Out-of-Anatolia: cultural and genetic interactions during the Neolithic expansion in the Aegean

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RESEARCH ARTICLE SUMMARY

ANCIENT DNA

Out-of-Anatolia: Cultural and genetic interactions during the Neolithic expansion in the Aegean

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INTRODUCTION: Neolithic farming cultures first developed in the Fertile Crescent around 10,000 years ago and later spread into Europe through the Aegean. How the Neolithic lifeways emerged in the Aegean, and particularly West Anatolia, has remained unknown, obscured by a lack of human ancient DNA from pre-Neolithic times.

RATIONALE: We studied population and cultural history of the Aegean using 30 new paleogenomes, including a 10,000-year-old individual from West Anatolia, combined with 408 published genomes. We also compiled a digitalized material culture that included 54 cultural traits from 16 sites from around 9000 years ago and joined this with 104 genomes from the same sites. This allowed us to reconstruct mobility and cultural change during the Neolithic transition in the Aegean.

RESULTS: We found at least 6000 years of genetic continuity in West Anatolia during the early Holocene, before the arrival of farming villages there. During this time, West Anatolians were in cultural exchange with their eastern neighbors from the Fertile Crescent, exploring sedentary lifeways. But these West Anatolians did not genetically mix with their neighbors in this early phase.

Things changed around 9000 years ago, when full-scale farming settlements began spreading across the Aegean. Our paleogenomic data show that this did not occur because of waves of migrant farmers from the east creating farming colonies in the Aegean and replacing local foragers. Rather, the transition unfolded as a fusion: Incoming groups of eastern origin joined together and genetically mixed with the descendants of the local foragers in the newly established villages. This was likely a complex process of coexistence and mutual innovation as well as eventual mixing. It further gave rise to the now-famous “Anatolian Farmer” genetic profile, which subsequently spread across the Aegean Sea and later throughout Europe. In this case, admixture with locals appears more limited and sporadic.

We further performed a comparative study of cultural and genetic data, asking whether cultural similarities among the 16 Neolithic settlements may be explained by their genetic similarities, which would be expected if culture was shaped by large-scale mobility and admixture history. We found that cultural similarities among villages could simply be explained by their geographic proximity, whereas their population genetic similarities did not have any explanatory power, implying that ideas mixed faster than people in this region.

CONCLUSION: The spread of Neolithic cultures in West Eurasia involved distinct mechanisms, from pure cultural adoption to mobility and admixture between incoming farmers and local foragers to rapid migration and spread. Further, cultural similarities among settlements were not shaped by large-scale mobility (as reflected in genetic data) but rather through background mobility. Our results thus challenge the widespread assumption that cultural entities frequently correspond to genetically homogeneous populations, supporting the archaeological adage, “pots don’t equal people.” Our study presents a fresh look at mechanisms of cultural change during one of humanity’s most transformative periods. ☐

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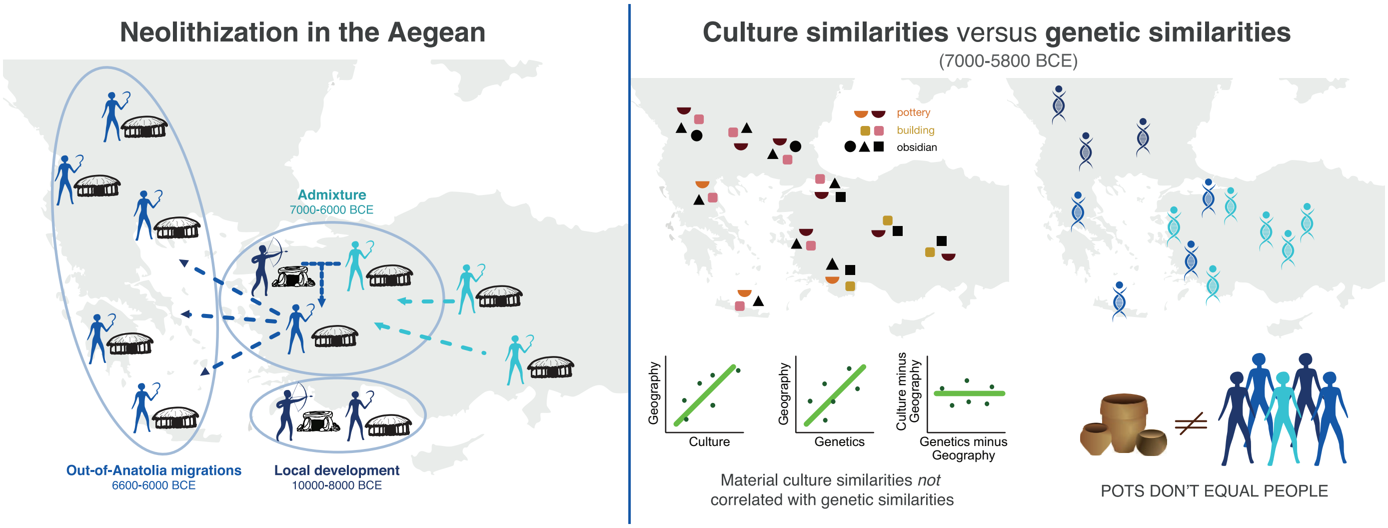

Diverse pathways to Neolithization and the uncoupling between cultural and genetic interactions in the Aegean. (Left) Neolithic practices in West Anatolia first started by cultural interactions, followed by mobility and admixture, and, lastly, migration into Europe. (Right) Comparative analysis of cultural and genetic similarity across 16 Neolithic settlements reveals no correlation between cultural and genetic similarities after controlling for geography.

ANCIENT DNA

Out-of-Anatolia: Cultural and genetic interactions during the Neolithic expansion in the Aegean

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West Anatolia has been a crucial yet elusive element in the Neolithic expansion from the Fertile Crescent to Europe. In this work, we describe the changing genetic and cultural landscapes of early Holocene West Anatolia using 30 new paleogenomes. We show that Neolithization in West Anatolia was a multifaceted process, characterized by the assimilation of Neolithic practices by local foragers, the influx of eastern populations, and their admixture, with their descendants subsequently establishing Neolithic Southeast Europe. We then coanalyzed genetic and cultural similarities across early Holocene Anatolian and Aegean Neolithic villages using 58 material culture elements. Cultural distances among villages correlate with their spatial distances but not with their genetic distances after controlling for geography. This suggests that cultural change was often decoupled from genetically visible mobility.

The emergence of sedentism and agriculture in West Eurasia was the outcome of a long social and economic process known as the Neolithic Transition, which started in Southwest Asia around 11,000 to 7000 BCE (*1*, *2*). Paleogenomic studies suggest that this transition largely emerged through cultural exploration by local foraging communities in different parts of the Neolithic core zones, namely the Levant, Upper (North) Mesopotamia, Zagros, and Central Anatolia, and their cultural exchanges, accompanied by limited levels of interregional mobility and genetic mixing (*3*–*6*). By contrast, the spread of Neolithic lifestyles and practices into Central and South Europe after 7000 BCE was driven by large-scale mobility, possibly originating from the Aegean (*7*–*11*). Cultural interactions prevailed in other areas, such as Baltic foragers adopting pottery (*12*) or North African indigenous populations embracing agriculture through cultural exchanges with Neolithic communities (*13*).

West Anatolia (i.e., the East Aegean coasts, East Marmara, and the Pisidian Lakes District) has a distinct trajectory in this picture. By ~9000 BCE, Aceramic or Pre-Pottery Neolithic (PPN) villages of sedentary foragers had emerged in the Fertile Crescent, including in Central Anatolia. However, despite a lack of major geographic borders between Central and West Anatolia, there were no comparable developments detected in West Anatolia between ~9000 and 7000 BCE apart from evidence for modest interregional contacts attested from changes in the stone tool assemblages (*14*–*17*). In fact, we know little of West Anatolia during the initial Holocene, except that its coastal areas (East Aegean and Marmara littorals) harbored forager groups with cultural connections to neighboring regions, as inferred from their stone tools (*18*–*22*).

The mid-8th millennium (mil.) BCE was a demographic turning point in the Neolithic development of Anatolia, when an episode of eastern mobility possibly of Upper Mesopotamian origin arrived in Central Anatolia (*23*, *24*). By the early 7th mil. BCE, villages with pottery, full-scale agriculture, and animal husbandry were being established across the Fertile Crescent. These agricultural villages, along with their material culture package, then continued to spread beyond the core zones into West Anatolia and, eventually, into Europe (*2*, *8*, *25*).

The emergence of multiple "Neolithic package" elements across West Anatolia between ~7000 and 6000 BCE has been interpreted as indicative of large-scale emigration from the Southwest Asian Neolithic core zones (*26*). Analysis of archaeological data has suggested various possible routes of human mobility or interaction that linked the emergence of West Anatolian Neolithic with its neighbors: one originating in Central Anatolia and/or Upper Mesopotamia and reaching Central-West Anatolia through Southwest Anatolia, another reaching Northwest Anatolia directly from Central Anatolia and/or Upper Mesopotamia, and also a maritime route connecting the Levant with Southwest or Central-West Anatolia (*2*, *27*, *28*). These models of West Anatolian demographic transformation have not yet been tested owing to the scarcity of representative paleogenomes.

Another hypothesis is that the Neolithization of West Anatolia involved only local groups (*29*) or cultural interactions and possibly admixture between eastern migrants and local foragers (*2*, *16*, *30*–*33*). This idea is inspired by the remarkable variation in their cultural preferences and subsistence strategies observed among 7th mil. BCE West Anatolian sites. Some villages had simple round huts, whereas other communities built more sophisticated rectangular buildings; some groups herded sheep and cattle, whereas others relied heavily on fishing; some villages used obsidian from Greece, some used obsidian from Central Anatolia, and some used nearly no obsidian but only local flint (*2*, *27*, *31*, *34*–*41*). These patterns have often been interpreted as the varying impact of local hunter-gatherers on different communities, but this notion has also not yet been tested genetically.

Overall, both the material culture and the limited paleogenomics data remain equivocal as to the origins of the West Anatolian Neolithic (*29*). The genetic affinities of the populations who lived in West Anatolia and the Aegean before 7000 BCE and how and whether they might have changed during the establishment of Neolithic settlements remain unclear. To what extent the observed material culture variation among Anatolian and Aegean Neolithic villages after 7000 BCE was driven by large-scale mobility and admixture processes (as was the case with the European Neolithic transition) is also unclear. In this work, we address these points using new paleogenomes from West and Central Anatolia, which allow us to describe the pre–7000 BCE population of West Anatolia, its continuity and transformation through

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the Neolithic period, and its connections with the Neolithic in Greece. We further measure material culture diversity across 58 traits among Anatolian and Aegean Neolithic villages and compare these with intervillage genetic and spatial distances, showing that cultural change can often be decoupled from genetically visible mobility.

Results and discussion

We produced 30 new paleogenomes from skeletal material from five West Anatolian settlements and from the Central Anatolian site of Çatalhöyük, all dated between 7800 and 6000 BCE (Fig. 1). The oldest individual was from Girmeler in Southwest Anatolia, dated to 7738 to 7597 calibrated (cal) BCE (*41*), and represented the oldest West Anatolian sequenced to date. Its endogenous ancient DNA content was only 0.7 to 0.9% in multiple libraries from which we produced a 0.11× paleogenome by using shotgun sequencing (data S1). The remaining 29 genomes were from post–7000 BCE Anatolia and had coverages 0.08 to 6.32× (median = 0.9×). Our data, combined with published data, cover West and Central Anatolia between 7500 and 6000 BCE with 98 genomes and comprise 11 settlements: Bademağacı in Southwest Anatolia; Ulucak in Central-West Anatolia; Bahçelievler, Pendik, Barcın, Aktopraklık, Menteşe, and Ilıpınar in Northwest Anatolia; and Musular, Çatalhöyük, and Tepecik-Çiftlik in Central Anatolia [Fig. 1, fig. S1, data S1 and S2, and supplementary text S1 (*42*)].

The local population of West Anatolia before widespread Neolithization by 7000 BCE

The site of Girmeler, in Southwest Anatolia, is located well outside the traditionally designated primary zones of Neolithization between the 12th and 8th mil. BCE (*41*, *43*) (Fig. 1 and fig. S1). The mound has nevertheless revealed evidence for PPN-like activities, including sedentary structures such as a lime-plastered floor and hearths, sickle blades and glume wheats, and flexed burials, together indicating connections to late 9th or early 8th mil. BCE PPN sites in Central Anatolia (e.g., Aşıklı and Boncuklu) [see supplementary text S1 (*42*)]. Meanwhile, the lack of ovicaprid hunting and the rarity of obsidian at Girmeler distinguish it from the Central Anatolian PPN (*41*, *43*). Girmeler also has parallels with Maroulas in the Aegean (*41*), including circular dwellings and subfloor burials as well as the presence of a flaked-type lithics industry and fishing (*43*). The Girmeler community may thus have been interacting with groups in the Neolithic core regions as well as with contemporary Aegean fisher-hunter-gatherers (*19*). In this study, we explored, whether the Girmeler community were locals or migrant PPN groups from Central Anatolia, the Levant, Cyprus, or Greece.

We compared the Girmeler genetic profile (*41*) with those from final Pleistocene and early Holocene populations from the broader region (fig. S1 and data S2). Whenever possible, we chose to perform analyses using either shotgun-sequenced genomes or 1240K single-nucleotide polymorphism (SNP) capture data, not mixing them. This was based on insights from our admixture simulations that used a new algorithm, genoMIX (*44*), which confirmed that analyses involving shotgun and capture data types together can (i) create technical-based clustering (*45*) and lead to false positive signals in f_4 tests of admixture and (ii) weaken statistical power in admixture modeling with qpAdm [figs. S2 to S5 and supplementary text S2 (*42*)].

By using multidimensional scaling (MDS), principal components analysis (PCA), and ADMIXTURE analysis, we found that the Girmeler genome consistently clustered with other final Pleistocene and early Holocene Anatolians (light and dark blue, respectively, Fig. 2; and figs. S6 to S8). In MDS and PCA space Girmeler had the most similar behavior with the 14th mil. BCE (Epipaleolithic) Central Anatolian Pınarbaşı genome (*4*) and the 7th mil. BCE (Neolithic) Northwest

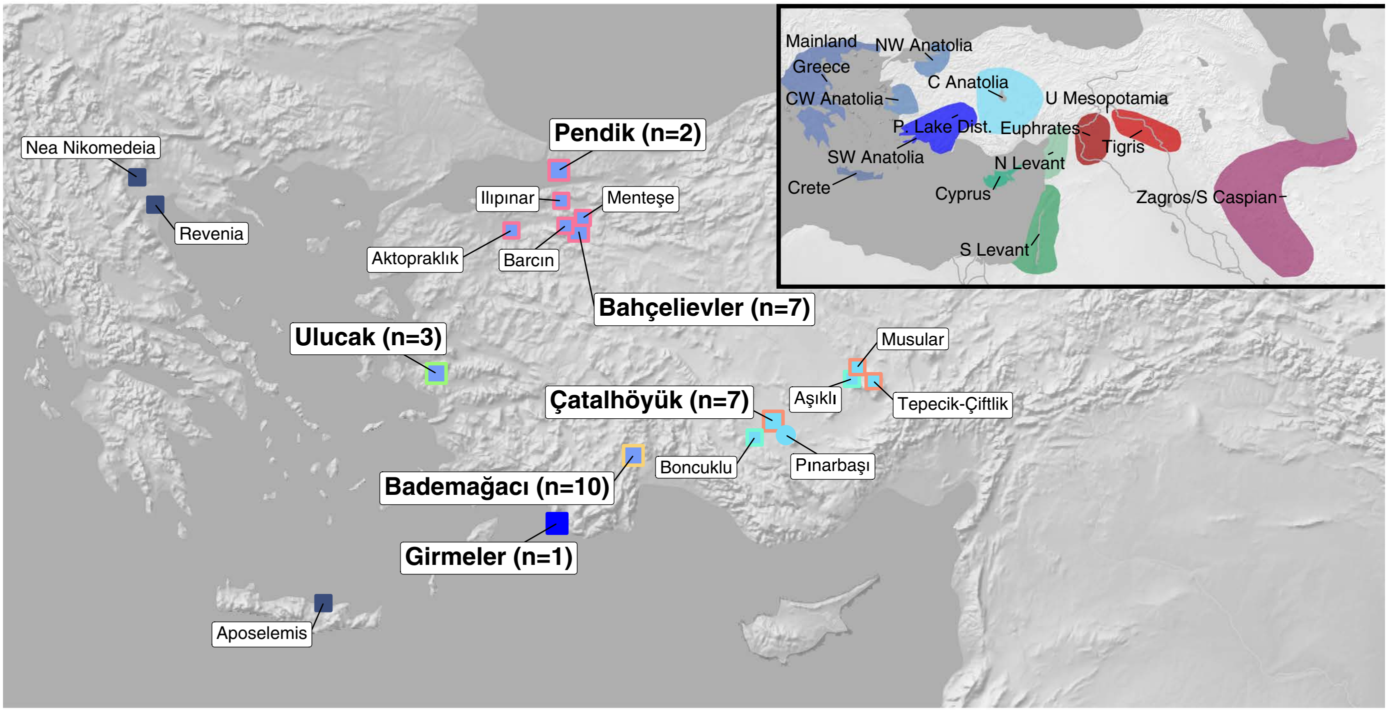

Fig. 1. Map of Aegean and Anatolian sites before 6000 BCE with paleogenomics data analyzed in this study. Smaller fonts and symbols indicate sites where only published genomic data have been included, whereas bold fonts and large symbols indicate sites where new paleogenomic data have been produced, with sample sizes shown in parentheses [data S1 and S2 and supplementary text S1 (*42*)]. We also used published data from Upper Mesopotamia, Zagros, Levant, and Cyprus (shown in the embedded map) as well as from the Balkans and other European sites in our analyses (fig. S1). To improve visualization, some of the locations were slightly shifted (the exact site coordinates can be found in data S1 and S2). Southwest (SW) Anatolia includes the Pisidia Lake District; Upper Mesopotamia includes both the Euphrates and Tigris regions.

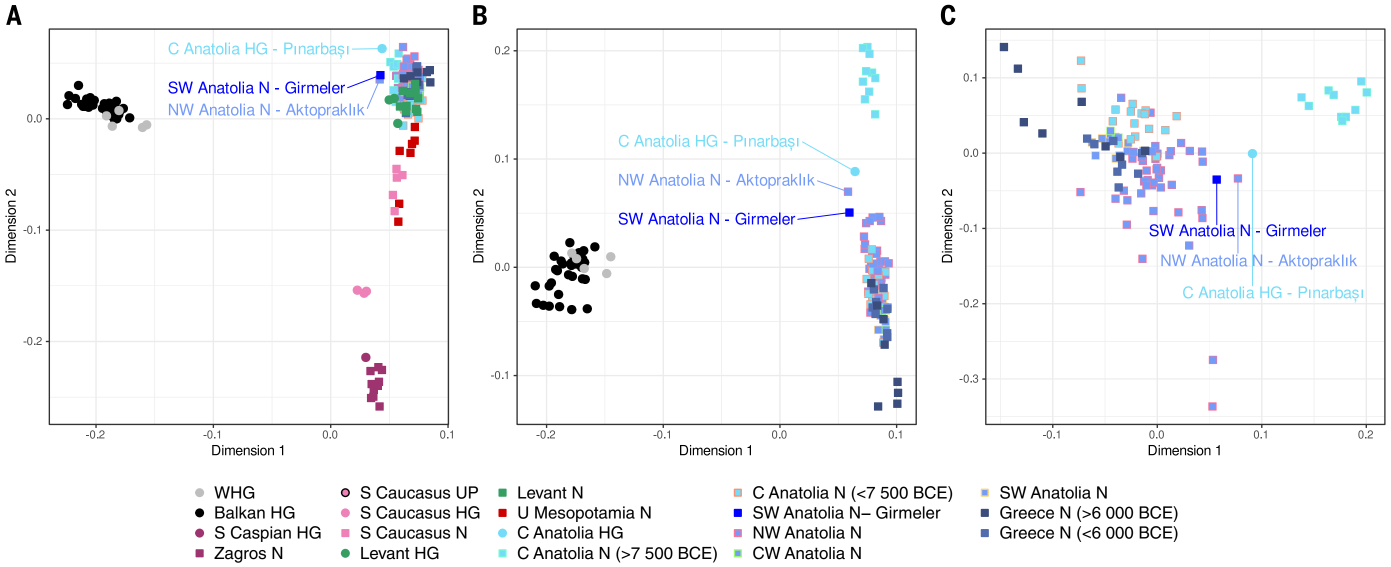

Fig. 2. Multidimensional-scaling plots describing genetic distances among early Holocene individuals from the broader region. (**A** to **C**) Distances were calculated by using the outgroup f_3 statistic (*42*). Graphs (A) to (C) have been drawn with progressively fewer populations to reveal broad- to fine-scale affinity patterns. UP, HG, and N suffixes indicate genomes of individuals from Upper Paleolithic (Mesolithic), hunter-gatherer, and Neolithic contexts, respectively. EHG and WHG represent genomes from East European and West European Mesolithic contexts (fig. S6). Note that genomes with low coverage (e.g., Cyprus) could not be included in this analysis but are included in the projection-based PCA (fig. S7). All post–7500 BCE genomes in Anatolia belong to the Ceramic (PN) period, except for Musular, which belongs to the PPN (fig. S1B).

Anatolian Aktopraklık genome (*25*) (Fig. 2, figs. S6 and S7, and data S2). Despite the five millennia separating Girmeler and Pınarbaşı, their genetic profiles were highly similar, such that all final Pleistocene and early Holocene genomes from the broad region were equally distant to both in f_4-tests (fig. S9 and data S3). qpAdm modeling of genetic ancestry sources of the Girmeler genome further suggested that it carried mixed ancestry between Balkan- and Levant-related sources of the final Pleistocene and early Holocene, again indistinguishable from the qpAdm model of Epipaleolithic Pınarbaşı (Fig. 3A and fig. S10B). On the other hand, Girmeler was distinct from PPN Cyprus on the PCA, with Cyprus shifted toward the Levant and Girmeler shifting toward the Balkans (fig. S7). The Girmeler qpAdm model was also distinct from those of contemporaneous (late 9th and early 8th mil. BCE) PPN-associated Central Anatolians, Aşıklı and Boncuklu (Fig. 3A). These Central Anatolians could be explained as admixed between ~65% Epipaleolithic Pınarbaşı–related and ~35% Upper Mesopotamia PPN–associated genetic sources (represented by 9th to 8th mil. BCE Çayönü) (Fig. 3A and data S4). Hence, Upper Mesopotamia–related ancestry appears to have arrived in Central Anatolia sometime between the 14th and 9th mil. BCE, without reaching Girmeler at detectable levels.

Even though Girmeler is represented by a single genome, its genomic profile is conspicuously distinct from any of its contemporaries from the core regions of the PPN. This implies that the Girmeler individual was not a migrant but a descendant of a local population that was sedentary and engaged in Neolithic-related practices, likely in cultural connection with its eastern neighbors, albeit without visible genetic interaction. This local development pattern appears to parallel Neolithization in the Zagros area, which also did not involve visible genetic contribution from other regions of the Fertile Crescent (*6*) but was culturally connected with them (*46*–*48*). By contrast, Neolithization in Central Anatolia and South Levant might have involved gene flow from eastern and northern sources, respectively (*4*, *6*).

The mixed origins of West Anatolian Neolithic villages

We next studied the demographic history of West Anatolia in the 7th mil. BCE, when food-producing Neolithic villages started spreading in the region. We found that post–7500 BCE West Anatolian genomes appear similar (albeit not the same, as we explain later in this section) to contemporaneous genomes from Central Anatolia, as previously noted (*29*). This genetic affinity between West and Central Anatolia after 7500 BCE can be observed both in MDS and PCA plots (Fig. 2 and figs. S6 and S7) and also in qpAdm models, where nearly all Central and West Anatolians studied can be modeled as admixed between Pınarbaşı or Girmeler and Çayönü (Upper Mesopotamia) (Fig. 3A). Using 1240K-generated Nevali Çori or Boncuklu Tarla instead of Çayönü also yields qualitatively similar results [figs. S11 and 12, data S4, and supplementary text S3 (*42*)]. A considerable fraction of the ancestors of West Anatolian Neolithic villages may thus have immigrated some centuries ago from Central Anatolia, Upper Mesopotamia, or genetically unsampled regions with possibly similar genetic profiles, such as the Upper Euphrates or North Levant. In fact, the presence of domestic pigs or pressure flaking in Central-West Anatolian sites, such as Ulucak, when these were absent in Central Anatolia [supplementary text S1 (*42*)] (*2*, *49*), may support an Upper Mesopotamian contribution alongside or instead of a Central Anatolian genetic contribution.

A PPN-associated population from the South Levant or Cyprus (*50*) arriving through seafaring in West Anatolia and founding Neolithic villages could be an alternative scenario. However, the genetic contributions of South Levant or Cyprus to West Anatolia appear limited, if any, notwithstanding the possibility of purely cultural contributions (*28*) and/or low-level genetic contributions from these regions to West Anatolia. This conclusion is based on the distinct genetic profiles between South Levant and West Anatolia (figs. S6, S7, and S13 to S16) and also because West Anatolia could not be systematically modeled as two-way admixture between Pınarbaşı or Girmeler and South Levant or Cyprus (figs. S11 and S17), as opposed to models that included Upper Mesopotamia [supplementary text S3 (*42*)].

The data imply a shift in the West Anatolian gene pool by the 8th or early 7th mil. BCE, driven by eastern gene flow and rendering West Anatolia similar to that of Central Anatolia. However, we noticed an exception to this pattern: the Aktopraklık individual with the sample ID AKT16, the oldest Northwest Anatolian in our dataset (6658 to 6578 cal BCE)

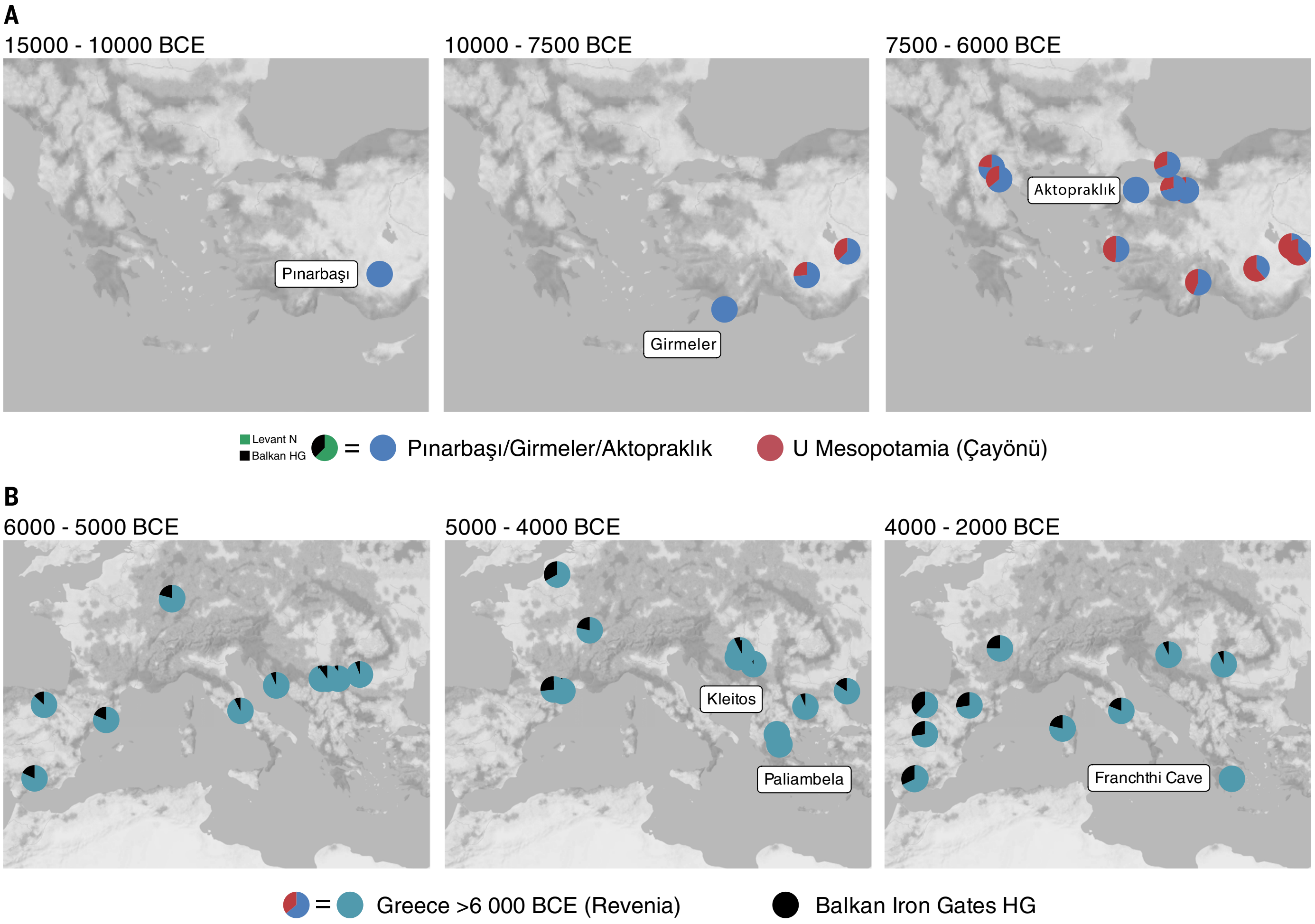

Fig. 3. qpAdm models of genomes from Anatolia, the Aegean, and South or Central Europe. (**A** and **B**) The pie charts show ancestry proportions of genomes from archaeological sites estimated by using statistically "feasible" qpAdm models (42). The time windows of the genomes included are indicated on top of the panels. The ancestry sources used in the models are shown in the key. (A) The key shows the qpAdm model for the genetic profile of Pınarbaşı, Girmeler, or Aktopraklık (blue), which can be modeled with early Holocene Levant (Levant N) and Balkans (Balkan HG) (fig. S10B). (B) The key shows the qpAdm model for pre–6000 BCE Greece (teal) represented by Revenia and Nea Nikomedeia, which can be modeled with Pınarbaşı, Girmeler, or Aktopraklık, with Çayönü representing Upper Mesopotamia [see also figs. S11 and S12, data S4, and supplementary text S3 (42) for models with Nevali Çori or Boncuklu Tarla instead of Çayönü]. qpAdm models of 1240K SNP capture-generated Neolithic Aposelemis (Crete) and Ilıpınar (NW Anatolia) with the same source genomes (shotgun-generated) were not feasible and are not shown, but additional analyses revealed that both populations have qualitatively the same profile as other Neolithic genomes from Greece or West Anatolia [supplementary text S4 (42)]. To improve visualization, some of the locations were slightly shifted (the exact site coordinates can be found in data S1 and S2).

published by Marchi *et al.* (25), not only stood out in MDS and PCA analyses as being different from other West Anatolians (Fig. 2) but also was indistinguishable from Pınarbaşı (Central Anatolia, 14th mil. BCE) and Girmeler (Southwest Anatolia, 8th mil. BCE) in qpAdm models and f_4 tests (Fig. 3 and figs. S9 and S10). AKT16 also clustered with Pınarbaşı in haplotype-sharing analyses with FineSTRUCTURE (51) (figs. S18 and S19). Low-coverage genome-wide capture data from three other 7th-mil. BCE Aktopraklık individuals (52) also indicated higher AKT16-like ancestry in these individuals than in neighboring villages, although Late Neolithic (after 6000 BCE) Aktopraklık capture genome did not carry such additional AKT16 affinity (fig. S20).

These observations confirm that AKT16 had higher western-related ancestry than other Anatolian Neolithic genomes, as observed earlier (25); however, this was not caused by the west-to-east admixture events proposed in that study but may instead be explained by population structure within Anatolia, which included genetic continuity within the region alongside east-to-west admixture. The Early Neolithic Aktopraklık population likely descended from the same pre-Neolithic gene pool to which Girmeler belonged, which may have inhabited all of West Anatolia into the 7th mil. BCE with limited eastern admixture.

Hereafter, we refer to the genetic profile represented by Pınarbaşı (ZBC_IPB001), Girmeler (gir001), and Aktopraklık (AKT16) as Early Holocene West Anatolian ancestry, given its inferred continuous local presence in West Anatolia until the early 7th mil. BCE. We found that Northwest and Southwest Anatolian 7th-mil. BCE genomes from Neolithic contexts (apart from Aktopraklık and Ilıpınar) could be modeled by using qpAdm with local West Anatolians (Girmeler or Aktopraklık) (28 to 53%) and post–7500 BCE Central Anatolia (Çatalhöyük) (47 to 72%) as sources (fig. S10C). We also found local Early Holocene West Anatolia to show higher affinity to 7th-mil. BCE West Anatolians than to contemporary Central Anatolians: All 126 tests of the form f_4(Yoruba, Pınarbaşı/Girmeler/Aktopraklık; <7500 BCE Central Anatolia, <7500 BCE West Anatolia) were positive, with 56% of these significant at z-score > 3 (Fig. 4 and figs. S18, S19, S21, and S22). These results strongly suggest that local Early Holocene West Anatolians admixed with incomers from Central Anatolia and/or from other regions to its east (e.g., Upper Mesopotamia) to eventually create the 7th-mil. BCE Neolithic West Anatolian gene pool identified in villages such as Bademağacı, Ulucak, Barcın, Bahçelievler, and Pendik.

We further observed considerable regional and intrasite heterogeneity in these admixture patterns within West Anatolia. f_4 tests, qpAdm modeling, f_3 tests, and haplotype-sharing analyses all indicated higher Early Holocene West Anatolian (i.e., local) ancestry in Northwest Anatolia than in Southwest or Central-West Anatolia, on average (Fig. 4 and figs. S23 to S27). The Ulucak genomes (~6700 BCE), the oldest West Anatolians in our dataset after the Girmeler genome, had lower local ancestry than most of their Northwest Anatolian contemporaries (figs. S24 and S25). Among the analyzed West Anatolian shotgun paleogenomes, some showed higher local ancestry than others, with heterogeneity even within the same site (fig. S25), Meanwhile, local ancestry levels were not correlated with the archaeological date of the individuals (fig. S28). These observations overall mark the variability of the admixture process with local groups, both in space and time.

Our results have major implications. First, the Aktopraklık data suggest that a Pınarbaşı- or Girmeler-like population persisted in West Anatolia until the mid-7th mil. BCE, with little or no genetic influence from its east, despite cultural contacts between regions (*16*). Second, between ~7500 and ~6500 BCE, West Anatolia received gene flow from Central Anatolia and/or more eastern regions (*2*), either gradually or by mass mobility, and these incoming groups were a major demographic contributor to the first Neolithic villages in the Aegean. Third, the Aktopraklık genome (AKT16) attests to local involvement in the development of the West Anatolian Neolithic (*53*), whereas the local admixture signature in West Anatolian post–7000 BCE genomes indicates admixture between incoming groups and locals. Fourth, we infer that local forager groups in West Anatolia either genetically integrated into incoming groups in a few centuries, or some groups may have survived while not mixing with villagers and later disappeared. In our data, none of the genomes sequenced from post–6500 BCE West Anatolia (all from Neolithic contexts) match the distinct local profile represented by Girmeler or Aktopraklık. Furthermore, we observed no temporal increase in local admixture proportions in Neolithic West Anatolian sites (fig. S28), as opposed to the extended pattern of local admixture observed in Europe (see next section).

The out-of-Anatolia expansion and lack of local admixture in Greece

Our data further provide new insights into the Neolithization of the West Aegean, i.e., present-day Greece. Based on material culture analyses, some scholars suggested that Greece was colonized by agriculturalists from the Levant or Cyprus moving along the coast (*54*), whereas others pointed to Anatolian origins (*33*). The observation that European Neolithic–associated genetic profiles were highly similar to those of Neolithic West Anatolians in turn points toward a Neolithic out-of-Anatolia event (*8*, *25*, *55*). However, because pre-Neolithic genomes from the Aegean were lacking, we had previously speculated that early Neolithic groups in West Anatolia and Greece could have been descendants of local foragers with that same genetic profile who had adopted village life by the 7th mil. BCE (*29*). This would imply that the demographic origins of the European Neolithic expansion lay in Southeast Europe instead of Anatolia. Our new results undermine this model: The European Neolithic–like genetic profile emerged only after 7000 BCE in West Anatolia through large-scale eastern mobility and local admixture (Fig. 3A) and is unlikely to have existed in Greece before 7000 BCE. These results provide the most direct indication yet of the mainly Anatolian demographic origins of the European Neolithic expansion (fig. S29).

The question then becomes the exact sources of those Anatolian populations and the routes they used. Genomes from before 6000 BCE from Greece are limited to a few sites, Nea Nikomedeia and Revenia in North Greece (*8*, *25*) and Aposelemis in Crete (*56*) (Fig. 1). The qpAdm models of all three sites were overall similar to those of West Anatolia, as noted earlier (*25*, *56*) (Fig. 3 and fig. S24). Outgroup f_3 and f_4 statistics also indicated higher similarity between Greece and West Anatolia relative to Central Anatolia (Fig. 4 and figs S26, S27, and S29).

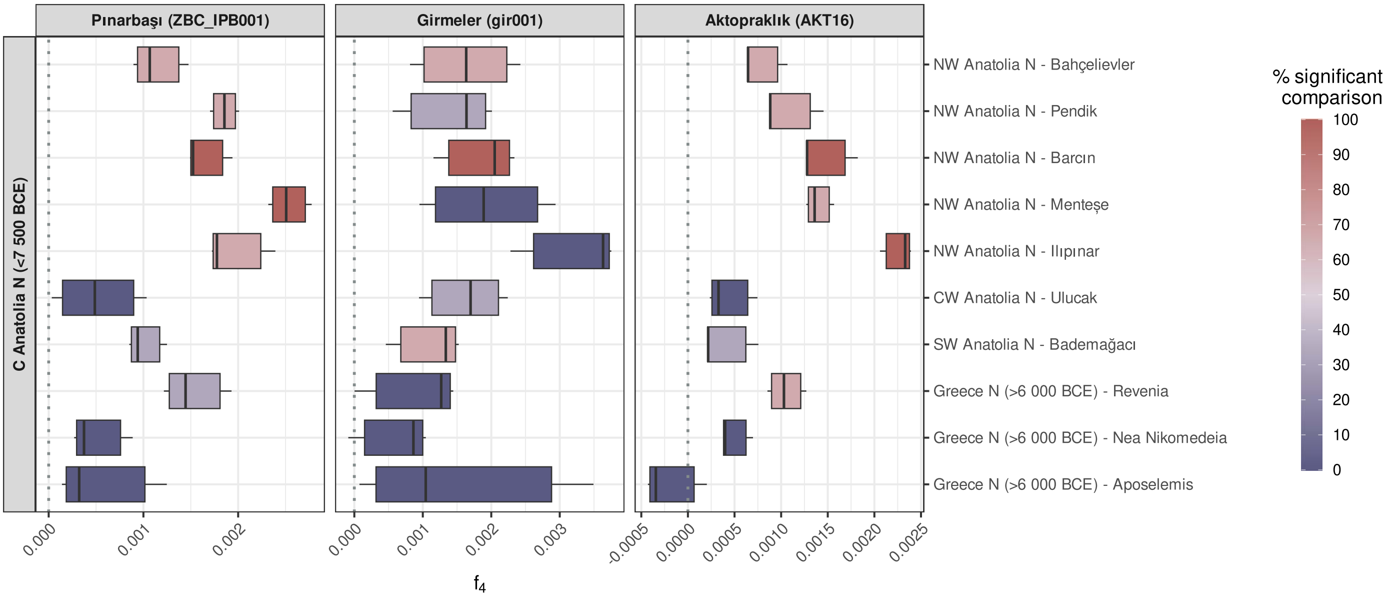

Fig. 4. The affinities of Epipaleolithic Pınarbaşı, Girmeler, and Aktopraklık genomes to Central Anatolia versus West Anatolia or Greece analyzed with f_4 tests. The populations on the left are Central Anatolians after 7500 BCE (Çatalhöyük, Musular, and Tepecik-Çiftlik), whereas those on the right are Neolithic groups from West Anatolia or Greece. The boxplots show the distribution of the f_4 statistics performed with groups of genomes per site; for example, the top left comparison involves three comparisons of the form f_4(Yoruba, Pınarbaşı/Girmeler/Aktopraklık; Çatalhöyük/Musular/Tepecik-Çiftlik, West Anatolia/Greece), one including Çatalhöyük, one including Musular, and one including Tepecik-Çiftlik. Color coding indicates the proportion of nominally significant tests out of all comparisons (at |z-score| > 3). The N suffixes indicate genomes identified with Neolithic contexts.

To increase our resolution for studying demographic connections, we imputed >0.25× shotgun genomes and >1× capture genomes (*42*) and estimated identical-by-descent (IBD) haplotype-sharing with the ancIBD tool (*57*) on these imputed genomes, a signal that informs on distant relatedness. We found shared segments of size 8 to 12 centimorgan (cM), representing distant relationships (e.g., >20 generations apart), between pre–6000 BCE North Greece and both Northwest and Central-West Anatolia (Fig. 5 and fig. S30). Clustering based on haplotype-sharing statistics, in turn, suggested strongest affinities to Northwest and Southwest Anatolia (figs. S18, S22, and S31). These observations do not pinpoint a single Anatolian region as the origin of westward expansion into Greece. We either lack the resolution to identify it, or the origins may have been dispersed, including both pan–Aegean Sea travel and possible land routes through Thrace.

The incomers must have encountered Mesolithic communities on the Aegean islands and in mainland Greece, with whom they were likely already in contact, given the presence of Greek (Melos) obsidian in Anatolia by the early 7th mil. BCE and possibly earlier (*28*, *49*, *58*). These Mesolithic communities in Greece have not yet been genetically sampled and could be similar to pre-Neolithic West Anatolian or the Balkan Mesolithic–related ("Balkan HG") gene pools. Irrespectively, admixture between such local Mesolithic groups and incoming Neolithic communities from Anatolia might be genetically detectable in Neolithic genomes from Greece (similar to the Girmeler- or Aktopraklık-like admixture signatures identified in West Anatolia relative to Central Anatolia). Such admixture may be expected given evidence for early genetic interactions between incoming Neolithic communities and local Mesolithic groups elsewhere in Southeast Europe. For example, burials at the Balkan sites of Lepenski Vir and Padina (in the Iron Gates region) dated to ~6200 to 5900 BCE (*59*) were estimated to carry 24 and 47% Anatolian ancestry, respectively (fig. S10C).

If Neolithic Anatolian populations first mixed with local foragers in West Anatolia before 7000 BCE and then expanded into Greece from there, then we could use the 7th–mil. BCE West Anatolian genetic profile as a reference to test for additional local admixture in Greece. We did not detect such additional Balkan HG-related or Girmeler-related admixture in genomes from Greece from the 7th to 5th mil. BCE (Figs. 3 and 4 and fig. S32). This was probably not a power issue, because, running qpAdm models on genomes admixed by simulation, we could identify ≥10% of Balkan HG-related admixture in a West Anatolian–like background (figs. S2 to S5). We could also construct qpAdm models for genomic data from 30 published European Neolithic sites across Southeast, South, and Central Europe (6000 to 2000 BCE), which indicated admixture between an early Neolithic Greece–related source (before 6000 BCE) and a Balkan HG–related source, with 4 to 38% contribution from the latter (figs. S33 to S35). By contrast, genomes from four later Neolithic (after 6000 BCE) sites in Greece were simply modeled as early Neolithic Greece (before 6000 BCE) without additional ancestry [Fig. 3, fig. S36, and supplementary text S4 (*42*)].

Different scenarios could equally explain these findings. One possibility is that Mesolithic groups survived in Greece after Neolithization but did not mix with the Neolithic communities on a large scale (up to ~10%; figs. S2 to S5). Another is that a large immigrant population or multiple episodes of mobility from Anatolia swamped the local Mesolithic population in Greece but did not have this effect in other regions (although comparisons of genetic diversity among populations do not support such a difference; figs. S37 to S40). Lastly, it is possible that populations from Central Anatolia or Upper Mesopotamia reached Greece through West Anatolia but before starting to admix with Girmeler-like local groups in West Anatolia. In this model, local Mesolithic groups in Greece may have fully integrated within incoming

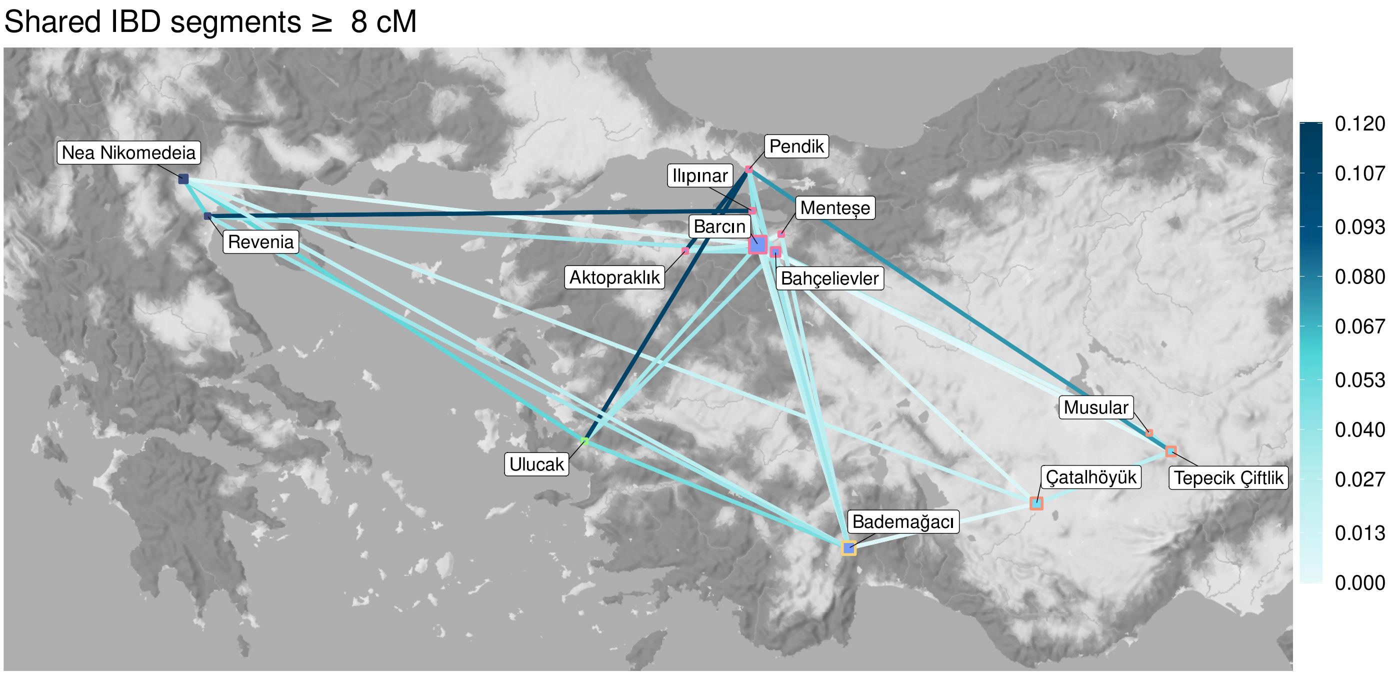
Shared IBD segments ≥ 8 cM

Fig. 5. IBD-sharing network across the Aegean showing distant genetic relatedness. The analysis was performed by using imputed ancient genomes from the study region and includes ≥8 cM IBD segments. The majority of these were 8 to 12 cM, and the only IBD segments >16cM were found between Nea Nikomedeia and Revenia in Greece and between Aktopraklık and Bahçelievler in Northwest Anatolia. The colors shown in the key indicate the strength of connections between pairs of genomes in any two sites. We calculated the strength given the number of comparisons and the maximum IBD sharing observed in the dataset. For example, if regions X and Y are represented by three and five genomes, respectively; if any two genomes share a maximum of four segments in the full dataset; and if across the 15 X-Y comparisons, there are seven segments in total shared, the X-Y connection strength is estimated as 7/(4 × 15) = 0.12 [figs. S30 and S41 to S45, data S5, and supplementary text S5 (*42*)].

Neolithic groups, concurrent with the demographic process observed in West Anatolia [supplementary text S4 (*42*)].

The evolution of material culture uncoupled from demographic dynamics in the Aegean Neolithization process

Our genetic data support a scenario in which the West Anatolian Neolithic arose by both large-scale mobility from Central Anatolia and the adoption of Neolithic cultural elements by local forager groups and their eventual admixture. This appears to align with previous proposals based on the material culture evidence that invoked both immigration and admixture with locals in West Anatolia (*27*). By contrast, the appearance of Neolithic cultural elements in Girmeler and in the Zagros area (*46*–*48*) without visible genetic change (*6*) (data S4) indicates the role of purely cultural contacts and/or local innovation in Neolithization. This suggests that both large-scale and genetically visible mobility as well as genetically invisible background mobility may have contributed to the spread of Neolithic culture.

These observations motivated us to systematically investigate whether sociocultural diversity across Neolithic villages in Southwest Asia and the Aegean might overall be correlated with their genetic similarity patterns (reflecting mobility and admixture). Such a result would arise if new cultural elements were mainly transmitted by large-scale mobility and admixture, as captured by genetic data. Alternatively, cultural patterns in the region could have been shaped by (i) purely cultural interactions, e.g., exchange networks; (ii) background mobility, i.e., small-scale mobility that may not be genetically as conspicuous as mass mobility, such as exogamy and mobility driven by individual motivations; or (iii) convergent cultural changes. Under these latter scenarios, we would expect no correlation between genetic and cultural affinities, which is our null hypothesis (*60*).

A first qualitative evaluation indicated little, if any, relationship between sociocultural and genetic similarities among settlements. For example, settlements extensively using Central Anatolian obsidian were not genetically closer to Central Anatolians. The presence of simpler architecture (semisubterranean round huts) was also not associated with higher local (Early Holocene West Anatolian) genetic ancestry [discussed in detail in supplementary text S6 (*42*)].

We then investigated these patterns quantitatively, calculating correlations between sociocultural and population genetic affinities among sites while controlling for geographic (spatial) proximity (*42*). For this, we collected and binary-coded material culture traits across 89 sites from Southwest Asia and Southeast Europe between 9500 and 5800 BCE. The information comprised 58 traits, including burial and ritual elements, architecture, pottery, lithics, and obsidian sources collected from the literature (data S6). By using this data matrix, we measured sociocultural distances using Jaccard dissimilarity among all pairs of sites and compared these with their geodesic distances (spatial distances representing the shortest path), separating the data into three periods: 9500 to 8500 BCE (early PPN), 8500 to 7000 BCE (PPN), and 7000 to 5800 BCE (Pottery Neolithic). As expected, sociocultural similarities could be explained by spatial proximity among sites in all periods (Spearman correlation coefficient $r > 0.21$, Mantel test $P < 0.01$). Moreover, we saw a decreasing correlation through the Neolithic (from $r = 0.48$ to 0.21; fig. S46). This may reflect the growing intensity of interregional cultural exchanges, which may parallel interregional genetic admixture through the Neolithic (*24*).

Next, we limited the dataset to 16 sites from 7000 to 5800 BCE that had both cultural and genetic data. We again found a positive correlation between geodesic and cultural distances ($r = 0.49$, $P = 0.001$), as between geodesic and genetic distances ($r = 0.58$, $P = 0.001$). Genetic affinities were also correlated with cultural affinities when tested directly ($r = 0.26$, $P = 0.033$). However, after controlling for the confounding effect of geography, genetic affinities did not explain any significant variation in cultural affinities ($P > 0.10$) (Fig. 6). Repeating the analysis with only Aegean and Anatolian sites, by testing each trait group separately, or with Girmeler affinity differences as genetic distances did not change the results (figs. S47 to S49).

We then asked whether genetic and spatial distances may have an equivalent impact on cultural distances, or whether spatial distance may have an additional impact on cultural distances not represented by genetic distances. This would be expected if background mobility, shaped by spatial proximity but not reflected in intervillage genetic distances, also shaped cultural patterns. To test this, we removed the effect of genetics using the same approach from geodesic and cultural distances. We found that spatial and cultural distances were still correlated ($r = 0.49$, $P = 0.001$) (Fig. 6 and fig. S50). This suggests that different modes of mobility, visible or invisible in genetic data but both independently structured by spatial proximity, simultaneously shaped the observed cultural similarity patterns across Neolithic sites in Southwest Asia and the Aegean.

Admittedly, our analysis does not have high resolution, as it combines data from multiple centuries of settlement occupation in single-digit records; the genetic information may also vary as new evidence becomes available. Still, it is worth noting that both qualitative and quantitative analyses point to the mismatch between genetic and cultural affinities in this period. We hypothesize that, at the regional level, sociocultural affinity patterns may be evolving more rapidly and plastically than genetic affinities captured by ancient DNA data, hence the lack of correspondence.

Conclusions

Our expanded genomic dataset has helped resolve long-standing questions on the earliest westward steps of the Neolithic expansion beyond the Fertile Crescent. By using the Girmeler and Aktopraklık genomes (*25*), we described the putative local gene pool of West Anatolia prior to Neolithization, which was genetically closely related to that of Central Anatolians from the PPN period but distinct in its lack of Upper Mesopotamian ancestry. The high similarity among Pınarbaşı, Girmeler, and Aktopraklık genomes, with dates ranging between ~13,000 to 6600 BCE, is most parsimoniously explained by the persistence of such a local population in the region. This emerging pattern of long-term continuity does not imply absolute genetic isolation and homogeneity in West Anatolia, but rather that mobility and admixture processes happened at levels too low to be observed with our current data.

The presence of PPN-related cultural elements in Girmeler provides another likely case of cultural interaction among regional communities shaped by low levels of continuous movement or background mobility. In other words, we see cultural change without mass movement discernable as genetic admixture, which resembles Neolithization in the Zagros region.

Moving forward in time, we infer that Neolithization in West Anatolia in the 7th mil. BCE involved both large-scale mobility from the east and cultural adoption by local groups (represented by the Aktopraklık genome from ~6600 BCE) as well as admixture between the two. The patterns that we observed resemble those observed in North Africa (*13*), where the expansion of Neolithic communities from Iberia appears to have triggered cultural change among locals. Through comparative analysis of material culture traits and ancient genomes for the first time to our knowledge, we tested the hypothesis that the observed cultural heterogeneity in regions of Neolithic expansion can be explained by heterogeneity in genetic admixture patterns, i.e., by cultural elements being shared through genetically visible mobility. We found no support for this: After controlling for spatial proximity, genetic similarity shows no correlation with cultural similarity. Instead, the transmission of sociocultural affinity patterns—even in ritual elements, such as burial practices (fig. S48)—may have been more rapid and fluid than genetic admixture processes, at least during the Aegean Neolithization. Accordingly, we found that intervillage spatial affinity still explains cultural similarities after removing the effect of

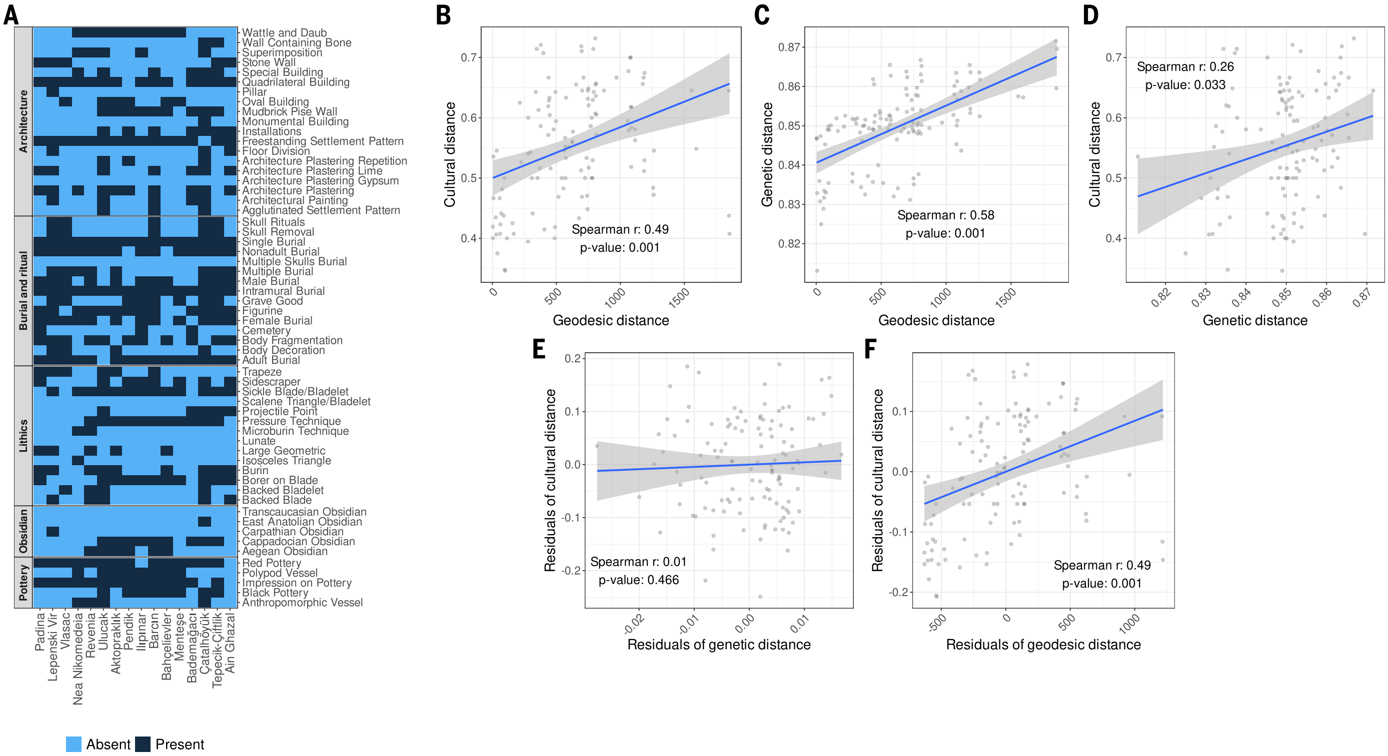

Fig. 6. The influence of geographic proximity and genetic similarity on material culture similarities among 7th-mil. BCE sites across Southwest Asia and the Aegean. (**A**) Presence or absence records of 58 material culture traits compiled from the literature for 16 Southwest Asian or Aegean sites covering 7000 to 5800 BCE and that have genetic data (see data S6 for the full dataset with 89 sites covering 9500 to 5800 BCE). (**B** to **D**) Correlations between pairwise distances among sites in material culture (Jaccard dissimilarity), geodesic distances (geographic shortest path estimates), and genetic distances (1-f_3) across the 16 sites (*42*). (**E**) Correlation between residuals of sociocultural and genetic distances after each was regressed on geodesic distances by using linear regression. Partial Mantel tests between cultural and genetic distances controlling for the effect of geography were nonsignificant ($r = -0.03$, $P = 0.56$), suggesting that the effect of genetic admixture on cultural variation can simply be explained by geographic proximity. (**F**) Correlation between residuals of sociocultural and geodesic distances after each was regressed on genetic distances by using linear regression. Partial Mantel tests between cultural and geodesic distances controlling for the effect of genetics were still significant ($r = 0.49$, $P = 0.01$), suggesting that spatial distances shape cultural variation independent of genetic admixture. In (B) to (F), the Spearman correlation coefficients and the Mantel test P values are shown inside the panels. See also figs. S46 to S50.

genetic similarity. This supports the notion that diverse types of mobility contributed to cultural variation in the Neolithic Aegean.

Our results call for further research on the following topics. One is the regional sources of gene flow into West Anatolia before 7000 BCE. A second is the veracity and possible reasons of local genetic contribution in the Neolithic populations of Greece. A third pertains to the prevalence of Neolithization without genetic admixture, as in Girmeler and the Zagros area, and the lack of correlation between sociocultural and population genetic similarities among Neolithic villages beyond their spatial proximity. These findings raise the possibility that, at the regional level, similarities in material culture may often be shaped by cultural transmission through exchange networks or by background mobility rather than by large-scale and genetically conspicuous mobility events [discussed in (*60*)]. Large-scale migration and genetic admixture were not always the main drivers of cultural spread in prehistory.

Materials and methods summary

For ancient DNA sequencing library preparation, we applied the Dabney extraction (*61*) and Meyer-Kirsher double-stranded library preparation protocols (*62*, *63*) on archaeological petrous bones and teeth. Sequencing was carried out on Illumina instruments (see data S1). We thus produced 30 shotgun-sequenced genomes and radiocarbon dated 5 of them at TÜBİTAK MAM. Sequencing reads were trimmed and merged for each library using Adapter Removal (version 2.3.1) (*64*) and mapped to the human reference genome (hs37d5) using *BWA aln/samse* (version 0.7.15) (*65*). After removing polymerase chain reaction duplicates, reads with >10% mismatches to the human reference genome, mapping quality < 30, and base pair count < 35 were discarded. We estimated contamination levels, biological sex, and uniparental haplogroups per library as well as genetic kinship among libraries using *PMDtools*, *ANGSD*, *contamMix*, and *READv2* (*66*–*72*). We accounted for postmortem damage by trimming 10 or 2 bp from the ends of reads for non–uracil DNA glycosylase (UDG)– or UDG-treated libraries, respectively.

We downloaded 453 published genomes from the literature and processed these with the same parameters (*42*), leading to a dataset of 483 ancient genomes. We prepared four separate pseudo-haploid datasets based on different SNP panels (the 1000 Genomes sub-Saharan African dataset with ~4.7 million SNPs (*24*), the 1240K Capture Array (*55*), the Human Origins SNP Array (*6*, *73*), and the 400K relatively unbiased SNP subset of 1240K (*74*) by randomly selecting one allele for each targeted SNP position by using *pileupCaller* (version 1.5.3.1). We also created an imputation dataset using all shotgun-produced ancient genomes with >0.25× coverage and capture-produced ancient genomes with >1× coverage ($n = 187$) and using the 1000 Genome Phase3 autosomal dataset as a reference panel with *GLIMPSE2* (*75*).

We developed the *genoMIX* software (*44*) to create admixed genomes from empirical data, which also allowed us to measure the effect of coanalyzing data of different types (shotgun and 1240K SNP capture). In population genetic analyses, we tried to avoid mixing data types when we could, and, in instances where this could not be avoided, we replicated results using the 400K relatively unbiased SNP subset of 1240K (*42*, *74*).

We used *EIGENSOFT* (*76*) to conduct PCA. We calculated outgroup f_3 and f_4 statistics using *AdmixTools* (*77*) to measure genome-wide similarity and admixture between populations. We also applied MDS to f_3-based distance matrices. Model-based clustering was performed by using *ADMIXTURE* (*78*), selecting Western Eurasian populations. We estimated runs of homozygosity with both *hapROH* (*79*) and *PLINK* (*80*). *Chromopainter* and *FineSTRUCTURE* (*51*) tools were applied for coancestry estimation on 75 imputed genomes. Ancestry proportions were estimated with *qpAdm* (*77*); here, we used "*Mbuti*, *Han*, *Papuan*, *Mixe*, *Ust_Ishim*, *Kostenki14*, *MA1*, *WHG*, *Levant_RaqefetCave_HG_CP*, *Morocco_Taforalt_CP*, *AfontovaGora3*, *Iran_N*" as "right" populations. Identical-by-descent segments in 59 to 109 imputed genomes were estimated using *ancIBD* (*57*).

Material culture traits from 89 final Pleistocene and early Holocene Southwest Asian and Southeast European archaeological sites were collected from the literature, binary coded, and analyzed for correlations with genetic and geographic distances. We computed pairwise Jaccard dissimilarity across sites for culture and geodesic distance; these we compared with 1-f_3–based genetic distances. We tested correlations among distances using the Mantel test in R (*81*). To control for a third variable in correlations (e.g., geographic distance or genetic distance), we used residuals from regressions.

A more detailed description of the methods is available in the supplementary materials (*42*).

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SUPPLEMENTARY MATERIALS

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Materials and Methods; Supplementary Text S1 to S6; Figs. S1 to S50; Table S1; References (*82*–*183*); MDAR Reproducibility Checklist; Data S1 to S6

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