasian mtDNA from haplogroups K and U6. In addition, mtDNAs belonging to haplogroups M10, M33, and M35 were observed in FPC/Lopinot members, suggesting a greater South Asian genetic contribution than previously observed.

Among Y-chromosome samples, three males from the FPC/Lopinot communities had Indigenous haplogroup Q-M3 haplotypes, confirming their presence in this population as well as their paternal relatedness (Table 1b and Table S6). Most of the remaining men had African E1b1a haplotypes or West Eurasian G2a, R1a and R1b haplotypes. In addition, one individual had an O2a2 haplotype, indicating East Asian paternal genetic ancestry (Shi et al., 2005; Wen et al., 2004). Thus, the expanded analysis revealed greater male genetic diversity than did the first phase of the study (Benn Torres et al., 2015).

Beyond these results, the GenoChip analysis also provided a finer degree of mtDNA and Y-chromosome haplogroup definition than obtained in our previous study (Tables S3–S6). For the mtDNA data, haplogroups identified with the GenoChip were usually resolved by 2–5 mutational steps further into the human mtDNA phylogeny than CR sequencing alone (van Oven & Kayser, 2009), while Y-chromosome SNP haplogroups were typically resolved by 3–5 additional mutational steps relative to those characterized through the combined STR and SNP genotyping analysis. These findings are consistent with our initial results with the GenoChip 1.0 (Elhaik et al., 2013, 2014), and affirm the utility of this custom microarray for anthropological genetic studies.

3.2 | Autosomal marker analysis

After applying quality control and validation measures, we obtained over 118,000 SNPs in 18 individuals from FPC/Lopinot and 32 Garifuna individuals for use in comparative analyses with comparative populations. These data proved to be very informative about the genetic histories of these two Indigenous Caribbean communities.

3.2.1 | Genetic diversity—F_{ST} estimates were calculated from autosomal SNP data for the two study and five comparative global populations determined to have highest ancestry of a particular geographic ancestry component (Figure S2, Table S7). Fixation indices were the smallest between the Garifuna and the Yoruban population (F_{ST} = 0.015), while the FPC/Lopinot population showed the greatest affinity with the Garifuna (F_{ST} = 0.127). The remaining F_{ST} indices were between 0.130 and 0.279 for all other comparisons between the comparative and the Caribbean groups. To ensure that differences in sample size were not driving our F_{ST} estimates, we reran this analysis restricting the sample sizes of all comparative groups to $n = 25$. None of the F_{ST} values changed substantially after this run, suggesting that our estimates were robust regardless of population size.

3.2.2 | Comparative geographic affinities—Using the autosomal data, PCA was used to visualize estimates of genetic distances between the Garifuna and the FPC/Lopinot communities and the reference populations (Figure 2). In the resulting plot, the first two PCs explained approximately 77% of the variation in the data, while the next two PCs explained approximately 16% of the variation. Considering the first two PCs, the reference populations clustered geo-graphically as expected, although the FPC/Lopinot and Garifuna individuals appeared somewhat distinct from each other. The FPC/Lopinot group formed a tight cluster in the middle of the plot, whereas Garifuna individuals were centrally located but more dispersed, trending toward the pole containing African and African-derived individuals.

The plot of the next two PCs appeared to separate the Americas from Eurasia and Africa, with admixed American populations being positioned in the middle (Figure 2). Both the FPC/Lopinot and Garifuna clustered with the comparative admixed groups, specifically Puerto Ricans (PUR) and Colombians from Medellin (CLM). However, unlike the reference populations positioned near the European group, the FPC/Lopinot and Garifuna clustered near the comparative African and African-derived groups. Similar to the plot of the first two PCs, Garifuna individuals were spread along the central portions of the plot and appeared somewhat distinct from the FPC/Lopinot group, whose members formed a condensed cluster.

3.2.3 | Global ancestry estimation—We used ADMIXTURE 1.3.0 (Alexander et al., 2009) and fastSTRUCTURE (Raj et al., 2014) to calculate our global ancestry estimates. The optimal K value ($K = 5$) was chosen based on cross-validation in ADMIXTURE and historical evidence regarding the general number of populations immigrating to these islands. Using $K = 5$ for ancestral population components, median ancestry estimations revealed varying ancestral proportions and substructure in the FPC/Lopinot and Garifuna communities. While both communities had high median proportions of African ancestry (39% in the FPC/Lopinot and 75% in the Garifuna), the proportions differed across European, East Asian, South Asian, and Indigenous American ancestries (Figure 3). East and South Asian ancestry were virtually absent in the Vincentian Garifuna, but present, albeit at low levels, in the FPC/Lopinot community (~9%). Both communities also appeared to have comparatively more European ancestry relative to East and South Asian ancestry, with about 31% median European ancestry in the FPC/Lopinot and 12% median ancestry in the Garifuna (Table 2, Figure S3). They further exhibited Indigenous American ancestry, with higher median amounts observed in the FPC/Lopinot community (13%) than in the Garifuna (5%). However, the distribution of Indigenous ancestry, as illustrated by the interquartile range values, was greater among the Garifuna (0.3–16%) than in the FPC/Lopinot community (12–13%) (Table 2). Despite this distribution, the mean ancestries between the groups were not significantly different for Indigenous American ancestry.

Beyond variation in the median ancestry values, population substructure also differed between the FPC/Lopinot and Vincentian Garifuna communities (Figure 4). The Garifuna appeared similar to the reference population from Barbados (ACB) and African Americans from the southwest United States (ASW). By contrast, the FPC/Lopinot community showed a distinct pattern of genomic ancestry which reflected its comparatively diminished African ancestry and greater contributions from other populations from around the world. In addition, the FPC/Lopinot community appeared more homogeneous with regard to individual ancestry components.

To further explore these results, we increased $K = 12$ to assess finer levels of substructure within the two Caribbean communities (Figure 4 and Figure S4). We again observed different patterns of genetic substructure in the FPC/Lopinot and Garifuna populations. While substructure analyses can sometimes distort real genetic components as a result of admixture especially in isolated groups, in our analysis, the FPC/Lopinot community had an ancestry component not present in the Garifuna or observed in any reference populations.

3.2.4 | Sex-biased gene flow—In addition to considering broad patterns of global ancestry within these Indigenous Caribbean communities, we explored the potential influence of sex-biased gene flow in these populations. We tested for sex-biased gene flow by comparing the mean ancestry estimated from the autosomes to that estimated from the X chromosome for all participants in our sample. To include the data from male participants in this analysis, we adjusted the log-likelihood based on the individual's sex to account for male hemizygosity on the X chromosome.

Among the Garifuna, no clear pattern of sex bias emerged, as evidenced by both the plot and the p-values (Figure 5, Table 3). However, we observed potential evidence of sex-biased gene flow in the FPC/Lopinot samples. As expected based on its population history, ancestry estimated from the X-chromosome was enriched for African and Indigenous American populations but was significantly lower for European populations. This result indicated genetic contributions from African and Indigenous American females as well as that from

European males. Interestingly, East Asian ancestry was also enriched along the X-chromosome relative to the autosomes, indicating that East Asian women also contributed to the FPC/Lopinot community. Alternatively, this enrichment for East Asian ancestry could also be reflective of Indigenous American ancestry that could occur as a result of shared ancestry between East Asian and Indigenous American populations. By contrast, there was no evidence of sex-biased gene flow for South Asian ancestry within the FPC/Lopinot group.

4 | DISCUSSION

The results of this genetic analysis affirmed our initial findings for the Indigenous communities of St. Vincent and Trinidad (Benn Torres et al., 2015) while also revealing new and important details about their population history.

4.1 | Haploid genetic markers

The expanded characterization of mtDNA and Y-chromosome diversity revealed that the Garifuna of St. Vincent have a mixture of Indigenous, African, and European haplogroups, and at relative frequencies consistent with those seen in our earlier study (Benn Torres et al., 2015). Of the African lineages, the FPC/Lopinot community had much lower frequencies of haplogroup L0 and L1 mtDNAs compared to the Garifuna community, with L2 and L3 mtDNAs being more common in each. In addition, we noted a wider range of Indigenous American and South Asian haplogroups in the FPC/Lopinot community and East Asian lineages not previously observed. These newly observed mtDNA and Y-chromosome haplogroups are the result of wider sampling and, for the Indigenous American haplogroups, possibly reflect gene flow with Indigenous peoples from South America that are known to have moved between Trinidad and the mainland throughout the late 19th century (Brereton, 1979). The different mtDNA M haplogroups observed in the FPC/Lopinot are also common within northeast India and East Asia (Chandrasekar et al., 2009), while Y-chromosome O2 haplogroups are commonly seen in East Asian populations (Shi et al., 2005; Wen et al., 2004). As discussed below, their appearance within the FPC/Lopinot community is consistent with historical records regarding the emigration of Indian and Chinese indentured laborers into Trinidad. On the basis of these results, the Garifuna and FPC/Lopinot communities appear genetically distinct from each other.

4.2 | Autosomal DNA markers

4.2.1 | Genetic diversity—Despite the geographic proximity of Trinidad and St. Vincent, the FPC/Lopinot and Garifuna Indigenous communities are genetically dis-similar, as seen in their F_{ST} estimates, a finding that likely reflects differences in their respective demographic histories. In addition to appearing distinct from the Garifuna, the FPC/Lopinot community also differs from other comparative groups, including both the representative African and Indigenous American populations. These differences may indicate that the comparative groups were not influential in shaping the diversity within the contemporary FPC/Lopinot population. Furthermore, as will be discussed below, the origins of Trinidad's enslaved African peoples appear to be somewhat different than the African peoples residing on other Caribbean islands.

4.2.2 | Comparative geographic affinities—Genetic differences between the Garifuna and FPC/Lopinot communities were evident in the PCA plots. In these plots, the reference populations cluster by geographic region, while the FPC/Lopinot sample forms a tight cluster in the center. The condensed cluster of the FPC/Lopinot further reflects its substantial group homogeneity, which was also observed in the substructure plots.

While members of the FPC/Lopinot community exhibit ancestry from other globally dispersed populations, gene flow into the FPC/Lopinot community appears to be have been structured by sex and generally limited, resulting in similar admixture signatures among individuals in the community. The exact sociocultural factors that contributed to this pattern are unclear. Trinidad's Indigenous populations were physically and socially marginalized during the European colonization of the island. This marginalization, coupled with demographically smaller population sizes, could have affected the pattern of genetic variation within the FPC/Lopinot community (Brereton, 2008; Ingram, 2009; Lipski, 1990). Thus, analysis of additional samples could improve our understanding of the scope of this historical trend.

Conversely, the Garifuna have a more dispersed distribution along the first principal component. Within the PCA plot, some Garifuna individuals fall close to the cluster of African and African-derived comparative populations, while others cluster nearer to the center of the plot, trending toward the comparative Indigenous American populations. This intergroup difference may reflect the semi-isolation of peoples within St. Vincent. Contemporary ethnography supports the idea that native peoples within the North Windward communities are somewhat economically and socially separated from the rest of the island population (Twinn, 2006). The broad distribution of Garifuna individuals on the PCA plot further illustrates the heterogeneity of genetic ancestries within this population. This heterogeneity may reflect varying frequencies of interaction and intermarriage with other Vincentians, which has been documented in 19th century records (Gullick, 1984).

4.2.3 | Global ancestry estimation—Previous studies of Caribbean islanders have found that ancestry estimates varies between island populations (Benn Torres et al., 2008; Deason et al., 2012; Moreno-Estrada et al., 2013; Simms, Rodriguez, Rodriguez, & Herrera, 2010; Vilar et al., 2014). These interisland distinctions in ancestry point to differences in historical, demographic, and sociopolitical factors present throughout each island's colonization period and postcolonial migrations (Heuman, 1997; Pérotin-Dumon, 1999; Whitehead, 1999). Such differences shaped mate choice and, ultimately, patterns of genetic variation within each island community.

In addition, considerable differences were also observed between the Indigenous Caribbean populations, as expected based on haploid marker analysis. In both communities, African, European, and Indigenous American ancestries accounted for upwards of 80% of their overall genomic ancestry. However, the median values for the ancestry estimates varied substantially between the two communities. We also observed notable differences between the study groups with regard to their population substructure. These differences in global ancestries and population substructure likely reflect differences in Trinidad's and St. Vincent's general histories, as discussed below.

4.3 | Historical context for genetic data

Archeological evidence from Trinidad's Banwari Trace site suggests that Indigenous peoples have inhabited the region since 7,800 YBP (Fitzpatrick, 2015; Harris, 1976). During initial migrations into the region, they exploited local resources and used Trinidad as a gateway into the island chain of the Lesser Antilles (Sued-Badillo, 2003). In 1498, the Spanish reached Trinidad, and, by 1592, they had established a permanent presence on the island (Rogoziânski, 1992; Williams, 1962). During the Spanish colonial period, the Indigenous population was decimated by disease and genocide, and exploited for labor within Trinidad and other Spanish-controlled regions of the Americas (Forte, 2004; Rogoziânski, 1992). Despite dramatic demographic changes spurred by Spanish colonization, Indigenous populations contested colonization and persisted in localized regions of the island (Cudjoe, 2016; Forte, 2005). Until the transfer to the British crown in 1797, Trinidad generally remained too undeveloped for large-scale plantation agriculture (Knight, 1990). After the British took control of Trinidad, they encouraged the development of plantation agriculture, with this economic shift resulting in substantial changes to the island's physical and demographic constitution (San Miguel & Monteith, 2011).

The earliest archeological evidence for human presence in St. Vincent dates to 1,650 YBP (Giovas & Fitzpatrick, 2014). During European colonization of the Caribbean, St. Vincent was initially left for Indigenous peoples, although the British later annexed the island and established a permanent presence there in 1763 (Palmié & Scarano, 2013; Whitehead, 1999). As with the native peoples of Trinidad, the Indigenous populations of St. Vincent were continuously exploited and displaced. In response, Indigenous St. Vincentians launched intense campaigns of resistance against European colonization (González, 1988; Kim, 2013; Palacio, 2000). Despite the demographic and cultural changes brought about by colonization, the native population on St. Vincent persisted and its descendants are present within contemporary Vincentian society. Within St. Vincent, the Garifuna identify themselves as descendants of African and Indigenous Caribbean peoples and are predominantly located in the southern portions of the island, while those who identify as Kalinago primarily descend from the local Indigenous population and are generally concentrated in the northern portion of the island (Fraser, 2014; Palmer, 2014).

Irrespective of their different colonial histories, the development of plantation agriculture and the arrival of enslaved Africans to the Caribbean had a profound impact on both St. Vincent and Trinidad (Thomas, 1997). According to historical records, in an effort to curb illegal slave trade, the British government mandated that a registry of enslaved peoples be created to help ensure that the trans-Atlantic importation of enslaved people had indeed ended (Higman, 1978; Roberts, 1977). Based on these registries, the enslaved population across the British Caribbean is recorded to have peaked at nearly 778,000 people in 1807 and declined to about 665,000 by the time of emancipation in 1834 (Higman, 1984). This registry of enslaved peoples also indicates that their birthplaces included Senegambia, Sierra Leone, Windward Coast, Gold Coast, Bight of Benin, Bight of Biafra, and Central Africa, as well as Mozambique on the east coast of Africa. While historians have noted the many ways in which census records are potentially biased due to competing motives of plantation owners, government officials, and other stakeholders, these registries provide some idea of the heterogeneous origins of African peoples enslaved in the British Caribbean colonies (Roberts, 1977; Solow, 2001). In fact, analysis of similar census records illustrates the demographic changes that occurred within the enslaved population which eventually resulted in African-derived peoples forming the most numerous segment of island populations relative to Indigenous Caribbean and European people (Knight, 1997).

Plantation agriculture was developed on the islands at different periods and, as a consequence, the sources of enslaved Africans varied across time and by island (Knight, 1997; Moreno & Cateau, 2011). On islands colonized by the British by the mid 18th century, including St. Vincent, enslaved peoples from the Windward Coast, Gold Coast, and the Bight of Benin were in the majority (Higman, 1984). On islands colonized and developed by the British in the 19th century, such as Trinidad, the majority of enslaved peoples came from Central Africa and the Bight of Biafra (Higman, 1984).

Early 19th century census records from Trinidad offer a closer snapshot of the enslaved laborers' origins. Roughly 79% of the African-born enslaved population came from 1 of 11 ethnicities/regions, including Ibo, Moco, Congo, Quaqua, Gold Coast, Coromante (Akan), Mine, Mandingo, Bibi, Chamba, and Arada (Higman, 1978). These census records also suggest a high level of assortative unions between members sharing regional origins within Africa. For example, in 1813, 303 of 646 unions involved pairing in which both members were from the Bight of Biafra (Higman, 1978). Post-emancipation also saw a significant migration of African peoples to Trinidad from various regions in West Africa, as well as St. Helena (Brereton, 1979). Comparable data for St. Vincent do not exist, although some census records superficially recognize the number of African-born enslaved people in 19th century St. Vincent (Office of Registry of Colonial Slaves and Slave Compensation Commission, n.d.).

In addition to the influx of European and African peoples to Trinidad and St. Vincent, later migrations of peoples to the islands impacted the demography of Indigenous communities. Shortly after emancipation in the Anglophone islands, the plantocracy needed to replace the labor lost from formerly enslaved peoples. As a result, they brought indentured laborers from South Asia, and to a lesser extent, China, to fill the labor void (Look Lai, 1993; Roopnarine, 2007). Shipping records and contract letters indicate that Trinidad accepted 143,939 South Asian indentured laborers, whereas St. Vincent received substantially fewer (2,472), with the remaining migrants being distributed across Guyana, Suriname, Guadeloupe, Jamaica, Martinique, French Guiana, Grenada, Belize, St. Lucia, St. Kitts, and St. Croix (Lal, 1998; Look Lai, 2004; Roopnarine, 2003).

Indian migrants to the Caribbean came from all social strata within populations found in the Indo-Gangetic plains of northern and eastern India and, to a lesser extent, southern India (Lal, 1998; Vertovec, 1994). In the latter half of the migratory period, the present-day state of Uttar Pradesh was the source of approximately 80% of the migrants, while Bihar and Bengal provided only 13% (Lal, 1998). The remaining laborers came from other regions of India including Madhya Pradesh and Punjab (Lal, 1998). Throughout this period of mass migration to the British West Indies from India, many migrants stayed within the Caribbean, with only about 22% making the return trip back to India (Vertovec, 1994). Consequently, this influx of South Asian people was influential in shaping the demography of the Caribbean, and in particular, Trinidad.

The histories of these islands help contextualize the patterns of genetic variation observed in our samples. As illustrated in the global ancestry estimates, both communities have genetic ancestry from African, European, and Indigenous American populations. However, the relative contributions of these ancestries differ between islands. For example, the frequency of African ancestry is higher among the Garifuna relative to the FPC/Lopinot, while there are higher values of European ancestry among the FPC/Lopinot relative to the Garifuna. Such differences likely reflect the later importation of enslaved African peoples into Trinidad relative to St. Vincent, and the interactions between Indigenous Caribbean peoples and other migrants on each island. In addition, the FPC/Lopinot and Garifuna have approximately similar proportions of Indigenous American ancestry.

Overall, the FPC/Lopinot sample is more genetically homogeneous than that of the Garifuna, with the extent of Indigenous ancestry being similar among members of the FPC/Lopinot community. This outcome was surprising in light of the history of Garifuna and Kalinago communities over the past several centuries. According to historical records, the British forcibly relocated nearly half of the purported number of Indigenous people on St. Vincent in the late 18th century, roughly 2,500 from an estimated 5,000 persons (Davidson, 1984; Gullick, 1984). Consequently, we had expected to see some sort of bottleneck effect in the Garifuna that had diminished genetic diversity in this community. Yet, given the lack of information about genetic diversity on St. Vincent prior to the exile, it may be complicated to detect such bottlenecks. Furthermore, there is also the possibility that, due to the trauma of exile among Indigenous persons and the economic interests of colonists, the historical records do not accurately account for the number of persons who were exiled, may have returned, or remained on the island. Nevertheless, our genetic data are generally consistent with previous anthropological genetic studies of Black Carib and Garifuna populations in showing differing degrees of Indigenous American ancestry among the sampled communities that likely resulted from this exile process (Crawford et al., 1984; Schanfield et al., 1984).

The homogeneity of the FPC/Lopinot community was also quite surprising given the general history of the island’s settlement. In this regard, we did not sample closely related family members and applied mitigative statistical methods to control for cryptic relatedness (see Methods). Accordingly, the homogeneity of the FPC/Lopinot community either reflects sampling effects or historical founder events that resulted in lower levels of genetic diversity within this community. In addition to differences in Indigenous American ancestry, the FPC/Lopinot exhibit ancestry from both East and South Asian populations, while the Garifuna have little such ancestry. This finding is supported by the historical records detailing the arrival of East and South Asian indentured laborers, primarily in Trinidad, beginning in the late 19th century (Ho, 1990; Weller, 1968).

With respect to differences in population substructure, we sought to further distinguish genetic ancestry by assessing substructure for up to 12 clusters (Figure S4). At $K = 12$, the FPC/Lopinot group forms its own cluster, while the Garifuna appear quite similar to African

American and Caribbean (Barbadian) comparative populations. While this result may possibly misrepresent the actual genetic components contributed through admixture, this distinct cluster in Trinidad may instead indicate the unique ancestral dynamics of this island community or a failure to identify appropriate reference populations. As mentioned above, historical sources suggest that Trinidad was home to a mix of African peoples different than those on other Caribbean islands, such as St. Vincent and Barbados (Higman, 1984; Warner-Lewis, 2003). The difference in African origins among Trinidadians is likely attributable to the relatively later development of plantation agriculture in combination with fluctuations of the sources of enslaved African labor throughout the colonial period (Higman, 1978, 1984). In addition, there were post-emancipation influxes of African peoples from Sierra Leone and St. Helena into Trinidad in the late 19th century (Brereton, 1979). Based on these observations, a finer resolution analysis designed to distinguish African ancestral components would further illuminate the Atlantic slave trade’s impact on genetic variability in the Caribbean.

To further elucidate the dynamics of gene flow affecting these Indigenous Caribbean communities, we estimated levels of sex-biased gene flow. For the Garifuna, we did not observe significant differences in ancestry between the autosomes and X-chromosomes. However, our analysis of the FPC/Lopinot community revealed that African, East Asian, and Indigenous American women and European men made much larger genetic contributions to the contemporary community, relative to African, East Asian, and Indigenous American men and European women. However, there does not appear to be sex-biased gene flow from South Asians in the FPC/Lopinot community. This general pattern, where the X-chromosome reflects strong African and Indigenous American ancestry and relatively diminished European ancestry, has been observed in other admixed populations throughout the Americas (e.g., Mathias et al., 2016).

Regardless, the differing degrees of sex-biased gene flow within these communities are difficult to explain from genetic data alone. They may be the result of sampling effects, or social dynamics that affected mate choice within island communities. For example, historical records indicate that, as Trinidad’s Indigenous populations endured Spanish and then British colonization, they became increasingly isolated in missions and localized regions of the island which may have limited opportunities for gene flow with surrounding groups (Brereton, 1979). The situation differed for St. Vincent’s Indigenous populations, as their higher concentrations in localized regions of the island did not appear to seriously limit gene flow with other Vincentians (Gullick, 1976, 1984). An expanded analysis of Vincentian samples, in addition to ethnographic and sociological perspectives on factors that have shaped mate choice, will help to verify sex-biased gene flow in these communities.

Despite persistent narratives suggesting that Indigenous Caribbean populations have gone extinct (Benn Torres, 2014; Castanha, 2010; Forte, 2002; Guitar, 2002), contemporary Indigenous Caribbean communities remain vital to an understanding of human history in the Caribbean region. Through analysis of their oral narratives, material culture, linguistic traits, and genetic data, we are able to provide new insights into the human history of this region of the world (Allaire, 1980; Benn Torres et al., 2015; Cudjoe, 2016; Ferreira, 2012; Forte, 2005; Giovas & Fitzpatrick, 2014). Furthermore, using a transdisciplinary approach to contextualize genetic data helps to elucidate the role of social factors in shaping genetic variation. In the case of the Indigenous Caribbean peoples of Trinidad and St. Vincent, differences in island and community histories have profoundly shaped their genetic diversity, resulting in different patterns of variation in the two groups, despite the relative geographic proximity. Future studies examining the population genetics and demography of these communities will benefit from larger sample sizes, as well as more refined analyses of non-European ancestral components to their genomes. Such analyses would be useful for dating admixture events and gaining an understanding of factors that shaped the genetic diversity of contemporary Caribbean populations.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

ACKNOWLEDGMENTS

We gratefully acknowledge the participation of Indigenous Caribbean individuals from Trinidad and St. Vincent, whose collaboration made this study possible. We also thank the Garifuna Heritage Foundation in St. Vincent and the Santa Rosa First Peoples Community of Arima in Trinidad for their support of this project.

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Funding information

National Cancer Institute (National Institutes of Health), Grant/Award Number: 1K07CA172294; National Geographic Society, Grant/Award Number: 2012 Geno 2.0 Award; The Vanderbilt Human Genetics Training Grant (part of the NIH/NIGMS Genetics Predoctoral Research Training Program), Grant/Award Number: T32GM080178; University of Notre Dame, Grant/Award Number: Small Grants for Research and Creative Work, Insti; University of Pennsylvania, Grant/Award Number: Faculty Research Fund

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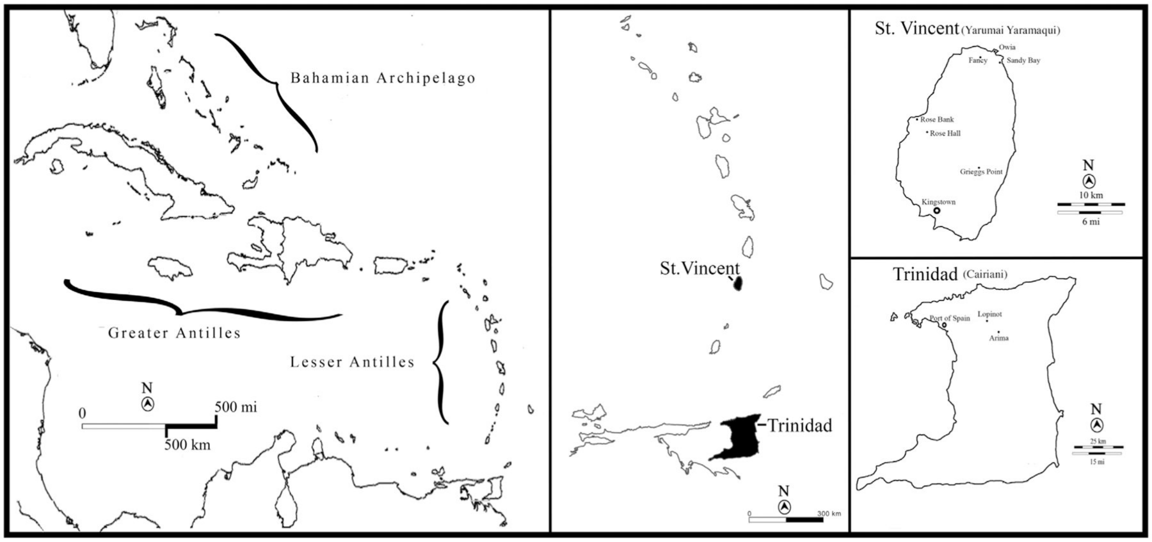

FIGURE 1.

Maps of Caribbean islands and sampled communities. (a) A map of the Caribbean basin; (b) a map of the study islands in the Lesser Antilles; (c) a map showing the sampling locales in St. Vincent and Trinidad (Indigenous names for the study islands are in parentheses, adapted from Sued-Badillo 2003.)

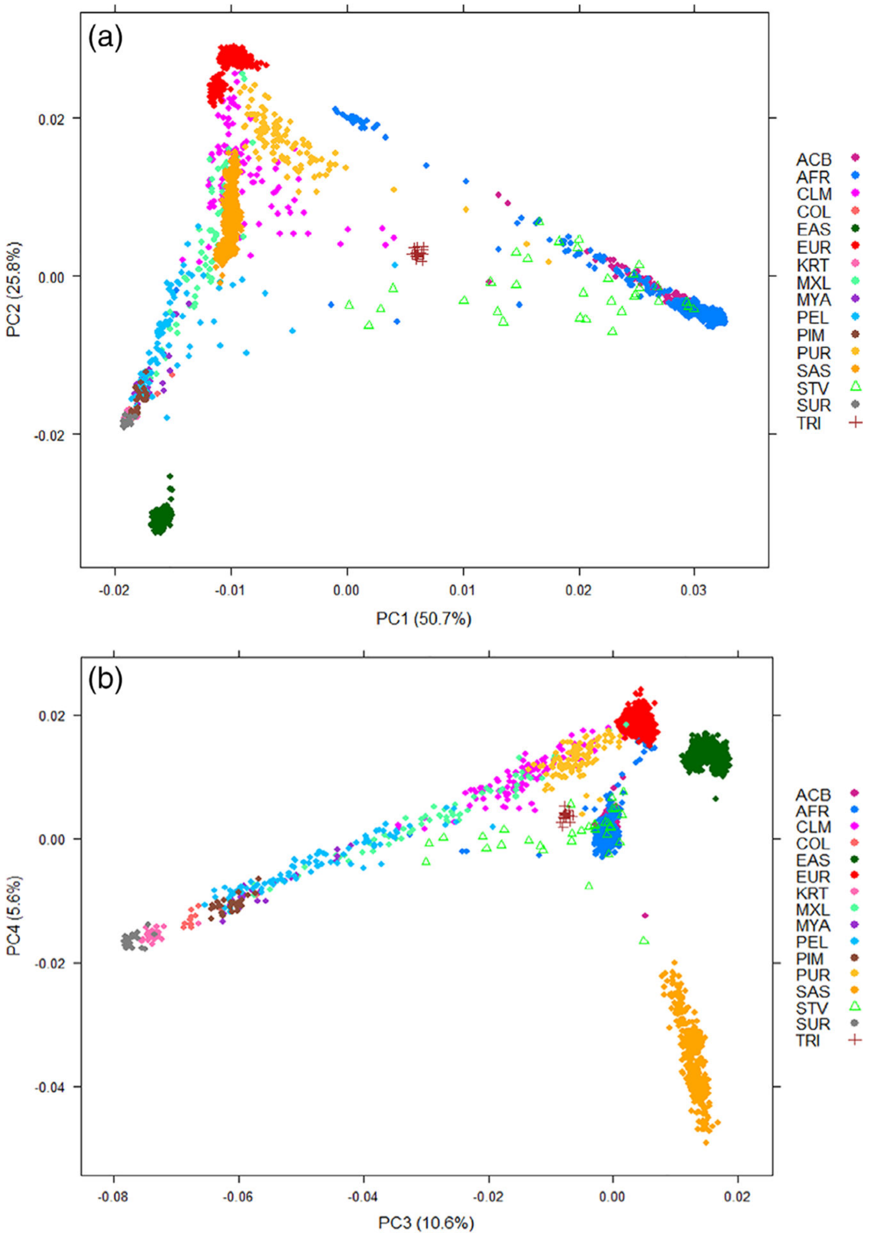

FIGURE 2.

PCA plots of comparative and study populations. (a) PC1 versus PC2, explaining 76.5% of the variation; (b) PC 3 versus PC 4, explaining 16.2% of the variation. A list of the comparative populations may be found in Table S6. PCA, principal components analysis

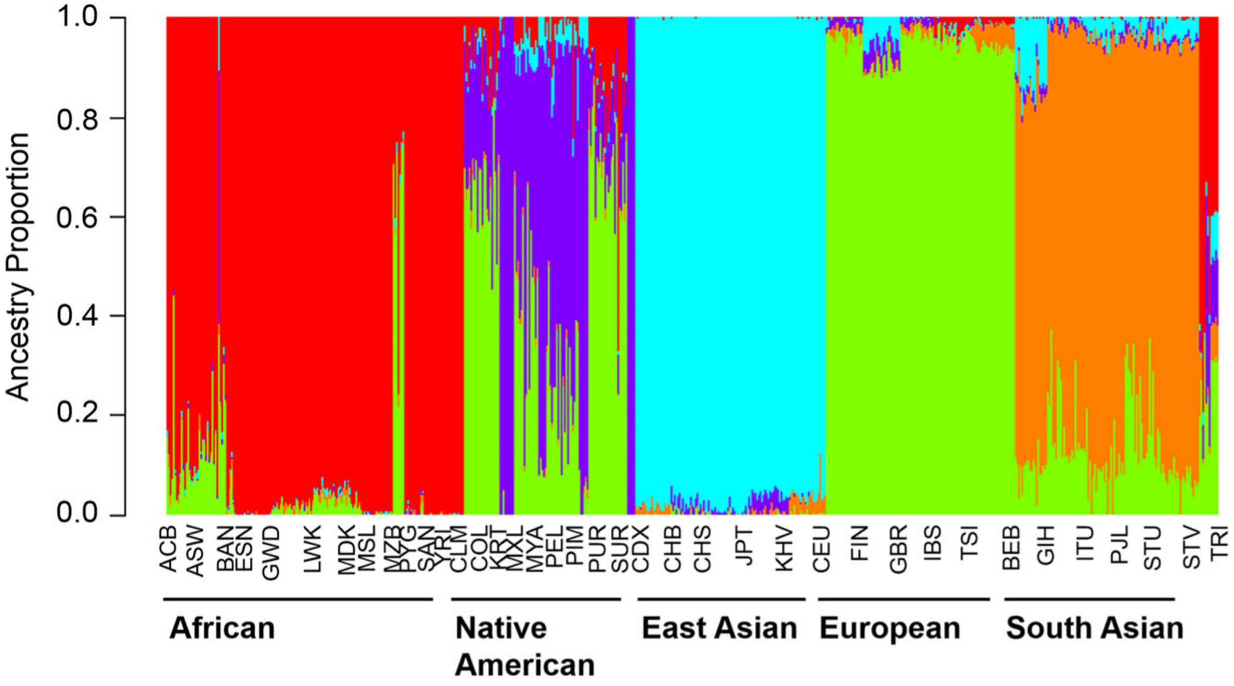

FIGURE 3.

Admixture plots of comparative and Indigenous Caribbean populations, $K = 5$

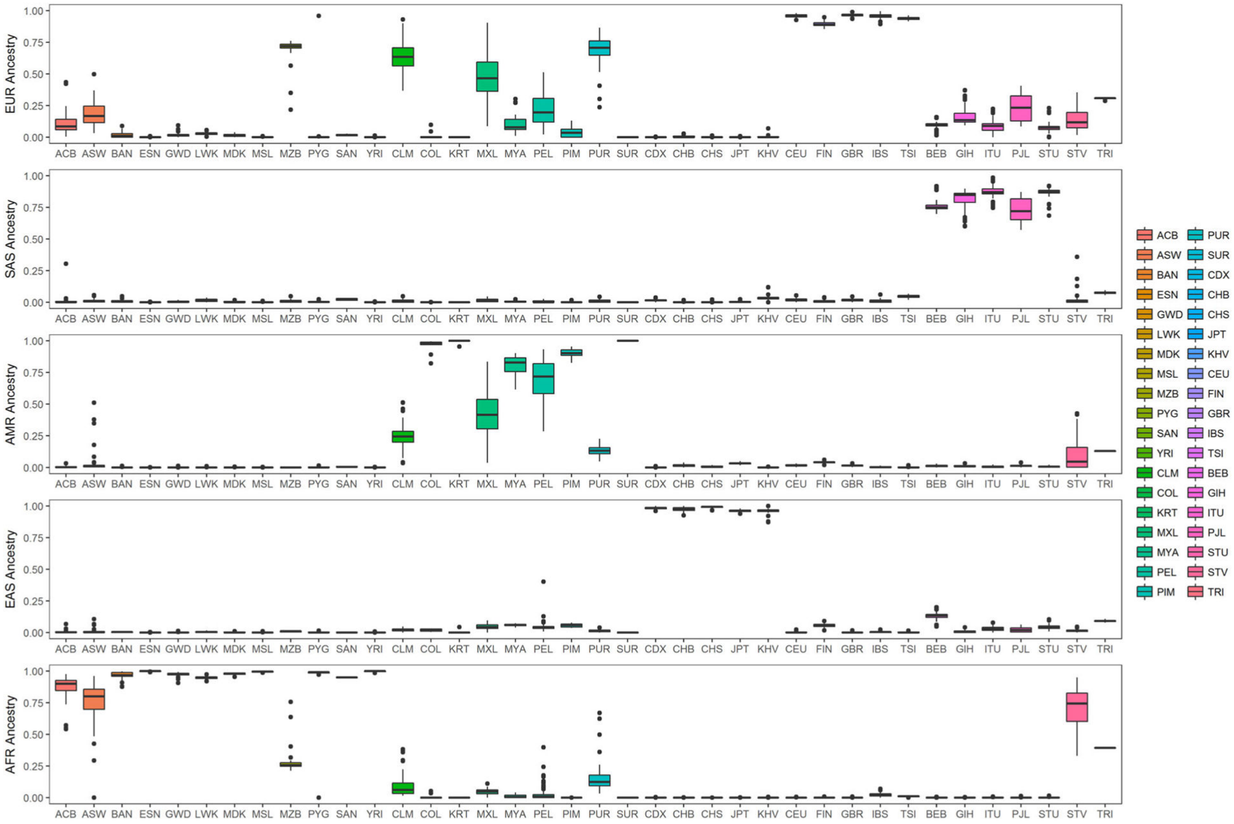

FIGURE 4.

Mean and median global ancestry estimates for Indigenous Caribbean and comparative populations

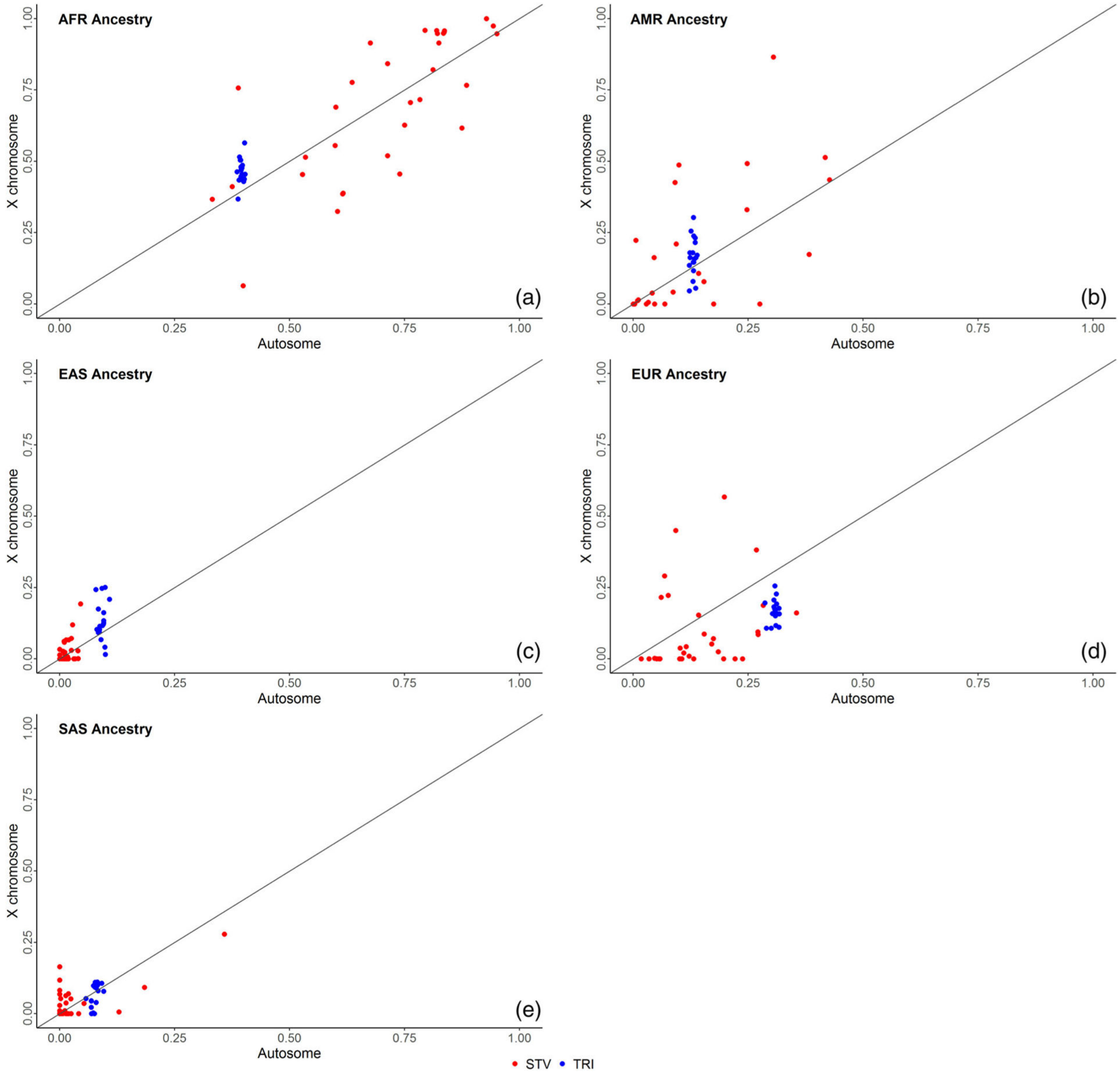

FIGURE 5.

Sex bias plots of proportional ancestry for (a) African (AFR), (b) Indigenous American (AMR), (c) East Asian (EAS), (d) European (EUR), and (e) South Asian ancestry in Indigenous Caribbean communities. Trinidad First People’s Community is shown in red and the Vincentian Garifuna in blue

TABLE 1

mtDNA and Y-chromosome haplogroup frequencies in FPC/Lopinot and Garifuna populations

a) mtDNA haplogroup data

	FPC	**FPC/Lopinot**	**Total FPC/Lopinot**	**SVG 1**	**SVG 2**	**Total SVG**
mtDNA Hg	***n* = 25**	***n* = 23**	***n* = 48**	***n* = 65**	***n* = 49**	***n* = 114**
A2	13	6	39.6%	7	1	7.0%
B1	0	1	2.1%	0	0	-
C1	3	1	8.3%	22	7	24.5%
D1	0	1	2.1%	0	0	-
H	0	0	-	0	1	0.9%
K	1	1	4.2%	0	0	-
L0	0	0	-	11	1	10.5%
L1	0	1	2.1%	2	5	6.1%
L2	2	4	12.5%	14	23	32.5%
L3	2	3	10.4%	9	10	16.7%
M10	0	1	2.1%	0	0	-
M33	4	2	12.5%	0	0	-
M35	0	1	2.1%	0	0	-
U5	0	0	-	0	1	-
U6	0	1	2.1%	0	0	-

b) NRY haplogroup data

	FPC	**FPC/Lopinot**	**Total FPC/Lopinot**	**SVG 1**	**SVG 2**	**Total SVG**
NRY Hg	***n* = 6**	***n* = 12**	***n* = 18**	***n* = 27**	***n* = 15**	***n* = 42**
E1b1a	3	3	33.3%	14	11	59.5%
G2a	0	1	5.6%	0	0	-
I1	0	0	-	2	1	7.1%
I2	0	0	-	1	0	2.4%
O2	0	1	5.6%	0	0	-
Q-M3	2	1	16.7%	3	1	9.5%
R1a	1	1	11.1%	0	0	-
R1b	0	5	27.8%	7	2	21.4%

Abbreviations: FPC, First People's Community; NRY, nonrecombining portion of the Y-chromosome.

TABLE 2

Median ancestry (IQR) and statistical tests of mean ancestry (*SD*) for Vincentian Garifuna (SVG) and Trinidad First People's community (TRI)

Population	**SVG**	**TRI**	***p*-value**
African			
Median (IQR)	0.745 (0.603–0.827)	0.394 (0.392–0.397)	
Mean (*SD*)	0.704 (0.171)	0.395 (0.005)	1.92×10^{-11}
Native American			
Median (IQR)	0.046 (0.003–0.159)	0.131 (0.127–0.134)	
Mean (*SD*)	0.107 (0.133)	0.130 (0.005)	.339
East Asian			
Median (IQR)	0.014 (0.009–0.021)	0.093 (0.086–0.096)	
Mean (*SD*)	0.016 (0.012)	0.092 (0.008)	$<2.2 \times 10^{-16}$
European			
Median (IQR)	0.118 (0.074–0.197)	0.308 (0.306–0.311)	
Mean (*SD*)	0.143 (0.085)	0.307 (0.008)	3.60×10^{-12}
South Asian			
Median (IQR)	0.004 (0.000–0.019)	0.077 (0.070–0.081)	
Mean (*SD*)	0.029 (0.072)	0.077 (0.009)	8.46×10^{-4}

Abbreviation: IQR, interquartile range.

TABLE 3

Comparison of autosomal and X-chromosome ancestry estimates for sex-biased gene flow

	Ancestry estimate				
	African	**American**	**European**	**East Asian**	**South Asian**
STV					
Autosomes	70.4%	10.7%	14.3%	1.6%	2.9%
X chromosome	69.5%	14.4%	9.8%	2.5%	3.7%
Relative increase or decrease on X	−1.28%	34.58%	−31.47%	56.25%	27.59%
p-value	.77	.22	.11	.20	.46
TRI					
Autosomes	39.5%	13.0%	30.7%	9.2%	7.7%
X chromosome	46.7%	16.6%	16.8%	13.4%	6.6%
Relative increase or decrease on X	18.23%	27.69%	−45.28%	45.65%	−14.29%
p-value	9.68×10^{-7}	3.77×10^{-2}	5.37×10^{-11}	1.75×10^{-2}	.23