

Exploring the African genetic influence in the first settlement founded by African slaves in America

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Abstract The present study aims to outline the genetic makeup of the current population of the town of Yanga (Veracruz State, Mexico), the first Latin American settlement founded by African slaves in Mexico. For this purpose, we carried out the genetic characterization of 60 individuals from Yanga, analysing 15 autosomal short tandem repeats (STRs) and interpreting the results in the context of the admixed population known as Mexican mestizos. The genetic contribution from the three most important human groups in the current admixed Yanga population was calculated using Structure software. We detected a high percentage of Amerindian (48%) and European inheritance (44.7%), and a much less important African contribution (7.3%). These results were then compared with 10 other Mexican mestizo populations. The results fit the tri-hybrid model for admixture characterized by a high genetic contribution from Europeans and Africans in the north—though the African influence is lower—and a decreasing contribution from these two populations to the south and southeast. Conversely, the Amerindian component presents maximum values in the south and minimum values in the north. The Amerindian and European genetic traces are related to their ancestral settlements, but the African contribution can be explained by other parameters. To understand the current African genetic traces, we have to assume that there was a redistribution of these population groups and an important admixture phenomenon which led to the dilution of the African ancestral genetic pool. Furthermore, admixture was favoured by conditions that allowed individuals who intermarried to ascend in social status. These reasons would explain why despite the fact that Yanga was founded by black slaves, high levels of African ancestry are not found in the current population.

Key words: Afro-Mestizos, Yanga, Palenque, microsatellites, admixture

Introduction

The genetic composition of Latin American mestizo populations is one of the most fascinating questions facing anthropology today. Most of these populations have Amerindian, European, and African components in different proportions. This is known as the tri-hybrid admixture model

(Lisker et al., 1996) based on the separate arrival of the three human groups to the New World.

Although there is still controversy about when the initial peopling of the American continent took place, the latest research supports the hypothesis of a recent settlement (18000 before present (BP)) across the Bering Strait (Tamm et al., 2007; O'Rourke and Raff, 2010).

The first European contact occurred in the late 15th century when the first Spanish explorers arrived in the New World. From this moment on the number of Europeans grew steadily, and by 1820 (Eltis, 1983) some 2.4 million had migrated to America. In the case of Mexico, the vast majority of these immigrants came from the Spanish regions of Andalusia and Extremadura.

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The first African slaves were brought to America as an alternative source of labour to the native peoples who had been decimated by epidemics and pressure from the Europeans. The earliest references describe the presence of Africans in the Caribbean in 1520 and in large numbers in continental America by the 16th century. It is estimated that in total between 12 and 15 million African slaves were brought to America (Lovejoy, 1982).

From then on, therefore, Africans, Europeans, and aboriginal Amerindians coexisted in the same territory, although with very different social structures and behaviour. For example, the first chroniclers described the behaviour of the natives as submissive, while Africans were generally considered to be disobedient, and escapes and insurrections were frequent. These African rebels were known as maroons (in Spanish 'cimarrones'), that is to say, fugitive black slaves, and the self-governing communities they founded were called 'palenques' (Landers, 2006).

The Palenque de San Basilio (Colombia) is considered to be the first free, black town in the New Continent (Sudarkasa, 1980). In 1713, the King of Spain, through the 'Cédula del Perdón,' granted the escaped slaves their freedom and assigned them the ownership of certain territories. However, according to other authors (Cruz-Carretero, 2005; Vinson and Restall, 2009), by 1630 there was already a free palenque, San Lorenzo de los Negros, which until 1932 was referred to as Yanga (Veracruz State, Mexico) in memory of the 'cimarrón' chief who led the first rebellion. In 1609, after 20 years of rebellion, the colonial government gave permission to Yanga to found a settlement (Memoria Política de México, 2014) for the first free African slaves in America. Since its foundation, and even today, Yanga acquired a symbolic value as a refuge for African fugitives and a landmark for African identity in Mexico (Rinaudo, 2011). The current population of Yanga is over 16000 and the economy of the area is based on growing corn and sugar cane.

The main objective of this work is to determine the proportion of African ancestry that currently exists in the town of Yanga using short tandem repeats (STRs); in other words, whether or not the history and the African identity of Yanga is reflected in its current genetic composition. The results will be interpreted in the context of Mexican mestizo populations.

Materials and Methods

Samples

Sixty samples were selected without considering donor phenotype or other characteristics. We chose this strategy because the objective of the study was not to trace the ancestry of individual donors, but rather to determine the genetic composition of a population with African origins and to find the parameters that could explain this distribution. Hair samples were plucked with tweezers from 60 healthy individuals whose four grandparents were all born in the town of Yanga (Veracruz). In order to avoid underestimating the genetic diversity, the donors chosen were unrelated. To be sure of this, the names from the surveys were compared and donors were asked if any other family members were included in the study. We received written consent from each of the donors

and also carried out a survey to obtain more information about their family origins.

Genetic markers

Traditionally, these markers have been used in forensic genetics (Butler, 2006), which has resulted in the characterization of a large number of population groups worldwide. This allows us to compare our results with those obtained in other studies and integrate the information in a geographical context, and therefore to study population characteristics such as admixture, genetic structure, and migration (Wang et al., 2008). In this study 13 common markers have been used for the populations (all except D2S1338 and D19S433).

DNA was extracted using the Chelex[®] method, and amplifications were carried out with the AmpF/STR[®] Identifier[™] kit. Genotypes were analysed by means of capillary gel electrophoresis using an ABI Prism[™] 310 Genetic Analyzer (Applied Biosystems).

The ancestral populations

In order to estimate the admixture composition of the Yanga population and another 10 mestizo groups from Mexico (Table 1, Figure 1), individual genotypes were compared to three ancestral populations, which should represent as closely as possible the populations from the tri-hybrid model.

The European population is represented by Andalusians from the southwest of Spain (Carvajal-Carmona et al., 2000). The African population selected was the Fangs (Calzada et al., 2004) from western central Africa (Equatorial Guinea) because a large proportion (approximately 34.5%) of the slaves came from this region (Salas et al., 2004). As regards the Amerindian reference, the Purépecha indigenous group was chosen because it was the indigenous population with the highest genetic distances relative to Fangs and Andalusians, $F_{ST} = 0.08$ and 0.05 , respectively (data not shown).

Statistical analysis

Allele frequencies, Hardy–Weinberg equilibrium, genetic distances (F_{ST}) and AMOVAs (molecular analysis of variance) were performed with the Arlequin 5.5.1.2 program (Excoffier et al., 2005). Admixture estimates were obtained by applying the Structure programme (Falush et al., 2003) using the admixture model with correlated frequencies and a separate α value to manage the asymmetric admixture observed in Mexican mestizo populations. We ran 35000 replications of the proposed tri-hybrid model ($K = 3$), with 25 iterations after a burn-in period of 5000. Thereafter, the output was analysed using CLUMPP software (Jakobsson and Rosenberg, 2007) and the DISTRUCT programme (Rosenberg, 2004). Genetic distances and the Pearson's correlation coefficient (r) were plotted by means of multidimensional scaling (MDS) using XLSTAT.

Results

Allele frequencies for 15 STRs in the Yanga population are shown in Table 2. For some samples incomplete profiles were obtained, perhaps because of the Chelex extraction;

Table 1. Geographical origins, sample size and bibliographical references of the admixture and ancestral populations used in this work

| Population | Geographical region | Sample size | Reference |
|------------------------------|---------------------|-------------|--------------------------------|
| <i>Admixed population</i> | | | |
| Chihuahua | North Center | 162 | Martínez-González et al., 2005 |
| Nuevo Leon | Northeast | 143 | Cerda-Flores et al., 2002a |
| Jalisco | West | 309 | Rubi-Castellanos et al., 2009 |
| Guanajuato | Center West | 331 | Rangel-Villalobos et al., 2010 |
| Yanga | Center-East | 60 | This study |
| Metztitlán | Center | 104 | Gorostiza et al., 2007 |
| México City | Center | 234 | Luna-Vázquez et al., 2005 |
| Puebla | Center | 313 | Rubi-Castellanos et al., 2009 |
| Veracruz | Center-East | 200 | Rangel-Villalobos et al., 2010 |
| Campeche | Southeast | 106 | Sánchez et al., 2005 |
| Yucatán | Southeast | 262 | Rubi-Castellanos et al., 2009 |
| <i>Ancestral populations</i> | | | |
| Fang | Africa | 115 | Calzada et al., 2004 |
| Andaluces | Spain | 198 | Sanz et al., 2001 |
| Purepechas | Center | 57 | Rubi-Castellanos et al., 2009 |

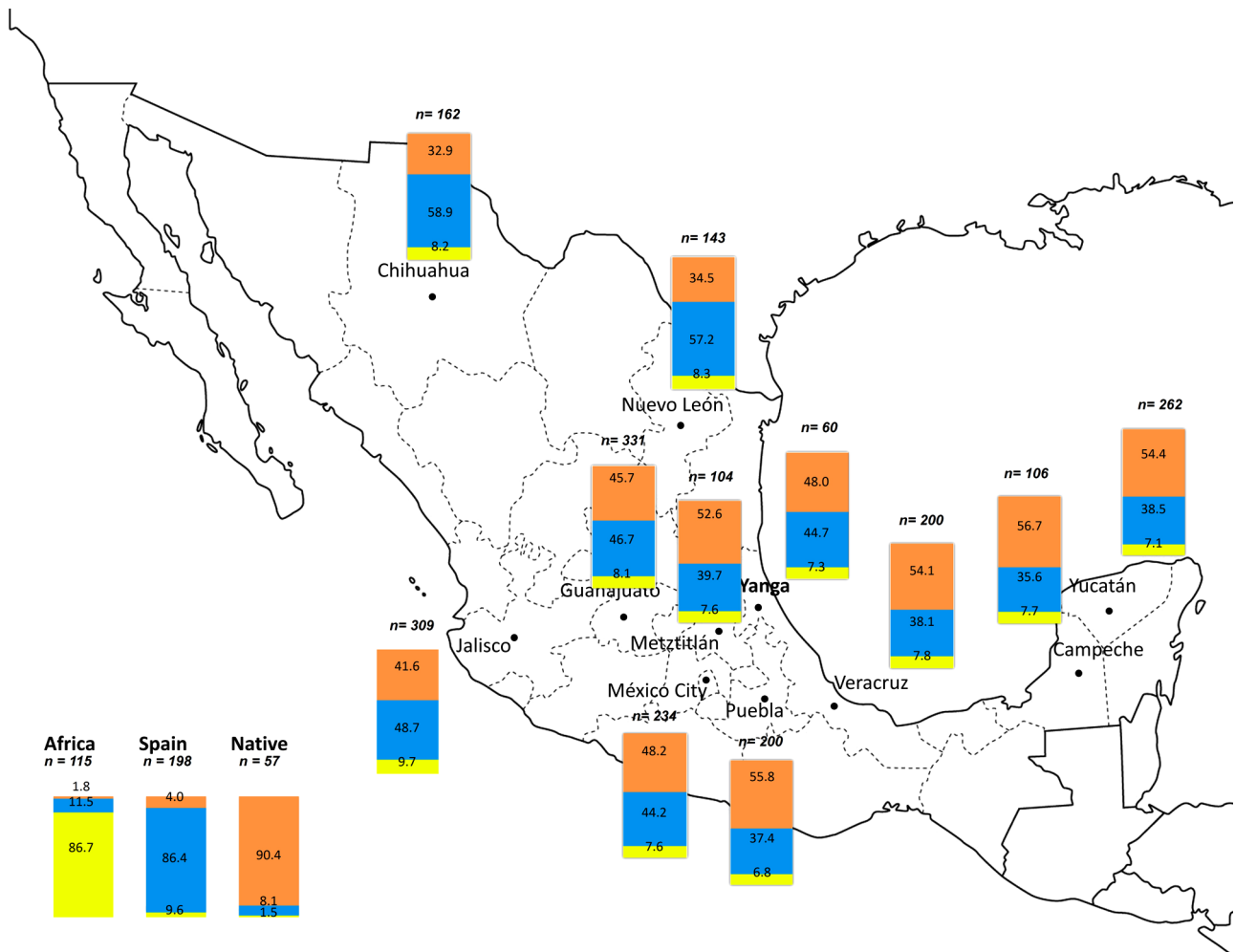


Figure 1. Populations included in this study: each bar represents the admixture estimates obtained from Structure analysis: Amerindian (grey for print; orange for online), European (dark grey for print; blue for online), and African (light grey for print; yellow for online) inheritance in Mexico. In the left bottom, the results of applying the Structure-District programs to the ancestral populations are shown. The number of samples and the percentage belonging to each of these populations are also included.

Table 2. Allele frequencies for the 15 STRs characterized for the Yanga population. All markers are under Hardy–Weinberg equilibrium, including D13S317 and FGA after the application of Bonferroni correction ($\alpha = 0.008$ and $\alpha = 0.001$, respectively)

| Allele | D8S1179 <i>n</i> = 58 | D21S11 <i>n</i> = 58 | D7S820 <i>n</i> = 57 | CSF1PO <i>n</i> = 54 | D3S1358 <i>n</i> = 59 | TH01 <i>n</i> = 55 | D13S317 <i>n</i> = 60 | D16S539 <i>n</i> = 55 | D2S1338 <i>n</i> = 54 | D19S433 <i>n</i> = 57 | vWA <i>n</i> = 59 | TPOX <i>n</i> = 46 | D18S51 <i>n</i> = 55 | D5S818 <i>n</i> = 60 | FGA <i>n</i> = 51 |
|---------|--------------------------|-------------------------|-------------------------|-------------------------|--------------------------|-----------------------|--------------------------|--------------------------|--------------------------|--------------------------|----------------------|-----------------------|-------------------------|-------------------------|----------------------|
| 6 | | | | | | 0.318 | | | | | | | | | |
| 7 | | | 0.018 | | | 0.409 | | | | | | | | 0.083 | |
| 8 | | | 0.044 | | | 0.027 | 0.075 | | | | | 0.402 | | 0.008 | |
| 9 | | | 0.035 | 0.019 | | 0.055 | 0.183 | 0.109 | | | | 0.076 | | 0.042 | |
| 9.3 | | | | | | 0.191 | | | | | | | | | |
| 10 | 0.078 | | 0.289 | 0.306 | | | 0.100 | 0.218 | | | | 0.033 | 0.009 | 0.067 | |
| 11 | 0.078 | | 0.281 | 0.306 | | | 0.250 | 0.282 | | | | 0.359 | | 0.542 | |
| 11.2 | | | | | | | | | | 0.009 | | | | | |
| 12 | 0.147 | | 0.219 | 0.306 | | | 0.200 | 0.300 | | 0.017 | | 0.130 | 0.136 | 0.192 | |
| 12.2 | | | | | | | | | | 0.026 | | | | | |
| 13 | 0.310 | | 0.096 | 0.046 | | | 0.117 | 0.073 | | 0.140 | | | 0.136 | 0.067 | |
| 13.2 | | | | | | | | | | 0.123 | | | | | |
| 14 | 0.250 | | 0.018 | 0.019 | 0.034 | | 0.075 | 0.018 | | 0.281 | 0.076 | | 0.145 | | |
| 14.2 | | | | | | | | | | 0.061 | | | | | |
| 15 | 0.112 | | | | 0.500 | | | | | 0.175 | 0.051 | | 0.145 | | |
| 15.2 | | | | | | | | | | 0.079 | | | | | |
| 16 | 0.026 | | | | 0.254 | | | | | 0.044 | 0.415 | | 0.082 | | |
| 16.2 | | | | | | | | | | 0.035 | | | | | |
| 17 | | | | | 0.169 | | | | 0.137 | | 0.305 | | 0.200 | | |
| 17.2 | | | | | | | | | | 0.009 | | | | | |
| 18 | | | | | 0.034 | | | | 0.059 | | 0.102 | | 0.055 | | 0.010 |
| 19 | | | | | 0.008 | | | | 0.304 | | 0.051 | | 0.036 | | 0.098 |
| 20 | | | | | | | | | 0.196 | | | | 0.009 | | 0.069 |
| 21 | | | | | | | | | 0.010 | | | | 0.018 | | 0.069 |
| 22 | | | | | | | | | 0.088 | | | | 0.018 | | 0.118 |
| 23 | | | | | | | | | 0.127 | | | | | | 0.118 |
| 24 | | | | | | | | | 0.069 | | | | 0.009 | | 0.147 |
| 25 | | | | | | | | | 0.010 | | | | | | 0.176 |
| 26 | | | | | | | | | | | | | | | 0.157 |
| 27 | | | | | | | | | | | | | | | 0.039 |
| 28 | | 0.052 | | | | | | | | | | | | | |
| 29 | | 0.172 | | | | | | | | | | | | | |
| 30 | | 0.284 | | | | | | | | | | | | | |
| 31 | | 0.078 | | | | | | | | | | | | | |
| 31.2 | | 0.138 | | | | | | | | | | | | | |
| 32 | | 0.034 | | | | | | | | | | | | | |
| 32.2 | | 0.190 | | | | | | | | | | | | | |
| 33.2 | | 0.034 | | | | | | | | | | | | | |
| 34.2 | | 0.009 | | | | | | | | | | | | | |
| 35.2 | | 0.009 | | | | | | | | | | | | | |
| p value | 0.514 | 0.377 | 0.919 | 0.184 | 0.384 | 0.179 | 0.049 | 0.709 | 0.937 | 0.523 | 0.836 | 0.752 | 0.793 | 0.103 | 0.033 |

however, good results for plucked hair samples were included in other studies (Sánchez et al., 2005; Barrot et al., 2007). Structure software was used to determine the individual and population admixture components depending on the contribution from parental populations. The results are displayed in a bar graph (Figure 1). These analyses show that Mexican admixed populations have a high percentage of Amerindian and European ancestry and a low percentage of African ancestry, ranging from 6.8% to 9.7%.

In order to show easily the tri-hybrid model and clearly understand the individual variation in each ancestral contribution, Figure 2 represents individual admixtures taking into consideration different numbers of clusters ($K = 3$).

The main genetic contribution from ancestral populations to Yanga is Amerindian (48%) and European (44.7%), whereas only 7.3% is of African ancestry. In general the Amerindian ancestry is the major lineage detected in the

south and centre of the Mexican Republic: 56.7% in Campeche, 55.8% in Puebla, and 54.4% in Yucatán.

The populations that have a higher African contribution are the ones from the northwest: Jalisco (9.7%), Nuevo León (8.3%), and Chihuahua (8.2%). These also show a higher European contribution (48.7%, 57.2%, and 58.9%, respectively).

In fact, the distribution pattern of African ancestry is similar to that of the European contribution, although it has much lower values for these same populations. This pattern is reversed when considering the Amerindian influence, i.e. it is higher in the south and lower in the north. The frequency distribution for African ancestry correlates inversely with the Amerindian one ($r = -0.619$; $P = 0.042$) and the latter also inversely with European ancestry ($r = -0.997$; $P = 0.0001$).

The genetic distances (F_{ST}) have been represented in an MDS with a level of stress = 0.197, which is a suitable value

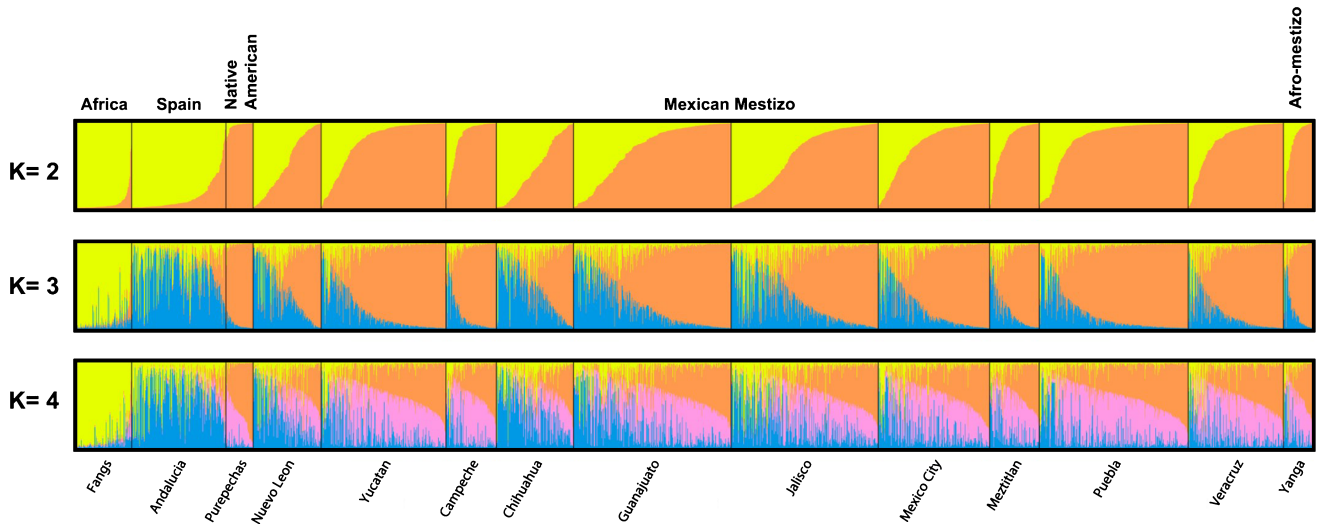


Figure 2. Population structure analysis of 11 mestizo populations considering different numbers of clusters: $K = 2$, $K = 3$, and $K = 4$.

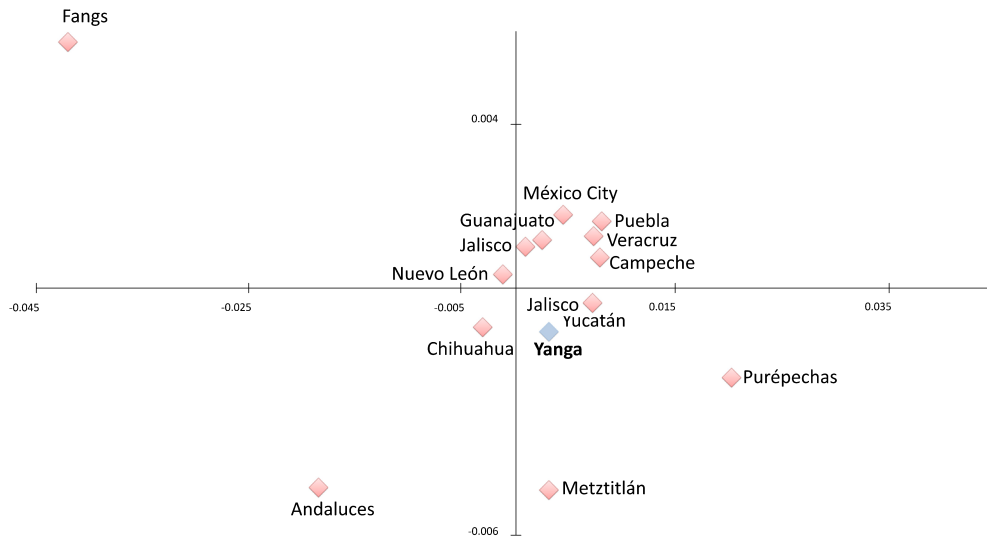


Figure 3. Multidimensional scaling (stress = 0.197) based on F_{ST} distances among the 11 mixed and 3 ancestral populations.

for the 14 populations studied (Sturrock and Rocha, 2000). The graph in Figure 3 shows that the mestizo populations form a homogeneous cluster. The vast majority of these populations are found around the area of European and Amerindian influence and coincide with the results obtained using Structure software (Figure 1). Yanga appears in the display close to the reference Amerindian group, and to a lesser extent to the Europeans. Moreover, the populations in the south and the southeast are closer to the Amerindian reference.

In this context Metztitlán is worthy of special mention as it lies at a considerable distance from the cluster formed by the other admixed populations. In fact, its position indicates that the influence of Amerindian and European ancestors is significant. In general in these latitudes the proportion of Amerindian ancestry in the gene pool of the populations tends to decrease and the European contribution to rise. However, the results show that the Metztitlán population has

a relatively high percentage of Native American ancestry.

In order to determine whether any genetic structure exists among the Mexican admixed populations, AMOVAs based on geographical area criteria were conducted (Table 3). The cumulative variability among groups, in both cases, was not significant ($F_{CT} = 0.0018$, $P = 0.0580$ and $F_{CT} = 0.0018$, $P = 0.0540$).

Discussion

Fifteen autosomal STRs have been used for the genetic characterization of the population. Previous studies demonstrate the robustness of these markers when analysing the phenomenon of admixture (de Assis Poiars et al., 2010; González-Herrera et al., 2010; Kraaijenbrink et al., 2014).

Two models can describe the different contributions from the ancestral groups to the Mexican mestizo populations.

Table 3. Results of AMOVAs applied to different criteria of the geographical groups

| Grouping criteria | Groups | Populations | | Variance | Fixation index | <i>P</i> |
|-------------------|----------------|---|---------------------------------|----------|-------------------|----------|
| Geography I | North | Nuevo León, Chihuahua, Jalisco, Guadalajara | Within populations | 99.72 | $F_{ST} = 0.0028$ | 0.000 |
| | Center | Metztlán, México City, Veracruz, Yanga | Among populations within groups | 0.10 | $F_{SC} = 0.0010$ | 0.000 |
| | South | Campeche, Yucatán, Puebla | Among groups | 0.18 | $F_{CT} = 0.0018$ | 0.058 |
| Geography II | North | Nuevo León, Chihuahua | Within populations | 99.72 | $F_{ST} = 0.0028$ | 0.000 |
| | Central north | Jalisco, Guadalajara | Among populations within groups | 0.10 | $F_{SC} = 0.0010$ | 0.000 |
| | Oriental coast | Veracruz, Yanga | Among groups | 0.18 | $F_{CT} = 0.0018$ | 0.054 |
| | Center | Metztlán, México City, Puebla | | | | |
| | Southeast | Campeche, Yucatán | | | | |

* Significant results ($P < 0.005$).

The first model presupposes that the African contribution should be lowest on the central high plateau and highest on the coast (Serrano, 1993), coinciding with the coastal regions of Veracruz and Acapulco that were collectors of African population. Veracruz was the principal slave harbour in the American continent. Acapulco's importance was based on the fact that it was the starting point and destination for the Manila Galleons (Schurtz et al., 1992), whose stevedores were usually of African origin (Campos, 1999). This hypothesis was based on classical markers which showed that the African contribution varied between 25.6% and 40.5% in Veracruz (Lisker and Babinsky, 1986) and 33.7% in Guerrero (Lisker, 1981). However, it was almost absent in the northern populations (Cerdeña-Flores and Garza-Chapa, 1989). The 7.2% of African contribution detected in Yanga does not fit this model.

The second hypothesis, based on new molecular techniques, describes a model in which there is a north-south gradient between a high frequency of European and African ancestry in the north and a significant Amerindian ancestry presence in the south. This distribution is justified by the presence of African slaves in the North who had escaped from the cotton plantations in the south of the USA (Green et al., 2000) and the preference of the European population to settle in the north (Licea-Cadena et al., 2006). On the other hand, the southeast was more hostile for Africans and Europeans (Menegus, 2006), as evidenced by the frequent revolts against these groups.

Studies based on uniparental markers, such as chromosome Y (xYAP), show an African contribution of only 1% in Guerrero (Bonilla et al., 2005), and similar low frequencies were detected in Costa Grande of Oaxaca (Rangel-Villalobos et al., 2008). Others studies, in this case based on sequencing of the hypervariable I region of the mitochondrial DNA, support this idea, detecting African variants in Chihuahua with values between 4.1% and 5% (Green et al., 2000). Analysis of autosomal markers has shown that the African contribution in Nuevo León (3.2%) was higher than the one obtained using classical markers (Cerdeña-Flores et al., 2002a). Human leucocyte antigen (Human Leukocyte antigen) studies also support the relatively high African gene

presence in the northern Mexican states, reaching a level of 5.02% in Nuevo León (Cerdeña-Flores et al., 2002b). Results of studies based on STRs provide further support for this idea and show a positive correlation between European and African contributions, while confirming an inverse correlation between these two contributions and the Amerindian one.

The interesting question, therefore, is what happened to the African populations to bring about the current distribution? Two complementary possibilities can be proposed, one methodological and one historical. Regarding the first, some authors consider that STRs underestimate the African contribution (Callegari-Jacques et al., 2003). However, this explanation seems unlikely given that analyses performed using 1814 ancestry informative markers (AIMs) agree with our results (Silva-Zolezzi et al., 2009). Another aspect is to consider the origin of the samples. During the 18th century the European and African populations were concentrated in urban areas (Cook and Borah, 1974), meaning that it would be interesting to determine if samples are from rural or urban regions.

The historical contributions are closely related to the dilution of the African genetic component and may be summarized in the following points: (i) the misconception that the founding population of Yanga was exclusively African, since chronicles describe that it was composed of 80 black men and 24 black women, some children and a few indigenous people (Laurencio and Pasquel, 1974); (ii) the high mobility of African people during the 18th century and the large number of Spanish people who settled in the city in 1768 (Cruz-Carretero, 2005); (iii) the introduction of slaves in America ceases after the 18th century (Aguirre-Beltrán, 1989); and (iv) social pressure in favor of admixing between Africans and other colonial groups in order to attain a higher status for their descendants (Barquera and Acuña-Alonzo, 2012).

Despite this model, a certain degree of geographical oscillation in the African contribution can be detected. The results of AMOVAs confirm that no genetic structure exists among mestizo populations, since the differences in their ancestral composition are not of sufficient importance for subdivisions to be created. In this sense, therefore, admixture behaves as a continuous variable.

Identity is a very complex concept and is related both to group membership and the perception of oneself (McNamara, 2012). Although this is a matter far beyond the objectives of this study, a brief comment on the results and their relation to the defence of identity in Yanga is of interest: the community of Yanga is proud of its history and its African roots, giving its members unique identity traits (Pérez Monfort, 2007). The results presented here confirm that identity—individual and collective—goes beyond the biological and genetic reality.

Conclusions

This study confirms, on the one hand, the value of STRs as a tool with which to study the admixture phenomenon in Latin America. In addition, the results support the existence of a tri-hybrid model that varies across Mexico depending on the contribution of the three ancestral populations (Amerindian, European, and African). In brief, it detects the existence of a north–south gradient in the contribution of European and African genetic components, although much less intense in the case of the latter. This gradient coincides inversely with the Amerindian contribution, which presents a maximum value in the south and southeast and a minimum value in the north.

On the other hand, it also confirms that the parameters that explain the distribution of European and indigenous contributions are related to their demographic and historical past, whereas the African contribution reflects the geographical redistribution that took place of the people of African descent, together with an important phenomenon of genetic dilution. In this context, Yanga would represent an interesting example as a collection centre of African population—given its uniqueness as the first free palenque of America—and a reference for Afro-American community identity despite its relatively low African genetic imprint.

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