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Genomic insights into the early peopling of the Caribbean

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The Caribbean was one of the last regions of the Americas to be settled by humans, but how, when, and from where they reached the islands remains unclear. We generated genome-wide data for 93 ancient Caribbean islanders dating between 3200-400 cal. BP and find evidence of at least three separate dispersals into the region, including two early dispersals into the Western Caribbean, one of which seems connected to radiation events in North America. This was followed by a later expansion from South America. We also detect genetic differences between the early settlers and the newcomers from South America with almost no evidence of admixture. Our results add to our understanding of the initial peopling of the Caribbean and the movements of Archaic Age peoples in the Americas.

Archaeological evidence suggests that people first moved into the Caribbean around 8000 calibrated years before present (cal. BP) (1, 2). Apart from Trinidad, which is located closer to the American mainland, the earliest securely dated archaeological sites in the region date to around 5,000 cal. BP and are located in Barbados, Cuba, Curaçao, and St. Martin, followed by Hispaniola and Puerto Rico (2). The location of these sites suggests that the early settlers took long and rapid leaps of exploration across the Caribbean Sea. As a result, there is no gradual wave of advance that would point backward to a point of origin. In the absence of clear chronological clues, archaeologists have relied on stylistic comparisons of artifact assemblages to suggest possible links between the Caribbean and surrounding mainland (3, 4), while others have studied the prevailing winds and currents to suggest possible dispersal routes (5).

Starting around 2800 cal. BP new people began to enter the islands. Their arrival marks the beginning of the Ceramic Age in the Caribbean as a distinctive new style of pottery starts to appear along with more permanent settlements and agricultural practices (1). Archaeological and genetic evidence indicates that the new settlers came from South

America (6, 7), but how they reached the islands is debated. Two models have been put forward: The traditional model suggests that people gradually moved northward through the Lesser Antilles until they reached Puerto Rico, and then eventually further west into Hispaniola and Cuba (6). Alternatively, it has been suggested that the new settlers first reached Puerto Rico, bypassing the Lesser Antilles before expanding southwards (8). Whichever way this expansion took place, it seems likely that the newcomers encountered indigenous communities in the islands, but the nature of their interactions are unclear (9).

To shed light on the population history of the Caribbean, we retrieved genome-wide data from 93 ancient Caribbean islanders from 16 archaeological sites dating between 3200-400 cal. BP (Fig. 1 and tables S1 to S3) (10). The skeletal samples derive from two distinct archaeological contexts, which are referred to as “Archaic” and “Ceramic”, respectively (10). The 52 Archaic-related individuals come from seven sites in Cuba and date to c. 3200-700 cal. BP, while the 41 Ceramic-related individuals stem from nine sites in Cuba, the Bahamas, Puerto Rico, Guadeloupe, and St. Lucia, dating around 1500-400 cal. BP (Fig. 1). To overcome the challenges posed

by poor DNA preservation, we used a hybridization capture method targeting ~1.2 million genome-wide SNPs (10). In addition, we report mtDNA haplogroups for 89 of the 93 individuals and Y-chromosome haplogroups for 40 of the 47 males (table S1). Contamination estimates were low (on average <1% on both nuclear and mitochondrial estimates) except for five individuals not included in the final dataset (table S4).

The mtDNA data reveal clear differences in haplogroup frequencies between the individuals from the two contexts (fig. S1). While most of the individuals from Cuba 3200-700 cal. BP carry haplogroups D1 and C1d (with a frequency of 47% and 30%, respectively), these haplogroups are less common among individuals from Ceramic-related contexts, including those reported in previous studies (11, 12). Overall, mtDNA diversity is higher among Ceramic Age individuals, with haplogroups B2, C1b, and C1c unique to this group (fig. S1).

To explore these differences at a genome-wide level, we performed a principal component analysis (PCA) on the capture data using twelve present-day Native American populations as reference (10) (Fig. 2A) and we find that the individuals fall into two distinct clusters consistent with their archaeological context. When plotting the ancient Caribbean individuals with other ancient and modern Native Americans (7, 13–17), we find that individuals from Ceramic Age contexts, including those from Cuba, cluster with present-day individuals from South America, as well as a published 1000-year-old genome from the Bahamas (7). In contrast, individuals from Archaic-related contexts in Cuba 3200-700 cal. BP cluster outside present-day Native American variation (fig. S2).

To assess whether the observed clustering reflects different genetic affinities, we grouped individuals by site and computed f_4 -statistics of the form f_4 (Mbuti, Test; Early San Nicolas, Preacher's Cave), measuring the amount of allele sharing between the tested groups (Test) and the 1000-year-old individual from the Bahamas (Preacher's Cave) (7) versus 4900-year-old individuals from California's Channel Islands (Early San Nicolas) (16) who represent a branch splitting off the main Native American lineage prior to the diversification of ancient Central and South Americans (Fig. 2B and table S5) (15). As expected, the individuals from Preacher's Cave show the highest affinity to the genome from the same site (7), followed by all other Ceramic-related groups. By contrast, all individuals from Cuba 3200-700 cal. BP show less affinity to the Bahamian genome, with one individual from the site of Cueva del Perico (CIP009) being slightly closer to the individuals from California's Channel Islands (16). These differences are largely driven by a greater similarity of Ceramic-related groups to present-day populations from northeastern South America (Fig. 2C and figs. S3 and S4) (7).

To test if the two groups derived from the same or distinct

ancestral populations we used *qpWave* (18), which estimates the minimum number of sources necessary to explain the genetic composition of an individual or group of individuals (10). This analysis was consistent with the groups deriving from at least two separate streams of ancestry (chi-square, $p=1.68e-17$), demonstrating that the distinction we observe in the PCA cannot be explained by genetic drift alone (table S6). This is also reflected in a supervised clustering analysis, which results in two separate components (fig. S5A) (10).

The radiocarbon dates associated with the individuals (Fig. 1B) indicate that both groups were present in the Caribbean at the same time. However, using *qpAdm* (19), we do not detect any notable levels of admixture, except for one individual (PDI009) from the Ceramic Age site of Paso del Indio in Puerto Rico who is dated to 1060-910 cal. BP and carries a minor proportion of Archaic-related ancestry ($13 \pm 7.7\%$) (table S7). Considering the mounting evidence of the influence of Archaic Age communities on the development of later Caribbean societies (20, 21), it is surprising to find so little evidence of admixture between the two groups. However, it is possible that the result is influenced by our limited sampling coverage of the transitional period and islands such as Hispaniola.

We also detect two distinct ancestries in Cuba around 2700-2500 cal. BP represented by the oldest individuals from Cueva del Perico (CIP009) and Guayabo Blanco (GUY002) (Fig. 3, A and B), suggesting multiple early dispersals into the western Caribbean, prior to the arrival of Ceramic Age groups. Using *qpWave* (18), we find that some of the oldest individuals in our dataset (i.e., CIP009 and the individuals from Guayabo Blanco) cannot be modeled as descendants of the same ancestral source (chi-square, $p=0.013$) (table S6). When we try to model CIP009 alongside other ancient Native American genomes (14–16) using *qpGraph* (18), a model where CIP009 branches off the main Native American lineage with the individuals from California's Channel Islands (16) and prior to the radiation of ancient South and Central Americans fits the data best (Fig. 3A). By contrast, all other Archaic-related individuals, including the 2500-year-old individual from Guayabo Blanco (GUY002), require additional gene flow from ancient South Americans to improve the models (Fig. 3B and fig. S6). Together, these results support multiple dispersals into the western Caribbean prior to the arrival of Ceramic Age groups. While it is difficult to determine where these early dispersals originated, it seems that at least one of them was connected to radiation events in North America prior to the diversification of Central and South Americans (14, 15).

After 2800 cal. BP, there followed another expansion, which originated in South America and is well attested archaeologically (1). When we model this expansion using the Ceramic Age genomes in our dataset, we find that a stepping-stone model with people originating in South America

gradually moving northwards through the Lesser Antilles fits the data better than a model assuming a southward expansion from Puerto Rico (Fig. 3C and fig. S7). However, since we do not have any individuals with Ceramic-related ancestry from the earliest phase of the Ceramic Age expansion (c. 2800-2200 cal. BP), it is difficult to model this process accurately. The expansion of Ceramic Age groups stalled in Puerto Rico for at least 1000 years before resuming sometime after 1500 cal. BP and it is generally assumed that the advance was halted by the presence of Archaic Age communities in Hispaniola and Cuba (1, 6). Our results are consistent with a temporal gap, as we do not detect any Ceramic-related ancestry in Cuba until 500 cal. BP. However, it is still unclear whether we are dealing with a period of genetic turnover (19, 22) or a more complex history of interaction with intermittent episodes of admixture similar to those that have been observed in other parts of the world (23, 24).

The new genetic evidence supports the notion that the Caribbean was settled and resettled by successive population dispersals that originated on the American mainland. We find support for at least three separate population dispersals into the region, including two early dispersals, one of which appears to be connected to radiation events in North America. Clearly, Archaic Age peoples had the seafaring abilities to conquer the Caribbean (5). In fact, there is mounting evidence to suggest that, far from being an insuperable barrier, the Caribbean Sea functioned as an “aquatic motorway” that people crossed frequently, despite its occasional unpredictability (25). The initial peopling of the Caribbean was later followed by another expansion from South America. As the newcomers arrived in the islands, they must have encountered descendants of the early settlers, but we find surprisingly little evidence of admixture, raising questions regarding the nature of their interactions and the role of the early settlers in the development of later Caribbean societies. Additional data and multiple lines of evidence will be needed to explore these questions further and to shed more light on the complex population history of the Caribbean.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Supplementary Text
Figs. S1 to S7
Tables S1 to S7
References (26–100)
MDAR Reproducibility Checklist

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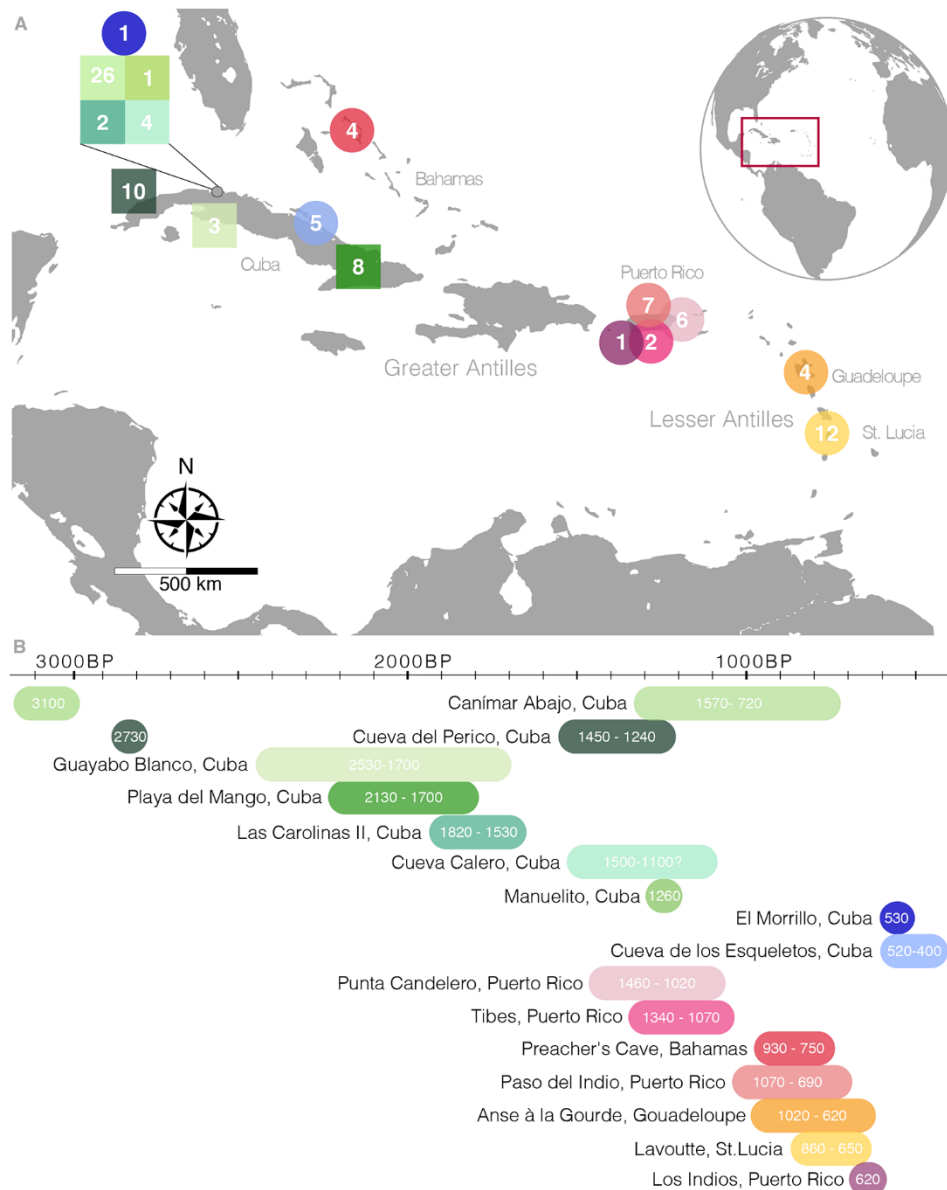


Fig. 1. Sites and samples. (A) Map of the Caribbean showing the location of the sites discussed in the text including the number of individuals analyzed per site. Squares represent sites with samples from Archaic-related contexts while circles denote Ceramic-related contexts. (B) Date ranges for each site are reported in calibrated years BP. Date ranges derive from directly dated skeletal remains and do not necessarily represent the entire period of occupation of the site. For sites with single individuals mean point dates are provided. The date ranges for the Cueva Calero individuals are based on archaeological context and indirect radiocarbon dates (10).

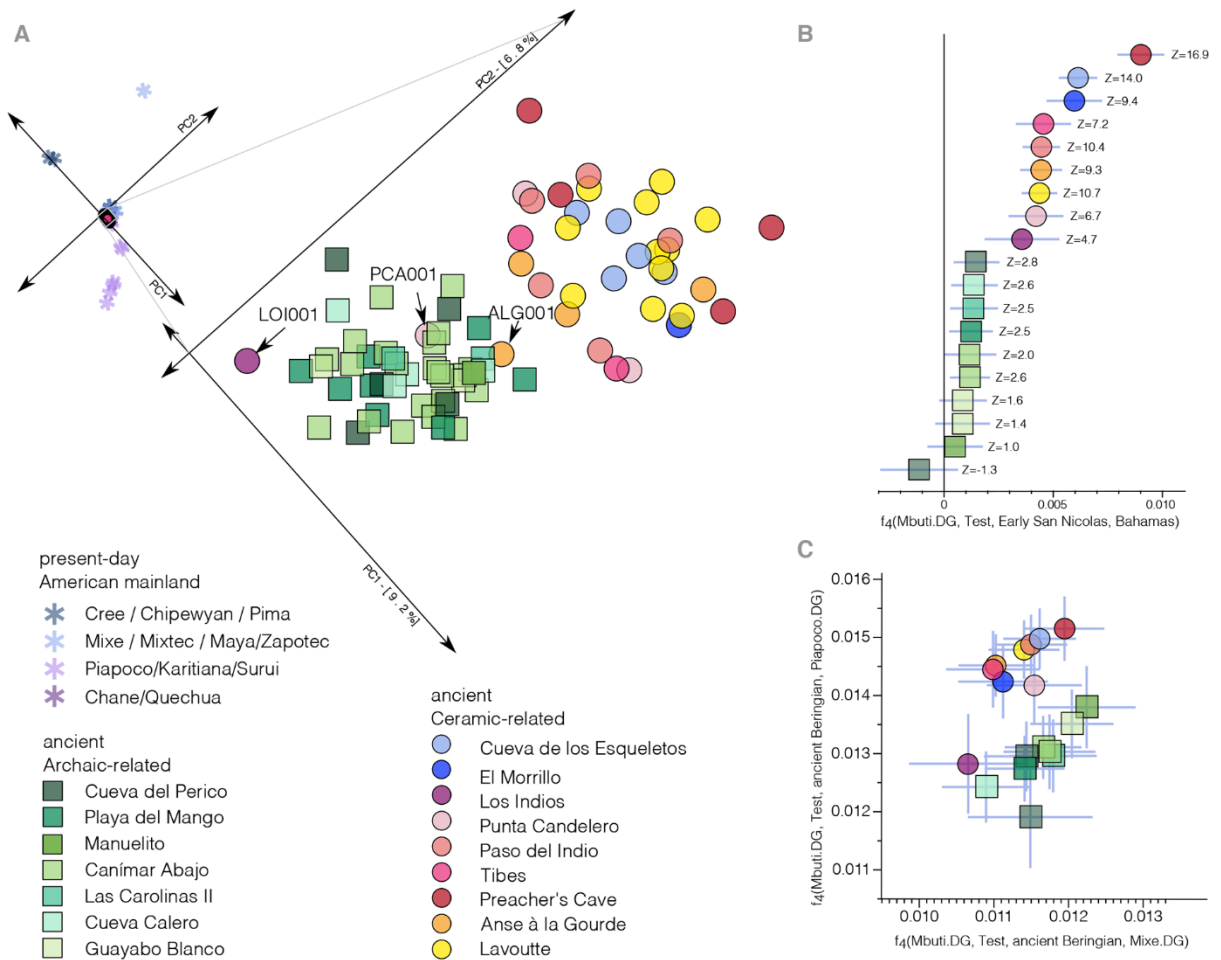


Fig. 2. Population substructure of ancient Caribbean islanders. (A) Principal component analysis (PCA) of ancient Caribbean islanders projecting the ancient individuals onto principal components calculated from present-day Native American populations (10). Three Ceramic Age individuals (ALG001, LOI001 and PCA001) cluster outside their main grouping, but f_4 -statistics indicate that they are more closely related to Ceramic-related than Archaic-related individuals (table S5). (B) f_4 -statistics measuring the differential affinities of ancient Caribbean islanders to 4900-year-old individuals from the California Channel Islands (Early San Nicolas) (16) and a published 1000-year-old individual from the Bahamas (7). The Bahamas genome serves as a proxy for ancient north-eastern South American components not available from the mainland. (C) Differential affinities of ancient Caribbean islanders to present-day Piapoco (y-axis) and Mixe (x-axis). Light blue lines indicate two standard errors. Squares indicate samples from Archaic-related contexts while circles denote Ceramic-related contexts.

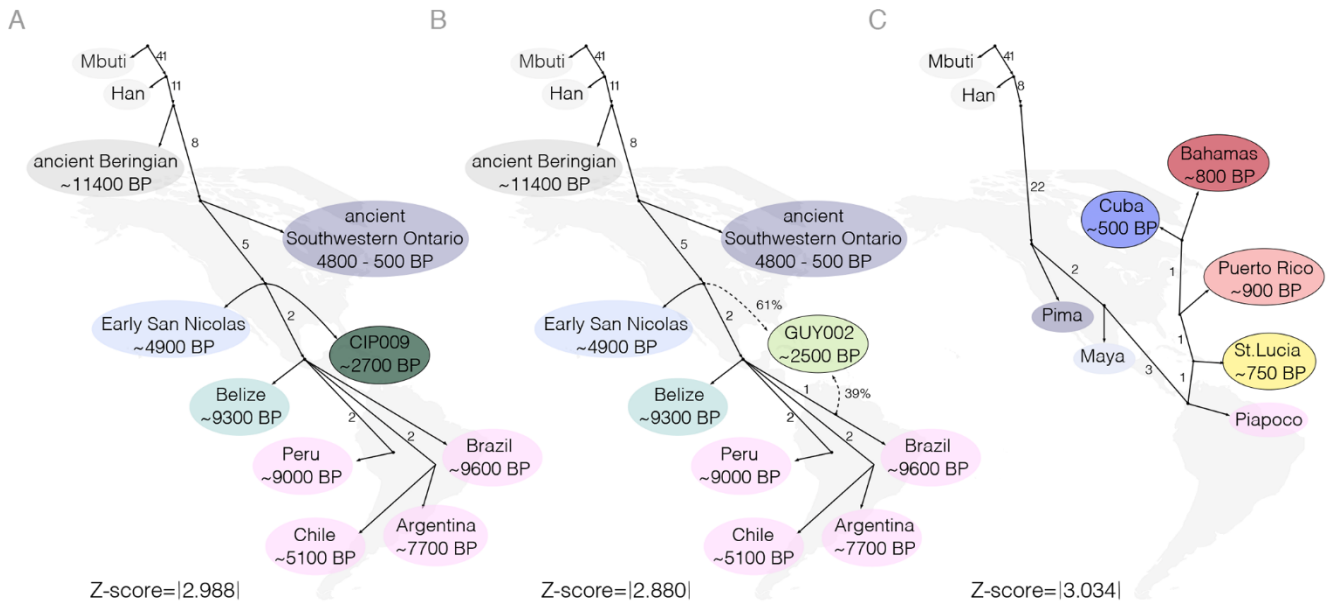


Fig. 3. Admixture graphs modeling the ancestry of ancient Caribbean islanders. (A to C) We show the best-fitting model for each individual or group as inferred from the final fit score (I_0) for individual CIP009 from the Cueva del Perico (A), individual GUY002 from Guayabo Blanco (B), and several Ceramic Age groups (C). CIP009 (2700 cal. BP) branches off the main Native American lineage together with individuals from the California Channel Islands (16) prior to the diversification of Central and South Americans, while GUY002 (2500 cal. BP) requires some South American-related ancestry to make the model fit. The expansion of South American groups after 2000 cal. BP can best be modeled as a stepping-stone process, while a southward model results in a worse fit (fig. S7). The geographical position of ancient groups corresponds to their approximate location. Arrows do not indicate dispersal routes and node placements do not show the actual geographic region where the split took place. Numbers to the right of solid edges are proportional to optimized drift; percentages to the right of dashed edges represent admixture proportions. Peru ~9000 BP includes Peru Cunchaicha 9000 BP and Peru Lauricocha 8600 BP (15). For other groups see the supplementary materials (10).

Genomic insights into the early peopling of the Caribbean

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