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Human mobility at Tell Atchana (Alalakh), Hatay, Turkey during the 2nd millennium BC: Integration of isotopic and genomic evidence

Tara Ingman[1]☉*, Stefanie Eisenmann[2]☉*, Eirini Skourtanioti[2], Murat Akar[3], Jana Ilgner[4], Guido Alberto Gnecchi Ruscone[2], Petrus le Roux[5], Rula Shafiq[6], Gunnar U. Neumann[2], Marcel Keller[7], Cäcilia Freund[2], Sara Marzo[4], Mary Lucas[4], Johannes Krause[2,8], Patrick Roberts[4], K. Aslıhan Yener[9]*, Philipp W. Stockhammer[2,10]*

1 Koç University Research Center for Anatolian Civilizations (ANAMED), Koc University, Istanbul, Turkey, 2 Department of Archaeogenetics, Max Planck Institute for the Science of Human History, Jena, Germany, 3 Department of Archaeology, Mustafa Kemal University, Alahan-Antakya, Hatay, Turkey, 4 Department of Archaeology, Max Planck Institute for the Science of Human History, Jena, Germany, 5 Department of Geological Sciences, University of Cape Town, Rondebosch, South Africa, 6 Anthropology Department, Yeditepe University, Istanbul, Turkey, 7 Estonian Biocentre, Institute of Genomics, University of Tartu, Tartu, Estonia, 8 Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany, 9 Institute for the Study of the Ancient World (ISAW), New York University, New York, NY, United States of America, 10 Institute for Pre- and Protohistoric Archaeology and Archaeology of the Roman Provinces, Ludwig Maximilian University, Munich, Germany

☉ These authors contributed equally to this work.
* tara.ingman@gmail.com (TI); eisenmann@shh.mpg.de (SE); akyener12@gmail.com (KAY); philipp.stockhammer@lmu.de (PWS)

Abstract

The Middle and Late Bronze Age, a period roughly spanning the 2nd millennium BC (ca. 2000–1200 BC) in the Near East, is frequently referred to as the first 'international age', characterized by intense and far-reaching contacts between different entities from the eastern Mediterranean to the Near East and beyond. In a large-scale tandem study of stable isotopes and ancient DNA of individuals excavated at Tell Atchana (Alalakh, located in Hatay, Turkey), we explored the role of mobility at the capital of a regional kingdom, named Mukish during the Late Bronze Age, which spanned the Amuq Valley and some areas beyond. We generated strontium and oxygen isotope data from dental enamel for 53 individuals and 77 individuals, respectively, and added ancient DNA data of 10 newly sequenced individuals to a dataset of 27 individuals published in 2020. Additionally, we improved the DNA coverage of one individual from this 2020 dataset. The DNA data revealed a very homogeneous gene pool. This picture of an overwhelmingly local ancestry was consistent with the evidence of local upbringing in most of the individuals indicated by the isotopic data, where only five were found to be non-local. High levels of contact, trade, and exchange of ideas and goods in the Middle and Late Bronze Ages, therefore, seem not to have translated into high levels of individual mobility detectable at Tell Atchana.

Introduction

The identification of human mobility, both of groups and of individuals, has long been a topic of much discussion within archaeology. The Near East during the 2nd millennium BC is a particularly promising arena to explore many of the questions targeting mobility patterns and effects, as it has often been discussed as an era of high levels of interregional connectivity in areas such as trade, diplomacy, and artistic expression, documented by both the material and textual records [1–8]. The wide-ranging social, cultural, and economic contacts of this period have long been understood to involve high levels of individual mobility on a broad scale and across a wide area, as the exchange and movement of traders, artisans, and representatives of kings is well documented [9–13]. However, there have been limited studies of individuals' life histories and broader demographic trends during this time period which are based in bioarchaeology, particularly in the Levant (though much of the isotopic work done on humans has been in both earlier and later periods [14–25]; for 3rd millennium BC Mesopotamia, see also [26]). This restricts the degree to which hypotheses regarding mobility can be effectively tested, although isotopic work done in 2nd millennium BC Middle and Late Bronze Age contexts in Egypt [27], modern Sudan [28, 29], Crete [30, 31], Greece [32, 33], Anatolia [34, 35], and Arabia [36] have indicated differing levels of individual mobility ranging from populations composed primarily of local individuals to those with very high levels of non-locals. Ancient DNA (aDNA) analysis has also begun to illuminate these issues in recent years, with work in the southern Levant [37–43], Iran [42, 44], Anatolia [42, 45–51], and the Aegean [52, 53] stretching across large transects of both time and space. Two recent studies have independently detected gene flow during the 2nd millennium BC from the northeast into the northern [49] and southern Levant [37] that seems to have ultimately originated from the Caucasus and/or Zagros regions. The role of northeastern Syria, northern Iraq, and southern Anatolia as intermediaries in between these distant regions remains unclear, though, due to a lack of sampling.

Tell Atchana (Alalakh), located in the Amuq Valley in modern day Turkey (Fig 1), is one among many urban sites in the Middle and Late Bronze Age (MBA and LBA, respectively; ca. 2000–1200 BC) Levant that functioned as the capital of a local kingdom named Mukish in the LBA, characterized by complex diplomatic and interregional relations and frequently shifting loyalties to bigger entities of the ancient Near East [54–57]. It is therefore a prime candidate for mobility studies, as there is a high likelihood that many different individuals from a wide range of origins both passed through and settled in the city.

Isotope and aDNA analyses are two tools that shed light on the movement of individuals from different angles. With strontium and oxygen isotope ratios from tooth enamel, it is possible to identify people of non-local origin via comparison of measured ratios in the tissue of an individual and the local baseline [58–60]. Analysis of aDNA, on the other hand, sheds light on a person's ancestry [61–63]; compared against a set of available ancient genomes of contemporary and older age from the same region and beyond, the genome of an individual holds key information about locality in terms of genetic continuity or discontinuity in an area through time or in terms of mobility as represented by genetically outlying individuals. While stable isotope analysis has been utilized in archaeology since the 1970s to explore questions of both diet and, later, mobility [58, 64–66], full genome aDNA analyses on a large scale only became available during the last decade [61, 67]. Independently, both methods have proven powerful tools in detecting human mobility and operate independently from archaeological concepts of burial traditions, but the exploration of their tandem potential has only recently started [68–70]. Nevertheless, the combination of both methods has yet to be applied systematically in the ancient Near East.

Fig 1. Regional map showing the location of Tell Atchana (base map data from Natural Earth: Https://www.naturalearthdata.com/. Map made by authors in ESRI ArcGIS).

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In this study, we seek to explore human mobility at Tell Atchana on the basis of the most direct source available, the human remains themselves. In order to explore patterns of mobility at the site, we performed strontium and oxygen isotope analysis and aDNA analysis on bones and teeth of individuals excavated at Tell Atchana from 2003–2017 from a wide range of different contexts. We publish here the first strontium and oxygen isotope data of 53 and 77 individuals, respectively. To an existing dataset of 28 individuals recently published by Skourtanioti et al. [49], we add genome-wide data for another ten individuals that were sampled for the first time and add additional aDNA data to an already published individual increasing its genomic coverage (ALA110, formerly ALA015 in Skourtanioti et al.). With this extensive, in-depth analysis of a large number of individuals from a single site, a study thus far unique for the ancient Near East, we demonstrate how isotope and aDNA data can complement or even contradict each other, and how both strands of evidence can be combined with the archaeological context in order to address questions regarding the nature and scale of individual mobility in the Near Eastern Bronze Age.

Background

Tell Atchana

Situated on the southward bend of the Orontes River in the modern state of Hatay, Turkey (see Fig 1), settlement at Tell Atchana (Alalakh) can be traced back to the terminal Early Bronze Age (EBA) or the earliest MBA (ca. 2200–2000 BC), flourishing throughout the MBA and LBA until its nearly complete abandonment ca. 1300 BC [55–57, 71]. The site was first excavated in the 1930s-1940s by Sir Leonard Woolley [54, 72], who exposed large horizontal swathes of what came to be known as the 'Royal Precinct' of the site (Fig 2) and uncovered a continuous sequence of 18 levels from Level XVII to Level O [54], the latter now known to date to the Iron Age (Table 1) [56, 71, 73]. K. Aslıhan Yener returned to the Amuq Valley in 1995 [74] and resumed ongoing excavations at Tell Atchana in 2003 [55, 56].

Texts from the palace archives dating from the MB II and LB I at Tell Atchana itself and from other sites that mention the city of Alalakh provide ample evidence about the city's significance as the capital of the region and its relations of exchange with its neighbors, such as Ebla, Ugarit, Halab, Emar (all located in modern Syria; see Fig 1), and cities in Cilicia, as well as entities located further away, like the state of Mitanni, Mari, the Kassite kingdom of Babylonia, the
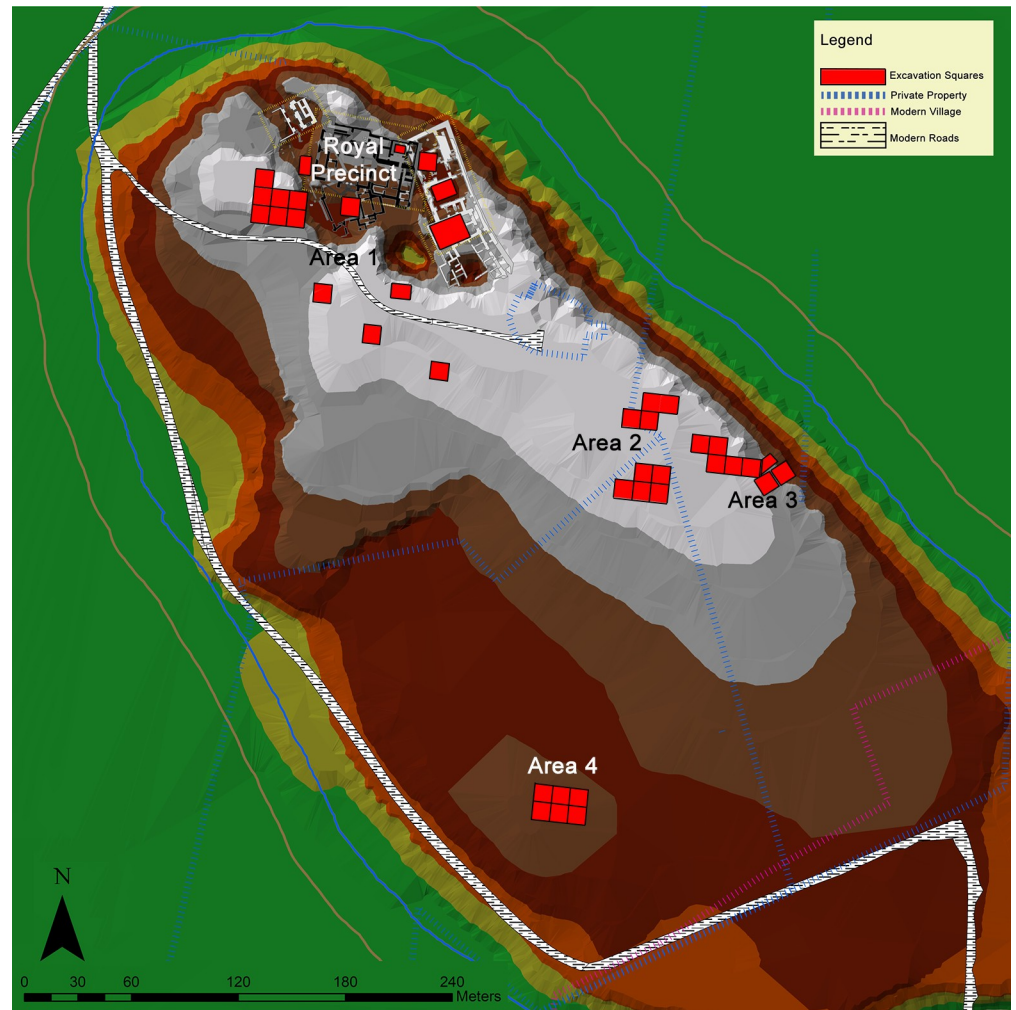
Fig 2. Map of Tell Atchana with excavation squares indicated (data courtesy of Alalakh Excavations Archive. Map made by authors in ESRI ArcGIS).

Hittites, and Middle and New Kingdom Egypt [5, 55, 75–81]. The textual record is matched by an archaeological record, particularly for the LBA, rich in imports (or objects imitating foreign styles) and architecture bearing foreign influences, including particular building methods, imported ceramic styles and small finds, and artistic motifs, such as Aegean-style bull-leaping scenes [54–57, 71, 81–99]. It is unclear how strongly this evidence was connected with the actual presence of people from abroad in permanent residence at Alalakh, however. While it is likely that at least some migrants lived and died at the site, it is impossible to make claims about the actual scale on the basis of texts and archaeology alone. It is also unclear whether these migrants were buried in the 342 graves which have been excavated to date, making the site a perfect candidate for targeted mobility studies.

Tell Atchana burial corpus. Burials at the site are present from the late MBA through the end of the LBA (stratigraphically, in contexts from Yener Periods 8–1; see Table 1) and have been found in every excavated area of the site. Tell Atchana has one of the largest numbers of recorded graves in the area, incorporating different burial types, goods, and locations, including examples inside the city itself (208 examples in total in various contexts, such as in

Table 1. Chronology of Tell Atchana.

Archaeological Era	Woolley Level	Yener Period	Excavated Areas	Main Architectural Features	Burials
Iron Age (ca. 1190–750 BC)	O	0	Royal Precinct (Area 1)	uncertain—poorly preserved	possible late burials?
Late Bronze II (ca. 1400–1300 BC)	I	1	Royal Precinct (Area 1), Areas 2, 4	Fort, Temple, houses	intra-city burials
	II	2	Royal Precinct (Area 1), Areas 2, 4	Northern and Southern Fortresses, Temple, houses	intra-city burials
	III	3	Royal Precinct (Area 1), Areas 2, 4	Temple, houses, workshops, Castle re-use	intra-city burials
Destruction ca. 1400 BC					
Late Bronze I (ca. 1650–1400 BC)	IV	4	Royal Precinct (Area 1), Site H, Areas 2–4	Palace, archive, houses, Castle, gate, western gate, workshops	extra-city cemetery, intra-city burials, Plastered Tomb
	V	5	Royal Precinct (Area 1), Site H, Areas 3–4	Temple, houses, workshops/domestic spaces	extra-city cemetery, intra-city burials
	VI	6	Royal Precinct (Area 1), Site H, Areas 3–4	Temple, workshops/domestic spaces	extra-city cemetery, intra-city burials
Fire/Conflagration ca. 1650 BC					
Middle Bronze II (ca. 1800–1650 BC)	VII	7	Royal Precinct (Area 1), Area 3–4	Palace, archive, temples, rampart, city wall, tripartite gate, domestic and workshop spaces	extra-city cemetery, intra-city burials
	VIII	8	Royal Precinct (Area 1)	Palace, Temple	intra-city burials

courtyards and other open spaces, in the ruins of abandoned buildings, and under intact floors) and in a cemetery located outside the city fortification wall in Area 3 (134 burials; see Fig 2) [100, 101]. The terms 'intra-city' and 'extra-city' are used here to differentiate these two groups, respectively. A total of 28 graves have been found in what appears to be another cemetery area within the city recently discovered in the south of the mound in Area 4 (see Fig 2) [101, 102]. The presence of both intra-city and extra-city burials provides a rare opportunity to compare the two funerary practices at a single site.

The vast majority of both intra- and extra-city burials are single, primary pit graves (n = 229), although there are a handful of secondary (n = 11) and/or multiple burials (n = 31), as well as cist graves (n = 2), pot burials (n = 17), and cremations (n = 12) [101, 103]. This variety is a starting place to look for the presence of non-locals, who could be associated with these minority types of burials. In the extra-city cemetery, grave goods are rare, with over half of the burials containing no grave goods; when they are present, they typically consist of one or two vessels and perhaps an article of jewelry, most often a metal pin or a beaded bracelet/necklace [100]. The intra-city burials, particularly those found in the Royal Precinct, are generally the richest in grave goods, with a wide variety of imported and local pottery, metal jewelry, and rarer items such as figurines and stone vessels [101, 103], supporting the suggestion that these burials represent a higher social class than the individuals interred in the extra-city cemetery [83, 100, 101, 103]. The exception to this, and the most intriguing burial at the site, is the Plastered Tomb. Located in the extra-city cemetery, it was built of several layers of plaster encasing four individuals that dates to the end of LB I [104–106]. This is the richest burial found at the site, with 13 vessels and numerous items of adornment, including beads made of gold, carnelian, and vitreous materials, pins of bronze and silver, and pieces of foil and stamped appliques made of gold. Due to its unique status, its unusual construction, and its rich assemblage of objects, it was a particular target for this study.

In addition to these broad burial groupings, several individuals have been recovered who seem to have died as a result of some type of misadventure and did not receive formal burials,

two of which are included in this study. The first, the so-called 'Well Lady' (ALA019), whose skeletal remains were found at the bottom of a well, was apparently thrown into the well while it was still in use, and homicide has been proposed as her manner of death [107]. The second, an adult female (ALA030), seems to have been killed during the destruction and collapse of a building in Area 3 [108].

The chronology of the burials. In Skourtanioti et al. [49], ^{14}C-AMS-dates were published for 27 individuals. To this, we add here seven dates for another six individuals (Table 2). All ^{14}C dates were produced at the Radiocarbon Laboratory of the Klaus-Tschira-Archäometrie-Zentrum at the Curt-Engelhorn-Zentrum Archäometrie gGmbH, Mannheim, Germany. From the 33 individuals that have been directly dated, 20 were located in the extra-city cemetery (including three individuals from the Plastered Tomb) and 13 were from intra-city contexts, including five from the intra-city cemetery area in Area 4 (Fig 3). The dates from the extra-city cemetery indicate that the beginning of its use dates back into the MB I (c. 2000–1800 BC), which makes it one of the oldest features that has been excavated at Tell Atchana to date. Furthermore, the radiocarbon dates of the extra-city cemetery show a general discrepancy with the archaeological dating: while the former suggests that all individuals sampled (with the exception of those in the Plastered Tomb) date to the MBA (c. 2000–1650 cal BC), the latter puts the main use of the cemetery into LB I (ca. 1600–1400 BC), with only very few burials dated to MB II (c. 1800–1650 BC) [100]. The reasons for this discrepancy could be general errors in the calibration curve for the Levantine area and/or that parts of the cemetery were only used during the MBA. It seems rather unlikely that by chance only those extra-city cemetery individuals which belong to the MBA were radiocarbon dated (for a detailed discussion of the dates and the stratigraphy see S1 File). Compared to the ^{14}C-results from the extra-city cemetery, the dates from the intra-city burials show a higher level of concordance with the archaeological (stratigraphic) dating, with only two out of 13 ^{14}C dates being substantially earlier (ALA016 and ALA020) and one later (ALA131) than expected.

Isotopic analysis background

The key principle in applying $\delta^{18}O$ and $^{87}Sr/^{86}Sr$ ratios to the study of past mobility is a comparison between the isotopic composition in the tooth enamel of excavated individuals and the

Table 2. [14]C dates newly published in this study.

Sample ID	Archaeological ID	[14]C age (BP)	$\delta^{13}C$ AMS [‰]	Cal BC 1σ	Cal BC 2σ	C [%]	C:N	Collagen (%)	Skeletal Material	[14]C Lab ID	Relative Date
ALA009.B	45.44, Locus 135, AT 17689	3552 ± 23	-17,5	1937–1829	2008–1774	38.8	3.2	4.3	RM[1]	MAMS-38608	early LB I
ALA009.C	45.44, Locus 135, AT 17689	3416 ± 30	-36,6	1747–1636	1872–1621	38.9	2.9	6	rib fragment	MAMS-38609	early LB I
ALA130.A	64.72, Locus 128	3375 ± 25	-14.6	1730–1622	1744–1547	42.7	3.2	8.0	petrous bone	MAMS-48944	LB I
ALA131.A	64.72, Locus 135	3099 ± 26	-24.1	1416–1306	1428–1287	43.2	3.2	3.3	petrous bone	MAMS-48945	LB I
ALA135.A	64.72, Locus 139	3438 ± 25	-19.2	1868–1690	1876–1636	30.8	3.3	4.2	petrous bone	MAMS-48946	early LB I
ALA136.A	64.72, Locus 141	3440 ± 25	-19.3	1868–1691	1878–1637	21.9	3.2	1.7	petrous bone	MAMS-48947	early LB I
ALA138.A	64.72, Locus 144	3383 ± 25	-21.6	1731–1626	1746–1569	36.5	3.2	6.5	petrous bone	MAMS-48948	early LB I

Dates were calibrated using OxCal v4.4.2 [109, 110].

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hydrologically and biologically available signatures at the same place. If a person spent their childhood prior to the completion of enamel formation of sampled permanent teeth at a different place than their adulthood (typically taken to be represented by the place where the individual was buried), this should result in a mismatch between the $\delta^{18}O$ and/or $^{87}Sr/^{86}Sr$ ratios in their teeth versus the environment, provided the bioavailable isotopic signatures of both places differ from one another [59, 111–122].

Stable oxygen isotopes ($\delta^{18}O$) of human tooth enamel are mainly derived from drinking water [112, 115, 117–119], which, in turn, is determined by the interaction of several factors, most importantly, elevation, temperature, humidity, and distance from the sea [111, 113, 114]. In the Amuq Valley, $\delta^{18}O$ values of modern precipitation average between -7‰ and -6‰ (Fig 4) [123–126], which is also consistent with measured Orontes water values from Syria [127–129]. However, climate change could have altered the bioavailable oxygen over time, and therefore intra-population analysis is generally the preferred method of evaluating $\delta^{18}O$ results [130].

Strontium in the human body, on the other hand, is incorporated via both food and water, with the biologically available $^{87}Sr/^{86}Sr$ composition at a location depending mainly on the underlying geological formations. ^{87}Sr forms during the radioactive decay of ^{87}Rb; therefore, while the amount of ^{86}Sr in each rock is stable, the amount of ^{87}Sr varies depending on the type of rock (which determines the initial quantity of ^{87}Rb and total Sr) and the rock's age. Weathering processes wash the strontium into soils and runoff water, where it is taken up by plants and then passed on to humans and animals alike, being incorporated into skeletal tissue and teeth during mineralization, as a substitute for calcium, without significant isotopic fractionation [59, 116, 121].

A knowledge of local geology is therefore crucial in order to establish a baseline for strontium isotopic studies. The surface of the Amuq Plain itself is made up mainly of alluvial sediments from the three major rivers (the Orontes, the Kara Su, and the Afrin) in the plain and eroded material from the highlands surrounding it [131] (Fig 5). The highlands to the south of the valley, which are part of the Arabian Platform [132], are made up of mostly limestone and other carbonate rocks of relatively young age (mainly Miocene and Eocene formations; $^{87}Sr/^{86}Sr$ ratios typically of 0.707–0.709 [133]). There are areas of basalt bedrock in some parts of the Kurt Mountains to the south, which are mostly from the Miocene and Eocene [131, 134], and these can be expected to have somewhat lower $^{87}Sr/^{86}Sr$ ratios (in the range of 0.703–0.705 [135, 136]). Basalt of a somewhat later age, from the Pliocene, can also be found in the northeast of the plain [132, 137, 138], and these areas may be expected to have roughly similar $^{87}Sr/^{86}Sr$ ratios.

The Amanus Mountains are much more geologically complex and consist mostly of formations of ultrabasic (or ultramafic) igneous (especially in the southern reaches), metamorphic, and sedimentary rock (particularly in the northern reaches) of more widely varying ages, with some formed as early as the (Pre)Cambrian [131, 134, 137, 139–141], including ophiolites, limestones, gabbro, and basalts, the majority of which are Mesozoic and later in age [137, 142, 143]. The $^{87}Sr/^{86}Sr$ ratios of ophiolites in the Kızıldağ area have been measured as 0.705 [144], and the gabbro fields in the same region can be expected to have similarly low values, comparable to basalt. The southwestern areas of the Amanus range, however, in the area of the Hatay Graben, are composed mainly of carbonates with $^{87}Sr/^{86}Sr$ values measured in the range of 0.7088–0.7090 [145]. Further north in the Amanus range, the clastic and carbonate formations are generally older (dating from the Paleozoic and Mesozoic eras) [146] and can therefore be expected to yield higher $^{87}Sr/^{86}Sr$ ratios compared to similar formations on the Arabian Platform to the south.
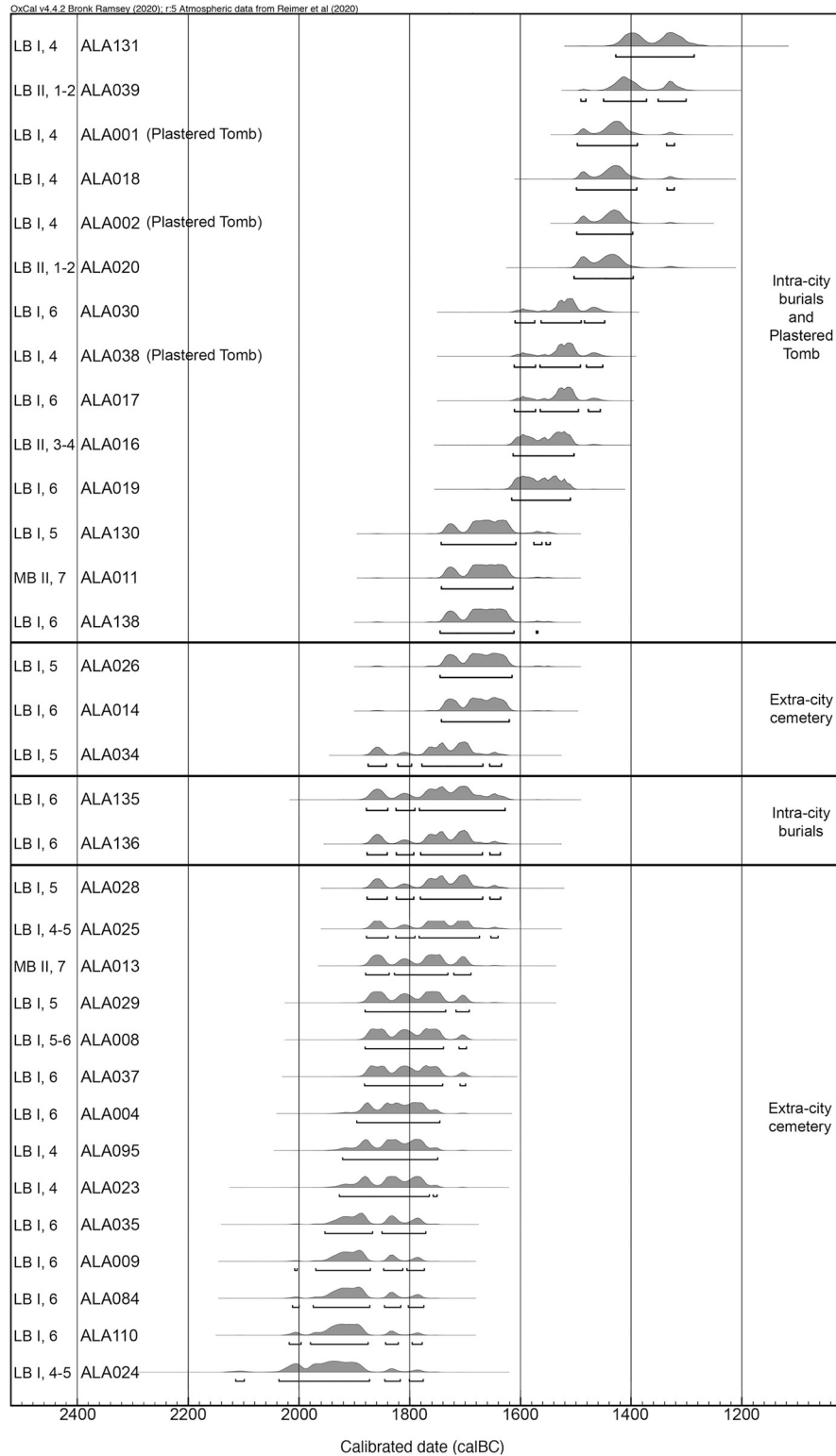
Fig 3. All ^{14}C dates from burials at Tell Atchana, including tentative archaeological dating to period and relative archaeological era (indicated as [ERA], [PERIOD] to the left of the individual sample IDs).
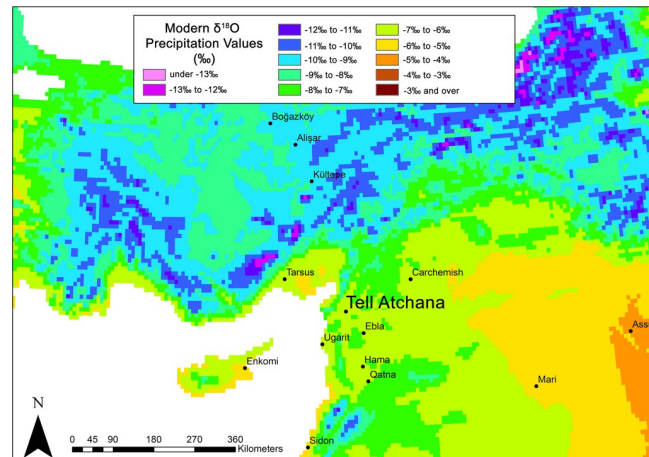
Fig 4. Mean annual δ^{18}O values for modern precipitation in the regions surrounding Tell Atchana (isotopic data from online isotopes in precipitation calculator [123–125]: Https://wateriso.utah.edu/waterisotopes/index.html. Map made by authors in ESRI ArcGIS).

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A strontium isotope pilot study was conducted by D. Meiggs [147] at Tell Atchana which focused mainly on archaeological faunal and modern environmental samples, although three human samples were also included. The modern environmental samples included both snail shells (six samples) and plants (six samples) collected from various locations around the valley, including one snail shell directly from Tell Atchana (sample AK01). Several of the unanalyzed shells collected during this project were used in the current study in order to compare the two sets of results (for further details, see S2 File). The ^{87}Sr/^{86}Sr ratios of modern samples analyzed by Meiggs ranged from 0.707851–0.714678 with a mean of 0.708998 [147], with the widest variation in ^{87}Sr/^{86}Sr ratios found in the samples from the Amanus Mountains (0.707851–0.714678), consistent with the varied geology encountered here. The samples from the alluvial plains of the valley floor showed comparatively lower ^{87}Sr/^{86}Sr variation (from 0.707942–0.708330), irrespective of if they originated from the northern or southern part of the valley
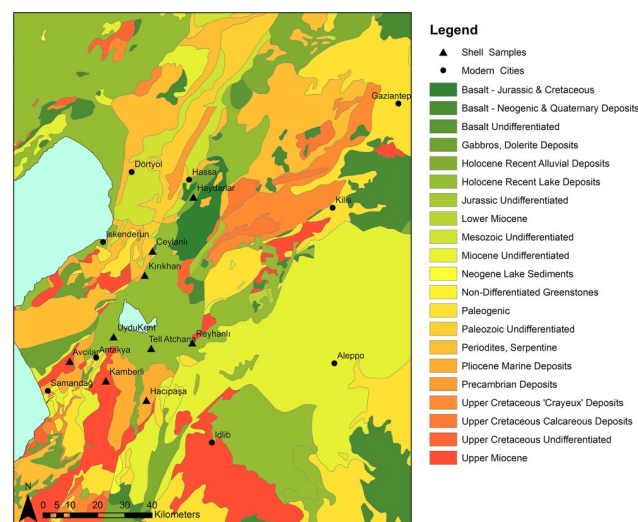
Fig 5. Geological map of the Amuq Valley and surrounding regions, with modern snail sample locations marked (data courtesy of the Amuq Valley Regional Project [AVRP]. Map made by authors in ESRI ArcGIS).

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[147]. The snail shell from the tell (AK01: 0.708550) had a slightly higher strontium ratio than those from the plain floor, but was within the range of the ancient faunal samples. The archaeological faunal samples analyzed by Meiggs consisted of teeth from eight ovicaprines and two deer. They provide a much smaller range of $^{87}Sr/^{86}Sr$ results, from 0.708196–0.70875, with a mean of 0.708396 [147]. This dataset therefore provides a local $^{87}Sr/^{86}Sr$ range (±2 standard deviations from the mean) of 0.708073–0.708718 that likely indicates where strontium signatures of individuals growing up at Alalakh or in its direct vicinity could be expected to fall, although herding practices may have included the use of pastures located on different soils than those used for crop cultivation. In this case, the available ancient faunal samples may not provide a sufficient representation of variation expected in humans.

These considerations show that it is crucial to evaluate where the majority of the food consumed by the individuals under study came from: only if the bulk of the diet was produced locally–i.e., at or in the vicinity of the site where an individual lived–will the strontium isotopic signature allow conclusions about the place of residency, and therefore questions of dietary make-up and catchment must be taken into account [59, 148, 149]. The archaeobotanical evidence of Alalakh is dominated by free threshing wheat (*Triticum aestivum/durum*) and barley (*hordeum vulgare*) [150], although pulses also make up significant portions of the assemblage in certain contexts, including lentils (*Lens culinaris*), fava beans (*Vicia faba*), and chick pea (*Cicer arietinum*) [151]. The Amuq Plain is well-situated for growing these plants, as it lies within the Mediterranean climate region, and an annual mean of 500–700 mm of precipitation, combined with seasonal flooding, allows for rain-fed cereal agriculture on a large scale [134, 152]. The faunal remains recovered from the site consist primarily of domesticates, namely a mix of cattle, sheep/goat, and pig, while wild taxa make up a considerably smaller percentage in most strata [153], although reaching levels as high as 31% in some contexts [154]. This means most animals that were consumed were not roaming free within the Amuq Valley but were managed by people. Occasional consumption of freshwater fish and shellfish occurred, based on their presence in the zooarchaeological assemblage, but not in significant quantities [154]. This suggests that the majority of the daily dietary input of Alalakh's citizens could have been produced locally.

However, not all of the food present at Alalakh was produced in the immediate vicinity of the site. Texts from the palace archives in Periods 7 (MB II) and 4 (LB I) describe regular shipments of food (including barley, emmer wheat, vetches, animal fodder, oil, beer, wine, and birdseed [e.g., texts AlT 236-308b, 320–328]) from Alalakh's vassal territories [79], and this non-local food, depending on where it was from and the bioavailable strontium of those areas, could have affected the strontium values of individuals who ate it. Most of the identified places where foodstuffs and animals were delivered from were within the control of Alalakh and seem to have been from the Amuq Valley and its immediate environs, although Emar, located to the east on the Euphrates River (see Fig 1), also delivered grain and sheep during Alalakh's sovereignty over that city in Period 7 [77], demonstrating that not all of the cities under Alalakh's sway were within the valley. It is unclear what the ultimate destination(s) of these received foodstuffs were–whether they were consumed by the palace denizens, redistributed to palace dependents, given as payment for services or against palace debts, or sold to other residents of Alalakh–but if certain portions of the population were consuming them in large proportions, this has the potential to change their $^{87}Sr/^{86}Sr$ ratios and to artificially inflate the numbers of non-locals identified.

DNA analysis background

The investigation and interpretation of genetic patterns of diversity between humans and groups of humans, usually referred to as populations, is one objective of the field of population

genetics. One major factor that shapes genetic variation between populations is geographic distance, as groups living closer to each other are naturally more likely to admix–meaning that individuals are more likely to procreate–than groups living farther apart [155, 156]. Another major factor involved in shaping genetic variation is time, due to continuous human mobility on different scales. The interpretive power of a single-site study such as the current one strongly depends on the availability of already published data of coeval and earlier periods from the Amuq Valley and the wider Near East and Anatolia in general (see below). Furthermore, to securely detect changes in the local gene pool and identify outlier individuals or even different genetic clusters within one place, data from many individuals and archaeological contexts are necessary.

One major difficulty in genetic studies in connection with the identification of genetic outliers at a place concerns the dating of this signal. Often, when an outlier is identified, it is rather difficult to establish whether the sampled individual itself or his/her ancestors immigrated. The combination of aDNA analysis with strontium and oxygen isotope analysis of the same individual is one way to resolve this issue, as migrants in the first generation can be identified (if the isotope signal in their teeth deviates from local baselines). On the other hand, the signal for a first-generation immigrant in the isotopic data can potentially be more closely refined by the aDNA data, due to the general geographic patterning of population genomic data. If an individual identified as a first-generation immigrant by isotopic analysis looks genetically very much like the other individuals at the site, it is likely that we are dealing with either regional/short distance migration or long-distance backwards migration.

In addition to the analysis of genetic ancestry between individuals within one site and between populations, aDNA analysis allows the detection of biological relationships amongst individuals. In some cases, pedigrees can be reconstructed from these [70, 157], which, from an archaeological point of view, can shed light on particular pedigree-related dynamics and practices at a site.

The earliest, and to date only, glimpse into the genetic makeup of the inhabitants of the Amuq Valley prior to Alalakh comes from six samples from Tell Kurdu, five of which date to the Early Chalcolithic between 5750–5600 BC and one of which is dated to the Middle Chalcolithic, 5005–4849 cal BC (2σ) [49]. Skourtanioti et al. [49] showed, with three different analyses (PCA, f_4-statistics, and $qpAdm$), that the Chalcolithic samples from Tell Kurdu harbor ancestries related primarily to western Anatolia and secondarily to the Caucasus/Iran and the Southern Levant, suggesting a gradient of ancestries with geographical characteristics already in place during that time in the Amuq Valley [49]. However, the samples from the MBA and LBA from Alalakh draw a genetic picture of the Amuq that is considerably changed: roughly 3000 years after the last individual from Tell Kurdu, the individuals from Alalakh, along with individuals from EBA and MBA Ebla in northwestern Syria, are part of the same PC1-PC2 space with Late Chalcolithic-Bronze Age Anatolians. They are, compared to samples from Barcın in western Anatolia and Tell Kurdu, all shifted upwards on the PC2 towards samples of Caucasus and Zagros/Iranian origin [49]. This shift in ancestry was formally tested with f_4-statistics of the format f_4(Mbuti, test; Barcın_N/TellKurdu_EC, X), which revealed that all the Late Chalcolithic-LBA populations from Anatolia and the northern Levant (X, i.e. Ebla and Alalakh) are more closely related to Iranian Neolithic individuals and/or Caucasus Hunter Gatherer individuals (*test*) than are the earlier Tell Kurdu and Barcın individuals [49]. A similar genetic shift towards Iranian/Caucasus-related populations was detected for the contemporary Southern Levant [37–39]. This means that in the period between 5000–2000 BC, gene flow from populations harboring Iranian/Caucasus-like ancestries, which also includes populations that are genetically similar to these but have not yet been sampled, and are thus unknown, affected southern Anatolia and the entire Levant, including the Amuq Valley. It is currently neither

possible to pinpoint the exact source population(s) that brought about these changes in the local gene pool nor to propose specific migration events.

Four genetic outlier individuals from Bronze Age Levantine contexts, one of them the so-called Well Lady from Alalakh (ALA019) and three from Megiddo (two of which are siblings), are shifted upwards on the PCA, the former towards individuals from Chalcolithic/Bronze Age Iran and Central Asia [49] and the latter towards the Chalcolithic/Bronze Age Caucasus. Strontium isotope analysis of the two siblings from Megiddo suggests that both grew up locally [37]. These outlier individuals from Megiddo and Alalakh attest that gene flow from the Caucasus/Iran (or genetically similar groups) into the Levant continued throughout the 2nd millennium BC.

Materials and methods

Sampling strategies and the datasets

All necessary permits were obtained for the described study, which complied with all relevant regulations. Permission for the Tell Atchana excavations and for the export and subsequent sampling of all material was granted by the Directorate of Cultural Heritage and Museums. Currently, $^{87}Sr/^{86}Sr$ results from tooth enamel samples are available for 53 individuals, $\delta^{18}O$ results for 77 individuals, and aDNA results for 37 individuals. aDNA data for ten of these 37 individuals are published here for the first time as well as improved data for one previously published individual (see below; see also S1 Table). Individuals for aDNA and isotope sampling were selected in order to be as representative as possible of the burial corpus as a whole, choosing individuals from all available intra- and extra-city contexts, different types of burials (primary and secondary, single and multiple), varying age groups (with an emphasis on adult individuals), and both sexes, with age and sex data based on osteological analysis conducted by R. Shafiq. Age estimation and sex determination was conducted using standard methodologies [158–161], with sex determination being corroborated by aDNA, where possible.

For aDNA analysis, we primarily targeted the petrous bone, the skeletal element which has been shown to best preserve human DNA, and as a secondary potential element, we used teeth [162–164]. For isotope analysis, we sampled tooth enamel, as has become standard practice in the field, due to the material's resilience to diagenetic alterations [165–167]. We preferentially used permanent second molars, as the M2 is formed between the ages of ca. 2–8 years [121, 168], thereby being more likely to show isotopic signals with minimal interference from breastfeeding effects [34, 169–171]. Where no second molar was available, the M3 (formed between ca. 7–14 years [168]), M1 (formed between ca. the last month in utero to 3 years of age [168]), or a premolar (formed between ca. 1–7 years, depending on which premolar [168]) were sampled in descending order of preference. Additionally, teeth which were found loose, i.e., already displaced from the mandible/maxilla at the time of excavation, were preferred over those imbedded in the bone, in order to preserve the integrity of the bone wherever possible. For this reason, it was not always possible to identify whether a tooth came from the right or left side. Where permanent teeth were unavailable (usually in the case of infants), deciduous teeth were sampled; in this case, the preference was again for second molars (dm2), followed by first molars (dm1). In a key difference from permanent teeth, however, deciduous teeth form *in utero* and in the first months after birth (dm2: ca. 16 weeks *in utero* to 11 months; dm1: ca. 14 weeks *in utero* to 6 months [168]). The results from deciduous teeth, therefore, do not reflect the dietary input of the sampled individual but rather that of the mother, since all the infant's nutritional needs are provided by the mother during the period of enamel formation. Environmental bulk reference samples (n = 16) for isotopic analysis were taken from modern and archaeological snails, as well as archaeological rodents (see below), in order to

establish a local range for biologically available strontium, both at Tell Atchana and across the Amuq Valley more broadly. Five bulk faunal samples were also taken for oxygen isotopic analysis; although these were not used as a baseline for evaluating the human results in a parallel way as the faunal strontium ratios, since human and faunal results are not directly comparable [64], they serve as an additional, discrete dataset that can be compared to that of the humans. Statistics were run in Statistical Package for the Social Sciences (SPSS Statistics) version 26 on the oxygen isotope results to test for significant differences within the sampled population using non-parametric Kruskal-Wallis H tests and post hoc Mann-Whitney U tests, where appropriate.

Analysis of aDNA–which, as an organic material, is subject to *post-mortem* decomposition–has a variable success rate: samples from 116 individuals from Alalakh were analyzed, but qualified 1240K SNP data could be produced only for 37 (including ten new in this study in addition to 27 in Skourtanioti et al. [49]). An "ALAXXX" sample number was assigned to each analyzed individual (see below). All samples were photographed and documented prior to any destructive sampling, and teeth were additionally CT scanned at the Max Planck Institute for the Science of Human History (MPI-SHH) in order to preserve a complete record of dental features.

Although the sampled skeletal assemblage does not reflect the excavated burials at Alalakh as a whole, as the sampled individuals are biased towards the extra-city cemetery (Table 3), it includes individuals from all Areas excavated by Yener. This imbalance is a result of the fact that nearly three-quarters of the intra-city burials were recovered during the previous excavations by Woolley (151 individuals of 208 intra-city burials = 72.6%) and are therefore unavailable for sampling, as Woolley did not keep the human remains he found. The situation is similar for the numbers of individuals sampled from each archaeological period (see Table 3), as the majority of the LB II individuals were excavated by Woolley [101]. Subadults as a group generally are also somewhat underrepresented among the analyzed individuals (Table 4), due to this study's preference for 2nd (and 3rd) permanent molars, but the proportions of age classes is, again, roughly representative of the available material. Given the limitations of available material, therefore, the sampled individuals are as representative as possible for the excavated burials as a whole [172], and, most importantly, cover all known contexts and burial types (see Table 4).

However, the excavated burials certainly do not represent the total population who lived and died at the city over the course of its history. It is possible that large swathes of individuals

Table 3. Contextual information of the total burial assemblage (location, date, and type), the numbers of graves available for sampling (i.e., excavated by Yener), and the numbers sampled for each analysis presented.

Context	Burials		Sampled For		
	Total	Total Available	Sr	O	aDNA
Intra-city	208	57	10	23	17
Extra-city	134	134	43	54	20
LB II	46	10	3	3	5
LB I	265	160	43	67	28
MB II	31	21	7	7	4
Primary inhumation	229	124	41	62	30
Secondary inhumation	11	9	6	6	2
Cist tomb	2	2	0	2	0
Plastered Tomb (# of individuals)	1 (4)	1 (4)	1 (4)	1 (4)	1 (3)
Non-burials–misadventure, homicide, etc.	3	3	2	1	2

Table 4. Demographic information of the total burial assemblage, the numbers of graves available for sampling (i.e., excavated by Yener), and the numbers sampled for each analysis presented.

Demographics	Burials		Sampled For		
	Total	Total Available	Sr	O	aDNA
Infant (0–2 years)	42	21	1	5	7
Child (2–13 years)	76	41	9	14	6
Adolescent (13–17 years)	21	12	3	4	1
Adult (17+ years)	81	112	38	49	22
Female	65	65	27	33	19
Male	62	62	16	24	18

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who lived at the site are currently missing from view due to their graves either not having been preserved due to taphonomic processes, not (yet?) having been recovered, or perhaps being archaeologically invisible, due to practices such as off-site burial.

Analytical methods

Stable oxygen isotopes. Sampling protocols and analysis procedures for stable oxygen isotope analysis of enamel carbonate follow those set out in Roberts et al. [173] (see also [174–176]). Teeth were cleaned to remove adhering material using air-abrasion, and a diamond-tipped drill was used to obtain a powder sample. The full length of the buccal surface was abraded in order to capture a representative bulk sample from the maximum period of formation. To remove organic or secondary carbonate contamination, the enamel powder was pretreated in a wash of 1.5% sodium hypochlorite for 60 minutes; this was followed by three rinses in purified H_2O and centrifuging, before 0.1 M acetic acid was added for 10 minutes. Samples were then rinsed again three times with milliQ H_2O and freeze dried for 4 hours. Enamel powder was weighed out into 12 ml borosilicate glass vials and sealed with rubber septa. The vials were flush filled with helium at 100 ml/min for 10 minutes. After reaction with 100% phosphoric acid, the CO_2 of the sample was analyzed using a Thermo Gas Bench 2 connected to a Thermo Delta V Advantage Mass Spectrometer at the Stable Isotope Laboratory, Department of Archaeology, MPI-SHH. $\delta^{18}O_c$ values were calibrated against International Standards (IAEA NBS 18: $\delta^{18}O$ -23.2±0.1‰, IAEA-603 [$\delta^{18}O$ -2.37±0.04‰]; IAEA–CO–8 [$\delta^{18}O$ -22.7 ±0.2‰,]). Repeated analysis of MERCK standards suggests that machine measurement error is ca. +/- 0.1‰ for $\delta^{18}O_c$. Overall measurement precision was determined through the measurement of repeat extracts from a bovid tooth enamel standard (n = 20, ±0.3‰ for $\delta^{18}O_c$).

Strontium isotopes. Sampling protocols and analytical procedures for strontium follow those set out in Copeland et al. [177]. Enamel powder was obtained with a diamond-tipped drill along the full length of the buccal surface after cleaning with air-abrasion. Up to 4 mg of enamel powder was digested in 2 ml of 65% HNO_3 in a closed Teflon beaker placed on a hotplate for an hour at 140°C, followed by dry down and re-dissolving in 1.5 ml of 2 M HNO_3 for strontium separation chemistry, which followed Pin et al. [178]. The separated strontium fraction was dried down and dissolved in 2 ml 0.2% HNO_3 before dilution to 200 ppb Sr concentrations for analysis using a Nu Instruments NuPlasma High Resolution Multi Collector Inductively Coupled Plasma-Mass Spectrometry (HR-MC-ICP-MS) at the Department of Geological Sciences, University of Cape Town. Analyses were controlled by reference to bracketing analyses of NIST SRM987, using a $^{87}Sr/^{86}Sr$ reference ratio of 0.710255. Data were corrected for rubidium interference at 87 amu using the measured ^{85}Rb signal and the natural $^{85}Rb/^{87}Rb$ ratio. Instrumental mass fractionation was corrected using the measured $^{86}Sr/^{88}Sr$ ratio and the exponential law, along with a true $^{86}Sr/^{88}Sr$ ratio of 0.1194. Results for repeat

analyses of an in-house carbonate reference material processed and measured as unknown with the batches ($^{87}Sr/^{86}Sr$ = 0.708909; 2 sigma 0.000040; n = 7) are in agreement with long-term results for this in-house reference material ($^{87}Sr/^{86}Sr$ = 0.708911; 2 sigma = 0.000040; n = 414).

aDNA. DNA data production of all eleven samples analyzed in this study took place in the dedicated aDNA facility of the MPI-SHH in Jena, Germany. The eleven samples belonged to ten individuals that were analyzed here for the first time and one individual that was already published as ALA015 in Skourtanioti et al. [49] but re-assigned here to individual ALA110. The initial reason for analyzing the petrous bone of ALA110 was the outlier position this individual takes up in the strontium isotope analysis (see below). During analysis of the aDNA data, we realized that the petrous bones of ALA015 and ALA110 belonged to one and the same context and individual and subsequently merged their data accordingly into ALA110, thus improving its aDNA data. In all samples analyzed, sampling targeted the inner-ear part of the petrous bone [164]. DNA extraction and double-stranded genomic libraries were prepared for four samples (ALA118, ALA120, ALA123, and ALA124) according to the MPI-SHH Archaeogenetics protocols for Ancient DNA Extraction from Skeletal Material, and Non-UDG treated double-stranded (ds) ancient DNA library preparation for Illumina sequencing, both archived and accessible at doi.org/10.17504/protocols.io.baksicwe and doi.org/10.17504/protocols.io.bakricv6, respectively. The library preparation protocol was modified with the introduction of partial Uracil DNA Glycosylase (UDG) treatment prior to the blunt-end repair, according to Rohland et al. [179]. Dual-indexed adaptors were prepared according to the archived MPI-SHH Archaeogenetics protocol accessible at doi.org/10.17504/protocols.io.bem5jc86.

For the remaining seven samples (ALA110, ALA128, ALA130, ALA131, ALA135, ALA136, and ALA138), DNA extraction was performed according to Rohland et al. [180], and single-stranded (ss) libraries (no UDG treatment) were prepared according to Gansauge et al. [181], both protocols using an automated liquid-handling system. All libraries were first shotgun sequenced (~5M reads) in a sequencing Illumina HiSeq4000 platform. Raw FastQC sequence data were processed through EAGER [182] for removal of adapters (AdapterRemoval [v2.2.0]) [183], read length filtering (>30b), mapping against hs37d5 sequence reference (BWA [v0.7.12]) [184], q30 quality filter, removal of PCR duplicates (dedup [v0.12.2]) [182], and DNA damage estimation (mapdamage [v2.0.6]) [185]. Two main characteristics of the sequenced reads were considered in order to select positive libraries for submission to an in-solution hybridization enrichment that targets 1,233,013 genome-wide and ancestry-informative single nucleotide polymorphisms (SNPs; "1240K SNP capture") [50]. The first is the proportion of DNA damage at the end of the reads (> ~5% C-T/ G-A substitution at terminal 5' and 3' base, depending on the UDG treatment of the library), and the second is the content of endogenous DNA (>0.1%) calculated as the portion of reads mapped against the hs37d5 reference over the total amount of sequenced reads after the length filtering. The enriched libraries were sequenced at the order of ≥20M reads, and the raw FastQC sequence data were processed through EAGER as described above. BAM (binary alignment map) files across libraries from the same sample were merged with samtools and dedup was rerun. Masked versions of the BAM files were created with trimBam (https://genome.sph.umich.edu/wiki/BamUtil:_trimBam), which masked the read positions with high damage frequency, that is, the terminal 2 and 10 bases for the partially UDG-treated ds libraries and ss libraries (no UDG), respectively. With "samtools depth" from the samtools, the coverage on X, Y, and autosomal chromosomes (v1.3) [186] was calculated on the masked BAM files, providing the bed file with the 1240K SNPs. X and Y coverage were normalized by the autosomal coverage (X-rate and Y-rate respectively), and females without contamination were determined by X-rate ≈ 1 and Y-rate ≈ 0, whereas males without contamination were determined by both rates ≈ 0.5.

Contamination on the mitochondrial DNA was estimated with Schmutzi [187], and on the nuclear DNA of males with ANGSD (MoM estimate is provided) [188]. Additionally, AuthentiCT was applied on the BAMs generated from ss libraries. This new method models the pattern of accumulation of damage-induced deamination across the length of ancient molecules and, therefore, can estimate contamination from modern sources [189]. Currently, the method can be only applied to ss-libraries without UDG treatment, whose molecules preserve the original damage.

Genotypes were called with the tool pileupCaller (https://github.com/stschiff/sequenceTools/tree/master/src/SequenceTools) according to the Affymetrix Human Origins panel (~600K SNPs) [42, 190], the 1240K panel [50], and the option randomHaploid, which randomly draws one read at every SNP position. The random calling was performed both on the original and the masked bam files of each ds library, and, for the final genotypes, we kept transitions from the masked and from the original bam files. For the ss libraries, genotypes were extracted from the original BAM files and the option 'singleStrandMode' that removes reads with post-mortem damage based on their alignment on the forward or the reverse strand of the human reference genome. Y-haplogroups were assigned to the male individuals after filtering the pileup from the masked BAMs for an updated list of ISOGG SNPs. For each of these SNPs, a record of their state (ancestral or derived) was collected. Then, it was manually checked whether the presence of diagnostic SNPs for a given haplogroup also included diagnostic SPNs from the root to the tip of the tree, or whether there were spurious jumps in the phylogeny because of damage.

When, after the 1240K enrichment, a ≥5x coverage on mitochondrial DNA was reached, consensus mitochondrial sequences were inferred using Schmutzi [187] and mapping with the CircularMapper [191] against the rCRS. A mapping quality filter of q30 and consensus quality score Q30 were applied. The mitochondrial haplogroups from the consensus sequences were assigned with Haplogrep [192].

The genome-wide data from the new individuals were combined with previously published ancient and modern data [39, 42, 45, 46, 49, 162, 193–220]. For readability, we kept most of the group labels used in Skourtanioti et al. [49], most importantly "Alalakh_MLBA", "ALA019" (genetic outlier) (n = 1), "Ebla_EMBA" (n = 9), "K.Kalehöyük_MLBA" (Kaman-Kalehöyük, n = 5), and "TellKurdu_EC" (n = 5), but dubbed individuals from Sidon with the label "Sidon_MBA" (instead of "Levant_MBA"; n = 5). A principal component analysis was performed on a subset of western Eurasian populations of the Human Origins Dataset using smartpca program of EIGENSOFT (v6.01) [221, 222] (default parameters and options lsqproject: YES, numoutlieriter:0).

The degree of genetic relationship among Alalakh_MLBA individuals (n = 34 after quality filtering) was assessed by applying and comparing two different methods: READ [223] and *lcMLkin* [224]. Read is a software that can estimate up to second degree relationships from low-coverage genomes by calculating the proportion of non-matching alleles for a pair of individuals (P0) in non-overlapping windows of 1 Mbps. P0 was normalized with the median of P0 from all pairs–assuming that most pairs are unrelated–in order to reduce the effects of SNP ascertainment, within-population diversity, and marker density.

LcMLkin uses a Maximum Likelihood framework on genotype likelihoods from low-coverage DNA sequencing data and infers k0, k1, and k2, the probabilities that a pair of individuals share, respectively, zero, one, or two alleles identical-by-descent (IBD), as well as the overall coefficient of relatedness (*r*). Two useful aspects of this method are that it serves for distinguishing between parent-offspring (k0 = 0) and siblings (k0≥0, depending on recombination rate) and can infer relatedness down to the 5th degree. However, a discrepancy from the expected k0, k1, k2, and *r* values can occur under scenarios of recent admixture, inbreeding,

contamination, and low-quality data. We ran *lcMLkin* on the masked bam files with the options -l phred and -g best.

Modelling of ancestry proportions was performed with *qpWave* and *qpAdm* programs from ADMIXTOOLS [v7.1] [190] using the following set of Right populations (also named outgroups or references): Mbuti.DG, Ami.DG, Onge.DG, Mixe.DG, Kostenki14, Eastern European hunter-gatherers (EEHG), Western European hunter-gatherers (WEHG), Levant_EP, and Anatolia_N (Barcın, Mentese and Boncuklu). These programs compute a matrix of f_4-statistics for the Right and Left populations (targets for *qpWave* and target and sources for *qpAdm*) in the form of $F_{ij} = F_4(L_1,L_j;R_1,R_j)$. Then, with a likelihood ratio test, the null model is compared against the full-rank model in which all columns of the matrix are independent. In the latter model, the *n* Left populations relate with the references through *n* waves of ancestry, which for *qpAdm*, implies that the target cannot be explained as a combination of the selected source populations (null model). Depending on the chosen cutoff, a tested null model with p-value ≤0.01 or ≤0.05 and/or infeasible admixture coefficients (outside 0–1 range) is considered a poor fit of the data and thus, it is rejected. For this group-based analysis, we kept only individuals who are not genetically related.

Results

Results of oxygen isotope analysis

The 77 individuals analyzed yielded a mean $\delta^{18}O_c$ of -5.2±0.9‰ and range from -7.3 to -3.2 (for a total range of 4.1‰; Fig 6 and Tables 5 and S1), with values clustering mainly between -6.0‰ and -4.0‰. A Kruskal-Wallis H test showed no statistically significant differences between intra- and extra-city graves ($\chi^2(1) = 1.667$, $p = 0.197$), burial types ($\chi^2(7) = 5.533$, $p = 0.595$), Yener Periods ($\chi^2(5) = 7.017$, $p = 0.219$), sex ($\chi^2(2) = 1.669$, $p = 0.434$), age ($\chi^2(4) = 3.696$, $p = 0.449$), based on the presence/absence of grave goods ($\chi^2(2) = 0.921$, $p = 0.631$), or between the MB II and LB I burials ($\chi^2(1) = 2.253$, $p = 0.133$). As there are only three LB II individuals with $\delta^{18}O_c$ results to date, meaningful statistical analysis could not be run on this small sample size.

Following recent suggestions that in-group statistical methods to identify outliers is a more reliable way of identifying non-locals within sets of $\delta^{18}O$ values than ranges of variation, which have been shown to be ca. 3‰ within a population [64, 130], there are no clear statistical outliers among the Tell Atchana dataset (median = -5.2, interquartile range = -4.5 –-5.8 = 1.3). The five archaeological faunal samples (all from domestic animals; Table 6) have a mean of -4.3 ±2.1‰ and a range from -2.2 to -7.2 (for a total range of 5‰). This is due to two particularly high results from AT 0263 and AT 3064, a cattle and an unidentified sheep/goat, respectively. Nevertheless, the results of the humans and fauna are broadly compatible.

Results of strontium isotope analysis

Every strontium isotope study is faced with the challenge of how best to establish the local bio-available $^{87}Sr/^{86}Sr$ range at the site under study. While two standard deviations from the mean of faunal/environmental samples have become common practice to set an objective cut-off to distinguish locals from non-locals [116], the material on which to base this mean is debated and varies between different studies. In this study, we used a mixed approach between ancient (snail shells, rodent teeth, sheep/goat teeth, and deer teeth) and modern faunal samples (snail shells) to establish (1) a local range for Alalakh and (2) a local range for the Amuq Valley in general, in order to be able to distinguish between those human individuals that grew up at Alalakh (locals), those who came to the site from within the Amuq (micro-regional migration),
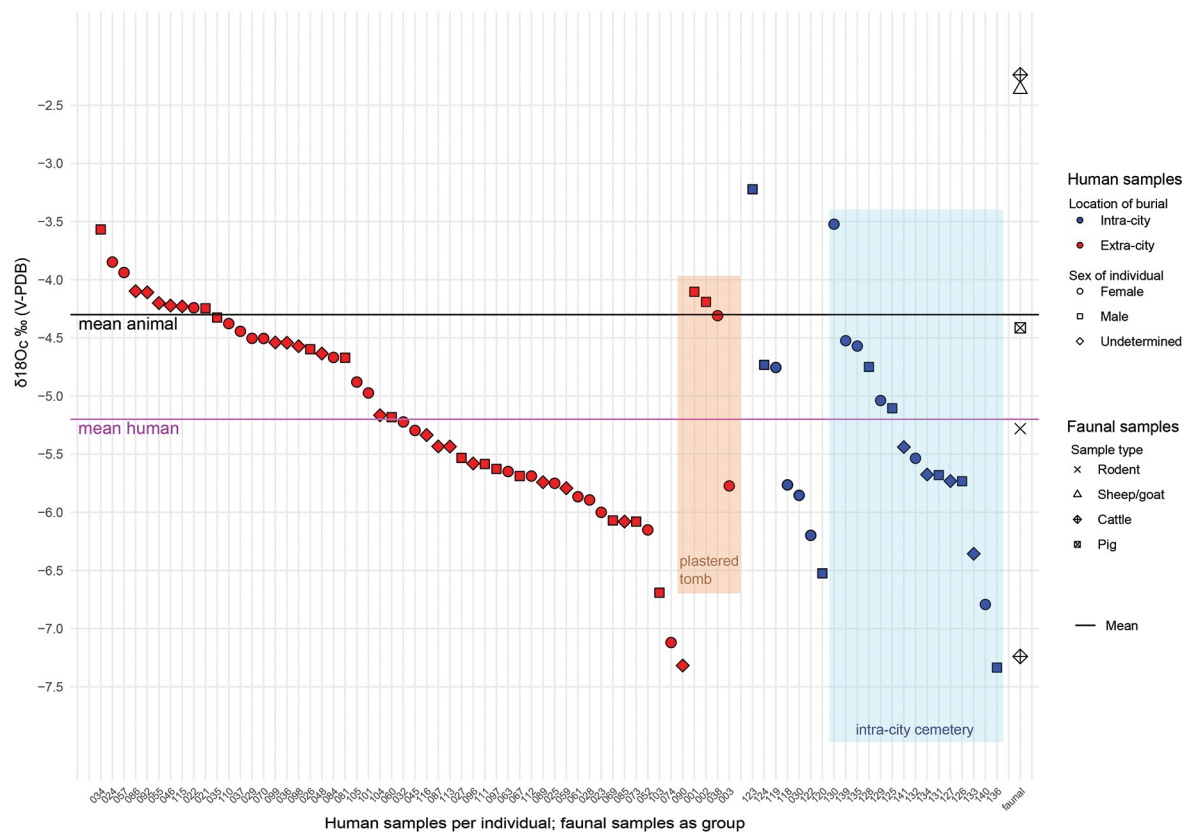
Fig 6. All δ¹⁸O_c ‰ (V-PDB) values of all samples analyzed in this study; continuous lines: Mean; pink line: Mean calculated from all human samples; black line: Mean calculated from all faunal samples.

and those originating from places outside the Amuq Valley (non-locals: migration over longer distances).

To estimate the typical local ^{87}Sr/ ^{86}Sr signature for humans at Alalakh, we measured, in addition to the existing samples from sheep/goat and deer teeth [147], ^{87}Sr/ ^{86}Sr ratios of five land snail shells and tooth enamel from two rodents from well-stratified archaeological contexts (see Table 6). As opposed to domesticates, rodents and snails are not managed by humans, and they obtain their food from within a small radius that should be representative for the strontium ratios available directly at the tell [166]. The snails and rodents offer a means to control whether the ovicaprines were grazing on pastures around Tell Atchana itself within the Amuq Valley, where the bulk of the humans' plant diet was likely produced, or whether the pastures were located on different geologies (e.g., in more mountainous areas on the fringes of the Amuq Valley). The ^{87}Sr/ ^{86}Sr ratios of the ancient snail shells and rodents clustered closely together between 0.708111 and 0.708544 (Fig 7) and largely overlapped with the ^{87}Sr/ ^{86}Sr ratios of the ovicaprines and deer from Meiggs' study [147], but, as expected, considering the differences in radius of movement, the ratios of the ovicaprines and deer have a wider range. Therefore, we can report positive results for the use of land snail shells as material to obtain bioavailable strontium signatures at Tell Atchana, contributing to a lively discussion in the literature where they have been used with varying success rates [166, 225–230]. The snails and rodents confirm that herding practices of the ovicaprines mostly included pastures in the environs of Alalakh. Thus, the combination of the ovicaprines and deer, together with the two rodents, likely indicates the most relevant local range to represent locality in humans at

Table 5. All individuals included in this study.

Sample ID	Arch. ID	$\delta^{18}O_c$ (‰) (VPDB)	$^{87}Sr/^{86}Sr$	aDNA[a]	Tooth Sampled (FDI)[b]	Location	Burial Type	Sex	Age	Yener Period[c]	Grave goods?[d]
ALA001	L03-3017, P.257	-4.1	0.708120	yes	RM_2 (47)	extra-city cemetery	Plastered Tomb	M	40–45 years	4	yes
ALA002	L03-3017, P.246	-4.2	0.708346	yes	LM_2 (37)	extra-city cemetery	Plastered Tomb	M	19–21 years	4	yes
ALA003	L03-3017, P.250	-5.8	0.708278	-	M^2	extra-city cemetery	Plastered Tomb	F	40–45 years	4	yes
ALA004	L03-3002, P.40	-	0.707630	yes	RM^2 (17)	extra-city cemetery	primary pit grave with bone scatter atop	M	40–45 years	6	no
ALA008	45.44.133	-	0.708431	yes	M^1	extra-city cemetery	primary, single pit grave	M	25–35 years	5–6	no
ALA009	45.44.135	-	0.708277	yes	RM^1 (16)	extra-city cemetery	primary, single pit grave	F	50–60 years	6	yes
ALA011	45.44.146	-	0.708525	yes	dm^1	Area 3 room	primary, single pit grave	M	3.5–4 years	7	yes
ALA013	45.44.152	-	0.708350	yes	di	extra-city cemetery	primary, single pit grave	F	0.5–1.5 years	7	yes
ALA014	45.45.9	-	0.708651	yes	RPM^2 (15)	extra-city cemetery	primary, single pit grave	M	35–55 years	6	no
ALA015	45.45.19	-	0.708406	$-^+$	PM	extra-city cemetery	primary, single pit grave	unk.	20–50 years	early 6	yes
ALA016	32.54.85	-	0.707937	yes	M	Royal Precinct, transitional layer	primary, single pit grave	F	65–75 years	3–4	yes
ALA017	32.57.160	-	0.708272	yes	M	Royal Precinct, under street	primary, single pit grave	F	17–25 years	6	yes
ALA018	42.29.44	-	0.708405	yes	I	Area 1, accumulation fill	primary, single pit grave	M	4–5 years	4	yes
ALA019	32.57.247	-	0.708456	yes	LM^1 (26)	Royal Precinct, bottom of well	accidental death/possible murder; no burial	F	40–45 years	6	N/A
ALA019	32.57.247	-	0.708474	yes	LM^2 (27)	Royal Precinct, bottom of well	accidental death/possible murder; no burial	F	40–45 years	6	N/A
ALA019	32.57.247	-	0.708540	yes	LM^3 (28)	Royal Precinct, bottom of well	accidental death/possible murder; no burial	F	40–45 years	6	N/A
ALA020	44.86.18	-	0.708043	yes	LM^3 (28)	Area 2, debris layer	primary, single pit grave	F	17–25 years	1–2	no
ALA021	45.44.43	-4.3	0.708201	-	M^2	extra-city cemetery	primary pit grave with complete individual and skeletal elements from a child	M	40–44 years	4	no
ALA022	45.44.56	-4.2	0.708176	-	M_2	extra-city cemetery	primary, single pit grave	F	20–30 years	4	yes
ALA023	45.44.65	-6.0	-	yes	dm2	extra-city cemetery	primary, single pit grave	F	6.5–7 years	4	yes
ALA024	45.44.68	-3.9	0.708258	yes	M^2	extra-city cemetery	primary, single pit grave	F	2–3 years	4–5	yes
ALA025	45.44.66	-5.8	0.708451	yes	M_2	extra-city cemetery	primary, single pit grave	F	13–14 years	4–5	yes
ALA026	45.44.70	-4.6	-	yes	dm_2	extra-city cemetery	primary, single pit grave	M	3.5–4 years	5	yes
ALA027	45.44.71	-5.5	0.708664	-	M_2	extra-city cemetery	primary, single pit grave	M	45–55 years	4–5	yes
ALA028	45.44.73	-5.9	0.708099	yes	M_2	extra-city cemetery	disturbed primary, single pit grave	F	30–40 years	5	no

(*Continued*)

Table 5. (Continued)

Sample ID	Arch. ID	$\delta^{18}O_c$ (‰) (VPDB)	$^{87}Sr/^{86}Sr$	aDNA[a]	Tooth Sampled (FDI)[b]	Location	Burial Type	Sex	Age	Yener Period[c]	Grave goods?[d]
ALA029	45.44.79	-4.5	0.708230	yes	M_2	extra-city cemetery	primary, single pit grave; reopened in antiquity	F	20–30 years	5	yes
ALA030	45.44.105	-5.9	0.708345	yes	M_2	Area 3 room	accidental death; no burial	F	40–44 years	6	N/A
ALA032	45.45.3	-5.2	0.708207	-	M_2	extra-city cemetery	primary, single pit grave	F	35–45 years	5	no
ALA033	45.45.4	-	0.709061	-	PM	extra-city cemetery	primary, single pit grave	F	35–45 years	6	yes
ALA034	45.45.6	-3.6	-	yes	M_2	extra-city cemetery	primary, single pit grave	M	35–45 years	6	no
ALA035	45.45.7	-4.3	-	yes	M_2	extra-city cemetery	primary pit grave with elements from multiple other individuals; disturbed? secondarily deposited?	M	25–35 years	6	no
ALA036	45.45.11	-4.5	-	-	M_2	extra-city cemetery	disturbed primary, single pit grave	unk.	10–11 years	6	no
ALA037	45.45.31	-4.4	0.707444	yes	M_2	extra-city cemetery	multiple individuals; secondary burial or possible slope wash disturbance	F	unk.	early 6	no
ALA038	L03-3017, P.236	-4.3	0.708409	yes	M^2	extra-city cemetery	Plastered Tomb	F	35–45 years	4	yes
ALA039	44.85.15	-	-	yes	-	Area 2 fill deposit	likely secondary, single pit burial	F	50–60 years	1–2	yes
ALA045	45.45.10	-5.3	0.708121	-	M_2	extra-city cemetery	primary, single pit grave	F	35–39 years	6	yes
ALA046	45.45.13	-4.2	-	-	M_2	extra-city cemetery	primary, single pit grave	unk.	20–50 years	6	yes
ALA048	45.45.23	-4.6	0.707851	-	M_2	extra-city cemetery	secondary burial of three mandibles	unk.	unk.	6	yes
ALA048	45.45.23	-4.6	0.708032	-	M_3	extra-city cemetery	secondary burial of three mandibles	unk.	unk.	6	yes
ALA052	45.45.33	-6.2	-	-	M_2	extra-city cemetery	primary, single pit grave	F	30–40 years	6	yes
ALA055	45.44.41	-4.2	0.708242	-	M_2	extra-city cemetery	primary, single pit grave	unk.	adult	4	yes
ALA057	45.45.50	-3.9	0.708769	-	M_2	extra-city cemetery	primary, single pit grave	F	35–55 years	early 7/8	yes
ALA059	45.44.55	-5.8	-	-	M^3	extra-city cemetery	primary, single pit grave	unk.	3–5 years	4	yes
ALA060	45.44.62	-5.2	0.708201	-	M_2	extra-city cemetery	secondary pit burial of two mandibles	M	adult	4	no
ALA061	45.44.67	-5.9	0.708090	-	M^2	extra-city cemetery	secondary, single pit burial	F	20–25 years	4–5	no
ALA063	45.44.82	-5.7	-	-	M_2	extra-city cemetery	primary, single pit grave	F	20–30 years	5	yes
ALA067	45.44.113	-5.7	0.708379	-	M^2	extra-city cemetery	primary, single pit grave	M	20–25 years	5	no
ALA069	45.44.120	-6.1	0.708078	-	M_2	extra-city cemetery	primary, single pit grave	M	25–35 years	5	yes
ALA070	45.44.121	-4.5	-	-	M^2	extra-city cemetery	primary, single pit grave with scattered remains of multiple individuals on top	F	40–50 years	6	yes

(*Continued*)

Table 5. (*Continued*)

Sample ID	Arch. ID	$\delta^{18}O_c$ (‰) (VPDB)	$^{87}Sr/^{86}Sr$	aDNA[a]	Tooth Sampled (FDI)[b]	Location	Burial Type	Sex	Age	Yener Period[c]	Grave goods?[d]
ALA072	L03-2025	-	0.708839	-	M^1	Area 2 mixed deposit	primary, single pit grave	F	17–25 years	4	no
ALA073	L03-3009	-6.1	-	-	M_2	extra-city cemetery	primary, pit grave with two individuals	M	35–45 years	6	yes
ALA074	L03-3011	-7.1	-	-	M_2	extra-city cemetery	primary, single pit grave	F	35–45 years	4	yes
ALA081	L03-3057	-4.7	0.708304	-	M^2	extra-city cemetery	primary, pit grave with two individuals	M	30–35 years	early 6	yes
ALA084	L03-3065	-4.7	0.708228	yes	M_2	extra-city cemetery	primary, single pit grave	F	25–30 years	early 6	no
ALA085	L03-3066	-6.1	0.708268	-	M_2	extra-city cemetery	primary, single pit grave	poss. F	25–35 years	early 6	yes
ALA086	L03-3054	-4.1	0.708206	-	M_2	extra-city cemetery	primary, single pit grave	unk.	8–13 years	6	yes
ALA087	L03-3027	-5.4	0.708112	-	M_2	extra-city cemetery	primary, single pit grave	unk.	12–15 years	6	no
ALA089	L03-3014	-5.7	0.708076	-	M_2	extra-city cemetery	primary, single pit grave with scattered remains of multiple individuals on top	unk.	6–11 years	6	no
ALA090	L03-3019	-7.3	-	-	M^2	extra-city cemetery	primary, single pit grave	unk.	15–19 years	4	no
ALA092	L03-3013	-4.1	0.708281	-	M^2	extra-city cemetery	primary, pit grave with two individuals	unk.	4–5 years	6	yes
ALA095	L03-3016	-	0.708391	yes	M_3	extra-city cemetery	primary, single pit grave with co-mingled remains of multiple individuals on top	M	25–35 years	4	no
ALA096	L03-3016	-5.6	-	-	M^2	extra-city cemetery	primary, single pit grave with co-mingled remains of multiple individuals on top	unk.	unk.	4	no
ALA097	45.44.53	-5.6	-	-	M_2	extra-city cemetery	primary, single pit grave	M	40–45 years	4	no
ALA098	45.45.23	-4.6	0.706801	-	M_2	extra-city cemetery	secondary burial of three mandibles	unk.	unk.	6	yes
ALA098	45.45.23	-4.6	0.706755	-	M_3	extra-city cemetery	secondary burial of three mandibles	unk.	unk.	6	yes
ALA099	45.45.23	-4.5	0.707977	-	M_2	extra-city cemetery	secondary burial of three mandibles	unk.	unk.	6	yes
ALA101	45.45.54	-5.0	0.708204	-	M^2	extra-city cemetery	primary, single pit grave	F	25–35 years	early 7/8	yes
ALA103	45.45.6a	-6.7	-	-	M_2	extra-city cemetery	primary, single pit grave	M	25–35 years	5	no
ALA104	45.45.45	-5.2	0.708223	-	M^2	extra-city cemetery	primary, pit grave with two individuals	unk.	ca. 3.5 years	7	yes
ALA105	45.45.43	-4.9	0.708214	-	M_2	extra-city cemetery	primary, pit grave with two individuals	F	35–45 years	7	yes
ALA110	45.45.48	-4.4	0.706770	Yes+	M^2	extra-city cemetery	primary, single pit grave	M	65–75 years	7	no
ALA110	45.45.48	-4.4	0.708303	Yes+	M_3	extra-city cemetery	primary, single pit grave	M	65–75 years	7	no
ALA111	L03-3015	-5.6	0.708436	-	M_2	extra-city cemetery	primary, single pit grave with co-mingled remains of individuals on top	M	20–35 years	6	no

(*Continued*)

Table 5. (Continued)

Sample ID	Arch. ID	$\delta^{18}O_c$ (‰) (VPDB)	$^{87}Sr/^{86}Sr$	aDNA[a]	Tooth Sampled (FDI)[b]	Location	Burial Type	Sex	Age	Yener Period[c]	Grave goods?[d]
ALA112	45.45.17	-5.7	-	-	M_2	extra-city cemetery	primary, single pit grave	F	20–30 years	6	yes
ALA113	45.44.31	-5.4	-	-	M_2	extra-city cemetery	primary, single pit grave	unk.	25–35 years	4	yes
ALA114	44.85.32	-	0.708554	-	M^1	Area 2 fill deposit	primary, single pit grave	F	40–45 years	1–2	yes
ALA115	45.44.21	-4.2	0.708201	-	M^2	Area 3 room	primary, single pit grave	unk.	adolescent	4	yes
ALA116	L03-3060	-5.3	-	-	dm_2	extra-city cemetery	primary, single pit grave	unk.	3–6 years	early 6	yes
ALA118	32.53.111	-5.8	-	yes*	RM^2 (17)	Royal Precinct, transitional layer	primary, single pit grave	F	45–50 years	3–4	yes
ALA119	32.53.136	-4.8	-	-	RM_2 (47)	Royal Precinct courtyard	primary, single pit grave	F	30–35 years	4	yes
ALA120	32.54.81	-6.5	-	yes*	LM_2 (37)	Royal Precinct, transitional layer	primary, single pit grave	M	1–2 years	3–4	yes
ALA122	44.95.9	-6.2	-	-	RM^2 (17)	Area 2 courtyard	primary, single pit grave	F	45–50 years	1–2	no
ALA123	45.44.147	-3.2	-	yes*	Rdm^2 (55)	Area 3 room	primary, single pit grave	M	3–4 months	7	no
ALA124	45.44.151	-4.7	-	yes*	dm^1	Area 3 room	primary, single pit grave	M	ca. 40 weeks	7	no
ALA125	64.72.100	-5.1	-	-	LM_3 (38)	Area 4 intra-city cemetery	primary, single burial in a possible mudbrick cist grave	M	55–65 years	5	yes
ALA126	64.72.101	-5.7	-	-	LM^2 (27)	Area 4 intra-city cemetery	primary, single burial in a stone and mudbrick cist grave	M	45–50 years	5	yes
ALA127	64.72.113	-5.7	-	-	RM^2 (17)	Area 4 fill deposit	loose teeth	unk.	unk.	LB I	N/A
ALA128	64.72.120	-4.8	-	yes*	RM_2 (47)	Area 4 intra-city cemetery	primary, single pit grave	M	35–45 years	5	yes
ALA129	64.72.123	-5.0	-	-	RM^2 (17)	Area 4 intra-city cemetery	primary, single burial in a stone and mudbrick cist grave	F	25–35 years	5	yes
ALA130	64.72.128	-3.5	-	yes*	dm2	Area 4 intra-city cemetery	primary, single pit grave	F	4–5 months	5	no
ALA131	64.72.135	-5.7	-	yes*	LM^2 (27)	Area 4 intra-city cemetery	primary, single pit grave	M	35–40 years	4	yes
ALA132	64.72.136	-5.5	-	-	M_2	Area 4 intra-city cemetery	primary, single pit grave	F	25–30 years	4	no
ALA133	64.72.137	-6.4	-	-	RM_2 (47)	Area 4 intra-city cemetery	primary, single pit grave	unk.	12–13 years	6	no
ALA134	64.72.138	-5.7	-	-	Rdm^2 (55)	Area 4 intra-city cemetery	primary, single pit grave	unk.	ca. 4 years	6	yes
ALA135	64.72.139	-4.6	-	yes*	Rdm^2 (55)	Area 4 intra-city cemetery	primary, single pit grave	F	5–6 years	6	yes
ALA136	64.72.141	-7.3	-	yes*	Ldm^1 (64)	Area 4 intra-city cemetery	primary, single pit grave	M	1.5–2 years	6	yes
ALA138	64.72.144	-	-	yes*	-	Area 4 intra-city cemetery	primary, single pit grave	M	1–2 months	6	no
ALA139	64.72.150	-4.5	-	-	LM^2 (27)	Area 4 intra-city cemetery	primary, single pit grave	F	50–53 years	5	yes
ALA140	64.72.153	-6.8	-	-	RM_3 (48)	Area 4 intra-city cemetery	primary, single pit grave	F	40–50 years	6	yes

(Continued)

Table 5. (Continued)

Sample ID	Arch. ID	$\delta^{18}O_c$ (‰) (VPDB)	$^{87}Sr/^{86}Sr$	aDNA[a]	Tooth Sampled (FDI)[b]	Location	Burial Type	Sex	Age	Yener Period[c]	Grave goods?[d]
ALA141	64.73.88	-5.4	-	-	LM$_2$ (37)	Area 4 intra-city cemetery	primary, single pit grave with partial remains of a second individual; reopened in antiquity to remove some skeletal elements	poss. M	17–18 years	4	no

[a]The ten individuals whose aDNA data is published here for the first time are marked with an asterisk (*). Individuals without (*) were published in Skourtanioti et al. [49]; (+) genomic data was published from ALA015 in Skourtanioti et al. [49], but this data actually belongs to individual ALA110. We have accordingly reassigned it to ALA110 in this study.

[b]"M" = unspecified molar; "PM" = unspecified premolar. Numbers in paratheses represent FDI World Dental Federation tooth identifications, where available based on the sampling restrictions outlined above.

[c]The majority of the Periods listed here are provisional, as many of the contexts are still under analysis, and may change as research progresses.

[d]"N/A" indicates that the sampled individual was not recovered from a grave proper, and thus the presence/absence of grave goods is not an applicable issue.

No data is indicated by '-'.

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Alalakh, returning a local range as two standard deviations from the mean (0.708401) of 0.708085–0.708717 (Table 7). By excluding the five snail shells from this calculation, we avoid a potential bias stemming from the snails' fixation to a very small radius on the tell that may be less representative for humans.

One way to check the accuracy of a local range obtained from the ancient faunal samples is by comparison against the $^{87}Sr/^{86}Sr$ ratios of young children: the likelihood of individual

Table 6. All faunal samples.

Sample ID	$^{87}Sr/^{86}Sr$	±2 SD internal	$\delta^{18}O$ (‰)(VPDB)	SD	Species	Context
AT 0263	-	-	-2.2	0.1	*Bos taurus*	Tell Atchana, Sq. 64.82.2
AT 1074	-	-	-7.2	0.0	*Bos taurus*	Tell Atchana, Sq. 64.82.17
AT 1141	0.708544	0.000010	-5.3	0.2	*Spalax leucodon*	Tell Atchana, Sq. 64.72.8
AT 11570	0.708440	0.000009	-	-	*Gastropoda*	Tell Atchana, Sq. 42.29.9
AT 12146	0.708411	0.000013	-	-	*Gastropoda*	Tell Atchana, Sq. 32.54.66
AT 12952	0.708296	0.000010	-	-	*Gastropoda*	Tell Atchana, Sq. 32.57.219
AT 2051	0.708111	0.000015	-	-	*Gastropoda*	Tell Atchana, Sq. 33.32.1
AT 3061	0.708418	0.000012	-	-	*Rodentia*	Tell Atchana, Sq. 64.73.9
AT 3064	-	-	-2.4	0.0	*Caprinae*	Tell Atchana, Sq. 64.73.7
AT 8302	-	-	-4.4	0.1	*Sus scrofa*	Tell Atchana, Sq. 64.82.56
AT 9580	0.708305	0.000011	-	-	*Gastropoda*	Tell Atchana, Sq. 45.44.94
G1.5A	0.708807	0.000013	-	-	*Gastropoda*	Kamberli (modern)
G2.2	0.707924	0.000013	-	-	*Gastropoda*	Kırıkhan (modern)
G2.6	0.707984	0.000012	-	-	*Gastropoda*	Reyhanlı (modern)
G3.3B	0.708359	0.000013	-	-	*Gastropoda*	Hacıpaşa (modern)
G3.4A	0.708661	0.000011	-	-	*Gastropoda*	Hacıpaşa (modern)
G4.2C	0.708302	0.000011	-	-	*Gastropoda*	UyduKent (modern)
G5.5	0.708522	0.000014	-	-	*Gastropoda*	Avcılar (modern)
G6.2A	0.708211	0.000015	-	-	*Gastropoda*	Ceylanlı (modern)
G6.7	0.707376	0.000014	-	-	*Gastropoda*	Haydarlar (modern)

Where samples have not been analyzed for a particular isotope, a '-' is used to indicate no data. The modern samples (as indicated in the Context column) were collected in surface survey near the cities listed. For the locations of the cities (all within the Amuq Valley), see Fig 5.

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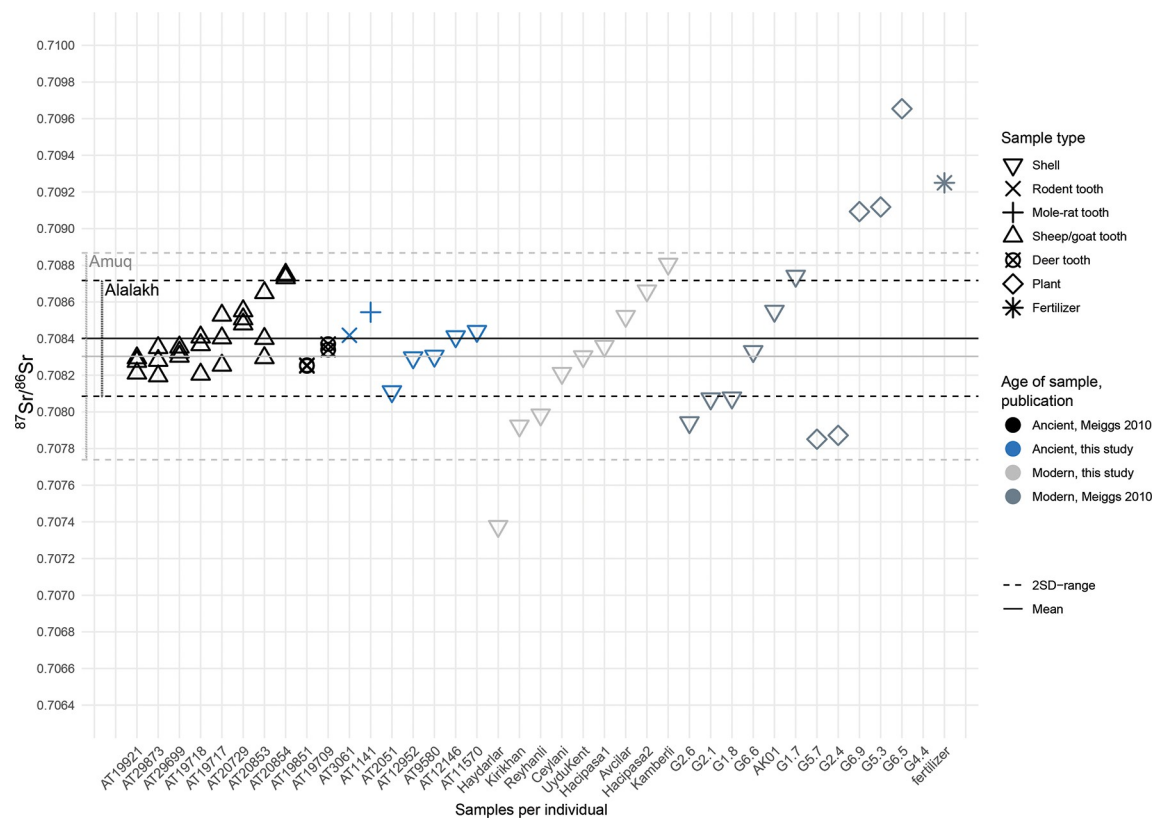
Fig 7. ^{87}Sr/^{86}Sr ratios of snail, plant, fertilizer, and animal samples from this study and Meiggs [147]; continuous lines: Mean; dotted lines: ±2 SD from mean; black dotted lines: Local range for Alalakh, calculated from sheep/goat, deer, and rodent teeth of both studies; grey dotted lines: Local range for the Amuq Valley, calculated from modern and ancient snail shells of both studies, using the mean of the five ancient snails from Alalakh as representative for this location, and excluding the modern samples AK01 and the outlier from Haydarlar. Note: sample G4.4 falls outside the ranges plotted in this graph and therefore appears blank.

mobility in sedentary societies should increase with age, so individuals dying at a young age are more likely to be local [229, 231–233]. All six individuals under the age of seven from Alalakh fall well inside the local range as determined by the archaeological fauna. In general, we believe that the range calculated from ancient faunal samples is representative for locality in humans, although in the case of individuals falling just outside this local range, we need to consider the option that these may only appear as outliers if they were consuming larger portions of non-local diet as compared to other inhabitants, as discussed above.

The modern snail samples taken from throughout the valley provide the opportunity to compare the ^{87}Sr/ ^{86}Sr ratios at the site with those from other locations in the Amuq Valley and serve to calculate a local range for the valley in general. The modern snail shells from our study (n = 9) show a high consistency with the snail shells from Meiggs' study (n = 6), with samples originating from the same geological units having similar ^{87}Sr/ ^{86}Sr ratios across both studies. The plant samples from Meiggs' study, on the other hand, are generally characterized by either extremely high or low ^{87}Sr/ ^{86}Sr ratios that cannot be explained by their location within the geological patchwork of the slopes of the Amanus mountains on the fringes of the Amuq Valley alone (for further discussion, see S2 File). We therefore decided to combine only the snail shells of both studies in our calculations of a local range for the Amuq Valley catchment area. The snail from Haydarlar, with the lowest ^{87}Sr/ ^{86}Sr ratio (0.707376) among the modern snails, constitutes an outlier compared to all other modern snails. Haydarlar is located

**Table 7. Comparison between possible local ranges.**

Description	n	Mean	Location	Local Range (+/-2 SD)	Comments
All ancient environmental samples (sheep/goat and deer teeth)	28	0.708396	Alalakh	0.708073– 0.708718	Meiggs [147]
All ancient environmental samples (5 snails, 2 rodents)	7	0.708361	Alalakh	0.708104– 0.708617	this study
All ancient snail shells	5	0.708313	Alalakh	0.708081– 0.708544	this study
All ancient environmental samples of both studies	35	0.708389	Alalakh	0.708077– 0.708700	Meiggs [147] and this study
Ancient samples of sheep/goat, deer and rodents' teeth	**30**	**0.708401**	**Alalakh**	**0.708085– 0.708717**	**Local range, Alalakh; Meiggs [147] and this study**
All modern environmental samples (snails and plants)	12	0.708998	Amuq Valley	0.705400– 0.712596	Meiggs [147]
Modern environmental samples, excluding pine needle outlier (Sample G4.4)	11	0.708482	Amuq Valley	0.707331– 0.709632	Meiggs [147]
All modern snail shells	6	0.708285	Amuq Valley	0.707716– 0.708855	Meiggs [147]
All modern snail shells	9	0.708238	Amuq Valley	0.707420– 0.709057	including Haydarlar outlier; this study
Modern snail shells combined with mean of ancient snails (excluding Haydarlar outlier and AK01 from Alalakh)	**14**	**0.708303**	**Amuq Valley**	**0.707739– 0.708868**	**Local range, Amuq: Meiggs [147] and this study**
Youngest individuals (0–6 years)	6	0.708340	Alalakh	0.708136– 0.708544	Humans, this study

on alluvial deposits of the Kara Su river valley on the northernmost fringes of the Amuq Valley. We conclude that the distinctly low isotopic signature of this snail stems from the basalt shields of Jurassic and Cretaceous age that are located along the slopes of the river valley, so that runoff water from these areas is naturally directed toward the riverbed and therefore impacts these adjacent areas, pulling the snail shell toward a lower ^{87}Sr/ ^{86}Sr ratio (see also S3 File) [166, 229]. This does not mean that the result should be considered incorrect, only that individuals growing up around this location may also have a comparable strontium signature that is distinctly lower than that of individuals from the rest of the Amuq Valley. We therefore excluded the snail shell from all further calculations of a local range for the Amuq Valley. Finally, we excluded the modern snail shell from Alalakh itself (sample AK01) and instead used the mean of the ancient snail shells (n = 5), since we expect these to be a better representative for the local signature directly at the tell in the past. With this method, we obtain a local range for the wider Amuq catchment area, based on 14 distinct data points, of 0.707739–0.708868 and a mean of 0.708303 that we see as best representing the strontium variation within the valley.

Applying the local range for Alalakh (708085–0.708717), out of a total of 53 human individuals, 40 plot within the range of Alalakh and another 8 plot outside the Alalakh range, but within the range for the Amuq Valley (0.707739–0.708868) (Fig 8; see also Table 5). Five individuals can be securely identified as non-locals to both Alalakh and the Amuq, plotting outside both local ranges (ALA110, ALA098, ALA037, ALA004, and ALA033). Nearly 10% of the sampled population (9.4%) is therefore identified as non-local to both Alalakh and the Amuq Valley.

All five non-local individuals were buried in the extra-city cemetery, and four of the five are stratigraphically dated to Period 6 (ALA110 is dated to Period 7 and is one of the earliest graves excavated in Area 3; see Table 2). Two are female (one adult–ALA033 –and one of unknown age–ALA037), two are adult males (ALA004 and ALA110), and one is of unidentified age and
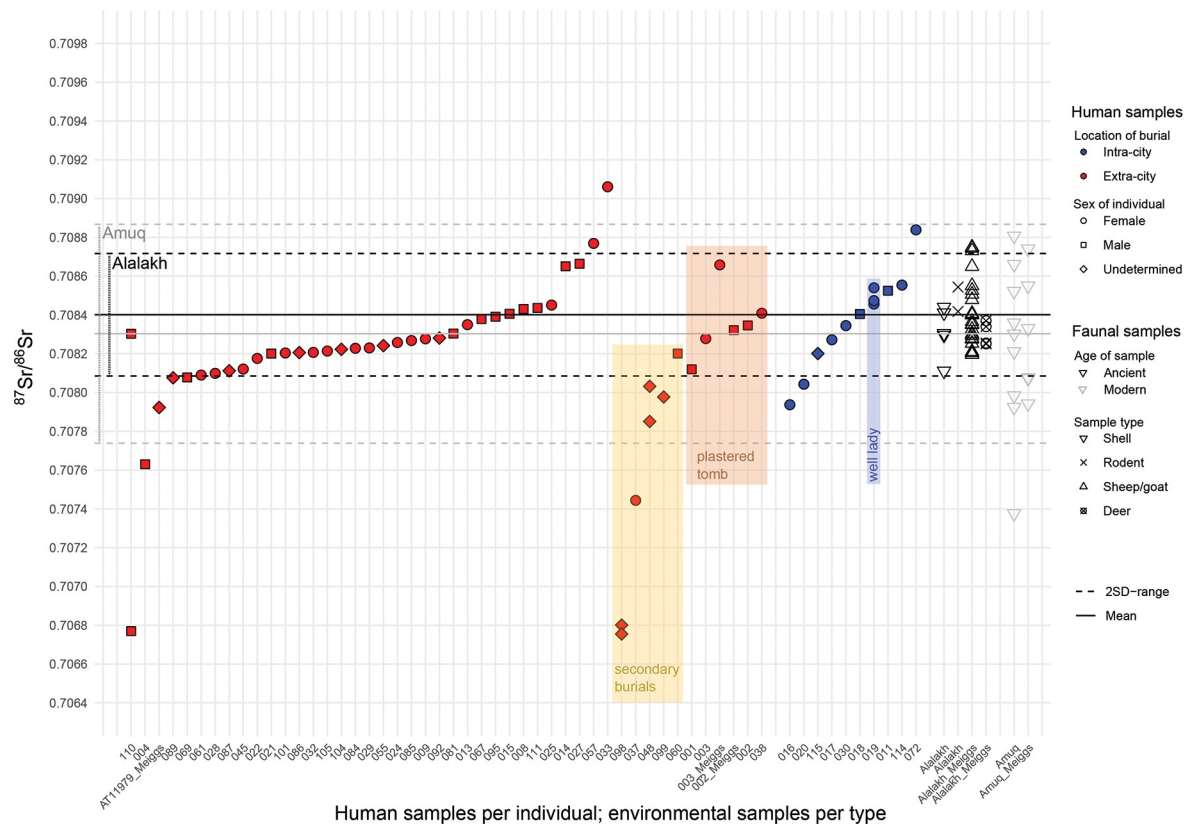
Fig 8. All ^{87}Sr/ ^{86}Sr results, plotted against local ranges. Continuous lines: mean; dotted lines: ±2 SD from mean. Black dotted lines: local range calculated from ancient faunal samples from Alalakh as explained in the Fig 7 caption; grey dotted lines: local range calculated from modern snails from the Amuq and the mean of ancient environmental samples from Alalakh as explained in the Fig 7 caption.

sex (ALA098). All three non-locals who have also been analyzed for oxygen isotopes (ALA110, ALA098, and ALA037) fall firmly within the range of local δ^{18}O values (see Table 5), indicating that, while they are not from the Amuq Valley, they grew up in areas with similar δ^{18}O values. Most interestingly, two of the five non-locals (ALA098 and ALA037) are secondary burials, as are secondarily buried individuals ALA048 and ALA099, two of those who likely came from within the Amuq Valley, rather than Alalakh itself (see Fig 8). In fact, only one of the sampled secondary burials (ALA060) falls within the local range for Alalakh (see Fig 8). In order to explore the timing of the migration of these non-locals, M3s were also analyzed when they were available, which returned a range of resulting patterns (see Fig 8). Like the M2 (0.707851), the M3 of ALA048 (0.708032) still falls within the group identified as local to the Amuq, but substantially closer to the Alalakh range, indicating that the move from within the Amuq to Alalakh may have occurred late during the formation of the M3 (likely during the end of childhood/ early adolescence), leading to this mixed signal. The M3 of ALA110 (0.708303) falls firmly within any local range calculated here and clearly shows that this individual moved to Alalakh in later childhood–i.e., between the formation of M2 and M3. ALA098, however, has similar ^{87}Sr/^{86}Sr values for both M2 (0.706801) and M3 (0.706755), both of which fall at the lowest end of the results reported here. It therefore appears that this individual spent their entire childhood and youth in another location, moving to Alalakh only in adulthood.

Out of the three human individuals sampled in Meiggs' study [147], two were analyzed again in this study (002_Meiggs = ALA002 and 003_Meiggs = ALA003). While both samples

from individual ALA002 have similar $^{87}Sr/$ ^{86}Sr ratios, ALA003 in Meiggs' study has a higher $^{87}Sr/$ ^{86}Sr ratio and plots outside the local range calculated here, as does the third human sample from Meiggs's study (AT 11979). Unfortunately, the teeth sampled by Meiggs were only identified to the level of molars, and, given the discrepancy between the M2 value obtained here and the one published by Meiggs [147], it is likely that the tooth sampled in Meiggs' study was either an M3 or an M1. In this case, the difference in the $^{87}Sr/$ ^{86}Sr ratio between the two samples from ALA003 would be explained by changes in the origins of food that could ultimately be linked to a change in place of residency during childhood. While a sample from an M1 would mean that ALA003 spent the first years of her life outside of Alalakh, a sample from the M3 would hint at a move away from Alalakh during later childhood/early adolescence and, consequently, a return to Alalakh later.

Results of aDNA analysis

All eleven new Alalakh samples analysed for aDNA produced good quality data (low contamination, $\geq$ 135,000 SNPs on 1240K; Table 8).

Remarkably, all individuals sampled from Alalakh, regardless of their context, are very homogeneous from a population genomics perspective, with only one exception (ALA019; compare PCA Fig 9). As described above (see Tables 3–5), the individuals cover all ages (ca. 40 weeks-75 years at death) and both sexes, as well as all burial contexts available for analysis. It is reasonable to assume, therefore, that the genomic data from Alalakh accurately describes the genetic variation within the bulk of the MBA-LBA population from Alalakh. Published data from other contemporary Levantine and Anatolian sites shows that most individuals cluster relatively close to each other in the PCA on a north-south cline, and their overall genetic differences are small [38, 39, 45, 49], yet detectable.

Therefore, with the help of *qpAdm* modeling, we can explore the role of Alalakh as an intermediary on this cline between contemporaneous individuals from sites located to the north in Anatolia and to the south in present day Lebanon [234]. For modeling, we have chosen individuals dating to the MBA and LBA from Kaman-Kalehöyük (n = 5 [45]) as a representative for central Anatolian groups and from Sidon (n = 5 [39]) as a representative for Levantine individuals to the south of Alalakh.

Table 8. Summary of aDNA data production for this study.

Sample ID	N° and type of libraries	Sex	N° SNPs on 1240K	ANGSD (MoM)	MT-coverage	Schmutzi	AuthentiCT	Y-haplo	MT-haplo
ALA110	1, ss	M	135815	-0.002	0.6	0.02	$\leq$0.01	-*NA*-	
ALA118	1, ds	F	297638		2.3	0.09			
ALA120	1, ds	M	931700	0.004	5.2	0.01		J2a1a1a2b2a3b1~	H92
ALA123	1, ds	M	713176	0.005	5.2	0.02		J2a1a1a2	X2d
ALA124	1, ds	M	443273	0.001	4.1	0.03		J1a2a1a~	
ALA128	1, ss	M	241913	0.030	1.7	0.02	$\leq$0.01	LT [K1]	
ALA130	2, ss	F	837689		38.4	0.01	$\leq$0.02		K1a4c1
ALA131	2, ss	M	590959	0.013	13.3	0.01	$\leq$0.02	J2a1a1a2b2a	K1a4a
ALA135	2, ss	F	847258		11.4	0.01	$\leq$0.02		R1a
ALA136	6, ss	M	186630	0.038	1.7	-*NA*-	$\leq$0.02	E1b1b1	
ALA138	2, ss	M	298445	0.011	19.7	0.01	$\leq$0.02	T1a1a	K1a

Ten individuals (ALA118, ALA120, ALA123, ALA124, ALA128, ALA130, ALA131, ALA135, ALA136, and ALA138) are published here for the first time. For ALA110, we add data from a new single stranded library. The initial genomic data for ALA110 was published in Skourtanioti et al. [49] under the identifier ALA015.
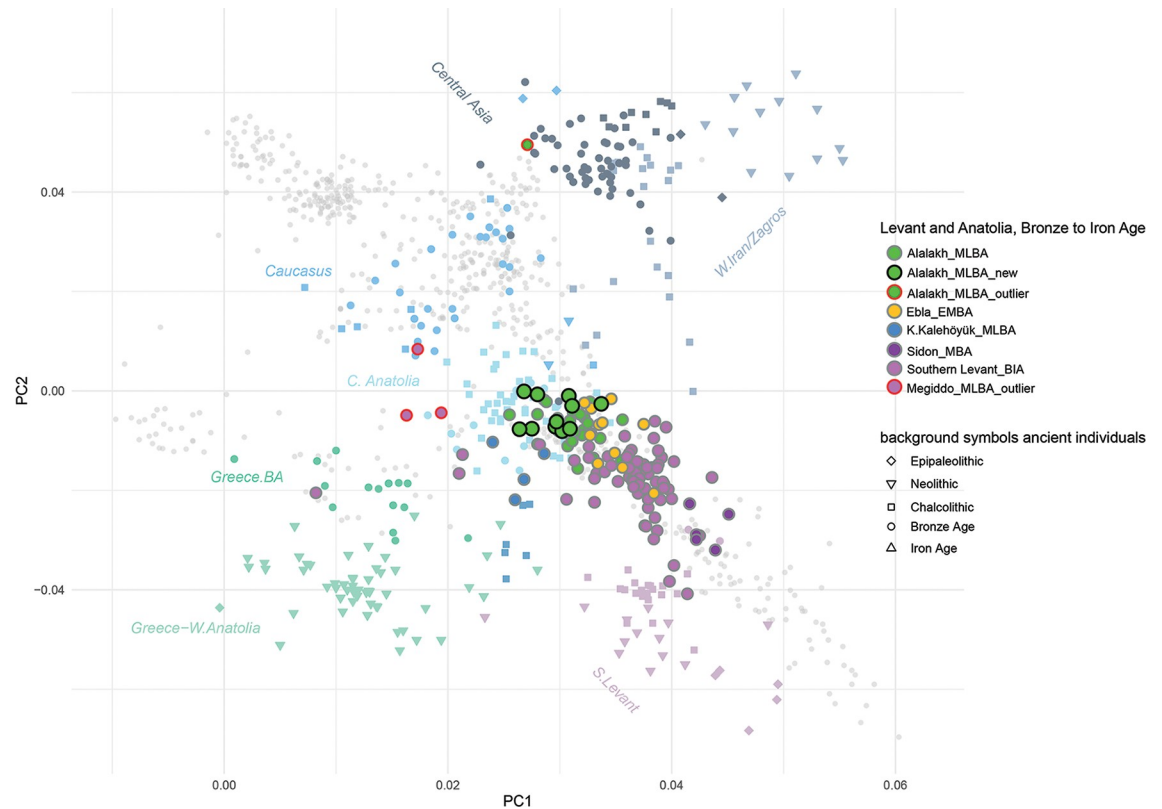
Fig 9. PCA: Scatterplot of PC1 and PC2 calculated on West Eurasian populations (Human Origins dataset; grey symbols) using smartpca with projection of ancient individuals (colored symbols).

As–at least for the Amuq Valley and the Southern Levant–there was gene flow during and/or after the Chalcolithic period, we tested models that used temporally proximal sources from Anatolia, Iran, the Caucasus, and the Southern Levant (Fig 10 and S2 Table). The results of this modeling show that Alalakh_MLBA (n = 33) can be adequately modeled as a three-way admixture model between an Anatolian ("Büyükkaya_Chl"; 29.5±4.4%), a Levantine ("Levant_Chl"; 33.9±3.8%), and an Iranian ("Iran_Chl"; 36.5±2.2%) source (p-value = 0.64). The same applies to Ebla_EMBA (p-value = 0.89), though with a lower coefficient from Büyük-kaya_EChl (21.5±5.6%). For Sidon_MLBA, the simpler two-way admixture model of Levant_Chl and Iran_Chl or W.Iran_N provides a better fit (p-value = 0.021 or p-value = 0.09, respectively). Three-way models fail for Sidon_MLBA (p-value < 0.01 or negative coefficients) (see Fig 10).

Overall, these models provide adequate descriptions for the positioning of the individuals from Alalakh, excluding outlier ALA019, on the PCA in between contemporary Anatolian and central/southern Levantine individuals by breaking their ancestry down to three major components of Anatolian, Levantine, and eastern origin. For Alalakh, Ebla, and Sidon, models fit better with Iranian than Caucasian sources. However, when the Tell Kurdu population is used instead of Büyükkaya as a geographically proximal source, models with Caucasus sources fit better for Alalakh when Levant_EBA is used as a third source instead [49]. Therefore, a clear distinction between possible source populations from an eastern (Iranian) or northeastern (Caucasus) source is not yet possible with the data available. Sources to the east/southeast (northern and southern Mesopotamia) also need to be considered here, but these remain completely unsampled as of yet. The existing gaps in available genomic data touch on yet
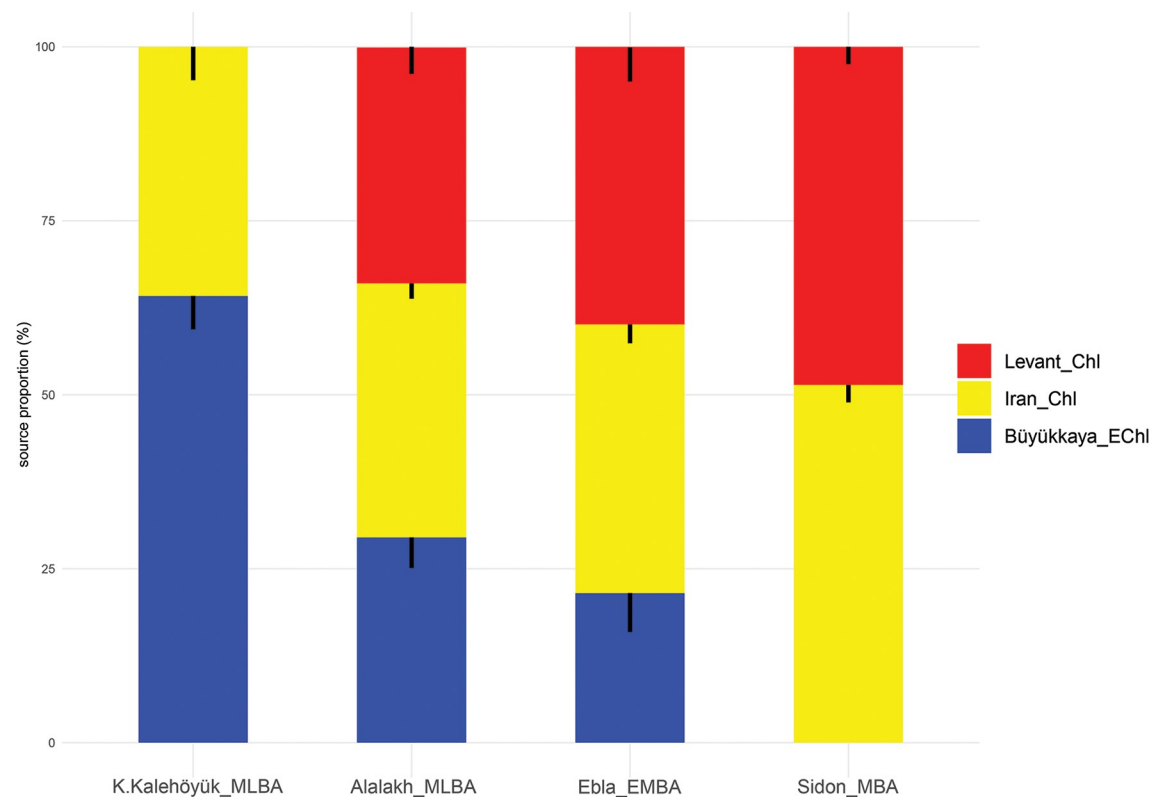
Fig 10. Admixture modeling (*qpAdm*) of Alalakh_MLBA, Ebla_EMBA, K.Kalehöyük_MLBA, and Sidon_MBA using Chalcolithic and Bronze age source populations. Source proportions are plotted with -1SE. Abbreviations: E = early, M = middle, L = late, BA = Bronze Age, Chl = Chalcolithic.

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another important issue when performing admixture modeling: the individuals we group together here to represent 'source populations' need to be seen as mere proxies. We do not suggest that any of these groups are the actual source for admixture events. Indeed, based on archaeological and textual evidence, populations from northern Mesopotamia are among the likely genetic sources at Alalakh, especially the Hurrians and the Amorites, both groups known from texts to have been on the move in the region in the 3rd and 2nd millennia BC and which are attested in considerable numbers in the Alalakh texts [49, 77–79, 235–241].

Kinship analysis. READ computed on the total of 35 individuals from Alalakh successfully assigned pairs ALA011-ALA123 and ALA001-ALA038 as first degree related and pair ALA002-ALA038 as second degree related (Fig 11). The latter two cases are individuals from the Plastered Tomb and are reported in Skourtanioti et al. [49]. However, the genetic relatedness between ALA001 and ALA002 remains unresolved with this method, as the estimated P0 for this pair lies within the 95% confidence interval of the second-degree cutoff, but surpasses it in the +2 SE, and therefore either a second or higher degree are possible. Plotting *r* against k0 estimated by *lcMLkin* clusters pairs in three main groups that correlate with the result of READ: pairs ALA011-ALA123 and ALA001-ALA038, pairs ALA002-ALA038 and ALA001-ALA002, and all the other unrelated pairs ($r \approx 0$) (Fig 12). For all related pairs, *r* is lower than expected, as suggested by the comparison with the degrees assigned by READ and by $r = 0.9$ between two different genomic libraries generated from the same individual (ALA039). Underestimation of *r* can be attributed to the lower quality of ancient data and has been reported before in Mittnik et al. [70], where genetic relatedness was explored in a large
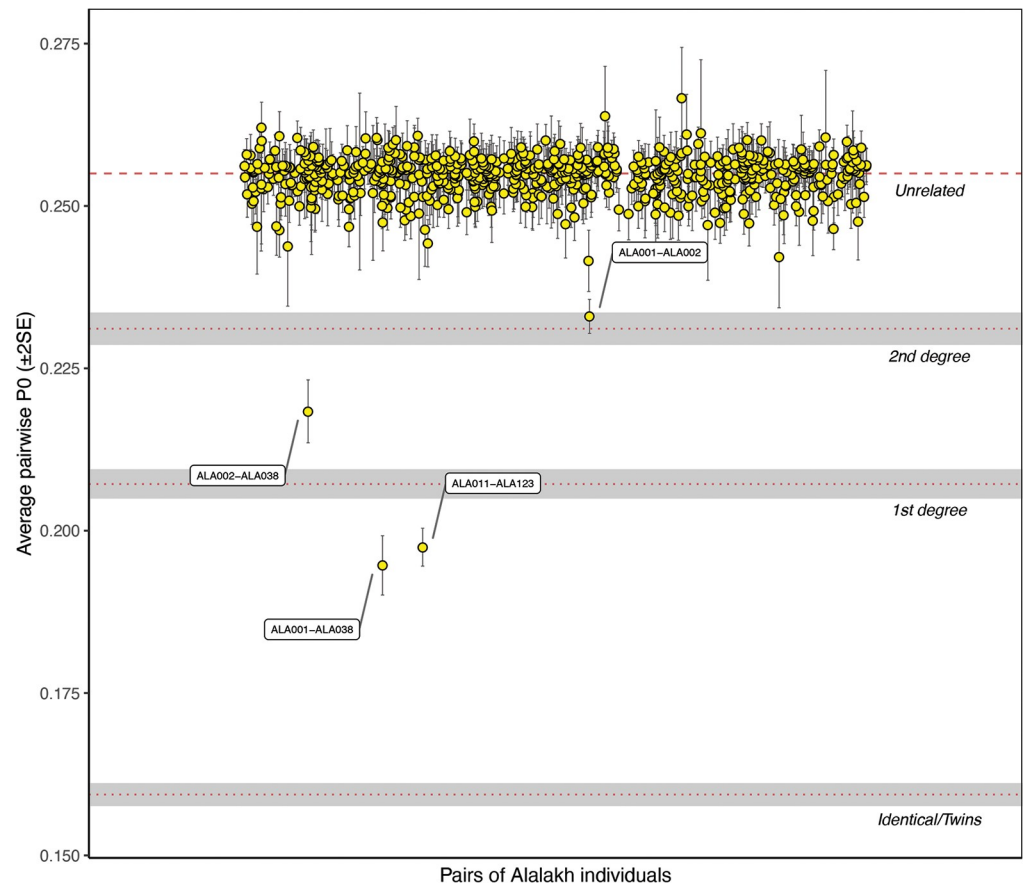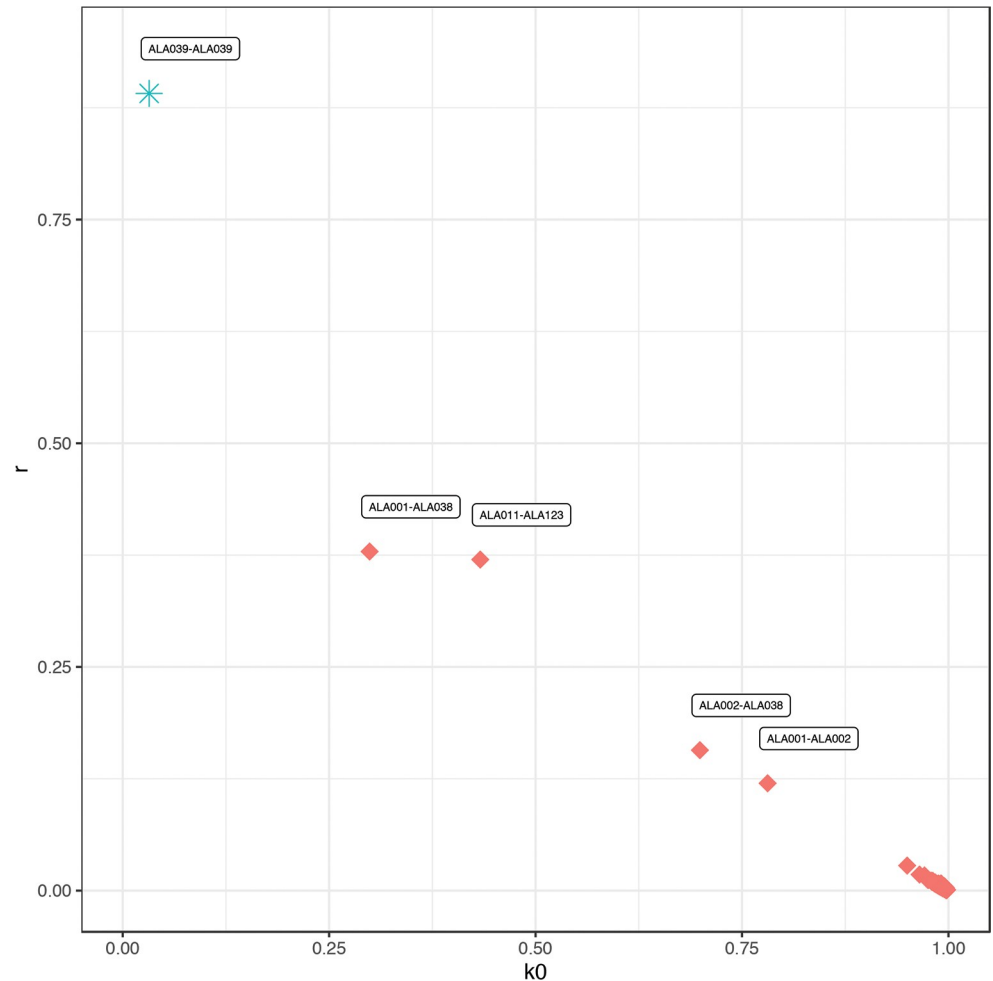
Fig 11. Kinship analysis with READ.

set of ancient individuals. However, the clustering of pairs ALA002-ALA038 ($r = 0.16$) and ALA001-ALA002 ($r = 0.12$) indicates that the latter likely also represents a second rather than a third-degree relationship. Interestingly, the two first-degree pairs ALA011-ALA123 and ALA001-ALA038 have both $r = 0.39$ but differ in the k0, and hence, suggesting a sibling-sibling and a parent-offspring relationship, respectively.

Altogether, therefore, kinship in the first and second degree can be securely identified between five individuals from Alalakh. In all cases, the deceased were buried in close spatial proximity to one another. Individuals ALA011 and ALA123, two small children who were buried next to each other inside a casemate of the Area 3 fortification wall [100, 108] are first degree relatives, making them direct siblings. The other three individuals come from the Plastered Tomb and are discussed further below.

Discussion

The aDNA analysis from Tell Atchana revealed that the sampled individuals are genetically very homogeneous–with the exception of ALA019 –and that the common ancestry at Alalakh was widespread over a larger area which stretched southeastward at least until Ebla. Consequently, aDNA's resolution for scenarios of micro-regional migration might be limited. The genetic homogeneity of the samples from Alalakh suggests that the recent ancestors of most individuals came from within the wider Amuq-Ebla region, rather than beyond, which

Fig 12. Kinship analysis with *lcMLkin*.

conforms well with the overall strontium and oxygen isotopic results that indicate a local upbringing within the Amuq Valley for the majority of sampled individuals.

Though the oxygen isotopic results are relatively homogenous, the strontium results are generally more informative. These suggest an overall population structure at the site during the MBA-LBA that was made up of a majority of people from the city itself. Based on the ancient faunal samples from Alalakh, we estimate that 40 individuals (75%) came from the city itself. The modern snail shells revealed that strontium ranges for many other locations within the Amuq Valley are comparable to those from Alalakh. This means we need to reckon with the possibility that a substantially larger portion of people than the eight that fall outside the Alalakh range but within the range calculated for the Amuq Valley originated within the Amuq Valley from sites other than Alalakh. Five individuals (9.4%) are identified as non-local to the whole Amuq Valley on the basis of the modern snail shells, one of which (ALA110) apparently moved to Alalakh during later childhood, resulting in the different ^{87}Sr/^{86}Sr ratios between M2 and M3 (see Fig 8 and Table 5). However, it should be kept in mind that the presence of non-local foodstuffs is well attested at Alalakh in both the MBA and LBA and, as discussed above, if this food was consumed by at least some of the population during childhood, it is possible that this could influence strontium ratios. This is less likely to be the case for the

five non-locals identified here, as their strontium ratios fall well outside the ranges established for both Alalakh and the Amuq Valley, but it could particularly be the case for those individuals falling closer to the margins of these ranges. It is therefore possible that some of the eight individuals identified here as local to the Amuq Valley (but not Alalakh itself) may fall into this (hypothetical, though reasonable, based on the evidence in hand) category of Alalakh residents who consumed enough non-local foodstuffs during childhood to modify their strontium ratios, thus making them appear in the results as non-locals to the city.

The only correlation between non-locals and any contextual variable such as burial location, type, or date, is the association of secondary burials with non-local individuals. One of these non-locals (ALA098) was found as part of a secondary burial consisting only of three mandibles. The other two mandibles, ALA048 and ALA099, are local to the Amuq, but not Alalakh. It therefore seems that all three of these individuals were born outside of Alalakh, although ALA048 and ALA099 seem to have grown up in the Amuq Valley (or somewhere with a similar isotopic signature). The wide separation between their $^{87}Sr/^{86}Sr$ ratios, however, indicates that all three spent their childhoods in different places (ALA098 = 0.706801; ALA048 = 0.707851; ALA099 = 0.707977), despite being buried together.

There are several potential explanations for this relationship between non-locals and secondary burials, not all of which are mutually exclusive. The most straightforward explanation is that these individuals moved to Alalakh at some point during their lives and then died and were buried there. If secondary burial was a stronger tradition in the area(s) where these individuals originally came from, it is possible that their families chose secondary burial for this reason, even though it was a minority practice at Alalakh itself [100, 101, 103]. However, given the nature of secondary burial, there are other possibilities. These individuals may have moved to Alalakh during their lifetimes, and, following their deaths, the majority of their remains could have been transferred back to their original settlement(s) for burial, with only parts of them remaining at Alalakh for burial. Alternatively, these individuals could have lived their entire lives elsewhere, but, after death, parts of the deceased could have been brought to Alalakh for burial, perhaps as a result of its status as a regional cult center [98, 99]. People who were able to do so may have chosen to inter a portion of their family's remains at the cult center for a variety of reasons, including gaining favor from the gods, in order to raise their social standing, or because they were ritual specialists who were expected and entitled to do so, although these scenarios are purely speculative.

Genomic data exists for three (ALA004, ALA037, and ALA110) of the five $^{87}Sr/^{86}Sr$ non-locals. All three individuals share the same genetic profile as the other individuals from Alalakh. There are two possible explanations for this pattern: the individuals could have come to Alalakh from a distance that is outside the Amuq but still within the wider Alalakh-Ebla catchment area, as the genomic data suggests, or this may be a case of backwards migration–the parents or grandparents of ALA004, ALA037, and/or ALA110 could have emigrated from the area around the Amuq, ALA004, ALA037, and ALA110 consequently spending their childhoods elsewhere, but later coming back to Alalakh and subsequently dying there. As the ancestors of the individuals would have originated from the Amuq region in this scenario, their genetic profile matches the other individuals sampled from Alalakh. In the case of ALA110, the additional M3 that was analyzed for $^{87}Sr/^{86}Sr$ plots within the local range for Alalakh and indicates that this individual's move to Alalakh occurred between M2 and M3 tooth formation, around the age of 7–10 (M2 tooth formation age = 2–8 years; M3 tooth formation age = 7–14 years) [162].

The case of the Well Lady (ALA019)

Aside from the bulk of genetic data from Alalakh that suggests regional ties over many generations, there is one outstanding case of long-distance mobility. Individual ALA019 –the Well

Lady–takes up an extreme outlier position in the PCA closest to sampled individuals from Bronze Age Iran/Turkmenistan/Uzbekistan/Afghanistan, which can be confirmed with *outgroup f_3* statistics [49]. While it is impossible to say exactly where to the east or northeast this individual (and/or her ancestors) came from, especially in the absence of data from nearby eastern regions like Mesopotamia, it is clear from the genetic data that either this individual or her recent ancestors migrated to the Alalakh region. The strontium isotope data allows us to narrow down the possibilities, and it seems that the Well Lady herself did not migrate, but rather her ancestors, as the ^{87}Sr/ ^{86}Sr ratios of all three molars sampled (M1, M2, and M3) fall within even the most narrowly defined local range for Alalakh (see Fig 8); however, due to a lack of research on bioavailable strontium isotopes in the Central Asian areas where the PCA suggests she came from, it is not currently possible to definitively rule out a childhood spent in these regions. A scenario in which she was part of a pastoral community that frequently came into contact with inhabitants of the Amuq Valley is unlikely, however, due to the low variation in all three ^{87}Sr/ ^{86}Sr ratios (M1 = 0.708456; M2 = 0.708474; M3 = 0.708540). The case of the Well Lady is therefore particularly interesting, not only because it is the only genetic outlier in a dataset of 37 individuals (if we add the Ebla data on top of that, in a dataset of 48 individuals), but also because the strontium evidence is consistent with her having spent her whole life at Alalakh; however, despite likely being a local of Alalakh, she did not receive a proper burial, instead found face down at the bottom of a well, with extremities splayed, indicating that she was thrown into the well.

The presence of this genetic outlier at Alalakh is generally not surprising, given the extensive genetic, archaeological, and textual evidence for long-distance contacts between both people and polities in the 2nd millennium BC, and it is doubtful that she was the only such outlier present in the city throughout its history, especially considering that she herself was apparently not migratory. Indeed, dental morphology of the Well Lady shows shoveling of I2 [242], a feature which is passed down genetically and is shared by three other individuals– 42.10.130, buried in the Royal Precinct, ALA012, buried in the extra-city cemetery, and ALA139, buried in the Area 4 cemetery–as well as ALA030 (the accident victim found in Area 3), ALA132, and ALA133 (both buried in the Area 4 cemetery), although the trait is less pronounced in these latter three individuals. Of these six individuals, only ALA030 has thus far yielded sufficient aDNA preservation, and this individual is not a genetic outlier among the Alalakh population. It is possible, therefore, that the former three individuals, which show pronounced I2 shoveling, may also be genetic outliers, similar to the Well Lady.

The Plastered Tomb: Evidence for local elites with kinship ties

The Plastered Tomb is the most elaborate, elite grave at Alalakh, judging from the grave construction and the richness of the burial goods [106]. While isotopic data could be generated for all four individuals in the tomb, genetic analysis only succeeded in three cases (ALA001, ALA002, and ALA038; ALA003 did not yield preserved aDNA), but these data illuminate the kinship ties between these individuals.
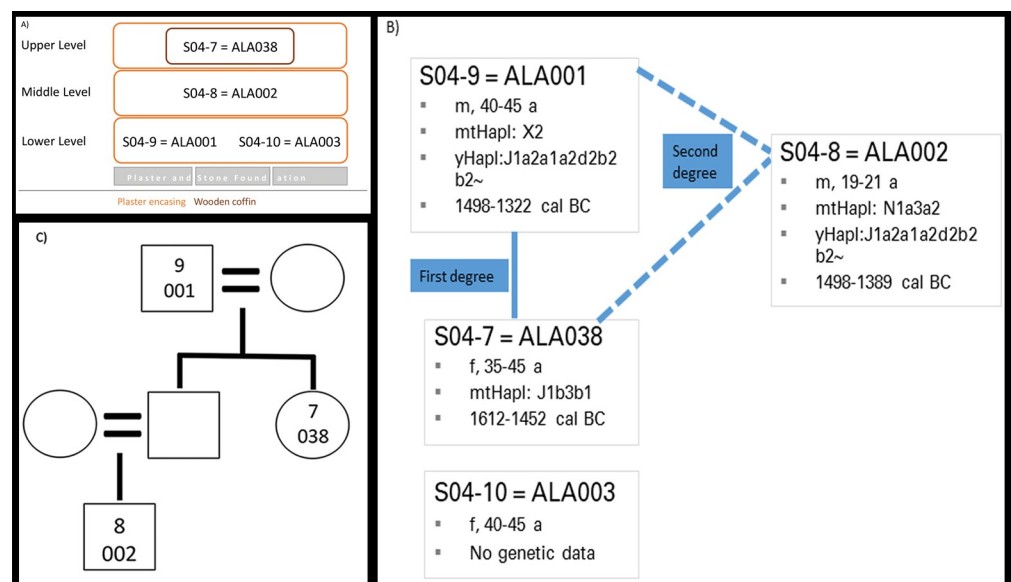
The four individuals buried in the Plastered Tomb were spatially arranged in three different layers atop each other, separated by plastering (Fig 13A). From a construction viewpoint, it is clear that the lowest two individuals, ALA001 and ALA003, were deposited first, and then the plastering over them was laid, sealing both bodies. On top, arranged above one another and separated by plastering, were individuals ALA002 and ALA038. ALA038 was, furthermore, placed in a wooden coffin (unpreserved, but attested by wood impressions in the plaster surrounding it) [101, 106]. While this general order of interments is clear [106], the time interval between each burial is not–there could have been between one to up to four separate events;

the semi-disarticulated state of ALA003's remains [104] suggests that even the lowest two individuals may not have originally been placed in the grave at the same time.

Osteological analyses concluded that three individuals in the grave were likely female and one individual (ALA001) male. ALA002 was tentatively ascribed as female on the basis of pelvic and cranial morphology and post-cranial robusticity [104, 105]. Genetic sexing has now revealed that this individual was actually male, which changes the arrangement of the tomb to an even sex ratio (2:2) [49]. According to the most recent analysis by R. Shafiq, the male individuals were estimated to have died at an age of 40–45 years (ALA001) and 19–21 years (ALA002); the two females were between 40–45 (ALA003) and 35–45 (ALA038) years old at death.

Multiple burials are common in the whole Levantine and Mesopotamian area during the MBA and LBA and are often associated with family burials, so even before genetic analysis, it was expected that these four individuals were related in some way [106]. The genetic data confirms, on the basis of READ [223] and *lcMLkin* [224], that all three successfully DNA sequenced individuals were biologically related (Fig 13B) [49]. None of them share the same mitochondrial haplogroup, which is exclusively passed on from mother to offspring. This means that first-degree relatives ALA001 and ALA038 are father and daughter, confirming the k0-based distinction of *lcMLkin* from siblings ALA011-ALA123. ALA002 must therefore be the nephew of ALA038 and the grandson of ALA001, linked to ALA001 via the male line, as they do not share the same mt-haplogroup but have the same Y-haplogroup (Fig 13C).

Stratigraphically, the tomb belongs to Period 4 at Alalakh and can be dated on the basis of the grave goods to the 15th century BC [106, 243]. The radiocarbon dates of ALA001, ALA002, and ALA038 all confirm this dating. Furthermore, the combination with the kinship and osteological data enables a more precise dating: the overlap in date ranges from 1498–1452 BC between ALA001 and ALA038 –father and daughter, and both adults in their thirties or forties at their age of death–can be used to place them more precisely in time: both must have died during the first half of the 15th century BC. The death of the grandson/nephew ALA002 would then be at the very latest during the first decades of the second half of the fifteenth century BC.

Fig 13. The Plastered Tomb. A) schematic representation of the spatial setting of the four individuals within the grave, after Yener [106]; B) osteological and genetic information of the Plastered Tomb individuals, including biological kinship; C) family tree.

https://doi.org/10.1371/journal.pone.0241883.g013

Examining these individuals as a group on a population genomics level shows that they cluster together with all other individuals from Alalakh and Ebla, excluding the Well Lady. Isotopic analysis confirms that ALA001, ALA002, and ALA038 likely grew up at Alalakh, while the difference in the strontium ratio of the two samples from ALA003 could indicate that this individual moved to Alalakh from within the Amuq Valley during early childhood (if an M1 was sampled by Meiggs [147]; see also above). Although it was not possible to generate genetic data for ALA003, her presence in the lower layer of the tomb and the semi-disarticulated state of her remains [104] suggest that she was also a part of this family group and was likely either from the same generation as ALA001 (perhaps his wife and/or his sister?) or an earlier one (perhaps his mother?). There are therefore selected members of at least three, possibly four, generations of a local, elite family buried in this unusual tomb that was very richly constructed and would have been sat prominently outside the city wall [101, 106]–a unique tomb constructed for, and likely by, local elites as a potent symbol of their social status and power.

Conclusions

Our investigation of the burial corpus at Alalakh via strontium and stable oxygen isotopic analysis, combined with both published [49] and new aDNA results, sheds light on aspects of human mobility at an urban center in the northern Levant during the MBA and LBA. The various lines of evidence reveal that most individuals grew up locally, with different levels of mobility, from long-distance to regional, indicated for a smaller number of individuals. We used overlap in datasets to refine signals for mobility, most notably by limiting the likely distance of the migrations. The strontium isotope data, due to its better refinement in outlier identification than the stable oxygen isotope data and to the different level it operates on than the aDNA data, proved to be best-suited for estimating numbers of non-locals and was even able to reveal that the Well Lady, though a remarkable genetic outlier, may have been local to Alalakh. Long-distance migration of the type demonstrated by this individual's ancestors appears (at least from the data currently available) to be rather rare.

The arising picture from Alalakh's population with regard to mobility is complex and does not directly correspond to certain burial traditions, with the exception of secondary burial, which tends to be associated with non-local individuals (though not exclusively or entirely: not all analyzed secondary burials are non-local, and not all non-locals were secondarily buried). As the case of the Well Lady indicates, though, we may be missing entire portions of the population due to their non-recovery for a variety of possible reasons. This example highlights how the vagaries of discovery and issues of representativeness influence mobility studies, and it is important to keep in mind that only a small portion of the total number of ancient inhabitants of the city has been recovered to date and is available for sampling.

Nevertheless, this study has revealed multiple scales and levels of mobility at Alalakh in the Middle and Late Bronze Ages, and shows, as have other recent studies in the ancient Near East [37, 39, 40], that the majority of sampled individuals were locals who likely lived, died, and were buried in close proximity to the place where they were born. This has important implications for understanding individual mobility in the Near Eastern Bronze Age: while such mobility is documented at relatively high levels both textually and archaeologically, it seems that–within the range and limitations the methods discussed here are able to determine–relatively few individuals were buried away from their childhood homes. The majority of cases of long-distance mobility may therefore have been on a temporary basis, for the duration of a diplomatic mission or a specific crafting commission, for example, rather than permanent relocations. This does not rule out longer periods of time spent as adults away from childhood homes, which would not be visible with the methods used here, since, in using tooth enamel,

we targeted childhood for isotopic analysis; some of these individuals could, for example, have spent most of their adult lives traveling with trade caravans. If this was the case, though, then these individuals either did not die during their travels (thus living to return to the area of their childhood and subsequently being buried there) or their remains were returned after their death elsewhere. The latter scenario could be the case for ALA060, the only secondary burial included in this study that was identified as a local. Similarly, these results also do not rule out the presence of non-locals at Alalakh, who could have spent considerable time living in the city as adults but who were not buried in the city. This lack of evidence for large numbers of non-locals buried at Tell Atchana, therefore, does not contradict the picture of the site as a center of exchange in the MBA and LBA but rather indicates that individual mobility was more likely restricted to adulthood and was generally followed by burial close to childhood homes. These results therefore contribute to the expanding range of mobility studies based in bioarchaeology that are increasingly illuminating patterns of group and individual movement during the first 'international age' in the ancient Near East and are enriching, not contradicting, our understandings of this time and the ways in which people and things moved during this period.

Supporting information

S1 Table. Isotopic results of all individuals, with sampled tooth indicated.
(XLSX)

S2 Table. Admixture modeling results.
(XLSX)

S1 File. The chronology of the burials: Detailed analysis of stratigraphy and radiocarbon dating.
(DOCX)

S2 File. Discussion of the modern snail shells and their underlying geology.
(DOCX)

S3 File. Comparison between modern environmental ^{87}Sr/ ^{86}Sr ratios in Meiggs [147] and the samples in this study.
(DOCX)

Acknowledgments

Author Contributions

Conceptualization: Tara Ingman, Stefanie Eisenmann, Eirini Skourtanioti, Murat Akar, Patrick Roberts, K. Aslıhan Yener, Philipp W. Stockhammer.

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