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Abstract

As the last American region settled by humans, yet the first to experience European colonization, the Caribbean islands have a complex history characterized by continuous migration, admixture, and demographic change. In the last 20 years, genetics research has transformed our understanding of Caribbean population history and revisited major debates in Caribbean anthropology, such as those surrounding the first peopling of the Antilles and the relationship between ancient Indigenous communities and present-day islanders. Genetics studies have also contributed novel perspectives for understanding pivotal events in Caribbean post-contact history such as European colonization, the Atlantic Slave Trade, and the Asian Indenture system. Here, I discuss the last 20 years of Caribbean genetics research and emphasize the importance of integrating genetics with interdisciplinary historic, archaeological, and anthropological approaches. Such interdisciplinary research is essential for investigating the dynamic history of the Caribbean and characterizing its impact on the bio-cultural diversity of present-day Caribbean peoples.

KEYWORDS

admixture, ancient DNA, genomics, Greater Antilles, Lesser Antilles, migration

1 | INTRODUCTION

The Caribbean islands (Figure 1) have a rich and complex history marked by constant migration and demographic change. The archipelago was one of the last island systems in the Americas settled by humans during the Holocene, and later became the setting for the first encounter between Indigenous Americans and European colonizers.^{1,2} The islands were also the first destination for the victims of the Atlantic Slave Trade and the birthplace of the American plantation with its concomitant system of racialized slavery.³ Due to this unique and dynamic past the Caribbean is a primary region of interest for anthropological research. The archipelago presents an excellent case study of how human populations cope with transformative social and biological processes such as migration, colonization, admixture, and creolization.

Until recently most research investigating the Caribbean past was focused on the archaeological, linguistic, and historic records. But in the last 20 years, our understanding of Caribbean history has been transformed by the growth of human genomics research. This growth has been rapid and exponential, especially for Caribbean paleogenomics studies. To provide some context, as of January 2015 no complete human genomes had been successfully sequenced from ancient Caribbean contexts. As of this writing, in December 2020, over 260 complete genomes spanning the last 3000 years of Caribbean history are now published.^{4–8} In addition, hundreds of high-resolution genomic data sets from present-day Caribbean islanders or Caribbean diasporic populations are now available.^{9–12} Taken together, this body of research has found that Caribbean genomes are diverse and heterogenous, a reflection of the complex social, historical, and biological processes that have shaped island populations over the last 7000 years (Figure 2). But, while the advent of population genomics has addressed some long-standing questions it has also posed many others; most of which cannot be answered without

[Correction added after first online publication on January 28, 2022. The legend in Figure 1 has been corrected.]

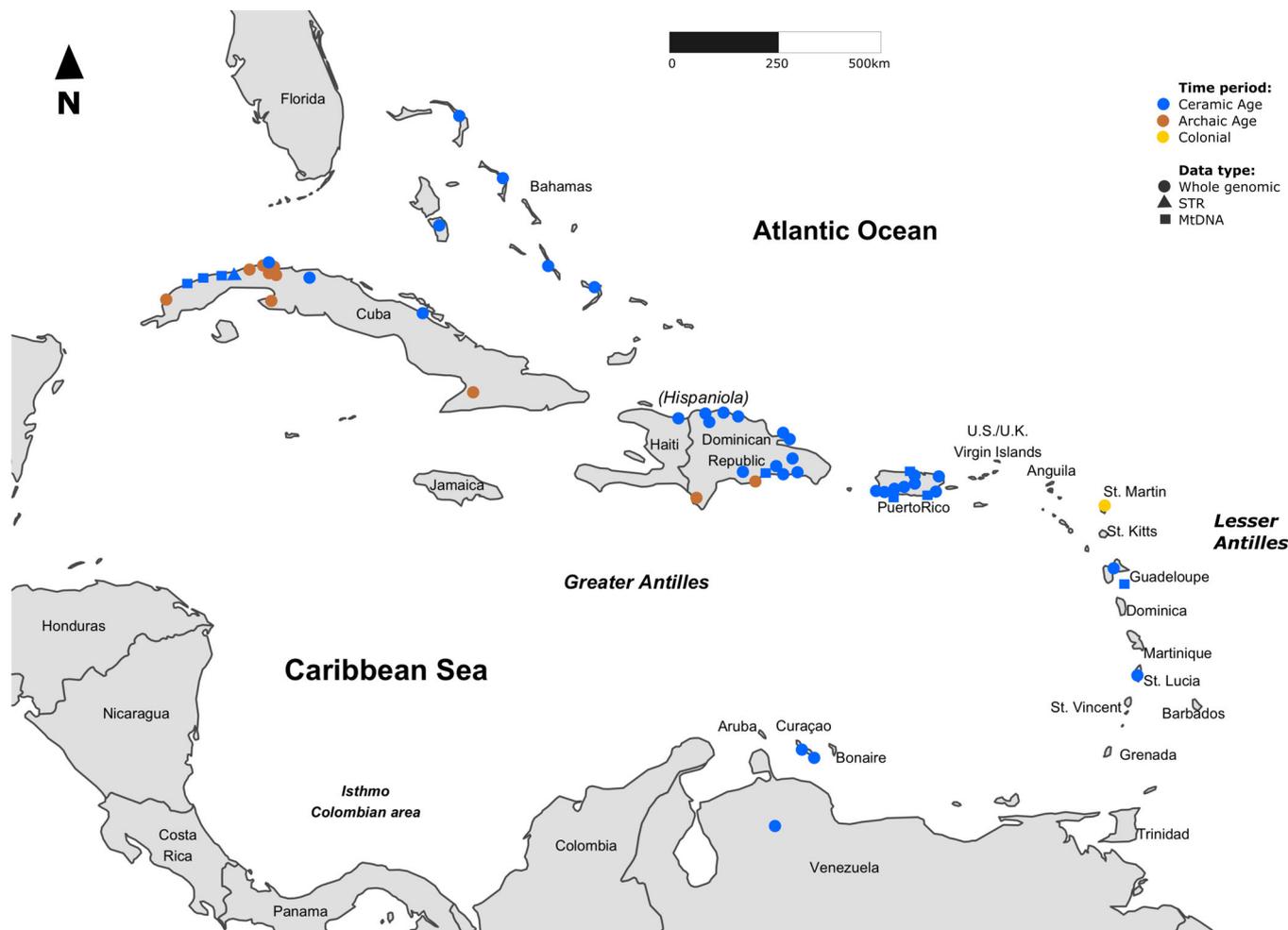


FIGURE 1 Map of the Circum-Caribbean basin with approximate locations of archaeological sites from which human ancient DNA has been recovered. STR, short tandem repeat; mtDNA, mitochondrial DNA. Source: References 4–8, 52–55

drawing upon additional sources of historic, (bio)archaeological or anthropological evidence.

Here, I review the major contributions of genetics research for understanding Caribbean population history. I begin by discussing the relevance of genetic data for addressing major debates about the Caribbean precontact period, including the first peopling of the Antilles and the relationship between ancient Indigenous communities and present-day islanders. Then, I describe how DNA studies have changed understanding of pivotal events during the post-contact period including European colonization, the Atlantic Slave Trade, and the Asian Indenture system. Throughout I describe how genetics research has characterized the influence of diverse ancestors—including Indigenous, European, African, East and South Asian peoples—in shaping the bio-cultural diversity of present-day Caribbean islanders. I emphasize the importance of integrating historical and archaeological sources of evidence for contextualizing genetic data and I highlight those areas with potential for future inquiry. This review concludes with a brief exploration of future directions and lists some of the current challenges of conducting anthropological genetics research with Caribbean populations.

2 | THE PRECONTACT CARIBBEAN

2.1 | Indigenous ancestors

Many questions remain unanswered about the initial settlement and precontact population history of the Caribbean. Archaeological evidence indicates the archipelago was first settled ~5000 years ago^{1,13}; although the island of Trinidad—which was still connected to mainland South America during the early Holocene¹⁴—has a much earlier date of initial human habitation, ~7000 years ago. The origins, number, and routes of these first population dispersals are unknown. Archaeological and linguistic data suggest potential source areas include the Isthmo-Colombian region, Central America (specifically the area around Belize, Honduras, and the Yucatan Peninsula) or South America.^{1,15,16} Although some scholars also proposed the Florida Peninsula as a potential source area,¹⁷ no strong evidence has yet been found in support of this hypothesis.¹⁸ This period is known as the Lithic or Archaic Age because island communities had technological toolkits including flaked and ground-stone tools, and

| Dates | Description |
|----------------|---|
| 2000 A.D. | Growth of Caribbean population genetics research. |
| 1834-1917 A.D. | Asian Indentureship period. Increased migration from East and South Asia to the Antilles. |
| 1834-1886 A.D. | Abolition of slavery and emancipation of the enslaved. |
| 1700-1830 A.D. | Growth of the Atlantic Slave Trade to the Caribbean. |
| 1520 A.D. | First African peoples arrive in the Antilles. |
| 1492 A.D. | European contact. Beginning of the colonization period. |
| 600 A.D. | Indigenous Caribbean groups expand and diversify. Start of the Late Ceramic Age |
| 400-500 B.C. | Arawak-speaking groups migrate from South America. Start of the Ceramic Age. |
| 5000 B.C. | Initial settlement of the Antilles. Start of the Archaic Age. |

FIGURE 2 Timeline of major events in Caribbean history described in the main text

horticultural subsistence strategies. In some locations of the Greater Antilles there is also evidence for small-scale pottery production during the Archaic period.¹⁹ Whether differences in these material traditions—stone tools in particular— represent multiple dispersals into the Caribbean has been a significant source of debate among Caribbean archaeologists.^{1,20} Material evidence suggests that Indigenous communities with Archaic Age material culture persisted in some of the Antilles since the first island settlement until the Contact period.²¹

The Caribbean Ceramic Age began ~2500 years ago when Arawak-speaking peoples from lowland South America entered the Antilles. These populations introduced novel ceramic industries and intensive agricultural technology to the archipelago.¹ The exact route by which Ceramic Age groups entered the Antilles is disputed. Two potential models have been proposed. The *Stepping Stone* model, largely based on ceramic typology but also supported by paleoenvironmental data,²² posits an island hopping route starting in the South American mainland passing through the Lesser Antilles and ultimately reaching the Greater Antilles.²⁰ In contrast, the *Southward Route* model, which is supported by computer simulations of maritime seafaring,^{23,24} as well as radiocarbon dating,^{13,25–27} posits direct maritime travel from South America to the Greater Antilles with subsequent expansion into the Lesser Antilles.¹³ Exactly how Archaic and Ceramic Age communities interacted during this period (e.g., coexistence, displacement, or admixture), and their respective

contributions to the development of Late Ceramic Age and Contact period populations continue to be topics of active research.¹

The number of population dispersals during this period has also been debated. The discovery of distinctive ceramic and lithic traditions, including zoomorph lapidary carvings resembling Andean condors, at Early Ceramic Age sites in Puerto Rico (most notably at the site of La Hueca-Sorcé in Vieques island) and the Lesser Antilles^{1,28} suggests that populations with distinctive material cultures co-existed in the Caribbean during the Early Ceramic Age. Similarities between these assemblages and material traditions found in precontact sites in Bolivia, Venezuela, and Colombia led several researchers to suggest that a separate dispersal event starting somewhere in the western Andean foothills may have also brought peoples to the Antilles.²⁸ Furthermore, other scholars have suggested that the emergence of novel ceramic traditions during the Late Ceramic Age may have been due to additional migratory waves from the continental mainlands.²⁰

Lastly, many gaps exist in our understanding of the early Contact period in the Caribbean. Much of what is known about Caribbean Indigenous peoples during this period is heavily influenced by the biases and perspectives of colonial writers.^{29–31} Their accounts reduce Indigenous communities to a few homogenous and largely dichotomous categories such as the “noble Indians” of the Greater Antilles, later renamed as Taino in the 19th century, and the “fierce Caribs” of the Lesser Antilles. Although these groupings are not based on Indigenous self-identification they continued to be deployed as valid analytical categories by anthropologists, archaeologists, and historians for much of the 20th century, and thus are now widely recognized and used in public discourse.^{30,32,33} Today, there is growing recognition that the uncritical use of these categories obscures the diversity of cultures coexisting in the Antilles during the Late Ceramic Age and early Contact period.^{1,32,34} Thus, much current archaeological and ethnohistorical research seeks to better characterize the ethnic diversity of precontact Caribbean Indigenous communities, their responses to colonization, and their relationship to present-day islanders.^{2,29,35,36}

2.2 | The first Caribbean genomes

In the last 20 years, genetics has emerged as an additional and important tool for studying precontact Caribbean history. DNA studies have contributed new insights toward major questions such as tracing the original peopling of the Antilles, characterizing subsequent dispersals, and examining the biocultural relationships between ancient Indigenous communities and present-day islanders. To investigate the genetic diversity of precontact populations in the Caribbean, DNA studies have relied upon two approaches: (1) Examining the Indigenous American ancestry of present-day populations, based on a large body of existing evidence that strongly suggests it derives at least partially from ancient island communities (as discussed below); or (2) Directly querying the ancient genomes recovered from human skeletal remains excavated from precontact archaeological contexts.

Studies carried out in the early to mid-2000s characterized the genetic diversity of Caribbean islanders using JC virus strains (Human polyomavirus 2), uniparental loci (mitochondrial DNA and Y-chromosome), and small panels of autosomal markers.^{37–41} This body of work found that contemporary islanders carry varying proportions of admixture from Indigenous American, European, African, and to a lesser degree, East and South Asian ancestors. In addition to characterizing broad patterns of global admixture, these studies were the first to suggest that Indigenous American ancestry among present-day islanders stemmed primarily from precontact Indigenous Caribbean populations.³⁷ This early research and subsequent follow-ups with larger sample sizes, denser geographic, and genomic coverage^{9,11,42–50} argued that contemporary islanders are a reservoir of precontact genetic variation and a source of information for reconstructing precontact Caribbean population history.

Beyond investigating modern genomes, some research also sought to directly assay precontact genetic variation by obtaining ancient DNA (aDNA) from human remains excavated at Caribbean archaeological sites. Despite the technical limitations of recovering aDNA in the adverse preservation conditions of the Caribbean tropics,⁵¹ these pivotal studies successfully used Sanger sequencing to characterize mtDNA and autosomal loci from the remains of Archaic and Ceramic Age individuals found in Cuba, Hispaniola and Guadeloupe.^{52–55} Subsequently, with the advent of next-generation sequencing and the development of improved techniques for aDNA recovery, Caribbean paleogenomics rapidly expanded. The first complete human genome from a precontact Caribbean context was published in 2018.⁶ This genome was recovered from a woman who lived ~1000 years before the present, and whose remains were found at the site of Preacher's Cave on Eleuthera island in the Bahamas. Today, genomic scale data sets have been produced from several precontact communities spanning large temporal sections of the Archaic and Ceramic periods in most of the Greater Antilles and several of the Lesser Antilles (Figure 1).^{4,7,8}

2.3 | DNA insights on precontact migration

Overall, the data derived from modern and ancient genomes shows that the precontact Caribbean was diverse and pluralistic, settled by multiple and successive dispersals from the mainland Americas.^{4,7,11,43,47,50,56} Consistent with archeological evidence, the aDNA data available to date finds genetic differences between Archaic and Ceramic Age Caribbean populations.^{4,7,52} However, while the origins of Ceramic populations are relatively well known, paleogenomic studies have reached differing conclusions regarding the origins and number of the first Archaic dispersals. For instance Fernandes and colleagues⁷ identified a single, homogenous ancestry component shared between Archaic individuals from Cuba and Hispaniola. This finding suggests Archaic populations arrived in the Antilles through a single dispersal event. In contrast Nägele et al.⁴ found high variability in the genetic composition of Archaic communities in Cuba, suggesting multiple dispersals may have occurred. Both studies found

the genetic diversity of Caribbean Archaic Age communities falls outside of present-day Indigenous American genetic variation. This suggests that the first Caribbean settlers originated in an as yet unknown population that is not closely related to contemporary Indigenous American groups.^{4,7} Thus, to date, the question of the mainland origins of Caribbean Archaic populations is still unresolved. Since currently available paleogenomic data sets provide insufficient resolution to fully address this question, it will be important to combine archaeological data with further aDNA research.

Future studies may seek to examine aDNA from human remains found at early sites in the Lesser Antilles, such as those from Trinidad, or in potential continental source areas such as the Isthmo-Colombian region, coastal Central America, or northern South America. Future prospection and excavation of submerged coastal and island landmasses may also uncover evidence of early human activity or habitation in the circum-Caribbean—including archaeological remains amenable for molecular sampling. Areas of interest include a now submerged chain of islands that extended between Jamaica and Central America in the early Holocene; submerged areas of Cuba, the Bahamas and some of the Lesser Antilles such as St. Martin; the land bridge that once connected Trinidad with South America; and submerged areas of the Yucatan peninsula or the Central American coast.^{14,57} If DNA preservation is sufficient, characterizing the genetic diversity of ancient individuals sampled from these contexts may allow for additional testing of archaeological hypotheses concerning the ultimate origins and genetic relationships of Caribbean Archaic communities with mainland populations.

In contrast to the uncertainty surrounding the first Archaic dispersals, there is broad agreement between genomic and archeological sources on the South American origins of Caribbean Ceramic Age populations. Studies investigating ancient and present-day genomes have identified genetic similarities between ancient Caribbean populations, present-day islanders and Indigenous populations from northeast South America.^{4,6–8,11,42,43,47,50,52–54} For example, aDNA studies found mtDNA lineages of South American origin, such as haplogroup C1b2, at very high frequencies in Caribbean Ceramic Age populations. Additionally, Caribbean populations also shared an autosomal ancestry component closely related to Indigenous Amazonian groups.^{4,6–8} These findings agree with a large body of linguistic¹⁶ and archaeological evidence^{1,20} which indicates that Ceramic Age Caribbean groups originated in the Orinoco River delta region of South America, in the present-day territories of Venezuela and Guyana.

Although the mainland source of Ceramic Age Caribbean populations is now well established, the scale of this migration and its impact on Caribbean biocultural landscapes are still topics of ongoing research.⁵⁸ For instance, most ancient DNA evidence points to a single wave of expansion out of South America and into the Antilles. But the possibility of multiple migrations originating in the same region or from the same genetic population cannot be confidently excluded with the available evidence.⁷

Similarly, the exact dispersal routes are still debated. Although paleogenetic analyses found support for the island-hopping *Stepping Stone* model,^{4,7} Bayesian modeling based on stringent application of

chronometric hygiene standards to over 2400 radiocarbon dates gathered from precontact Caribbean sites provides strong evidence in support of the *Southward Route* hypothesis.¹³ Lastly, while additional dispersals from other parts of South America, such as the Andean foothills, have been proposed on the basis of archaeological evidence,²⁸ the aDNA studies conducted to date have not detected Andean ancestries among Caribbean Ceramic Age populations.^{4,7,8}

Additionally, the nature of interactions between newly arrived Ceramic Age migrants and island Archaic populations are still unknown. Despite material and genetic evidence that these groups coexisted for several hundred years in some of the Greater Antilles—most notably in western Cuba²¹—few instances of genetic admixture have been identified.^{4,7} For instance Fernandes and colleagues⁷ reported that among 201 individuals excavated from Ceramic associated contexts, only three individuals from the La Caleta and Diale 1 sites in Hispaniola carried a signal of genetic admixture with Archaic populations. Similarly, out of 41 Ceramic associated individuals examined, Nägele et al.⁴ identified only one individual with a small proportion of Archaic-related ancestry from the site of Paso del Indio in Puerto Rico. Why did populations with Archaic and Ceramic material cultures intermix so little, and what was the nature of their social interactions? Further research integrating genetic data with other lines of evidence is clearly needed to answer this question.

An important caveat underlying all of these inferences are the current spatial gaps in paleogenomic sampling. Most ancient human genomes recovered to date from precontact Caribbean sites were obtained from the northern and western Caribbean, especially from the Greater Antilles. Specifically, Archaic and Ceramic genomes have been sequenced from individuals buried at sites in the Bahamas, Cuba, northern Haiti, Dominican Republic, Puerto Rico, and three of the Lesser Antilles: St. Lucia, Guadeloupe, and Curaçao (Figure 1).^{4,7,8,52–54} The genetic diversity of ancient Caribbean peoples living in other areas of the Antilles, such as Jamaica, southern Haiti, Trinidad and most of the Lesser Antilles have yet to be characterized. As more archaeological and genomic data are generated, especially from currently unsampled archaeological contexts, a more detailed picture of ancient population movements and interactions associated with the Archaic to Ceramic Age transition is likely to emerge.

2.4 | Island founders and genetic drift

Several lines of evidence suggest that the demographic history of Indigenous Caribbean populations was strongly impacted by genetic drift. First, most ancient Indigenous communities in the Greater Antilles had low mtDNA diversity relative to continental Indigenous American populations.^{8,52,53} Similar patterns of low diversity are found in populations with demographic histories marked by genetic bottlenecks or isolation.⁵⁹ A notable exception to this pattern is the Guadeloupe archipelago, a group of three islands in the Lesser Antilles (Figure 1). An aDNA study published in 2015⁵⁴ found that Late Ceramic Age communities in Guadeloupe had high mtDNA diversity, differing haplogroup frequencies and distinct funerary practices

between burial sites. It is possible that this divergent pattern arose because several distinct groups, with potentially different demographic histories, inhabited Guadeloupe before European contact.

Second, several Caribbean mtDNA clades exhibit phylogenetic signatures consistent with undergoing one or more founder effects. A founder effect occurs when a small number of individuals establishes a new population. Since the newly formed population only has a subset of its ancestral genetic variation this event leads to reduced diversity and an increased frequency of founder variants or haplotypes over time. For example, Martínez-Cruzado and colleagues⁴³ investigated 488 Indigenous American mtDNA haplotypes identified in a sample of 800 individuals representative of the modern Puerto Rican population.⁴⁴ Of these 488 haplotypes, 104 were assigned to lineage C1b2, representing 21% of the total data set. Using aDNA, Nieves-Colón and colleagues⁸ reported that C1b2 was also the most common mtDNA lineage found in Ceramic Age communities from Puerto Rico, making up ~33% of all precontact haplotypes. Clade C1b2 exhibits a starlike phylogenetic pattern consistent with a founder event seeded by a small group of maternally related individuals followed by subsequent expansion and differentiation of derived lineages.^{8,43} In an in-depth study of mtDNA variation among Puerto Ricans, Martínez-Cruzado⁴³ proposed that this founder event may be connected to the expansion of Arawak-speaking populations with intensive agricultural technology during the Caribbean Ceramic Age. Due to this founder event, lineage C1b2 continues to be extremely common among Puerto Ricans today.^{8,50} Similar island founder events and subsequent reductions in mtDNA haplotype diversity have also been documented in precontact populations from Cuba⁵² and Hispaniola,⁵³ and among Indigenous and Garifuna groups in the Lesser Antilles.^{47,60}

Third, demographic reconstructions indicate that Ceramic Age Caribbean populations had relatively small effective population sizes (N_e)—between 1000 and 2000 individuals—compared with coeval populations from the continental Americas.^{6–8,42} Several mtDNA studies suggest that low N_e and increased susceptibility to drift may have led to genetic isolation and differentiation of island mtDNA pools over time, even between geographically close Caribbean communities.^{8,47–49,52–54,56} In contrast, studies examining autosomal loci find evidence for high inter-island mobility and gene flow during the Caribbean Ceramic Age.^{6,7,11} Most recently, Fernandes and coauthors⁷ detected kin relations between ancient individuals buried on different islands. Altogether, these findings suggest that regional interaction networks—which are well documented archaeologically^{1,36}—may have buffered the effects of low N_e by maintaining genetic diversity across the archipelago.

The extent to which regional interaction networks in the Caribbean were maintained through the establishment of social or familial connections is still unknown. Several authors have proposed that matrilineal or avunculocal kinship networks existed among late Ceramic Age Caribbean societies.^{61,62} Although this hypothesis could explain discrepancies in patterns of gene flow between uniparental versus autosomal loci, it has yet to be systematically tested with genetic data. Under the avunculocal hypothesis, matrilineally related males would reside in the household of a maternal uncle

concentrating political power and resources under a single matrikin group. Unrelated females would then move with the husband's family upon marriage.⁶¹ It is unclear whether this residence pattern was widespread across the Antilles or practiced widely beyond members of the political elite. Although Fernandes and colleagues⁷ identified three genetically related males buried at different sites in Hispaniola, this sample size is too small to test for statistically significant differences in male versus female mobility and residence patterns. Thus, while the genetic data available to date suggests that males engaged in intra-island mobility it does not demonstrate avunculocal residence patterns or exclude a role for females in mediating inter-island exchange and connectivity. Additional research examining detailed patterns of uniparental versus autosomal genetic variation among males and females buried at distinct sites is needed to reconstruct residence patterns and understand their role in shaping the genetic diversity of precontact Caribbean societies. Ultimately, the largest reduction in genetic diversity among Indigenous communities in the Caribbean was caused not by random drift or sex-biased migration patterns but by European contact.^{7,8,11}

2.5 | Contact and colonization: The genomic impact

The arrival of European colonizers in the late 15th century caused the decline and transformation of Indigenous Caribbean populations. Exposure to novel diseases, enslavement, warfare, forced and voluntary displacement profoundly affected island communities, especially in the Greater Antilles which were the first sites of European settlement.^{29,63} Furthermore, European colonizers transformed the demography of the islands by importing enslaved peoples from across the Americas and Africa to work in the newly established mines and plantations.^{3,29,64} Indigenous and African peoples resisted colonization through rebellion, flight, and other means. Some fled from Hispaniola and Puerto Rico to the Lesser Antilles where they joined local groups in launching raids and attacks on newly formed European settler towns.²⁹ Others founded maroon communities in the remote interior of islands like Jamaica, Hispaniola, Cuba, and St. Croix.^{65,66} In St. Vincent and Dominica, Indigenous and Black communities successfully fought off European advances well into the 18th century.⁶⁷ These events and population movements reshaped the patterns of genetic diversity, population structure, ancestry, and admixture that existed before contact.

Beyond impacting population structure, colonial perspectives also shaped historical discourses regarding the fate of Indigenous Caribbean peoples. Census records and other texts from the early colonial period describe the rapid disappearance of Indigenous Caribbean communities.²⁹ Subsequent interpretations of these texts led to a widely popularized extinction narrative. This interpretation posits that Indigenous Caribbean peoples became extinct soon after contact due to disease, genocide, replacement, and absorption or acculturation into creole colonial society.^{35,68,69} In contrast with this narrative, recent scholarship has postulated an alternative scenario emphasizing

survival, continuity, and resurgence.³¹ This alternative interpretation suggests that while Indigenous Caribbean populations were greatly impacted by colonization, they did not disappear entirely. As described by Benn Torres⁷⁰ the survival narrative is supported by several lines of evidence. First, recent scholarship has recognized that colonial-era records failed to accurately document the number of Indigenous peoples living in the Antilles during European occupation. It is therefore possible that surviving communities were not counted in official documents.^{29,31,35} Second, anthropologists and ethnohistorians have documented persistent expressions of Indigenous cultural practices and identities throughout the Antilles into the present-day.^{31,36,68} And third, government recognized and self-identified Indigenous communities are present on several islands. In addition, Indigenous resurgence movements exist throughout the archipelago and in the Caribbean international diaspora.^{31,69} Because of these disputing narratives, extinction versus survival, the relationship of precontact Indigenous Caribbean peoples to present-day islanders, and their role in the formation of today's island communities continue to be vigorously debated. Due to the prominent position DNA data have assumed in shaping notions of identity and belonging, genetic studies have become an increasingly important and consequential part of this debate.^{70–73}

2.6 | Continuity and genetic legacies

The first indications of potential genetic continuity between ancient and present-day islanders came from population history studies mapping patterns of mtDNA and JC viral strain diversity.^{37,39} These studies documented high proportions of Indigenous American ancestry among Puerto Ricans; especially among self-identified communities of Indigenous descent in the island's mountainous interior.³⁷ Subsequent works documented a strong sex bias in the distribution of Indigenous American ancestry: high proportions of Indigenous American ancestry in mtDNA and conversely low proportions in Y-chromosome and autosomal loci.^{11,12,44,45,50} Varying proportions of Indigenous American mtDNA ancestry have also been documented in other Caribbean populations from the Greater^{48,49,74,75} and Lesser Antilles,^{9,46–48,76} and among Maroon communities.^{65,77}

It is possible, and even likely, that some of this Indigenous American ancestry stems from Indigenous peoples who were transported from the continental mainlands to the Caribbean during the colonial period.^{43,71} However, several lines of supporting evidence suggest most of the Indigenous American genetic component of present-day islanders can be attributed to local continuity and not replacement. Most Caribbean populations share a regional pattern of high frequencies of Indigenous American A2 and C1 mtDNA haplogroups.^{43,44,47–50} Similar haplogroup distributions are also found among Ceramic Age populations.^{4,7,8,53,54} This suggests that present-day mtDNA haplogroup patterns probably originated in the precontact period and persisted over time. Additionally, several Indigenous American mtDNA lineages found in the Caribbean today bear signatures of local evolution and diversification. These lineages are unlikely to have originated

outside of the archipelago and may represent locally evolved diversity.^{43,50}

Most recently, aDNA studies identified traces of precontact genetic ancestry in the genomes of modern Caribbean peoples. For instance, mtDNA haplotypes from Ceramic Age Caribbean communities were identified among Puerto Ricans and other islanders.^{7,8} Many of these lineages are uncommon or entirely absent outside of the Caribbean today.^{7,8,50} Additionally, comparisons with autosomal loci demonstrate that populations in Cuba and Puerto Rico have a close genetic relationship to Ceramic Age groups from the Greater Antilles.^{6,7} Interestingly, no Archaic Age ancestry has been identified among present-day populations.^{4,7} This suggests that Ceramic Age groups were the primary contributors to present-day Indigenous Caribbean genetic diversity. More research including broader sampling of present-day islanders and additional ancient populations is still needed to fully characterize the genetic links between past and present island communities.

In summary, ample genetic evidence demonstrates that present-day Caribbean islanders are at least a partial reservoir of precontact genetic variation. However, the demographic shifts brought by European contact have strongly impacted and reshaped the apportionment of this diversity. Several mtDNA lineages from Ceramic Age populations did not persist into the present-day, and Caribbean islanders vary in the extent of autosomal ancestry they can trace to precontact populations.^{6–8,11,42,43,74} Thus, far from representing a static snapshot of ancient genetic diversity, present-day Caribbean genomes reflect the dynamic combination of precontact, colonial, and postcolonial demographic processes. Today, Ceramic Age Caribbean diversity can even be found outside of the Antilles as modern populations expand into the transnational Caribbean diaspora.

3 | THE POST-CONTACT CARIBBEAN

3.1 | Of admixture and ancestry: Tracing post-contact Caribbean population history

Starting in the 15th century, European colonization and intercontinental migration drastically transformed the demography of the Antilles. Due to its central geographic location and its early importance to the overseas colonial enterprise, the Caribbean became the initial American destination for European settlers in the 15th and 16th centuries. These settlers established the first *encomiendas* and plantations, forced labor systems which led to the enslavement of Indigenous Caribbean communities and the forcible transport of millions of enslaved peoples from across Africa and the circum-Caribbean basin to the Antilles.^{3,78} Subsequently, after the abolition of slavery in the 19th century, Caribbean plantations attracted thousands of indentured laborers from Europe, Africa, South, and East Asia.⁷⁹ This pattern of continuous migration and exchange reshaped the genetic diversity of Caribbean populations.^{11,80}

Over the last two decades, research into Caribbean post-contact population history has largely focused on investigating the impact of

historical migrations on extant patterns of genetic structure and admixture. Most of these studies can be broadly classified into four, sometimes overlapping, research categories: (1) Local histories focusing on one or more island communities and often seeking to characterize the impact of local sociocultural and historical processes on biocultural diversity,^{9,10,38–40,43,45,49,50,60,65,75,77,81–88} (2) Regional histories surveying broad patterns of genetic diversity across several islands which are usually grouped together due to some unifying geographic, historical or linguistic factor (e.g., the Lesser Antilles, the former French colonies, the Anglophone islands),^{11,46–48,74,76,89} (3) Large scale surveys or meta-analyses of genomic variation in the Americas that include island or diasporic Caribbean populations,^{12,80,90,91} and (4) Biomedical or evolutionary genetic studies investigating the impact of population history on human health and phenotypic diversity.^{41,92,93} Although all of these studies characterize overall patterns of genetic structure, ancestry and admixture, some of them also focus on specific questions such as tracing subcontinental ancestries, dating and characterizing historical migration pulses, or identifying founder events and reconstructing their impact on present-day genetic variation. Throughout more than 20 years of research attempting to disentangle the Caribbean's complex post-contact population histories, genetic studies have used a broad array of genomic elements such as JC viral genotypes,³⁹ uniparental markers (especially mtDNA),^{46,49,50} panels of autosomal informative markers (AIMs),^{45,89} genomewide single-nucleotide polymorphism (SNP) panels,^{10–12} and, more recently, whole sequencing of both historic and present-day human genomes.^{5,42}

Overall, this large body of work has found that most Caribbean islanders can trace their genetic ancestries to two or more continental populations. However, despite some historical commonalities, differing colonial and postcolonial experiences as well as extensive sex-biased admixture have created heterogenous patterns of genetic structure and ancestry across the archipelago (Figure 3).^{11,12,74,80,89,90} Understanding the differential contributions of Indigenous American, European, African, and South and East Asian ancestors to the biocultural diversity of present-day islanders is a major topic of ongoing research in Caribbean population history studies.

3.2 | European settlers

Although the major sources of European migration to the Antilles are well documented in the historical record, DNA studies have contributed new perspectives on the timing, scale, and impact of these movements, as well as the distribution of European settlement within the Antilles. European migration to the Caribbean began with the arrival of Spanish *conquistadores* to the Greater Antilles in the 15th century.⁹⁴ Although pirates and buccaneers routinely raided Spanish settlements in the 15th and 16th centuries, other European powers did not formally enter the region until the early 17th century. At that time French, Dutch and British colonists occupied most of the Lesser Antilles, eventually moving westwards into Jamaica and Hispaniola. In the ensuing decades, many Europeans arrived as settlers, mercenaries, and missionaries, but others, especially from the British Isles and

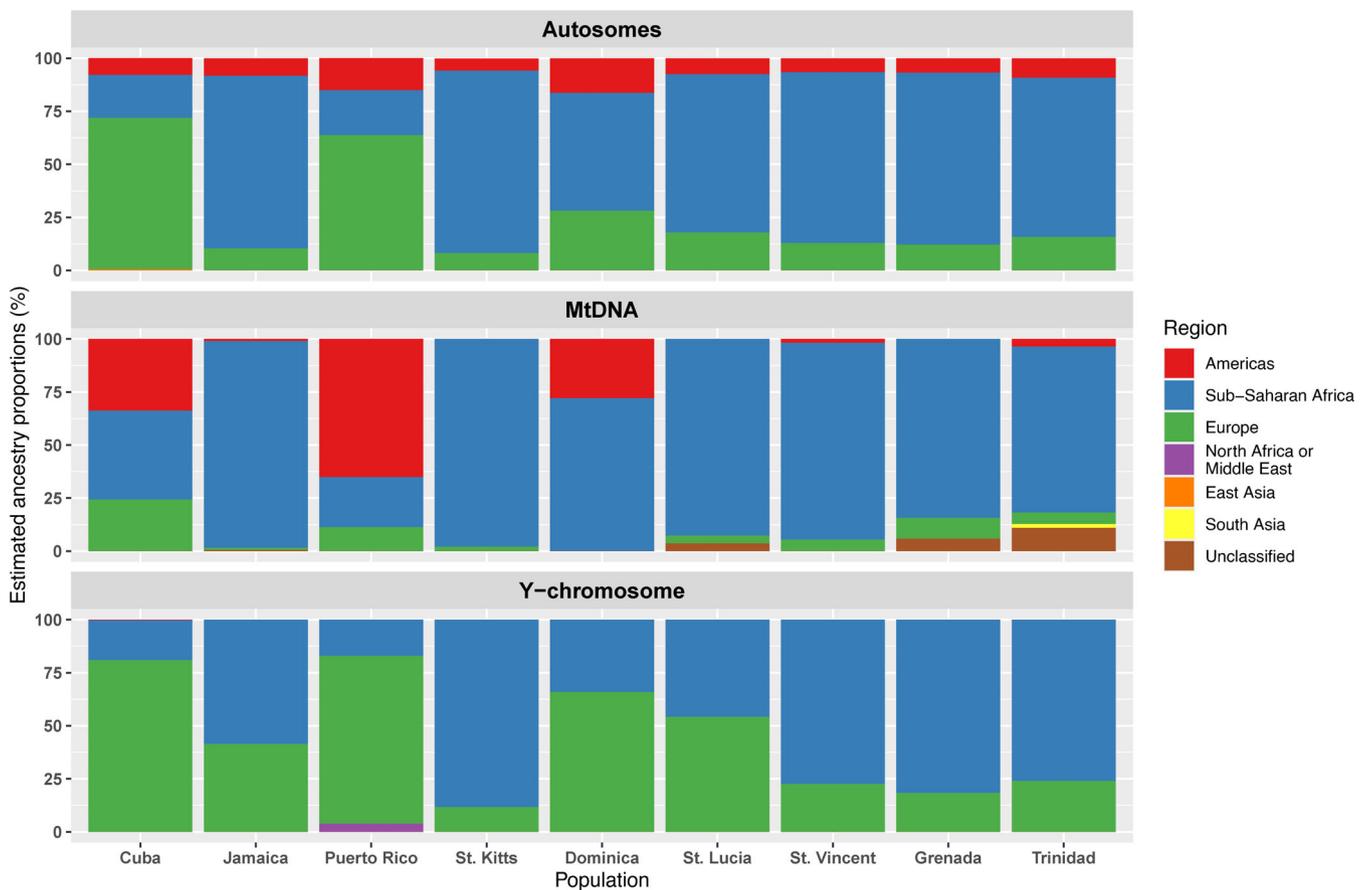


FIGURE 3 Comparison of genetic ancestry proportions across autosomal, mitochondrial, and Y-chromosome loci in nine Caribbean populations. Estimated ancestry proportions were gathered from the published literature. mtDNA, mitochondrial DNA. Source: References 10, 44–46, 49, 50, 75, 86, 89, 91

Scotland, arrived as indentured servants or contract laborers.^{78,95} Although European women participated in these migrations—traveling alone or as part of family units—European men far outnumbered them.⁹⁶ In general, European migration to the Antilles during the colonial period was motivated, shaped, and structured by imperial expansion policies, political relations between colonial states, the requirements of plantation labor, and colonial norms and regulations on inter-ethnic unions.^{78,94,96} These social factors and policies influenced who migrated to the Antilles, where they settled, who they started families with and how these families contributed to the bio-cultural diversity of creole Caribbean communities.

Genetic research has identified several main trends in the European ancestries of present-day Caribbean islanders. First, proportions of European genetic ancestry differ between Caribbean populations; and sometimes within a single island.^{10–12,45,75} For the most part, these genetic structure patterns are consistent with historical settlement trends such as the locations of primary plantation centers, port cities, or other landmarks.^{10,45} However these patterns are also strongly sex-biased.

In most admixed Caribbean populations European ancestry is disproportionately enriched in paternally inherited loci such as the Y-chromosome, while Indigenous American and African ancestry are

found at higher frequencies in maternally inherited mtDNA and X-chromosome loci.^{11,12,80} This sex-biased pattern reflects the unequal gender relations of Caribbean slave societies, where many—sometimes coerced—unions took place between European men and Indigenous or African women.^{96,97} However, although most Caribbean populations share this pattern of sex-biased admixture, paternally inherited European ancestry is heterogeneously distributed.⁹⁸ While some populations, such as Cubans and Puerto Ricans carry between 80% and 85% European paternal ancestries,^{49,50} others, such as Afro-Caribbean populations in the Lesser Antilles carry much less, between 30% and 40% (Figure 3; Table A1).^{46,91} These sex-biased ancestry patterns may also vary within a single island such as in the case of Cuba, where European paternal ancestry is highest in the Eastern versus the Western provinces in response to colonial settlement trends.^{10,75}

Second, sources of European ancestry vary between islands in alignment with the historical distribution of European colonial powers. For example, in former Spanish colonies such as Cuba, Puerto Rico and Dominican Republic, many islanders can trace European sub-continental ancestries to Iberia, the Canary Islands and Southern Europe.^{10,11,81} Similarly, in the former French colony of Guadeloupe, most European uniparental lineages can be traced to Western and

South-Western Europe, among contemporary French and Italian populations.⁷⁶

Third, a strong founder event shaped the genetic diversity of European settler populations in the Greater Antilles. On the basis of dense SNP genotyping,¹¹ identified a Latino-specific European ancestral component in the autosomal genomes of Cubans, Puerto Ricans, and Dominicans. This indicates that due to a reduced number of founders, long-term isolation from the founding population, and the consequent action of genetic drift, the European ancestry component of present-day islanders has diverged from that of contemporary Iberian populations. Subsequent studies of uniparental markers in Puerto Ricans also reached similar conclusions.⁸¹ Whether comparable patterns of drift are also found in the European ancestry components of other Caribbean populations is currently unknown and an interesting avenue for future genetic research. Investigating founder effects, in European ancestry components or otherwise, is relevant for the identification of rare variants and other patterns of deep structure which may be found at higher frequencies among Caribbean islanders due to the action of genetic drift. These rare variants and patterns may be of phenotypic, evolutionary, or medical importance as the recent research by Belbin and colleagues⁹³ has shown.

Fourth, consistent with the historical record, pulses of European migration to the Caribbean pre-date European settlement in the continental Americas. By analyzing the size and distribution of European autosomal haplotypes in the genomes of present-day islanders, the timing of first admixture has been dated to around 16–17 generations ago for the Greater Antilles (circa 1490–1520 assuming a 30-year generation time), and between 14 and 15 generations ago for Cuba specifically.¹⁰ To test if additional pulses of European migration occurred, these studies also fitted haplotype tract-length distributions modeled under admixture scenarios including one or several European ancestry pulses to the observed tract-length distributions of admixed Caribbean islanders.^{10,11} In both cases models proposing a single European pulse were the best fit, suggesting that most European ancestry found today in the Greater Antilles stems from the early colonial period. For comparison, similar analyses conducted with South American populations dated the timing of first admixture to between 9 and 14 generations ago and found evidence of multiple pulses of European admixture.⁹⁹ These later pulses likely correspond to more recent dispersals from the 19th and 20th centuries, when waves of Western and Central Europeans came seeking refuge and economic opportunity to the Americas.¹⁰⁰ Although historical evidence indicates that some of these migrants also arrived in the Greater Antilles—especially after the South American wars of independence and the Spanish American war in the 19th century¹⁰⁰—the genetic data available to date suggests that these later movements had a comparatively smaller impact on the genetic diversity of present-day islanders.

Interestingly, in the case of Puerto Rico there is discrepancy between these genetic findings and the historical record of the late colonial period. Extensive historical documentation demonstrates that a large, second wave of European migration to Puerto Rico took place in the 19th century when the Spanish Crown incentivized European

Catholics to settle in its American colonies through edicts such as the Royal Decree of Graces of 1815.¹⁰¹ These incentives attracted significant numbers of migrants from several Spanish regions including Catalonia, the Balearic and Canary Islands, other areas of Europe such as Corsica and France, and even among the creole elites of other Circum-Caribbean colonies.^{102–105} How these population movements shaped extant patterns of European ancestry in Puerto Rico is still a matter of ongoing research. By examining mtDNA diversity patterns, Díaz-Zabala and coauthors⁸¹ estimated that ~47% of Eurasian mtDNA lineages found among contemporary Puerto Ricans arrived during the early colonial period. The remainder, ~53%, are thought to have arrived later, possibly between 17th and 19th centuries. Based on these findings, the authors suggest that European migrations in the late colonial period likely had a stronger impact on the apportionment of mtDNA versus autosomal genetic diversity due to the larger participation of women in the re-settlement of family units in the late versus early colonial periods. The differing participation and roles of women in migratory and creolization processes throughout the colonial period may be one of several factors that explain the large discrepancies in ancestry proportions between autosomal and uniparental markers among Puerto Ricans today. Note that present-day Puerto Ricans carry—on average and with significant geographic variation—~64% European ancestry, 21% African ancestry, and 15% Indigenous American ancestry in the autosomal genome (Figure 3).⁴⁵ These proportions contrast sharply with the patterns observed in paternally inherited Y-chromosome loci (~85% European ancestry, 85% African ancestry, <1% Indigenous American ancestry) and the maternally inherited mtDNA genome (~60%–61% Indigenous American ancestry, 25%–27% African ancestry, 12%–15% European ancestry).^{44,50} It is possible that further research among other Caribbean populations may reveal similar discrepancies and more complex patterns of recent admixture among different European ancestors.

Lastly, another avenue for future research is the application of paleogenomic approaches to historic and colonial archaeology. To date, no aDNA studies have examined the genetic diversity of colonial European settlers or early creole populations in the Caribbean. Such research may contribute toward addressing questions related to European migration patterns, local histories, the process of creolization, and even gain insights into the health status, dietary patterns, and daily lives of populations in colonial settlements.

3.3 | African ancestors and Afro diasporic communities

The Atlantic Slave trade to the Caribbean began in the 16th century with the first arrival of enslaved Africans to the Spanish colonies of Hispaniola, Puerto Rico, and Cuba. In subsequent years the trade expanded, reaching a peak during the 18th and 19th centuries.^{64,97,106}

By the time of emancipation in the 19th century, it is estimated the British forcibly transported ~2.3 million enslaved Africans, at a rate of about 50,000 people a year, to their Caribbean possessions. The Spanish for their part imported around 750,000 enslaved Africans to

their Caribbean colonies, while the French imported over 1 million enslaved people—most of whom were headed to the plantation colony of Saint Domingue on Hispaniola (modern Haiti).^{64,95} Due to preferential importation of male slaves, sex ratios of enslaved peoples on Caribbean plantations were highly skewed.⁹⁷ As a result, the demography of the islands shifted. Africans and their descendants became, on average, between 60% and 90% of the population.^{95,97} Thus, over time, most Caribbean colonies saw the rise of a creole population with mixed European, African and Indigenous heritage.¹⁰⁷

Although slave traders and colonial authorities documented the ship ports, coasts, and regions from which they extracted human cargo, these documents alone are not sufficient for understanding the origins of the enslaved within Africa. Moreover, specific information about the ethnicities, identities, professions, livelihoods, and health of the enslaved, as well as any aspect of their cultures or personalities that was of little interest to the slave traders, is largely missing from the documentary record.¹⁰⁶ Thus, to gain a fuller picture of the African diaspora to the Caribbean and the impact of African peoples on present-day biocultural diversity, it is necessary to combine insights from several fields including history, archaeology, and genetics.¹⁰⁸

Until recently, few genetic studies had been conducted investigating the African diaspora in the Caribbean.¹⁰⁹ However, the last 10 years have seen an increase in scholarly interest toward this topic. Overall this recent body of work has found that African ancestries in the Caribbean are diverse and heterogenous, as demonstrated by several key findings.

First, proportions of African ancestry vary widely between and within Caribbean populations. Many of these differences can be attributed to social, political, and economic factors such as differing experiences with colonization, distance or proximity to African slaving ports, the centrality of chattel slavery to each island's economic system, the extent of maroonage and resistance, colonial regulations on marriage and domestic relations, and the timing of abolition or emancipation.^{10,11,74,87,89,109–111} For example, Benn Torres and colleagues⁸⁹ identified distinct patterns of genetic structure between self-identified Afro-Caribbean populations in the Anglophone Antilles (Dominica, Grenada, St. Kitts, St. Lucia, St. Thomas, St. Vincent, Jamaica, and Trinidad). While all populations had high proportions of African ancestry, Afro-Caribbeans from Dominica had significantly higher proportions of Indigenous American ancestry than other groups. Dominica and Grenada were French colonies before falling under British control.⁹⁵ French Caribbean colonies such as Dominica saw the rise of an upwardly mobile creole social class which included peoples of mixed European and African descent. This contrasted with the situation in most British colonies where a “one-drop” rule of racial classification meant that anyone with African heritage was excluded from social and economic mobility.¹⁰⁷ Additionally, in the 17th century part of Dominica's territory was designated as a reserve for the Indigenous Kalinago people.⁹⁵ This reserve became a stronghold of maroonage and resistance for Indigenous and Black peoples throughout the colonial era.⁶⁷ Thus, differing experiences of colonial rule, Indigenous resistance, and creolization on Dominica likely played a large role in shaping the distinctive patterns of genetic structure and ancestry seen among the island's Afro-descendant peoples. This

example illustrates the heterogeneity of the African diasporic experience in the Antilles.

Second, consistent with the documented patterns of the Atlantic Slave Trade,¹⁰⁶ most Caribbean islanders have African genetic ancestries traceable to West and West-Central Africa, in areas such as Senegambia, the Bights of Benin and Biafra, Cameroon, Ghana, and, to a lesser degree, Angola in coastal Southwestern Africa.^{10,11,74,80,83,89,91,110–112} However, individual studies have found distinct origins within these broad sub-continental areas. For example, Schroeder et al.⁵ sequenced the genomes of three 17th century enslaved individuals known as the Zousteeg Three whose skeletal remains were found on the island of St. Martin in 2010.¹⁰⁸ The three individuals, one female and two males, had dental modifications indicative of an African origin, but the specific areas from where they came were unknown. Ancient DNA data indicated that the Zousteeg Three had different genetic origins within Africa. While two individuals shared genetic affinity with present-day populations from Nigeria and Ghana, the other was most similar to present-day Bantu speakers from northern Cameroon. This finding emphasizes the diversity of African peoples who arrived to the Caribbean during the Atlantic Slave Trade and thus has important implications for our understanding of the Caribbean creolization process.^{106,107}

Third, genomic studies suggest that most Caribbean populations received multiple pulses of African ancestry.^{10,11} In admixed populations from the Greater Antilles for example, the first pulse has been dated to ~15 generations ago (circa 1550 assuming a 30-year generation time), broadly coinciding with the first documented introduction of enslaved peoples from coastal West Africa during Spanish occupation. A second and stronger pulse, dated to ~7–8 generations ago coincides with a documented increase in slave importation from Central Africa during the late 18th century.¹¹ Additionally, some genetic studies have found evidence of admixture between African diasporic populations in the Americas.^{10,111} For instance, Fortes-Lima and colleagues¹⁰ found evidence of a late pulse of African ancestry ~3–4 generations ago circa the late 19th or early 20th centuries. The authors suggest this pulse may be explained by the recent influx of afro-descendant populations from Haiti into Cuba during the first decades of the 20th century. These findings highlight the complexity of the Afro-Caribbean diaspora and demonstrate how recent inter island population movements continue to shape the genetic diversity of afro-descendant communities.

In sum, genetic studies have contributed new insights to our understanding of the Caribbean experience with the Atlantic Slave Trade and the biocultural diversity of present-day Afro-Caribbean peoples. When interpreted alongside other forms of evidence such as historical documents, archaeological and osteological remains, this research has great potential for documenting the lives of African ancestors and restoring some of the links between ancient and present-day populations that were severed through experiences of marginalization and violence.¹⁰⁸ However, more work remains to be done. At present, population genetic databases do not fully represent the full spectrum of African diversity. The uncritical use of these data sets may lead to skewed conclusions regarding the population history of afro-descendant communities.¹¹³ Additionally, Afro-Caribbean

populations are severely underrepresented in current genomics research making up just 1.15% of all genome-wide association studies.¹¹⁴ This underrepresentation results in exclusion from the advances of clinical research and genomic medicine and increases risk for detrimental health outcomes.

3.4 | East and South Asian ancestors

After the abolition of slavery in the 19th century, several colonial powers turned to contract labor and indentured servitude to address the resulting shortage of plantation workers. Between 1834 and 1917 over 500,000 indentured laborers, from China, India, Portugal and parts of Africa, arrived in the Antilles (Figure 4). Most laborers were transported to the sugar plantations of British colonies such as Trinidad and Jamaica, but some also arrived in Cuba and the Caribbean coast of Costa Rica. A large number of these migrants settled permanently, further transforming the demography of Caribbean

populations. Their labor was instrumental for powering the economic sugar boom the Caribbean experienced during the 19th and early 20th centuries.^{79,100,115}

Extensive anthropological research has been conducted among self-identified *Culí* communities of East Indian descent living in the coastal region of Puerto Limón in Costa Rica.^{115,116} Combining long-term ethnographic research, including the collection of detailed pedigrees, with the use of uniparental markers, Castri and coauthors¹¹⁶ found this community descends from a small number of indentured migrants transported from Central India. Interestingly, differences in the sub-continental ancestries of mtDNA and Y-chromosome loci suggest that the male and female ancestors of the *Culí* came from different parts of Central India and migrated to the Americas at different times. This finding is supported by the pedigree data which traces only four couples as the ancestors of all modern *Culí* families at Puerto Limón.¹¹⁵ This study also found evidence of admixture with European, African, and Indigenous peoples in the population history of the *Culí*.



FIGURE 4 East Indian migrants photographed in Trinidad, ca. 1890–1896. Source: Photography provided by the DeGolyer Library at Southern Methodist University. Attribution: SMU Central University Libraries, no restrictions, via Wikimedia Commons

In contrast to the studies conducted in Costa Rica, the impact of indentured migration to the island Caribbean is relatively understudied. But even though systematic research into this topic has yet to be done, evidence of East and South Asian ancestry among admixed islanders has been reported in several studies. For instance, Benn Torres et al.⁴⁷ identified an mtDNA lineage of South Asian origin (M33a) in two Indigenous individuals from the First People's Community of Trinidad. In Cuba, the recent study by Fortes-Lima and colleagues¹⁰ found 37 individuals carried notable proportions of East Asian autosomal ancestry. Furthermore, ongoing genomics research among Afro-Caribbeans in Trinidad has also found significant proportions of South and East Asian autosomal ancestry in these communities.¹¹⁷

These findings are consistent with the historical record and track the development of the British indenture system during the 19th century. Historical documents indicate that starting in 1806, ~17,000 Chinese laborers, mostly from Guangdong and Fujian province, were transported to British colonies such as Trinidad, and to other sugar-producing islands like Cuba. Additionally, after 1838, Indian laborers from areas of northwest and south India, such as Uttar Pradesh, Bengal, Bihar, and Madras, were also brought to the Antilles in great numbers.^{118,119} Because of these initial labor movements and subsequent migration waves during the 20th century, Chinese and Indian diasporic communities exist today in Cuba, Trinidad, Jamaica, and other Caribbean islands. How these translocated East and South Asian communities interacted with other island groups, despite legal, structural, and cultural barriers to do so,^{118,119} as well as their role in shaping the biocultural diversity of Caribbean societies is an interesting avenue of future anthropological genetics research.

4 | CONCLUSION: THE FUTURE OF CARIBBEAN ANTHROPOLOGICAL GENETICS

DNA studies have contributed major insights for understanding Caribbean population history especially with regards to pivotal events such as the initial peopling of the Antilles, European colonization, the Atlantic Slave Trade and the Asian indenture. Overall, the insights derived from modern and ancient Caribbean genomes have expanded understanding of pre-colonial period dynamics by testing archaeological hypotheses about the peopling of the Caribbean, challenging the descriptions of colonial-era sources and raising new questions about the diversity of the Caribbean's Indigenous populations. Such research has also characterized the biological links between ancient and modern populations and contributed novel perspectives on the impact of Indigenous, European, African, East, and South Asian ancestors on current biocultural diversity. The broad conclusion that can be drawn from this large body of research is that Caribbean populations have varied and complex genomic histories reflecting the heterogeneous experiences of migration, contact and colonization that took place in the Antilles during the last 7000 years.

However, many questions still remain unanswered and would benefit from further research. For instance, despite the use of high-

resolution paleogenomic data sets, it has not been possible to pinpoint the exact mainland origins of the first Caribbean populations. Thus, tracing the first peopling of the Caribbean and the start of the Archaic Age remains a focus for future studies. Additionally, although paleogenomics has contributed to reconstructing Ceramic Age dispersals, most of the currently available data sets are focused on the islands of the northern Caribbean, mostly the Bahamas and Greater Antilles. Expanding sampling coverage to include ancient populations from archeological contexts beyond the Greater Antilles, including prospection of coastal and submerged sites in the circum-Caribbean basin, may contribute novel insights to our understanding of ancient population movements, inter-island mobility, and interaction networks in the Antilles. Lastly, the recent discovery that genetic admixture was rare between Archaic and Ceramic Caribbean populations has raised even more puzzling questions about the Archaic to Ceramic transition. Far from resolving this issue, aDNA findings have posed additional questions which will only be answerable by integrating genetic data sets with archaeological evidence.

Furthermore, most aDNA research in the Caribbean to date has focused on the precontact period. No paleogenomic data has been generated from the early contact period, and very little is available from the colonial period.⁵ Genetic data have great potential for supplementing research in historic and plantation archaeology, investigating the Afro-Caribbean diaspora or the history of maroon societies.^{65,66,77} When interpreted along with other sources of evidence such as archaeological materials and historical documents, such genetic data sets could provide new perspectives on the process of creolization and ethnogenesis in the colonial Caribbean.⁸⁹ While the use of aDNA to address these questions has been limited by a dearth of systematically studied contact period sites in the Antilles^{1,2} and poor organic preservation,¹²⁰ further interdisciplinary research, integrating novel approaches from paleogenomics, bioarchaeology, and ethnohistory may fill these important gaps.

Future research efforts may also include the application of genomics to investigate health and disease patterns over time in the Caribbean. Such studies have great potential for elucidating precontact Indigenous health by using aDNA to identify potential disease agents or confirm paleopathological differential diagnoses.^{120,121} Ancient DNA analysis can also aid in characterizing pathogen strains involved in epidemic outbreaks documented in the historical record.⁶³ By combining such research with ethnohistoric evidence, novel insights could be gained about the social and economic factors impacting health outcomes in historic island populations. Finally, genetic approaches could also supplement bioarchaeological research seeking to characterize major health transitions in the Caribbean such as those brought on by the Columbian exchange,¹²² the Atlantic Slave Trade or 20th century urbanization. Investigating these historic trends may have implications for the health of present-day islanders.

Here I must emphasize that while genetic insights are important, genetic approaches alone cannot fully address the questions that remain unanswered about the history and evolution of Caribbean societies. Instead, it is necessary to deploy integrative research approaches that draw from multiple sources of evidence and several

BOX 1 GLOSSARY

Ancestry: In population genetics, ancestry refers to the proportion of genetic variation inherited from an individual's ancestors. Genetic ancestry differs from genealogical ancestry in that the latter refers to the full set of ancestors in an individual's pedigree, irrespective of their role in transmitting genetic information.

Ancestry informative markers (AIMs): Polymorphic genetic variants that can be used to estimate ancestry and admixture proportions because their alleles vary significantly in frequency between population groups.

Ancient DNA (aDNA): Genetic material obtained from historic, archaeological or paleontological remains. Ancient DNA can be obtained from biological tissues such as bone or teeth, or from substrates such as sediments. It is present in low quantities and is usually degraded, fragmented and highly susceptible to external contamination.

Autosomes: In humans, the autosomes are any of the chromosomes numbered 1–22 which are present in two copies within the cell nucleus. Autosomal loci are inherited from both parents and subject to recombination during cell division.

Colonization: In the context of Caribbean history, colonization refers to a process of migration and subsequent settlement which resulted in the appropriation of lands and the subjugation of native populations by foreign powers.

Creolization: The process by which elements of different cultures are blended together to create novel cultural expressions. In the Caribbean, creolization often refers to the mixture of cultural elements derived from Indigenous Caribbean, Sub-Saharan African and European ancestral populations.

Encomienda: A system of regulated forced labor employed by the Spanish crown during the colonization of the Americas. Under the *encomienda*, European settlers were granted land estates and charged with evangelizing to the Indigenous peoples (*encomendados*) inhabiting the lands. The settlers, or *encomenderos*, also had the right to exact tribute from the *encomendados* in the form of unpaid labor, minerals, or agricultural production.

Genetic Admixture: The mixing of two or more previously diverged genetic lineages or populations.

Genotyping: The process of determining the allelic states of a set of polymorphic genetic variants.

Haplogroup: A set of haplotypes (see below) that share a common ancestor and belong to the same lineage.

Haplotype: A set of polymorphisms inherited together on the same DNA segment. Haplotypes are defined by a combination of allelic states. All haplotypes belonging to the same haplogroup share a common set of lineage defining polymorphisms. But, some haplotypes may also contain additional polymorphisms that evolved after the divergence from the common ancestor.

Indentureship: A system of regulated labor in which a person is contracted, or indentured, to provide labor for a specific period of time. Individuals may enter the indentureship voluntarily or as a form of bondage due to debt repayment or judicial punishment. In the Caribbean, European colonial powers used the indentureship system to provide labor for plantation agriculture.

JC virus (Human polyomavirus 2): A DNA virus which is capable of establishing persistent infection in humans and can be vertically transmitted from parents to offspring. The JC virus has co-diverged with human populations and therefore can be used as marker for reconstructing human migration and population history.

Maroons: Self-liberated African and African-descendant peoples who escaped slavery and formed independent, free settlements outside of the control of the colonial state. In the Caribbean, Indigenous peoples also participated in the formation of maroon communities.

Migration: The movement of populations or individuals from one geographic area to another. If migration occurs into a previously inhabited area and contact between populations occurs, admixture may ensue.

Mitochondrial DNA (mtDNA): The circular genome of the mitochondrion. In eukaryotic organisms, mtDNA is passed on clonally from mothers to offspring without recombination.

One-drop rule: Socially defined rule of racial classification in which a person with any known or suspected African ancestry (“one drop”) is considered Black and assigned a minoritized or lesser status. The one-drop rule arose in colonial North American slave societies and persisted in US legislation until the early 20th century.

Short tandem repeat (STR): Short tracts of repeated sequence motifs, approximately one to six base pairs long, that can be repeated continuously between 5 and 50 times. STRs are used for genetic identification or to determine proportions of genetic relatedness

Single nucleotide polymorphism (SNP): Genetic variation that arises due to a mutation occurring in a single base. SNPs are the most common form of polymorphic genetic variation in humans.

Y-chromosome: One of the human sex chromosomes. The Y-chromosome has a non-recombining portion which contains genes responsible for male sex-determination. It is passed on exclusively from fathers to male offspring.

forms of knowledge production. The insights derived from fields such as (bio)archaeology, history, ethnography, demography, and from local and traditional knowledge systems,¹²³ provide the necessary foundation on which anthropological geneticists should rely in formulating research questions, defining hypotheses, informing sampling approaches, designing analytical models, and ultimately, imbuing genetic findings with context, meaning, and significance. For example, in a recent book, Benn Torres and Torres Colón¹²⁴ describe the importance of integrating ethnographic and community-based participatory research methods to an ongoing study of genetic ancestry among Afro-Puerto Rican communities. Before collecting DNA samples, the researchers engaged in extensive ethnographic fieldwork, conducting in-depth interviews, and collecting individual and community histories in order to characterize social networks and ascertain self-assigned ethnic and racial identities. The outcome of this work allowed them to re-define their study population and design a sampling strategy that aligned with how Afro-Puerto Rican communities define themselves; as a geographically dispersed group of communities which remains connected through participation in active social networks. This case demonstrates that while genetics approaches are an essential component of anthropological genetics research, by themselves they are insufficient to characterize the full complexities of human biocultural diversity. To generate substantial insights about the past and present of Caribbean societies, anthropological genetic studies must be supported by the scaffolding that nongenetic perspectives can provide.

Lastly, to ensure that the future of Caribbean anthropological genetics is equitable, ethical, and sustainable, future research efforts should contribute towards collaborations and structures that empower locally-led research and train Caribbean students. Many Caribbean nations face significant challenges in sustaining locally led genomics research initiatives.¹²⁵ These challenges include lack of research funding and institutional support, economic policies that devalue or defund scientific research, austerity measures that strip resources from public and higher education,¹²⁶ crumbling scientific infrastructures,¹²⁷ and the impact of natural disasters.^{128,129} Additionally, “brain drain” emigration patterns push many scientific professionals away from the islands to work and study abroad or in former colonial metropolises.¹²⁶ These challenges hinder the establishment and maintenance of local research capabilities, and make it difficult to comprehensively train undergraduate and graduate students. To build an ethical, equitable, and sustainable field of Caribbean anthropological genetics, researchers who work with Caribbean populations must invest in local capacity building and equitable collaborations, where local researchers and institutions are not just sample providers but instead considered equal partners in designing, conducting, and publishing research with their own communities. Finally, future research should also empower student training through inclusion in local projects and opportunities for bilateral trainee exchanges. This will ensure that the next generation of Caribbean scientists can ask the next generation of research questions. It is only through this integration of local scientific perspectives and input from local stakeholders that we can gain a full and complete picture of the Caribbean past and its impacts on the present.

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DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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APPENDIX A

Table A1

TABLE A1 Estimated ancestry proportions from autosomal, mtDNA and Y-chromosome loci gathered from the literature for nine Caribbean populations (Input data for Figure 3)

| Source | Population | N | Locus | European ancestry | African ancestry | Indigenous American ancestry | East Asian ancestry | South Asian ancestry | North African or Middle Eastern ancestry | Unclassified | Notes |
|-------------------------------|------------|------|--------------|-------------------|------------------|------------------------------|---------------------|----------------------|--|--------------|---|
| Fortes-Lima et al. (2018) | Cuba | 860 | Autosomal | 0.7061 | 0.2067 | 0.0767 | 0.0104 | 0.0000 | 0.0000 | 0.0000 | Estimated with RFMix assuming K = 4 model |
| Marcheco-Teruel et al. (2014) | Cuba | 1019 | Autosomal | 0.7200 | 0.2000 | 0.0800 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | |
| Marcheco-Teruel et al. (2014) | Cuba | 943 | mtDNA | 0.2670 | 0.3880 | 0.3450 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | |
| Marcheco-Teruel et al. (2014) | Cuba | 384 | Y-chromosome | 0.8180 | 0.1770 | 0.0050 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | |
| Mendizabal et al. (2008) | Cuba | 245 | mtDNA | 0.2200 | 0.4500 | 0.3300 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | |
| Mendizabal et al. (2008) | Cuba | 132 | Y-chromosome | 0.8000 | 0.2000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | |
| Benn Torres et al. (2007) | Dominica | 50 | mtDNA | 0.0000 | 0.7200 | 0.2800 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | Self-identified Afro Caribbean |
| Benn Torres et al. (2007) | Dominica | 21 | Y-chromosome | 0.6590 | 0.3410 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | Self-identified Afro Caribbean |
| Benn Torres et al. (2013) | Dominica | 37 | Autosomal | 0.2810 | 0.5560 | 0.1620 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | Self-identified Afro Caribbean |
| Benn Torres et al. (2007) | Grenada | 51 | mtDNA | 0.0980 | 0.8431 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0588 | Self-identified Afro Caribbean |
| Benn Torres et al. (2007) | Grenada | 35 | Y-chromosome | 0.1830 | 0.8170 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | Self-identified Afro Caribbean |
| Benn Torres et al. (2013) | Grenada | 48 | Autosomal | 0.1210 | 0.8110 | 0.0680 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | Self-identified Afro Caribbean |

TABLE A 1 (Continued)

| Source | Population | N | Locus | European ancestry | African ancestry | Indigenous American ancestry | East Asian ancestry | South Asian ancestry | North African or Middle Eastern ancestry | Unclassified | Notes |
|--------------------------------|-------------|-----|--------------|-------------------|------------------|------------------------------|---------------------|----------------------|--|--------------|--------------------------------|
| Benn Torres et al. (2007) | Jamaica | 53 | Y-chromosome | 0.4170 | 0.5830 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | Self-identified Afro Caribbean |
| Benn Torres et al. (2012) | Jamaica | 75 | Y-chromosome | 0.4110 | 0.5890 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | Self-identified Afro Caribbean |
| Benn Torres et al. (2013) | Jamaica | 44 | Autosomal | 0.1030 | 0.8140 | 0.0830 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | Self-identified Afro Caribbean |
| Deason et al. (2012) | Jamaica | 400 | mtDNA | 0.0100 | 0.9750 | 0.0100 | 0.0000 | 0.0000 | 0.0000 | 0.0050 | |
| Bryc et al. (2010) | Puerto Rico | 27 | mtDNA | 0.0741 | 0.1852 | 0.7407 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | |
| Bryc et al. (2010) | Puerto Rico | 26 | Y-chromosome | 0.7308 | 0.1923 | 0.0000 | 0.0000 | 0.0000 | 0.0769 | 0.0000 | |
| Martínez-Cruzado et al. (2005) | Puerto Rico | 800 | mtDNA | 0.1150 | 0.2720 | 0.6130 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | |
| Via et al. (2011) | Puerto Rico | 642 | Autosomal | 0.6370 | 0.2120 | 0.1520 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | |
| Vilar et al. (2014) | Puerto Rico | 326 | mtDNA | 0.1500 | 0.2500 | 0.6000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | |
| Vilar et al. (2014) | Puerto Rico | 121 | Y-chromosome | 0.8500 | 0.1500 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | |
| Benn Torres et al. (2007) | St. Kitts | 48 | mtDNA | 0.0208 | 0.9792 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | Self-identified Afro Caribbean |
| Benn Torres et al. (2007) | St. Kitts | 33 | Y-chromosome | 0.1170 | 0.8830 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | Self-identified Afro Caribbean |
| Benn Torres et al. (2013) | St. Kitts | 47 | Autosomal | 0.0820 | 0.8590 | 0.0580 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | Self-identified Afro Caribbean |
| Benn Torres et al. (2007) | St. Lucia | 55 | mtDNA | 0.0364 | 0.9273 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0364 | Self-identified Afro Caribbean |
| Benn Torres et al. (2007) | St. Lucia | 24 | Y-chromosome | 0.5420 | 0.4580 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | Self-identified Afro Caribbean |
| Benn Torres et al. (2013) | St. Lucia | 50 | Autosomal | 0.1790 | 0.7450 | 0.0750 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | Self-identified Afro Caribbean |
| Benn Torres et al. (2007) | St. Vincent | 55 | mtDNA | 0.0545 | 0.9273 | 0.0182 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | Self-identified Afro Caribbean |

(Continues)

TABLE A 1 (Continued)

| Source | Population | N | Locus | European ancestry | African ancestry | Indigenous American ancestry | East Asian ancestry | South Asian ancestry | North African or Middle Eastern ancestry | Unclassified | Notes |
|---------------------------|-------------|----|--------------|-------------------|------------------|------------------------------|---------------------|----------------------|--|--------------|--------------------------------|
| Benn Torres et al. (2007) | St. Vincent | 21 | Y-chromosome | 0.2250 | 0.7750 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | Self-identified Afro Caribbean |
| Benn Torres et al. (2013) | St. Vincent | 51 | Autosomal | 0.1280 | 0.8060 | 0.0650 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | Self-identified Afro Caribbean |
| Benn Torres et al. (2007) | Trinidad | 55 | mtDNA | 0.0545 | 0.7818 | 0.0364 | 0.0000 | 0.0182 | 0.0000 | 0.1091 | Self-identified Afro Caribbean |
| Benn Torres et al. (2007) | Trinidad | 33 | Y-chromosome | 0.2400 | 0.7600 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | Self-identified Afro Caribbean |
| Benn Torres et al. (2013) | Trinidad | 43 | Autosomal | 0.1580 | 0.7500 | 0.0920 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | Self-identified Afro Caribbean |