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Evaluating Greek Population Structure and Admixture Signals with Modern Genomic Summaries

Weining Zhang

Winchester College, Winchester, UK
walterzhang99@gmail.com

Abstract. Greece lies at the intersection of southeastern Europe, Anatolia and the eastern Mediterranean, regions connected by repeated population movements. Here we use publicly available genome-wide SNP data to examine the genetic structure of modern Greek populations in relation to neighbouring and historically connected groups. 257 individuals from 19 population groups were analysed using pairwise F_{ST}, PCA, ADMIXTURE, and admixture f_3 statistics. Pairwise genetic differentiation and principal component analysis place the Greek samples within a broader eastern Mediterranean continuum, whereas admixture identifies a predominant ancestry profile alongside components shared across southern Europe, Anatolia and the Levant. Admixture f_3 tests yielded no significantly negative result when Greek was the target. When Greek was included as one source proxy, several target populations produced negative statistics at the conventional $Z < -3$ threshold, and a subset remained significant after correction for multiple testing. Together, these complementary analyses describe modern Greek population structure as layered and regional, shaped by both retained local ancestry and recurrent population interaction.

Keywords: modern Greeks, genetic structure, population admixture, eastern Mediterranean

1. Introduction

The Aegean Basin has long been a key contact zone between southeastern Europe, Anatolia, and the Levant, with Greece acting as a geographic bridge between Europe and the Near East. Its population history has been shaped by movements associated with the Neolithic transition, Bronze Age exchange networks, historical empires, and later migration. Genome-wide studies have also shown that genetic variation within Europe often follows geography, so populations separated by shorter distances tend to show greater genetic similarity than populations from more distant regions [1, 2]. Modern Greek population structure should therefore be considered within a wider geographic continuum rather than as an isolated genetic unit.

Ancient DNA has substantially improved our understanding of the Aegean past. Bronze Age Minoans and Mycenaeans derived at least three quarters of their ancestry from Neolithic populations related to early farmers of western Anatolia and the Aegean, with most of the remaining ancestry related to populations of the Caucasus and Iran. Mycenaeans also carried additional ancestry ultimately related to eastern European hunter-gatherers or steppe-associated groups [3]. Later studies have identified further temporal and regional variation. Genome-wide data from the Aegean palatial

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civilizations showed that gene flow during the Middle Bronze Age contributed to the formation of later Aegean populations [4], while a larger study of individuals from Crete, mainland Greece, and the Aegean islands documented multiple phases of eastern and central/eastern European-related gene flow between the Neolithic and Iron Age [5]. Research across the wider Southern Arc has likewise shown that southeastern Europe and West Asia were connected by repeated, multidirectional population movements rather than a single migration event [6].

These ancient DNA studies provide essential historical context, but they do not remove the need to examine present-day populations directly. Modern genomes reflect both ancient ancestry and subsequent events, including population movement during the Roman and medieval periods [7]. Because modern Greeks occupy the same geographic crossroads, their genomes may preserve echoes of both ancient and more recent interactions with the Balkans, Anatolia, and the Levant. Previous genome-wide research has also identified shared genetic structure across Greece, the southern Balkans, southern Italy, and the eastern Mediterranean [8]. However, the interpretation of modern data requires caution: present-day populations are not unchanged representatives of ancient groups, and similarity in PCA or ADMIXTURE does not by itself demonstrate a specific historical migration.

In this study, we analyzed publicly available genome-wide SNP data from modern Greeks and neighbouring populations. We used pairwise F_{ST}, PCA, ADMIXTURE, and admixture f_3 statistics to address three questions: (1) where Greek samples lie within regional genetic variation; (2) which sampled populations show relatively low or high differentiation from Greeks; and (3) whether the data contain evidence of simple two-source admixture involving populations related to modern Greeks. By combining several complementary summaries, we aimed to provide a clear and reproducible description of modern Greek population structure and to evaluate how geographic continuity, population-specific differentiation, and shared regional ancestry are expressed across the eastern Mediterranean.

2. Materials and methods

2.1. Dataset compilation and population selection

We used publicly available Human Origins-style genome-wide SNP data and metadata distributed through the Allen Ancient DNA Resource (AADR) [9]. Only present-day individuals were included. The final dataset contained 257 individuals assigned to 19 population labels: Greek, Albanian, Bulgarian, Cypriot, Georgian, Egyptian, Assyrian, Turkish, Turkish Balikesir, Turkish Jewish, Sardinian, Italian Sardinian, northern Italian, southern Italian, Sicilian, Syrian, Lebanese, Lebanese Christian, and Lebanese Muslim. These groups were selected to represent southeastern Europe, Anatolia, the Caucasus, the Levant, North Africa, and the central and eastern Mediterranean.

Population labels were taken from the source metadata and were used as analytical groupings. They should not be interpreted as internally homogeneous ethnic or historical populations. Sample sizes also differed among groups, which may influence PCA and model-based clustering results.

2.2. Data filtering and quality control

Quality control was conducted in PLINK v1.9 [10]. SNPs and individuals with more than 5% missing data were excluded. SNPs with Hardy-Weinberg equilibrium $P < 1 \times 10^{-6}$ were removed, and closely related individuals with an estimated relatedness value greater than 0.125 were excluded. Before quality control, the dataset contained 597,573 SNPs and 257 individuals. After the

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missingness and Hardy-Weinberg filters, 584,875 SNPs remained, and all 257 individuals were retained.

Linkage-disequilibrium pruning was performed using a sliding window of 50 SNPs, a step size of 5 SNPs, and an r^2 threshold of 0.2. After restriction to the autosomal sites used for pruning, 131,241 of 580,920 SNPs were retained. The LD-pruned dataset was used for PCA and ADMIXTURE so that groups of highly correlated markers did not dominate the analyses.

2.3. Pairwise F_{ST}

Pairwise F_{ST} was calculated for all 171 pairs of the 19 population labels. F_{ST} summarizes allele-frequency differentiation between populations, with values closer to zero indicating lower differentiation within the analysed marker set [11]. The output included an F_{ST} estimate, standard error, and Z score for each population pair. For visualization, negative point estimates were set to zero because small negative values can arise from sampling variation and do not represent biologically meaningful negative differentiation. The pairwise estimates were arranged in a symmetric matrix and visualized as a heatmap. Average-linkage hierarchical clustering was applied to the rows and columns to summarize similarities among the F_{ST} profiles.

2.4. Principal component analysis

PCA was performed using smartpca in EIGENSOFT v7.2.1 [12]. PCA reduces genome-wide allele-frequency variation to a small number of axes and is widely used to visualize population structure [13, 14]. Default settings were used, with outlier iterations disabled. The PCA displayed in Figure 2 contains all 257 individuals retained after quality control. PC1 and PC2 explained 0.92% and 0.76% of the total variance, respectively. Because the first two components explain only a small fraction of total variation, their interpretation was based on broad clustering patterns rather than strict population boundaries.

2.5. ADMIXTURE analysis

Individual ancestry components were estimated using ADMIXTURE v1.3 [15] with the LD-pruned dataset. Values of K from 2 to 10 were evaluated, where K represents the number of modelled ancestry components. Cross-validation error was used to compare values of K, and K = 8 was selected as the main descriptive result. For visualization, individuals were grouped by population and ordered within each population by similarity across their complete K = 8 ancestry profiles; this display order does not represent time or geography. ADMIXTURE components were treated as statistical patterns within the sampled dataset, not as direct representations of discrete ancient populations. This distinction is important because ADMIXTURE results can change with sample composition, sample size, marker selection, and the chosen value of K [16].

2.6. Admixture f_3 statistics

Admixture f_3 statistics were calculated using ADMIXTOOLS 2 following the framework f_3 (Target; Source 1, Source 2) [17]. A negative statistic with $Z < -3$ is conventionally treated as evidence that the target population is consistent with ancestry from two lineages related to the selected source populations. It does not require the sampled present-day sources to be the actual historical source populations. Because multiple combinations were tested, $Z < -3$ was treated as a nominal threshold; Bonferroni-adjusted significance across all 2,907 tests was also evaluated.

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We first tested all combinations of the form f_3 (Greek; X, Y), with Greek as the target and X and Y drawn from the other sampled populations. We then evaluated statistics of the form f_3 (Target; Greek, Y), in which Greek was one of the two source proxies. In the second analysis, a significantly negative value means that the target is consistent with admixture between a lineage related to the sampled Greeks and a lineage related to Y. It does not, by itself, demonstrate direct or directional gene flow from Greece into the target population.

3. Results

3.1. Pairwise genetic differentiation

The pairwise F_{ST} heatmap showed generally low differentiation across many of the sampled eastern Mediterranean and southern European populations, together with several more distinct comparisons (Figure 1). The highest F_{ST} values involving Greek were observed with Assyrian (F_{ST} = 0.015) and Turkish Balikesir (F_{ST} = 0.014). Greek also showed comparatively higher differentiation from Bulgarian and Cypriot in this dataset (F_{ST} = 0.006 for both comparisons). Lower point estimates were observed between Greek and several Georgian, Turkish, Lebanese, and Turkish Jewish groups (approximately F_{ST} = 0.001). Taken together, these estimates place Greek within a broad zone of low regional differentiation rather than identifying a single nearest neighbouring population.

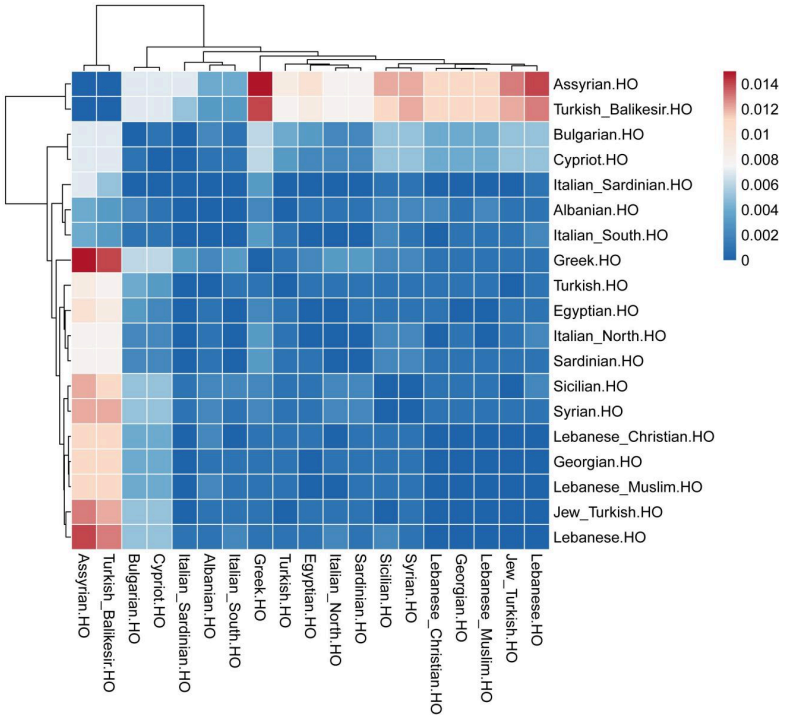


Figure 1. Pairwise F_{ST} among the 19 sampled populations

Across all population pairs, Assyrian and Turkish Balikesir had the highest average F_{ST} relative to the other sampled groups. Their positions in the heatmap set them apart from the broader cluster of populations with lower differentiation. This contrast suggests that regional connectivity was accompanied by population-specific histories, with demographic isolation, local drift, and endogamy as plausible contributors. The concordance between their heatmap positions and their ADMIXTURE

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profiles strengthens the evidence that they represent distinctive structures within the sampled regional landscape.

3.2. Principal component analysis

PCA summarized the major axes of variation among the 257 individuals (Figure 2). The sampled populations formed several partially overlapping clusters rather than completely discrete groups. Greek individuals occupied an intermediate region of the plot relative to southern European, Balkan, Anatolian, and Levantine samples. This pattern is consistent with the broader observation that genetic structure in Europe and the eastern Mediterranean often follows geography [1, 2].

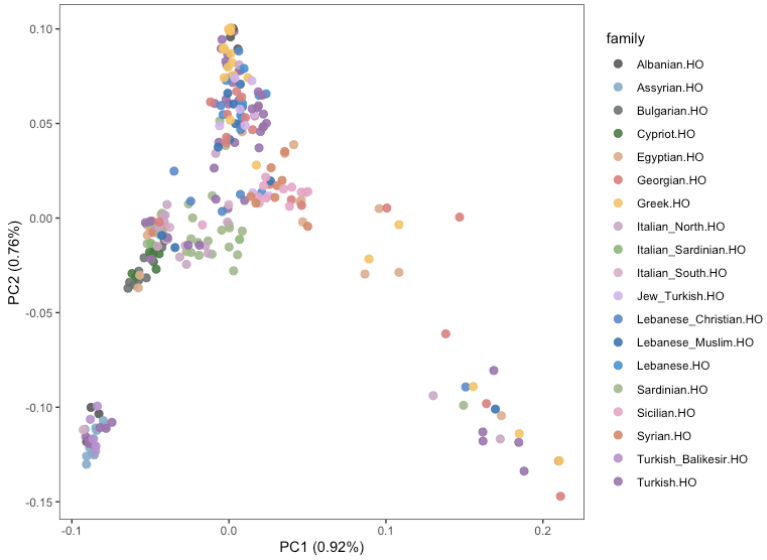


Figure 2. PCA of Greek and neighbouring populations

Some populations formed relatively compact clusters, whereas others showed wider within-group dispersion. Greek samples lay within a partially overlapping distribution that linked southern European and Balkan populations with Anatolian and Levantine groups. This intermediate placement reinforces a broad geographic cline across the Aegean and suggests that Greek population structure reflects both regional continuity and connections to neighbouring populations. PC1 and PC2 captured this main regional axis, while the wider dispersion within several groups points to additional population structure beyond the first two components.

3.3. ADMIXTURE analysis

At K = 8, the individual-level ancestry profiles showed both between-population structure and variation within several population groups (Figure 3). Component C5 was the largest component in 14 of the 20 Greek individuals and accounted for an average of 61.5% of the inferred profile across the Greek samples. Smaller components in the Greek profiles were also present in southern European, Anatolian, and Near Eastern populations. Neighboring populations showed different but overlapping component profiles. Turkish Balikesir and Assyrian samples appeared comparatively homogeneous at this value of K, consistent with their more distinct profiles in the F_{ST} analysis.

The combination of a predominant C5 profile and smaller components shared with surrounding groups gives the Greek samples a layered but coherent ancestry pattern. Similar component sharing

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across southern European, Balkan, Anatolian, and Near Eastern populations is consistent with sustained regional connectivity across the Aegean [14, 18]. In contrast, the comparatively homogeneous profiles of Turkish Balikesir and Assyrian highlight more localized population structure. Thus, the K = 8 model distinguishes a broad zone of shared ancestry from several population-specific profiles, supporting repeated regional interaction alongside retained local ancestry. The components remain model-derived summaries [16], but their comparative distribution is informative about the structure of the sampled populations.

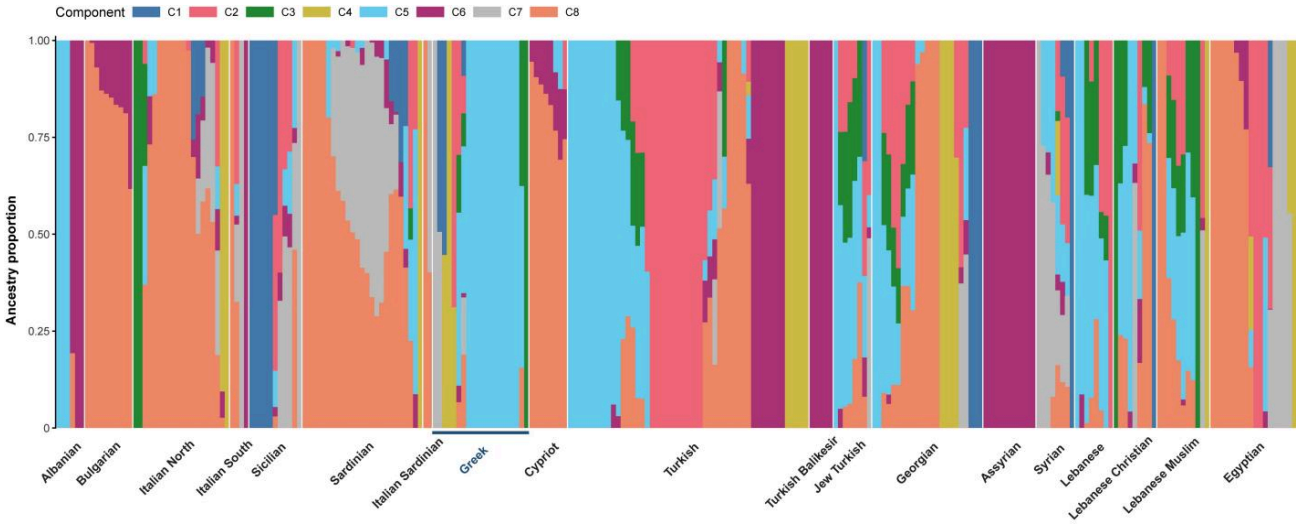


Figure 3. Individual ancestry profiles inferred by ADMIXTURE at K = 8

3.4. Admixture f_3 results

We first tested whether the Greek population could be modelled as an admixed target using f_3 (Greek; X, Y). No tested source pair produced a significantly negative statistic at $Z < -3$. Thus, the analysis did not detect an admixture signal for Greek using the sampled source pairs; this result does not exclude histories involving unsampled or closely related source lineages.

Viewed alongside ancient DNA evidence of multiple ancestry shifts in the Aegean [3-6], the target tests leave open more complex histories involving unsampled or closely related regional sources. This possibility is also compatible with previous evidence of shared regional ancestry [8] and with the descriptive ADMIXTURE pattern, but the non-significant f_3 results alone do not distinguish among these explanations.

We next included Greek as one of the source proxies in tests of the form f_3 (Target; Greek, Y). At the conventional $Z < -3$ threshold, 13 tests produced nominally significant negative statistics. The strongest result involved Egyptian.HO as the target with Greek.HO and Assyrian.HO as source proxies ($Z = -9.19$). Additional nominal signals involved Georgian.HO, Italian_South.HO, Cypriot.HO, Bulgarian.HO, and Turkish_Balikesir.HO as targets (Figure 4). Seven negative results remained significant after Bonferroni correction across the 2,907 tests, involving Egyptian.HO, Georgian.HO, Italian_South.HO, and Cypriot.HO as targets. These statistics indicate that each target is consistent with admixture between lineages related to the sampled Greek population and the alternative source proxy; they do not identify actual historical source populations or the direction of gene flow.

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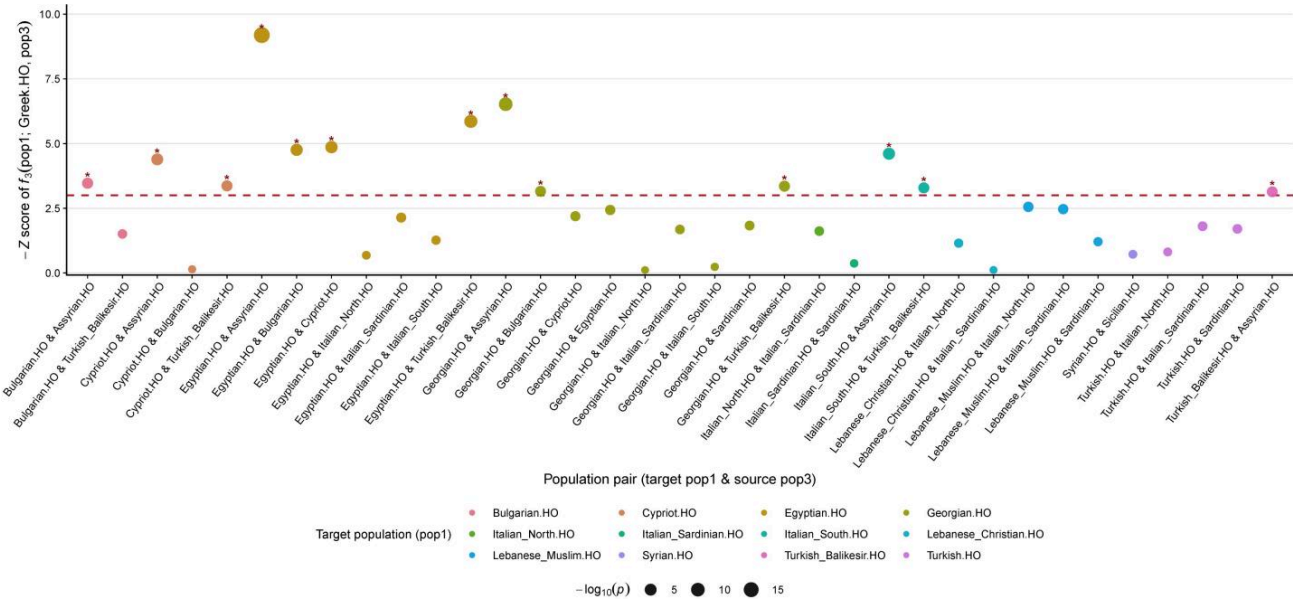


Figure 4. Admixture f_3 statistics with Greek as one source proxy

Earlier genome-wide work described Turkish population structure as heterogeneous and connected to several Eurasian regions [19]. In the present analysis, only one nominally significant source-proxy test had a sampled Turkish group (Turkish_Balikesir.HO) as the target, and it did not remain significant after Bonferroni correction. More broadly, relatively low F_{ST} or PCA proximity alongside different f_3 outcomes shows that genetic similarity and admixture-test results summarize complementary aspects of the data.

4. Discussion

Together, F_{ST}, PCA, ADMIXTURE, and admixture f_3 identify modern Greeks as a distinguishable population that is nevertheless deeply embedded within southeastern European and eastern Mediterranean genetic variation. F_{ST} and PCA reveal a broad regional continuum, ADMIXTURE resolves a predominant Greek profile alongside components shared with neighbouring groups, and f_3 highlights asymmetric mixture signals involving several eastern Mediterranean targets. The convergence of these results supports a history in which local continuity and recurrent regional interaction jointly shaped modern Greek population structure.

The PCA position of the Greek samples follows the geographic structure observed across Europe, where genetic variation often forms clines rather than sharp national boundaries [1, 2]. Their intermediate position across PC1–PC2 is consistent with Greece acting as a bridge across the Aegean. The F_{ST} results add a complementary view: the smallest rounded values involving Greek occurred with several Turkish, Georgian, Lebanese, and Turkish Jewish groups, while the Greek–Cypriot estimate was somewhat higher. Rather than identifying a single nearest population, the combined pattern reveals multiple axes of affinity extending across the Balkans, Anatolia, and the Levant. In this sense, the Aegean emerges as a permeable zone in which geographic continuity and repeated interaction coexist with recognizable population structure.

ADMIXTURE at K = 8 provided a complementary view of this structure. Greek individuals were characterized by a predominant component together with several components shared across neighboring populations, placing them within a broader pattern of eastern Mediterranean genetic variation. This layered profile is consistent with the combined effects of retained local ancestry and

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recurrent interaction across the Aegean [14, 18]. Although ADMIXTURE components are model-dependent and should not be equated directly with ancient populations [16], their distribution highlights both the coherence of the Greek samples and their genetic connections with surrounding southern European, Anatolian, and Near Eastern groups. Together with the PCA and FST results, these findings support a regional history shaped by both continuity and repeated population exchange.

The two f_3 analyses test different target hypotheses and are therefore not contradictory. No f_3(Greek; X, Y) test crossed $Z < -3$, so no admixture signal was detected for Greek using the sampled source pairs. In contrast, several f_3 (Target; Greek, Y) tests were negative, including seven that remained significant after Bonferroni correction. These results show that Greek.HO can represent one lineage in successful two-source tests for several target populations, but they do not establish a Greek-specific ancestral source or the direction of gene flow. Ancient Egyptian genomes also document changes in ancestry composition through time [20], reinforcing the value of interpreting modern source-proxy results within a changing regional context.

Ancient DNA provides a plausible historical context for this complexity. Minoans and Mycenaeans carried substantial ancestry related to Neolithic Aegean and Anatolian farmers, together with ancestry related to the Caucasus and Iran; Mycenaeans also carried additional eastern European- or steppe-related ancestry [3]. Subsequent studies have identified further gene flow during the Bronze Age and regional differences between Crete, mainland Greece, and the Aegean islands [4, 5]. The Southern Arc study demonstrated repeated movements between southeastern Europe and West Asia [6]. Regional population-genetic work has likewise described the Caucasus as an asymmetric semipermeable barrier, with geography shaping different levels of connectivity among the Near East, Anatolia, and the East European plain [21]. Genome-wide data from the first millennium CE also show that later Roman- and medieval-period migrations contributed to present-day Balkan variation [7]. The modern patterns observed here are therefore more likely to reflect several historical layers than one continuous or one-directional process.

The relationship among Greece, Cyprus, southern Italy, and the wider Mediterranean provides an especially informative example of this layered regional history. Previous genome-wide studies have identified shared ancestry across southern Italy, Greek-speaking islands, Albania, and Cyprus [8]. Y-chromosome data further indicate substantial shared pre-Ottoman paternal ancestry between Greek and Turkish Cypriots [22], while palaeogenomic modelling of early Neolithic Cypriots supports mixed Anatolian- and Levantine-related origins for the sampled early settlers [23]. Together, these findings point to a long-lived interaction network linking the Aegean, Cyprus, and southern Italy through Neolithic expansion, Bronze Age connectivity, and later maritime movement. The single Greek.HO label used here probably averages part of this regional variation; geographically detailed Greek sampling could reveal how these ancestry layers differ between mainland and island populations.

The study nevertheless has a defined analytical scope. Population sample sizes were uneven, the Human Origins panel represents a preselected subset of genomic variation, and present-day groups provide imperfect proxies for past populations. PCA, ADMIXTURE, and F_{ST} summarize complementary aspects of structure, while f_3 evaluates a simplified two-source model without estimating the date of admixture. Because ancient individuals were not analysed directly, the results are strongest as a regional description of modern population structure and as a foundation for more explicit historical modelling.

Future work should include more geographically detailed Greek samples, balanced regional reference populations, and directly comparable ancient genomes. Formal methods such as outgroup

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f_3, f_4 statistics, qpAdm, and admixture graphs could test specific ancestry models, while linkage-disequilibrium-based methods could help estimate the timing of more recent admixture [18]. Repeated ADMIXTURE runs and full cross-validation records should also be retained to evaluate model stability. These additions would make it possible to move from a descriptive regional analysis toward better-supported historical hypotheses.

Overall, the results place modern Greeks within a broad southeastern European and eastern Mediterranean genetic continuum while preserving a distinguishable population profile. The predominant ADMIXTURE component, the intermediate PCA position, the generally low regional F_{ST} values, and the pattern of f_3 signals together support a history of local continuity embedded within repeated population exchange. Greece therefore emerges as a genetic crossroads: connected to the Balkans, Anatolia, the Levant, Cyprus, and southern Italy, yet retaining a coherent regional structure of its own. Combining this modern pattern with ancient DNA and explicit demographic modelling will help resolve when and how its different ancestry layers were formed.

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