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The ancestry and geographical origins of St Helena's liberated Africans

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Summary

The island of St Helena played a crucial role in the suppression of the transatlantic slave trade. Strategically located in the middle of the South Atlantic, it served as a staging post for the Royal Navy and reception point for enslaved Africans who had been "liberated" from slave ships intercepted by the British. In total, St Helena received approximately 27,000 liberated Africans between 1840 and 1867. Written sources suggest that the majority of these individuals came from West Central Africa, but their precise origins are unknown. Here, we report the results of ancient DNA analyses that we conducted as part of a wider effort to commemorate St Helena's liberated Africans and to restore knowledge of their lives and experiences. We generated partial genomes (0.1–0.5×) for 20 individuals whose remains had been recovered during archaeological excavations on the island. We compared their genomes with genotype data for over 3,000 present-day individuals from 90 populations across sub-Saharan Africa and conclude that the individuals most likely originated from different source populations within the general area between northern Angola and Gabon. We also find that the majority (17/20) of the individuals were male, supporting a well-documented sex bias in the latter phase of the transatlantic slave trade. The study expands our understanding of St Helena's liberated African community and illustrates how ancient DNA analyses can be used to investigate the origins and identities of individuals whose lives were bound up in the story of slavery and its abolition.

Introduction

Between the 16th and 19th centuries, over 12.5 million Africans were abducted from their homelands in Africa to be sold into slavery in the Americas.[1] Historical records have revealed a great deal about the changing volume and structure of the transatlantic trade in enslaved Africans, but where in Africa they originated has been much more difficult to ascertain.[2–4] Recently, ancient and modern DNA studies have started to provide new information on the ancestral origins and experiences of enslaved Africans and their descendants in the Americas and elsewhere.[5–14] Meanwhile, archaeologists have stressed the importance and value of involving descendant communities in study design and research, as modeled on the New York African Burial Ground Project and others.[15–18]

The island of St Helena in the South Atlantic played a crucial role in the history of the transatlantic slave trade and its abolition. Between 1840 and 1867, St Helena received approximately 27,000 "liberated Africans" who had been rescued from slave ships by the Royal Navy (Figure 1; Table S1). Most of these individuals did not stay long on the island, as they were moved on to South Africa or the British colonies in the Caribbean and South America as indentured laborers. However, a small number of liberated Africans were allowed to settle on the island and, of those who did, many lived well into the 20th century. While there is no recognized descendant community on the island today, it is clear that hundreds if not thousands of descendants of St Helena's liberated Africans must exist on as well as off the island.[19]

The origins of St Helena's liberated Africans are likely to have been diverse. Records in the Transatlantic Slave Trade Database[1] indicate that the vast majority originated in West Central Africa, and a lesser number came from the Bight of Benin and the port of Quilimane in Southeast Africa (Table S1). These numbers are consistent with data from the vice-admiralty courts, which reveal that the majority of slave-carrying prizes bound for St Helena had been captured off the coast of West Central Africa (Figure 1), as well as personal accounts of Royal Navy personnel stationed on the island, which suggest that the majority of Africans had come from the Congo, Angola, and Benguela regions and a small number came from

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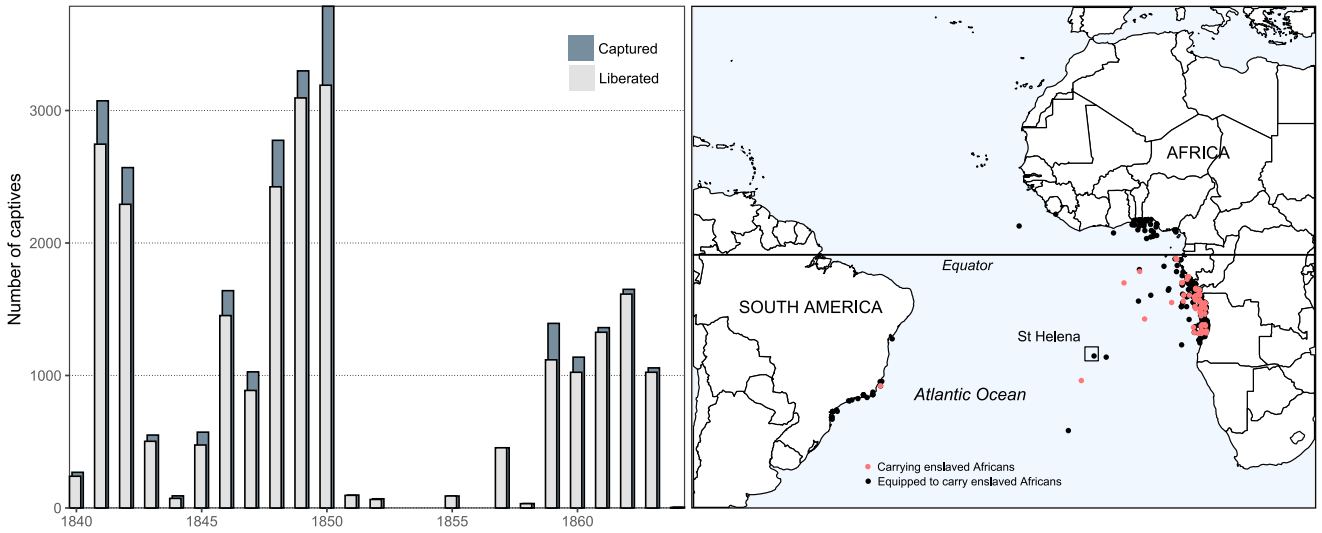

Figure 1. St Helena's liberated Africans
(A) Number of liberated Africans disembarked on St Helena between 1840 and 1872.
(B) Locations of slave ships captured by the Royal British Navy between 1840 and 1872 and brought to St Helena according to data from the vice-admiralty court at St Helena.[20]

Mozambique.[20] However, where exactly they originated or from how far inland they had traveled before reaching one of the coastal shipping points remains unclear.

Professionally led archaeological excavations on the island, carried out in 2007 and 2008 ahead of roadwork in connection with the construction of the island's first airport, led to the discovery of two large unmarked graveyards in Rupert's Valley on the north side of the island.[21] In total, the remains of 325 individuals were recovered from 178 graves and it quickly became clear that they were most likely the remains of liberated Africans who had died on the island in the mid-19th century. The exhumation of the remains provoked mixed feelings in the community, but most St Helenians accepted it as a necessity.[19] However, there was broad consensus that the remains should be reburied, although it was initially unclear how and where exactly reburial should take place.[22] Following public consultation on the reburial plan, the remains were eventually reburied in Rupert's Valley during a ceremony in August 2022 and plans are currently underway to create a memorial and interpretation center at the site in order to commemorate St Helena's liberated Africans and to provide opportunities for knowledge transfer.[23]

We set out to investigate the origins and identities of St Helena's liberated Africans by using ancient DNA analyses as part of a wider effort to restore knowledge of their lives and experiences.[22,23] We discussed the project with members of the community during a visit to the island in September and October of 2012. The feedback we received was very positive overall, with many Saints (to use their own shorthand) seeing particular value in information that might be gleaned about the origins of the island's liberated Africans. Since then, certain members of the community have developed a specific interest in the work. Fueled by their curiosity to delve deeper into their own family history and to uncover possible connections with St. Helena's liberated Africans, they have taken commercial DNA tests and were curious to learn what they could reveal (see also Abel and Schroeder[24]). We discussed the results of the project and the science underlying commercial DNA testing during a webinar (due to Covid restrictions) in November 2022, and there are plans to use the results as educational resources and in the context of the planned interpretation center on the island.

Material and methods

Sampling

We sampled 63 individuals for ancient DNA (aDNA) analysis (Figure 2). To minimize damage to the remains, we sampled a single tooth from each individual. The sampled individuals included 32 adult males, 16 adult females, and 15 subadults whose genetic sex could not be determined on the basis of skeletal traits (Table S2).[21] Teeth with evidence of cultural dental modification were avoided during sampling because they carry cultural information.[25,26] All laboratory work was carried out in dedicated aDNA clean lab facilities at the University of Copenhagen following established guidelines. Prior to sampling, the teeth were cleaned with paper towels and a 10% commercial bleach solution. The teeth were sampled with diamond-coated cutting discs targeting the cementum-rich layer of the tooth roots.[27] For more details, see supplemental information.

DNA extraction and library preparation

We extracted DNA from approximately 100 mg of bone by using a silica-based method with a pre-digestion step to reduce the amount of microbial contamination.[27] The DNA extracts were then built into DNA sequencing libraries via a blunt-end library preparation kit from NEB (E6070, New England Biolabs) and Illumina-specific adapters.[28] Libraries were amplified and indexed with a single six nucleotide index, purified with SPRI beads, and eluted in 60 μL. The optimal number of PCR cycles was determined by qPCR.[28]

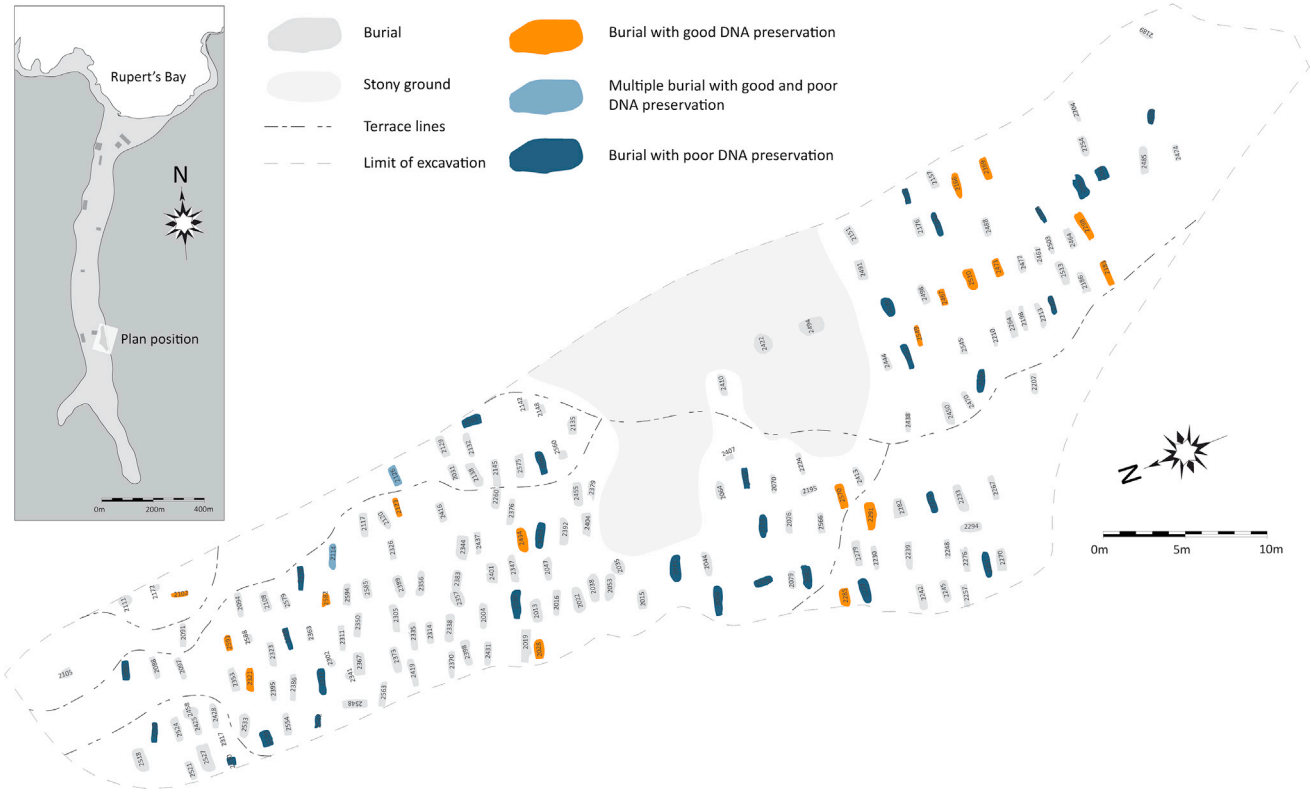

Figure 2. Burial plan of Rupert's Valley
Burial plan showing the location of the 178 burials excavated in 2007 and 2008. Burials sampled for aDNA are marked in color.

After purification, the libraries were quantified with an Agilent 4200 TapeStation and pooled in equimolar amounts. To assess the level of DNA preservation in the samples, we first screened all 63 libraries by using shallow shotgun sequencing across three lanes of an Illumina HiSeq 2500 flow cell run in 100 SR mode.

Whole-genome enrichment and sequencing

To increase the human DNA content of the aDNA libraries, 20 libraries with human endogenous DNA content > 0.1% were selected for whole-genome enrichment (WGC) and further sequencing. The libraries were enriched with the myBaits Human Whole Genome Enrichment Kit (Daicel Arbor Biosciences, Ann Arbor, MI), which uses biotinylated RNA bait transcribed from genomic DNA to enrich aDNA libraries in human DNA.[29] The enrichment was performed following manufacturer's instructions (myBaits Kit manual version 2.3.1) with a single round of enrichment and the enriched libraries were purified, amplified, and pooled as described above and sequenced across three additional lanes of an HiSeq 2500 flow cell run in 100 SR mode. For more details, see supplemental information.

Data processing

Base-calling was done with Illumina software CASAVA 1.8.2. Adapter sequences and low-quality stretches of DNA were removed with AdapterRemoval 2.0.[30] After trimming, reads shorter than 30 bp were removed and the trimmed and filtered reads were aligned to the human reference genome build 37 (hg19) and the revised Cambridge Reference Sequence (rCRS)[31] via *bwa aln*.[32] PCR duplicates were identified and removed with picard-tools MarkDuplicates. We used MapDamage 2.0[33] to assess aDNA damage patterns and to rescale mapping quality scores of bases most likely derived from damage. Contamination estimates were performed with Schmutzi[34] and hapCon.[35]

Sex determination and genetic relatedness

We carried out sex determination by calculating the observed fraction of Y chromosome reads compared to the total number of reads mapping to both sex chromosomes, following the approach and thresholds suggested by Skoglund et al.[36] Genetic relatedness between pairs of individuals was determined with READ,[37] which was developed to identify genetic kin relationships from low coverage ancient genomes by estimating pairwise distances *P*0 between pairs of individuals from pseudo-haploid genotypes (i.e., one randomly sampled allele per individual and SNP site) in non-overlapping windows of 1 Mbps.

Uniparental marker analysis

mtDNA and Y chromosome haplogroups were determined with HaploGrouper[38] on the basis of the phylogenetically informative sites obtained from PhyloTree build 17[39] and the ISOGG Y-DNA haplogroup tree 2019 (version 15.73) (https://isogg.org/tree/index.html). Genotypes for these sites were extracted from the BAM files of the St Helena individuals as consensus alleles after filtering for base and mapping quality of 20. Principal-component analysis (PCA) of mtDNA haplogroup frequencies (Figure S2) was carried out with the prcomp function in R version 4.2.1 and plotted in Rstudio version 2022.12.0 + 353.

Genome-wide ancestry estimates

To assess the genetic affinities of the individuals in our dataset, we performed PCA with three different reference datasets: (1) a global

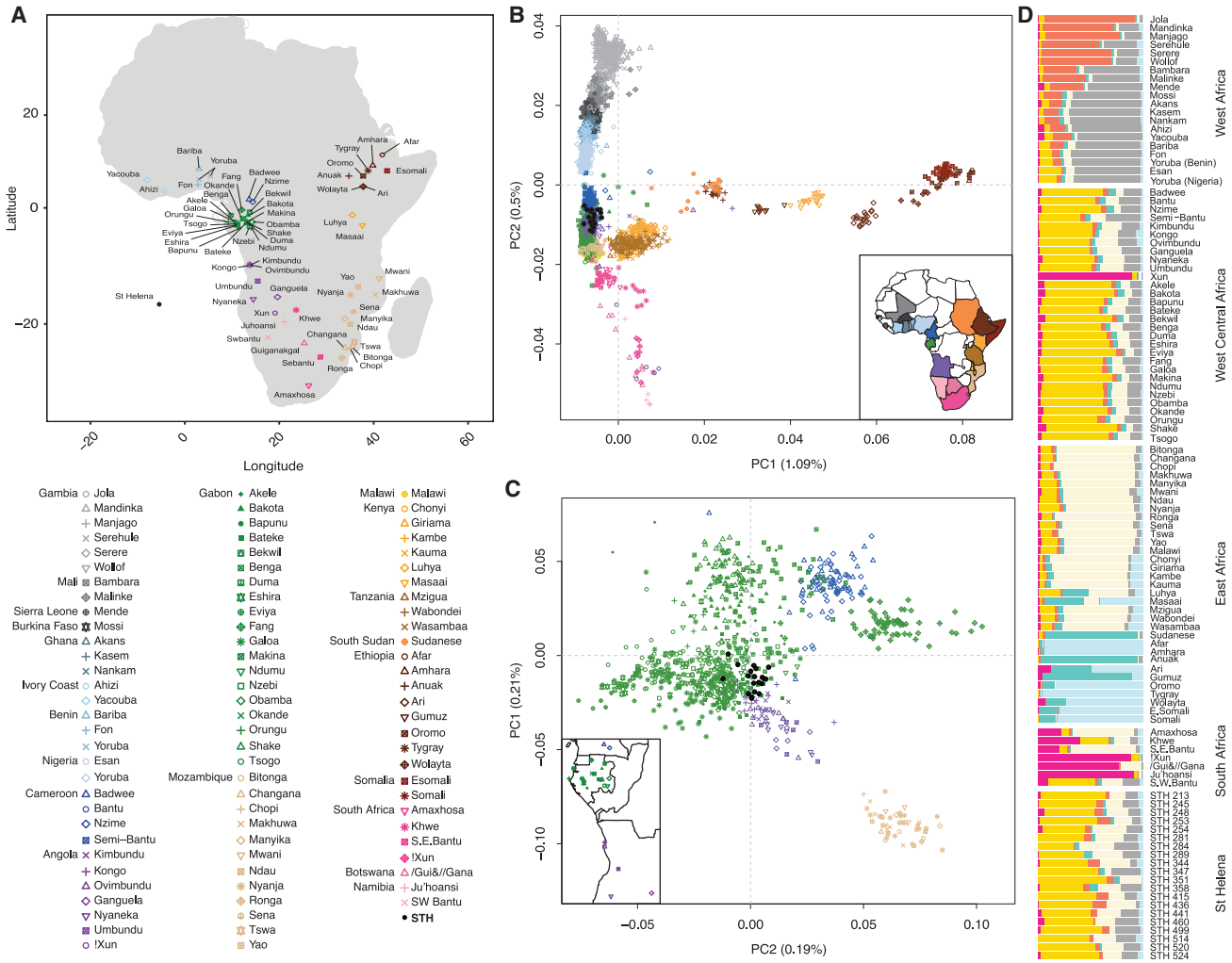

Figure 3. The ancestry of St Helena's liberated Africans

(A) Map showing the location of African reference populations.[41–49]

(B) Principal-component analysis of 3,098 individuals from 90 African reference populations and the 20 individuals from St Helena.

(C) Principal-component analysis of 1,121 individuals from 39 reference populations from only West Central Africa and Mozambique and 20 St Helena individuals.

(D) ADMIXTURE[54] analysis (K = 7) for 20 St Helena individuals and 90 reference populations. The results of the full ADMIXTURE[54] run can be seen in Figure S7.

dataset of 938 individuals from 53 global reference populations from the HGDP[40] genotyped at 644,117 SNPs, (2) a pan-African dataset containing 216,168 SNPs for 3,098 individuals from 90 present-day populations from sub-Saharan Africa (Figure 3A),[41–49] and (3) a smaller African dataset of 414,839 SNPs for 1,121 individuals from 39 populations from Angola, Gabon, Cameroon, and Mozambique (Table S11).[41–43] The datasets were merged with PLINK[50,51] and the St Helena individuals were added as pseudo-haploid calls by sampling a random read at every SNP position in the dataset (see supplemental information for more details).[52] PCA was performed with *smartpca*[53] with the option *lsqproject* to project the St Helena individuals onto PCs calculated for the modern reference populations and plotted in Rstudio version 2022.12.0 + 353.

Unsupervised ADMIXTURE[54] was run on the pan-African dataset with default settings for K = 2 to K = 10. For each K, we ran 50 replicates starting at different seed values and kept the replicate with the best log likelihood for each value of K. We determined the values of K that produced the lowest cross-validation (CV) error values. The lowest CV error value was obtained with K = 7 (Figure S7). Admixture results were plotted with R and are shown as bar plots (Figures 3D, S7, and S8). For Figure 3D, we show the average ancestry proportions for each of the populations in the reference dataset, except for the St Helena individuals for which we show the individual ancestry proportions.

Weighted identity-by-state (wIBS) analysis

To further explore the relationship between the individuals in our dataset and the reference populations, we calculated pairwise identity-by-state (IBS) scores weighted by allele frequency.[55] To avoid biases caused by small sample sizes, we only calculated the weighted IBS (wIBS) scores for individuals from reference populations with more than five individuals. We then calculated the mean and standard deviation of the wIBS scores for each of the St Helena individuals against all reference individuals and used

them to transform the raw wIBS scores into *Z* scores. To be able to exclude reference populations as possible source populations, we performed a series of pairwise permutation tests comparing the reference population with the largest mean wIBS score (population A) to each of the other reference populations (population B). In each instance of this test, we shuffled the wIBS scores between the individuals in our dataset and each member of the reference populations 100,000 times to obtain the null distribution for the difference in mean wIBS scores, under the assumption of no difference between them. An individual was deemed to be more closely related to population A than B when 5% or fewer values from the null distribution were greater than the observed (non-permuted) difference between A and B. The p values were Bonferroni adjusted for the number of tests performed. To validate the wIBS results, we computed a series of *D*-statistics of the form *D(Outgroup, STH; A, B)* where *A* is the reference population with the highest wIBS score and *B* represents any other given population in the reference panel. We computed *D*-statistics with *AdmixTools*[56] by using the genotypes of 103 Chinese individuals (CHB) from the 1000 Genomes project as the "outgroup." Assuming that each of the individuals in our dataset has the highest genetic affinity to population *A* (i.e., the population with the maximum wIBS score) we expect that *STH* will share more alleles with population *A* than population *B*, resulting in $D \leq 0$. For more details, see supplemental information.

Results

Initial screening of the libraries revealed varying levels of DNA preservation, with human endogenous DNA contents ranging from 0% to 48% (Table S3). After whole-genome capture and further sequencing, we obtained 20 low coverage genomes with an average depth of coverage between 0.1× and 0.5× (Tables S3 and S4). All libraries exhibited features typical of aDNA, including short average fragment lengths (<100 bp) and characteristic fragmentation and deamination patterns (Table S4). Genome-wide contamination estimates based on the male haploid X chromosome were low, ranging between 1.4% and 6.3% (Table S6). Individuals 254 and 351 yielded higher mtDNA-based contamination estimates, but their genome-wide estimates were comparable to those of the other individuals and within the accepted range, which is why we decided not to exclude them from the study.

Genetic sex and biological relatedness

The molecular sexing results revealed that the majority (17/20) of individuals in our dataset were males (Table S7). For the 16 adults in the dataset, the DNA results were consistent with previously published results on the basis of skeletal morphometric analyses.[21] In addition, we were able to determine the sex of four subadults whose biological sex could not be determined on the basis of their skeletal morphology.[21] Of those, three were identified as males and one as female. The kinship analysis revealed no close (i.e., first or second degree) relationships between the sequenced individuals in the dataset (Figure S4).

Uniparental markers

As expected, all the St Helena individuals were assigned to various subclades within African mtDNA macro-haplogroup L (Table S8). The most common haplogroup was haplogroup L2a1f, which is frequently found in West Central Africa and is thought to have originated there around 5,000 years ago before spreading southwards with the Bantu expansion.[57–59] Overall, the frequency distribution of mtDNA haplogroups among the individuals from St Helena appears most similar to populations in West and West Central Africa (Figure S1). This is also reflected in a PCA based on mtDNA haplogroup frequencies, where the individuals from St Helena fall closest to modern reference populations from West Africa (Figure S2).

All except one of the male individuals were assigned to Y chromosome haplogroup E1b1a1 or one of its various subclades (Table S8). E1b1a1 is the most common and diversified Y chromosome haplogroup in sub-Saharan Africa.[60–62] It is thought to have originated in West or West Central Africa around 40,000 years before present, and spread to Southern Africa and East Africa with the Bantu expansions.[62] Today, it is especially common among Niger-Congo speakers across West and West Central Africa and it also found among African-descendant communities outside of Africa.[9,10,14,63,64] Individual 436 was assigned to haplogroup B2a1a1a1, which appears widely distributed across sub-Saharan Africa, although it seems to be more common among some populations from Cameroon.[65–67]

Genome-wide ancestry estimates

The PCA results are shown in Figure 3. In Figure 3B, the St Helena individuals can be seen to cluster with populations from West Central Africa, specifically with populations from Angola, Cameroon, and Gabon. At a more regional scale, the individuals cluster most closely with reference populations from Angola and Gabon (Figure 3C). By contrast, Cameroon and Mozambique can most likely be excluded as possible regions of origin on the basis of this analysis. The PCA results are mirrored in the ADMIXTURE[54] results (Figure 3D), which indicate that the individuals from St Helena carry ancestry proportions that are most similar to those found in present-day Bantu-speaking populations from West Central Africa, particularly to those living in present-day Angola and Gabon.

To evaluate the effects of low coverage on the PCA and ADMIXTURE[54] results, we randomly down-sampled the individual with the highest depth of coverage (individual 213) to 60,000, 30,000 and 15,000 overlapping sites and generated ten independent replicates for each. The results indicate that, down to 30,000 overlapping sites, the results of the PCA do not change substantially (Figure S6). However, at 15,000 sites, we do observe a slightly wider spread in the placement, and we therefore caution that, for individuals with fewer than 30,000 overlapping sites, the placement in the PCA might be inaccurate. For the ADMIXTURE[54] analysis, we repeated the analysis three

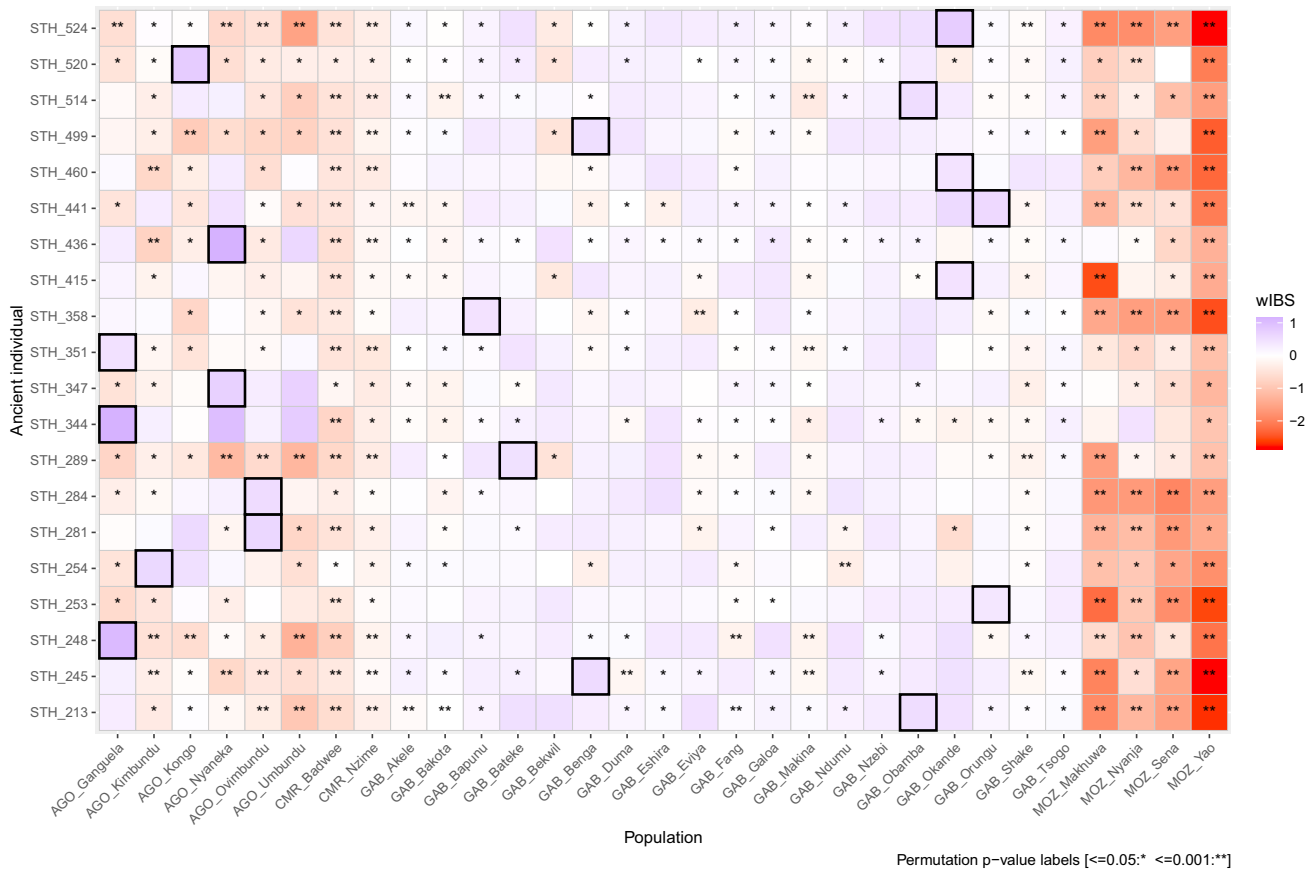

Figure 4. Heatmap showing the normalized (*Z* scores) pairwise wIBS scores between the St Helena individuals and reference populations

Highlighted squares indicate the reference population with the highest wIBS score for each of the St Helena individuals. Populations that can be excluded as likely source populations on the basis of a permutation test are marked with * (p value $\leq$ 0.05) and ** (p value $\leq$ 0.001).

times for individual 213 by using 60,000, 30,000, and 15,000 overlapping sites (Figure S8). The results indicate that the analysis is fairly robust even for individuals with as few as 15,000 overlapping sites.

wIBS analysis

Figure 4 shows the normalized wIBS scores for each of the individuals in our dataset. The non-normalized wIBS scores are listed in Table S12 and plotted in Figure S9. Highlighted squares mark the reference population with the highest wIBS score. Populations that can be excluded as possible source populations based on pairwise permutation tests are marked with * ($p \leq 0.05$) and ** ($p \leq 0.001$). These results are further supported by the *D*-statistics and their corresponding *Z* scores (Table S13), which indicate that none of the reference populations are significantly closer to the individuals from St Helena than the one with the maximum wIBS score ($|Z| < 3$) (Figure S10). On the basis of these results, we can exclude the populations from Cameroon and Mozambique as possible source populations for the individuals in our dataset. Conversely, several of the populations from Angola and Gabon cannot be excluded.

Discussion

Our fine-scale assessment of the ancestry and geographical origins of St Helena's liberated Africans suggests that the 20 individuals we were able to sequence most likely originated somewhere within the general area between northern Angola and Gabon. These results are consistent with historical sources, which suggest that during the course of the 19th century the trade from Central Africa shifted from the region around Luanda and Benguela in central Angola, which had dominated the supply and shipment of enslaved Africans hitherto, to northern Angola, particularly the region between southern Gabon and Ambriz, north of Luanda.[68] In fact, the trade from northern Angola during this period appears to have been orders of magnitude larger than that from other regions.[68] It therefore seems likely that the majority of liberated Africans who were brought to St Helena between 1840 and 1867 originated there.

Our results also indicate that, despite their general affinity with populations from Central Africa, the individuals probably did not derive from a single source population.

This is most clearly seen in the wIBS results, which suggest that some of the individuals are more closely related to present-day populations from Angola, while others show greater affinity to populations from Gabon (Figure 3). These observations are consistent with historical accounts, which suggest that St Helena's liberated Africans were ethnically and linguistically diverse.[20] Thus, several accounts agree that St Helena's liberated Africans spoke numerous languages, although they disagree to what extent they were mutually intelligible. According to one observer, the "Benguelan" language was the most common, while different dialects or "jargons" of the Congo were also being spoken.[69] Overall, multiple lines of evidence combine to indicate that the majority of St Helena's liberated Africans came from diverse communities within the general area of northern Angola, the Congo, and Gabon.

Our analyses also reveal that the majority of individuals in our dataset (17/20) were male. This is consistent with osteological analyses of the human remains from Rupert's Valley, which reported that 82% of the individuals for whom sex could be determined were male.[21] Historical sources suggest that a larger proportion of males were transported over the Atlantic over the period of the slave trade as a whole: roughly two-thirds of the captives were male and one-third female.[70] This male bias appears to have been particularly pronounced during the last phase of the transatlantic slave trade during the mid-19th century and our results are consistent with these figures.[20,70]

Our results are broadly consistent with expectations based on historical sources, but they also highlight some of the limitations of using a genetic approach.[24] The mtDNA and Y chromosome results are consistent with an origin in Central Africa, but they lack resolution. The genome-wide analyses help narrow down the range of possible source populations within Africa, but we are still unable, at this point, to identify specific source populations with certainty. This is partly due to the fact that African populations are still grossly underrepresented in genome-wide association studies (GWASs) and other studies of human genetic variation.[71,72] In fact, there are over 2,000 ethnolinguistic groups in sub-Saharan Africa, and only a small number of those have been sampled for genetic studies. For example, there are no individuals from the Congo in our reference dataset, which limits our ability to identify source populations from that area.

Another limitation is that we only have modern reference data. This is problematic because human populations or ethnic groups are not bounded, static units, frozen in time, but dynamic entities whose composition can change over time in response to external pressures or internal dynamics.[73] For example, it has been argued that warfare, raids, and violence led to the internal displacement of thousands of people in Angola during the period of the transatlantic slave trade, and it can be assumed that the same is true for other areas as well.[74] It is still unclear to what extent these movements transformed the genetic landscape of Africa, but it seems unlikely that it has remained unchanged since the time of the slave trade.[24] In particular, some admixture between populations is likely to have occurred over the past 200 years.

Despite these limitations, our study provides yet another example of how aDNA analyses can help restore histories of populations for whom the details of their past have been obscured by forced displacement and colonial violence.[5,9,14] Such knowledge can complement historical sources, but it can also be used to challenge dominant colonial narratives that were largely written by those who carried out the displacement and violence. In that sense, DNA is simply another source of information that can be used to reconstruct historic events and lived experiences, and we hope that by illustrating the history and condition of a few, we can illustrate the condition of the many.

At this point, our ability to identify the origins of individuals is limited by sparse sampling of ethnic groups and/or entire geographic regions, which reduces our ability to detect such fine-scale structure as has been reported for other parts of the world (e.g., Europe[75]). However, this limitation is likely to be overcome in the near future as denser sampling of different ethnic groups across Africa reveals the fine-scale genetic structure and complex admixture histories of African populations. Our study was also limited by the fact that we were only able to generate data for a relatively small number of individuals. Future research based on a larger sample may yet reveal more complex histories, while genetic testing involving the local community on St Helena has the potential to reveal long-lost connections with living descendants on and off the island.[76]

Data and code availability

The raw sequence files and the mapped data are available on the European Nucleotide Archive (ENA) website under project accession number PRJEB31303 (https://www.ebi.ac.uk/ena/browser/view/PRJEB31303).

Supplemental information

Supplemental information can be found online at https://doi.org/10.1016/j.ajhg.2023.08.001.

Acknowledgments

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Author contributions

H.S., K.R.B., A.H., and M.T.P.G. designed the research and acquired funding; J.W. and E.J. carried out sampling; A.P., J.W., E.J., K.R.B., and H.B. provided historical and archaeological background information; M.S.V. performed the lab work; M.S.V., A.J., J.R.M., C.F.L., M.C.Á.A., S.G., J.V.M.M., G.R., D.I.C.D., A.H., and H.S. performed the data analyses; M.S.V., J.R.M., A.P., H.B., A.H., and H.S. interpreted the results; H.S. and M.S.V. wrote the manuscript with contributions from J.R.M., A.P., H.B., A.H. and the remaining authors.

Declaration of interests

The authors declare no competing interests.

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