A unified genealogy of modern and ancient genomes*

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Abstract

The sequencing of modern and ancient genomes from around the world has revolutionized our understanding of human history and evolution. However, the problem of how best to characterize ancestral relationships from the totality of human genomic variation remains unsolved. Here, we address this challenge with non-parametric methods that enable us to infer a unified genealogy of modern and ancient humans. This compact representation of multiple datasets explores the challenges of missing and erroneous data and uses ancient samples to constrain and date relationships. We demonstrate the power of the method to recover relationships between individuals and populations, as well as to identify descendants of ancient samples. Finally, we introduce a simple non-parametric estimator of ancestor geographical location that recapitulates key events in human history.

One-Sentence Summary:

The largest genealogy of modern and ancient genomes yet constructed delivers insights into human history and evolution.

Our ability to determine relationships among individuals, populations and species is being transformed by population-scale biobanks of medical samples (1, 2), collections of thousands of ancient genomes (3), and efforts to sequence millions of eukaryotic species for comparative genomic analyses (4). Such relationships, and the resulting distributions of genetic and phenotypic variation, reflect the complex set of selective, demographic and molecular processes and events that have shaped species such as our own (5–8).

However, learning about evolutionary events and processes from the totality of genomic variation, in humans or other species, is challenging. Combining information from multiple data sets, even within a species, is technically demanding: discrepancies between cohorts due to error (9), differing sequencing techniques (10, 11) and variant processing (12) can lead to noise that can easily obscure genuine signal. Furthermore, few tools can cope with the vast data sets that arise from the combination of multiple sources (13). Also, statistical analysis typically relies on data reduction techniques (14, 15) or the fitting of parametric models (16–19), which may provide an incomplete picture of the complexities of evolutionary history. Finally, data access and governance restrictions often limit the ability to combine data sources (20).

The succinct tree sequence data structure provides a potential solution to many of these problems (13, 21). Tree sequences extend the fundamental concept of a phylogenetic tree to multiple correlated trees along the genome, necessary when considering genealogies within recombining organisms (22). Importantly, the tree sequence, and the mapping of mutation events to it, reflects the totality of what is knowable about genealogical relationships and the evolutionary history of individual variants. A tree sequence is defined as a graph with a set of nodes representing sampled chromosomes and ancestral haplotypes, edges connecting nodes representing lines of descent, and variable sites containing one or more mutations mapped onto the edges (Fig. 1A). Recombination events in the ancestral history of the sample create different edges and thus distinct, but highly correlated trees along the genome. Tree sequences can not only be used to compress genetic data (13), but also lead to highly efficient algorithms for calculating population genetic statistics (23).

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Here, we introduce, validate and apply non-parametric methods for inferring time-resolved tree sequences from multiple heterogeneous sources to efficiently infer a single, unified tree sequence of ancient and contemporary human genomes. We note that while humans are the focus of this study, the methods and approaches we introduce are valid for most recombining organisms.

To generate a unified genealogy of modern and ancient human genomes, we integrated data from three modern datasets: the 1000 Genomes Project (TGP) which contains 2,548 sequenced individuals from 26 populations (6), the Human Genome Diversity Project (HGDP), which consists of 929 sequenced individuals from 54 populations (8), and the Simons Genome Diversity Project (SGDP) with 278 sequenced individuals from 142 populations (7). 154 individuals appear in more than one of these datasets (24). In addition, we included data from three high-coverage sequenced Neanderthal genomes (25–27), a

single Denisovan genome (28), and high coverage whole genome data from a nuclear family of four (a mother, a father, and their two sons with average coverage of 10.8x, 25.8x, 21.2x, and 25.3x) from the Afanasievo Culture, who lived ~4.6 thousand years ago (kya) in the Altai Mountains of Russia (Table S1). Finally, we used 3,589 published ancient samples from over 100 publications compiled by the Reich Laboratory (24) and three sequenced ancient samples: Loschbour, LBK-Stuttgart, and Ust'-Ishim (5, 29) to constrain allele age estimates. These ancient genomes were not included in the final tree sequence due to the lack of reliable phasing for the majority of samples.

We built a unified genealogy from these datasets using an iterative approach (Fig. 1B). We first merged the modern datasets and inferred a tree sequence for each autosome using *tsinfer* version 0.2 (24, 30). We then estimated the age of ancestral haplotypes with *tsdate*, a Bayesian approach that infers the age of ancestral haplotypes with good accuracy and scaling properties (Fig. 1C and figs. S1–S5) (24, 31). Note that *tsdate* can be used to date any valid tree sequence, not only those inferred by *tsinfer*. *tsdate* can also use ancient samples to improve date estimates (Fig. 1D). We identified 6,412,717 variants present in both ancient and modern samples. A lower bound on variant age is provided by the estimated archaeological date of the oldest ancient sample in which the derived allele is found. Where this was inconsistent with the initial inferred value (559,431, or 8.7% of variants) we used the archaeological date as the variant age.

Finally, we integrated the Afanasievo family and four archaic sequences with the modern samples and re-inferred the tree sequence. The Afanasievo family have high coverage and comparably reliable haplotype phasing and were included to demonstrate the ability of our approach to incorporate high quality ancient samples.

The integrated tree sequences of each autosome together contain 26,958,720 inferred ancestral haplotype fragments, 231,073,278 edges, 91,172,114 variable sites, and 245,631,834 mutations. We infer that 38.7% of variant sites require more than one change in allelic state in the tree sequence to explain the data. This may indicate either recurrent mutations or errors, all of which are represented by additional mutations in the tree sequence. If we discount mutations that are likely indicative of sequencing errors (24), we find that 13,513,873 sites contain at least two mutations affecting more than one sample, implying that up to 17.5% of variable sites could result from more than one ancestral mutation. A high proportion of sites with over ~100 mutations on chromosome 20 have sequencing or alignment quality issues as defined by the TGP accessibility mask (6) or are in minimal linkage disequilibrium to their surrounding sites (fig. S6), suggesting they are largely erroneous. Moreover, analysis of data simulated with an empirically-calibrated error profile and evaluation of enrichment of multiple mutations at sites with known elevated mutation rates, suggests that the majority of the multiple mutations we identify are likely explained by error, but a minority (c. 20%) are the result of genuine recurrence or back mutation (24). We chose to retain such sites so that our inferred tree sequences are lossless representations of the original data sources; however, future iterative approaches to the removal of such probable errors are likely to improve use cases such as imputation.

To characterize fine-scale patterns of relatedness between the 215 populations of the constituent datasets, we estimated the time to the most recent common ancestor (TMRCA) between pairs of haplotypes from these populations at the 122,637 distinct trees in the tree sequence of chromosome 20 (~300 billion pairwise TMRCAs). In this and other analyses we present data from this chromosome as it is representative of genome-wide patterns. After performing hierarchical clustering on the average pairwise TMRCA values, we find that samples do not cluster by data source (which would indicate artifacts), but reflect patterns of global relatedness (Fig. 2 and Interactive fig.S1). We conclude that our method of integrating datasets is therefore robust to biases introduced by different datasets.

In this genealogy, numerous features of human history are immediately apparent, such as the deep divergence of archaic and modern humans, the effects of the Out of Africa event (Fig. 2A), and a subtle increase in Oceanian/Denisovan MRCA density from 2,000-5,000 generations ago (Fig. 2B). Multiple populations show recent within-group TMRCAs, suggestive of recent bottlenecks or consanguinity. The most extreme cases occur when a population consists of a single individual in our dataset, such as the Samaritan individual from the SGDP where we see a logarithmic average within-group TMRCA of ~ 1,000 generations, which is caused by multiple MRCAs at very recent times (Fig. 2C) and is consistent with a severe bottleneck and consanguinity in recent centuries (32). Indigenous populations in the Americas, an Atayal individual from Taiwan, and Papuans also exhibit particularly recent within-group TMRCAs (Fig. 2).

Tree sequence based analysis of descent from ancient sequences

To validate the dating methodology, we used simulations to show that the integration of ancient samples improves derived allele age estimates under a range of demographic histories (Fig. 1D). To provide empirical validation of the method, we tested how best to infer allele ages that are consistent with observations from ancient samples. Thus, we inferred and dated a tree sequence of TGP chromosome 20 (without using ancient samples) and compared the resulting point estimates and upper and lower bounds on allele age with results from *GEVA* (33) and *Relate* (34). This resulted in a set of 659,804 variant sites where all three methods provide an allele age estimate. Of these, 76,889 derived alleles are observed within the combined set of 3,734 ancient genome samples, thus putting a lower bound on allele age. The estimated allele ages from *tsdate* and *Relate* showed the greatest compatibility with ancient lower bounds, despite the fact that the mean age estimate from *tsdate* is more recent than that of *Relate* (Fig. 3A) (24).

Next, to assess the ability of the unified tree sequence to recover known relationships between ancient and modern populations, we considered the patterns of descent to modern samples from Archaic sequences on chromosome 20. Simulations indicate that this approach detects introgressed genetic material from Denisovans at a precision of ~86% with a recall of ~61% (24). We find descendants among non-archaic individuals, including both modern individuals and the Afanasievo, for 13% of the span of the Denisovan haplotypes on chromosome 20. The highest degree of descent among modern humans is in Oceanian populations as previously reported (28, 35–37) (Fig. 3B). However, the tree sequence also reveals how both the extent and nature of descent from Denisovan haplotypes varies greatly

among modern humans. In particular, we find that Papuans and Australians carry multiple fragments of Denisovan haplotypes that are largely unique to the individual (Fig. 3C). In contrast, other modern descendants of Denisovan haplotypes have fewer blocks which are more widely shared, often between geographically distant individuals.

Examining the other ancient samples in the unified genealogy, we find the greatest amount of descent from the haplotypes of the Afanasievo family among individuals in Western Eurasia and South Asia (fig. S7A), consistent with findings from the genetically similar Yamnaya peoples and supporting a contemporaneous diffusion of Afanasievo-like genetic material via multiple routes (38). For the Neanderthals, where there are three samples of different ages, our simulations indicate that interpretation of the descent statistics is complicated by varying levels of precision and recall among lineages. Nevertheless, recall is highest at regions where introgressing and sampled archaic lineages share more recent common ancestry and precision is higher for the Vindija sample, which is more closely related to introgressing lineages. Examining patterns of descent from Vindija haplotypes across autosomes indicates that modern non-African groups carry similar levels of Vindija-like material (fig. S8), supporting suggestions that the proportions are similar between East Asians and West Eurasians (39) and inconsistent with other reports (26, 40).

Non-parametric inference of spatio-temporal dynamics in human history

Tree sequence based analysis of ancient samples demonstrates an ability to characterize patterns of recent descent. We developed a simple estimator of ancestor spatial location that uses the coordinates of descendants of a node, combined with the structure of the tree sequence, to provide an estimate of ancestors' geographic position (24). Briefly, this is accomplished by determining the coordinates of a parent node in the tree sequence as the midpoint of its immediate children (24), an approach that performs well in simple simulations (fig. S9). The approach can use information on the location of ancient samples, though it does not attempt to capture the geographical plausibility of different locations and routes. The inferred locations are thus a model-free estimate of ancestors' location, informed by the tree sequence topology and geographic distribution of samples.

We applied our method to the unified tree sequence of chromosome 20, excluding TGP individuals (which lack precise location information). We find that the inferred ancestor location recovers multiple key events in human history (Fig. 4 and Movie S1). Despite the fact that the geographic center of sampled individuals is in Central Asia, by 72 kya the average location of ancestral haplotypes is in Northeast Africa and remains there until the oldest common ancestors are reached. Indeed, the inferred geographic center of gravity of the 100 oldest ancestral haplotypes (which have an average age of ~2 million years) is located in Sudan at 19.4 N, 33.7 E. These findings reflect the depth of African lineages in the inferred tree sequence and are compatible with well-dated early modern human fossils from eastern and northern Africa (41, 42). We caution if we analyzed data from a grid sampling of populations in Africa the geographic center of gravity of independent lineages at different time depths would shift. In addition, migrations occurring within the last few thousand years (43, 44) mean that present day distributions of groups in Africa and elsewhere may not represent those of their ancestors, and thus we may have a distorted

picture of ancient geographic distributions (45). Nevertheless, the deep tree structure is geographically centered in Africa in autosomal data, just as it is for mitochondrial DNA and Y chromosomes (46, 47).

By 280 kya, the estimated geographic center of human ancestors is still located in Africa, but many are also observed in the Middle East and Central Asia and a few are located in Papua New Guinea. At 140 kya, more ancestors are found in Papua New Guinea. This is almost 100 kya before the earliest documented human habitation of the region (48). However, our findings are potentially consistent with the proposed timescales of deeply diverged Denisovan lineages unique to Papuans (37) and possibly admixture with unsampled, "ghost" lineages. At 56 kya, some ancestral lineages are observed in the Americas, earlier than the estimated migration times to the Americas (49). This effect is possibly attributable to the presence of ancestors that predate the migration and did not live in the Americas, but whose descendants now exist solely in this region (50); the same effect may also explain observations from Papua New Guinea. Additional ancient samples and more sophisticated inference approaches are required to distinguish between these hypotheses, since there remains considerable uncertainty about the true age of any single ancestor (24). Nevertheless, these results demonstrate the ability of inference methods applied to tree sequences to capture key features of human history in a manner that does not require complex parametric modeling.

Discussion

A central theme in evolutionary biology is how best to represent and analyze genomic diversity to learn about the processes, forces and events that have shaped organismal history. Historically, many modeling approaches focus on the temporal behavior of individual mutation frequencies in idealized populations (51, 52). More recently, modelling techniques have shifted to focus on the genealogical history of sampled genomes and the correlation structures arising through recombination (22, 53). Critically, a single (albeit extremely complex) set of ancestral relationships exist that, coupled with how mutation events have altered genetic material through descent, describes what we observe today.

However, developing efficient methods for inferring the underlying genealogy has proved challenging (54, 55). The methods described here produce high quality dated genealogies that include thousands of modern and ancient samples. These genealogies cannot be entirely accurate, nevertheless, they enable a wealth of analyses that reveal features of human evolution (23, 56–60). That our highly simplistic geographic estimator captures key events suggests that more sophisticated approaches, coupled with the ongoing program of sequencing ancient samples, will continue to generate new insights into our history. Specifically, the methods developed here provide a framework for testing different models of human migration and demographic history, such as Neanderthal absorption models (61), using a parametric and explicitly spatial simulation framework. However, the accuracy of any ancestral geographic inference method will be limited when the distribution of sampled individuals does not reflect the location of the samples' ancestors.

Our study also highlights the importance of accommodating genotype error and recurrent mutation in the analysis of genomic variation. While a large number of sites are inferred to carry multiple mutations, we find that the majority of these likely reflect genotype error and potentially errors arising from paralogy (particularly at sites requiring high numbers of mutations), though there remains a significant signal of recurrent mutation, as previously reported (62, 63). Similarly, we find some evidence for certain classes of error in ancient sequence leading to false "correction" of variant ages. We choose to retain all additional mutations in the analyses described in this paper, including those which are highly likely to reflect sequencing error, as this reflects the input data used to build the tree sequence and any effort to remove mutations corresponding to errors will itself introduce bias. We caution that the absolute ages we report have some degree of error, in part due to these errors in the sequencing datasets. Estimates from simulations show that genotype error may cause an upwards bias of up to 16% in age estimates derived from modern samples (fig. S3), but we also find that removing sites that are highly likely to be erroneous has a marginal effect on age estimates (fig. S10). Improving methods to detect and correct, or mitigate against the impact of genotype errors is an important direction for future research.

Because the tree sequence approach aims to capture the structure of human relationships and genomic diversity, it provides a principled basis for combining data from multiple different sources, not just correcting errors, but also enabling tasks such as imputing missing data. Although additional work is required to integrate other types of mutation, a reference tree sequence for human variation - along with the tools to use it appropriately (13, 23) - potentially represents a basis for harmonizing much larger and wider sets of genomic data sources and enabling cross data-source analyses. We note that reference tree sequences could also enable data sharing and preserve privacy in genomic analysis (20) through compression of cohorts against such a reference structure.

There exists room for improvement as well as new opportunities for genomic analyses that use the dated tree sequence structure. Our approach requires phased genomes, a particular challenge for ancient samples. However, it should be possible to use a diploid version of the matching algorithm in *tsinfer* to jointly solve phasing and imputation. This also has the potential to alleviate biases introduced by using modern and genetically distant reference panels for ancient samples (64). In addition, our approach to age inference within *tsdate* only provides an approximate solution to the cycles that are inherent in genealogical histories (65) and could be extended to model heterogeneity in mutation rates. There are also many possible approaches for improving the sophistication of spatio-temporal ancestor inference.

The unified genealogy presented in this work represents a foundation for building a comprehensive understanding of human genomic diversity, including both modern and ancient samples, which enables applications ranging from improving genome interpretation to deciphering our earliest roots. Although much work is still required to build the genealogy of everyone, the methods presented here provide a solution to this fundamental task.

Supplementary Material

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Acknowledgments:

Data and materials availability:

Newly reported sequencing data from the Afanasievo family is available from the European Nucleotide Archive, accession number PRJEB43093; phased variant data for the family is available from the European Variation Archive, accession number PRJEB46983. All publicly available datasets used in this paper are available from their original publications, *tsinfer* is deposited to Zenodo at doi:10.5281/zenodo.5168051 and available at https://tsinfer.readthedocs.io/ under the GNU General Public License v3.0 (30), *tsdate* is deposited to Zenodo at doi:10.5281/zenodo.5168040 and available at https://tsdate.readthedocs.io/ under the MIT License (31), and *tskit* is deposited to Zenodo at doi:10.5281/zenodo.5465773 and available at https://tskit.readthedocs.io/ under the MIT License (66). All code used to perform analyses in this paper is deposited to Zenodo at doi:10.5281/zenodo.5172104 and can be found at https://github.com/awohns/unified_genealogy_paper (67). Unified tree sequences of the HGDP, SGDP, and TGP autosomes are available from Zenodo at https://doi.org/10.5281/zenodo.5495535 (68). Unified tree sequences of the HGDP, SGDP, TGP, and high coverage ancient autosomes are available at https://doi.org/10.5281/zenodo.5512994 (69). Tree sequences were compressed using the tszip utility; see the documentation at https://tszip.readthedocs.io/ for further details.

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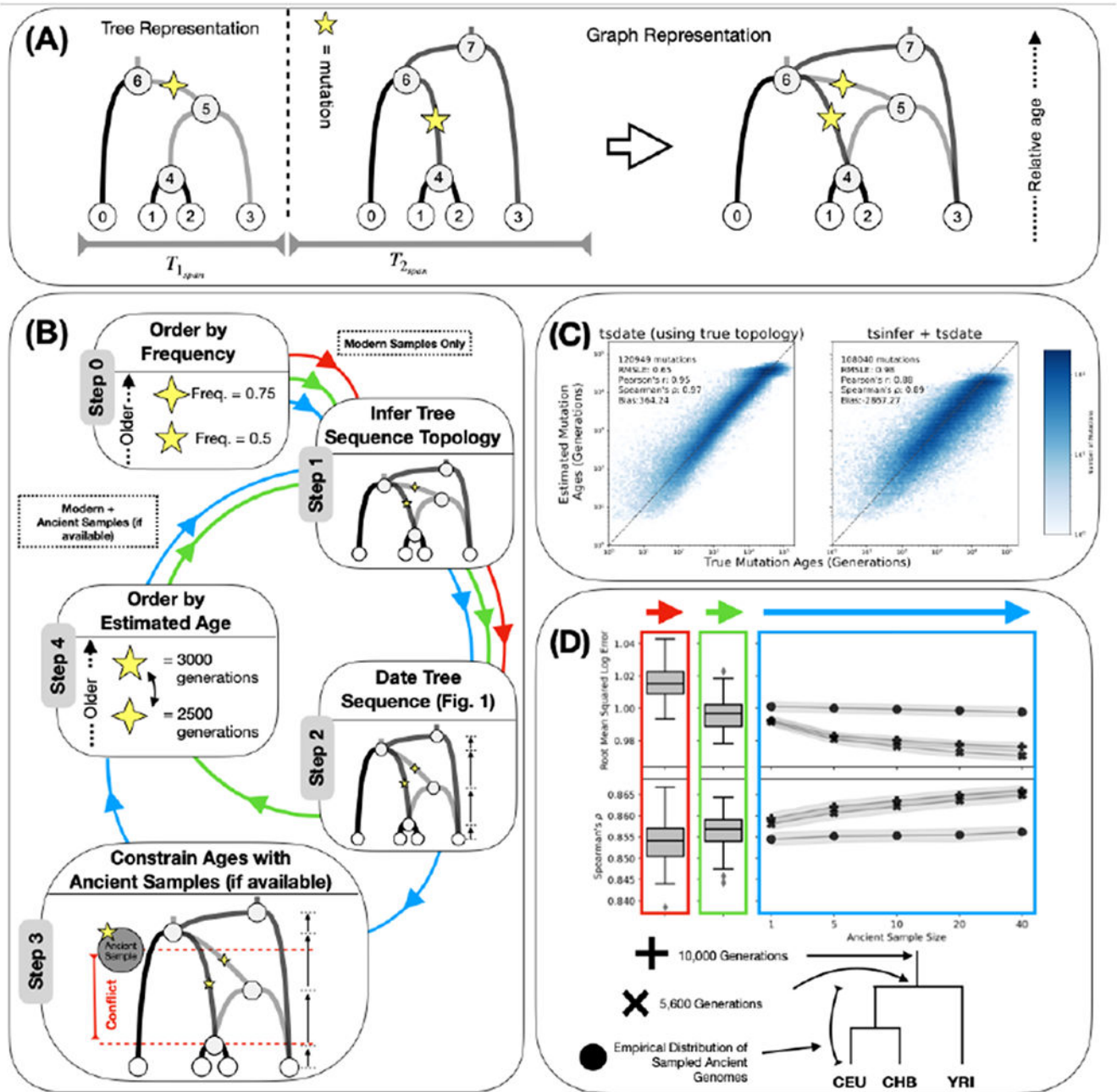
Fig. 1. Schematic overview and validation of the inference methodology.

(**A**) An example tree sequence topology with four samples (nodes 0-3), two marginal trees, four ancestral haplotypes (nodes 4-7), and two mutations. T_{span} measures the genomic span of each marginal tree topology, with the dotted line indicating the location of a recombination event. The graph representation is equivalent to the tree representation. (**B**) Schematic representation of the inference methodology. Step 0: alleles are ordered by frequency; the mutation represented by the four-point star is considered to be older. Step 1: the tree sequence topology is inferred with *tsinfer* using modern samples. Step 2: the tree sequence is dated with *tsdate*. Step 3: node date estimates are constrained with the known

age of ancient samples. Step 4: ancestral haplotypes are reordered by the estimated age of their focal mutation; the five pointed star mutation is now inferred to be older. The algorithm returns to Step 1 to re-infer the tree sequence topology with ancient samples. Arrows refer to modes of operation: Steps 0, 1 and 2 only (red); Steps 0, 1, 2, 4, 1, and 2 (green) and Steps 0, 1, 2, 3, 4, 1, 2 (blue) (24). (**C**) Scatter plots and accuracy metrics comparing simulated (x-axis) and inferred (y-axis) mutation ages from *msprime* neutral coalescent simulations, using *tsdate* with the simulated topology (left) and inferred topology from *tsinfer* (right). (**D**) Accuracy metrics, root-mean squared log error (top) and Spearman rank correlation coefficient (bottom), with modern samples only (first panel), after one round of iteration (second panel) and with increasing numbers of ancient samples (colored arrows as in panel B). Ancient samples from three eras of human history are considered as in the schematic (24).
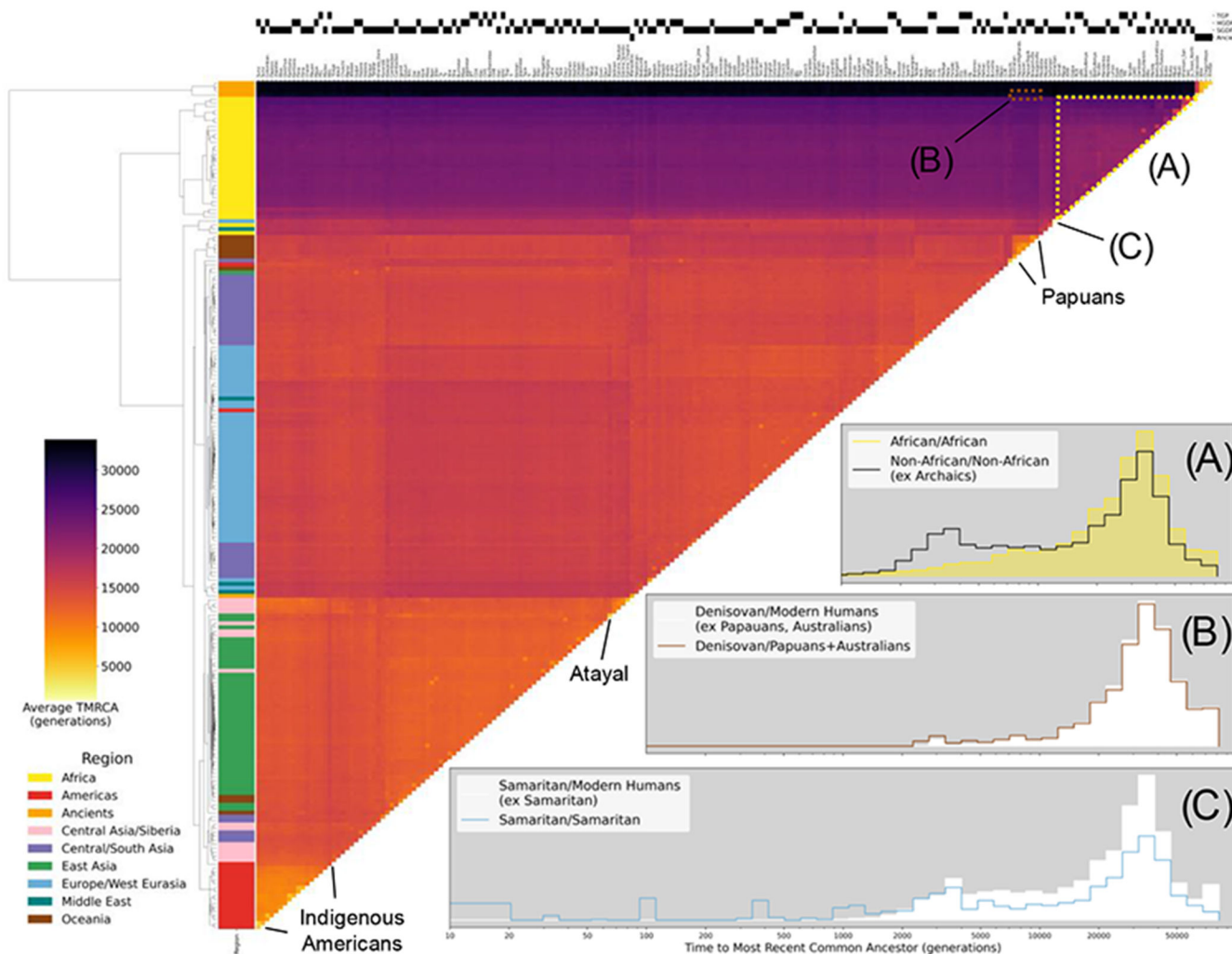
Fig. 2. Clustered heatmap showing the average time to the most recent common ancestor (TMRCA) on chromosome 20 for haplotypes within pairs of the 215 populations in the HGDP, TGP, SGDP, and ancient samples.

Each cell in the heatmap is colored by the logarithmic mean TMRCA of samples from the two populations. Hierarchical clustering of rows and columns has been performed using the UPGMA algorithm on the value of the pairwise average TMRCAs. Row colors are given by the region of origin for each population, as shown in the legend. The source of genomic samples for each population is indicated in the shaded boxes above the column labels. Three population relationships are highlighted using span-weighted histograms of the TMRCA distributions: (**A**) average distribution of TMRCAs between all non-African populations (black line) compared to African/African TMRCAs (solid yellow). (**B**) Denisovan and Papuan/Australian TMRCAs (solid line), compared to the Denisovan against all non-Archaic populations (solid white). This subtle but unique signal of elevated recent ancestry between the Denisovan and Papuans/Australians is particularly evident in Interactive fig. S1 at https://awohns.github.io/unified_genealogy/interactive_figure.html. (**C**) TMRCAs between the two Samaritan chromosomes (solid line), compared to the Samaritans/all other modern humans (solid white). Selected populations with particularly recent within-group

TMRCAs are indicated. Duplicate samples appearing in more than one modern dataset are included in this analysis. Interactive Figure S1 is an interactive version of this figure and is available at: https://awohns.github.io/unified_genealogy/interactive_figure.html.
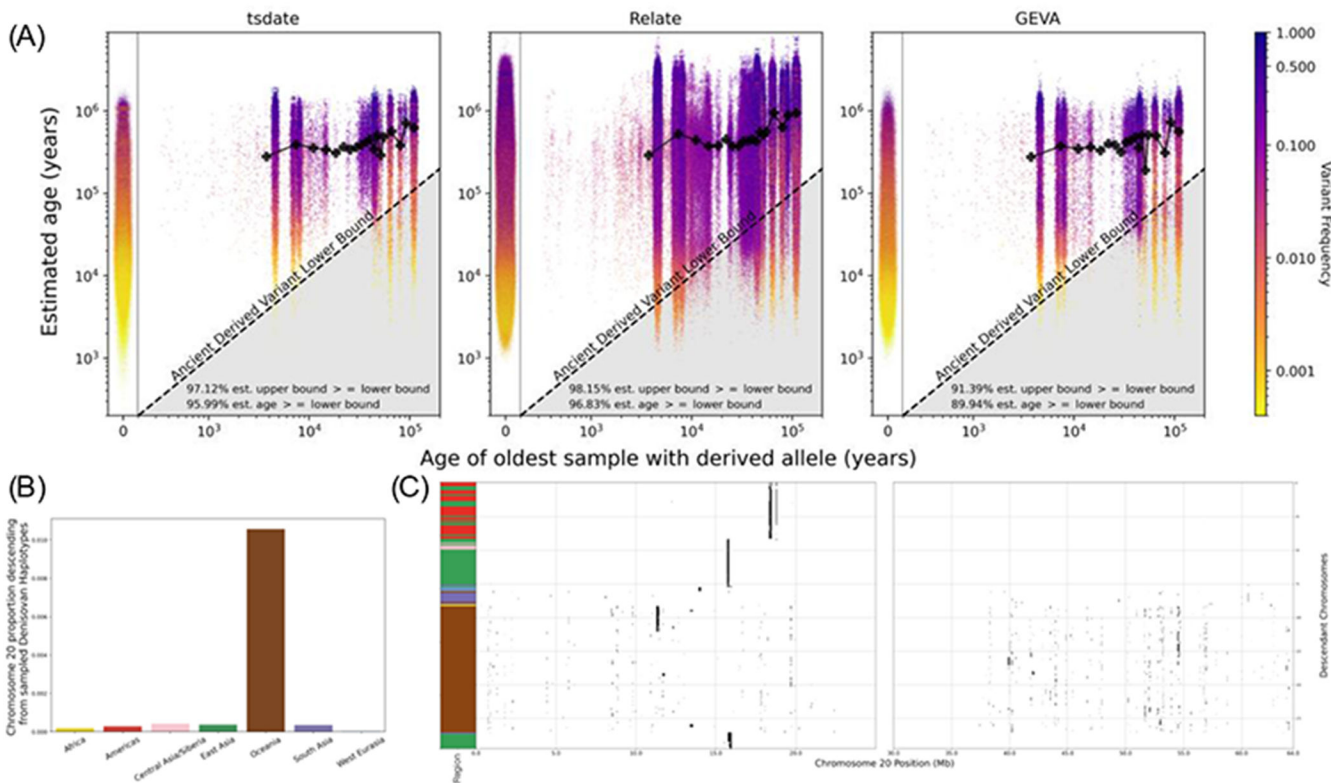
Fig.3. Validation of inference methods using ancient samples.

(**A**) Comparison of mutation age estimates from *tsdate*, *Relate* and *GEVA* with 3,734 ancient samples at 76,889 variants on chromosome 20 (note that *Relate* estimates ages separately for each population in which a variant is found). The radiocarbon- dated age of the oldest ancient sample carrying a derived allele at each variant site in the 1000 Genomes Project is used as the lower bound on the age of the mutation (diagonal lines). Mutations below this line have an estimated age that is inconsistent with the age of the ancient sample. Black lines on each plot show the moving average of allele age estimates from each method as a function of oldest ancient sample age. Plots to the left show the distribution of allele age estimates for modern-only variants from each respective method. Additional metrics are reported in each plot. (**B**) Percentage of chromosome 20 for modern samples in each region that is inferred to descend from Denisovan haplotypes, calculated with the genomic descent statistic (57). (**C**) Tracts of descent along chromosome 20 descending from Denisovan haplotypes in modern samples with at least 100 kilobases (kb) of total descent (colors as in Fig. 2).
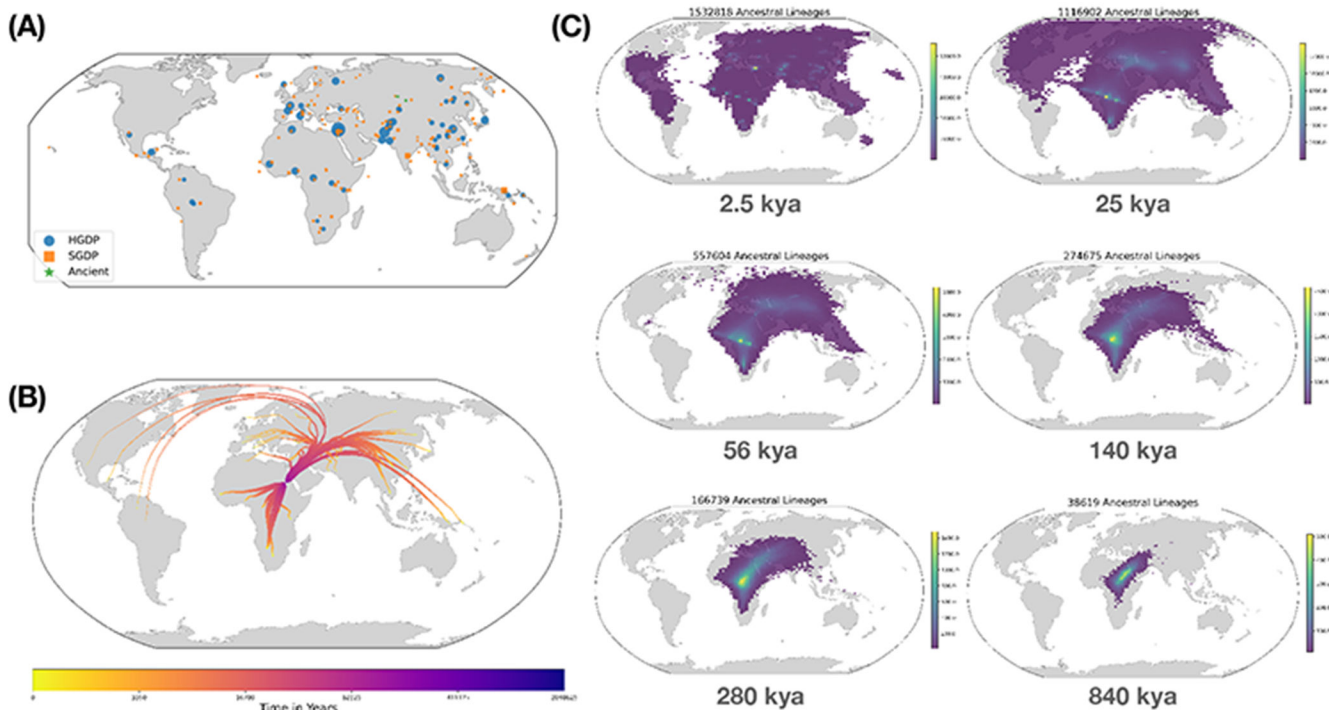
Fig. 4. Visualization of the non-parametric estimator of ancestor geographic location for HGDP, SGDP, Neanderthal, Denisovan, and Afanasievo samples on chromosome 20.

(**A**) Geographic location of samples used to infer ancestral geography. The size of each symbol is proportional to the number of samples in that population. (**B**) The average location of the ancestors of each HGDP population from time t=0 to ~2 million years ago. The width of lines is proportional to the number of ancestors of each population over time. The ancestor of a population is defined as an inferred ancestral haplotype with at least one descendant in that population. (**C**) 2d-histograms showing the inferred geographical location of HGDP ancestral lineages at six time-points. Histogram bins with fewer than 10 ancestors are not shown. Note that the geographic concentration of ancestors at more recent times is an artifact of uneven sampling and our geographic inference method.