Peopling of the Americas as inferred from ancient genomics

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In less than a decade, analyses of ancient genomes have transformed our understanding of the Indigenous peopling and population history of the Americas. These studies have shown that this history, which began in the late Pleistocene epoch and continued episodically into the Holocene epoch, was far more complex than previously thought. It is now evident that the initial dispersal involved the movement from northeast Asia of distinct and previously unknown populations, including some for whom there are no currently known descendants. The first peoples, once south of the continental ice sheets, spread widely, expanded rapidly and branched into multiple populations. Their descendants—over the next fifteen millennia—experienced varying degrees of isolation, admixture, continuity and replacement, and their genomes help to illuminate the relationships among major subgroups of Native American populations. Notably, all ancient individuals in the Americas, save for later-arriving Arctic peoples, are more closely related to contemporary Indigenous American individuals than to any other population elsewhere, which challenges the claim—which is based on anatomical evidence—that there was an early, non-Native American population in the Americas. Here we review the patterns revealed by ancient genomics that help to shed light on the past peoples who created the archaeological landscape, and together lead to deeper insights into the population and cultural history of the Americas.

Before the advent of genomics, genetic evidence for the peopling of the Americas relied on studies of mitochondrial DNA (mtDNA)[1–7] and the non-recombining portion of the Y chromosome[8–10]. Although these uniparental markers provided a broad outline of the peopling of the Americas, they are limited in what they can reveal of potentially complex ancestries, population structure and admixture, can be overprinted by gendered and sex-biased cultural practices, and are more susceptible to genetic drift and lineage loss[11,12]. Problems of lineage loss are compounded in the Americas, where the majority of studies of uniparental markers are in present-day populations, which may not be representative of past populations or genetic diversity, owing to the demographic collapse of Indigenous groups after the sixteenth century introduction of infectious diseases by European peoples, and the collateral blows of warfare, famine, enslavement and exploitation[13,14].

Broader and deeper insights into the population history of the Indigenous peoples of the America came with the study of genomes[15], which provide a mosaic of numerous independent genealogies. Their power was expanded when it became possible to recover genomes of the past[16–18]. The first ancient American genome[19], that of a child from the Anzick Clovis site in Montana, dated to 12,800 calibrated years before present, was published in 2014. Since then, genomes of numerous ancient individuals across the Americas have been sequenced (Fig. 1), and are revolutionizing our understanding of the population history of the Americas[20].

However, it is important to stress that our understanding of the history is by no means complete, not least because the number of ancient genomes from the Americas is relatively small, with fewer from North America than South America, because of different heritage preservation laws, as well as Indigenous traditions regarding ancient remains[11,21]. Acknowledging that some interpretations will probably change in coming years, we summarize the currently known genomic evidence for the peopling of the Americas.

Archaeological and geological parameters

The earliest secure archaeological evidence of anatomically modern humans in northeast Asia dates to around 31.6 thousand years ago (ka) at the Yana RHS site[22,23]. This puts humans in the Arctic in the broader vicinity of, although still a considerable distance from, the jumping off point for the Americas, before the onset of the final period of the Pleistocene. By this time, continental ice sheets had begun to build, leading to a decline in global sea levels[24], a process that culminated in the Last Glacial Maximum (LGM) approximately 23–19 ka.

Once relative sea levels in the north Pacific fell around 50 m below their present level, the continental shelf in the Bering Strait region became dry land, creating an approximately 1,800-km-wide (measured north–south) land bridge—the central portion of the region known as Beringia—that linked Asia and America. The land bridge was traversable

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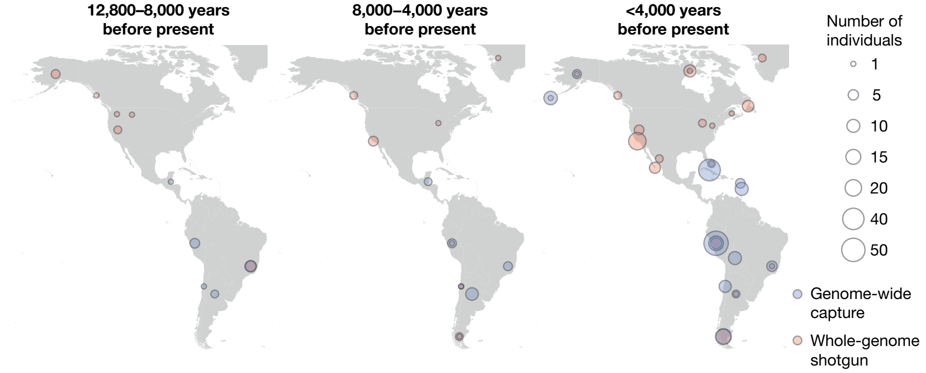

Fig. 1 | Ancient whole-genomes and genome-wide SNP capture analyses from the Americas. Whole-genome (red circles) and genome-wide SNP capture (blue circles) analyses sorted by time and geography. The size of the circles indicates the number of individuals.

possibly as early as around 30 ka, and until it was breached by rising postglacial seas approximately 12 ka[24–27]. Beringia was largely ice-free, although at times, as during the LGM, cold and harsh conditions may have limited movements[20,25,28]. After 12 ka, groups could no longer walk to America, and instead had to cross the Bering and Chukchi Seas, which required seafaring technologies, along with the skills and strategies to cross frigid, frequently storm-prone and seasonally ice-bound waters[29]. This difference in the means and challenges of travel, as well as changes in adaptive strategies, probably also explains the gap between the earliest currently accepted archaeological evidence for the arrival of ancestral Native American populations (around 15.5–15 ka) and the next major population dispersal into the Americas—of the Palaeo-Inuit (previously, Palaeo-Eskimo) (about 5.5 ka)[29,30].

When people first crossed the land bridge is not known, in part owing to the limited archaeological record of northeast Asia. After the Yana occupation, the next oldest archaeological site known, Diuktai Cave in Siberia, was not occupied until 16.8 ka[31]. The absence of evidence over the approximately 15,000 years separating these occupations could be due to groups having abandoned the region[32]. But it is also in some measure owed to the archaeological near-invisibility of what would have been small and highly mobile populations, the vast area to be searched for their sites, and the relatively limited archaeological work that has been carried out in this remote region[33].

The earliest presence of people in eastern Beringia dates to 14.2 ka at the Swan Point site in Alaska[34]. However, this cannot date the first peoples' arrival, as humans were already in North and South America by around 15.5–15 ka[35–38]—the so-called 'pre-Clovis' period (the label is solely a chronological referent; Clovis culture did not extend into South America). The earliest substantial and widespread human presence—the Clovis archaeological complex in North America and contemporaneous groups in South America—appears around 1,500 years later. Whether pre-Clovis and Clovis populations represent historically related groups is not known. Still older sites have been reported south of the continental ice sheets, including ones that predate the LGM[39–41], although the latter remain undemonstrated or disputed[42].

A human presence south of the continental ice sheets by approximately 15.5 ka necessitates a reconsideration of the route(s) that people used to travel southward from Alaska[20]. During the LGM, the Cordilleran and Laurentide ice sheets—which blanketed much of present-day Canada and reached into the northern USA—effectively blocked passage south as early as around 23 ka (Fig. 2). The traditional notion was that people travelled through an ice-free corridor that opened in postglacial times along the eastern flank of the Rocky Mountains[43,44]. This idea has recently been challenged by geological evidence that shows that the corridor was not fully ice-free until around 15–14 ka, and by ancient DNA from both fossil bison and lake sediments, indicating that the plants and animals that hunter-gatherers would have needed for food along the roughly 1,500-km route were not available in the corridor region until about 13 ka[45,46]. Thus, this route would not have been viable early enough for the first peoples' travels.

The absence of an interior route suggests that the first peoples moved south along the Pacific coast. Glacial ice blocked that route as early as around 23 ka, but with the post-LGM retreat long reaches were ice-free after 17 ka and, by 16–15 ka, the coast was largely clear and supported the resources necessary for human travellers[47–49]. A coastal route would have enabled people to reach the Americas south of the continental ice sheets well before the earliest currently accepted archaeological presence. It has been suggested that Clovis groups arrived later via the ice-free corridor[44], but the earliest archaeological evidence of people in the corridor region postdates Clovis time, and appears to mark a northbound rather than a southbound movement[50].

Ancient genomics and first peoples

Genomes from individuals at the Yana RHS site, and the Mal'ta site (dated to 24 ka), show that Siberia was occupied by a population designated 'Ancient North Siberian' (ANS) individuals[51]. This structured population diverged from West Eurasian populations some 39 ka (95% confidence interval, 45.8–32.2 ka), shortly after their split from East Eurasian populations[51–53]. Although the ANS ultimately disappeared as a separate population, traces of their genetic legacy occur in later ancient and some present-day groups, most notably Native American populations, and to varying degrees in Indigenous Siberian groups[51,54,55]. This suggests that the geographical distribution of the ANS in the late Pleistocene must have extended, on aggregate, across most of Siberia and possibly into Beringia.

Current evidence suggests that around 23–20 ka, there was gene flow between an ANS group and an East Asian group. It was previously hypothesized that admixture might have taken place in or east of the Lake Baikal region, or perhaps further north and east in western Beringia, based on the known locations of the populations involved (one in Siberia and the other in eastern Asia)[51]. Additional evidence will be needed to resolve which, if either of those scenarios is correct. Regardless, gene flow between these populations ultimately gave rise on separate occasions (evident in different admixture proportions) to at least two distinct lineages[51,54,56]. One, the 'Ancient Palaeo-Siberians' (based on the genome of the Kolyma individual, dated to 9.8 ka, from the Duvanny Yar site, northeast Siberia[51]), formed the ancestral population of present-day groups of northeast Siberia, such as the Chukchi, Koryak and Itelmen (whose languages fall within the Palaeo-Siberian linguistic family[57]). The other lineage became the basal American branch, whose descendants ultimately crossed to the Americas[51,54,58,59].

A possible alternative to the timing of the formation of that basal American branch is based on the observation that Afontova-Gora 3 individual (dated to 18 ka[60]), shares more genetic drift with Native American individuals than does Mal'ta[61]. This finding suggests that admixture between Ancient North Siberian and East Asian populations was with a population more closely related to Afontova-Gora 3 than to Mal'ta, and thus that the formation of the basal American lineage took place after the LGM, rather than before. However, without additional constraints on the divergence time of the Afontova-Gora 3 and Mal'ta

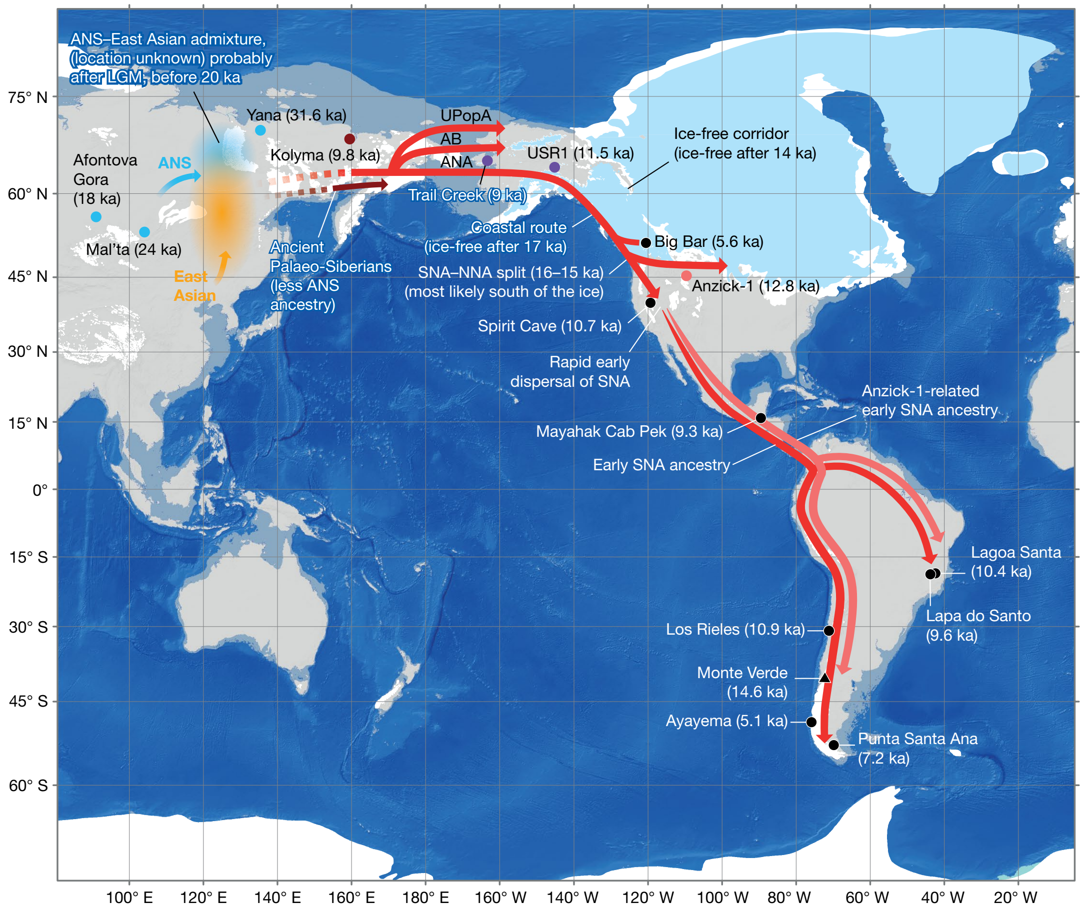

Fig. 2 | Schematic of the processes of human dispersal and divergence into and within the Americas in the Pleistocene. ANA, ancestral Native American individuals; AB, ancient Beringian individuals; ANS, ancient North Siberian individuals; NNA, northern Native American individuals; SNA, southern Native American individuals; UPopA, unsampled population A. Circles indicate key sites and ancient human genomes as well as their ages. The position of the North American ice sheets at the LGM is shown in white, and the position of the ice sheets at 15.5 ka in blue. The Bering Land Bridge (Beringia) is shown at its LGM position.

populations, no secure inferences can be made about the timing of the admixture. It remains possible that gene flow occurred even before 24 ka (the age of Mal'ta), as long as it happened after the population represented by Mal'ta diverged from the population represented by Afontova-Gora 3. Therefore, precisely where and when the basal American branch emerged remains uncertain.

Nonetheless, its emergence must have been before approximately 21–20 ka (thus suggesting admixture before the LGM), as by then the basal American branch had begun to diverge into separate lineages, and none shows evidence of subsequent gene flow from Ancient Palaeo-Siberian or other northeast Asian populations[58,59]. It is noteworthy that Native American individuals have only ANS and East Asian ancestry; northeast Siberian individuals have different ANS and East Asian proportions, as well as additional ancestries[51,54]. This suggests that the basal American branch was geographically isolated early on, perhaps in western Beringia (northeast Asia) or further to the south[54,58]. One possibility is that the inhospitable climate and environment of the LGM led to the separation of the groups and the isolation of the basal American branch, and subsequent divergences within it. This could have happened if—as has been suggested—portions of the regions were abandoned during this time[31,32], although for reasons noted above, the issue of abandonment is debated and difficult to test.

LGM isolation is in keeping with the Beringian standstill model[56,62–65], which proposes that dispersal into the Americas did not happen immediately, but instead followed an extended pause, possibly in the region of the land bridge. From that isolated population, several lineages emerged: unsampled population A (UPopA), a 'genetic ghost' of which little is currently known, 'Ancient Beringian' individuals, and 'Ancestral Native American' (ANA) individuals[59] (Fig. 2). All three populations ultimately crossed into North America, but the deep divergence and limited gene flow between them indicates that they probably did so in separate movements.

Although the Ancient Beringian individuals crossed into Alaska, they evidently did not continue farther south; no members of this population are known from south of the continental ice sheets. At some point after around 9 ka (the age of the Trail Creek Cave individual, the most recent Ancient Beringian known from Alaska), this population disappeared; Indigenous groups who live in the region today are not closely related[58,59]. Nonetheless, Ancient Beringian individuals are closer to other past and present Native American individuals than to any other contemporary human population.

There were successive internal splits within the ANA lineage: the first at around 21–16 ka when the 'Big Bar' lineage branched off from the ANA line[59] and then at about 15.7 ka (95% confidence interval 17.5–14.6 ka), when there was a split between Northern Native American (NNA) and Southern Native American (SNA) populations[19,56,66–68]. As the Big Bar lineage is known from the Pacific Northwest but not from Alaska, and is phylogeographically earlier than the NNA–SNA split, it must have diverged as groups moved south from eastern Beringia (Alaska)[59,66]. This suggests that the NNA–SNA split occurred even farther to the south, consistent with the fact that NNA–SNA groups are genetically equidistant to Ancient Beringian individuals[58].

This evidence suggests that Ancestral Native American individuals crossed Beringia and reached North America south of the continental ice sheets ahead of Ancient Beringian individuals. Alternative possibilities include that all of these populations diverged while occupying the same region of northeast Asia or Beringia, although that requires an extended period of a strong population structure, for which there is currently no evidence. Or perhaps all groups arrived in eastern Beringia as part of the same population[58], after which NNA–SNA groups split and moved south of the continental ice sheets. This too seems less likely given that Ancient Beringian and Ancestral Native American peoples are associated with very different cultural repertoires[20,31,69], although cultural divergence may not be congruent with population divergence[70]. Resolving which of these is correct will require additional evidence.

The dispersal patterns of NNA and SNA groups, once south of the continental ice sheets, were quite different. NNAs appear to have remained in northern North America; the suggestion that they may have reached South America[68] has not been supported[21]. At some time in the Holocene—perhaps after the disappearance of Ancient Beringian peoples—NNA groups must have shifted further northward, as they are presently in Alaska and the Yukon[58,59,68].

There is archaeological evidence of people at around 12.6 ka in the ice-free corridor region, which was by then traversable. This evidence points to a northward dispersal of people whose material culture appears historically related to the older Clovis tradition[50]. Yet, Clovis falls on the SNA branch, and there is no evidence of SNA groups in Alaska today[19]. This implies several possible scenarios: that the Clovis culture included NNA individuals; that there was more than one back-track into the Arctic and the NNA groups who live presently in the region were a different and later northward movement; or that the NNA–SNA split occurred north of the continental ice sheets[66,71]. Current evidence cannot eliminate either of the first two possibilities. If the last is correct, it must also shift northward the divergence of the Big Bar lineage, which seems unlikely, given the closely timed splitting of the Big Bar, NNA and SNA groups, as well as the widespread distribution of SNA groups south of the continental ice sheets after around 16 ka[59,72].

In contrast to NNA groups, SNA populations rapidly spread southward, which is evident in the close genetic links between ancient individuals who lived at roughly the same time (around 10 ka) but thousands of kilometres apart in North and South America[21,59,68]. The rapidity of the SNA dispersal matches what was long suspected of early movements based on the near-contemporaneity of the earliest archaeological sites in North and South America[73]. It may not have been a single radiation; there appear to have been at least two late Pleistocene pulses of SNA groups into South America, given the different degrees of affinity that ancient individuals in Argentina, Brazil and Chile have to Anzick[21,74]. It is also important to acknowledge that the apparent rapidity of the dispersal probably masks slower, smaller-scale movements within and between habitats, although such would be within the error of radiocarbon dating and hence largely undetectable archaeologically[75].

The relatively small size of the incoming population[62,76,77], and the vast distances that they and their descendants covered in their initial movement throughout the hemisphere, increased the chances of isolation and divergence, as is evident in repeated splitting within the SNA lineage as groups made their way south[59], which in turn led to considerable ancestry variability in ancient South Americans[21,67,78].

A notable corollary to the peopling process is seen in the genetic history of dogs, which were possibly domesticated in Siberia or Beringia in the late Pleistocene, and show mtDNA lineage splits from there and into the Americas that roughly coincide with the major splits within the dispersing human populations[79]. It is not surprising that their divergences parallel one another: people could have travelled to the Americas without dogs, but dogs would not have travelled to the Americas without people. As human groups became isolated from one another, so too did the dogs that accompanied them.

To date, there is no genomic evidence that any population from a region other than northeast Asia was an important source of America's first peoples. The controversial claim that the first peoples came from Europe via the North Atlantic, based on an ostensible similarity in stone-tool technology between the Solutrean culture of Pleistocene Europe and Clovis in North America[80], was undermined by the genome of the Anzick Clovis child, which sits squarely on the SNA branch of Ancestral Native American peoples[19]. No ancient or present-day genome (or mtDNA or Y chromosome marker) in the Americas has shown any direct affinities to Upper Palaeolithic European populations[11,81].

Similarly rejected is the assertion that ancient and more-recent skeletons with distinct crania—so-called 'Palaeoamericans'—had different ancestry, possibly related to European, Aboriginal Australian, Japanese Ainu or Polynesian populations, and thus were only distantly related to present-day Native American groups[82–84]. All 'Palaeoamericans' sequenced to date, including those from early in the peopling process (for example, individuals from the Spirit Cave (Nevada, USA, dated to 10.7 ka), Lagoa Santa (Brazil, dated to 10.4 ka) and Kennewick (Washington, USA, dated to 9 ka)), fall well within Native American genetic diversity[21,56,59,85].

In fact, it has now been shown that, with the exception of the later arriving Palaeo-Inuit and Inuit Thule groups, all ancient human genomes from the Americas have closer affinities to contemporary Native American peoples than to any other present-day populations worldwide[11,19,21,56,66–68].

Holocene histories

The millennia of the Holocene saw continued movement of people, both from northeast Asia across the now-open Bering and Chukchi Seas and within the Americas (Fig. 3).

The earliest evidence of groups crossing the Bering Strait appears with the Ocean Bay archaeological tradition, around 5.2 ka[29,30], which is generally consistent with the mid-Holocene population divergence and dispersal also seen in the genomic record[86,87].

Athabaskan groups in northern North America, members of the NNA branch, have slightly more East Asian genetic ancestry than other NNA (or SNA) groups[56]. It was recently suggested that this genetic signal was introduced by 'proto-Palaeo-Eskimos'[86]—ancestors of the 4-thousand-year-old Saqqaq individual from Greenland[88]—with the gene flow into NNA groups estimated to have occurred in Alaska around 5,000–4400 years ago[61,86,89]. However, this interpretation is problematic, given that Ancient Palaeo-Siberians are more closely related to Athabaskan individuals, than is the population related to Saqqaq[51]. In fact, the Ancient Palaeo-Siberians represent the major ancestral component of present-day Palaeo-Siberian peoples[57]—groups such as Ket and Koryak[51,89]. This is evidenced by the Koryak being the closest contemporary population possessing the extra Asian signature found in Athabaskan individuals[58]. Thus, the source population providing additional Asian gene flow into Athabaskan individuals must have been genetically close to the ancestors of contemporary Palaeo-Siberians, Palaeo-Inuit and of Native American peoples. In effect, elements of that population made it to the Americas more than once.

Given that this extra East Asian signal is lacking in Ancient Beringian individuals[58,59], we infer that the contact between this population and Athabaskan peoples took place following the disappearance of Ancient Beringian individuals from Alaska, but before the arrival of Palaeo-Inuit in that same region (thus, between 9 and 5.5 ka as currently estimated)[58,59]. It is hypothesized that language elements were exchanged in this process as well: linguists have argued for links between Athabaskan and the Yeniseian-speaking Ket of central Siberia[86,90]. Leaving aside criticisms of this hypothesis on linguistic grounds[91], the genetic relationship between Ket and Athabaskan is not straightforward[51,89] and, in any case, it is impossible to use ancient DNA to confirm linguistic links[70,86,92].

The later Holocene history of the North American Arctic is marked by two distinctive pan-Arctic archaeological traditions: the earliest Palaeo-Inuit cultures appear in the archaeological record of far northern North America and Greenland around 5.2 ka; they disappear around

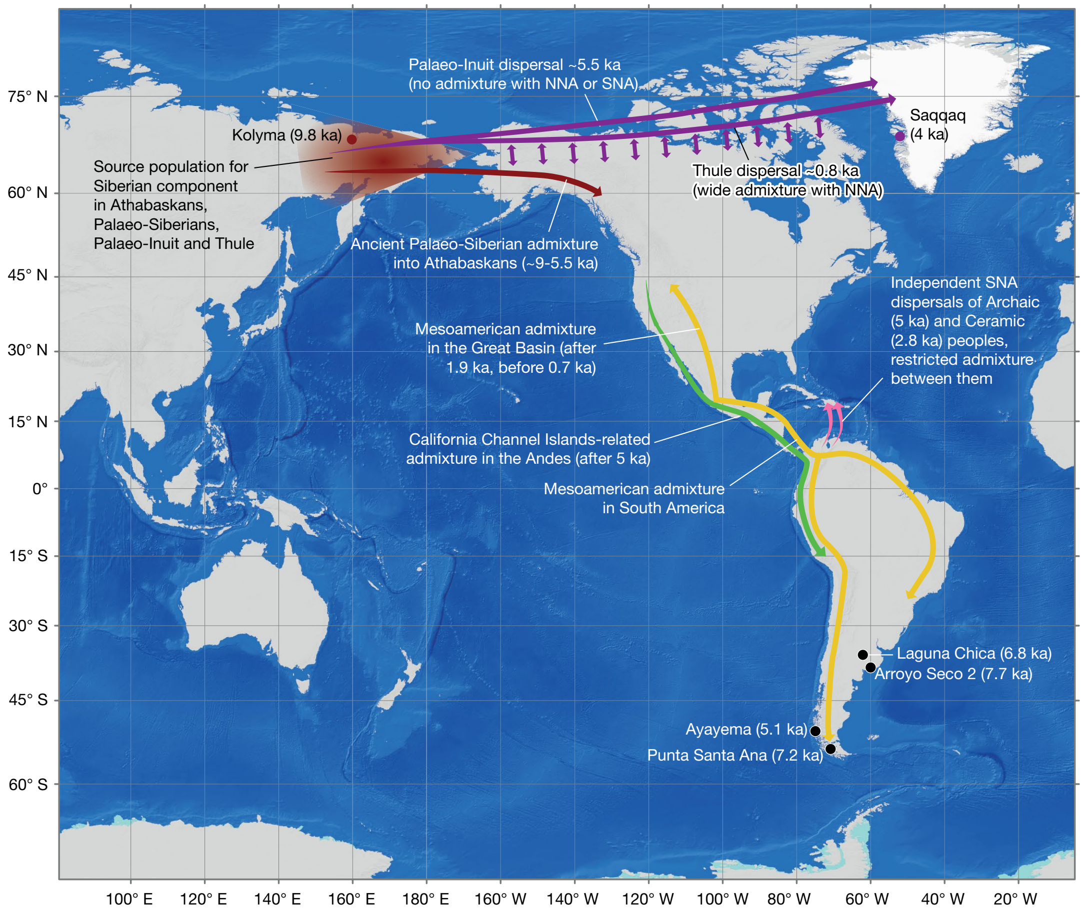

Fig. 3 | Schematic of the processes of human dispersal and divergence into and within the Americas in the Holocene, and to the Caribbean Islands and Greenland in the late Holocene. Circles indicate key sites and ancient human genomes as well as their ages. Glacial ice and sea levels are shown in their present-day position.

AD 1500 (and over that time have different designations depending on age, location and cultural repertoires[30]). They are followed and eventually replaced by people of the Thule culture (previously, Neo-Eskimo), who are generally considered to be the ancestors of present-day Inuit and Iñupiat. Additionally, there is evidence of back migration from the Americas to Siberia, in the genetic composition of ancient Ekven (around 2 ka) and contemporary Chukchi peoples[15,51,63].

Before analyses using ancient genomics, it was unclear how Palaeo-Inuit groups related to one another, or to contemporary Inuit, Aleutian Islanders, Siberian populations, or Athabaskan individuals and other Native American peoples[86,93]. The Saqqaq individual is distinct from Native American individuals and, as noted, is closer to Palaeo-Siberian groups, such as Koryak and Chukchi[88]. Thus, the Palaeo-Inuit represent a population dispersal into the Americas from Siberia that is altogether independent of other Indigenous American peoples[61,87,88]. The limited number of Palaeo-Inuit individuals sequenced so far carry the same mtDNA haplogroup (D2a1[93]), which is consistent with evidence from the Saqqaq genome that the founding population was of small size[88].

The Thule culture developed in the Bering Strait and coastal areas of Alaska, perhaps as early as around AD 200, but around AD 1200 spread rapidly eastward, appearing in Greenland almost simultaneously[29,30]. Genetically, the Thule are a mix of Palaeo-Inuit-related groups and Native American peoples[58,61], and thus it remains unclear whether Thule represent an independent migration into the Americas from Siberia (perhaps having admixed with back-migrating Athabaskan individuals), or if they emerged within Alaska. The Native American component in Inuit derives from NNA groups[58], as might be expected given their geographical proximity.

Palaeo-Inuit and Inuit Thule groups overlapped for several centuries, but archaeologists have questioned whether they ever were at the same place at the same time[94]. Genetically, there is some evidence of admixture between the Palaeo-Inuit and Inuit Thule[87], and also admixture with Athabaskan individuals[86]. However, the degree of gene flow was probably limited—as is also apparent in the genetically distinct dogs that accompanied each of their dispersals[95,96]. Regardless, the Palaeo-Inuit ultimately disappear from the archaeological and genomic records, for reasons still unknown.

The Norse Vikings of Greenland were the first European individuals who reached the Americas (around AD 1000), and based on the occurrence of Norse wares in Indigenous sites they may have met Palaeo-Inuit or, more probably (based on the timing), Inuit Thule and Native American peoples[97]. There is ancient genomic evidence of substantial admixture within Viking Age populations that reflects their complex trading and raiding networks[98], yet there is none that indicates admixture with either Palaeo-Inuit or Inuit Thule. If there was Norse gene flow into Indigenous communities in the Americas, evidence could be sought in individuals who lived between AD 1000–1500.

Farther south during the middle and late Holocene, ancestors of present-day Mesoamerican peoples were expanding and interacting with other SNA populations in both North and South America[59]. This Mesoamerican-related gene flow, which includes traces of UPopA, is evident in the Great Basin of western North America sometime after 1.9 ka, but before 700 years ago (based on genomes from two individuals from Lovelock Cave, Nevada)[59].

The Mesoamerican expansion into South America is evident in several present-day populations, although in different proportions on opposites sides of the Andes, and over an extended period[59]. There is also suggestive evidence of a second, 'non-Anzick' SNA lineage, with an affinity to ancient individuals from the California Channel Islands, who spread into South America around the middle Holocene (approximately 5 ka) and who largely replaced earlier-arriving SNA groups, including descendants of the population with close affinities to Anzick[21,78]. How this ancestry might relate to the Mesoamerican expansion is not clear.

During the middle and late Holocene there were at least two major episodes of population movement onto the Caribbean Islands. The first, after around 6 ka during the Archaic period[99], was originally thought to represent the movement of two separate South American populations[100,101]. However, a subsequent study detected only a single stream of South American ancestry[102]. Sometime after about 2.5 ka, Ceramic Age peoples arrived from northern South America, from a source population that includes Amazon groups, which is consistent with the proposed relationship between the Caribbean Taino and other Arawakan languages of the northern Amazon[101]. The Ceramic and Archaic populations overlapped for an unknown period of time, although there is currently only very limited evidence of admixture[100,102].

By the late Holocene across Central and South America, populations had essentially ‘settled in’, and in many regions there is population continuity over the several millennia before the arrival of European individuals. There is, of course, also continued movement and admixture of populations, although on a much smaller spatial scale than in earlier periods[21,67,74,78]. Even in areas that later saw empires rise, such as that of the Inca, their expansion over large areas did not necessarily involve widespread population movements as seen, for example, during the Neolithic and later times in Eurasia[103]. Even so, these expansions resulted in the genetic landscape becoming far more diverse[67,72,78].

Possible evidence of Pacific contacts

At roughly the same time that Inuit peoples were crossing the Bering Sea to Alaska, Polynesian seafarers reached the remote eastern Pacific island of Rapa Nui (Easter Island). There has long been controversy as to whether they continued east and made landfall on the South American continent (an additional distance of around 3,700 km against unfavourable currents) or whether Native American peoples had sailed westward into the Pacific. Initial genomic studies of the present-day peoples of Rapa Nui suggested a low level of Native American ancestry, estimated to have occurred between AD 1280 and 1425, although how it might have come remains unclear[104]. However, given the ambiguity in the timing of when the admixture occurred, and on the basis of the results of a later study of two ancient Rapa Nui individuals, the inference of Native American ancestry on Rapa Nui was dismissed[105].

The possibility of contact with Pacific peoples has returned with a recent study of several hundred present-day Indigenous peoples who occupy islands in the Pacific Ocean and along the coast of Mesoamerica and South America. Polynesian individuals with Native American admixture most closely related to the Zenu of Colombia are found on half a dozen widely separated eastern Pacific islands. The admixture event is estimated to have occurred in the thirteenth century, far earlier than a European presence in the Pacific, and about the time many of these islands were first settled[106]. It is proposed that this represents the dispersal of Native American individuals into the eastern Pacific, but a more likely scenario—given the abundant archaeological evidence that ties Pacific island settlement to seafaring Oceanic peoples—is that Native American ancestry on these islands is a result of Pacific peoples having visited South America and admixed or returned with Native American individuals. The question of the timing and nature of pre-Columbian Polynesian contacts with Native American peoples will probably only be resolved with the analysis of ancient Polynesian individuals, who could carry a stronger Native American signal than the one detected in present-day Pacific Islanders.

Larger patterns and processes

On a continental scale, ancient genomic and archaeological evidence point to a rapid initial spread throughout the Americas, which was also accompanied by marked cultural changes[20]. The genomic record also confirms that having passed through a substantial bottleneck[62,77], populations increased steeply in the millennia after their arrival, in what may have been “one of the most substantial growth episodes in modern human population history”[62,76].

Despite the rapidity of their initial radiation, the ancient genomic record also reveals that after their dispersal, groups in many regions more or less settled into place. This resulted in population continuity that in some areas extended over thousands of years, which possibly reflects long-sustained but relatively small populations and perhaps a more-limited geographical extent of interaction and exchange[21,56,59,67,78,85].

Population continuity sometimes occurred even under ecological conditions that are thought to be more likely to result in abandonment and replacement. For example, in the western Great Basin of North America, several middle Holocene millennia of severe aridity and drought caused the density of the human population to decline sharply. The archaeological record before and after this period is quite different, and was once thought to signify new group(s) having replaced the previous inhabitants[107]. However, there are strong affinities between the genomes before (the Spirit Cave individual) and after those intervening millennia (Lovelock Cave individuals at 2 and 0.7 ka), even granting the Mesoamerican admixture in the younger of the Lovelock individuals[59].

In other instances ancient genomes reveal discontinuities of two sorts: first, in cases in which ancient individuals have links to present-day people, but not to the people now living in that area (in essence, there was regional abandonment)[21,108]. An example of this are the Palaeo-Inuit, whose DNA fragments appear among some contemporary Athabaskan individuals[15,86]. A second form of discontinuity is in cases in which an ancient population vanished altogether, in the sense that no contemporary individuals derive from that population, such as the Ancient Beringian populations[58]. That said, because the Ancient Beringian population was present in the Arctic for more than 10,000 years, theirs was not in any meaningful sense a ‘failed migration’. Caution is appropriate in making statements regarding population discontinuity or replacement, as ancient samples are inevitably limited relative to the size and distributions of the ancient populations. Regardless, there is reason to suspect that early in the peopling process, small, isolated, dispersing bands pioneering unfamiliar lands who strayed far from distant homelands or kin, and without nearby populations to seek mates, could have disappeared in a few tens or hundreds of years because of a lack of sufficient numbers or from an inability to cope with stochastic events in their new-found environment[109].

Apparent as well is evidence of isolation, owing to both geographical and social barriers. This can be seen in genomic (and also mtDNA and Y chromosome) differences in populations on either side of the Andes, which may also reflect an initial southward dispersal down both sides of the mountain chain, a separation that was maintained over time by the challenge of moving east–west across the mountains[15,72,78,110]. On a smaller scale, there are patterns of regional isolation, seen for example in the divergence of populations between low and high elevation[67,78,111], on islands[21,68] and in the more-remote margins of the continent[59,74].

Social isolation is inferred, for example, from the ancient genomes of middle Holocene-age groups living on the British Columbia coast[66], who are distinct from contemporaneous populations living just a few hundred kilometres inland[59], despite the relative ease of travel—via the Fraser River—between the two areas. The natural richness and diversity of the region apparently allowed groups to inhabit different environmental settings and from that, perhaps, emerged boundaries that maintained population separation.

It is important to emphasize that genomic continuity or discontinuity—or isolation or admixture—are relevant only to the biology of a population, and may not and need not have had a substantial bearing on cultural patterning. For example, Clovis and Western Stemmed Tradition (WST) stone-tool technologies that are present in the Late Pleistocene, are sufficiently distinct that they have been attributed to 'genetically divergent, founding groups'[37]. Yet, as the close similarity between the Anzick (Clovis) and Spirit Cave (Western Stemmed Tradition) genomes shows, they were made by peoples who had strong genetic affinities[59]. Cultural continuity, discontinuity, drift or admixture can proceed independently of population processes. In effect, both population and social dynamics had critical and at times independent roles in shaping the genetic and cultural landscape of regions, and this was true particularly in later periods and in regions in which strong territorial boundaries were established or overrun[11,70,74,112].

Beyond population history

Ancient genomics have also been used to address hypotheses of disease history[108]. For example, it was shown that bacterial strains related to *Mycobacterium tuberculosis*, which is responsible for tuberculosis, were present in humans from Peru 1 ka[113]. Thus, tuberculosis may not have been introduced in the Americas by European individuals, as previously believed, but was present in some pre-Columbian form. Notably, it was found that ancient *Mycobacterium* strains are most closely related to *Mycobacterium pinnipedii*, which is found in seals and sea lions, suggesting that pre-Columbian tuberculosis was transmitted to humans through sea mammals. Thus far, ancient pathogen studies of the Americas are limited, but have the potential to help in understanding the history and long-term health consequences of the introduction of a range of infectious diseases by European peoples, against which Native American communities had only limited or no immunity[14,20,114].

Analyses of ancient DNA can also identify changes in allele frequencies due to natural selection that are driven by changes in environmental conditions and diet, and thereby generate new insights into the interaction between genetic factors and environmental factors that affect disease prevalence—as might have been experienced, for example, when humans first entered the American tropics[115]. The benefits of addressing human disease histories through ancient and contemporary population genomics have recently been reviewed elsewhere[108]. Studies using ancient genomics to address disease issues are still relatively rare, especially among Native American peoples[116,117]. Combining contemporary DNA and functional studies of ancient DNA could constitute a powerful approach to gaining new and beneficial insights into the evolution and underlying genetic causes of lifestyle and metabolic diseases in Native American individuals[108].

To achieve that potential will require more collaborative relationships to be established between the Indigenous and scientific communities[118]. This is necessary to redress a deep legacy of distrust among Native American peoples that is the result of a long history of unethical and exploitative research on Indigenous populations[11,118–121]. Research communities nowadays have stronger guidelines for genetic research on human participants and seek to better protect Indigenous interests, for example, by prohibiting secondary and unapproved uses of samples in ways that are culturally harmful[119,120,122,123]. Nevertheless, in most instances such oversight pertains principally (often solely) to genetic studies with living people, and not to ancient individuals[119]. The use of ancient DNA adds a measure of complexity regarding access to human remains, consent for research on those remains, ownership and distribution of data, most especially in cases in which the ancient individuals are held by an institution and deemed unaffiliated to a community or specific tribe[118,119,121].

Across and between the research and Indigenous communities, efforts are being made to develop ethically sound and collaborative best practices for the study of ancient individuals[118,119], including questioning the ethics of the scientific 'bone rush' that has marked the first decade of ancient genomic research[124]. Time and proper engagement will enable more collaborative relationships to be established[118]. There are already positive developments in that direction, with greater efforts at consultation and cooperation among interested parties to these studies[118,119]. These efforts made possible the application of ancient genomics in what had been highly divisive repatriation cases, such as that of Kennewick Man (the Ancient One), which was resolved with the collaboration of The Confederated Tribes of the Colville who provided DNA samples[85], and of the Spirit Cave individual, when the Fallon Paiute–Shoshone Tribe and Nevada State Museum agreed on moving forward with genomic analyses[59].

Looking ahead to the genomic past

Ancient genomics has transformed our understanding of the population history of the Americas. Nonetheless, there is much we still do not know. For one, it remains unclear whether the claims of very early (for example, before the LGM) archaeological sites[39,41] in the Americas south of the continental ice sheets are legitimate. If they are, it is unclear how these sites fit the extant genomic scenario in which ancestral Native American peoples had not yet emerged as a distinctive population in northeast Asia. If humans were present in the Americas at that time, this suggests that there was an early human presence about which we currently have no secure evidence, archaeological or genetic. Yet, it is also important to stress that there are no ancient genomes from any individuals in the Americas before Clovis times. Hence, it is not known whether pre-Clovis-age populations are on one or the other of the NNA–SNA lines, before that split or another group altogether[21]. In the absence of skeletal remains from the earliest sites in the Americas, ancient environmental genomics may prove helpful, as DNA from higher organisms—plants, animal and humans—can be obtained directly from ancient sediments and could potentially reveal a human presence[46,125–127].

An Australasian genomic signal, albeit faint, has been documented in one ancient individual and present-day individuals from a relatively small region of Brazil[56,59,128]. No other ancient individuals or present-day peoples in South America, North America or northeast Asia contain that signal[59,74]. It has proven difficult to determine whether the signal was present in a highly structured initial population and its absence from regions outside of Brazil is a vagary of sampling; or whether it represents an earlier population in the Americas that had largely disappeared before the arrival of ancestral Native American individuals, with only a slight degree of introgression; or even whether it was a case of later Holocene movement well after the initial spread of peoples throughout the Americas, although given the number of ancient individuals sequenced to date, this last possibility seems increasingly less likely.

As the Australasian signal is scattered across different areas of the genome, it would seem that it is not a case of genetic convergence, or a 'false-positive' signal[21]. Part of the challenge to resolving this issue is the lack of genomic evidence of pre-Clovis-age individuals, which could at least resolve whether the Australasian signal arrived with an earlier group. Similarly, there is a relatively sparse genomic record of Pleistocene human remains from Asia, and the origins and spread of the Australasian signal, if present, should be sought through sequencing of more such individuals—particularly from northeast Asia. It is noteworthy that a recent ancient genome study found evidence of the Australasian genetic signal among hunter-gatherer populations of mainland Southeast Asia dating to the mid-Holocene[129].

Thus, there remains the possibility that other populations contributed to the ancestry of Native American peoples, and some of those populations may be genetic ghosts as, for example, UPopA[59], or are related in ways yet undetected. It is also likely that there were more lineage splits and movements within ancestral Native American populations than the ones that have been detected so far.

Finally, although the ancient genomic record has demonstrated wide-ranging dispersals, extended periods of continuity, episodes of population replacement and evidence of gene flow and admixture, it is largely silent on the question of why people moved (or stayed in place), what occurred when different groups encountered one another (aside from admixture), why some groups vanished and how these processes relate to the record and variation of material culture seen archaeologically[20]. Those questions will require far more integration of the genomic and archaeological records[11,20,70,103], that extend beyond simply noting correlations[74] between genomic and cultural changes. After all, cultural changes can occur independently of population admixture, and not all population admixture leads to cultural changes[20,70].

Note added in proof: The Australasian signal has recently been detected in present day Native American individuals who inhabit the Pacific coast region of South America[130]. This indicates that the range and structure of that signal is greater than previously known. It is inferred that the Australasian signal was introduced by a population that entered the Americas via the Pacific coast[130], but the absence of that signal from ancient individuals in that region, and also from Central and North America, remains unexplained.

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