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Pleistocene North African genomes link Near Eastern and sub-Saharan African human populations

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North Africa is a key region for understanding human history, but the genetic history of its people is largely unknown. We present genomic data from seven 15,000-year-old modern humans from Morocco, attributed to the Iberomaurusian culture. We find a genetic affinity with early Holocene Near Easterners, best represented by Levantine Natufians, suggesting a pre-agricultural connection between Africa and the Near East. We do not find evidence for gene flow from Paleolithic Europeans into Late Pleistocene North Africans. The Taforalt individuals derive one third of their ancestry from sub-Saharan Africans, best approximated by a mixture of genetic components preserved in present-day West and East Africans. Thus, we provide direct evidence for genetic interactions between modern humans across Africa and Eurasia in the Pleistocene.

The Sahara poses an eco-geographic barrier for human migration between North and sub-Saharan Africa, aside of intermittent greening periods (1). Sub-Saharan Africa is home to the most deeply diverged genetic lineages among present-day humans (2) and the general view is that all Eurasians mostly descend from a single group of humans that dispersed outside of sub-Saharan Africa around 50-100 thousand years before present (yBP) (3). This group likely represented only a small fraction of the genetic diversity within Africa, most closely related to a Holocene East African group (4). Interestingly, present-day North Africans share a majority of their ancestry with present-day Near Easterners, but not with sub-Saharan Africans (5). Thus, from a genetic perspective, present-day North Africa is largely a part of Eurasia. However, the temporal depth of this genetic connection between the Near East and North Africa is poorly understood and has only been indirectly estimated from present-day mitochondrial DNA variation (6, 7).

Due to challenging conditions for DNA preservation relatively few ancient genomes have been recovered from Africa. Genome-wide data from 23 individuals have been reported from South and East Africa, with the oldest dating back to 8100 yBP (4, 8, 9). In North Africa, a genomic study of Egyptian mummies from the first millennium BCE showed that

the genetic connection between the Near East and North Africa was established by that time (5). However, the genetic affinity of North African populations at a greater time depth has remained unknown.

We present genome-wide data from seven individuals from Grotte des Pigeons near Taforalt in eastern Morocco (10), which were directly dated between 15,100 and 13,900 calibrated years before present (cal. yBP) (table S1). They provide a critical reference point to understand the deep genetic history of North Africa and the broader Middle East (Fig. 1). The Taforalt individuals are associated with the Later Stone Age (LSA) Iberomaurusian culture, whose origin is debated. They may have descended either directly from the manufacturers of the preceding Middle Stone Age (MSA) technologies (Aterian or local West African bladelet technologies) or from an exogenous population with ties to the Upper Paleolithic techno-complexes of the Near East or southern Europe (10, 11).

For nine Taforalt individuals (table S2) we created double-indexed single-stranded DNA libraries (12) for next generation sequencing from DNA isolated from petrous bones. We then used in-solution capture probes (13) to enrich libraries for the whole mitochondrial genome and ~1240k single nucleotide polymorphisms (SNPs) in the nuclear genome (14).

The DNA fragments obtained from seven individuals, six genetic males and one female, had post-mortem degradation characteristics typical of ancient DNA (tables S3 to S5 and fig. S6). We reconstructed the mitochondrial genomes of all seven individuals (102-1,701X coverage, unmerged libraries, table S4), with low level of modern human contamination (1-8%; table S4). For the nuclear data analysis, which is more susceptible to contamination than mitochondrial data, we analyzed five individuals, four males and one female, based on coverage (table S3, merged libraries) and negligible modern human contamination for males (1.7-2.5%; table S5). For each individual, we randomly chose a single base per site as a haploid genotype. We intersected our new data with a panel of worldwide present-day populations, genotyped on the Affymetrix Human Origins (HO) array for 600k markers, as well as ancient genomic data covering Europe, the Near East and sub-Saharan Africa (4, 8, 15-17). The final data set includes 593,124 intersecting autosomal SNPs with 183,041-544,232 SNP positions covered for each of the five individuals (table S3). For group-based analyses involving other ancient individuals, we adopted the population labels from the original studies (4, 16). We found an overall high genetic relatedness between the Taforalt individuals, suggesting a strong population bottleneck (fig. S26).

We analyzed the genetic affinities of the Taforalt individuals by performing principal component analysis (PCA) and model-based clustering of worldwide data (Fig. 2). When projected onto the top PCs of African and West Eurasian populations, the Taforalt individuals form a distinct cluster in an intermediate position between present-day North Africans (e.g., Amazighes (Berbers), Mozabite and Saharawi) and East Africans (e.g., Afar, Oromo and Somali) (Fig. 2A). Consistently, we find that all males with sufficient nuclear DNA preservation carry Y haplogroup E1b1b1a1 (M-78; table S16). This haplogroup occurs most frequently in present-day North and East African populations (18). The closely related E1b1b1b (M-123) haplogroup has been reported for Epipaleolithic Natufians and Pre-Pottery Neolithic Levantines (“Levant_N”) (16). Unsupervised genetic clustering also suggests a connection of Taforalt to the Near East. The three major components that comprise the Taforalt genomes are maximized in early Holocene Levantines, East African hunter-gatherer Hadza from north-central Tanzania, and West Africans (K = 10; Fig. 2B). In contrast, present-day North Africans have smaller sub-Saharan African components with minimal Hadza-related contribution (Fig. 2B).

We calculated outgroup- f_3 statistics of the form $f_3(\text{Mbuti}; \text{Taforalt}, \text{Test})$ across worldwide ancient and present-day test populations. Consistent with previous analyses, we find that ancient Near Eastern populations, especially Epipaleolithic Natufians and early Neolithic Levantines, show the highest outgroup- f_3 values with Taforalt (Fig. 3A). This is confirmed

by f_4 symmetry statistics of the form $f_4(\text{Chimpanzee}, \text{Taforalt}; \text{NE}_1, \text{NE}_2)$ that measure a relative affinity of a pair of Near Eastern groups to Taforalt. A positive value indicates that NE_2 is closer to Taforalt than NE_1 is. We consistently find positive f_4 values when NE_2 are Natufian/Levant_N and NE_1 are other populations ($Z = 2.2$ -11.0 standard error (SE); table S6). Congruent to the outgroup- f_3 results, Natufian shows higher affinity to Taforalt than does Levant_N ($Z = 2.2$ SE, table S6). This indicates that the early Holocene Levantine populations, overlapping with or postdating our Taforalt individuals by up to 6,000 years (16), are most closely related to Taforalt among Near Eastern populations. Next, we tested if the Taforalt individuals have sub-Saharan African ancestry by calculating $f_4(\text{Chimpanzee}, \text{Test}; \text{Natufian}, \text{Taforalt})$. We observe significant positive f_4 values for all sub-Saharan African and significant negative values for all Eurasian populations, supporting a substantial contribution from sub-Saharan Africa (Fig. 3B). West Africans, such as Mende and Yoruba most strongly pull out the sub-Saharan African ancestry in Taforalt (Fig. 3B and figs. S15 and S16).

We investigated if two first-hand proxies, Natufians and West Africans, are sufficient to explain the Taforalt gene pool or whether a more complex admixture model is required. We thus tested if Natufians could be a sufficient proxy for the Eurasian ancestry in Taforalt without explicit modeling of its African ancestry (fig. S18). This is inspired by proposed archaeological connections between the Iberomaurusian and Upper Paleolithic cultures in southern Europe, either via the Strait of Gibraltar (19) or Sicily (20). If this connection is true, both the Upper Paleolithic European and Natufian ancestries will be required to explain the Taforalt gene pool. For our admixture modeling with *qpAdm* (16), we chose outgroups that can distinguish sub-Saharan African, Natufian and Paleolithic European ancestries but are blind to differences between sub-Saharan African lineages (11). A two-way admixture model, comprising Natufian and a sub-Saharan African population, does not significantly deviate from our data ($\chi^2 p \geq 0.128$) with 63.5% Natufian and 36.5% sub-Saharan African ancestry on average (table S8). Adding Paleolithic European lineages as a third source only marginally increased the model fit ($\chi^2 p = 0.019$ to 0.128; table S9). Consistently, using *qpGraph* (21) we find that a mixture of Natufian and Yoruba reasonably fits the Taforalt gene pool ($|Z| \leq 3.7$; fig. S19 and table S10). Adding gene flow from Paleolithic Europeans does not improve the model fit and provides an ancestry contribution estimate of 0% (fig. S19). We thus find no evidence of gene flow from Paleolithic Europeans into Taforalt within the resolution of our data.

We further characterized the sub-Saharan African-related ancestry in the Taforalt individuals using f_4 statistics in the form $f_4(\text{Chimpanzee}, \text{African}; \text{Yoruba/Mende}, \text{Natufian})$. We

find that Yoruba/Mende and Natufians are symmetrically related to two deeply divergent outgroups, a 2000 yBP ancient South African (“aSouthAfrica”) and Mbuti Pygmy, respectively ($|Z| \leq 1.564$ SE; table S11). Since f_4 statistics are linear under admixture, we expect Taforalt not to be any closer to these outgroups than Yoruba or Natufians if the two-way admixture model is correct. However, we find instead that Taforalt is significantly closer to both outgroups (“aSouthAfrica” and “Mbuti”) than any combination of Yoruba and Natufians ($Z \geq 2.728$ SE; Fig. 4). A similar pattern is observed for the East African outgroups Dinka, Mota and Hadza (table S11 and fig. S20). These results can only be explained by Taforalt harboring an ancestry that contains additional affinity with South, East and Central African outgroups. None of the present-day or ancient Holocene African groups serve as a good proxy for this unknown ancestry, because adding them as the third source is still insufficient to match the model to the Taforalt gene pool (table S12 and fig. S21). However, we can exclude any branch in human genetic diversity more basal than the deepest known one represented by aSouthAfrica (4) as the source of this signal: it would result in a negative affinity to aSouthAfrica, not a positive one as we find (Fig. 4). Both an unknown archaic hominin and the recently proposed deep West African lineage (4) belong to this category and therefore cannot explain the Taforalt gene pool.

Mitochondrial consensus sequences of the Taforalt individuals belong to the U6a ($n = 6$) and M1b ($n = 1$) haplogroups (15), which are mostly confined to present-day populations in North and East Africa (7). U6 and M1 have been proposed as markers for autochthonous Maghreb ancestry, which might have been originally introduced into this region by a back-to-Africa migration from West Asia (6, 7). The occurrence of both haplogroups in the Taforalt individuals proves their pre-Holocene presence in the Maghreb. We analyzed the seven ancient Taforalt in combination with four Upper Paleolithic European mtDNA genomes (22, 23) and present-day individuals belonging to U6 and M1 (7) in BEAST v1.8.1 (24). Using a human mtDNA mutation rate inferred from tip calibration of ancient mtDNA genomes (23), we obtained divergence estimates for U6 at 37,000 yBP (40,000-34,000 yBP for 95% highest posterior density, HPD) and M1 at 24,000 yBP (95% HPD, 29,000-20,000 yBP) (table S15). Our estimates are considerably younger than those of a study using present-day data only (45,000 \pm 7000 yBP for U6 and 37,000 \pm 7000 yBP for M1) (7), though similar to those of (25). Moreover, we observe an asynchronous increase in the effective population size for U6 and M1 (fig. S24). This suggests that the demographic histories of these North and East African haplogroups do not coincide and might have been influenced by multiple expansions in the Late Pleistocene (25). Notably, the diversification of haplogroup U6a and M1 found for Taforalt is dated to ~24,000 yBP (fig. S23), which is close in time to

the earliest known appearance of the Iberomaurusian in Northwest Africa (25,845-25,270 cal. yBP at Tamar Hat (26)).

The relationships of the Iberomaurusian culture with the preceding MSA, including the local backed bladelet technologies in Northeast Africa, and the Epigravettian in southern Europe have been questioned (13). The genetic profile of Taforalt suggests substantial Natufian-related and sub-Saharan African-related ancestries (63.5% and 36.5%, respectively), but not additional ancestry from Epigravettian or other Upper Paleolithic European populations. Therefore, we provide genomic evidence for a Late Pleistocene connection between North Africa and the Near East, predating the Neolithic transition by at least four millennia, while rejecting a potential Epigravettian gene flow from southern Europe into northern Africa within the resolution of our data. Archaeogenetic studies on additional Iberomaurusian sites will be critical to evaluate the representativeness of Taforalt for the Iberomaurusian gene pool. We speculate that the Natufian-related ancestral population may have been widespread across North Africa and the Near East, associated with microlithic backed bladelet technologies that started to spread out in this area by at least 25,000 yBP ((10) and references therein). However, given the absence of ancient genome data from a similar time frame for this broader area, the epicenter of expansion, if there was any, for this ancestral population remains unknown.

Although the oldest Iberomaurusian microlithic bladelet technologies are found earlier in the Maghreb than their equivalents in northeastern Africa (Cyrenaica) and the earliest Natufian in the Levant, the complex sub-Saharan ancestry in Taforalt makes our individuals an unlikely proxy for the ancestral population of later Natufians who do not harbor sub-Saharan ancestry. An epicenter in the Maghreb is plausible only if the sub-Saharan African admixture into Taforalt either post-dated the expansion into the Levant or was a locally confined phenomenon. Alternatively, placing the epicenter in Cyrenaica or the Levant requires an additional explanation for the observed archaeological chronology.

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the archaeological interpretation. M.L., B.N. and S.N. performed laboratory works with the help of A.P. and M.M. M.L., C.J., C.P. and W.H. analyzed data. M.L., C.J., J.K., C.P., A.B., L.H., N.B. and M.M. wrote the manuscript with input from all co-authors. **Competing interests:** A.B. keeps an additional affiliation with the MPI-EVA; they supported his excavation and worked with him on the site. This is also reflected in the co-authorship of J.H., director of MPI-EVA, who initially conceived part of the study together with A.B. The authors declare no conflict of interests. **Data and materials availability:** Genomic data (BAM) are available through the Sequence Read Archive (accession number SRP132033) and consensus mitogenome sequences (FastA) in GenBank (accession numbers MG936619-25).

SUPPLEMENTARY MATERIALS

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Supplementary Text

Figs. S1 to S26

Tables S1 to S16

References (28–114)

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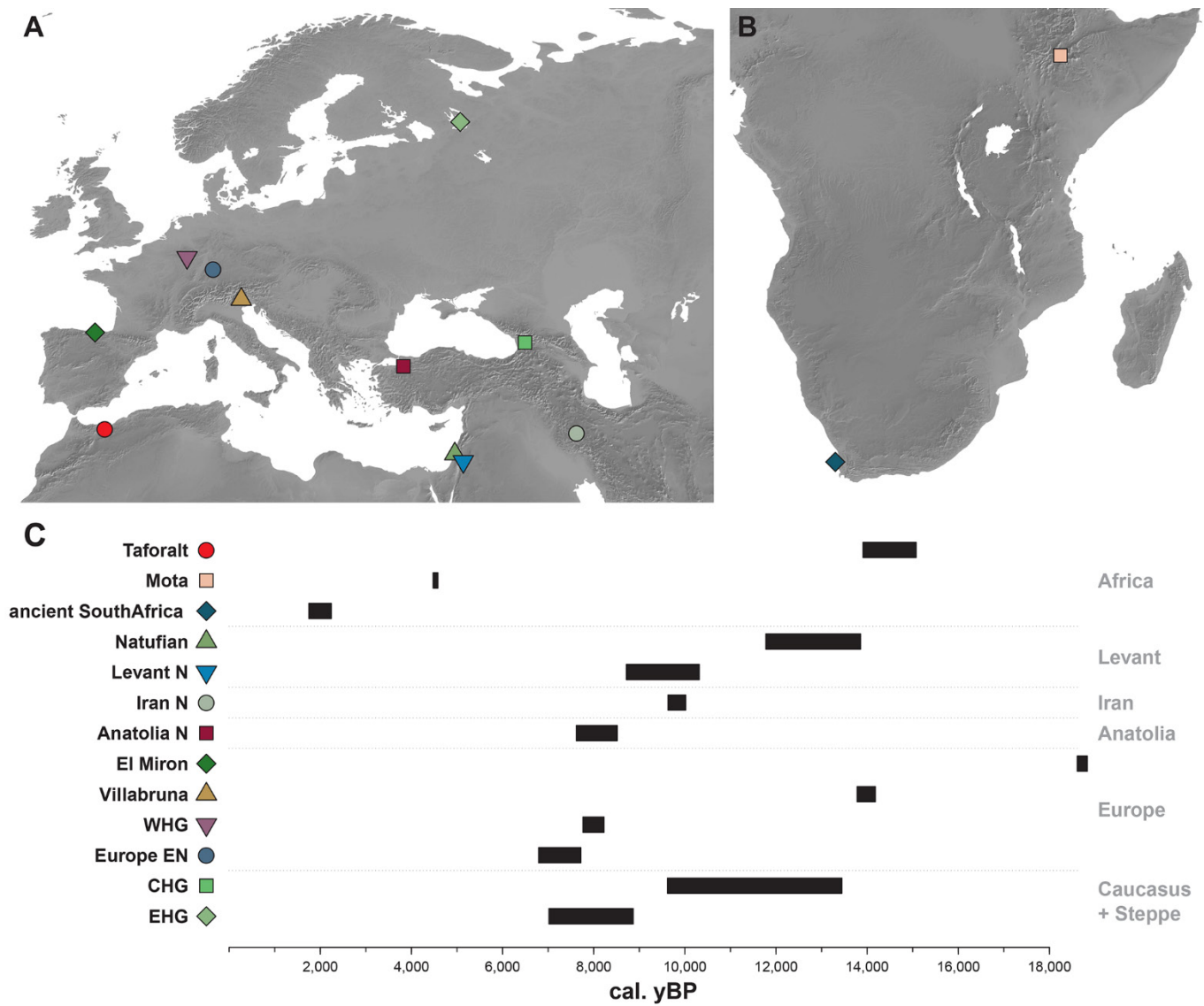


Fig. 1. Spatiotemporal locations of the Taforalt and other ancient genomes. (A and B) Geographic locations of representative ancient genomes from West Eurasia and Africa included in our analysis. The Pleistocene Taforalt site is marked by a red-colored circle. (C) The date range of each ancient group is marked by black bars, representing the range of 95% confidence interval of radiocarbon dating across all dated individuals (cal. yBP on the x-axis). Group labels are taken from previous studies reporting each ancient genome (4, 16, 27).

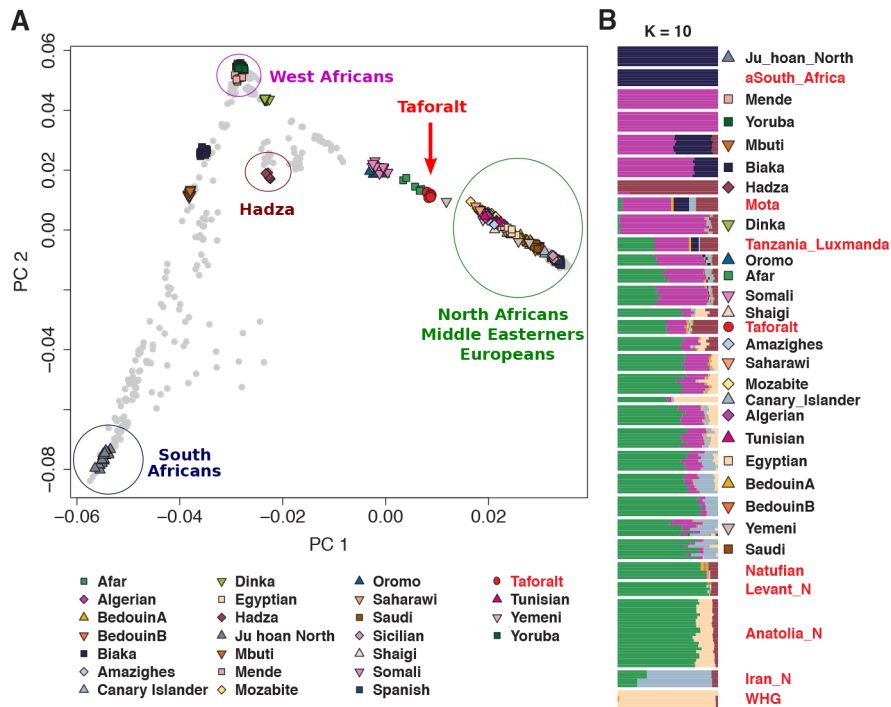


Fig. 2. A summary of the genetic profile of the Taforalt individuals. (A) The top two PCs calculated from present-day African, Near Eastern and South European individuals from 72 populations. The Taforalt individuals are projected thereon (red-colored circles). Selected present-day populations are marked by colored symbols. Labels for other populations (marked by small grey circles) are provided in fig. S8. (B) ADMIXTURE results of chosen African and Middle Eastern populations ($K = 10$). Ancient individuals are labeled in red color. Major ancestry components in Taforalt are maximized in early Holocene Levantines (green), West Africans (purple) and East African Hadza (brown). The ancestry component prevalent in pre-Neolithic Europeans (beige) is absent in Taforalt.

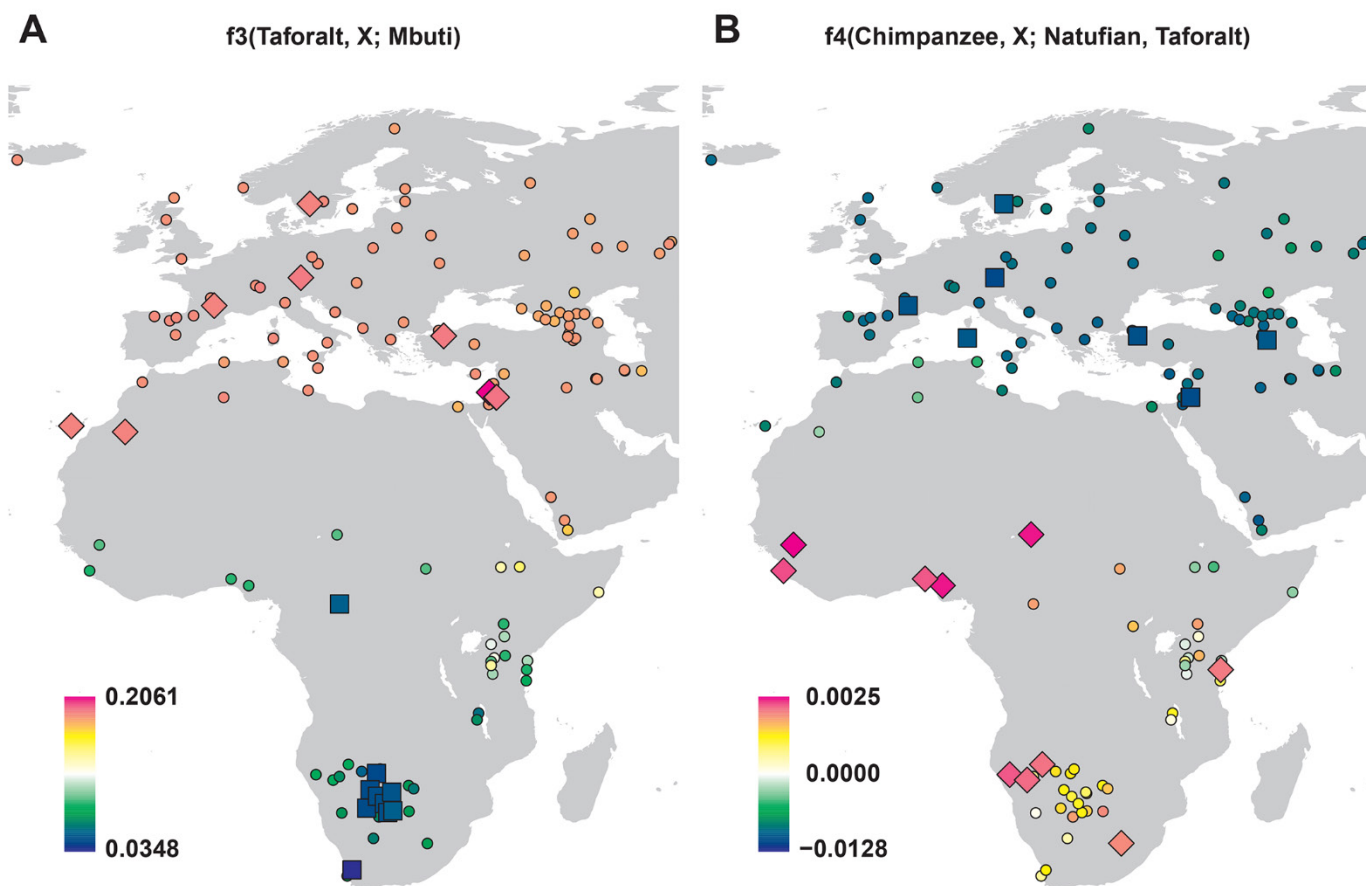


Fig. 3. The geographic distribution of the genetic affinity of Taforalt with worldwide populations. (A) Mean shared genetic drift with Taforalt measured by outgroup- f_3 statistics in the form $f_3(\text{Taforalt}, X; \text{Mbuti})$. Warm colors are for populations genetically close to Taforalt. Large diamonds and squares represent the ten highest and lowest f_3 values, respectively. Early Holocene Levantine groups, Natufian and Levant_N, show the highest affinity with Taforalt. The statistics and their associated SEs for the top 30 signals are presented in fig. S14. **(B)** Extra genetic affinity with Taforalt in comparison to Natufian measured by f_4 statistics in the form $f_4(\text{Chimpanzee}, X; \text{Natufian}, \text{Taforalt})$. Large diamonds and squares represent the ten most positive and negative f_4 values, respectively. Sub-Saharan Africans show high positive values, with West African Yoruba and Mende being the top, supporting the presence of sub-Saharan African ancestry in Taforalt. In contrast, all Eurasian populations are genetically closer to Natufians than to Taforalt. The statistics and their associated SEs for the top 30 signals are presented in fig. S16.

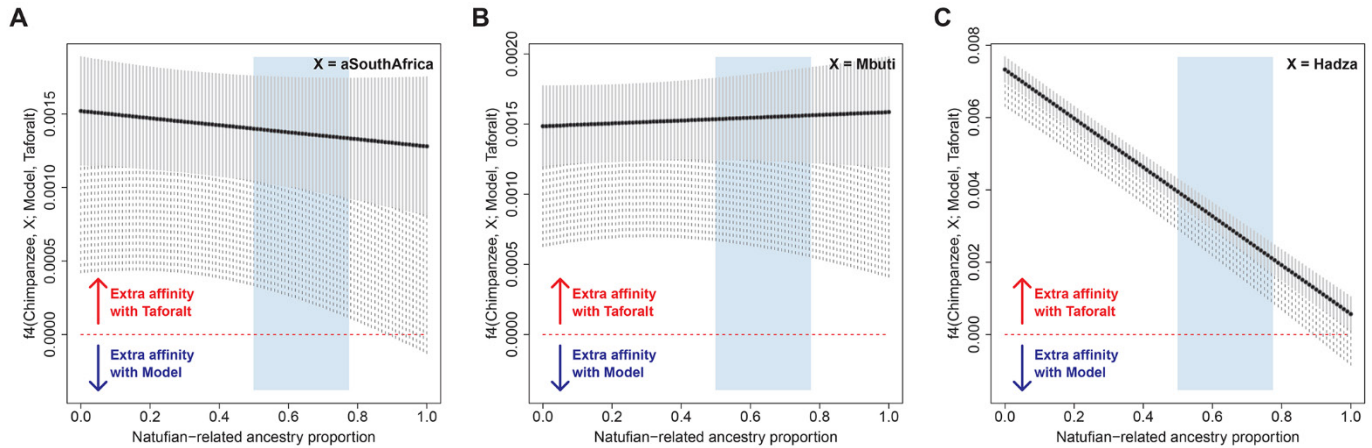


Fig. 4. Relative genetic affinity of representative sub-Saharan African groups to a mixture of Yoruba/Natufian and Taforalt, measured by $f_4(\text{Chimpanzee}, \text{African}; \text{Yoruba}+\text{Natufian}, \text{Taforalt})$ using (A) aSouthAfrica, (B) Mbuti and (C) Hadza as the African group. F_4 statistics were calculated for the proportions of Natufian-related ancestry ranging from 0% to 100% by an increment of 1%. The colored rectangle marks a plausible range of Natufian ancestry proportion on the x-axis, estimated by our qpAdm modeling ($0.637 \pm 2 \times 0.069$). Thick grey solid lines and dotted grey lines represent ± 1 SE and -3 SE ranges, respectively. SEs were calculated by 5 cM block jackknifing.