Where are the Caribs? Ancient DNA from ceramic period human remains in the Lesser Antilles

F. Mendisco¹, M. H. Pemonge¹, E. Leblay¹, T. Romon², G. Richard³, P. Courtaud¹ and M. F. Deguilloux¹

¹Université de Bordeaux, UMR 5199 PACEA, Equipe Anthropologie des Populations Passées et Présentes, Allée Geoffroy ST Hilaire, Pessac Cedex 33615, France
²Institut National de Recherches Archéologiques Preventives Guadeloupe, centre de Saint-Claude, rue des Gommiers Blancs Parnasse, Saint-Claude 97120, France
³Conseil regional de la Guadeloupe, Avenue Paul Lacaze, Basse-Terre 97100, France

The identity and history of the indigenous groups who occupied the Lesser Antilles during the ceramic periods remain highly controversial. Although recent archaeological evidence has challenged hypotheses concerning the organization of human groups in this region, more biological data are needed to fully inform the discussion. Our study provides, to our knowledge, the first palaeogenetic data for Late Ceramic groups of the Guadeloupe archipelago, yielding crucial information concerning the identities of these groups. Despite the generally poor DNA preservation in the tested remains, we were able to retrieve Hypervariable Region 1 sequences from 11 individuals and mitochondrial single-nucleotide polymorphisms from 13 individuals. These novel data provide interesting preliminary results in favour of a common origin for all Saladoid Caribbean communities, i.e. the first ceramic groups of the region, as well as for a local continuity between the Saladoid and post-Saladoid groups. A combination of the genetic data obtained and several pieces of cultural evidence allows us to propose that two different groups inhabited the Guadeloupe archipelago during the Late Ceramic period, with the possible occupation of the La Désirade and Marie-Galante islands by groups affiliated with the Taíno communities. The working hypotheses proposed here appear consistent with recent archaeological evidence.

1. Introduction

When Europeans first reached the Caribbean archipelago in the late fifteenth century, they described four distinct human groups: an agriculturalist group called the Taínos, who inhabited Hispaniola, Puerto Rico, eastern Cuba and most likely Jamaica and the Bahamas; a hunter–gatherer group called the Ciboneys (or Guanajutabeyes), who occupied western Cuba; and two distinct groups in the Lesser Antilles known as the Arawaks and the Island Caribs. Some scholars consider the Ciboneys to be the direct descendants of the first migrants to arrive in the region approximately 6000 BC [1,2]. The Taínos of the Greater Antilles and the Arawaks of the Lesser Antilles are considered to be the descendants of the first agriculturists originating from South America, and they have been associated with the Saladoid culture in particular [1,2]. The Saladoid culture is the name given to the first ceramic groups living in the Middle Orinoco region of South America. Five hundred years BC, the Saladoid ceramic culture arrived in the Antilles, consisting of agriculturalists who built permanent settlements near areas of cultivation [2,3]. The end of the seventh century AD marked a period of crucial change in Antilles history, which led to the fragmenting of Saladoid culture into several smaller groups (often called Post-Saladoid groups within the Lesser Antilles).

Although there may be a consensus concerning the origins of the Taínos and the Arawaks, the existence and origin of the Island Caribs remains the subject of
intense debate. Island Caribs were first viewed as the descendants of the mainland Caribs, who originally occupied the area north of the Amazon and eventually spread to parts of Guyana, Venezuela and Colombia [1,2]. Mainland Caribs were once thought to have left the Orinoco river area to settle in the Caribbean at approximately AD 1200, after which time they were referred to as the Island Caribs. Europeans chronicled these people as ferocious nomadic hunters who raided Arawak and Taíno villages for their women, eventually completely replacing the Arawaks. However, more current analyses no longer portray the Island Caribs as male invaders who arrived from the South American mainland, and the image of the Caribs as cannibals is now thought to have been invented by Europeans to justify the slave trade [4]. Moreover, no gaps in the archaeological record can be linked to potential Carib migration waves prior to contact, and the archaeological continuity observed in the Lesser Antilles—from the post-Saladoïd period to the contact period—lends strong support to the idea of local evolution [1,4,5].

Another ongoing debate concerns the genetic relationships between the native groups in the Greater and Lesser Antilles. Although a clear separation exists between the Taínos and Amerindians from the Lesser Antilles in the form of distinct social organizations (e.g. the highly hierarchized society of the Taínos versus the egalitarian societies of the Lesser Antilles) and archaeological cultures, archaeological data also indicate that the inhabitants of the Caribbean region maintained widespread contact networks, including prolonged periods of exchange between the Caribbean and the continent [6–8]. Notably, numerous instances of artefact exchange have been found between the communities of the Lesser and Greater Antilles [9], suggested the potential for gene flow as well. To date, the only biological data available with which to test for genetic links between the various Caribbean groups are dental morphology data [10]. The results showed that differences in material cultures could be linked to distinct biological backgrounds, which was interpreted to support the hypothesis that the different native groups originated from different migration waves and preserved their biological integrity through time (i.e. a lack of gene flow). Of course, new genetic data from these ancient groups could significantly change the direction of the debate.

All Amerindian groups from the Caribbean region are thought to have gone extinct soon after contact. Mainstream history tells that these peoples were decimated by war, famine, disease and emigration, such that they had completely disappeared by the end of the sixteenth century. To replace the decreasing indigenous populations, Europeans brought African slaves to the region, who came to constitute the major substratum of present-day Caribbean populations. Today, only small ethnic Carib communities remain in St Vincent and in the Carib Territory of Northeast Dominica.

Recently, genetic analyses have been introduced into the debate surrounding the origins of the Caribbean peoples, providing crucial data concerning the English-speaking Caribbean groups of the Lesser Antilles [11], the Black Carib groups of Belize [12] and Honduras [13], and the population of Puerto Rico [14,15]. The results proposed corroborate the historical accounts that the indigenous populations were drastically reduced and that they left only scant traces in extant gene pools, most notably in the Lesser Antilles. Revealing high levels of genetic admixture with West African populations, these analyses clearly illustrate the limitations of using modern Caribbean genetic data to unravel the origins and evolution of native groups. To overcome the limits induced by lineage extinction and recent admixture, palaeogenetic analyses have been developed. To date, ancient DNA (aDNA) data have only been published for individuals from the Greater Antilles: the first palaeogenetic study focused on Taíno remains from the Dominican Republic [16] and a second focused on Ciboney remains from western Cuba [17]. The authors concluded that the aDNA data supported the view that the Cibones and Taínos derived from successive migration movements emanating from the same area around the Orinoco Delta in South America.

Our study describes novel aDNA sequences obtained from native remains originating from the Guadeloupe archipelago (composed of the islands of Guadeloupe, Marie-Galante and La Désirade in the northern part of the Lesser Antilles; figure 1) and dating from the sixth to seventeenth centuries AD. As ceramic assemblages from this region show clear influences from both the Greater Antilles and the southeast Lesser Antilles [18], these islands represent a key logistical position for analysing the genetic affinities...
between human groups from the Lesser and Greater Antilles. The palaeogenetic results we obtained are discussed at different geographical levels: (i) at the sub-continental level, our results permitted us to characterize the origin of these ancient groups, which should inform the debate concerning the identity of the Island Caribs; (ii) at the regional level, the data revealed new insights into the genetic affinities between the Lesser Antilles human groups and the other Caribbean communities and allowed us to assess the extent of genetic divergence between groups marked by different material cultures; and (iii) at the local level, the sequences we retrieved provide crucial findings concerning the relationship between individual identity and funerary practices in these peoples.

2. Material and methods

(a) Archaeological sites and samples
Bone or dental remains from 38 individuals were collected from 11 pre-Columbian archaeological sites on the islands of Guadeloupe, La Désirade and Marie-Galante. The locations of these sites are detailed in figure 1. The archaeological contexts in which they were found, as well as the measured radiocarbon dates, allowed us to associate all the remains used in this study with either the Saladoid (BC 500 to AD 600) or post-Saladoid (AD 600–1500) cultures. The funerary contexts of the archaeological sites were extremely variable, from scattered and transformed remains found within cavities (islands of La Désirade and Marie-Galante) [19], to primary burials discovered in outdoor sites [20]. All information concerning collection dates and context is detailed in table 1. When possible, the samples were collected in situ during site excavations using strict protocols to avoid contamination and ensure optimal sample preservation; in particular, samples were directly deposited into hermetically sealed sterile bags and immediately stored at −20°C.

Table 1. Detailed characteristics of the archaeological sites studied.

<table>
<thead>
<tr>
<th>site</th>
<th>period</th>
<th>radiocarbon datation</th>
<th>individuals</th>
<th>sample</th>
<th>context</th>
</tr>
</thead>
<tbody>
<tr>
<td>Basse-Terre</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gare-Maritime (Basse-Terre)</td>
<td>Saladoid—Hueca</td>
<td>cal. AD 250 – 450</td>
<td>1</td>
<td>bone fragments</td>
<td>dumping ground</td>
</tr>
<tr>
<td>St Claude</td>
<td>post-Saladoid</td>
<td></td>
<td>2</td>
<td>bone fragments</td>
<td>burial (inland settlement)</td>
</tr>
<tr>
<td>Roseau (Capesterre Belle Eau)</td>
<td>post-Saladoid—</td>
<td></td>
<td>2</td>
<td>teeth</td>
<td>dumping ground</td>
</tr>
<tr>
<td></td>
<td>Cayo</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grande Anse (Trois-Rivières)</td>
<td>post-Saladoid</td>
<td>—</td>
<td>16</td>
<td>bone fragments</td>
<td>burial (littoral settlement)</td>
</tr>
<tr>
<td>Grande-Terre</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anse St Marguette</td>
<td>post-Saladoid</td>
<td>—</td>
<td>1</td>
<td>teeth</td>
<td>burial (littoral settlement)</td>
</tr>
<tr>
<td>Ilet Gosier</td>
<td>post-Saladoid</td>
<td>—</td>
<td>1</td>
<td>teeth</td>
<td>burial (littoral settlement)</td>
</tr>
<tr>
<td>Desirade</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Voute a Pin</td>
<td>post-Saladoid</td>
<td>cal. AD 1312 – 1427</td>
<td>2</td>
<td>bone fragments</td>
<td>burial (cave)</td>
</tr>
<tr>
<td>Marie-Galante</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Morne Rita (Capesterre-de</td>
<td>post-Saladoid/early</td>
<td>cal. AD 1475 – 1664</td>
<td>3</td>
<td>bone fragments</td>
<td>burial (cave)</td>
</tr>
<tr>
<td>Marie-Galante)</td>
<td>colonial)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grotte Blanchard</td>
<td>post-Saladoid</td>
<td>cal. AD 1289 – 1445</td>
<td>4</td>
<td>bone fragments</td>
<td>burial (littoral settlement)</td>
</tr>
</tbody>
</table>

(b) DNA extraction
Sample processing and analyses were performed using standard precautions to minimize the risk of exogenous DNA contamination. The procedures were performed in the aDNA facilities of the laboratory of Past and Present Populations Anthropology (Université de Bordeaux, UMR PACEA) in a laboratory dedicated to aDNA analysis, as described in [21].

The samples collected in situ using precautions against contamination were cleaned with a sterile surgical blade in a sterile hood. The samples manipulated by archaeologists or anthropologists without precautions prior to DNA extraction were first cleaned with a sterile surgical blade, washed with dilute bleach and irradiated for 15 min with ultraviolet light to eliminate potential surface contamination. Each sample was ground, and the resultant powder was incubated overnight at 55°C with agitation in a lysis solution (0.5 M EDTA, NaOH, 1–2 mg ml⁻¹ Proteinase K and 0.5% N-lauryl sarcosyl). For some samples, DNA was extracted using a phenol/chloroform-based protocol [21], whereas for others, DNA was extracted using the NucleoSpin Extract II kit (Macherey-Nagel, Düren, Germany), according to a previously described protocol [22]. An extraction blank was systematically co-extracted with the ancient samples during each extraction session. At least two independent DNA extractions were carried out for each sample. For the majority of individuals, two different samples were analysed.
Table 2. Mitochondrial haplotypes (Ht) and haplogroups (Hg) retrieved for the Guadeloupe archipelago.

<table>
<thead>
<tr>
<th>Ht</th>
<th>samples</th>
<th>HVR-1 polymorphisms</th>
<th>mt-SNPs</th>
<th>Hg</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ht-01</td>
<td>St Claude-11</td>
<td>16223T 16290T 16319A 16362C</td>
<td>12007A-64T</td>
<td>A2</td>
</tr>
<tr>
<td>Ht-02</td>
<td>Grande Anse-1</td>
<td>16111T 16218T 16223T 16290T 16319A 16362C</td>
<td>64T A2</td>
<td></td>
</tr>
<tr>
<td>Ht-03</td>
<td>St Claude-8</td>
<td>16223T 16270T 16290T 16319A 16362C</td>
<td>64T A2</td>
<td></td>
</tr>
<tr>
<td>Ht-04</td>
<td>Grande Anse-12</td>
<td>16223T 16290T 16318T 16319A 16362C</td>
<td>12007A-64T  A2</td>
<td></td>
</tr>
<tr>
<td>Ht-05</td>
<td>Voute à Pin-1, Cadet-2</td>
<td>16223T 16298C 16325C 16327T</td>
<td>493G C1b</td>
<td></td>
</tr>
<tr>
<td>Ht-06</td>
<td>Voute à Pin-2</td>
<td>16051G 16223T 16298C 16311C 16325C 16327T 16335G</td>
<td>7697A C1d1</td>
<td></td>
</tr>
<tr>
<td>Ht-07</td>
<td>Cadet-1</td>
<td>16223T 16298C 16311C 16325C 16327T</td>
<td>15930A C1c</td>
<td></td>
</tr>
<tr>
<td>Ht-08</td>
<td>Cadet-3</td>
<td>16223T 16362C</td>
<td>2092T D1</td>
<td></td>
</tr>
<tr>
<td>Ht-09</td>
<td>Grande Anse-2</td>
<td>16223T 16325C 16362C 16390A</td>
<td>2092T D1</td>
<td></td>
</tr>
<tr>
<td>Ht-10</td>
<td>Cadet-4</td>
<td>16223T 16325C 16362C</td>
<td>12007A A2</td>
<td></td>
</tr>
<tr>
<td></td>
<td>— Grande Anse-352</td>
<td>—</td>
<td>16325C C1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>— Blanchard</td>
<td>—</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(c) Amplification, cloning and sequencing of the Hypervariable Region 1
Mitochondrial haplotypes were determined by sequencing a 393 bp fragment of the mitochondrial Hypervariable Region 1 (HVR-1) (nts 16008–16401) using four overlapping primer pairs: L15989 and H16158, L16112 and H16239, L16190 and H16322, and L16268 and H16401 [23,24]. PCR amplifications were performed according to the protocol described by Deguilloux et al. [21], with the exception that 3 μl of the DNA extracts obtained from the NucleoSpin Extract II kit were used in each reaction, which were amplified for 40 cycles. At least two separate amplifications of each mitochondrial fragment were performed for each DNA extract. To detect possible contamination from external DNA, extraction and amplification blanks were used as negative controls. To detect artefacts generated by DNA degradation and Taq polymerase errors, some of the PCR products were cloned using the Topo TA cloning kit (Invitrogen). The ‘authentic’ sequences were deduced from the consensus sequence of several clones from multiple amplification products and multiple extracts.

(d) Single-nucleotide polymorphism genotyping
To confirm and refine the sequence haplogroup attribution, eight specific single-nucleotide polymorphisms of the mitochondrial coding region (mtSNPs) characterizing the founding Native American haplogroups A2, B2, C1b, C1c, C1d1, C1d2 and D1 [25–27] were amplified using iPLEX Gold technology (Sequenom), as described in a previous work [22]. In addition, eight Y-chromosomal SNPs were also amplified to characterize the major Amerindian paternal lineages: C-M216, Q-M242, Q-M346, Q-M3, Q-M19, Q-M194, Q-M199 and Q-SA01 [28–31]. All primers used for these analyses are shown in the electronic supplementary material, table S1.

(e) Statistical analysis
To estimate the genetic affinities between our samples and extant populations from the surrounding regions, data from three Caribbean, eight Mesoamerican and 37 South American groups, representing a total of 4465 HVR-1 sequences, were compiled from the literature. In addition, to test the inter-island relationships of the Caribbean region during the ceramic periods, 34 previously described mtDNA sequences from ancient groups of the Greater Antilles were used [16,17]. All references and genetic characteristics concerning these groups are detailed in the electronic supplementary material, table S2.

Two within-group diversity indices [nucleotide (π) and haplotype diversity (Hd)] were computed using ARLEQUIN package v. 3.5.1.3 [32] to measure intra-population mtDNA variation. A genetic distance matrix between the LCG group and comparison populations was also generated using the ARLEQUIN package. Genetic distances were calculated from mtDNA-haplotypes (considering sequences between positions 16024 and 16365) using the Tamura and Nei distance model [33] with the suggested correction gamma value of 0.26 for mitochondrial HVR-1 data [34]. To visualize the patterns of genetic differentiation, pairwise FST values were plotted on a multidimensional scaling plot using the XLSTAT-Pro v. 7.5 software program and on a map using the SURFER software program (v. 8.0; Golden Software). A PCA analysis was performed for ancient and modern-day populations described in the electronic supplementary material, table S2, using the XLSTAT-Pro 7.5 software program.

3. Results
DNA was obtained from 13 human remains, out of the 38 tested, distributed over the entirety of the Guadeloupe archipelago, and dating from between AD 1200 and 1600 (table 2). The low amplification efficiency we observed (34%) could be attributed to the unfavourable environment of the Caribbean region, as tropical conditions are not conducive to the preservation of human remains and DNA [35]. It should be noted that we observed differences in the quality of DNA preservation between the ancient samples based on the sites of conservation. Although reproducible sequences could be readily obtained from the samples collected from cavities (about 50% of authentic PCR products), a statistically significant lower PCR success rate could be noted for samples originating from outdoor sites (30% of authentic PCR products; p (t-test) = 0.005).

(a) Sequence authentication
Several basic authentication criteria for aDNA were followed, including the use of a dedicated laboratory, cloning of amplification products to detect PCR artefacts (electronic supplementary material, figure S1) and multiple reactions to

http://rstb.royalsocietypublishing.org/
determine the reproducibility of the results [36,37]. These precautions, combined with the following facts, make us confident concerning the authenticity of the retrieved sequences. In particular: (i) the blanks showed no signs of contaminating Amerindian sequences; (ii) European-specific sequences originating from the researchers who directly participated in this study were never observed during the analyses (electronic supplementary material, table S3); (iii) all consensus haplotypes and haplogroups were determined using multiple replicates (i.e. samples from independent extracts and amplifications performed at different times); (iv) the mutational patterns of the clones were consistent with those previously described for aDNA (electronic supplementary material, figure S1); and (v) all results from the HVR-1 sequencing and mtSNP genotyping were consistent.

(b) mtDNA sequence variation
Mitochondrial haplogroups could be characterized for 13 of the samples, and the results revealed the presence of three distinct Amerindian mitochondrial lineages: A2 (n = 5), C1 (n = 5) and D1 (n = 3). Reproducible haplotypes were recovered for 11 samples, as presented in table 2. The 11 HVR-1 sequences were classified into 10 different mtDNA-haplotypes, of which nine were found in a single individual and one was shared by two individuals of this ancient group. We compared these 10 mtDNA-haplotypes with our reference database, which revealed exact matches for seven of the mtDNA-haplotypes. Two mtDNA-haplotypes (Ht-05 and Ht-09) were found in the ancient Taíno and Ciboney groups of the Greater Antilles, and they are also distributed throughout all regions of Meso- and South America, as they represent the C1 and D1 haplogroup founding sequences. Similarly, haplotypes Ht-01 and Ht-07 were not informative as they are also found in numerous modern Amerindian communities. On the other hand, three of the described haplotypes have very limited distributions among extant populations. One of these A2 haplotypes (Ht-04) has only been reported for a single native Mexican individual [38], and another C1 haplotype (Ht-06) has only been reported for one native Mexican individual and one Garifuna from Honduras [13,38]. Furthermore, a match was found for the one D1 haplotype (Ht-08) with an individual from northern Brazil [39]. Finally, the three remaining haplotypes (Ht-02, Ht-03 and Ht-10) could not be matched to any individuals from our database.

(c) Y-chromosome analysis
Very few positive results were obtained for the Y-chromosome SNP analyses, highlighting the fact that degradation of nuclear genomic DNA in ancient human samples remains a problem. However, the paternal lineage of one individual from the Grotte Cadet site was identified. This sample (Cadet-1) was assigned to the Q-M3 paragroup. Today, this haplogroup is most commonly found among Native American populations and widespread throughout the Americas [40,41].

(d) Sequence and population diversity
The distribution of the mitochondrial haplogroups in the pre-Columbian LCG group was as follows: 38.5% A2, 38.5% C1 and 23% D1. The B2 mitochondrial haplogroup was not detected in the ancient LCG group. The observed haplotypic diversity (Hd = 0.9636 ± 0.0510), which was calculated using the 11 retrieved HVR-1 sequences, was one of the highest described for any Central and South American population, although it was close to the values described for other extant populations in Cuba, Mexico and Amazonia, as well as the Moxos and Andean groups (electronic supplementary material, table S2). However, considering the low number of sequences evaluated, these results must be interpreted with care.

A map representing the genetic distances based on the HVR-1 data between the ancient LCG sequences and extant populations from Meso- and South America is shown in figure 2a (FST values are detailed in the electronic supplementary material).
supplementary material, table S4). Based on this analysis, the LCG group showed the strongest genetic affinities with extant groups from northern South America. Indeed, the ancient LCG group could not be significantly differentiated from extant groups in Venezuela (Wayuu, Guahibo), Colombia, Guiana (Apalai, Waunana) or Amazonia. However, given the small number of sequences considered, we also conducted the same type of analysis using all of the ancient HVR-1 sequences available for ancient groups from the West Indies (i.e. including the Taino and Ciboney sequences). As illustrated in figure 2b, the same pattern of genetic affinities was observed when we considered all of the ancient Caribbean samples. The ancient Caribbean groups could not be significantly differentiated from native Colombians inhabiting the Amazon area ($F_{ST} = 0.016$) [42], and they were only slightly differentiated from the Amazonian and Colombian populations ($F_{ST} = 0.079$ and 0.064, respectively) [43,44]. The PCA analysis, based on the haplogroup frequencies, confirmed the affinity of the LCG group with some South American groups (such as the Apalai, Guahibo or Arawak), especially owing to the high percentages of C1 haplogroup (electronic supplementary material, figure S3).

4. Discussion

Despite intense interest in the evolutionary history of indigenous Caribbean populations, to date, only two aDNA studies had been conducted on populations of the Caribbean region, and notably, only in the Greater Antilles [16,17]. This situation has been partly owing to the environmental conditions of the Caribbean region, which are not favourable to DNA preservation—a fact that is highlighted by the low amplification efficiency observed in our analyses. However, our study also revealed a clear correlation between DNA preservation and micro-environmental conditions, since a statistically higher PCRs success rate was observed for samples originating from caves (in Marie-Galante and La Désirade), than for samples obtained from outdoor sites. Despite the difficulties encountered dealing with these Caribbean human remains, we report, to our knowledge, the first palaeogenetic data from the Lesser Antilles associated with the late phase of the Late Ceramic Age (AD 1200–1600).

The mitochondrial gene pool of the LCG was characterized by the presence of three Amerindian mitochondrial haplogroups (A2, C1 and D1). This composition of haplogroups indicates a clear affinity with extant populations of the northern parts of South America, although it was not discriminating enough to clarify the precise origin of the studied groups. The statistical analyses we conducted indicated that the closest genetic relationships were with several Amazonian communities that speak a language of the Equatorial-Tucanoan family, such as native Colombians or Amazonians [42–44]. It is worth noting that the closest relationships were not found with communities located along the northern coast of South America, but with inland indigenous populations. This clustering of the ancient LCG and inland continental groups may reflect migrations that took place throughout the Amazon and Orinoco basins. These migratory movements, which often occurred along waterways, could have favoured the colonization of the Caribbean islands, or at least diffusion of the Saladoid ceramic culture to this region [1,2,15].

We also noted that the $F_{ST}$ patterns obtained for either the LCG group alone or for the group including all of the ancient Caribbean communities were very similar (figure 2). These results suggest a common origin for these groups, even considering the small number of available ancient Caribbean samples. It is also worth noting that all of the ancient Caribbean communities for which genetic data were obtained existed during a critical historical period, namely between the first ceramic age and the early colonial period. As a consequence, the genetic homogeneity observed for all the ancient Caribbean groups supports the hypothesis of local evolution of the ceramic populations in the Greater and Lesser Antilles with a Saladoid/post-Saladoid regional continuity, as supported by the archaeological evidence [45].

Only weak genetic affinities were observed between the ancient Caribbean groups, including our LCG sample, and the extant populations of Mesoamerica. This observation underscores the low amount of gene flow between both regions during the ceramic periods. However, it should be noted that two rare mitochondrial haplotypes (Ht-04 and Ht-06) were shared between the LCG group and a few native individuals from Mexico and Honduras (Garifunas) [13]. The Garifunas, or ‘Black Caribs’, are thought to have arisen from an admixture of West African slaves who survived the wreck of two British ships carrying slaves to the West Indies and indigenous people from the Lesser Antilles (specifically from the St Vincent Islands) [12,13]. The fact that this specific haplotype was shared between ancient LCG and Garifuna individuals supports both the historical accounts and the genetic affinities between the Late Ceramic groups from the Guadeloupe archipelago and St Vincent Island.

Three of the 11 mitochondrial sequences characterized in our LCG group have not been described before (Ht-02, Ht-03 and Ht-10). Of course, we cannot exclude the possibility that the scarcity of data available in the literature is responsible for the low number of shared haplotypes. However, the current distribution of genetic sequences observed for the LCG group is consistent with the major changes to the Caribbean gene pool that occurred following colonization and slavery. It is well known that the indigenous populations, who represented the initial workforce of the European colonizers, were drastically and rapidly reduced by war, disease, emigration and slavery [2,11,14,15]. Important native groups were displaced following the arrival of the Spanish in Greater Antilles, which resulted in many Tainos finding refuge in the Lesser Antilles [46], and following the importation of many Amerindian slaves from the Lesser Antilles as well as from mainland Meso- and South America [11,14]. We can detect the echoes of these events in our results, which are consistent with the disappearance of numerous native lineages and the redistribution of other significant lineages throughout the circum-Caribbean region. This profound restructuring of the native gene pool is also supported by the low observed genetic affinity between the ancient and extant groups in the Caribbean region. As a consequence, if a relatively large number of Native Amerindian mitochondrial lineages have been maintained in the gene pool of certain extant groups (notably in Greater Antilles [14,47]), they are probably not completely representative of the ancestral gene pool.

The palaeogenetic data obtained in this study allow us to address, at a local level, several biological and cultural phenomena. The human samples analysed in this study originated from a variety of funerary contexts. On the one hand, the human remains originating from mainland Guadeloupe were found in primary burials located next to ‘houses’ (carbet) in outdoor sites [20]. Samples from these sites belonged to the maternal lineages A2 (five samples) and
D1 (one sample). On the other hand, the human remains originating from the islands of La Désirade and Marie-Galante were found scattered in caves. In addition, for some of these human remains, as in the case of Cadet, anthropologists found the presence of numerous cut marks, traces of disarticulation and defleshing, as well as voluntary perforations [19]. The samples from these two islands belonged to the C1 (five samples) and D1 (two samples) maternal lineages, which reflects the genetic diversity observed for ancient communities from the Greater Antilles. Despite the low number of samples considered, a striking correlation was found between differences at the archaeological level (most notably in terms of funerary practices) and differences at the genetic level (at least in terms of mitochondrial haplogroup frequencies). Based on these observations, the obvious question arises as to whether different groups occupied these sites. One likely hypothesis is that the individuals discovered on the islands of La Désirade and Marie-Galante were related to the Taínos populations, which were genetically and archaeologically distinct from the native groups of the Lesser Antilles found on mainland Guadeloupe. Current archaeological evidence indicates that the Taínos appear to have expanded their territory into the north of the Lesser Antilles, as far as Martinique [6,46], which could explain their presence on the islands of Marie-Galante and La Désirade. It may also be the case that the burial sites on Marie-Galante and La Désirade were used for particular functions or special rituals, as previously proposed for the site of Morne Cybèle on La Désirade [6,48]. Finally, the correlation between archaeological evidence and biological differentiation in these groups is consistent with an increase in the number of ceramic styles in time and space, which suggest cultural fragmentation during the post-Saladoid period [45]. This cultural regionalism may have been correlated with decreased gene flow between these different groups, which may have resulted in the genetic differentiation observed between the ancient groups of the Guadeloupe archipelago.

Finally, one goal of this project was to address the controversial issue of the origin and existence of the so-called Island Caribs. Today, the theory of Island Caribs migration waves from mainland South America to the Caribbean around the twelfth century is widely questioned. In this context, it is interesting to note that our ancient LCG group is genetically differentiated from extant communities that are thought to be descendants of the mainland Caribs (FST = 0.27 for the Kalina of Guiana), which would support the lack of a common origin for the ancient communities of Guadeloupe and the mainland Caribs. However, it remains possible that the 'Island Caribs' migrated much later than previously thought, perhaps during the late pre-colonial/early colonial period (e.g. associated with the Cayo material culture) [49,50]. Unfortunately, our data do not allow us to test this hypothesis of a late, large-scale arrival of newcomers in the Lesser Antilles. Therefore, the nature of the Island Caribs remains unresolved, and this question should be further analysed using palaeogenetic/palaeogenomic analyses with greater numbers of human remains from the Lesser Antillean region, dating between the twelfth century and the contact period.

5. Conclusion

Our study provides, to our knowledge, the first palaeogenetic data from native groups of the Lesser Antilles associated with the late phase of the Late Ceramic Age (AD 1200–1600). These novel, albeit preliminary, results provide interesting evidence in support of a common origin (northern South America) for the Saladoid ceramic groups of the Greater and Lesser Antilles followed by local evolution leading to the emergence of diversified post-Saladoid cultures. Moreover, the genetic data we obtained in combination with cultural arguments, allow us to propose that different groups occupied the Guadeloupe archipelago during the Late Ceramic Age. We believe that our results clearly highlight the importance of considering both archaeological and anthropological data (necessitating a true interdisciplinary approach) to better characterize the identities of the individuals under study. Finally, the dramatic reshaping of the gene pool of the ancient native Caribbean groups has been clearly reconfirmed by our findings, which highlight the necessity of broadening our sampling of aDNA in the Caribbean region, both in time and space, to allow for a better understanding of native Caribbean group dynamics.

Acknowledgements. We thank everyone who participated directly in the excavations of the human remains submitted for our palaeogenetic analyses.

Funding statement. This research was made possible by funding from the Guadeloupe Region (Conseil regional de la Guadeloupe), the INRAP (Institut National de Recherches en Archéologie Préventives) and the CNRS (Centre National de la Recherche Scientifique). This research is partly funded by a ministerial grant from the Research National Agency as a programme of prospects investments ANR-10-LABX-52 (CAP project; dir: M.F.D.; University of Bordeaux, LaScArBx-ANR; 2012–2014).

References


