



Figure 4 | USR1 demographic history in the context of East Asians, Siberians and other Native Americans. **a**, SMC++-inferred effective population sizes with respect to time for Athabascans (NNA), Karitiana (SNA), Han, Koryaks and USR1 (Supplementary Information section 19.1). We used these demographic histories as a basis for fitting a joint model for these populations. **b**, A ‘backbone demography’ was fitted excluding USR1 using momi2, a maximum likelihood approach based

Using frequency-based and ‘enhanced’ D statistics, we found no support for USR1 being closer to Papuans (a proxy for Australasians) than other Native Americans.

We leveraged the position of USR1 on the Native American branch before the NNA–SNA split to re-assess the origins of Athabaskan and Eskimo populations by fitting admixture graphs. We considered a whole-genome dataset, including Siberian, East Asian, Native American and Eskimo groups, as well as Mal’ta (Supplementary Information section 17). The heuristic approach in TreeMix²³ showed that the best proxies for the Asian component in Athabascans and Greenlandic Inuit are Koryaks and the Saqqaq individual, respectively. We then used an incremental approach to fit an f -statistic-based admixture graph¹⁹, including the Kets, which have previously been suggested to share a linguistic and perhaps a genetic link with Athabascans^{10,26}. This approach recapitulated the TreeMix results, and yielded a model in which both Athabascans and Greenlandic Inuit derive from the NNA branch. However, the Asian ancestry in Athabascans is most closely related to the Asian component in Koryaks, whereas the Saqqaq genome is the best proxy for the Siberian component in the Greenlandic Inuit (Fig. 3). We infer the latter is a consequence of Palaeo- and Neo-Eskimos having been derived from a similar Siberian population^{1,15}. This model appears to be a good fit to the data, as the observed f statistic that deviated the most from the model prediction yielded $Z = 3.27$. We also tested the robustness of this model and these predictions by computing individual D statistics and by re-fitting the model using alternative datasets (Supplementary Information section 17.3).

Finally, we inferred the demographic history of USR1 with respect to Native Americans, Siberians and East Asians, using two independent methods: diCal2²⁷ and momi2²⁸ (Supplementary Information sections 18, 19). diCal2 results indicate that the founding population of USR1, Native Americans and Siberians had a very weak structure from around 36 ka up to about 24.5 ka (Supplementary Table 7), which is when the ancestors of USR1 and Native Americans began to diverge substantially from Siberians. USR1 diverged from other Native Americans around 20.9 ka, with a period of ensuing moderate gene flow between them (Supplementary Tables 6 and 7), as indicated by a simulation study that showed a significant increase in likelihood when comparing a ‘clean split’ model to an ‘isolation with migration’ model (Supplementary Information section 18.4). Using momi2 and SMC++²⁹, we estimated a backbone demography in which Karitiana and Athabascans split around 15.7 ka, whereas their ancestral population split from Koryaks about 23.3 ka (Fig. 4). With momi2, we inferred the most likely branch (the population immediately ancestral to NNA and SNA) and time (around 21 ka) for the USR1 population to join the backbone demography,

on a site frequency spectrum (Supplementary Fig. 27), along with the most likely join-on point for USR1 onto the backbone demography (Supplementary Information section 19). We show the likelihood heat map for the latter; warmer colours correspond to a higher likelihood of USR1 joining at a given point. These estimates agree with those obtained using diCal2, a method based on haplotype data (Supplementary Information section 18).

while allowing for possible gene flow between USR and other populations (Fig. 4b and Supplementary Information section 19); results that are consistent with ref. 13 and the diCal2 inference.

These new findings, along with existing data, allow us to place Ancient Beringians within the broader context of the Pleistocene peopling of the Americas. The founding population of Native Americans (consisting of Ancient Beringians and NNA and SNA) began to diverge from ancestral Asians as early as around 36 ka, probably in northeast Asia, as there is no evidence of people in Beringia or northwest North America at this period. A high level of gene flow was maintained between them and other Asians until as late as around 25 ka^{2,13}. The subsequent isolation of the Native American founding population about 24 ka roughly corresponds to a decline in archaeological evidence for a human presence in Siberia³⁰. Both changes may result from the same underlying cause: the onset of harsh climatic conditions during the LGM². These findings, coupled with a divergence date of around 20.9 ka between USR1 and other Native Americans, are in agreement with the Beringian standstill model⁹ (Supplementary Information section 21). Ancient Beringians and the common ancestor of NNA and SNA began to diverge around 20.9 ka, after which gene flow ensued, although whether this only involved the latter or the already differentiated NNA and SNA branches cannot be determined owing to the shallow divergence times among groups.

These findings allow us to consider possible scenarios regarding where ancient Native American populations diverged (Fig. 2 and Supplementary Information sections 20, 21). Scenarios 3–5 require extended periods of strong population structure marking Ancient Beringians, NNA and SNA as separate groups, for which we do not see compelling genetic evidence; these can therefore be rejected. Scenarios 1 and 2 are compatible with our evidence of continuous gene flow among these groups, but differ as to the location of the Ancient Beringians versus NNA and SNA split at 20.9 ka, whether in northeast Asia (scenario 1) or eastern Beringia (scenario 2). Each has strengths and weaknesses relative to genetic and archaeological evidence: scenario 1 best fits the archaeological and palaeoecological evidence, as the earliest securely dated sites in Beringia are no older than around 15–14 ka, and the LGM cold period is unlikely to be associated with northward-expanding populations³⁰. Scenario 2 is genetically most parsimonious, given evidence of continuous gene flow between the Ancient Beringians and NNA and SNA, suggesting their geographical proximity 20.9–11.5 ka, and that all three were isolated from Asian and/or Siberian groups after about 24 ka and form a clade.

Scenarios 1 and 2 are both consistent with the NNA–SNA split at around 15 ka² having occurred in a region south of eastern Beringia.