Isotopic and DNA analyses reveal multiscale PPNB mobility and migration across Southeastern Anatolia and the Southern Levant

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Growing reliance on animal and plant domestication in the Near East and beyond during the Pre-Pottery Neolithic B (PPNB) (the ninth to eighth millennium BC) has often been associated with a "revolutionary" social transformation from mobility toward more sedentary lifestyles. We are able to yield nuanced insights into the process of the Neolithization in the Near East based on a bioarchaeological approach integrating isotopic and archaeogenetic analyses on the bone remains recovered from Nevalı Çori, a site occupied from the early PPNB in Turkey where some of the earliest evidence of animal and plant domestication emerged, and from Ba'ja, a typical late PPNB site in Jordan. In addition, we present the archaeological sequence of Nevalı Çori together with newly generated radiocarbon dates. Our results are based on strontium ($^{87}Sr/^{86}Sr$), carbon, and oxygen ($\delta^{18}O$ and $\delta^{13}C_{carb}$) isotopic analyses conducted on 28 human and 29 animal individuals from the site of Nevalı Çori. $^{87}Sr/^{86}Sr$ results indicate mobility and connection with the contemporaneous surrounding sites during the earlier PPNB prior to an apparent decline in this mobility at a time of growing reliance on domesticates. Genome-wide data from six human individuals from Nevalı Çori and Ba'ja demonstrate a diverse gene pool at Nevalı Çori that supports connectedness within the Fertile Crescent during the earlier phases of Neolithization and evidence of consanguineous union in the PPNB Ba'ja and the Iron Age Nevalı Çori.

Neolithization | Near East | $\delta^{18}O$ and $\delta^{13}C$ isotopes | $^{87}Sr/^{86}Sr$ | ancient DNA

The classic model of "Neolithization" argues that there was a dramatic shift between mobile hunting and gathering to an increasingly sedentary herder/cultivator-based lifestyle as a result of growing economic reliance on animal and plant domestication during the Pre-Pottery Neolithic (PPN) in Southwestern Asia (1–4). Although the "Fertile Crescent" (FC) has often been seen as a vital region of early pathways to "agriculture," this process was heavily dependent on the distribution of the wild progenitors of domesticates, like wheat, barley, pulses, goat, sheep, pig, and cattle (5–12) in the FC (13), including the Levantine corridor, Southeastern (SE) Anatolia (which makes up a significant part of Upper Mesopotamia), and Zagros region, located at the western wing, the northeastern fringe, and the eastern wing of the FC, respectively. Nevertheless, despite decades of research into the "origins of agriculture," direct insights into the complex mechanisms underlying Neolithization, especially the pace, patterns, and the relationship between sedentism and the integration of hunting-gathering and agricultural lifeways, are still insufficiently understood (2, 14, 15). In particular, the correlation between sedentism and the adoption of agriculture has been hotly debated, especially in light of almost-sedentary Levantine Natufian hunter-gatherer communities (16–24).

Besides individual mobility during a lifetime, the importance of larger migrations during the process of Neolithization is also under debate. Early from the Pre-Pottery Neolithic A (PPNA) to the Pre-Pottery Neolithic B (PPNB) stages, it is marked by evidence for long-distance interactions throughout the wider region of the FC, where the presence of exotic objects, like obsidian, minerals, and lithic raw materials (25–27), shared ritual/cultural practices (28, 29) and feasting (30–33) increased. Ba'ja (ca. 7250 to 6800 cal. BC) in the late PPNB Southern Levant is a typical site of the "mega-site phenomenon," i.e., the sudden aggregation of population, enlargement of settlement size, and increased social differentiation, which has been explained under different models (34). One of these argues that domesticated species diffused as "packages" from their agricultural "homeland" in SE Anatolia (35, 36). However, there is also evidence indicating that the late PPNB Southern Levantine plant production was based on the cultivation of crops with a long history of local management (37). How these cultural similarities and the modes of exchange relate to human heritage and population connectedness between SE Anatolia

Significance

We present the integrative bioarchaeological study on the Pre-Pottery Neolithic B (PPNB) in the Southeastern Anatolia by combining isotopic data ($^{87}Sr/^{86}Sr$, $\delta^{18}O$, and $\delta^{13}C_{carb}$), new radiocarbon dates, and genome-wide data recovered from human skeletal remains from the site of Nevalı Çori. We also report human genome-wide data from post-Neolithic Nevalı Çori and the late PPNB site of Ba'ja in the Southern Levant. Our combined isotope and ancient DNA data fill a research gap between prehistoric Anatolian and Levantine populations. Our results indicate a decline in human mobility after the first phase of the PPNB in the Southeastern Anatolia accompanied by increasing reliance on domesticated resources and evidence of consanguinity in the PPNB Levant.

and the Levant are still unclear (38–40) with indirect diffusion of ideas or direct interaction like larger migrations and individual mobility associated with trade, marriage, and other factors, all being proposed to explain the interplay between the different regions of the FC (3).

During the PPNA and PPNB, an enigmatic type of site with T-shaped pillars (TSP) emerged and flourished in SE Anatolia and has been seen as an iconic part of the early Neolithization process. The TSP themselves are believed to signify humans, with low reliefs representing head, arms, and clothing like belts and loincloth, and are often decorated with a variety of animal motifs, including snakes, scorpions, aurochs, and gazelles, and geometric patterns in low and high relief (41). Nevalı Çori is one of the key representative sites of the TSP society, the excavation of which not only documented the earliest occurrence to date of domesticated einkorn (42, 43) but also recovered a large amount of animal bones living in wooded habitats (*Bos, Sus, Cervus*, etc.) and open landscapes (*Ovis, Capra, Gazella*, etc.) (11, 44–46). Excavations at Nevalı Çori unearthed a series of five PPNB layers (47–51), i.e., phases I–V, with phase I being the oldest, based on its flint industry and architectural remains (47–51). In close proximity to Nevalı Çori (within a radius of ca. 60 km), the site of Göbekli Tepe is famously believed to have been the ritual center of this TSP society, many sites among which remain unexcavated or buried under the alluvium of the Harran Plain (52, 53). The younger layer (layer II) of the early and middle PPNB architectural phases at Göbekli Tepe is partially contemporaneous with the occupation of the earlier phase at Nevalı Çori for ca. 300 y, and both are characterized by smaller pillars (<2 m, compared with those of PPNA at Göbekli Tepe), rectangular stone buildings, and terrazzo floors (50, 54). The potential relatedness and dynamic interactions between these two sites, and the wider social landscape, require further investigation, however.

The social organization and subsistence strategies of the TSP society are key to better understanding the cultural transformations and the interplay of forager lifeways with the initial stages of agriculture. There has been so much work on subsistence in the FC given the focus on agricultural origins but much less on direct insights into mobility. Nevertheless, modes and degrees of human mobility strongly influence their cultural and social organization and have been central to arguments of agricultural dispersal across the regions (6, 55–58). However, the identification of human mobility on the basis of material culture has posed severe challenges (59). Multidisciplinary bioarchaeological approaches, especially archaeogenetic and isotopic analyses of $^{87}Sr/^{86}Sr$ and $\delta^{18}O$, have increasingly served as powerful tools for investigating past mobility (60–65). The only available strontium isotope dataset for reference in SE Anatolia so far was generated for Körtik Tepe in the Upper Tigris region of the PPNA period (66), and bioarchaeological datasets aiming to investigate human mobility (Sr isotopic and archaeogenetic data) are missing for the TSP society in the Upper Euphrates. Furthermore, aDNA studies have documented the progressive reduction in genetic differentiation between populations from the Levant, Northwestern–Southcentral Anatolia, and as far as Zagros since the Neolithic, thereby shedding light on genetic admixture of a broad spatiotemporal scale within the FC (67–70). Geographically located among these regions, SE Anatolia is the critical missing link into further elucidating mobility patterns since the earliest phases of Neolithization.

In order to overcome this lack of data, we have conducted an integrative bioarchaeological analysis of human and animal remains from one of the key sites of the earliest Neolithic, i.e., Nevalı Çori. We report $^{87}Sr/^{86}Sr$, $\delta^{18}O$ and $\delta^{13}C_{carb}$ data from 44 molar enamel samples belonging to 28 human individuals excavated from subphases PPNB I (ca. 8700 to 8300 BC), PPNB II (ca. 8300 to 7900 BC) and PPNB III (ca. 7900 to 7500 BC) and later periods. The site was reoccupied during the Halaf Culture (ca. 5500 to 5000 BC), Early Bronze Age I (EBA I, ca. 2900 to 2800 BC), the Iron Age (IA, ca. 1200 to 30 BC), and finally the Roman Imperial period (RI, ca. first to third century CE) (71) based on both archived and newly reported 14C data of bone and cereal materials recovered in situ (Dataset S4). Their distribution ranges from the PPNB to the RI occupation layers as follows: 23 samples (n = 13 individuals) dating to the early (I), middle (II), and late (III) layers of the PPNB, three samples (n = 2 individuals) from the period of Halaf Culture, nine samples (n = 6 individuals) from the EBA I, eight samples (n = 5 individuals) from the IA, and two samples (n = 2 individuals) from the RI. Additionally, we conducted strontium, carbon, and oxygen isotope measurements on 29 animal samples, most of which are gazelles, sheep/goats, and pigs recovered from PPNB Nevalı Çori (Dataset S3), aiming to identify a baseline for the local bioavailable strontium and to explore possible changes in subsistence strategies. We also developed human genome-wide data from PPNB Nevalı Çori and Ba'ja to explore evidence for transregional population mobility in the landscape of polycentric development of Near Eastern cultivation and domestication (27, 37). After sampling 35 individuals from Nevalı Çori and 24 from Ba'ja (archaeological background is provided in *SI Appendix*, Note S1 and Fig. S1), genome-wide data were successfully recovered from three PPNB individuals (NEV009, BAJ020, and BAJ022) due to the challenging preservation conditions. Supraregional comparisons of population genetics from these two sites with other early groups across the Near East have been conducted to achieve more insights into connections within the northwest wing of the FC and, more broadly, within the whole of Southwestern Asia. The detailed contextual and osteological information, as well as the shotgun metagenomic sequencing evaluation of all sampled individuals, are presented in Datasets S1 and S5.

Results

Strontium Isotope Analysis of Human Remains. In Figs. 1*B* and 2*A*, the range between the solid lines shows the bioavailable local strontium signature of Nevalı Çori [0.707818 to 0.708052 (mean ± 2 SD)] calculated based on the $^{87}Sr/^{86}Sr$ ratios of pigs (n = 6) and fox (n = 1) as archaeological fauna enamel expected to provide a more local range (Dataset S2). The resulting range is compatible with the geological background in the Urfa region, where limestone bedrock provides a significant contribution to strontium isotopic composition (*SI Appendix*, Note S2). We define any data falling outside the Nevalı Çori local baseline as "nonlocal" values. However, what this means in terms of cultural significance can vary. For instance, for people who are not completely sedentary, a nonlocal $^{87}Sr/^{86}Sr$ ratio could reflect use of a broader home range area across different geological contexts. During the subphase PPNB I, 6 out of 7 individuals showed nonlocal values, while only 1 out of 6 individuals is nonlocal during PPNB II–III, and none of the subsequent periods (from the Halaf Culture to the RI) provide nonlocal signatures. In order to contextualize the Nevalı Çori results within the wider region, a local range of bioavailable $^{87}Sr/^{86}Sr$ at Göbekli Tepe, drawn from the published values of Lang et al. (72) determined from gazelle bones and enamel of 0.708025 to 0.708255 (mean values ± SD), was used. As wild animals (73), the values of gazelles, which have never been domesticated, tend to be more dispersed, and we therefore used ±1 SD instead of ±2 SD, which has also been applied in other
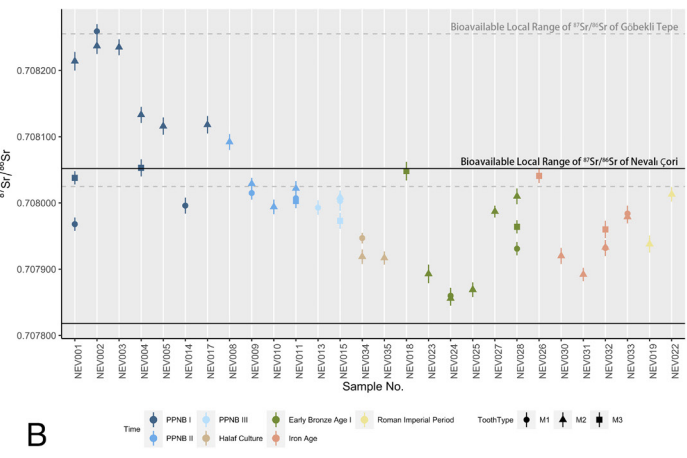
Fig. 1. *A*) Map of the prehistoric FC and Anatolia, with relevant sites in the text. *B*) Scatterplot of the ^{87}Sr/^{86}Sr ratios of the individuals from Nevalı Çori (Dataset S1); the range between the gray dashed lines shows the bioavailable ^{87}Sr/^{86}Sr interval based on the data from gazelles excavated at Göbekli Tepe; the range between the dark solid lines shows the bioavailable ^{87}Sr/^{86}Sr interval of Nevalı Çori based on the data of the archaeological animal remains measured in this study (Dataset S2).

studies, including the original publication of these gazelles (72), for a more conservative local range (64, 74).

Our ^{87}Sr/^{86}Sr ratios for human enamel samples from Nevalı Çori ranged from 0.707856 to 0.708259 (n = 44). An obvious decrease in mobility among the Nevalı Çori inhabitants occurred at the transition from PPNB I to II, as evident from the numbers of nonlocals in each period. Among the nonlocals from PPNB I, NEV001 shows the largest variation in the ^{87}Sr/^{86}Sr ratios, with the lowest value measured in the M1, which indicates that the individual's mother spent her pregnancy and breastfeeding period in a geological location compatible with Nevalı Çori. Meanwhile, this individual had a nonlocal value for the M2 and a local value for the M3 (Fig. 1*B* and Dataset S1). Similarly, NEV004 exhibits intraindividual variations in ^{87}Sr/^{86}Sr ratios also with M2 being nonlocal and M3 being local but M1 missing. Both NEV001 and NEV004 indicate a similar pattern of mobility: Both individuals seem to have been active around the Göbekli Tepe region during their later childhood (ca. 3 to 7 y old; *SI Appendix*, Note S5.2.2) and returned to Nevalı Çori later in their lifetimes (ca. 8 to 14 y old). Moreover, the ^{87}Sr/^{86}Sr ratios of the M1 and M2 of NEV002 are both highly consistent with the range of the Göbekli Tepe region, with the fact that NEV002 died between the ages of 12 to 15 y (Dataset S1), indicating that this individual was born outside Nevalı Çori and had lived beyond this area, although there is no indication from or differentiation in burial practices that would distinguish it from other contemporary individuals.

Stable Isotope Analyses of Human Remains. All tooth enamel samples measured for ^{87}Sr/^{86}Sr were also analyzed for $\delta^{13}C_{carb}$ and $\delta^{18}O_{carb}$. Forty-four matching $\delta^{13}C_{carb}$ and $\delta^{18}O_{carb}$ values were generated from all the 28 individuals ranging in periods from the PPNB to the RI. The $\delta^{13}C_{carb}$ values all fall into a range between –14‰ and –11‰ (Dataset S1 and *SI Appendix*, Fig. S2), which indicates an overall reliance on C_3 resources without significant diachronic variation. This fits well with archaeobotanical evidence for the dominant crops at the site being wheat (*Triticum* spp.) and pulses (e.g., *Lens* and *Pisum*) (42), as well as with the natural vegetation, highlighting that the graze and browse available for domesticated animals would have been made up primarily of C_3 plants, with the use of forested habitats perhaps also indicated by the relatively low values (75). Our results agree with the previously published $\delta^{13}C$ data of collagen material (76) that the people at

Nevalı Çori lived on a heavily vegetarian diet based on C_3 plants. The newly published modeling research (77) quantified the plant biomass contribution as being as high as up to 90% in some individuals (average 87%). This overall reliance on plants may help to explain the close apparent linkage between growing reliance on domesticated resources and a reduction in mobility following the early PPNB phase.

The $\delta^{18}O_{carb}$ values of the human samples vary widely from –7.3‰ to –1.7‰, with values becoming higher over time. Twenty-one previously published $\delta^{18}O_{carb}$ values from Nevalı Çori (78) range from ca. –8.6‰ to –6.4‰, except for an extremely high outlier at the value of –5.55‰. The latter dataset therefore partially overlaps with the new data, agreeing with those from the PPNB I subphase in this study (–7.3‰ to –4.3‰), although they are, overall, lower. This was probably due to the limited temporal coverage and the dates of the previous sampling, which seem to have concentrated on the very early PPNB, although specific dating was not provided. For the $\delta^{18}O$ data presented in this study, we applied ANOVA and the Tukey Honestly Significant Difference (HSD) test, which indicated that both PPNB I and II values differ from those of the post-PPNB individuals, especially for PPNB I, of which the measured difference with EBA I is –3.9‰ (CI: –6.2, –1.7), with the Halaf Culture is –5‰ (CI: –8.2, –1.9), with the IA is –4.8‰ (CI: –7.1, –2.5), and with the RI is 4.6‰ (CI: 0.9, 8.3). However, no clear distinction is demonstrated between PPNB III individuals and their post-PPNB counterparts, and no isotopic meaningful difference can be inferred from individuals among the PPNB subphases (*SI Appendix,* Fig. S4 and Dataset S9). The change in $\delta^{18}O$ values over time could be related to different factors working together, like climate change or anthropogenic changes—e.g., mobility patterns or drinking water sources from different altitudes. However, the increase in the newly reported $\delta^{18}O$ values from the PPNB to later periods is consistent with Holocene $\delta^{18}O$ increases documented in paleoenvironmental records in the Eastern Mediterranean area, including the speleothem profiles from the Incesu Cave in Southcentral Anatolia, Turkey (79), and from the Soreq Cave in the Southern Levant (80), and of the stalagmites from the Sofular Cave in Northern Turkey (81, 82). The $\delta^{18}O$ ratios of the body water of large mammal and human enamel are systematically related to the isotope values of drinking water ($\delta^{18}O_{dw}$), with $\delta^{18}O_{precip}$ being calculated from $\delta^{18}O_{carb}$ (with an intermediate step of conversion to $\delta^{18}O_{phosphate}$ values using a series of equations) (83–85) (*SI Appendix*, Note S5.1.1). On a
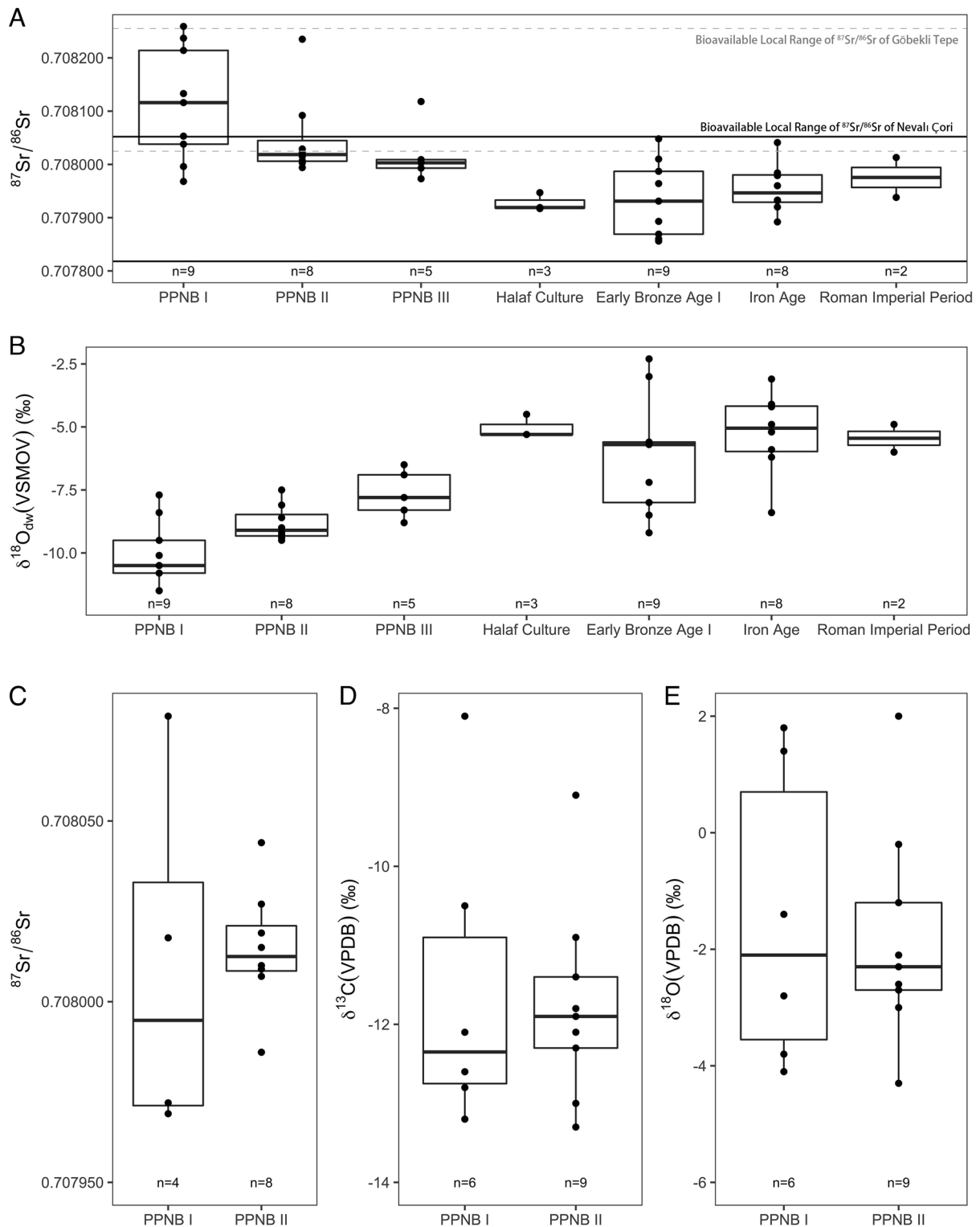
Fig. 2. *A*) Box plot of the $^{87}Sr/^{86}Sr$ ratios of the individuals from Nevalı Çori; the range between the gray dashed lines presents the bioavailable $^{87}Sr/^{86}Sr$ interval based on the data from gazelles excavated at Göbekli Tepe, and the range between the dark solid lines shows the bioavailable $^{87}Sr/^{86}Sr$ interval of Nevalı Çori. *B*) Box plot of $\delta^{18}O_{dw}$ (drinking water) values of the Nevalı Çori human samples grouped in different periods, spanning from the PPNB to the RI; VSMOW, Vienna standard mean ocean water. *C*) The $^{87}Sr/^{86}Sr$ ratios of the gazelles from Nevalı Çori grouped into PPNB I and II. *D*) $\delta^{13}C_{carb}$ values of the gazelles from Nevali Çori grouped into PPNB I and II. *E*) $\delta^{18}O_{carb}$ values of the gazelles from Nevalı Çori grouped into PPNB I and II.

larger temporal scale, there seems to be a warming trend in this region, which has gradually become closer to the modern environment, as represented by the annual mean precipitation $\delta^{18}O$ values ranging from –8‰ to –6‰ that generally agree with the $\delta^{18}O_{dw}$ values from post-PPNB (Fig. 2*B* and *SI Appendix,* Fig. S3) (86, 87).

Isotope Analyses of the PPNB Animals. First, as mentioned above, we primarily used pigs and fox to represent the local $^{87}Sr/^{86}Sr$ baselines in our study on the ecological understanding that these animals tend to be closely integrated with settlements at this time based on zooarchaeological identification (11, 12). Second, 26 matching $\delta^{18}O$ and $\delta^{13}C_{carb}$ data and 28 $^{87}Sr/^{86}Sr$ data were newly generated from 29 animal individuals recovered from the different PPNB subphases of Nevalı Çori (Dataset S3). In contrast to the above taxa (pig and fox), we use gazelle as a better marker of human use of the wider landscape and hunting. The scatterplot of the mammalian $\delta^{18}O$ and $\delta^{13}C_{carb}$ data (*SI Appendix*, Fig. S5 and Dataset S3) reveals that NC0289 and NC0518 (both gazelles) had C_4 food intake. Evidence for the widespread distribution of C_4 plants throughout temperate Eurasia is extremely low (75), and C_3 resources were dominant in the local vegetation (75). However, notable cover of C_4 plants in communities of sand dunes, salt marshes, and disturbed sandy ground of warm regions were found. Mediterranean, Irano-Turanian, and Hyrcanian ecosystems with high summer temperature, intensive light, nutrient-poor soils, and dry conditions are suitable habitats for C_4 plants (88–90). Therefore, there would have likely been C_4 food resources available for gazelles moving widely across the arid regions in Anatolia and the Levant.

The lack of a significant C_4 signal among the human individuals in this study is likely due to either the low frequency of C_4-consuming individuals among the whole gazelle population or a limited consumption of gazelles overall due to seasonal aspects of grazing and hunting. It is also possible that the hunted animals were only used for special feasts/occasions at specific times, especially in light of the fact that the inhabitants at Nevalı Çori depended largely on a plant-based diet as mentioned above (77, 78). It is worth noting that the box plot of the Nevalı Çori gazelles, clustered by stratigraphic level, shows that variation in PPNB II is lower than that in PPNB I for all isotopes (Dataset S3 and Fig. 2 *C–E*), which potentially indicates a shrinking of the meat resource catchment area from PPNB I to II. Additionally, $^{87}Sr/^{86}Sr$ data of the gazelles from Nevalı Çori are distinct from the PPNA and early–middle PPNB Göbekli Tepe (*SI Appendix*, Fig. S6), which show higher averages and, in general, greater variability. However, we should caution that variability cannot necessarily be directly compared between these two limestone-based sites due to local contingencies in geology. These two facts together possibly indicate declining mobility of hunters from the PPNA to PPNB along with a weakening of the dependence on a hunting-gathering economy over time.

Genetic Analysis of Human Remains. All the six genetically analyzed individuals passed quality control, including low contamination rates and ca. 0.25× coverage on 1,240K markers (≥300,000 SNPs) (SNP, Single Nucleotide Polymorphism), except one low-coverage sample BAJ020 (ca. 47,000 SNPs). A complete summary of quality assessment of the data, along with information on molecular sexing and uniparental haplogroups, is provided in Datasets S5 and S6.

To get an overview of the population genetic structure, we first computed a principal component analysis (PCA) using SNP array data (Human Origins, ca. 600,000 SNPs) from 85 modern western Eurasian populations. We then projected ancient individuals from this and relevant other studies onto the first two principal components (Fig. 3). Notably, the PPNB individuals from Ba'ja and Nevalı Çori (level II; NEV009) are separated along the PC2 and PC1. The former fall within the cluster formed by PPN individuals from the Southern Levant and one published sample from Ba'ja (BAJ001) (67), whereas NEV009 is placed along the PC1 between
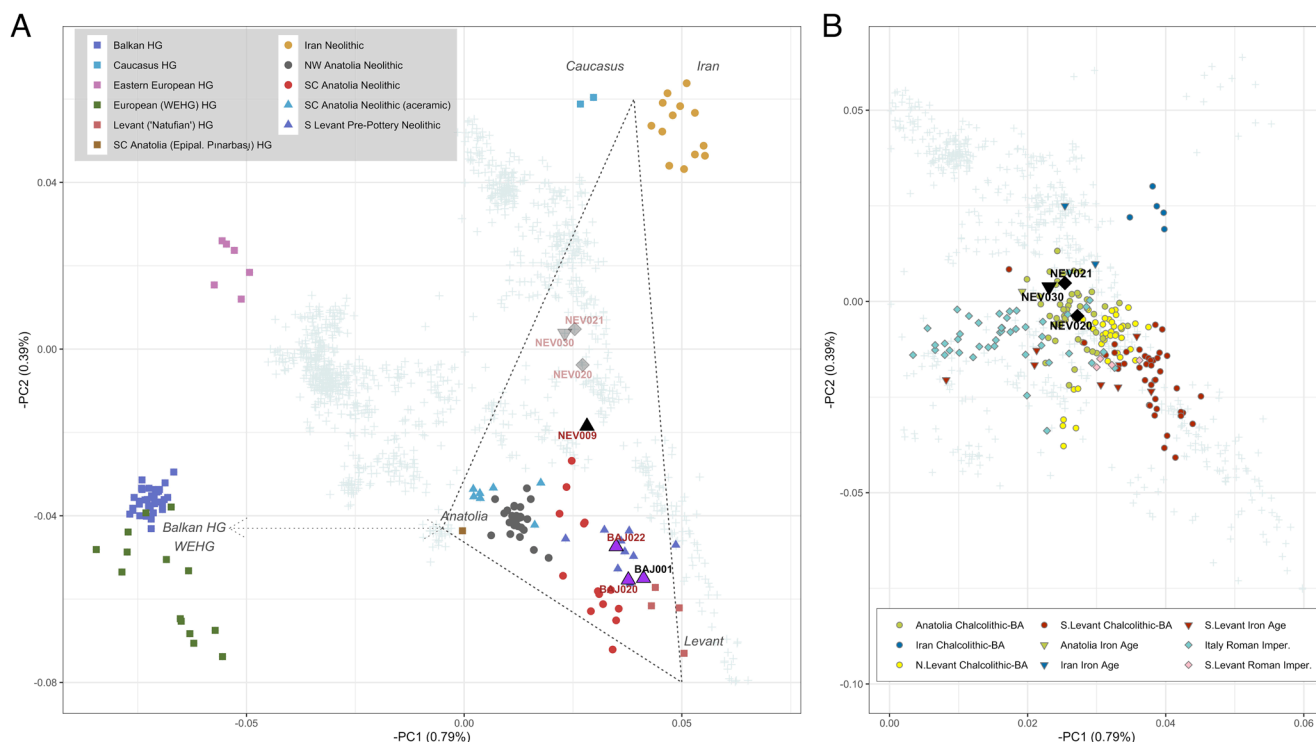

Fig. 3. Scatterplot of the PC1 and PC2 generated with *smartpca* on Human Origins (HO) data of 85 modern West Eurasian populations (light gray cross symbols). Ancient datasets (colorful points) were projected with the *lsqproject* option. *A*) Coordinates of the PPNB Nevalı Çori (NEV) and the Ba'ja (BAJ) individuals (black and purple upward triangles, respectively) with their IDs. The drawn polygon outlines the Early Holocene individuals from southwestern Asia, and the double arrow represents the more distal genetic link between the Anatolian HG and European HG. For reference, the IA and RI Nevalı Çori individuals are plotted in faded colors. *B*) The three later Nevalı Çori individuals are plotted along with post-Chalcolithic Southwest Asia and Rome from the Imperial Period. Abbreviations: HG = hunter-gatherers, NW = Northwestern, S = Southern, SC = Southcentral.

the cluster of Anatolian hunter-gatherers (HG) and PPN farmers and the Levantine cluster of PPN and Epipaleolithic (EP) individuals. However, NEV009 can be distinguished from these two groups along the PC2, being shifted toward the direction of the Early Holocene Iranian (Neolithic Iran; "Iran N") and Caucasian HG ("CHG") individuals. The intermediate coordinates between the Early Holocene Anatolia, the Southern Levant, and Iran/Caucasus suggests varying genetic affinity with these populations. However, a higher genetic similarity can be proposed based on the distances between all the Neolithic individuals from within the Anatolia (including NEV009) and the Levant compared with Iran.

Almost eight millennia later, the three Nevalı Çori individuals dated to the IA and RI carry a distinct ancestry profile in contrast to the earlier inhabitants (68). Consistent with broad-scale post-Neolithic population mixing across the FC and the Caucasus (91, 92), all three individuals cluster with the Chalcolithic and Bronze Age Anatolian individuals. Interestingly, some other individuals from Rome during the RI overlap with the two Nevalı Çori RI. These new data indicate genetic continuity from the Bronze Age through the Iron Age and the Roman Imperial period and further corroborate the argument that people of the Anatolian origin contributed to the population of ancient Rome (93).

To gain further insights into ancestry patterns identified via our PCA, we tested several scenarios of asymmetric allele sharing. To delineate the evolutionary relationship between PPNB Nevalı Çori and Ba'ja and other Neolithic individuals, D-statistics of the form (outgroup, test; pop 3 and pop 4) were calculated (Fig. 4). As a four-population test, a D-statistic measures the excess of allele sharing between test and either pop 3 or pop 4, in which cases the statistic is expected to be negative or positive, respectively. For this

analysis and the admixture modeling, the individuals were grouped and/or labeled by the site and period. Besides BAJ020 and BAJ022, the group "Ba'ja PPNB" comprised the previously published individual BAJ001. Collectively, Ba'ja PPNB exhibits evidence of gene flow from populations related to Anatolia when compared with the "Natufian" HG. This also applies to the PPN individuals from 'Ain Ghazal further to the north in Jordan. Furthermore, the genetic affinity with Anatolia might be stronger in 'Ain Ghazal than Ba'ja, although not significantly [Z = 1.3 for D (Mbuti, Anatolia Barcın–Menteşe N; 'Ain Ghazal PPN, Ba'ja PPNB)].

Nevalı Çori PPNB (NEV009) shares significantly more alleles with the Anatolian gene pool than the Levantine populations do, which indicates a common ancestry among the Anatolian populations. However, when we contrast NEV009 with the Anatolian populations, significant differences can be captured for test being western European HG (WEHG) and the Balkan HG (Z ≤ –6.5) (Fig. 4A). These test populations broadly represent a post–Last Glacial Maximum lineage that prevailed in Europe and had a higher affinity to the Anatolian hunter-gatherer from Pınarbaşı and present-day Near Easterners (67, 94). Consistently, NEV009 also shares less alleles with Pınarbaşı compared with the other Anatolian farmers, indicating a less direct genetic link to this ancestral Anatolian population. On the other direction, a trend for increased affinity of NEV009 with the Early Holocene Iranian/Caucasian and Levantine can be drawn, especially when NEV009 is contrasted with Pınarbaşı—but stands below the significance threshold.

To address how the various signals from the D-statistics can be fitted under certain admixture models, we run qpAdm exploring
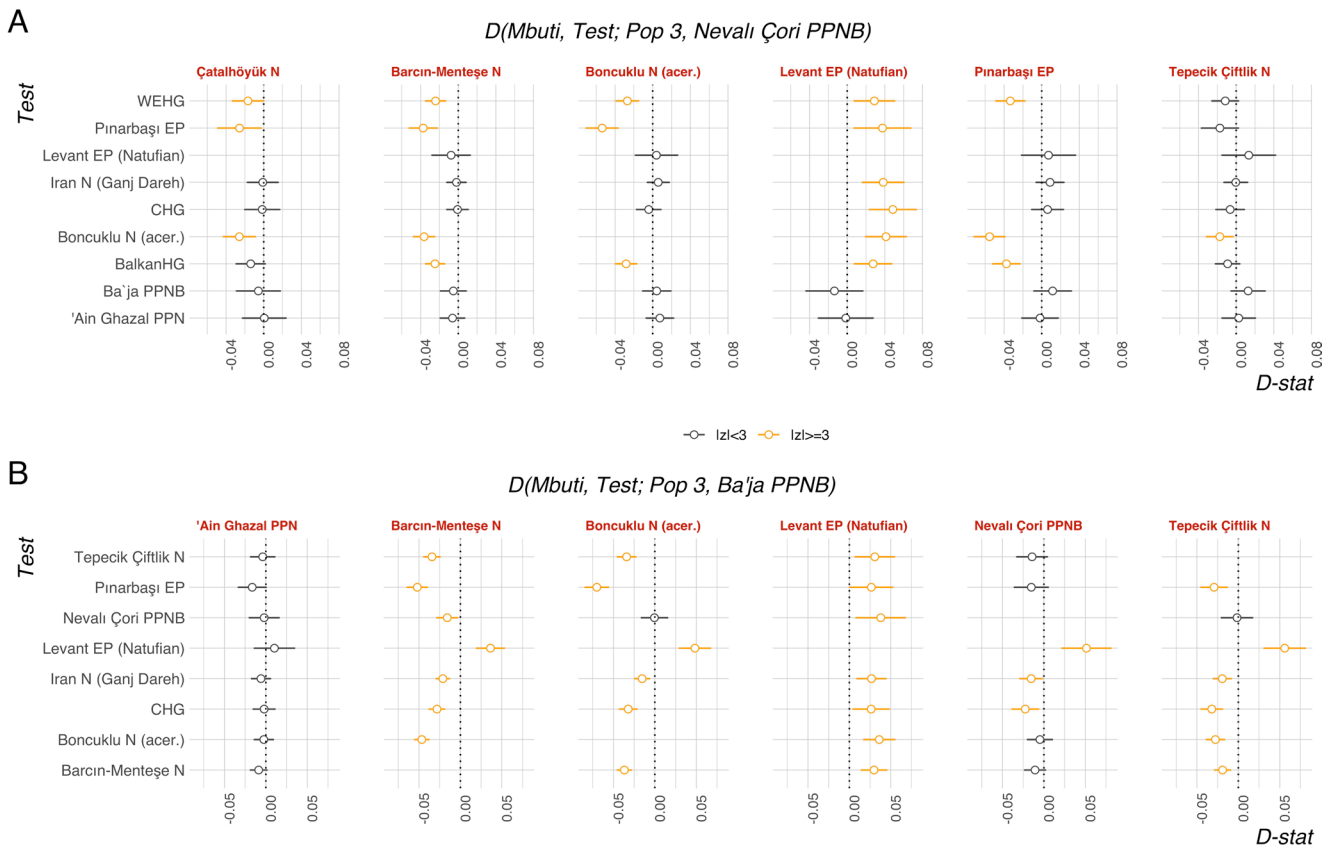
Fig. 4. D-statistics for allele-sharing differences between the Early Holocene Southwest Asian and European populations and A) Nevalı Çori PPNB (NEV009) or B) Ba'ja PPNB. Significant statistics (|Z| ≥ 3) are annotated in orange, and error bars are plotted as ±3 SE. For both groups, results are presented by pop 3 (columns). EP = Epipaleolithic, PPN = Pre-Pottery Neolithic, N = Neolithic, HG = hunter-gatherers, CHG = Caucasus HG, and WEHG = European (western) HG.

combinations from genetically and geographically distant sources within the FC (distal modeling) (*SI Appendix*, Fig. S7 and Dataset S7). To increase the resolution of the analysis, populations such as WEHG, CHG, and Levant EP ("Natufian") were added to the set of reference populations, which serve as a scaffold to relate the target with the source populations (*Materials and Methods*). In agreement with previous results, the later seventh millennium BC Anatolian farming communities require additional ancestry related to the 'Ain Ghazal Levant (i.e., Barcın–Menteşe) or Ganj Dareh Iran (i.e., Tepecik Çiftlik) compared with Pınarbaşı HG and the PPN farmers from Boncuklu. In stark contrast, Nevalı Çori cannot be modeled as a two-way combination from Pınarbaşı HG and either Iran N or Levant PPN. Instead, all three sources are necessary. Notably, this three-way admixture model becomes adequate only when CHG is removed from the reference populations, which can be explained by the real source of the Iranian-related source being linked to CHG-like populations as well, which agrees with the suggestion that CHG and Ganj Dareh Neolithic are interchangeable as sources of inland admixture for most cases (95). Furthermore, the high Levantine coefficient (45 ± 15%)—in spite of the lack of significant D-statistics for excessive affinity with the Levant—might result from a lower resolution owing to the low sample size of Nevalı Çori. Therefore, we take a qualitative rather than a strictly quantitative interpretation of the qpAdm model.

To gain insights into parental relatedness, we inferred runs of homozygosity (ROH) using the software hapROH (96). We analyzed five individuals from Ba'ja and Nevalı Çori spanning from the PPNB to the RI periods, with as low as ca. 25% coverage on 1,240K SNPs (Fig. 5). Populations having reduced effective population sizes exhibit a higher frequency of short ROH due to background relatedness (97). PPN famers from Boncuklu in Southcentral Anatolia and some early farmers from Iran have a higher proportion of short ROH equivalent to small mating pools

in contrast to the seventh millennium BC farmers from Northwestern Anatolia, a pattern already previously observed (96, 98). Similarly, high levels of short-range ROH [4 to 8 centimorgan (cM)] are observed within PPN Levant including the previously published individual from Ba'ja (BAJ001). On the contrary, the PPNB individual NEV009 exhibits lower levels of short ROH, which suggests larger population sizes on average, comparable with those later Anatolian farmers. Interestingly, in total, 3/5 individuals exhibit long-range ROH (≥20 cM), with the oldest being PPNB BAJ022 with an overall ROH distribution equivalent to offspring of a close-kin union (e.g., parents being first or second cousins). A similar conclusion can be drawn for the IA NEV030. However, the most striking evidence for consanguinity comes from the IA individual NEV020 whose ROH length distribution matches the parental scenario of full siblings (*SI Appendix*, Fig. S8).

Discussion

Foundation of the TSP Horizon in the Final PPNA. With the rapid amelioration of the climate after the Younger Dryas, an increase in population and settlements took place in the Tigris Basin and Upper Euphrates, also correlated with simultaneous changes in human behavior and productive subsistence strategies (87, 100, 101). Subsequently, wider settlement distributions evidently declined, while at the same time, occupation in the Urfa region increased as embodied by the appearance of the TSP sites (102). This change in settlement patterns has been interpreted as a "Late PPNA Hunter-Crisis" (102–105) corresponding to a rapid climate change interval indicated by a spike in the GISP2 potassium data (106, 107), which heralded the rise of the TSP communities. From the PPNA to early PPNB, Göbekli Tepe was a ritual center in the Urfa region characterized by its magnificent monolithic
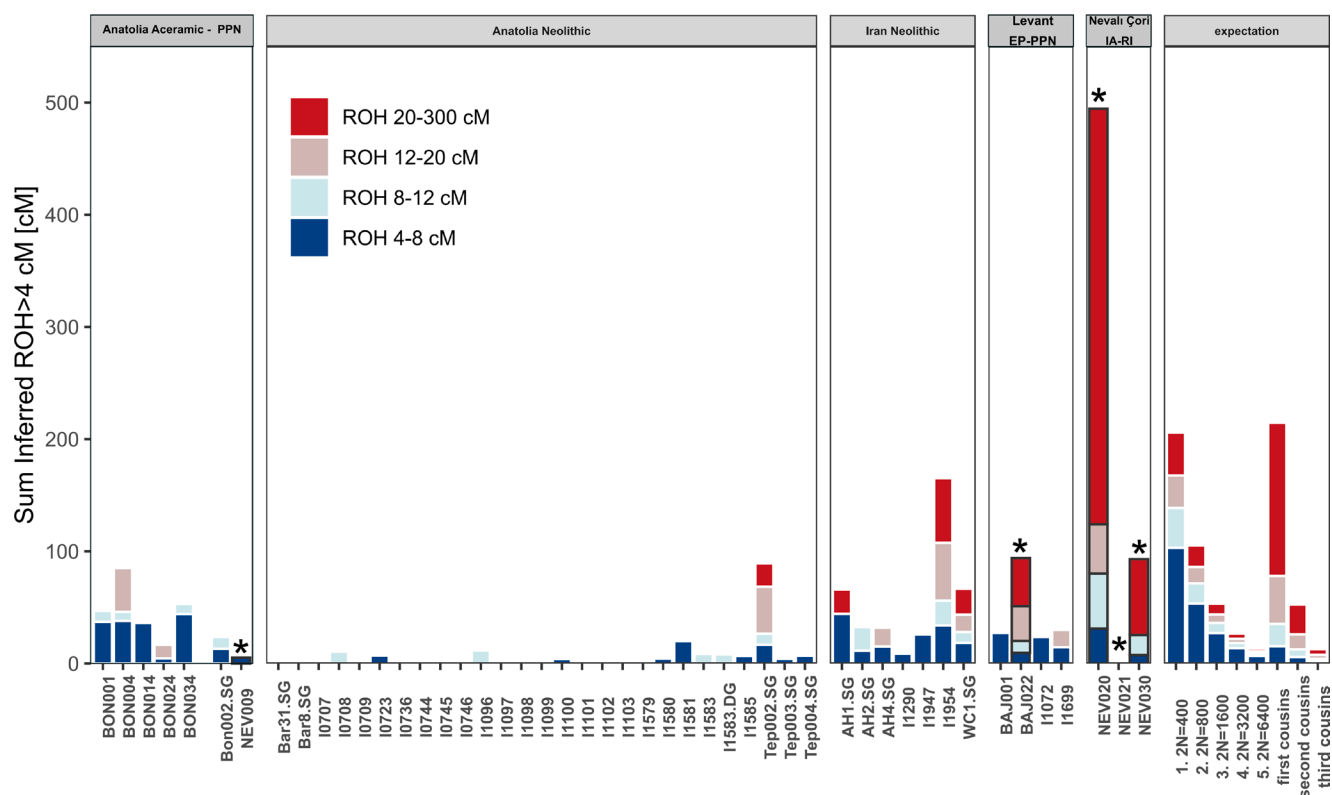

Fig. 5. Inference of Runs Of Homozygosity (ROH) from 1240K data using hapROH (99). The ROH distribution in the individuals of the present study (NEV009, NEV020, NEV021, NEV030, and BAJ022) and the published individuals from other Southwest Asian EP and Neolithic contexts.

structures. The hypothesized large events held in the TSP buildings might have been part of routine gathering and feasting events that the surrounding communities participated in (33). Göbekli Tepe is not the only place in the Urfa region where the geological context consists of a mixture of Eocene and Miocene limestones (*SI Appendix*, Note S2), the signature of which can be distinguished from that of Nevalı Çori. The other sites of the TSP are of similar geological context as Göbekli Tepe. Therefore, "Göbekli Tepe" here refers not only to the site itself but also to the TSP society as a whole, which covers the interactive sphere in the Urfa region from the PPNA to PPNB, including Karahan Tepe, Sefer Tepe, Harbetsuvan Tepesi, and so on (Fig. 1*A*) (102, 108). Taking the region represented by the bioavailable strontium signature of Göbekli Tepe into account, prior to this point, the interactive sphere of PPNB Nevalı Çori seems to have extended across a larger area. On top of that, the fact that the nonlocal $^{87}Sr/^{86}Sr$ ratios of Nevalı Çori humans during PPNB I match the $^{87}Sr/^{86}Sr$ signature of a broader area in the Urfa region where the other TSP sites located is very likely to be the consequence of mixed strontium intake across the whole area where TSP people were active by means of frequent interaction and networks. This supports the hypothesis that the establishment of the TSP ritual system was part of a demand for unifying and organizing the people in the Upper Euphrates to engage in concerted hunting events and other cultural practices (102, 109–112). In turn, these collective activities further consolidate the ritual system, and social stability was strengthened, with more connections being built among more stable communities in the area.

A trans-FC comparison of the populations at a genetic level is also now possible, given the credit that Nevalı Çori fills the missing connection within the northwest wing of the FC. Individual NEV009 was shown to not only descend from the Early Holocene populations like those from the Southcentral Anatolia but also traced part of her ancestry to populations in the southern and eastern wings of the FC (i.e., Levant and Iran). Compared with recent genomic data from individuals at the northeast wing of the FC (Mardin, Nemrik 9, Shanidar, and Bestansur) (95), both Nevalı Çori and neighboring PPN Çayönü (113) are distinct since the presence of the Levantine-associated ancestry is not required to model the other eastern Mesopotamian sites. This pattern could reflect substructure within the FC owing to geography and could have been shaped even before the onset of the PPN. As more data are obtained, a consensus is reached, whereby gene flow after the HG in the PPN and the Neolithic populations from Anatolia cannot be explained under a uniform model with respect to the timing and its origin. When Nevalı Çori and the HG from Pınarbaşı were tested as source populations for the other PPN and Neolithic Anatolian sites, the model fit improved compared with the model with Neolithic Iran or Levant (instead of Nevalı Çori) only for the PPN Boncuklu. For the other groups (e.g., Barcın–Menteşe and Tepecik Çiftlik), the fit was less good (*P* value < 0.05, Dataset S7). Furthermore, in the Levant, both PPN 'Ain Ghazal and Ba'ja individuals saw an increase in their affinity to the Anatolian populations compared with the preceding population of "Natufians." Both the chronological alternations of Levantine and the Anatolian ancestral components indicated the increasingly intensive interaction network across the FC during the PPN periods. Considering the rich record of shared elements in the material culture, contacts between the Levant and SE Anatolia could have been established via bidirectional gene flow (1, 3), eventually reaching the farmers as north as Barcın and Menteşe in the Northwestern Anatolia, while such signatures were not traced in Southcentral Anatolia during the PPN period (Boncuklu site). Overall, these variegated connections in material culture and

genetics point to different spheres of interactions between Anatolia, the Levant, and the Upper Mesopotamia. The genetic variability among populations from Mesopotamia suggests that the range from Southern to Eastern Anatolia and Northern Iraq contained different niches of blending ancestries that could have variably contributed to other populations in the Levant and the rest of Anatolia. Another genetic evidence, the ROH estimated on NEV009 and Çayönü individuals (113) indicate that these individuals belonged to a population of a larger effective population size compared with the coeval individuals from the Southern Levant, Western Iran, and Southcentral Anatolia. This corroborates different demographics in Upper Mesopotamia, which could have promoted long-range mobility resulting in many of the observed genetic signals in ancestry. Additional genetic data from the neighboring areas would be critical for investigating the overall dynamic transition that SE Anatolia experienced during the PPNB.

Disconnection and Collapse of the TSP Horizon. Our human and faunal $^{87}Sr/^{86}Sr$ from Nevalı Çori highlight the contrast between PPNB I and II, showing a dwindling mobility and hunting catchment, which might be interpreted as a transition in lifestyle, subsistence strategies, and social organization. Already published evidence suggests an increased reliance on cultivation at Nevalı Çori; wheats in all the PPNB layers are morphologically domestic (42, 114). Similarly, zooarchaeological research (10, 11, 115) has demonstrated that the biodiversity of faunal remains began to decrease toward the end of the ninth millennium cal. BC in SE Anatolia, which corresponds to the transition from PPNB I/II to III/IV at Nevalı Çori, showing a degradation of a broad-spectrum diet/economy and a gradual move away from the hunter-gatherer lifestyle. As the most common taxon recovered at Nevalı Çori, the fraction of gazelle in the assemblages of faunal remains decreased from PPNB I/II to IV/V, while the percentage of sheep and goats increased (11, 71). It is also noted that the proportion of female cattle at PPNB I/II Nevalı Çori was higher than that during the PPNA Göbekli Tepe (11, 115). *Ovis, Capra,* and *Sus* remains recovered from Nevalı Çori were, in part, from domestic caprines and pigs, which is indicated by diachronic changes in their frequencies during the site's occupation and their significantly smaller body sizes compared with their wild relatives at other sites (Göbekli Tepe, Cafer Höyük) in the region, and demographic profiles are consistent with early Neolithic husbandry systems rather than hunting regimes of foragers (116). Additional evidence for the domestic status of some *Ovis, Capra,* and *Sus* comes from the $\delta^{15}N$ analyses showing that the early stockkeepers of Nevalı Çori deliberately fed these animals with legumes (76).

In contrast to Nevalı Çori, there is no evidence for the development of agriculture at Göbekli Tepe during this key turning point in the PPNB, perhaps due to conflicting belief systems, e.g., that cultivation and domestication may have been taboo as they challenged the traditional hunting-gathering mentality or lifestyle—different societies sometimes may have radically different systems of value (117), or pressure from the environment and resources, e.g., water stress, which would restrict the development of agriculture without irrigation strategies, or simply used as different parts of the landscape and social system. An unstable animal-driven protein supply could have motivated people to practice a mixed subsistence pattern, with both hunting-gathering and farming acting as risk-buffering strategies, which might also suggest that the TSP ritual system did not collapse abruptly as reflected in the fact that the construction of monumental architecture continued at Nevalı Çori into PPNB II and III (71).

According to the strontium isotopic results, there are still some individuals (e.g., NEV008, NEV003, and NEV017) from post-PPNB I that fall into the $^{87}Sr/^{86}Sr$ range of Göbekli Tepe and other TSP communities, and these individuals may have continued to engage in the maintenance of the traditional belief system and social networks manifested by TSP, with other members at Nevalı Çori investing more in cultivation and domestication, becoming more sedentary.

Overall, however, the high mobility seen in PPNB I gradually declined at Nevalı Çori, with the proportion of hunting in the mixed subsistence model also declining until sedentary agriculture dominated, which marks the end of PPNB I as a key turning point. As subsistence farming increasingly overshadowed hunting and gathering, larger numbers of inhabitants could be fed within large, more sedentary communities. This perhaps further undermined ties among the TSP system, with Göbekli Tepe losing its prestige position as the main ritual center before becoming finally abandoned. The cult buildings were no longer prevalent at the end of PPNB Nevalı Çori, either (71). Meanwhile, the process of Neolithization led to a decentralized network among different socioeconomic communities. This brand-new social structure paved the way for the emergence of autonomous communities in the late Neolithic across a wider region (118–120). Another direction of research, that focuses on the familial relationships within communities (e.g., ref. 121), provides further insights into the inner-community organization during the late Neolithic in the Southern Levant. The presence of a consanguineous individual from Ba'ja—although too small a sample size to indicate a social practice—aligns with intrasite morphological analysis in the neighboring site of Basta in the late PPNB (7500 to 7000 cal. BC), which supports extensive social endogamy (122). If more genetic data in the future statistically support the fact that this endogamy phenomenon roots in a cultural preference, it would likely suggest that it was a way of strengthening the inner bonds within the relatively more autonomous and seclusive communities of the later Neolithic.

Conclusion

To contribute more insights into the dynamic process underlying the Neolithization across the FC, we have integrated bioarchaeological analyses on human and animal bones recovered from Nevalı Çori and Ba'ja during the PPNB. Based on the results of our isotopic data and the newly integrated timescale of Nevalı Çori, a decline in mobility and growing reliance on domesticates took place by ca. 8300 BC at the end of its first subphase of the PPNB, at a time of increasing apparent social detachment from Göbekli Tepe and its underlying system of living and associated world views. Göbekli Tepe's loss of centrality as a result of new modes of mobility and subsistence after the early phase of the PPNB appears to have resulted in the increasing independence of the sites formerly connected under the TSP phenomenon. In spite of local transformations in modes of mobility and societal organization, our genome-wide data for the PPNB human individuals from Nevalı Çori and Ba''ja provide evidence for long-distance connectedness within the FC during this time. The evidence of consanguinity in the late PPNB Ba'ja further raises the question of how the PPN societies were internally organized and calls for additional future analyses on potential endogamy in the sense of cultural behavior and social practice. These dual aspects of human mobility investigation via isotope and genetics of both inner/intersocieties in the FC and within-/trans-Neolithic time highlight the potential of tandem molecular analyses to yield nuanced insights into the process of the Neolithization in the Near East.

Materials and Methods

Excavation and Sampling. All human and animal individuals analyzed in this research were excavated and documented with their archaeological and osteological information from the sites of Nevalı Çori and Ba'ja, as well as the radiocarbon dates of the chronological phases of Nevalı Çori (Datasets S1, S4, S8, and S10). Access to the so-far mostly unpublished documentation of the excavations at Nevalı Çori under the direction of Harald Hauptmann is possible upon request in the archive of the Institute of Prehistory and Early History, Heidelberg University. The burial information of sampled individuals from both sites is provided in *SI Appendix*. The human remains from Nevalı Çori were exported in 1991 based on an export permit issued by the Museum Şanlıurfa, which permitted archaeometric analyses under the auspices of the University of Göttingen Anatomy Laboratory and subsequent permanent storage of the remains at Göttingen; the animal remains from the same site were collected at the LMU Institute of Palaeoanatomy archives. The Ba'ja human samples were provided by the Ba'ja Neolithic Project excavation team.

Regarding the human remains recovered from Nevalı Çori, there was no specific sex bias in the sampling of the various phases. Our contextual interpretation is based on the still-unpublished archaeological documentation of Harald Hauptmann and his team, which is accessible in the Hauptmann archive at the University of Heidelberg. No identifiable grave constructions in the PPNB phase were visible, and there are no distinguishable differentiations in burial practices for the PPNB samples. Stone cists were identified during the EBA and RI. When preservation was sufficient, we sampled multiple molars per individual to detect potential mobility during a single lifetime (Fig. 1*B* and Dataset S1). Regarding the sampling strategy for the enamel of both humans and other fauna, we took the bulk fragment samples across a large range along the buccal side of each tooth to get a more integrated and averaged isotopic signal to avoid the potential bias caused by partial sampling in which way the measured ratio/value only represents partial or seasonal duration. We selected the teeth of the ungulate animals (*Bos, Ovis, Capra,* and *Gazella*) with limited length to attenuate the amplitude of intratooth isotopic change along the time of enamel maturation. The "bulk" samples from these individuals provide an average assessment of their local dietary, hydrological, and geological context for comparison with the human material.

Isotope Analyses. The pretreatment of tooth enamel samples for both strontium and stable isotope analyses was conducted at the Stable Isotope Laboratory of the Department of Archaeology, Max Planck Institute of Geoanthropology (formerly the Max Planck Institute for the Science of Human History, MPI-SHH), Jena, Germany (MPI-GEA).

Stable carbon and oxygen isotopes were analyzed by a Thermo Scientific Gas Bench II connected to a Thermo Delta V Advantage Mass Spectrometer at the same laboratory. Stable carbon and oxygen isotope values were compared against the International Atomic Energy Agency standards (603, CO08, and NBS 18). The calibration process and analytical uncertainty are presented in the *SI Appendix,* Note S5.1.3. We applied the equations provided in Szpak et al. (123) to calculate overall uncertainty using the check and calibration standards measured in all analytical sessions producing data presented in this paper. Full details can be found in Datasets S11 and S12 and *SI Appendix,* Note S5.1.3.

Strontium isotope analysis was undertaken at the clean laboratory in the Department of Geological Sciences at the University of Cape Town. Following strontium elemental separation, the radiogenic $^{87}Sr/^{86}Sr$ ratios were measured using the Nu Instruments Nu Plasma HR MC-ICP-MS and referenced to a value of 0.710255 for NIST SRM987.

The full details of the protocols and rationales of the methods are described in *SI Appendix,* Note S5. Statistical analysis was carried out using JMP 11.0 and R 3.63; map illustration was carried out with QGIS 3.16.6.

Genetic Analyses. All the samples analyzed for aDNA were processed in the designated facilities of the MPI-SHH and the Max Planck Institute for Evolutionary Anthropology (MPI-EVA) in Germany. After the DNA extraction, genomic libraries were prepared with the single-stranded protocol, which efficiently immortalizes ultrashort chemically damaged (single-stranded) DNA with Illumina adapters (124). The metagenomic content of the libraries was analyzed after shallow sequencing on an Illumina HiSeq4000 platform (ca. 5 mio reads). The proportion of endogenous DNA (sequence reads mapping to the human reference genome sequence hs37d5) and the presence of deamination patterns were the main criteria to evaluate whether aDNA preservation was sufficient for employing

the targeted enrichment of ca. 1.2 mio nuclear markers (SNPs) after Haak et al. (99), Mathieson et al. (125), and Fu et al. (126). The enriched libraries were then sequenced at 20 to 40 mio reads, and the sequencing data were processed through the pipeline Efficient Ancient Genome Reconstruction (EAGER) (127). The processed sequences in binary alignment map format (bam) were examined for contamination using three different methods (128–130), and pseudodiploid genotypes were called with the program pileupCaller (https://github.com/stschiff/sequenceTools) and the option "singleStrandMode." Libraries with qualified genotype data (i.e., low contamination and ≥ 40,000 SNPs) were checked for relatives or duplicate individuals by calculating the pairwise rate of mismatching alleles (131, 132) and were merged with the latest release of publicly available genotype datasets of ancient and modern individuals [v50.0] (https://reich.hms.harvard.edu/allen-ancient-dna-resource-aadr-downloadable-genotypes-present-day-and-ancient-dna-data) focusing on speficid published dataset relevant for our analyses [additional citations we've provided in the comment attached to this sentence].

We conducted an analysis of population structure with smartpca (133, 134) on the Human Origins (HO) SNP array data of 1,264 individuals from West Eurasia and projected all ancient individuals with the option lsqproject. We then used the package ADMIXTOOLS [v57.1] (135) and run the tools D-statistics and qpWave/qpAdm. With qpAdm, we modeled a target as a combination of coefficients from n source populations. The fit of the models and the admixture coefficients are estimated from a matrix of allele correlations (D/f_4-statistics) between the target, the sources, and a set of reference populations ("right pops" in the parameter file). As reference populations, we chose the modern Mbuti, Onge, Ami, Mixe, and the ancient Ust'Ishim hunter-gatherer from Russia, individuals MA1, and AfontovoGora3 grouped as "Ancestral North Eurasians" (ANE), Eastern European HG (EEHG), Kostenki14 hunter-gatherer from Russia, Balkan HG, Natufian HG from Israel, and CHG (Dataset S7).

Data, Materials, and Software Availability. Sources for all downloaded data are presented in Datasets S1–S12. The genome-wide data reported in this study can be accessible as fastq and BAM files through the European Nucleotide Archive (ENA) under the study name PRJEB58620.

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