

1 **Classification:**

2 **BIOLOGICAL SCIENCES: Genetics**

3

4 **Title: Origins, admixture dynamics and homogenization of the African gene pool**
5 **in the Americas**

6

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73 **Keywords:**

74 African diaspora, Transatlantic Slave Trade, admixture dynamics, *mestizaje*

75

76 **Abstract**

77 The Transatlantic Slave Trade transported more than 9 million Africans to the Americas
78 between the early 16th and the mid-19th centuries. We performed genome-wide
79 analysis of 6,267 individuals from 22 populations and observed an enrichment in West-
80 African ancestry in northern latitudes of the Americas, whereas South/East African
81 ancestry is more prevalent in southern South-America. This pattern results from distinct
82 geographic and geopolitical factors leading to population differentiation. However, we
83 observed a decrease of 68% in the African gene pool between-population diversity
84 within the Americas when compared to the regions of origin from Africa, underscoring
85 the importance of historical factors favoring admixture between individuals with
86 different African origins in the New World. This is consistent with the excess of West-
87 Central Africa ancestry (the most prevalent in the Americas) in the US and Southeast-
88 Brazil, respect to historical-demography expectations. Also, in most of the Americas,
89 admixture intensification occurred between 1,750 and 1,850, which correlates strongly
90 with the peak of arrivals from Africa. This study contributes with a population genetics
91 perspective to the ongoing social, cultural and political debate regarding ancestry, race,
92 and admixture in the Americas.

93

94 **Significance Statement**

95 Differently from most genetic studies, that have estimated the overall African ancestry
96 in the Americas, we perform a finer geographic analysis and infer how different African
97 groups contributed to North-, South-American and Caribbean populations, in the
98 context of geographic and geopolitical factors. We also perform a formal comparison of
99 information from demographic history records of the Transatlantic Slave Trade with
100 inferences based on genomic diversity of current populations. Our approach reveals the

101 distinct regional African ancestry roots of different populations from North-, South-
102 America and the Caribe and other important aspects of the historical process of
103 *mestizaje* and its dynamics in the American continent.

104

105 **Introduction**

106 The Transatlantic Slave Trade was an international enterprise involving Brazilian,
107 British, Danish, Dutch, French, German, Portuguese, Spanish and Swedish traders.
108 They brought over 9 million Africans to the Americas between the early 16th and the
109 mid-19th centuries. African regions of origin included far away locations as Senegambia
110 is from Tanzania. Destiny ports in the Americas were also distant as Newport in New
111 England is from Buenos Aires (1, 2). The Transatlantic Slave Trade shaped the genetic
112 structure of American continent populations (3–11). While most genetic studies have
113 estimated the overall African ancestry in the Americas, a finer geographic analysis is
114 needed to infer how different African groups contributed to North-, Central-, South-
115 American and Caribbean populations. The geopolitical factors that permeated the
116 African Diaspora have been seldom discussed at a continental scale, despite its potential
117 influence on the genetic structure of populations. Furthermore, a formal comparison of
118 information from demographic history records of the Transatlantic Slave Trade with
119 inferences based on genomic diversity of current populations has not been performed.

120

121 Here we perform a joint analysis of genetic data and historical records of the
122 Transatlantic Slave Trade to address the following questions: (i) Is there a
123 correspondence between the geographic origin of specific African populations of the
124 Diaspora and specific destinations in the Americas?; (ii) Was admixture dynamics in the
125 Americas associated with the dynamics of arrivals of African slaves?; (iii) Considering

126 the geographic extension and the massive demographic magnitude of the African
127 Diaspora, as well as the level of *between-populations* genetic differentiation in the
128 African regions of origin of slaves, did the Transatlantic Slave Trade lead to a higher,
129 similar or lower level of *between-population* differentiation of the African gene pool in
130 the Americas?

131

132 **Results and Discussion**

133 We combined genome-wide data from 25 populations: 9 admixed of the Americas, 11
134 Africans, 2 Europeans and 3 Native Americans (Fig. 1, *SI Appendix*, Table S1 and
135 section 1.1) and created a dataset of 6,267 unrelated individuals with >10% of African
136 ancestry (*SI Appendix*, sections 1 and 2). Using ADMIXTURE (12), we identified two
137 continental (European and Native American) and four African-specific ancestry
138 clusters, named based on their association with geographic regions (*SI Appendix*, Table
139 S1, represented by different colors in Fig. 1): (i) West-Central African (blue), (ii)
140 Western African (purple) and, (iii) South/East African (yellow), which are prevalent in
141 the Americas, as well as (iv) Northern Ugandan (NU, cyan), which accounts for a very
142 low proportion of African ancestry in the Americas. Hereafter, while in African
143 individuals, the proportion of ADMIXTURE ancestry clusters are relative to their whole
144 genome ancestry (Fig. 1A, *SI Appendix*, Table S1), in American continent individuals,
145 these proportions are relative to the sum of the four African ancestry clusters (Fig 1A).
146 We also estimated haplotype-based population admixture proportions (13, 14) in
147 populations of the Americas, that in Fig. 2A and B, and *SI Appendix*, Table S3, are
148 relative to the total contribution of African populations.

149

150 *Ancestry correspondence between African and admixed American continent*
151 *populations, and the influence of geography and geopolitics*

152 The West-Central Africa-associated ancestry cluster is the most prevalent African
153 cluster in the Americas, including African-Caribbean from Barbados (72% of African
154 ancestry), Northeastern Brazilians (57%), Afro-Peruvians (56%) and US African-
155 Americans (54-55%) (blue in Fig. 1, *SI Appendix*, Table S1 and section 2.1). Moreover,
156 haplotype-based analysis(13, 14) reveals a higher contribution from Yoruba-like and
157 Esan-like populations (from Nigeria, mean: 38%) than from Kwa/Gur-like populations
158 (from Ghana, mean: 18%) (Fig. 2A and B, *SI Appendix*, Table S3).

159 The Western Africa-associated ancestry cluster has its highest proportions in Puerto
160 Ricans (38% of African ancestry), Colombians (27%) and US African-Americans (19-
161 20%, purple in Fig. 1, *SI Appendix*, Table S1), while Brazilians have the lowest
162 proportion (<9%), limited to a Mandinka-like (Gambia) contribution and with no
163 Mende-like (Sierra Leone) contribution (Fig. 2A and B, *SI Appendix*, Table S3).

164 The South/East Africa-associated ancestry cluster, in contrast, shows its highest
165 proportion in South and Southeast Brazil (44% and 54% of total African ancestry,
166 respectively) (yellow in Fig. 1 and *SI Appendix*, Table S1). Haplotype-based methods
167 (13, 14) identified two different sources of gene flow associated with the South/Eastern
168 Africa ancestry cluster: one from Mbukushu-like populations (Botswana, Western
169 Bantu speakers from Southern Africa, 20-24% to South/Southeast Brazil) and one from
170 Luhya-like populations (Kenya, Eastern Bantu speakers from Eastern Africa, 17-20% to
171 South/Southeast Brazil, Fig. 2A and B, *SI Appendix*, Table S3). Western- and Eastern-
172 Bantu speakers historically correspond to the two streams of the Bantu migrations in the
173 last 4000-2500 years (10, 15, 16).

174 This emerging portrait of the African ancestry in the Americas suggests an influence of
175 geography and geopolitics. Geographical factors include: (i) the latitudinal proximity
176 between Western Africa and Caribe-Central/North America, as well as between
177 South/East Africa and Southern Brazil, (ii) the winds and ocean currents, that shaped
178 two navigation systems: the North-Atlantic, with voyages mostly to North America, and
179 the South-Atlantic, with voyages predominantly to Brazil (17). Indeed, West Central
180 Africa- and West Africa-associated ancestry clusters are more commonly observed in
181 northern latitudes, while the South/East Africa-associated ancestry cluster is more
182 evident in southern latitudes.

183 Differently, the Portugal possessions in the Americas (Brazil) and its influence in South
184 and East African coasts (current Angola and Mozambique)(18) exemplify the
185 geopolitical factors that affected, in particular, the distribution of the South/East Africa-
186 associated ancestry cluster. While the Portuguese Crown had earlier privileged relations
187 with the kingdoms of Benin in nowadays Nigeria, it later extended its influence to
188 Bantu-speaking areas such as Congo/Angola and Mozambique (19). Indeed,
189 Portuguese-Brazilian slave trade routes departed from Luanda and Cabinda (Angola)
190 and from Zanzibar (Tanzania) and Inhambane (Mozambique) during 18th and 19th
191 centuries (1). The abolition of slavery by the British in 1807, who controlled the North
192 Atlantic route, also led Portuguese traders to prefer routes in the South Atlantic(20).
193 Therefore, geography (inter-continental distances and climatic factors affecting
194 transatlantic navigation) and geopolitics (European colonial influences and possessions)
195 influenced the geographic and linguistic diversity of African emigrants as well as
196 favored the regional differentiation of African ancestry in the Americas.

197

198 ***The dynamics of African admixture in the Americas accompanied the dynamics of***
199 ***arrivals of African slaves***

200 Remarkably, linkage-disequilibrium-based inference (14) shows that all the studied
201 admixed populations of the Americas exhibit the signature of an intensification of
202 admixture in the interval from 1750 to 1850 (Fig. 2C, *SI Appendix*, section 3), revealing
203 a continental trend. This trend is consistent with results by Baharian et al. (3), focused
204 in the US. Importantly, this time interval matches or is immediately subsequent to
205 regional peaks of number of slaves arriving from Africa to US, Barbados, Puerto Rico
206 and Brazil (*SI Appendix*, Fig. S4). Thus, in most of the Americas, the arrival of the
207 largest contingent of Africans between 1700 and 1850 (*SI Appendix*, Figs. S4) was
208 almost synchronic with intensive admixture, a process that was also characterized by
209 positive ancestry-based assortative mating (6).

210 ***The African gene pool is more homogenous between-populations in the Americas***
211 ***than in Africa***

212 Figure 1 suggests that African ancestry clusters are more homogeneously distributed
213 between admixed American continent populations than between the African populations
214 that contributed to the Transatlantic Slave Trade. Considering only the African gene
215 pool, the largest differentiation, measured by the *African-Specific Genetic Distance*
216 (*ASGD*, Fig. 3 and *SI Appendix*, section 4 and Figs. S5), is observed between African
217 populations (mean: 0.057, mean excluding populations with marginal contribution to
218 the Americas [Nilotics and Sandawe: 0.53]), followed by differentiation between
219 African vs. America's populations (mean: 0.043) and between populations of the
220 Americas (mean: 0.018, 32% of the *ASGD* between African populations) (Wilcoxon
221 test, $p < 10^{-6}$ for the three pairwise comparisons, Fig. 3).

222 To better understand this pattern of *between-populations* homogenization of the African
223 gene pool in the Americas, and for the geographic regions represented in our dataset for
224 which there are historical demography records of origin and destination of Africans(1),
225 we compared: (i) proportions of West-Central Africa-, Western Africa- and South-East
226 Africa-associated ancestry clusters (Fig. 1) with (ii) expected proportion of these
227 ancestry clusters, estimated from the proportions of arrivals from different locations
228 (Fig. 4 ,*SI Appendix*, Table S5, S6 and section 5). Overall, for New World populations
229 the proportions of South-Eastern African and Western African ancestry clusters are
230 highly correlated with the expected ancestry based on the numbers of arrivals to
231 Americas ports and departures from African ports (Spearman rho= 0.89, p = 0.02).
232 However, for the West-Central African ancestry cluster the correlation does not reach
233 significance (Fig. 4). For the entire American continent, we observe an excess of the
234 observed West-Central Africa ancestry clusters (47.7% observed vs. 40% expected,
235 being this a conservative estimation of the difference, see *SI Appendix*, section 5, p = <
236 2.2e-16), mainly determined by Southeastern Brazil and the US populations. The
237 poorest concordance between observed and expected ancestries is observed in
238 Southeastern Brazil, that presents more of the West-Central African ancestry cluster
239 (37%) than expected (20%) (p = < 2.2e-16) and complementarily, less of the South/East
240 African ancestry cluster than expected based on arrivals (55% observed vs. 76%
241 expected (p < 2.2 x 10⁻¹⁶). The US population also shows an excess of the West-Central
242 African ancestry cluster (54.7% observed vs. 43.1% expected, p < 3.33⁻¹⁶), compensated
243 by a deficit of the Western African ancestry cluster (19.1% observed vs. 27.7%
244 expected, p < 3.33⁻¹⁶). Therefore, the *between-population* homogenization of the African
245 gene pool in the Americas is partly explained by the excess of the West-Central Africa
246 ancestry cluster in Southeast Brazil and in the US (Fig. 4). The higher between-

247 population homogeneity of the African gene pool in the Americas contributes to a more
248 statistical power of genetic association studies involving individuals with African
249 ancestry from different populations of the Americas.

250 In conclusion, genetic data trace the African genetic roots of admixed individuals of the
251 Americas to a broad geographic extension (from Western Africa to East Africa),
252 associated with a high linguistic diversity (Niger Kordofanian non-Bantu and Western-
253 and Eastern-Bantu language speakers). Considering the level of *between-populations*
254 genetic differentiation in the African regions of origin of slaves, historical facts that
255 homogenized the *between-populations* component of genetic diversity have
256 predominated over facts that tend to maintain or increase it. This latter group of facts
257 includes geographic (i.e. inter-continental distances and maritime winds/currents) and
258 geopolitical factors (i.e. specific European colonial influences and possessions and the
259 abolition of the slavery by British in 1807), that shaped an association of Western
260 African ancestry with northern latitudes and South/East African ancestry with southern
261 latitudes. Contrastingly, the following facts have contributed to gene flow between
262 individuals with different African ancestries and thus, to the *between-populations*
263 homogenization of the African gene pool in the Americas: (i) despite their specific
264 European origins, traders/vessels transported slaves, frequently illegally, to different
265 American continent ports (1, 18, 21); (ii) *forced amalgamation*, which is the preference
266 of slave owners for slaves from different geographic and linguistic origins, so that they
267 could not understand each other, and thus, reducing the risk of riots (22); and (iii) the
268 role of islands such as Jamaica and Barbados, that centralized parts of arrivals of
269 African slaves, and re-distributed them to different parts of the Americas (2). Moreover,
270 the *between-population* homogenization of the African gene pool in the Americas is
271 partly explained by the excess of the West-Central Africa ancestry cluster (the most

272 prevalent in the Americas) in US and Southeast Brazil respect to demographic
273 expectations, which suggest a spread of this ancestry in the American continent.
274 Interestingly, in most of the Americas, the arrival of the largest contingent of Africans
275 between 1,700 and 1,850 was almost synchronic with the intensification of admixture,
276 which implies that this time interval was critical to shape the structure of the African
277 gene pool in the New World. This study contributes with a population genetics
278 perspective to the ongoing social, cultural and political debate regarding ancestry, race,
279 and admixture in the Americas (23, 24).

280

281 **Methods**

282 We analyzed a dataset including 6,267 unrelated individuals with more than 10% of
283 African ancestry for 533,242 SNPs (*SI Appendix*, Table S1). We inferred population
284 structure and admixture using ADMIXTURE (12) and Principal Component Analysis
285 (25) for unlinked SNPs and ChromoPainter and fineSTRUCTURE (13) for haplotype-
286 based analyses. Admixture dynamics was inferred using GLOBETROTTER (14).
287 Demographic information of embarked and disembarked African slaves was obtained the
288 African Voyages database (<http://www.slavevoyages.org/voyage/search>). Genetic
289 differentiation between populations considering only the African gene pool was estimated
290 using the *African-ancestry genetic distance* (AAGD, *SI Appendix*, section 4.1).
291 Flowcharts and masterscripts of the analyses are available in the EPIGEN Scientific
292 Workflow (26) web (<http://ldgh.com.br/scientificworkflow>). Details of Methods are in
293 the *SI Appendix*.

294

295 Data Availability: EPIGEN-Brazil data are deposited in the European Nucleotide
296 Archive (PRJEB9080 (ERP010139), accession no. EGAS00001001245, under EPIGEN

297 Committee Controlled Access mode. The Nilotics and Kwa/Gur datasets are deposited
298 in dbGaP at phs001705.v1.p1 and phs000838.v1.p1, respectively. The Botswana and
299 Tanzania datasets from Sarah Tishkoff Lab are available at dbGaP accession number
300 phs001396.v1.p1 and SRA BioProject PRJNA392485.

301

302 **Acknowledgments**

303 We thank Sergio D Pena, Marcia Beltrame, Rosangela Loschi, Eduardo F Paiva,
304 Fabrício Santos, Renan Souza, Claudio Struchiner, Ricardo Santos and Garrett
305 Hellenthal for advice, discussions and criticisms. **Funding:** The EPIGEN-Brazil
306 Initiative is funded by the Brazilian Ministry of Health (Department of Science and
307 Technology from the Secretaria de Ciência, Tecnologia e Insumos Estratégicos) through
308 Financiadora de Estudos e Projetos. The EPIGEN-Brazil investigators received funding
309 from the Brazilian Ministry of Education (CAPES Agency). ETS, MHG, VB, TPL and
310 MFLC were supported by Brazilian National Research Council (CNPq), Minas Gerais
311 Research Agency (FAPEMIG) and Pró-Reitoria de Pesquisa da Universidade Federal de
312 Minas Gerais. MHG performed part of this study as CAPES-PDSE fellow, VB was a
313 CAPES-PEC-PG fellow. MLS was a TWAS-CNPq PhD fellow. Tishkoff laboratory is
314 funded by the National Institutes of Health (1R01DK104339-0 and 1R01GM113657-
315 01). EMBLEM is funded by the Intramural Research Program of the Division of Cancer
316 Epidemiology and Genetics, National Cancer Institute (NCI) (HHSN261201100063C
317 and HHSN261201100007I) and, in part, by the Intramural Research Program, National
318 Institute of Allergy and Infectious Diseases (SJR), National Institutes of Health,
319 Department of Health and Human Services. Bioinformatics support was provided by the
320 Sagarana HPC cluster, CPAD-ICB-UFMG, Brazil. **Author contributions:** The project
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323 analyzed genetic data. RL and RZ performed laboratory experiments. ETS supervised
324 bioinformatic and statistical analyses. MD, RHG, HG, ACP, MFLC, MLB, BLH, SMM,
325 SJC, SAT and MY contributed with data. MHG, VB, AWB, MY, SAT contributed to
326 data interpretation. MHG, VB and ETS wrote the manuscript. All authors read the
327 manuscripts and contributed with suggestions. **Competing interests:** The authors
328 declare no competing interests.

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330 **References**

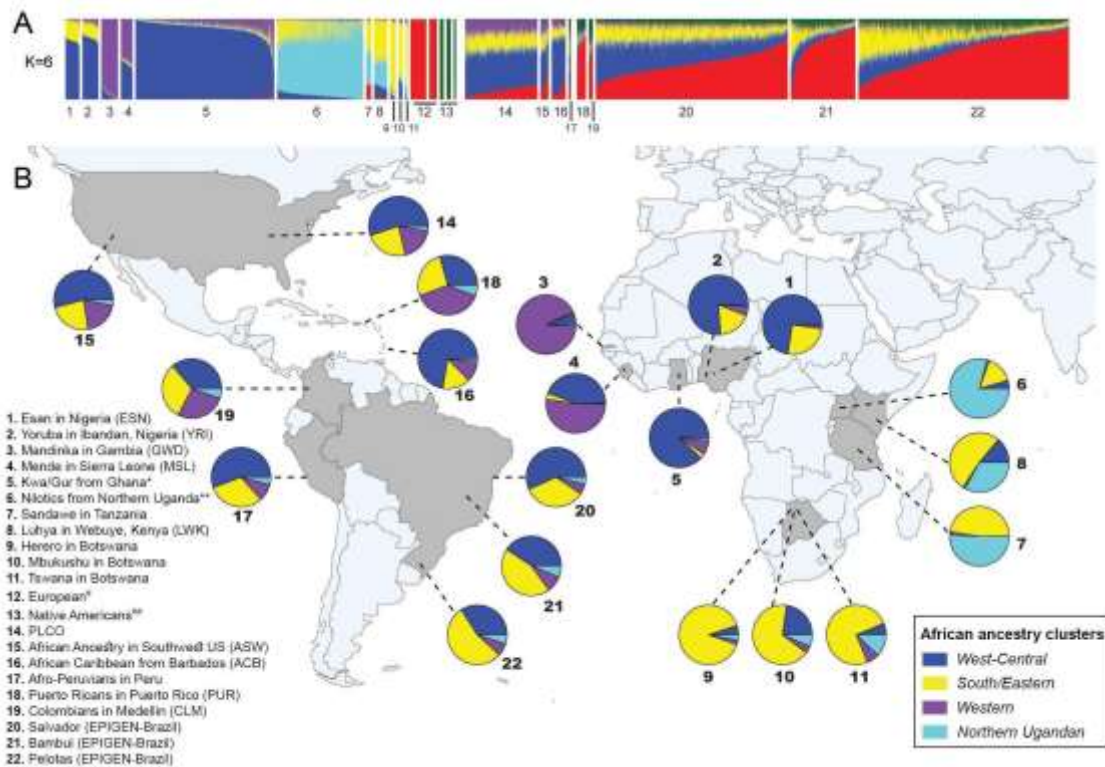
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393

394 **Figures and Legends:**



395

396 **Fig. 1. Ancestry analysis of African and admixed populations of the Americas**

397 **inferred using ADMIXTURE (K=6).** (A) Vertical bar plot showing the total African,

398 European and Native American proportions of the ancestry clusters (*SI Appendix*, Fig.

399 S1 and section 2.6.1.). *The Kwa/Gur dataset includes approximately 35 ethno-

400 linguistic groups, predominantly from the Kwa and Gur Niger-Congo linguistic

401 group(27). **The Nilotics dataset includes predominantly three ethno-linguistic groups

402 in Northern Uganda (Langi, Acholi and Lugbara) from the Nilotic linguistic group²⁷;

403 #the Europeans are: Iberian Population in Spain (IBS) and Utah residents with Northern

404 and Western European ancestry (CEU), in this order in the ADMIXTURE bar plot;

405 ##the Native Americans are: Shima, Ashaninka and Aymara, respectively from Borda

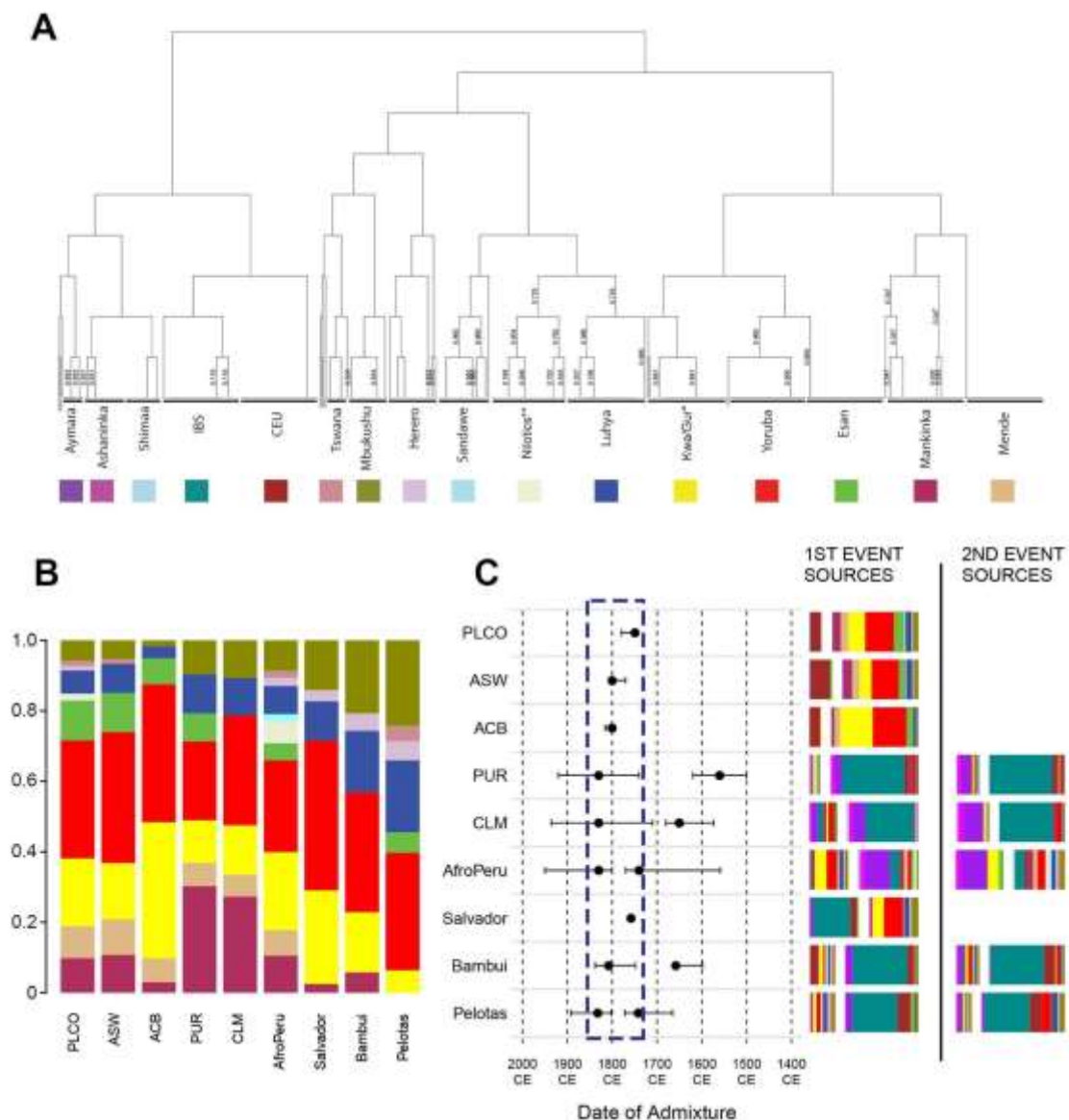
406 et al. (in preparation); the PLCO (Prostate, Lung, Colorectal and Ovarian Cancer

407 Screening) data is comprised of African-Americans from East USA. (B) Percentages of

408 subcontinental African ancestry clusters. For admixed populations of the American

409 continent these percentages are relative to the total African ancestry (i.e. the sum of the
410 four African associated clusters: West-Central, Western, Southern/Eastern, Northern
411 Ugandan).

412



413

414 **Fig. 2. Haplotype-based clustering of parental individuals and admixture**

415 **inferences for admixed American continent populations. (A) fineSTRUCTURE tree**

416 **of parental individuals. *The Kwa/Gur dataset includes approximately 35 ethno-**

417 **linguistic groups, predominantly from the Kwa and Gur linguistic group²⁷. **The**

418 **Nilotics dataset includes predominantly three ethno-linguistic groups from Northern**

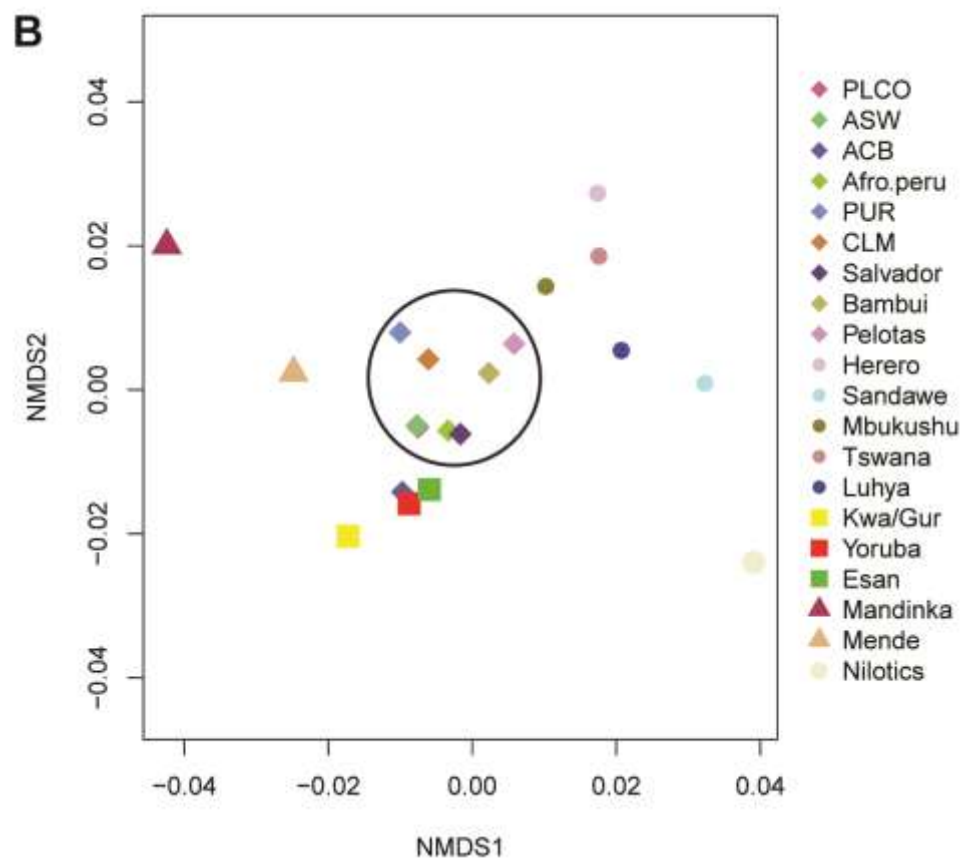
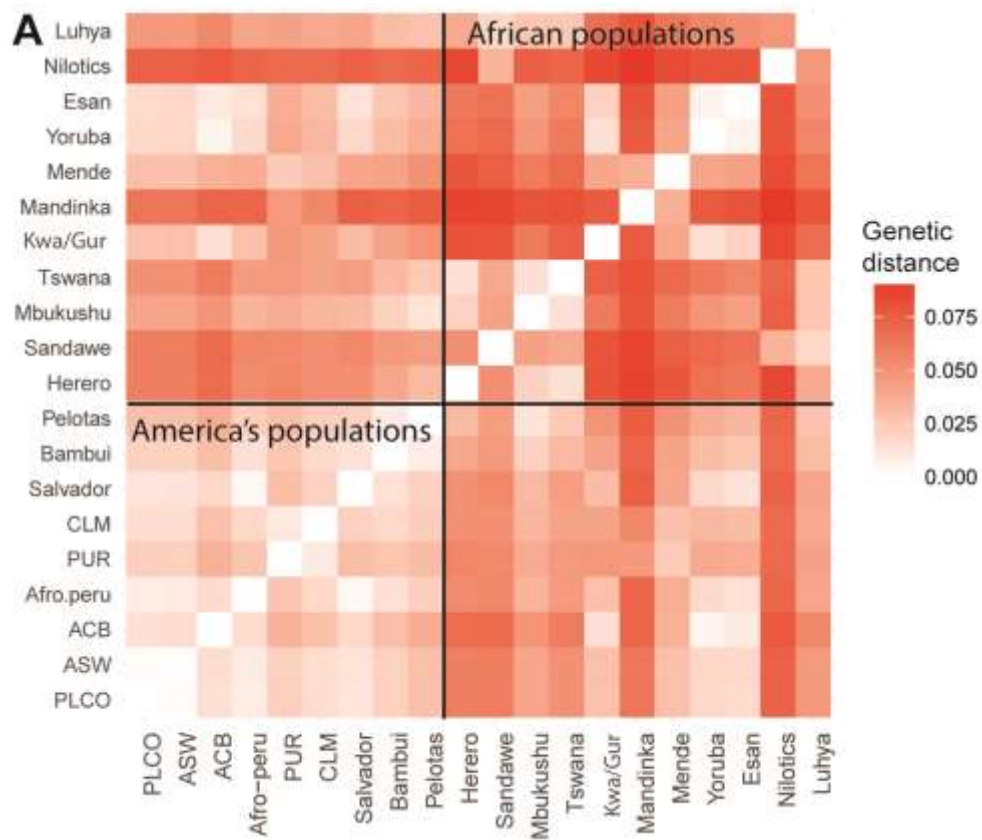
419 **Uganda (Langi, Acholi and Lugbara) of the Nilotic linguistic group²⁷. (B)**

420 **Subcontinental contributions relative to the total African ancestry in admixed**

421 **populations inferred by the MIXTURE MODEL. (C) GLOBETROTTER inference of**

422 admixture events for each admixed population. Inferred date(s) and 95% confidence
423 intervals are represented by dots and horizontal lines in the graph, respectively. Dashed
424 rectangle in the admixture dates plots highlights the most dynamic period for admixture.
425 Beside the dating graph, we represented the inferred admixing sources (bars) for one
426 and two events. Bar size represents the genetic contribution of the source. Each color
427 corresponds to the contribution of each parental population. CEU=Utah Residents
428 (CEPH) with Northern and Western Ancestry-USA, IBS=Iberian population in Spain,
429 CLM=Colombians from Medellin, PUR=Puerto Ricans from Puerto Rico,
430 ACB=African Caribbeans in Barbados, ASW= African Americans in Southwest USA,
431 PLCO= African Americans from East USA.
432

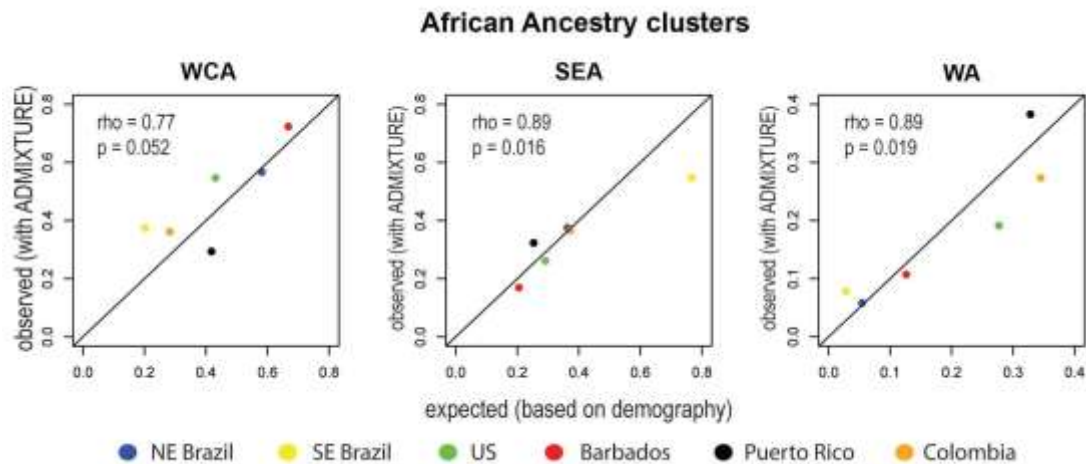
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434

435 **Fig. 3. Pairwise genetic distances of the African gene pool between populations of**
436 **the American continent and Africa.** (A) Heatmap Matrix and (B) Multidimensional
437 scaling of the African gene pool genetic distances. We used solid squares, triangles and
438 circles to represent populations associate with WCA: West-Central Africa, SEA:
439 South/East Africa and WA: Western Africa ancestry clusters. The admixed American
440 continent populations are highlighted with the circle with the exception of the ACB
441 population which clustered closer to the WCA ancestry-associated populations.
442 CLM=Colombians from Medellin, PUR=Puerto Ricans from Puerto Rico,
443 ACB=African Caribbeans in Barbados, ASW= Americans of African ancestry in South
444 western USA, PLCO= African-Americans from Eastern USA.
445

446



447

448 **Fig. 4. Observed and expected proportions of genomic African ancestry clusters in**
449 **the Americas.** We compared (i) the observed proportions of genomic African ancestry
450 clusters (inferred using ADMIXTURE [Alexander et al. 2009]) in the vertical axis, with
451 (ii) expected proportions of genomic African ancestry clusters, estimated based on
452 demographic historical records from the African Voyages Database¹, in the horizontal
453 axis (see *SI Appendix* and Table S3 for details). rho: Spearman's coefficients of
454 correlation, p: significances. The significance was evaluated using randomization tests
455 of 10,000 replications. WCA: West-Central Africa, SEA: South/East Africa, WA:
456 Western Africa.

457