

Ancient human genomes suggest three ancestral populations for present-day Europeans

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Analysis of ancient DNA can reveal historical events that are difficult to discern through study of present-day individuals. To investigate European population history around the time of the agricultural transition, we sequenced complete genomes from a ~7,500 year old early farmer from the Linearbandkeramik (LBK) culture from Stuttgart in Germany and an ~8,000 year old hunter-gatherer from the Loschbour rock shelter in Luxembourg. We also generated data from seven ~8,000 year old hunter-gatherers from Motala in Sweden. We compared these genomes and published ancient DNA to new data from 2,196 samples from 185 diverse populations to show that at least three ancestral groups contributed to present-day Europeans. The first are Ancient North Eurasians (ANE), who are more closely related to Upper Paleolithic Siberians than to any present-day population. The second are West European Hunter-Gatherers (WHG), related to the Loschbour individual, who contributed to all Europeans but not to Near Easterners. The third are Early European Farmers (EEF), related to the Stuttgart individual, who were mainly of Near Eastern origin but also harbored WHG-related ancestry. We model the deep relationships of these populations and show that about ~44% of the ancestry of EEF derived from a basal Eurasian lineage that split prior to the separation of other non-Africans.

Ancient DNA studies have demonstrated that migration played a major role in the introduction of agriculture to Europe, as early European farmers were genetically distinct from ancient European hunter-gatherers^{1,2} and closer to present-day Near Easterners^{2,3}. Europeans today, however, are genetically intermediate, which has led to attempts to model them as a mixture of those two ancestral populations². A two-way mixture model is difficult to reconcile, however, with the fact that nearly all present-day Europeans also have ancestry from a third source: an Ancient North Eurasian (ANE) population^{4,5} that also contributed ancestry to Native Americans⁶.

To clarify the population transformations that accompanied the agricultural transition in Europe, we sequenced the genomes of nine ancient European individuals (Fig. 1A; Extended Data Fig. 1). We sequenced to 19-fold coverage the genome of “Stuttgart”, a ~7,500 year old individual found in Stuttgart in southern Germany who was buried in the context of artifacts from the first widespread Neolithic farming culture of central and northern Europe, the *Linearbandkeramik* (LBK). We sequenced to 22-fold the genome of “Loschbour”, an ~8,000 year old individual

found in the Loschbour rock shelter in Heffingen Luxembourg, from a skeleton that was discovered in the context of Mesolithic hunter-gatherer artifacts (SI1; SI2). We also sequenced DNA from seven ~8,000 year old remains from Mesolithic hunter-gatherers from the Motala site in southern Sweden, with the highest coverage individual (Motala12) at 2.4-fold. We mapped the sequences to the human reference genome (*hg19*), and for the two high coverage individuals (Stuttgart and Loschbour) inferred genotypes⁷ (SI2).

A central challenge in ancient DNA research is to distinguish authentic sequences from contamination. In initial sequencing libraries prepared from all nine individuals, the rate of C→T and G→A mismatches to the human genome at the ends of the DNA molecules was >20% compared with <1% for other nucleotides, suggesting authentic ancient DNA^{8,9} (SI3). We inferred a mitochondrial DNA (mtDNA) consensus for each sample, and based on the number of reads that differed from the consensus, estimated contamination levels of 0.3% for Loschbour, 0.4% for Stuttgart, and 0.01% - 5% for the Motala individuals (SI3). Stuttgart belonged to mtDNA haplogroup T2, typical of Neolithic Europeans¹⁰, while Loschbour and all Motala individuals belonged to haplogroups U5 and U2, typical of pre-agricultural Europeans^{1,8} (SI4). Based on the ratio of sequences aligning to chromosomes X and Y, we infer that Stuttgart was female while Loschbour and five Motala individuals were male¹¹ (SI5). Loschbour and four Motala males belonged to Y-chromosome haplogroup I, showing that this was a predominant haplogroup in pre-agricultural northern Europeans^{12,13} (SI5).

To generate large amounts of data, we built sequencing libraries using the enzyme uracil DNA glycosylase, which decreases the rate of C→T and G→A errors due to ancient DNA damage (SI3). After correcting for genotyping error, we estimate that heterozygosity (the number of differences per nucleotide between an individual's two chromosomes) is 0.00074 for Stuttgart, at the high end of present-day European (SI2). Heterozygosity is 0.00048 for Loschbour, lower than in all other present-day humans we analyzed. Combined with the higher proportion of deleterious heterozygous observed in Loschbour compared with Stuttgart or present-day humans (SI6), this finding is consistent with the ancestors of Loschbour having experienced small population sizes since separation from the ancestors of the other samples. By analyzing sites known to affect phenotype, we inferred that neither Stuttgart nor Loschbour could digest milk

into adulthood, that both had a >99% probability of dark hair, that Loschbour probably had darker skin than Stuttgart, and that Loschbour had a >50% probability of blue eyes while Stuttgart had a >99% probability of brown eyes (SI7). The *AMY1* gene coding for salivary amylase had 6, 13, and 16 copies in Motala12, Loschbour and Stuttgart respectively, in the range of present-day populations (Extended Data Fig. 2) (SI 8), suggesting that high copy counts of *AMY1* in humans are not entirely due to selection since the switch to agriculture¹⁴.

To determine how the ancient genomes relate to each other and to present-day humans, we analyzed 2,196 individuals from 185 populations genotyped at 594,924 autosomal single nucleotide polymorphisms (SNPs) using the Affymetrix Human Origins array⁵ (SI9) (Extended Data Table 1). We identified a set of “West Eurasian” populations as those that cluster with Europe and the Near East in an ADMIXTURE¹⁵ analysis (SI9 and Extended Data Figure 3). Principal Component Analysis (PCA)¹⁶ of the West Eurasian individuals separates Near Eastern and European populations along parallel south-north gradients, with a handful of mostly Mediterranean populations in between (Fig. 1B). The gradient in the Near East stretches from the Levant to the North Caucasus, and in Europe from Sardinia to the Baltic. This plot is qualitatively different from previous PCAs of Europeans in which the first and second PCs have correlated well to geography^{17, 18}; we ascribe this to our heavy sampling of Near Eastern populations, which causes the first PC to be more dominated by European-Near Eastern differences. We projected onto the PCs genetic data from ancient individuals^{2, 19, 20}, which reveals that European hunter-gatherers like Loschbour and Motala fall outside the variation of West Eurasians in the direction of European differentiation from the Near East. This pattern is suggestive of present-day Europeans being admixed between ancient European hunter-gatherers and ancient Near Easterners, an inference that we confirm below. Loschbour clusters with ~7,000 year old hunter-gatherers from Spain²⁰, allowing us to propose a “West European Hunter-Gatherer” (WHG) meta-population. The Motala individuals cluster with ~5,000 year old Neolithic hunter-gatherers² from the Pitted Ware Culture (PWC) in Sweden, suggesting a “Scandinavian Hunter-Gatherer” (SHG) meta-population that maintained biological continuity across the Neolithic transition. Stuttgart clusters with two early farmers—the ~5,300 year old Tyrolean Iceman¹⁹ and a ~5,000 year old southern Swedish farmer² from the Funnel Beaker Culture—suggesting an “Early European Farmer” (EEF) meta-population similar to present-day

Sardinians¹⁹. Two Upper Paleolithic Siberian samples project beyond the variation of Europeans on the second PC (Fig. 2A), suggesting that they may derive from the Ancient North Eurasian (ANE) population previously shown to have contributed to Europeans^{4,5}.

PCA is a powerful technique for measuring genetic similarity, but its interpretation in terms of history is difficult, as gradients of variation due to admixture may arise under a variety of different histories²¹. To test if present-day Europeans were formed by admixture of populations related to Loschbour, Stuttgart and MA1, we analyzed $f_3(X; Ref_1, Ref_2)$ statistics which measure the correlation in nucleotide frequency differences between a test sample and two populations: $(X-Ref_1)$ and $(X-Ref_2)$. If the three populations are related by a simple tree, the statistic is expected to be positive⁵. However, if X is admixed between populations related to Ref_1 and Ref_2 , the statistic can be negative and provides evidence of admixture in population X ⁵. For each present-day West Eurasian population, we tested all possible modern reference populations with at least 4 individuals, along with Loschbour, Stuttgart, Motala12 and MA1 (Table 1). For the majority of European populations ($n=18$) the lowest f_3 -statistic is observed with Loschbour and a Near Eastern population as references, suggesting that many Europeans derive from a mixture between WHG and populations related to present-day Near Easterners. Only Sardinians form their lowest f_3 -statistic with Loschbour-Stuttgart so the mixture process is unlikely to have been a simple WHG-EEF one (Table 1). Other European populations form their lowest f_3 -statistics with MA1-Stuttgart, which we hypothesize reflects the cline of increasing relatedness to MA1 in Fig. 1B. In the Near East, no population has its lowest f_3 -statistic with Loschbour or Motala12, but all have their lowest f_3 -statistic with Stuttgart (Table 1), suggesting that most of the ancestry of this sample may be directly inherited from populations of the ancient Near East, while modern Near Easterners have additional influences related to Africa, North Eurasia, or South Asia (Table 1).

To determine whether a mixture of just two ancestral populations can explain the negative f_3 -statistics we observe or whether more populations are required, we analyzed f_4 -statistics^{5,22}. We began by analyzing $f_4(X, Stuttgart; Loschbour, Chimpanzee)$, which measures whether Loschbour shares more alleles with West Eurasian population X or with *Stuttgart* (Extended Data Fig. 4). This statistic is positive for nearly all Europeans showing that Stuttgart has less WHG ancestry than present-day Europeans. However, it is negative for all Near Easterners, suggesting

that the ancestors of Stuttgart were not unmixed migrants from the Near East^{1, 2, 10} (Extended Data Table 1), consistent with the clustering of Stuttgart with Europeans in the PCA of Fig. 1B. We replicated this signal in subsets of SNPs that are uniformly ascertained (Extended Data Table 2). In SI10, we estimate that the proportion of Near Eastern ancestry in Stuttgart is definitely less than 100% and possibly as little as 61%. Further analyses of f_4 -statistics, however, show patterns that cannot all be explained by a history of Loschbour-related mixture. For example, the statistic $f_4(X, Stuttgart; MA1, Chimpanzee)$ has a qualitatively different geographic distribution than the same statistic replacing MA1 with Loschbour, in that it is positive in both Europeans and Near Easterners whereas the latter is positive only in Europeans (Extended Data Tables 1 and 2). This and related statistics are correlated to a statistic previously shown to document a signal of ANE-related admixture into Europe^{4,5} (Extended Data Fig. 5), indicating that these f_4 -statistics are reflecting ANE admixture rather than WHG admixture. Extended Data Fig. 6 visually illustrates the different admixture patterns by plotting onto a map of West Eurasia f_4 -statistics that reflect the degree of allele sharing of each West Eurasian population with different pairs of ancient populations. We formally tested whether the f_4 -statistic patterns are reflecting a history of more than one historical admixture event by using a method that tests the consistency of a matrix of f_4 -statistics with descent from a specified number of ancestral populations²³. We reject the scenario of most European population descending from a mixture of just two populations ($P < 10^{-12}$), but find that a scenario in which most European present-day populations descend from as few as three ancestral population is consistent with the data to the limits of our resolution (SI11).

Motivated by these observations, we modeled Europeans as a three-way mixture of ANE (of which MA1 is a member), WHG (Loschbour), and EEF (Stuttgart). To test the consistency of this model with our data, we used the ADMIXTUREGRAPH software²², which fits a tree with discrete admixture events and reports f -statistics that differ by more than three standard errors between the estimated and fitted values (SI12). Our model-building was motivated by three observations (SI12): (1) Eastern non-Africans (Oceanians, East Asians, Native Americans, and Onge, indigenous Andaman islanders²⁴) are genetically closer to ancient Eurasian hunter-gatherers (Loschbour, Motala12 and MA1) than to Stuttgart; (2) Every eastern non-African population except Native Americans is genetically equally close to Loschbour, Motala12, and MA1, but Native Americans are genetically closer to MA1 than to European hunter-gatherers⁶;

and (3) All three hunter-gatherers and Stuttgart are genetically closer to Native Americans than to other eastern non-Africans. We jointly fit models to data from Loschbour, Stuttgart, MA1, Karitiana and Onge (SI12), and found that there was a unique model with two admixture events that fit the data; models with one or zero admixture events could all be rejected (SI12). One of the inferred admixture events is the ANE gene flow into both Europe⁶ and the Americas⁶ that has previously been documented. The successful model (Fig. 2A) also suggests $44 \pm 10\%$ “Basal Eurasian” admixture into the ancestors of Stuttgart: gene flow into their Near Eastern ancestors from a lineage that diverged prior to the separation of the ancestors of Loschbour and Onge. Such a scenario, while never suggested previously, is plausible given the early presence of modern humans in the Levant²⁵, African-related tools made by modern humans in Arabia^{26, 27}, and the geographic opportunity for continuous gene flow between the Near East and Africa²⁸.

Our fitted model (Fig. 2A) allows us to estimate fractions of ANE/WHG/EEF ancestry for each European population (SI12). To explore the robustness of these estimates, we developed an independent method for estimating mixture that only assumes that MA1 is a representative of ANE, Loschbour of WHG, and Stuttgart of EEF. Specifically, we studied f_4 -statistics of the form $f_4(X, Stuttgart; Outgroup_1, Outgroup_2)$, measuring the correlation in allele frequency difference between X and Stuttgart, and a pair of outgroups with no recent shared history with Europeans. We chose divergent outgroups (SI13) that are differentially related to ANE, WHG and EEF, and then expressed the f_4 -statistics for each European population as a linear combination of $f_4(Loschbour, Stuttgart; Outgroup_1, Outgroup_2)$ and $f_4(MA1, Stuttgart; Outgroup_1, Outgroup_2)$, fitting the mixture coefficients that minimize the difference between expected and observed f_4 -statistics. The mixture coefficients agree between this method and the ADMIXTUREGRAPH modeling, increasing our confidence in both analyses (Extended Data Table 3, SI13).

Our estimates of mixture proportions (Fig. 2B and Extended Table 3) indicate that EEF ancestry in Europe today ranges from as little as around 30% in the Baltic to as high as around 90% in the Mediterranean (a previous study² inferred 11% in Russians to 95% in Sardinians, but fit a two-population mixture model). The north-south gradient is also consistent with patterns of identity-by-descent (IBD) sharing²⁹, in which Loschbour shares more segments with northern Europeans and Stuttgart with southern Europeans (SI14). We infer that southern Europeans received their

European hunter-gatherer ancestry mostly via EEF, while Northern Europeans acquired up to 50% additional WHG-related ancestry. Europeans also have ANE ancestry (up to ~20%), which is widespread across Europe, but quantitative less as the WHG/(WHG+ANE) ratio is ~0.6-0.8 for most Europeans (SI12). The history behind the ANE ancestry in West Eurasia is not simple, as the Near East has little or no WHG ancestry but substantial levels of ANE ancestry there especially in the North Caucasus (SI12; Fig. 1B; Fig. 2). Loschbour and Stuttgart had little or no ANE ancestry, indicating that it was not as pervasive in central Europe around the time of the agricultural transition as it is today. (By implication ANE ancestry was also not present in the ancient Near East; since Stuttgart which has substantial Near Eastern ancestry lacks it.) However, ANE ancestry was already present in at least some Europeans (Scandinavian hunter-gatherers) by ~8,000 years ago, since MA1 shares more alleles with Motala12 than Loschbour: $f_4(\text{Motala12}; \text{Loschbour}; \text{MA1}, \text{Mbuti}) = 0.003$ ($Z=5.2$ standard errors from zero) (SI12). While SHG may have contributed ANE ancestry to modern Europeans, it cannot have been the only population that did so, as no European population has its lower f_3 -statistic with it in Table 1, and few populations fit a model of EEF-SHG admixture (SI12).

While our three-way mixture model fits the data for most European populations, two sets of populations are poor fits. First, Sicilians, Maltese, and Ashkenazi Jews have EEF estimates beyond the 0-100% interval (SI13) and they cannot be jointly fit with other Europeans in the (SI12). These populations may have more Near Eastern ancestry than can be explained via EEF admixture (SI13), an inference that is also suggested by the fact that they fall in the gap between European and Near Eastern populations in the PCA of Fig. 1B. Second, we observe that Finns, Mordovians, Russians, Chuvash, and Saami from northeastern Europe do not fit our model (SI12; Extended Data Table 3). To better understand this, for each West Eurasian population in turn we plotted $f_4(X, \text{Bedouin2}; \text{Han}, \text{Mbuti})$ against $f_4(X, \text{Bedouin2}; \text{MA1}, \text{Mbuti})$, using statistics that measure the degree of a European population's allele sharing with Han Chinese or MA1 (Extended Data Fig. 7). Europeans fall along a line of slope >1 in the plot of these two statistics. However, northeastern Europeans fall away from this line in the direction of Han. This is consistent with Siberian gene flow into some northeastern Europeans after the initial ANE admixture, and may be related to the fact that Y-chromosome haplogroup N^{30, 31} is shared between Siberian and northeastern Europeans^{32, 33} but not with western Europeans. There may in

fact be multiple layers of Siberian gene flow into northeastern Europe after the initial ANE gene flow, as our analyses reported in SI 12 show that some Mordovians, Russians and Chuvash have Siberian-related admixture that is significantly more recent than that in Finns (SI12).

This study raises two questions that are important to address in future research. A first is where the EEF picked up their WHG ancestry. Southeastern Europe is a candidate as it lies along the geographic path from Anatolia into central Europe, and hence it should be a priority to study ancient samples from this region. A second question is when and where ANE ancestors admixed with the ancestors of most present-day Europeans. Based on discontinuity in mtDNA haplogroup frequencies in Central Europe, this may have occurred during the Late Neolithic or early Bronze Age ~5,500-4,000 years ago³⁵. A central aim for future work should be to collect transects of ancient Europeans through time and space to illuminate the history of these transformations.

Supplementary Information is linked to the online version of the paper. The fully public version of the Human Origins dataset can be found at http://genetics.med.harvard.edu/reichlab/Reich_Lab/Datasets.html, whereas a version with additional samples that require users to sign a letter indicating that they will abide by specified usage conditions is available on request from DR.

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Author contributions

EEE, JBu, MS, SP, JKe, DR and JKr supervised the study. IL, NP, AM, GR, SM, PHS, JGS, SC, KK, QF, CdF, KP, WH, MMey, and DR analyzed genetic data. FH, EF, DD, MF, J-MG, JW, AC and JKr obtained archaeological material. AM, CE, RB, KB, SS, CP and JKr processed ancient DNA. IL, NP, SN, GA, HAB, EB, OB, HB-A, JBe, FBe, FBr, GBJB, FC, MC, DECC, LD, GvD, SD, SAF, IGR, MG, MH, BH, TH, UH, ARJ, RKi, EK, TK, VK, RKh, AK, LL, SL, RWM, BM, EM, JM, TN, LO, JP, FP, OLP, VR, IR, RR, HS, AS, EBS, AT, DT, ST, IU, OU, MV, PZ, LY, TZ, CC, MGT, SAT, LS, KT, RV, DC, RS, MMet, SP and DR assembled the genotyping dataset. IL, DR and JKr wrote the manuscript with help from all co-authors.

Author information

The authors declare no competing financial interests except for JM who is an employee of 23andMe.

Table 1: Lowest f_3 -statistics for each West Eurasian population

<i>Ref₁</i>	<i>Ref₂</i>	Target pop. for which these two reference pops. give the most negative $f_3(X; Ref_1, Ref_2)$
Loschbour	Stuttgart	Sardinian
Loschbour	Near East (Abkhasian ^A , Armenian ^B , Georgian ^C , Iraqi_Jew ^D)	Estonian ^A , Finnish ^A , Icelandic ^A , Lithuanian ^A , Mordovian ^A , Russian ^A , Orcadian ^B , Belorussian ^C , Czech ^C , Norwegian ^C , Ukrainian ^C , Basque ^D , English ^D , French_South ^D , Spain_North ^D , Scottish ^D , Spanish ^D
Stuttgart	North Eurasia (MA1 ^E , Piapoco ^F)	Albanian ^E , Ashkenazi_Jew ^E , Bergamo ^E , Bulgarian ^E , Croatian ^E , French ^E , Greek ^E , Hungarian ^E , Maltese ^E , Sicilian ^E , Tuscan ^E , Abkhasian ^E , Chechen ^E , Cypriot ^E , Druze ^E , Lezgin, Turkish_Jew ^E ; Adygei ^F , Balkar ^F , Iranian ^F , Kumyk ^F , North_Ossetian ^F , Turkish ^F
Stuttgart	African (Esan ^G , Gambian ^H , Kgalagadi ^I)	BedouinA ^G , BedouinB ^G , Jordanian ^G , Lebanese ^G , Libyan_Jew ^G , Moroccan_Jew ^G , Palestinian ^G , Syrian ^G , Yemenite_Jew ^G ; Tunisian_Jew ^H ; Saudi ^I
Stuttgart	South Asian (Gujarati3 ^J , Vishwabrahmin ^K)	Armenian ^J , Georgian ^J , Georgian_Jew ^J , Iranian_Jew ^J , Iraqi_Jew ^K

Note: We group populations into five categories of similar Ref_1 and Ref_2 , using a capital letter superscript to indicate the Ref_2 population in each pair. The Z-scores for populations are < -4 except where marked in gray. Extended Table 1 gives the quantitative values of each f_3 -statistic.

Figure Legends

Figure 1: Map of West Eurasian populations and Principal Component Analysis. (a)

Locations of ancient and present-day samples analyzed, with color coding matching the PCA. We show all sampling locations for each population, which results in multiple points for some populations (e.g. Spain). (b) PCA on all present-day West Eurasians, with the ancient and selected eastern non-Africans projected. European hunter-gatherers fall beyond modern Europe in the direction of European differentiation from the Near East. Stuttgart clusters with other Neolithic Europeans and present-day Sardinians. MA1 falls outside the variation of modern day West Eurasians in the direction of southern-northern differentiation along dimension 2 and between the European and Near Eastern clines along dimension 1.

Figure 2: Modeling of West Eurasian population history. (a) A three-way mixture model that is a statistical fit to the data for many European populations, ancient DNA samples, and non-European populations. Present-day samples are colored in blue, ancient samples in red, and reconstructed ancestral populations in green. Solid lines represent descent without mixture, and dashed lines represent admixture events. For the two mixture events relating the highly divergent ancestral populations, we print estimates for the mixture proportions as well as one standard error. (b) We plot the proportions of ancestry from each of three inferred ancestral populations (EEF, ANE and WHG) as inferred from the model-based analysis.

Figure 1

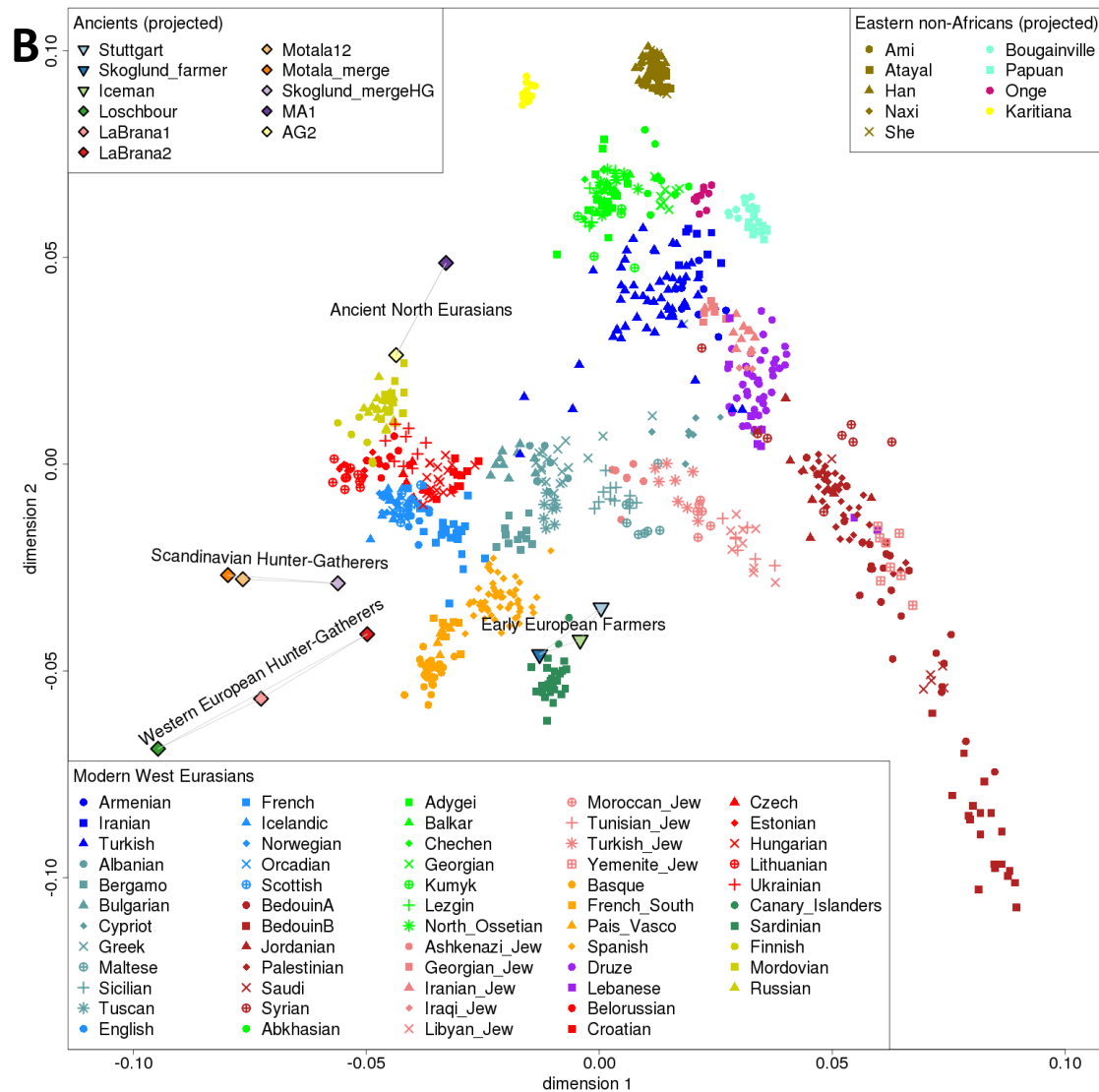
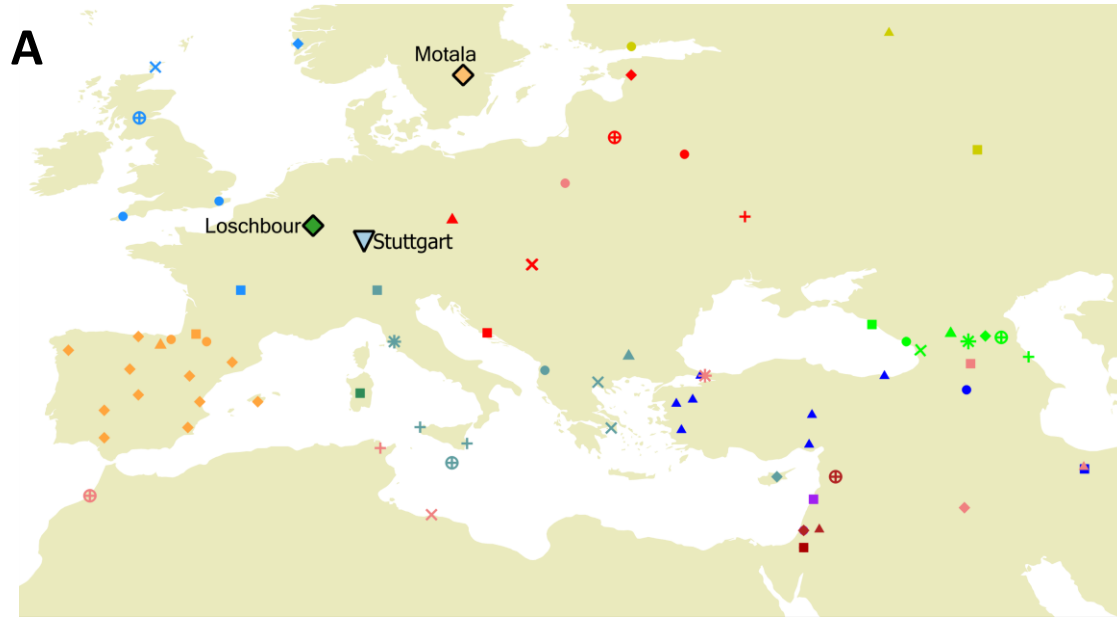
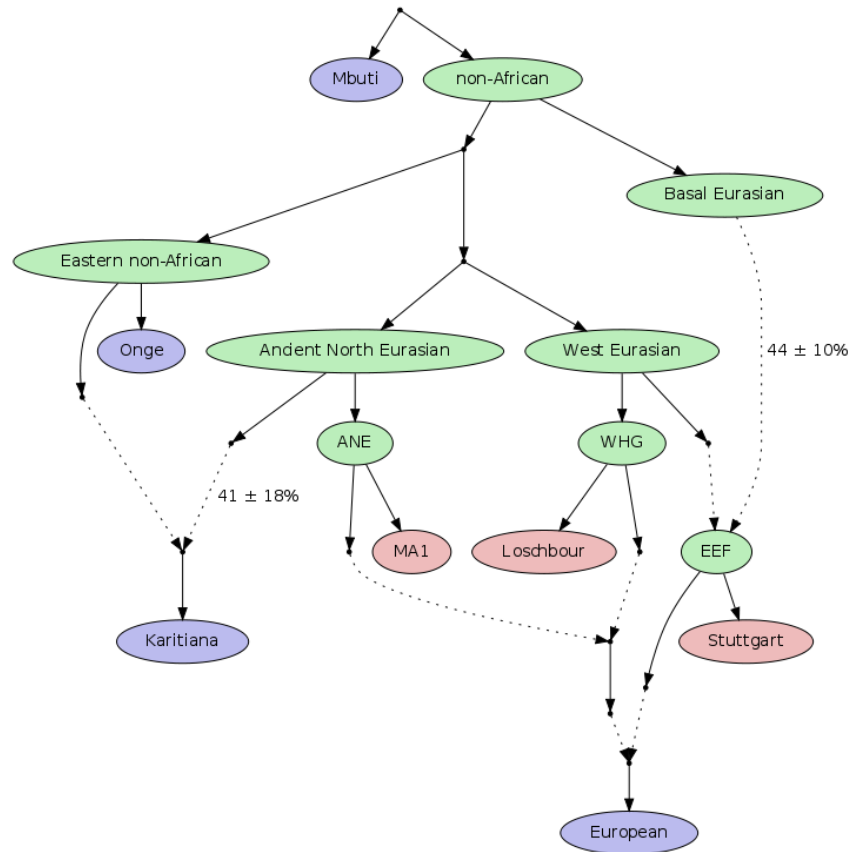
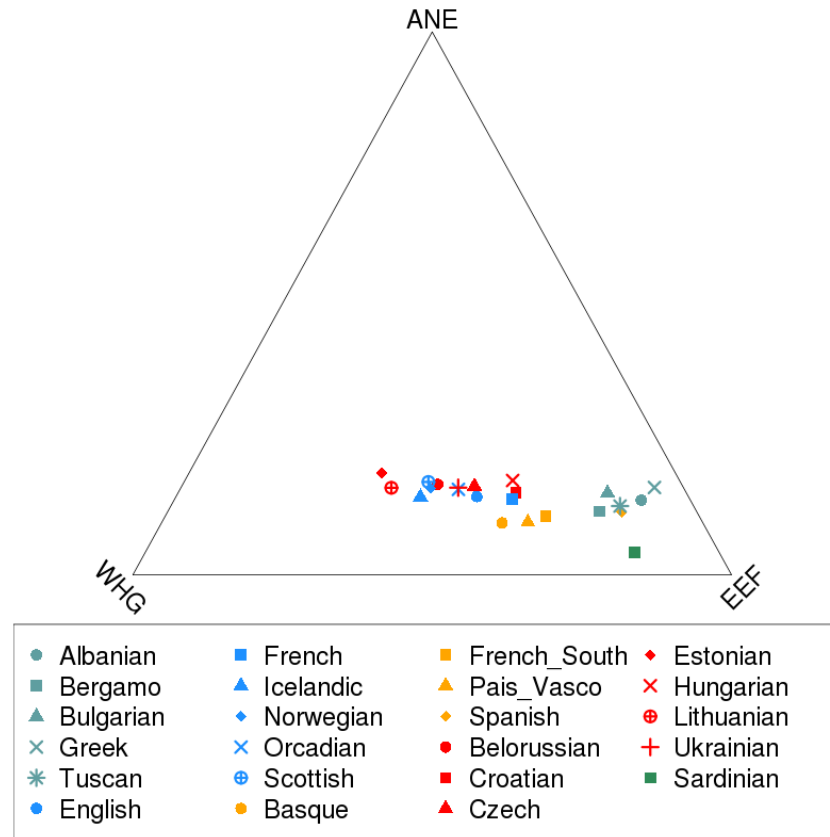


Figure 2

A



B



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