

The population history of northeastern Siberia since the Pleistocene

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Northeastern Siberia has been inhabited by humans for more than 40,000 years but its deep population history remains poorly understood. Here we investigate the late Pleistocene population history of northeastern Siberia through analyses of 34 newly recovered ancient genomes that date to between 31,000 and 600 years ago. We document complex population dynamics during this period, including at least three major migration events: an initial peopling by a previously unknown Palaeolithic population of ‘Ancient North Siberians’ who are distantly related to early West Eurasian hunter-gatherers; the arrival of East Asian-related peoples, which gave rise to ‘Ancient Palaeo-Siberians’ who are closely related to contemporary communities from far-northeastern Siberia (such as the Koryaks), as well as Native Americans; and a Holocene migration of other East Asian-related peoples, who we name ‘Neo-Siberians’, and from whom many contemporary Siberians are descended. Each of these population expansions largely replaced the earlier inhabitants, and ultimately generated the mosaic genetic make-up of contemporary peoples who inhabit a vast area across northern Eurasia and the Americas.

Northeastern Siberia (the modern Russian Far East) is one of the most remote and extreme of the environments that were colonized by humans in the Pleistocene epoch. Extending from the Taimyr Peninsula in the west to the Pacific Ocean in the east, and north from the border between China and Russia to the Arctic Ocean, the region is currently home to dozens of diverse ethnolinguistic groups. Recent genetic studies of the indigenous peoples of this land have revealed complex patterns of admixture, which are argued to have occurred largely within the past 10,000 years^{1–3}. Humans have been in the region for far longer^{4–6}, but their origins and the demographic processes of this deeper population history are largely unknown. The earliest, most secure archae-

ological evidence for human occupation in this region comes from an artefact-rich, high-latitude (approximately 70° N) site on the Yana River (Siberia) named Yana RHS, which dates to 31,600 calibrated years before present (taken as AD 1950)⁴ (Fig. 1). Yana RHS yielded a flake-based stone tool industry and sophisticated bone and ivory artefacts, which are reminiscent of technologies seen in the Upper Palaeolithic in Eurasia and southern Siberia^{5,7} (Extended Data Fig. 1). By the time of the Last Glacial Maximum (LGM) at about 23–19 thousand years ago (ka)⁸, the archaeological culture seen at Yana RHS had disappeared from northeastern Siberia. Instead, archaeological lithic assemblages at this time are dominated by a distinctive microblade technology, which

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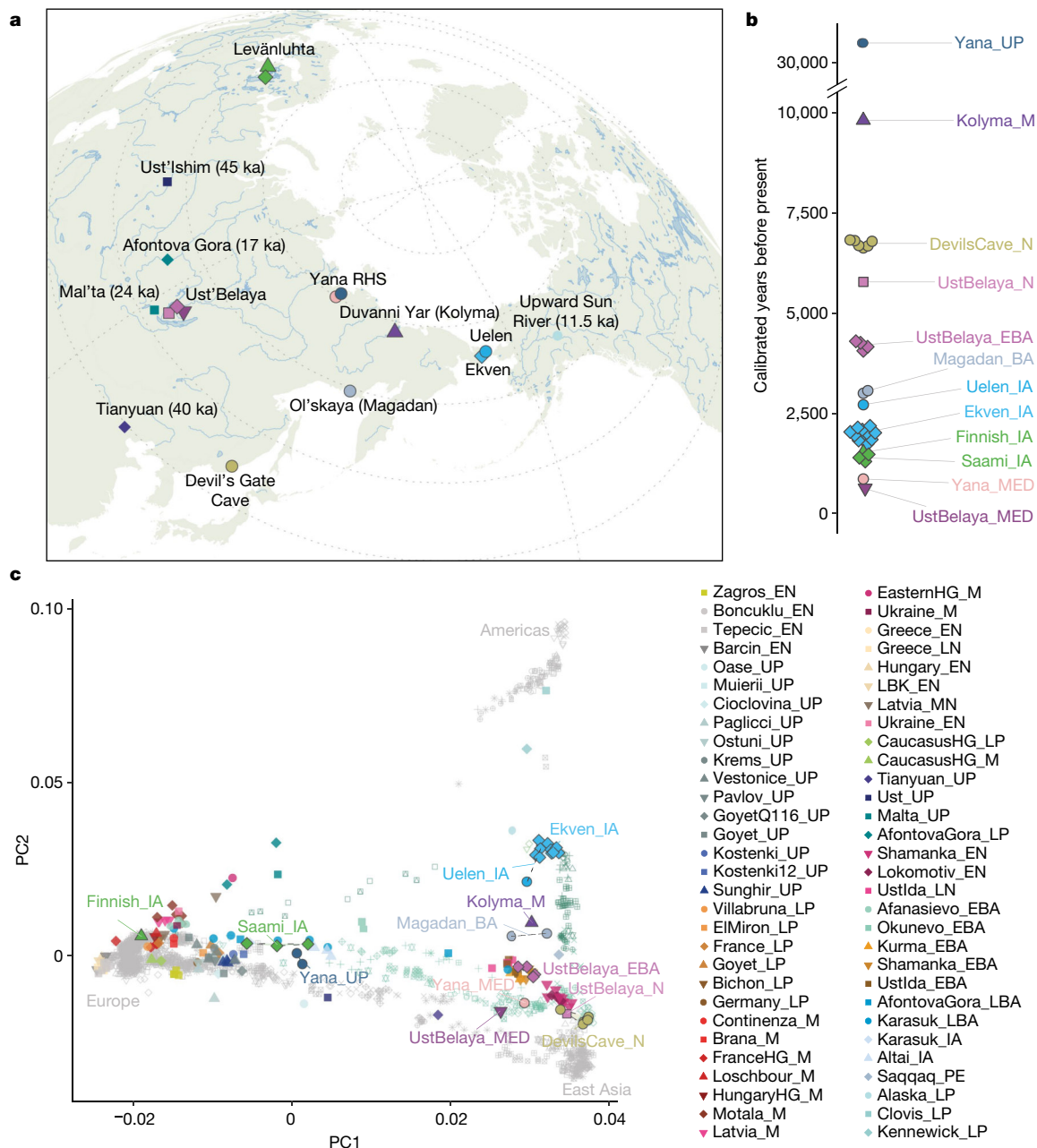


Fig. 1 | Genetic structure of ancient northeast Siberians. **a**, Sampling locations of newly reported individuals, as well as select previously published individuals with dates in parentheses. **b**, Sample dates. **c**, Principal component (PC) analysis of 257 ancient individuals projected onto a set of 1,541 modern Eurasian and American individuals.

Abbreviations in group labels: UP, Upper Palaeolithic; LP, Late Palaeolithic; M, Mesolithic; EN, Early Neolithic; MN, Middle Neolithic; LN, Late Neolithic; N, Neolithic; EBA, Early Bronze Age; LBA, Late Bronze Age; IA, Iron Age; PE, Palaeo-Eskimo; MED, Medieval; HG, hunter-gatherer.

spread in a time-transgressive manner north and east out of the Amur region^{9,10}. This tradition did not reach Chukotka or cross the Bering land bridge (Beringia) until the end of the Pleistocene—later than the earliest known sites in the Americas. Changes in material culture in northeastern Siberia continued into the late Holocene epoch, but it remains debated whether these successive cultural complexes represent in situ technological evolution or migrations of distinct groups of people. In the case of the latter, it is unclear how these groups may have been related to each other, to contemporary Siberians, or to Native Americans, whose ancestors may have emerged in this region (or, at the very least, traversed it en route to Beringia).

To investigate these questions, we used single-end shotgun sequencing to generate whole genomes of 34 ancient individuals with associated radiocarbon ages that range from 31,600 to 600 calibrated years before present (Fig. 1, Supplementary Information 1, 2, Supplementary

Tables 1, 2). Our data include samples from ancient individuals that are key for understanding Siberian population history: two high-quality genomes sequenced from fragmented milk teeth (Supplementary Information 2) that were recovered from Yana RHS (Yana1 and Yana2, which produced genomes at 25× and 7× coverage, respectively), which are the oldest Pleistocene human remains found to date at such high latitude; a high-coverage genome (14× coverage) of an individual from the Duvanni Yar site at the Kolyma River (Kolyma1), dated to about 9.8 ka; 14 genomes from ancient individuals from sites in far eastern Chukotka (Ekven and Uelen) and the northern coast of the Sea of Okhotsk (Ol'skaya, near the city of Magadan), ranging in age between 3 and 2 ka; 6 individuals from the approximately 7,600-year-old site of Devil's Gate Cave in northern East Asia¹¹; 6 genomes of individuals from southern Siberia (Ust'Belaya in the Lake Baikal region) dating to between 6.5 ka and 0.6 ka; an individual from the Yana River but from

a different locality than Yana RHS, here named ‘Young Yana’ (dated to 0.8 ka); as well as 4 individuals from the Levänluhta site in southwestern Finland, dated to approximately 1.5 ka. We analysed these data in the context of large panels of previously published ancient and present-day individuals (Supplementary Information 3, Supplementary Tables 3, 4).

Upper Palaeolithic peoples at Yana RHS

The Yana RHS human remains represent the earliest direct evidence of human presence in northeastern Siberia, a population that we refer to as Ancient North Siberians (ANS). The two Yana RHS individuals were unrelated males who carry mitochondrial haplogroup U (which is predominant among ancient West Eurasian hunter-gatherers) and Y chromosome haplogroup P1, which is ancestral to haplogroups Q and R—which are widespread among present-day Native Americans and Eurasians, respectively^{12,13} (Extended Data Fig. 2, Supplementary Information 4, 5, Supplementary Table 1). Genetic clustering using outgroup- f_3 statistics demonstrates broad genetic similarities with a wide range of present-day populations across Northern Eurasia and the Americas. This contrasts with other Upper Palaeolithic Eurasians, such as those from Sungir¹⁴ and Tianyuan¹⁵—who share similar amounts of genetic drift with present-day populations that are geographically more restricted to western Eurasia and East Asia, respectively (Extended Data Fig. 3). Despite their extreme northeastern Siberian geographical location, the Yana RHS individuals are genetically closer to West Eurasians, although symmetry tests using f_4 statistics reject tree-like clade relationships between them, early West Eurasians (Sungir) and East Asians (Tianyuan) (Extended Data Fig. 3d, e, Extended Data Table 1, Supplementary Information 6). Using admixture graphs and outgroup-based estimation of mixture proportions, we find that ANS can be modelled as early West Eurasian with an approximately 22% contribution from early East Asians (Extended Data Fig. 3f, Supplementary Information 6). Demographic modelling of the high-coverage individual Yana1 using a site-frequency-spectrum-based framework indicates an early divergence of the ANS lineage at about 39 ka (95% confidence interval (CI) 32.2–45.8 ka), concomitant with substantial gene flow (approximately 29%; 95% CI 21.3–40.1%) from East Asians, an event that probably occurred very soon after the latter diverged from West Eurasians 43.1 ka (95% CI 33.4–48.6 ka) (Fig. 2a, Supplementary Information 7). Thus, the ANS population represents a distinct lineage with affinities to both early West Eurasians and early East Asians, albeit in a 2:1 ratio. These complex relationships among early Eurasian groups are also supported by the presence of East Asian ancestry and mitochondrial haplogroup M in Western Europe by 35 ka^{16,17}. Finally, we estimate about 2% Neanderthal ancestry in the Yana RHS genomes, which is contained in longer genomic tracts than in present-day individuals, as also shown for other Upper Palaeolithic Eurasians^{14,16} (Supplementary Information 6).

We next investigated how the Yana RHS individuals relate to an ancient Siberian population represented by the Mal'ta individual (dated to 24 ka) from the Lake Baikal region (previously termed ‘Ancestral North Eurasians’), from which Native Americans derive around 40% of their ancestry¹⁸. We find that the Mal'ta individual shares more alleles with the Yana RHS individuals than with other West Eurasian hunter-gatherers (for example, f_4 (Mbuti, Mal'ta; Sungir, Yana) > 0; $Z = 3.99$) (Extended Data Table 1, Supplementary Information 6). The Mal'ta and Yana RHS individuals also exhibit a similar pattern of genetic affinities to both early West Eurasians and East Asians, consistent with previous studies^{19,20}. In admixture graphs, the Mal'ta individual can be successfully fit as a descendant of the ANS lineage, with a minor contribution from an early Eurasian lineage that is ancestrally related to Late Palaeolithic hunter-gatherers from the Caucasus (Extended Data Fig. 3e, f). The Ancestral North Eurasian lineage of the Mal'ta individual can thus be considered a descendant of the ANS lineage, and our results therefore suggest that—by 31.6 ka—people related to the ANS were probably widespread across northeastern Eurasia.

The two Yana RHS individuals were contemporaneous, which provides an opportunity to investigate relatedness and levels of inbreeding

at this remote Upper Palaeolithic settlement. We find that the two individuals were not closely related and did not exhibit signatures of recent inbreeding, with a moderately large estimate of recent effective population size of up to 500 individuals (Extended Data Fig. 4, Supplementary Information 4, 5). Our results mirror those observed at Sungir, an early (approximately 34,000-year-old) European Upper Palaeolithic site located about 4,500 km southwest of Yana RHS, which reinforces the view that wide-ranging mate exchange networks were present among Upper Palaeolithic foragers across the pre-LGM landscape¹⁴.

Ancient Palaeo-Siberians and Native Americans

Following the occupation at Yana RHS, there is an absence of archaeological sites in northeastern Siberia. The area is re-occupied in the later part of the LGM, about 20 ka, when sites preserving a very distinctive stone tool technology become widespread. This gap in the archaeological sequence is critical, as it was within the intervening period that the population ancestral to Native Americans emerged^{18,21}, although no genomes from individuals of this age have been recovered in northeastern Siberia to date. We find that the Kolyma1 individual (dated to 9.8 ka)—who represents a lineage that formed after about 30 ka, which we name ‘Ancient Palaeo-Siberian’—documents the first major genetic shift that we observe in the region (Extended Data Fig. 5). Principal component analysis, outgroup- f_3 statistics and mitochondrial DNA and Y chromosome haplogroups (G1b and Q1a1b, respectively) demonstrate a close affinity between Ancient Palaeo-Siberians and present-day Koryaks, Itelmen and Chukchis, as well as with Native Americans (Extended Data Fig. 5, Supplementary Information 6). Admixture graph modelling shows that the Kolyma1 individual derives from a mixture of East Asian and ANS-related ancestry, similar to that found in Native Americans, although the East Asian contribution is greater in Kolyma1 than in Native Americans (75% versus 63%) (Extended Data Fig. 3f, Supplementary Information 6). For both Ancient Palaeo-Siberians and Native Americans, ANS-related ancestry is more closely related to Mal'ta than to the Yana individuals (Extended Data Fig. 3f), which rejects the hypothesis that the Yana lineage contributed directly to later Ancient Palaeo-Siberians or Native American groups.

We then estimated the demographic parameters of population history models that included the Ancient Palaeo-Siberian Kolyma1 and Native Americans, represented either by Ancient Beringians²¹ (the Upward Sun River 1 (USR1) individual) or present-day Native Americans (Karitiana individuals; Supplementary Information 7). We find that their ancestors diverged at about 30 ka (95% CI 26.8–36.4 ka) from present-day East Asians (represented by Han individuals), consistent with previous results²¹; the subsequent divergence of Ancient Palaeo-Siberians from the population ancestral to Ancient Beringians or Native Americans occurred at about 24 ka (95% CI 20.9–27.9 ka) (Fig. 2, Supplementary Information 7). We infer that both Ancient Palaeo-Siberians and Ancient Beringians received ANS-related gene flow at a similar time (Kolyma1 at 20.2 ka (95% CI 15.5–23.7 ka) and USR1 at 19.7 ka (95% CI 13.3–23.5 ka)). This gene flow amounts to 16.6% (95% CI 7.5–22.2%) of ANS ancestry into the Kolyma1 individual and 18.3% (95% CI 9.8–20.3%) of ANS ancestry into USR1, which is comparable to the estimates we obtained using admixture graphs. An alternative model with a single admixture pulse in the ancestral population of the Kolyma1 and USR1 individuals showed a comparable likelihood (Supplementary Information 7), but differences in the estimated proportions of ANS-related ancestry between Kolyma1 and USR1 favour the two-independent-pulses model. The Kolyma1 individual thus represents the closest relative to the ancestral Native American population in northeastern Siberia that has been found to date.

Changes in climatic conditions are commonly put forward as principal drivers of Pleistocene population movement and regional abandonment in Siberia. We used palaeoclimatic modelling to infer geographical locations in Siberia that were suitable for human occupation between 48 and 12 ka to further investigate this hypothesis. When humans were present at Yana RHS, interstadial climatic conditions meant that a large stretch of the Arctic coast of northeastern Siberia was

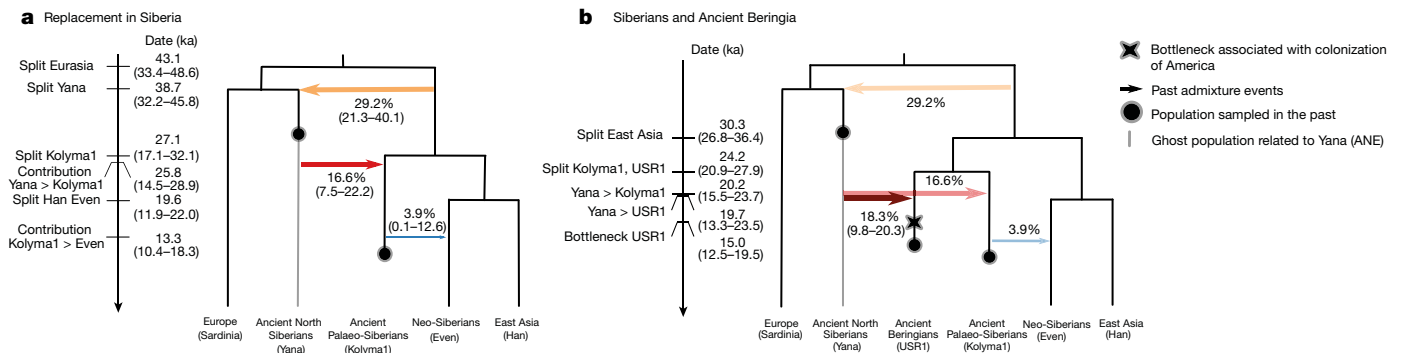


Fig. 2 | Demographic modelling of Siberian and Native American populations. a, b, Inferred parameters for models with ancient and modern Siberian populations (a) and Siberian and Ancient Beringian populations (b). Dates of events (ka) are indicated on the left, and admixture estimates are given as percentages along the arrows. Point parameter estimates are shown with associated 95% CI in parentheses. Neanderthal contribution was modelled as an unsampled ('ghost')

suitable for human occupation (Extended Data Fig. 6, Supplementary Information 8). Conditions in the region became harsher during the LGM, which is consistent with the absence of archaeological sites in the area at this time. However, our models suggest the existence of a refugium across southern Beringia during the LGM (for example, see Alaska in the '22 ka' panel of Extended Data Fig. 6a), consistent with previous reports²². Therefore, a possible scenario for gene flow during the formation of the early Native American and Ancient Palaeo-Siberian gene pools may have involved early ANS-related groups occupying southern Beringia during the LGM, and subsequently admixing with East Asian-related peoples who expanded northwards towards the end of the LGM. This scenario would also be consistent with a divergence of Ancient Beringians from ancestral Native Americans in eastern Beringia rather than in Siberia, which is supported by genetic data (scenario 2 in ref. ²¹). Alternatively, the closer affinity of both Kolyma1 and Native Americans to Mal'ta, rather than the Yana RHS individuals, could suggest a more-southwesterly location (Lake Baikal region) for the admixture, with a northward expansion after the LGM. The alternative scenario is supported by archaeological evidence for a movement south during the LGM, although the genetic isolation that is observed between Asians and ancestral Native Americans after about 23 ka would have required the maintenance of a structured population during the LGM—this, in turn, implies that Ancient Palaeo-Siberians and ancestral Native Americans occupied different refugia. Regardless, our results support the broader implication that glacial and post-glacial climate change was a major driver of human population history across northern Eurasia.

Holocene transformations across Siberia and Beringia

Our genomic data provide further insights into the timing and the origins of peoples involved in more-recent gene flow during the Holocene, across what was by then the Bering Sea. The Saqqaq individual from Greenland (dated to 4 ka²³)—representing Palaeo-Eskimos—clusters with the Kolyma1 individual, but shows a greater affinity to East Asians than Kolyma1 (Fig. 1, Extended Data Table 1). By modelling the Saqqaq individual as a mixture of Ancient Palaeo-Siberians (represented by Kolyma1) and East Asians (represented by the Devil's Gate Cave individuals), we estimate that the Saqqaq individual contains around 20% East Asian ancestry (Extended Data Fig. 7a, b, Supplementary Information 6, Supplementary Table 5). Individuals from the Uelen and Ekven Neo-Eskimo sites (dated to 2.7–1.6 ka), located on the Siberian shore of the Bering Sea, cluster closely with contemporary Inuit individuals (Fig. 1, Extended Data Fig. 8a). We fit them as a mixture of 69% Ancient Palaeo-Siberian (Kolyma1) and 31% Native American ancestry (represented by the Anzick individual associated with Clovis assemblages), thereby documenting a 'reverse'

Neanderthal population contributing 3% into the ancestors of all Eurasian populations, and an extra 0.5% into the Asian lineage. Neanderthal effective population size and split times were fixed according to recent estimates based on the genome-wide site frequency spectrum³⁴. Shaded arrows for the model in b indicate admixture proportions that were fixed to values estimated under model a. ANE, Ancestral North Eurasians.

gene flow across the Bering Sea (from northwestern North America to northeastern Siberia). This is consistent with linguistic evidence for a back-migration into Siberia of a population speaking a language from the Eskimo–Aleut family (Extended Data Table 1; Extended Data Fig. 7, Supplementary Information 6, 9, Supplementary Table 5). The source population of this gene flow post-dates the divergence of the USR1 individual from other Native Americans (at about 20.9 ka²¹), as the individuals at Ekven share more alleles with ancient Native Americans (individuals Anzick-1 and Kennewick Man) than with Ancient Beringians (USR1); this confirms previous results from present-day Inuits²⁴ (Extended Data Table 1). Using linkage-disequilibrium-based admixture dating²⁵ with the Saqqaq and Anzick-1 individuals as source populations, we find a significant signal of admixture linkage disequilibrium, with an estimated date of 100–200 generations before the age of the individuals (Supplementary Information 6). Although these estimates show considerable uncertainty (owing to the limited sample size and genomic coverage), they nevertheless indicate that gene flow from Native Americans into Siberia took place possibly as early as about 5 ka (about 100 generations before the earliest individual from Uelen and Ekven), well after the disappearance of Beringia. Finally, we investigated the genetic affinity between North American populations who speak Na-Dene languages (including Athabascans) and Siberian populations²⁶, which has previously been suggested to relate either to gene flow from a Palaeo-Eskimo source²⁷ or to an unknown source population that was more closely related to Koryaks²¹. We find that the Kolyma1 individual is a better proxy for this source population than the Saqqaq individual, using both admixture graph modelling (Supplementary Information 6) and chromosome-painting symmetry tests (Extended Data Fig. 5); this provides additional evidence against a genetic contribution from a migration of Palaeo-Eskimos (Saqqaq) to contemporary speakers of Na-Dene languages.

The Holocene archaeological record of northeast Siberia is marked by further changes in material culture. We used a temporal transect of ancient Siberians from about 6 ka to 500 years ago to investigate whether these cultural transitions were associated with genetic changes. We find that, in a principal component analysis of present-day non-African populations, most contemporary Siberian populations are arranged along two separate genetic clines. The majority of individuals (referred to as 'Neo-Siberians') lie on an east–west cline that is stretched out along principal component 1, between European individuals at one end and East Asian individuals at the other (Fig. 1). A secondary cline between East Asians and Native Americans along principal component 2 includes speakers of Palaeo-Siberian languages and Inuit populations (Extended Data Fig. 8c). Estimated mixture proportions show that Ancient Palaeo-Siberian ancestry (Kolyma1) was common in other Siberian regions until the early Bronze Age (Extended Data Fig. 7),

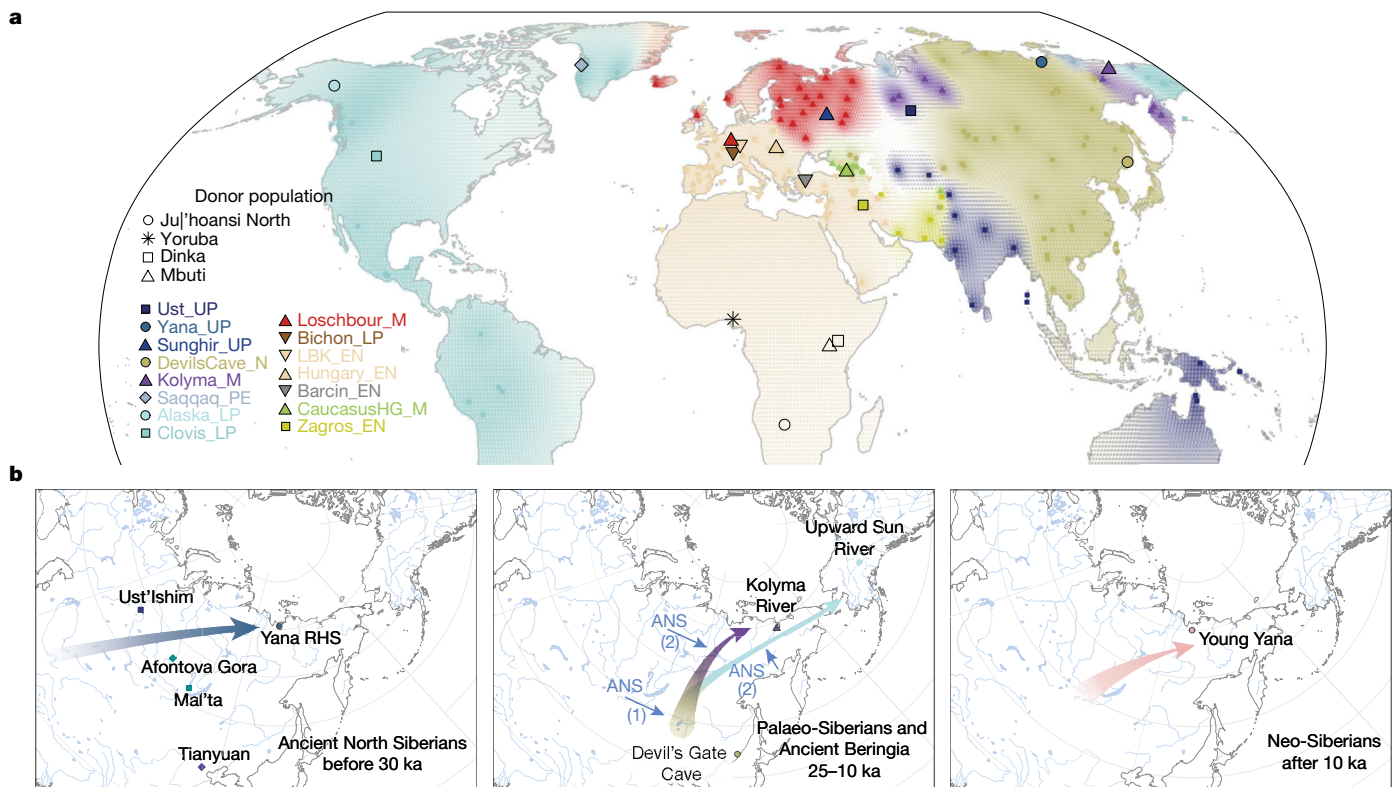


Fig. 3 | Genetic legacy of ancient Eurasians. **a**, Worldwide map of top haplotype donations inferred by chrompainter. Coloured symbols represent a modern recipient population; the colour and shape indicate the donor population that contributes the highest fraction of haplotypes to that recipient population. Geographical locations of donor populations used in this analysis (modern Africans and ancient Eurasians) are indicated by the corresponding larger symbols with a black outline added. Extended regions of shared top donors are visualized by spatial interpolation of the

respective donor population colour. **b**, Major hypothesized migrations into northeast Siberia. Arrows indicate putative migrations that gave rise to ANS (left), Ancient Palaeo-Siberians (middle) and Neo-Siberians (right). Key sample locations for the respective time slice are indicated with symbols. Small blue arrows in the middle panel indicate possible ANS admixture scenarios: (1) admixture in southern Siberia and (2) admixture in Beringia.

but thereafter was largely restricted to the northeast; this is exemplified by an individual from Ol'skaya dated to 3 ka, who closely resembles present-day Koryaks and Itelmen. Using present-day Even individuals to represent Neo-Siberians in our demographic model, we find evidence for a divergence from East Asians at about 20 ka, with only low levels (about 4%) of Ancient Palaeo-Siberian gene flow at around 13 ka (Fig. 2, Supplementary Information 7). Thus, our data provide evidence for a second major population turnover in northeastern Siberia in which Neo-Siberians expanding northwards largely replaced Ancient Palaeo-Siberians; this pattern is also evident in chromosome-painting analyses of present-day populations (Fig. 3). A notable exception are the Ket (an isolated population that speaks a Yeniseian language), who have previously been described as rich in 'Ancestral North Eurasian' ancestry and as having genetic links to Palaeo-Eskimos²⁶. The Ket fall on a secondary cline parallel to Neo-Siberians in the chromosome-painting analysis, and carry about 40% Ancient Palaeo-Siberian ancestry (Extended Data Figs. 8c, 7). Our findings are consistent with the proposed linguistic link between the Yeniseian-speaking Ket and Na-Dene-speaking Athabascan populations (Supplementary Information 9), likely through shared ancestry with an Ancient Palaeo-Siberian meta-population that was more widespread across northern Eurasia before the expansion of Neo-Siberian peoples.

Our Holocene transect reveals additional complexity in recent times, with evidence for further episodes of gene flow and local population replacements. A notable example is found in the Lake Baikal region in southern Siberia; here, the genomes from Ust'Belaya and neighbouring Neolithic and Bronze Age sites show a succession of three distinct genetic ancestries over an approximately 6,000-year period. The earliest

individuals show predominantly East Asian ancestry (represented by individuals from Devil's Gate Cave) (Fig. 1, Extended Data Figs. 7, 8, followed by a resurgence of Ancient Palaeo-Siberian ancestry (up to about 50% ancestry) in the early Bronze Age, as well as the influence of West Eurasian steppe ancestry (about 10% ancestry from individuals associated with the Afanasievo culture) (Extended Data Fig. 7, Supplementary Table 5). This is consistent with previous reports of gene flow from an unknown Ancestral North Eurasian-related source into Lake Baikal hunter-gatherers²⁸. Our results suggest a southward expansion of Ancient Palaeo-Siberians as a possible source. This is consistent with the replacement of Y chromosome lineages observed at Lake Baikal, from predominantly haplogroup N in the Neolithic to haplogroup Q during the early Bronze Age²⁸. Finally, the most recent individual from Ust'Belaya (about 600 years old) falls along the Neo-Siberian cline and is similar to the Young Yana individual from northeastern Siberia (about 760 years old), demonstrating the geographical extent of the Neo-Siberian demographic expansion in the recent past. We show that most populations on the Neo-Siberian cline can be modelled as predominantly East Asian, with varying proportions of West Eurasian steppe ancestry; the largest proportions of this latter ancestry are observed among Altaian populations, both of the present day and in more-recent Bronze Age and Iron Age archaeological contexts (Extended Data Fig. 7, Supplementary Table 5). Together, these findings demonstrate considerable population movement and admixture throughout southern and eastern Siberia during the Holocene, in which groups dispersed in multiple directions—but without clear evidence of the wholesale population replacement seen earlier in the Pleistocene.

Finally, we investigated the geographical extent of these processes of population flux across northern Eurasia. The notable spatial pattern of Ancestral Palaeo-Siberian and East Asian ancestry in present-day populations (Fig. 3) suggests that Ancient Palaeo-Siberian ancestry was once widespread, probably as far west as the Ural Mountains. At the western edge of northern Eurasia, genetic and strontium-isotope data from ancient individuals at the Levänluhta site (Supplementary Information 1) document the presence of Saami ancestry in southwestern Finland in the late Holocene, at about 1.5 ka. This ancestry component is currently limited to the northern fringes of the region, which mirrors the pattern that is observed for Ancient Palaeo-Siberian ancestry in northeastern Siberia. However, although the ancient Saami individuals contain ancestry from an eastern source, we find that this is modelled better by East Asians than by Ancient Palaeo-Siberians, which suggests that the influence of Ancient Palaeo-Siberians probably did not extend across the Ural Mountains into western Eurasia (Extended Data Fig. 7, Supplementary Table 5). East–west gene flow continued to shape the gene pool of the Finnish population into the very recent past. We observe West Eurasian admixture in present-day Saami; by contrast, present-day Finns have greater Siberian ancestry than the ancient Levänluhta individual (Extended Data Table 1), who may represent the Scandinavian component in the dual-origin (Uralic and Scandinavian) gene pool of Finns today.

Discussion

Our findings reveal that the population history of northeastern Siberia is far more complex than previously inferred from the contemporary genetic record. It involved, at a minimum, three major population expansions and subsequent large-scale replacements during the late Pleistocene and early Holocene, with smaller-scale population fluxes since then. These three major waves are also clearly documented in the archaeological record. The initial movement into the region represents a now-extinct ANS population diversifying at about 38 ka, soon after the basal split between West Eurasians and East Asians, which is represented by the archaeological culture found at Yana RHS^{4,29}. This finding is consistent with other studies that have shown that this period was a time of rapid expansion of early modern humans across Eurasia¹³. The arrival of people who carried ancestry from East Asia and their admixture with descendants of the ANS lineage at about 20–18 ka led to the formation of the Ancient Palaeo-Siberian and Native American lineages. In the archaeological record, this is reflected by the spread of a microblade technology that accompanies the post-LGM contraction of the once-extensive mammoth steppe¹⁰. This group was, in turn, largely replaced by Neo-Siberians in the early to mid-Holocene. Our data suggest that the Neo-Siberians received ANS-related ancestry indirectly through admixture with Ancient Palaeo-Siberian groups at about 13 ka, and possibly later from Bronze Age groups from the central Asian steppe after around 5 ka. A signal of Australasian ancestry that has been observed at a very low frequency in some modern and ancient South American populations^{30–32} is not evident in any of the ancient Siberian or Beringian samples sequenced here, or in previous studies²¹.

We find that—despite the complex pattern of population admixture throughout the past 40,000 years—the first inhabitants of northeastern Siberia (represented by the Yana RHS individuals) were not the direct ancestors of either Native Americans or present-day Siberians, although traces of their genetic legacy can be observed in ancient and modern genomes across America and northern Eurasia. These earliest ancient Siberians (the ANS) are known from a handful of other ancient genomes (those of the Mal'ta and Afontova Gora individuals); they are the descendants of one of the early modern human populations that diversified as Eurasia was first settled by our species, and are thus highly distinct. The ANS were later partially assimilated with a group with East Asian affinity who formed the Ancient Palaeo-Siberians (represented by Kolyma1); this group also probably once had a wide geographical distribution across northern Eurasia. The genetic legacy of Ancient Palaeo-Siberians among present-day Siberians is more limited, being restricted to groups in northeastern Siberia. Importantly, this legacy is

also evident in the Americas, which implies that the majority of Native American genetic ancestry is likely to have originated in northeastern Siberia rather than south-central Siberia, as has been inferred from modern mitochondrial and Y chromosome DNA³³. The Neo-Siberians, who occupy much of the range that was previously inhabited by ANS-related and Ancient Palaeo-Siberian groups, represent a more recent arrival that originated further south. The replacement processes we have revealed for the northeastern portion of Siberia are mirrored in far-western Eurasia by the regional displacement and admixture of the Saami people during the late Holocene. This suggests that similar processes probably took place in many other parts of the northern hemisphere.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, statements of data availability and associated accession codes are available at <https://doi.org/10.1038/s41586-019-1279-z>.

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Additional information

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METHODS

No statistical methods were used to predetermine sample size. The experiments were not randomized and investigators were not blinded to allocation during experiments and outcome assessment.

Sample processing and DNA sequencing. The ancient DNA work was conducted in dedicated ancient DNA clean-room facilities at the Centre for GeoGenetics (Natural History Museum, University of Copenhagen) according to strict ancient DNA standards. DNA was extracted from the samples following established protocols^{35,36}. Sequencing libraries were built from the extracts and amplified as previously described^{37,38}, and sequenced on the Illumina platform. Raw reads were trimmed for Illumina adaptor sequences using AdapterRemoval³⁹, and mapped to the human reference genome build 37 using BWA⁴⁰ with seeding disabled⁴¹. Final analysis BAM files were obtained by discarding reads with mapping quality ≤ 30 , removing PCR duplicates with MarkDuplicates (<http://picard.sourceforge.net>) and local realignment using GATK⁴² (Supplementary Information 2, 3).

Authentication, mitochondrial DNA and chromosome Y analyses. Authentication for ancient DNA was carried out by examining fragment-length distributions and nucleotide-substitution patterns that are characteristic for ancient DNA damage, using mapDamage⁴³. Levels of contamination were estimated for all individuals on mitochondrial DNA sequences using schmutzi⁴⁴, as well as on chromosome X for male individuals using ANGSD⁴⁵. Mitochondrial DNA sequences were reconstructed using endoCaller from schmutzi⁴⁴, and haplogroups assigned with HaploGrep⁴⁶. Y chromosome haplogroups were assigned from reads overlapping single-nucleotide polymorphisms (SNPs) included in the Y-chromosome DNA haplogroup tree from the International Society of Genetic Genealogy (<http://www.isogg.org>, version 13.37), as previously described¹⁴. Phylogenetic analysis was carried out on haploid SNP calls from high-coverage individuals obtained with samtools and bcftools⁴⁷, using RAXML⁴⁸ with the ASC_GTRGAMMA model¹³ (Supplementary Information 2, 4).

Analysis panels. Autosomal analyses were carried out on three analysis panels of ancient and modern individuals^{3,14,16,18,20,21,23,28,30,31,35,49–69} and different sets of SNPs. Panel 1 ('HO 1240K') includes modern individuals from worldwide populations genotyped using the Affymetrix HumanOrigins array⁵⁰, merged with ancient individuals with data from shotgun sequencing or genomic capture (the 1240K panel⁷⁰). Panel 2 ('SGDP/CGG 2240K') includes shotgun sequencing data for modern and ancient individuals, as well as selected ancient individuals with genomic capture, all genotyped at SNPs included in the 2240K capture panel^{16,61}. Panel 3 ('CGG WGS') includes all genome-wide SNPs genotyped across high-coverage modern and ancient individuals with shotgun sequencing data. Genotyping was carried out separately for each diploid individual using samtools and bcftools⁴⁷, and filtered as previously described¹⁴ (Supplementary Information 3). Pseudo-haploid genotypes for low-coverage ancient individuals were obtained by sampling a random high-quality read at each covered SNP position of the respective panels.

Population structure and admixture modelling. Population structure was investigated with principal component analysis using smartpca⁷¹. Principal components were inferred using modern as well as high-coverage ancient individuals, followed by projection of low-coverage individuals using lsqproject. Genetic affinities of ancient and modern individuals were investigated with the f -statistic framework⁷², using outgroup- f_3 statistics for estimation of shared genetic drift¹⁸ as well as f_4 statistics for allele-sharing analyses. Standard errors were estimated using a weighted block jackknife with five-megabase block size. Admixture graph modelling was carried out using qpGraph, and outgroup-based estimation of admixture components using qpAdm from the ADMIXTOOLS package⁷² (Supplementary Information 6).

Relatedness and identity-by-descent analyses. Relatedness among the ancient individuals was quantified using the kinship coefficient estimator implemented in KING⁷³, obtained from a pairwise identity-by-state matrix inferred with realSFS, implemented in ANGSD⁴⁵ (Supplementary Information 5). Genomic segments that were homozygous-by-descent or identical-by-descent were inferred for all high-coverage individuals using IBDseq⁷⁴. Distributions of number and total length of homozygous-by-descent segments for effective population sizes were obtained by simulating 100 haploid individuals from a simple two-population demography¹⁴ using msprime⁷⁵.

Demographic modelling. The parameters of alternative demographic scenarios were inferred on the basis of the joint site frequency spectrum, by approximating the likelihood of a given model with coalescent simulations using fastsimcoal2⁷⁶. Demographic modelling was carried out on selected ancient individuals from the CGG WGS panel, merged with a set of genomes of present-day individuals from the Simon's Genome Diversity Project⁶⁸. We discarded singleton SNPs for this analysis to minimize the influence of possible sequencing errors in the ancient individuals. Confidence intervals were obtained using a block-bootstrap approach, resampling blocks of one megabase. Parameters in coalescent time were scaled to time in years, assuming a mutation rate of 1.25×10^{-8} per generation per site⁷⁷ and a generation time of 29 years⁷⁸ (Supplementary Information 7).

Haplotype-sharing analyses. Haplotype-based analyses of population structure were carried out using ChromPainter⁷⁹ on all individuals with diploid genotypes in both the HO 1240K and WGS datasets. We used shapit⁸⁰ to reconstruct phased haplotypes for each individual. Chromosome painting was then carried out as previously described⁸¹. We first estimated the parameters N_e and θ on a subset of individuals (chosen from diverse modern and ancient groups) and chromosomes (2, 9, 16 and 22) using 10 iterations of the expectation-maximization algorithm, separately for each dataset. Chromosome painting for inferring global population structure related to the ancient individuals was then performed by painting all non-African modern individuals as recipients, using African as well as high-coverage ancient individuals as possible donors. Population structure was investigated by multidimensional scaling on the co-ancestry matrix obtained from ChromPainter, both for length and number of shared chunks. For the analysis of Siberian ancestry in present-day Athabascan groups, a second analysis was carried out by painting all Native American groups, using modern Africans and ancient individuals from outside the Americas as potential donors. We quantified differential sharing of pairs of Native American populations A and B with a particular donor group using the symmetry statistic³⁰

$$S(A, B) = \frac{\text{Chunk length recipient A} - \text{Chunk length recipient B}}{\text{Chunk length recipient A} + \text{Chunk length recipient B}}$$

Standard errors were estimated using a block jackknife, dropping each of the 22 chromosomes in turn.

Palaeoclimatic modelling. We used palaeoclimatic modelling to identify regions with the most suitable climatic conditions, in steps of 1,000 years from 48 to 12 ka. We collated a geo-referenced database of modern human fossil and archaeological dated remains, including 936 modern human occurrences across all time intervals. All palaeoclimatic data were gridded to a 1×1 -degree resolution, and all occurrences within a grid cell were aggregated to a single occurrence. Palaeoclimatic conditions were simulated under the HadCM3 (Hadley Centre Coupled Model, version 3) atmospheric-ocean general circulation model, and we selected the three seasonal variables that maximized the climatic signal information: autumn total precipitation, summer average temperature and autumn average temperature. An ensemble of seven different algorithms was used to characterize the climatic niche of modern humans, using the package biomod2. We validated the accuracy of the climatic suitability predictions using cross-validation within each time period. To identify regions with the most suitable climatic conditions across all time periods (from 48 to 12 ka), we estimated the median suitability (and standard deviation) across time intervals for each grid cell (Supplementary Information 8).

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this paper.

Data availability

Sequence data have been deposited in the European Nucleotide Archive (ENA) under accessions PRJEB29700 and PRJEB26336.

Code availability

Source code with functions for calculating f -statistics is available as an R package at GitHub (<https://github.com/martinsikora/admixr>)

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