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Anthropological Genetics Perspectives on the Transatlantic Slave Trade

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UNCORRECTED MANUSCRIPT

Abstract

During the Trans-Atlantic Slave Trade (TAST), around twelve million Africans were enslaved and forcibly moved from Africa to the Americas and Europe, durably influencing the genetic and cultural landscape of a large part of humanity since the 15th century. Following historians, archaeologists, and anthropologists, population geneticists have, since the 1950's mainly, extensively investigated the genetic diversity of populations on both sides of the Atlantic. These studies shed new lights into the largely unknown genetic origins of numerous enslaved-African descendant communities in the Americas, by inferring their genetic relationships with extant African, European, and Native American populations. Furthermore, exploring genome-wide data with novel statistical and bioinformatics methods, population geneticists have been increasingly able to infer the last 500 years of admixture histories of these populations. These inferences have highlighted the diversity of histories experienced by enslaved-African descendants, and the complex influences of socio-economic, political, and historical contexts on human genetic diversity patterns during and after the slave trade. Finally, the recent advances of paleogenomics unveiled crucial aspects of the life and health of the first generation of enslaved Africans in the Americas. Altogether, human population genetics approaches in the genomic and paleogenomic era need to be coupled with history, archaeology, anthropology, and demography in interdisciplinary research, to reconstruct the multifaceted and largely unknown history of the TAST and its influence on human biological and cultural diversities today. Here, we review anthropological genomics studies published over the past 15 years and focusing on the history of enslaved-African descendant populations in the Americas.

Keywords: Population Genetics, Anthropology, Admixture, Slave Trade, Paleogenomics.

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Introduction

The Trans-Atlantic Slave Trade (TAST) was one of the largest forced migrations in recent human history. Between the 15th and the 19th century, more than 12 million Africans were enslaved and forcibly removed from their homeland to be deported to the Americas and Europe (1). The vast majority of them were deported to South America and the Caribbean (around 43% and 52%, respectively), a minority (around 5%) to North America, and only a reduced fraction (< 1%) to mainland Europe (2).

Enslaved Africans were taken from African slaving regions that stretched thousands of miles, from present-day Senegal to Angola and, around the coast, Mozambique and Madagascar. According to historical sources (2,3), from 1501 to 1867, enslaved Africans were forcibly embarked mainly from eight coastal regions (**Figure 1**): 5.7% embarked from Senegambia, 3.2% from Sierra Leone, 2.7% from the Windward Coast, 9.6% from the Gold Coast, 16.1% from the Bight of Benin, 12.3% from the Bight of Biafra, 46.3% from West Central Africa, and 4.1% from Southeast Africa. The West Central African coast was thus the largest slaving and embarkation region throughout most of the TAST, focused mainly South of the Congo river. The Gold Coast, the Bight of Benin, and the Bight of Biafra became increasingly prominent slaving and embarkation regions after the mid-17th century, as the TAST expanded with Plantation Economy in the Americas (**Figure 1**).

During more than 300 years, slavers dehumanized their human cargo with a profusion of organized psychological and physical abuses and violence. They forbade slaves to use their name, language, and religion, repeatedly broke-up families, and, with the crossing of the Atlantic Ocean and extensive migrations within the Americas, severed all possible roots between the captives and their original homeland, culture, and people (4). As a direct and dreadful consequence, enslaved-African descendants throughout the Americas have little knowledge of their origins in continental Africa; a gap that can only partially be filled with historical sources (5).

Indeed, historians investigated marine and customs manifests, commercial and tax records and deeds, and other sources to reconstruct TAST routes, possible African ethnic origins of deportees (**Figure 1**), and, in some rare instances, the genealogies of enslaved-African descendants in the Americas (2). Nevertheless, due to imprecise, missing, or falsified records, the prominence of illegal slave-trade which leaves scarce written traces, and the difficulties to transpose ethnic and linguistic categories used during the TAST era into present-day ethnic categories, large parts of the history of enslaved-African descendants remain obscure (5). In this historical context that radically changed the cultural and genetic landscape of the Americas (6,7), molecular and population genetics since the mid-20th century offered new tools to help reconstruct the migrations and demographic histories of enslaved-African descendant populations.

In this review, we examine population genomics articles published over the past 15 years and focusing on the genetic history of enslaved-African descendant communities in the Americas today. The genetic determination of phenotypes and disease risks have been widely studied in connection to TAST

migrations and admixture in the Americas (8–10), and the subject of several major reviews (6,11,12). Instead, we chose to focus primarily here on the complex interactions between genetic inferences about populations' origins, migrations, and admixture histories, and the cultural, anthropological, and historical contexts during and after the TAST era.

Origins of enslaved-African descendants inferred with genetics

Since the 1950s, anthropological genetics research investigated the links between genetic variation patterns observed today across Africa, Europe, and the Americas, and those observed in enslaved-African descendant communities in the Americas, to narrow their possible geographic origins from either continent. To do so, patterns of shared genetic ancestry between present-day enslaved-African descendant communities and worldwide populations were inferred using population genetics methods and, at first, markers such as blood groups, HLA, or uniparentally-inherited mitochondrial DNA and/or Y-chromosome markers (13–15).

With the advances of molecular genetics at the genome-wide scale since the 2000s, and with the developments of novel bioinformatics methods, reconstructing the genetic origins of enslaved-African descendants has reached unprecedented resolution (7,16,17). These studies have shown that virtually all such populations are genetically admixed and share recent genetic ancestries with European, African, and Native American populations today. Furthermore, geneticists have revealed the tremendous variability of genomic admixture patterns across enslaved-African descendant populations, each echoing the specific history of slavery and European colonization they experienced.

As an illustration of a genome-wide study, Patin et al. (18) investigated the African genetic origins of US self-reported enslaved-African descendants from three large-scale cohorts totalling 5244 participants from four states. Compared to genetic variation from 1955 individuals from 14 populations living in former slaving regions of Africa's Atlantic shores, they found that US participants had, on average, 75% of African genetic ancestry, and 25% of (mostly) European genetic ancestry (18). Furthermore, the identified African genetic components shared a recent common ancestry, on average, for 13% with Senegambian populations today, 7% with those from the Windward Coast, 50% with those from the Bight of Benin, and up to 30% with those from present-day Gabon and Angola, thus reflecting the highly diverse origins of African populations having contributed to the gene-pool of enslaved-African descendants in the USA.

Furthermore, population geneticists identified important variation in the African genomic ancestry across Brazil (19,20), a country that received the majority (~70%; ~4.8 million) of all enslaved-Africans deported to continental Latin America during the TAST (**Figure 1**). African ancestries ranged, on average, from 14.7% in the inland South-East of Brazil, and mainly originated from the South-West and South-East of Africa, to 50.8% in the North-East of the country (**Figure 2**), with West African origins more frequent in this later region (21,22). This further illustrated how the genomic heritage of enslaved-African descendants in the Americas can also vary within a country.

With similar population genomics approaches, other studies have identified variable African admixture patterns in numerous enslaved-African descendant populations throughout the Americas (**Figure 2**), with, for instance, around 89% of African ancestry in enslaved-African descendants from Jamaica (23), 88% in Barbados (24), 78% in Peru (25), 77% in Choco (Colombia) (26,27), 71% in Rio de Janeiro (Brazil) (27), 70% in Saint Vincent (28), and 38% in eastern Cuba (29); each population being also highly variable in relative contributions from each continental African regions.

During the TAST era, enslaved Africans actively mobilized to create systems of resistance against the inhuman repression that accompanied slavery, and escaped captivity, a phenomenon often called *marronnage*. This is characterized by massive escapes of slaves who then grouped in small and independent communities of free-people, known as Maroon communities, who developed specific linguistic, political, religious, and domestic traditions (30,31). Genomics investigations of the history of Maroon communities remain overall scarce (32,33). However, Fortes-Lima et al. (27) recently investigated four Noir Marron communities from French Guyana and Surinam. The results highlighted high levels of genomic inbreeding, high (~98%) African genetic ancestry originated mainly from the Bight of Benin (**Figure 3A-B**), and more precisely from Gbe-speaking populations in Benin (34,35), and reduced Native American and European ancestries, altogether resulting from more than 350 years of genetic and cultural isolation in the South-American rainforest (36). This relatively simple admixture pattern, with apparently very few different African source populations, substantially differs from those observed in numerous other enslaved-African descendant populations in the Americas who could not escape bondage and often show genomic contribution from multiple African sources as well as substantial admixture with European and Native American populations (7,17,22).

Beyond the African origins of enslaved-African descendant populations, population geneticists also identified numerous populations with significant three-way admixture between African, European, and Native American sources. Interestingly, European source populations have been shown to have contributed differently to the gene-pools of enslaved-African descendant populations (17), in possible relation with each European emigration policies and preferred TAST routes (5). Enslaved-African descendant populations in Spanish or Portuguese former colonies in the Americas share the majority of their European common genetic ancestry with the Iberian Peninsula rather than with Northern-Western Europe, while the opposite is observed in enslaved-African descendants from the former British colonial empire (7,27,37). Consistently, enslaved-African descendant populations in locations having experienced changes of European empire dominion, such as some Caribbean islands, are sometimes found to bear more variable signatures of admixture from different European regions.

Finally, Native American populations have been dramatically impacted by European colonization, which triggered substantial levels of genetic admixture with African deported populations via joint enslavement and social marginalization, and/or joint resistance and escape from European domination in Maroon communities (23,28,29,37). Nevertheless, as Native American populations have suffered dramatic demographic reductions during European colonization, population geneticists have faced major challenges to

reconstruct precisely their contribution to the genetic landscape of enslaved-African descendant populations, because genetic datasets from Native American populations relatively unaffected by post-Columbus admixture were largely lacking until recently (38–40).

Reconstructing the admixture histories of enslaved-African descendants with genetics

Several population genetics methods have been developed during the past 10 years to infer, from genomic data only, how many recurring or more temporary events of admixture, and their associated timings and respective intensities, have shaped the observed genetic patterns in admixed populations today (41–43). Applied to enslaved-African descendant populations in the Americas, results could then, *a posteriori*, be compared to historical sources to better understand which major historical events and socio-cultural changes, during or after the TAST era, significantly influenced genomic patterns, and propose possible explanatory mechanisms.

For instance, an unprecedentedly detailed investigation of genomic patterns in enslaved-African descendant communities in the US, analysed together with extensive demographic data in an interdisciplinary framework, highlighted that admixture between European and African descendant populations likely occurred during at least two major periods (44). The first admixture period likely occurred during the Plantation Economy era (~1700s-1850s) mainly in the Southern part of the country, before the US civil war. The second admixture period occurred later, during the early 20th century, after the massive South-to-North migration of emancipated-slave descendant communities. These results thus showed that slavery and its abolition did not explain, alone, genetic admixture patterns (7,45,46). Indeed, admixture in the US occurred first long before the abolition of slavery, most often as a result of sexual coercion of slave-owners and despite the “Code Noir” and other laws forbidding intermarriages between communities; and roughly two generations after the abolition of slavery, indirectly as a result of migrations and changes in intercommunity relationships, despite the persistence of segregation laws until the late 20th century.

Furthermore, African and European emigration waves throughout the Americas have been massive long after the TAST, during the late 19th and throughout the 20th century (1,4). This led to major social changes among communities and, for instance in Brazil, population geneticists proposed that it likely substantially increased the relative amount of European-derived genomic ancestry in the general population (17,21,22). Altogether, these results highlight the importance of specific socio-cultural relationships among enslaved and non-enslaved descendant communities for shaping genomic diversity patterns of enslaved-African descendant populations, both during and long after the TAST era (**Figure 2**).

More generally, together with most references cited above, population geneticists identified discrepancies between the TAST demographic history and the expected resulting genetic patterns in enslaved-African descendant populations. Historians have demonstrated that African males represented the vast majority of deported-slaves compared to females, as a consequence of the massive demand for an exhausting-labour force for which males were thought to be better adapted than females (2). Nevertheless, geneticists found very strong biases towards European males reproducing with African females that shaped

admixture patterns in enslaved-African descendant communities (16,27). Indeed, socio-cultural discriminations, prejudice, and segregation, often enforced legally in particular after the expansion of Plantation Economy, resulted, throughout and after the TAST era, in a strong reproductive isolation between enslaved and non-enslaved communities. In a largely patriarchal and patrilocal context, this resulted in extremely limited signatures of non-slave females having reproduced with slave males, while non-slave males reproducing with slave females, often coercively as demonstrated by historians, could be more often tolerated by the socio-politically dominant European-descendant communities (47). While this pattern is qualitatively ubiquitous during the TAST, substantial differences in the intensity of this sex-biased admixture across enslaved-African descendant populations are observed throughout the Americas (6,17,23).

Socio-cultural relationships inherited from the TAST era influence genetic patterns and interpretations

Overall, complex cultural processes resulted in variable forms of reproductive isolation between enslaved and non-enslaved communities during and after the TAST across the Americas. These local barriers to panmixia depended largely on the legal and societal categorization of individuals in either community. In addition, these categories have changed over time when different legislations were established, such as the “Code Noir” in North America, the “Sistema de Castas” in Latin America, and segregation laws during colonial and post-colonial eras after the TAST. Over time, these shifting societal barriers influenced, in turn, identity-constructions and mate choices, further enhancing cultural and reproductive isolation and determining the social status of admixed individuals.

These community constructions are, to some extent, reflected in individual self-report categorization in national population census questionnaires. Among 23 continental American countries, the last census questionnaires record up to four questions about self-reported indigenous, ethnic, linguistic, or racial identity (only four countries use explicitly the word “race” or its literal translation). Apart from French Guyana where no self-categorizations are recorded, the census questionnaires’ categories are based on self-reported imprecise skin-color criteria, genealogical ancestry and cultural affinities, linguistic practices, or mixtures of these criteria. 14 countries out of 22 propose a category based on self-reported African descent, seven of which propose the word “Black” (or its translation) as an alternative naming for the same category, and three of 14 which distinguish the “Afro-descendant” category from the “Black” category. Additionally, four countries among the 22 consider only a “Black” category without explicit reference to “Africa”. Furthermore, eight countries out of the 22 propose a separate category for “explicitly” admixed individuals of African descent (“Mulata/o”, “Creole” or “Mixed”), two countries have a separate “Brown” category, and three countries gather some or all these labels under the broader “Afro-descendant” category. In this complex categorization patchwork, population geneticists showed that self-perception of ancestry and self-reported identities overlapping national census categories are often at odds with individuals’ genomic ancestries and admixture patterns (48–50). This is due to the fact that self-constructed cultural identities emerge from multiple familial and societal experiences superimposing self-perceived phenotypic features. This process is

thus much more complex than simple mendelian inheritance which only reflects a very specific (genetic) part of an individual's history, furthermore only very partially translated into complex phenotypic features such as skin-color (51).

Therefore, it is often difficult to compare average African genomic ancestries across population genetics studies (**Figure 2**), mainly due to the heterogeneity of inclusion criteria of sampled individuals (7). Indeed, some studies consider cohorts sampled from the general population with inclusion criteria based on geography, and/or medical or socio-economic status, rather than self-reported ancestral origins or census categories (21,29). Other studies focus instead on groups of individuals from census categories in relation to African descent (20,44,52), shown above to possibly designate different populations with different demographic histories across the Americas. In general, whether participating individuals have known genealogical relationships with enslaved-Africans during the TAST, with post-slavery African-immigrants, with admixed populations, or categorized as "Afro-descendants" based on phenotypic features only, remains too often undiscussed in population genetics studies.

Furthermore, lack of anthropological information about participants' inclusion criteria can introduce possible confounding factors in genome-wide association studies (GWAS) due to cryptic genetic stratification, even when elaborated bio-statistical approaches allow to correct for genetic-relatedness heterogeneities in case and control samples (53,54). Finally, investigations of differential adaptation and natural selection pressures signatures in the genomes of enslaved-African descendant populations may also be affected by confusions in individual categorization, as groups of individuals with, in fact, largely differing demographic and admixture histories may a priori be gathered in a single target population (18).

Altogether, the genetic patterns of enslaved-African and non-enslaved descendant communities in the Americas are highly variable across the continent. They depend on the genetic origins of the founding individuals, on the genetic origins of subsequent migration waves into each community and socio-cultural processes of assimilation or rejection of the new migrants, and on admixture processes and inter-community relationships regarding barriers to reproduction and their prevalence in the societies, during and long after the TAST. It is thus crucial to consider the detailed local historical and anthropological contexts to elucidate the evolutionary history of enslaved-African descendant communities.

TAST history research entering the paleogenomics era

Archaeology of the slave-trade has often been described as an "archaeology of the invisible", as, by definition, slaves' material possessions were scarce, numerous sites related to slaves' history (housing, cells or transit centres, etc.) were not primarily built to withstand the erosion of time or have been actively destroyed during history, and as the memory of slaves' burial-sites has often been lost (55–58). Nevertheless, bioarchaeological investigations, together with isotopic and paleopathological methods, contributed invaluablely to our understanding of the TAST era, questioning the conditions of life of slaves, reconstructing historical migrations, the socio-economic history of slaves amidst slave-societies, and the health status in Maroon or enslaved communities (59).

Analogously to archaeology, paleogenomics, the study of ancient DNA (aDNA), focusing on remains linked to the TAST, often face inextricable difficulties, particularly in tropical environments. Indeed, DNA often preserves poorly under intense seasonal climatic change and reduced protection of skeletal remains, which is often the case for slave burial-sites in the Caribbean and the Americas. Nevertheless, aDNA analyses may yield invaluable information, as it provides direct insights into the genetic reality of populations in the past; contrarily to modern-DNA which only provides incomplete information about the genealogical histories underlying genetic patterns observed today. In this context, the technical improvements of paleogenomics over the last decade brought new promising results about the history of enslaved populations during the TAST (60,61).

A recent study (62) successfully generated aDNA data from remains of three enslaved-Africans buried shortly after the beginning of the colonisation of Mexico City in the 16th century. The study showed that mitochondrial, Y-chromosome, and autosomal aDNA from these individuals shared a recent common ancestry with different ethnolinguistic groups from different African former slaving regions (**Figure 3C-D**), despite being buried together. Furthermore, investigating the non-human DNA extracted together with human DNA in these samples, geneticists identified sequences likely belonging to *Treponema pallidum pertenuis* (a bacteria strain responsible for human yaws) and from hepatitis B virus, and matched statistically these sequences with bacterial and virus strains typically found in West African patients, respectively (62,63). In another recent study, Sandoval-Velasco et al. (64) investigated skeletal remains excavated in large graveyards from St Helena island, midway between the coasts of Angola and Brazil. Between 1840 and 1867, historical records showed that approximately 27,000 enslaved-Africans who escaped at sea were subsequently re-captured by the British Royal Navy and disembarked on St Helena, of whom ~8000 died and were buried on the island (65). Successfully obtaining aDNA for 20 individuals, authors found that this genetic material shared common ancestries mainly with several West Central African populations rather than other African regions.

Paleogenomics investigation of the TAST era can thus provide new knowledge about the unknown African origins of deportees, forced migrations across the Americas, admixture histories throughout the TAST, and key information about familial relationships among remains, further revealing familial-anthropology and funeral practices in societies with slaves. Finally, as illustrated above, paleo-metagenomics approaches can further unveil the epidemiological status of enslaved communities, and the phylogeographic history of human diseases during this era. This unequivocally demonstrates the future potential of paleogenomics investigation of TAST-related remains to fill major gaps of the history of this era.

Conclusions

Altogether, population genetics has repeatedly shown the diverse African and European origins of enslaved-African descendants throughout the Americas and the Caribbean. These results also show that the genomic make-up of enslaved-African descendant communities reflects the specific histories of marooning and rebellion, subjugation, social segregation, and legal emancipation experienced by these populations during

more than 500 years, hence further demonstrating how the complex history of the TAST has shaped, in the long-term, human genetic landscapes observed today for both enslaved and non-enslaved descendant communities.

Today, genome-wide genotype data can relatively easily be obtained and analysed with increasingly powerful statistical inference methods. It is therefore now crucial for geneticists to investigate in detail the genomic diversity patterns of enslaved-African populations at a very local scale, and explicitly parametrize, in historical, adaptive, and GWAS inferences, the influence of complex anthropological contexts having determined, over time, identity and categorisation constructions, as well as inter-community barriers to admixture. Furthermore, with the advances of local-ancestry mapping approaches, massive efforts should be undertaken to better understand the complex history of genetic admixture between enslaved-African populations and autochthonous American populations, which will also require further sampling at a local scale accompanied with anthropologic, ethnologic and demographic information for the same populations.

Finally, the influence of the TAST on genetic diversity patterns of African populations has seldom been explored (66–68), despite extensive historical and demographic work having shown the multifaceted influence of the TAST in continental Africa (69,70). It is imperative that geneticists fill this gap to better understand, not only the TAST itself, but genetic diversity patterns observed within Africa today (71). Indeed, by triggering massive population movements of communities escaping slavery and strongly influencing pre-existing inter-community socio-economic and cultural relationships, the TAST likely deeply influenced genetic patterns observed today within the continent.

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Figure Legends

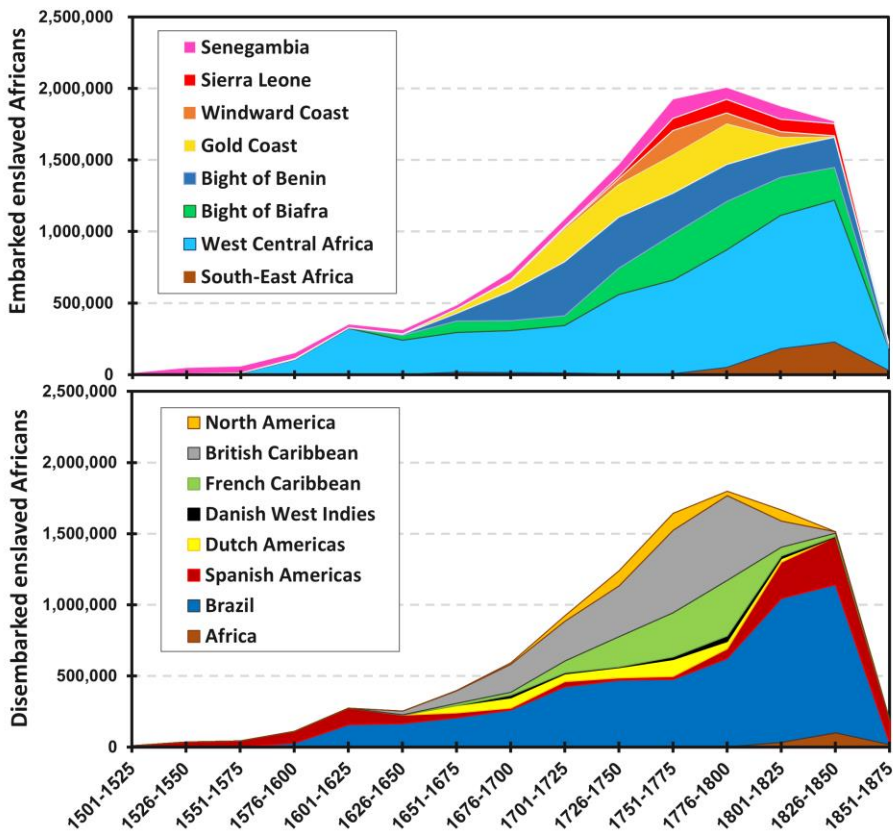


Figure 1. Census of enslaved Africans who were forced to leave Africa from 1501 to 1875 estimated from historical sources (2). (Top panel), estimated census for each major TAST embarkation region. (Bottom panel), estimated census for each major TAST dis-embarkation region in the Americas and Africa (tables can be found at <https://www.slavevoyages.org/estimates/L8KDKZCH>).

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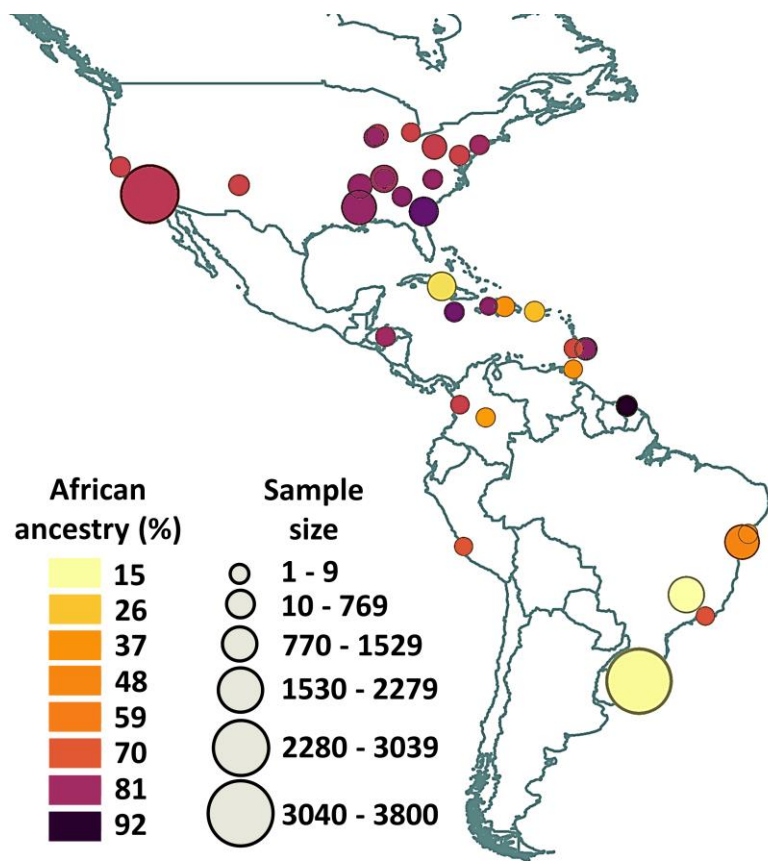


Figure 2. African genetic ancestries averaged proportions throughout the Americas estimated in previous genome-wide studies focussing on enslaved-African descendant populations (18,21,23,25,27–29,37,72). Size of the dots are proportional to the sample sizes used in each study.

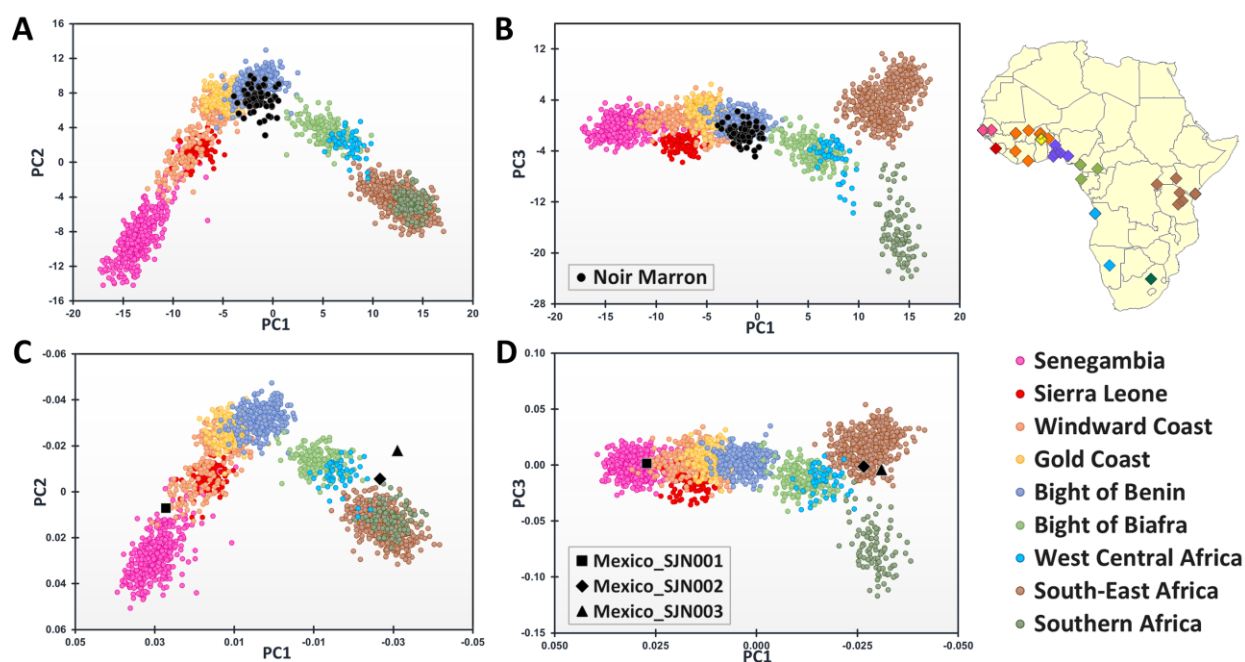


Figure 3. First three major axes of Principal Component Analyses (PCA) projections of genome-wide single nucleotide polymorphisms (SNPs) genotyped in sub-Saharan African modern populations with enslaved-African descendants in South and Central America (Noir Marron and ancient remains in Mexico, respectively). This illustrates the varying genetic resemblance between the enslaved-African individuals and their descendants in the Americas with genetic variation from 43 African populations grouped in nine major historical regions of enslavement and embarkation in Africa (Map panel). (Panels **A-B**) Principal components 1-2-3 projecting 229,586 autosomal SNPs genotyped in 64 Noir Marron individuals from French Guiana, originally investigated in (27), with 1976 sub-Saharan African modern samples; (Panels **C-D**) Principal components 1-2-3 projecting 30,163 autosomal SNPs genotyped in three ancient samples from early 16th century Mexico, originally presented in (62), with the same 1976 sub-Saharan African modern samples. Further information about modern African populations and SNP set merging included in these analyses can be found elsewhere (27).