

## Demogenomic modeling of the timing and the processes of early European farmers differentiation

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## **Abstract:**

The precise genetic origins of the first Neolithic farming populations, as well as the processes and the timing of their differentiation, remain largely unknown. Based on demogenomic modeling of high-quality ancient genomes, we show that the early farmers of Anatolia and Europe emerged from a multiphase mixing of a Near Eastern population with a strongly bottlenecked Western hunter-gatherer population after the Last Glacial Maximum. Moreover, the population branch leading to the first farmers of Europe and Anatolia is characterized by a 2,500-year period of extreme genetic drift during its westward range expansion. Based on these findings, we derive a spatially explicit model of the population history of Southwest Asia and Europe during the late Pleistocene and early Holocene.

## **One-Sentence Summary:**

Early European farmers emerged from multiple post LGM mixtures and experienced extreme drift during their westward expansion.

In recent years, genetic analyses of skeletal remains from early Neolithic farmers have fundamentally enriched our knowledge of the communities that became sedentary and invented food-production (1, 2). Nonetheless, the genetic origins of the first Western Eurasian farmers remain elusive. To date, palaeogenetic findings revealed that early European farmers were genetically distinct from Holocene European hunter-gatherers (HGs) (3, 4), with limited genetic exchange in early phases of the farming expansion, and more intense exchange at later stages (5, 6). Most continental European farmers likely descend from populations inhabiting the Aegean basin (7), but their ultimate genetic origins are still a matter of debate. Whereas early Neolithic Aegeans are clearly connected to Central Anatolians (8), they also show some affinities with Pre-Pottery Neolithic farmers of the southern Levant (9), suggesting a Near Eastern origin of these populations, potentially related to the spread of farming from the Fertile Crescent (10). However, Aegeans are genetically distant from early farmers from the Zagros region, the eastern wing of the Fertile Crescent, which was interpreted as evidence for the adoption of farming by genetically distinct groups of hunter-gatherers in Southwest Asia (11). There is however evidence of genetic continuity between Central Anatolian HGs and early farmers (12), indicating an earlier westwards migration from the Levant. Moreover, some Central Anatolian individuals show genetic affinities to Caucasus HGs as represented by the genome from Kotias in Georgia (10, 13, 14), who are thought to be closely connected to early Iranian Neolithic farmers (9) as well as to steppe populations (15–17).

These paleogenetic findings mostly stem from the interpretation of descriptive and summary statistics (e.g. Principal Component and admixture analyses,  $f$ -statistics), usually computed on low coverage genomes and/or on ascertained sets of SNPs (18) that are difficult to integrate into demogenetic analyses. In fact, previous analyses have estimated divergence times between

ancestors of Neolithic and HG groups (11, 14), but the underlying models were very simplistic. Therefore, we still lack a detailed historical scenario of population demography, divergence and migration that is embedded in a spatially explicit and temporal framework, for the inference of which whole genomes of good sequencing quality are a prerequisite.

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To reconstruct the ancestry of Neolithic populations of Southwest Asia and Europe and the processes that contributed to their differentiation from HGs, we therefore produced high-resolution genomes of early Holocene farmers and HGs (Table 1) arranged along a geographical and temporal transect from the Near East via the Aegean along the Danube to the Rhine (Fig. 1, Fig. S1A).

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## Results

### *Genetic structure and affinities of ancient individuals*

Multidimensional scaling (MDS) performed on the neutral portion of the genome (Fig. 2A) of modern and ancient individuals reveals three main ancient groups: i) a cluster of European HGs, ii) a cluster including an early Neolithic individual (WC1) from Wezmeh Cave in Iran and a Caucasus Mesolithic HG (KK1) from Western Georgia, and iii) a cluster with all other Holocene individuals. Consistent with previous analyses based on ascertained SNPs (4, 19), European and Anatolian Neolithic samples show strongest affinities with modern Sardinians, with the exception of one English (CarsPas1) and two NW Anatolian (Bar8, AKT16) individuals who are found closer to modern individuals from other parts of Southern Europe. In contrast, Palaeolithic and Mesolithic HGs are distinct from all modern Western Eurasians. The Iranian early Neolithic and the Caucasus Mesolithic HG individuals appear closest to modern genomes from Iran and the Caucasus, suggesting some genetic continuity in those regions.

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### ***Demogenomic modeling assumptions***

We first contrasted alternative models of population differentiation using high-resolution ancient genomes that were representative of the three main clusters described above. Sampled individuals from a given cluster were assumed to come from populations belonging to a large structured metapopulation, made up of interconnected but mostly unsampled populations, formally described as a continent-island model (Excoffier 2004; Excoffier et al. 2013). In this framework, the sampled islands receive a single pulse of gene flow from the continent shortly before sampling time. The three metapopulations were called *Western*, *Central* and *Eastern* and model the Western HGs, the Anatolian/Aegean/European early farmers, and the Iranian early farmers, respectively. Additional ancient individuals were then added successively to the initial model to infer their ancestry and various relationships with other individuals (see Supp. Text - Demographic inferences with *fastsimcoal2*). Thus, more complex models were progressively built, resulting in the historical scenario shown in Fig. 3A.

### ***All European and Anatolian farmers share a remote common ancestry with CHGs***

Contrary to previous interpretations (9), we find that Caucasus HGs (represented by KK1) and early European and Anatolian farmers are related, and descend from a population ancestral to the *Central* metapopulation. This ancestral population received about 14% (95% CI 8-26%) of its gene pool from the *Western* metapopulation some 14.2 kya (95% CI 13.7-19.0, Fig. 3A, Fig. S31, Supp. Table 4). The ancestors of the Iranian Neolithic population were not affected by this initial admixture: they diverged from the *Eastern* metapopulation 13.6 kya (95% CI 11-24.6), from which the *Central* metapopulation already split ~15.8 kya (95% CI 14.3-25.6). These analyses thus suggest that even though Caucasus HGs show closer genetic affinities with early Iranian farmers (Fig. 2A-B), they share a common ancestry with all Anatolian and European early farmers.

### ***Ancestors of early Anatolian and Aegean farmers admixed twice with Western HGs***

We find that the ancestors of early Anatolian and Aegean farmers, but not Caucasus HGs, received a second pulse of gene flow (15%, 95% CI 6-17) from the *Western* metapopulation ~12.9 kya (95% CI 9.4-13.9), and all models not including this additional admixture are clearly rejected (Fig. S33, Supp. Table 4). Thus, the ancestors of early European and Anatolian farmers are the product of repeated episodes of gene flow from the *Western* metapopulation, and further diverged from Caucasus HGs due to an intense period of genetic drift between 13 and 9 kya (Fig. 3).

### ***Anatolian and Aegean farmers differentiation***

Aegean populations from NW Anatolia (from the archeological sites of Aktopraklık and Barcın) and Northern Greece (from Nea Nikomedeia) seem to have diverged from each other at about the same time ~9.1-9.3 kya (95% CI 9.1-12) shortly before they were sampled, potentially indicating a spatial diffusion of all Aegean populations around that time. Contrastingly, early farmers from Central Anatolia (represented by a genome from Boncuklu) have diverged earlier ~10.5 kya (95% CI 10.5-11). Furthermore, Anatolian and Aegean populations show varying amounts of recent additional gene flow from the *Western* metapopulation, suggesting different levels of interaction with surrounding HGs. Indeed, genomes from Northern Greece show a lower degree of introgression (3%, 95% CI 1-11) than those from Boncuklu (10%, 95% CI 3-15), Barcın (12%, 95% CI 6-16), and especially Aktopraklık (17%, 95% CI 11-18) (Fig. S33-35-37, Supp. Table 4). The high level of *Western* metapopulation admixture found in Aktopraklık, a site previously described as influenced by both Epipalaeolithic and Neolithic traditions (20), is in line with the admixture analysis (Fig 2B) and *f*-statistics (Fig. S43).

### ***A stepwise, demic expansion of Neolithic farmers into Central Europe***

To better understand the spread of early farmers into Europe, we modelled the genetic differentiation of three early Neolithic populations from Central Serbia, Lower Austria and Southern Germany (Fig. S38). We find that a simple model with a strict stepwise migration of early farmers originating in the wider Aegean region (NW Anatolia or Greece) and extending to Serbia along the Balkans and the so-called Danubian corridor, then to Austria, and eventually Southern Germany, is better supported than a scenario allowing for long-distance migration from the Aegean directly to Lower Austria (Fig. S39A, Supp. Table 4). We also find that early farming communities incorporated a few HG individuals (2-7%, compatible with previous estimates of 3-9% (7, 21, 22)) at each modeled stage of their dispersal along the Danubian corridor. Scenarios without *Western* metapopulation introgression into early farmer populations are rejected. Even though we modelled this introgression from the *Western* metapopulation, closely related to the Danube Gorges Mesolithic individuals from Vlasac, we cannot exclude that it actually occurred from other Western European HGs like those related to Loschbour and Bichon (Fig. 4H), since previous work suggested that different Mesolithic backgrounds could have introgressed into early farmer gene pools in different regions (21).

### ***An LGM divergence between Eastern and Western metapopulations***

Our model also provides novel insights on the deep branching of pre-Neolithic populations. The divergence between the ancestors of the *Western* and *Eastern* metapopulations is estimated to date back to the LGM ~25.6 kya (95% CI 17.3-31.3). This is much younger than the previously inferred divergence time between the ancestors of Iranian and Aegean early farmers (46-77 kya) (11) or between European early farmers and Western European HGs (27-76 kya) (14), which were both obtained under a simple model with constant population sizes and no admixture. We would get



older divergence times (27-37 kya) between the ancestors of these two HG groups if we also used models without population size changes, but the fit to the data would be worse (Fig. S31A). Comparing two Western European HGs from the sites of Bichon and Loschbour to our newly-sequenced Mesolithic individuals from the Danube Gorges reveals that they already split during the LGM ~22.8 kya (95% CI 16.8-24.7) (Fig. S41, Supp. Table 4), and that Bichon and Loschbour populations diverged from each other approximately a thousand years later.

***The reduced diversity in European hunter-gatherers is due to a massive LGM bottleneck***

Genetic diversity as quantified by the heterozygosity at neutral sites is much lower in HGs than in early farmers, with the exception of NW Anatolians (Fig. 2C), in agreement with previous results (10, 23). Furthermore, HG genomes also show a generally larger proportion of short runs of homozygosity (2-10Mb ROHs, Fig. 2D, Fig. S20A) (24) indicative of remote inbreeding within European HGs and thought to be due to their small population size (25), in line with *MSMC2* analyses (Fig. S25). However, we estimate HG effective population sizes to actually be larger than those of most early farmers (Fig. 3A), particularly those from Anatolia (Bon002, AKT16 and Bar25) which show small effective population sizes in the order of a few hundred individuals in agreement with their relatively high proportion of short ROHs. The lower diversity observed among European HGs thus seems rather due to a very strong LGM bottleneck, which we estimate equivalent to a single human couple for one generation, or 20 individuals for 10 generations (Fig. 3A, Fig. S31, Supp. Table 4).

## Discussion

### *Evolutionary insights gained from explicit demographic modeling*

Our sequencing of ancient genomes at >10X, which triples the number of high quality whole genomes available for early Holocene in Europe, has allowed us to perform genetic analyses on an unbiased set of markers minimally impacted by selection, and thus ideally suited for reconstructing the population history of Western Eurasia from the Late Pleistocene to the Early Holocene. In addition to confirming some previous interpretations, our modeling provides several new insights about the demographic processes preceding and underlying the Neolithic transition and spread.

First, we found that European HGs had already split into two Western and Central subgroups ~23 kya, and passed through a very severe LGM-driven bottleneck that is responsible for their low level of genetic diversity (Fig. 2C). Contrary to previous interpretations (25, 31), HGs are generally found to have larger population sizes than contemporary early farmer populations (Fig. 3A) which explains why they show close genetic affinities on the MDS (Fig. 2A) despite long divergence times and a wide geographic distribution. Conversely, it suggests that the Neolithic transition was linked to a reduction in local effective population sizes, potentially due to sedentarization (32) and restricted gene flow.

Second, we have evidenced that HGs from the Caucasus are phylogenetically related to the ancestors of early farmers from Europe and Anatolia as both show the traces of an ancestral admixture event between the *Western* and *Eastern* metapopulations (Figs. 2A-B). Despite this historical proximity, our model still predicts the observed affinity of the Caucasus HG genome to the Iranian Neolithic farmer (compare Fig. 2B and Fig. S42, as well as Fig. 2A and 3B).

Third, we can show how specific demographic processes affected the genetic divergence of past populations. Genomic data simulated under the final demographic scenario leads to population

relationships very similar to those observed on an MDS (compare Fig. 2A and 3B) and a simplified admixture graph (18) compatible with all  $f$ -statistics calculated on the real data (Fig. S45-46), both providing an *a posteriori* validation of our model-based approach. By simulating additional genomes from unsampled populations or timepoints (Fig. 3), we further predict that the population ancestral to all sampled individuals was genetically close to ancestors of Iranian early farmers and 5 Caucasus HGs; European HGs then considerably drifted after their LGM bottleneck, explaining their outlier position on the MDS. The ancestors of European and Anatolian early farmers, however, were first brought towards the center of the MDS by two consecutive admixture events with the *Western* metapopulation, and then pushed orthogonally towards the upper right by >2,500 10 years of intense genetic drift, possibly due to recurrent founder effects during their dispersal through Anatolia. Even though European and Anatolian early farmers were previously recognized to be genetically intermediate between other Near Eastern groups (12), or considered to be a mixture of other ancient populations (6), this initial admixture signal remained hidden to previous approaches as it was eroded by later genetic drift (Fig. S42): Whereas populations simulated 15 shortly after the two main admixture events with the *Western* metapopulation indeed appear as admixed (i.e. MetaCentral (489g), Aegeans (445g) on Fig. 3B), this signal progressively disappears through time, and these populations eventually look like having a completely independent gene pool (e.g. in the admixture analyses of Fig. S42). Their more central position on the MDS later on is then due to admixture with the *Western* metapopulation and surrounding 20 farmers modeled as the *Central* metapopulation.

### ***A spatially explicit scenario of population differentiation***

Even though our demogenomic model (Fig. 3A) can explain observed population affinities, we are aware that it has temporal and geographical gaps that will only be filled by gathering further genomic data. In particular, high quality samples from the Northern and Southern Levant as well as representatives of Eastern HGs are needed to complete and confirm our conclusions.

Nonetheless, the timing and sequence of demographic events that emerge from our analyses suggest a spatially explicit scenario of population differentiation during the LGM and early Holocene (Fig. 4). Under this scenario, the very strong bottleneck in the population ancestral to European HGs that occurred after their divergence from the *Eastern* metapopulation was probably due to a contraction into a small LGM refugium, potentially located in milder Western Mediterranean coastal regions (Fig. 4B). It was followed by a rapid differentiation of these HGs in two separate refugia (Fig. 4C), corresponding to what archaeologists identified as the areas of distribution of Solutrean and Epigravettian lithic traditions in Europe (26, 27).

Following a period of range expansion after the LGM (Fig. 4D), representatives of the *Central* metapopulation, likely descendants of the Epigravettian refugial population, mixed ~14.2 kya with the population ancestral to both Caucasus HGs and Anatolian/Aegean early farmers. Given the former geographical distribution of the glacial refugia, this admixture likely happened during the Bölling interstadial period in a region encompassing Southeastern Anatolia and the Northern Levant or even in neighboring regions such as Central and Eastern Anatolia or the Turkish South coast (Fig. 4E).

The subsequent demographic processes explaining the differentiation between Central Anatolian and Aegean farmers are more difficult to pinpoint and locate. The inferred low population size of the ancestors of Anatolian/Aegean farmers after their split from Caucasus HGs during the Older Dryas (~12.9 kya; Figs. 3A and 4F) could be due to a westward range expansion and associated

recurrent founder effects during the Allerød interstadial, a period with relatively favorable climatic conditions during which they would have also further admixed with Epipalaeolithic HGs in Anatolia (Fig. 4G). The fact that early farmers from Central Anatolia share the same admixture event and drift with Aegean farmers suggests they were part of the same expansion wave. However, their close genetic proximity with Epipalaeolithic Central Anatolian foragers (12) questions this scenario and rather indicate that admixed groups existed in Central Anatolia in pre-Neolithic times, or had moved there from the Fertile Crescent, adopting fully developed farming practices at a later stage. Indeed, early aceramic sites like Boncuklu and Aşıklı on the Anatolian Plateau show experiments in crop cultivation and caprine management ~9.7 kya (28, 29).

In contrast, the migration to NW Anatolia (Fig. 4H) likely occurred at the time of the fully developed ceramic Neolithic characterized by the establishment of widespread mixed farming (30). Further support for such a demic diffusion scenario to NW Anatolia by a direct (coastal) route and not via the Konya plain region comes from  $f$ -statistics showing Levantine populations sharing more drift with Aegeans than with Central Anatolian Neolithic individuals (Fig. S48). This signal could either be due to i) some long distance gene flow between the Aegeans and a Levant-like population, ii) a higher level of *Western* metapopulation admixture observed in Boncuklu (Fig. S47), or iii) an early migration of the Boncuklu ancestors from the Fertile Crescent to Central Anatolia, combined with some later gene flow between people from the Fertile Crescent and the ancestors of Aegeans. However,  $f$ -statistics analyses reveal that early farmers from the Aegean are rather heterogeneous in their levels of shared drift with several populations, including Levantine HGs and early Iranian farmers (Fig. S49), suggesting that the Neolithization of the Aegean was a more complex process. Nonetheless, our results imply that even though the initial spread of the Neolithic must have been through cultural diffusion in the Fertile Crescent among genetically

already well differentiated groups, its extension to other parts of Anatolia and along the Danubian corridor occurred through demic diffusion processes (Fig. 4H).

In sum, our population modelling allowed us to extract novel, unexpected, but complementary and far more detailed information on population affinities than what one could conclude from summary statistics or multivariate analysis alone. In addition, it provides a time frame for the differentiation of the major groups populating SW Asia and Europe from the LGM until the introduction of agriculture, and highlights the crucial role of climatic changes in promoting population fragmentation and secondary contacts (33).

## References and Notes

1. J. Peters, A. von den Driesch, D. Helmer, M. Saña Seguí, Early Animal Husbandry in the Northern Levant. *Paléorient*. **25**, 27–48 (1999).
2. D. Q. Fuller, G. Willcox, R. G. Allaby, Cultivation and domestication had multiple origins: arguments against the core area hypothesis for the origins of agriculture in the Near East. *World Archaeol.* **43**, 628–652 (2011).
3. B. Bramanti, M. G. Thomas, W. Haak, M. Unterlaender, P. Jores, K. Tambets, I. Antanaitis-Jacobs, M. N. Haidle, R. Jankauskas, C.-J. Kind, F. Lueth, T. Terberger, J. Hiller, S. Matsumura, P. Forster, J. Burger, Genetic discontinuity between local hunter-gatherers and central Europe's first farmers. *Science*. **326**, 137–140 (2009).
4. P. Skoglund, H. Malmström, M. Raghavan, J. Storå, P. Hall, E. Willerslev, M. T. P. Gilbert, A. Götherström, M. Jakobsson, Origins and genetic legacy of Neolithic farmers and hunter-gatherers in Europe. *Science*. **336**, 466–469 (2012).
5. I. Mathieson, I. Lazaridis, N. Rohland, S. Mallick, N. Patterson, S. A. Roodenberg, E. Harney, K. Stewardson, D. Fernandes, M. Novak, K. Sirak, C. Gamba, E. R. Jones, B. Llamas, S. Dryomov, J. Pickrell, J. L. Arsuaga, J. M. B. de Castro, E. Carbonell, F. Gerritsen, A. Khokhlov, P. Kuznetsov, M. Lozano, H. Meller, O. Mochalov, V. Moiseyev, M. A. Rojo Guerra, J. Roodenberg, J. M. Vergès, J. Krause, A. Cooper, K. W. Alt, D. Brown, D.

- Anthony, C. Lalueza-Fox, W. Haak, R. Pinhasi, D. Reich, Genome-wide patterns of selection in 230 ancient Eurasians. *Nature*. **528**, 499–503 (2015).
6. I. Lazaridis, N. Patterson, A. Mittnik, G. Renaud, S. Mallick, K. Kirsanow, P. H. Sudmant, J. G. Schraiber, S. Castellano, M. Lipson, B. Berger, C. Economou, R. Bollongino, Q. Fu, K. I. Bos, S. Nordenfelt, H. Li, C. de Filippo, K. Prüfer, S. Sawyer, C. Posth, W. Haak, F. Hallgren, E. Fornander, N. Rohland, D. Delsate, M. Francken, 5 J.-M. Guinet, J. Wahl, G. Ayodo, H. A. Babiker, G. Bailliet, E. Balanovska, O. Balanovsky, R. Barrantes, G. Bedoya, H. Ben-Ami, J. Bene, F. Berrada, C. M. Bravi, F. Brisighelli, G. B. J. Busby, F. Cali, M. Churnosov, D. E. C. Cole, D. Corach, L. Damba, G. van Driem, S. Dryomov, J.-M. Dugoujon, S. A. Fedorova, I. Gallego Romero, M. Gubina, M. Hammer, B. M. Henn, T. Hervig, U. Hodoglugil, A. R. Jha, S. Karachanak-Yankova, R. Khusainova, E. Khusnutdinova, R. Kittles, T. Kivisild, W. Klitz, V. Kučinskas, A. Kushniarevich, L. Laredj, S. Litvinov, T. Loukidis, R. W. Mahley, B. Melegh, E. Metspalu, J. Molina, J. Mountain, K. Näkkäläjärvi, D. Nesheva, T. Nyambo, 10 L. Osipova, J. Parik, F. Platonov, O. Posukh, V. Romano, F. Rothhammer, I. Rudan, R. Ruizbakiev, H. Sahakyan, A. Sajantila, A. Salas, E. B. Starikovskaya, A. Tarekegn, D. Toncheva, S. Turdikulova, I. Uktveryte, O. Utevska, R. Vasquez, M. Villena, M. Voevoda, C. A. Winkler, L. Yepiskoposyan, P. Zalloua, T. Zemunik, A. Cooper, C. Capelli, M. G. Thomas, A. Ruiz-Linares, S. A. Tishkoff, L. Singh, K. Thangaraj, R. Villems, D. Comas, R. Sukernik, M. Metspalu, M. Meyer, E. E. Eichler, J. Burger, M. Slatkin, S. Pääbo, J. Kelso, D. Reich, J. Krause, Ancient human genomes suggest three ancestral populations for present-day Europeans. *Nature*. **513**, 409–413 (2014).
7. Z. Hofmanová, S. Kreutzer, G. Hellenthal, C. Sell, Y. Diekmann, D. Díez-Del-Molino, L. van Dorp, S. López, A. Kousathanas, V. Link, K. Kirsanow, L. M. Cassidy, R. Martiniano, M. Strobel, A. Scheu, K. Kotsakis, P. Halstead, 20 S. Triantaphyllou, N. Kyriasi-Apostolika, D. Urem-Kotsou, C. Ziota, F. Adaktylou, S. Gopalan, D. M. Bobo, L. Winkelbach, J. Blöcher, M. Unterländer, C. Leuenberger, Ç. Çilingiroğlu, B. Horejs, F. Gerritsen, S. J. Shennan, D. G. Bradley, M. Currat, K. R. Veeramah, D. Wegmann, M. G. Thomas, C. Papageorgopoulou, J. Burger, Early farmers from across Europe directly descended from Neolithic Aegeans. *Proc. Natl. Acad. Sci. U. S. A.* **113**, 6886– 25 6891 (2016).
8. G. M. Kılınç, D. Koptekin, Ç. Atakuman, A. P. Sümer, H. M. Dönertaş, R. Yaka, C. C. Bilgin, A. M. Büyükkarakaya, D. Baird, E. Altınışik, P. Flegontov, A. Götherström, İ. Togan, M. Somel, Archaeogenomic analysis of the first steps of Neolithization in Anatolia and the Aegean. *Proc. Biol. Sci.* **284** (2017), doi:10.1098/rspb.2017.2064.

9. I. Lazaridis, D. Nadel, G. Rollefson, D. C. Merrett, N. Rohland, S. Mallick, D. Fernandes, M. Novak, B. Gamarra, K. Sirak, S. Connell, K. Stewardson, E. Harney, Q. Fu, G. Gonzalez-Fortes, E. R. Jones, S. A. Roodenberg, G. Lengyel, F. Bocquentin, B. Gasparian, J. M. Monge, M. Gregg, V. Eshed, A.-S. Mizrahi, C. Meiklejohn, F. Gerritsen, L. Bejenaru, M. Blüher, A. Campbell, G. Cavalleri, D. Comas, P. Froguel, E. Gilbert, S. M. Kerr, P. Kovacs, J. Krause, D. McGettigan, M. Merrigan, D. A. Merriwether, S. O'Reilly, M. B. Richards, O. Semino, M. Shamooun-Pour, G. Stefanescu, M. Stumvoll, A. Tönjes, A. Torroni, J. F. Wilson, L. Yengo, N. A. Hovhannisyian, N. Patterson, R. Pinhasi, D. Reich, Genomic insights into the origin of farming in the ancient Near East. *Nature*. **536**, 419–424 (2016).
10. G. M. Kılınc, A. Omrak, F. Özer, T. Günther, A. M. Büyükkarakaya, E. Bıçakçı, D. Baird, H. M. Dönertaş, A. Ghalichi, R. Yaka, D. Koptekin, S. C. Açıkan, P. Parvizi, M. Krzewińska, E. A. Daskalaki, E. Yüncü, N. D. Dağtaş, A. Fairbairn, J. Pearson, G. Mustafaoğlu, Y. S. Erdal, Y. G. Çakan, İ. Togan, M. Somel, J. Storå, M. Jakobsson, A. Götherström, The Demographic Development of the First Farmers in Anatolia. *Curr. Biol.* **26**, 2659–2666 (2016).
11. F. Broushaki, M. G. Thomas, V. Link, S. López, L. van Dorp, K. Kirsanow, Z. Hofmanová, Y. Diekmann, L. M. Cassidy, D. Díez-del-Molino, A. Kousathanas, C. Sell, H. K. Robson, R. Martiniano, J. Blöcher, A. Scheu, S. Kreutzer, R. Bollongino, D. Bobo, H. Davoudi, O. Munoz, M. Currat, K. Abdi, F. Biglari, O. E. Craig, D. G. Bradley, S. Shennan, K. R. Veeramah, M. Mashkour, D. Wegmann, G. Hellenthal, J. Burger, Early Neolithic genomes from the eastern Fertile Crescent. *Science*. **353**, 499–503 (2016).
12. M. Feldman, E. Fernández-Domínguez, L. Reynolds, D. Baird, J. Pearson, I. Hershkovitz, H. May, N. Goring-Morris, M. Benz, J. Gresky, R. A. Bianco, A. Fairbairn, G. Mustafaoğlu, P. W. Stockhammer, C. Posth, W. Haak, C. Jeong, J. Krause, Late Pleistocene human genome suggests a local origin for the first farmers of central Anatolia. *Nat. Commun.* **10**, 1218 (2019).
13. E. Skourtanioti, Y. S. Erdal, M. Frangipane, F. Balossi Restelli, K. A. Yener, F. Pinnock, P. Matthiae, R. Özbal, U.-D. Schoop, F. Guliyev, T. Akhundov, B. Lyonnet, E. L. Hammer, S. E. Nugent, M. Burri, G. U. Neumann, S. Penske, T. Ingman, M. Akar, R. Shafiq, G. Palumbi, S. Eisenmann, M. D'Andrea, A. B. Rohrlach, C. Warinner, C. Jeong, P. W. Stockhammer, W. Haak, J. Krause, Genomic History of Neolithic to Bronze Age Anatolia, Northern Levant, and Southern Caucasus. *Cell*. **181**, 1158–1175.e28 (2020).
14. E. R. Jones, G. Gonzalez-Fortes, S. Connell, V. Siska, A. Eriksson, R. Martiniano, R. L. McLaughlin, M. Gallego Llorente, L. M. Cassidy, C. Gamba, T. Meshveliani, O. Bar-Yosef, W. Müller, A. Belfer-Cohen, Z. Matskevich, N.



- Jakeli, T. F. G. Higham, M. Currat, D. Lordkipanidze, M. Hofreiter, A. Manica, R. Pinhasi, D. G. Bradley, Upper Palaeolithic genomes reveal deep roots of modern Eurasians. *Nat. Commun.* **6**, 1–8 (2015).
15. I. Lazaridis, The evolutionary history of human populations in Europe. *Curr. Opin. Genet. Dev.* **53**, 21–27 (2018).
16. I. Mathieson, S. Alpaslan-Roodenberg, C. Posth, A. Szécsényi-Nagy, N. Rohland, S. Mallick, I. Olalde, N. Broomandkhoshbacht, F. Candilio, O. Cheronet, D. Fernandes, M. Ferry, B. Gamarra, G. G. Fortes, W. Haak, E. Harney, E. Jones, D. Keating, B. Krause-Kyora, I. Kucukkalipci, M. Michel, A. Mittnik, K. Nägele, M. Novak, J. Oppenheimer, N. Patterson, S. Pfrengle, K. Sirak, K. Stewardson, S. Vai, S. Alexandrov, K. W. Alt, R. Andreescu, D. Antonović, A. Ash, N. Atanassova, K. Bacvarov, M. B. Gusztáv, H. Bocherens, M. Bolus, A. Boroneanț, Y. Boyadzhiev, A. Budnik, J. Burmaz, S. Chohadzhiev, N. J. Conard, R. Cottiaux, M. Čuka, C. Cupillard, D. G. Drucker, N. Elenski, M. Francken, B. Galabova, G. Ganetsovski, B. Gély, T. Hajdu, V. Handzhyiska, K. Harvati, T. Higham, S. Iliev, I. Janković, I. Karavanić, D. J. Kennett, D. Komšo, A. Kozak, D. Labuda, M. Lari, C. Lazar, M. Leppek, K. Leshtakov, D. L. Vetro, D. Los, I. Lozanov, M. Malina, F. Martini, K. McSweeney, H. Meller, M. Mendušić, P. Mirea, V. Moiseyev, V. Petrova, T. D. Price, A. Simalcsik, L. Sineo, M. Šlaus, V. Slavchev, P. Stanev, A. Starović, T. Szeniczey, S. Talamo, M. Teschler-Nicola, C. Thevenet, I. Valchev, F. Valentin, S. Vasilyev, F. Veljanovska, S. Venelinova, E. Veselovskaya, B. Viola, C. Virag, J. Zaninović, S. Zäuner, P. W. Stockhammer, G. Catalano, R. Krauß, D. Caramelli, G. Zariņa, B. Gaydarska, M. Lillie, A. G. Nikitin, I. Potekhina, A. Papathanasiou, D. Borić, C. Bonsall, J. Krause, R. Pinhasi, D. Reich, The genomic history of southeastern Europe. *Nature*. **555**, 197–203 (2018).
17. V. M. Narasimhan, N. Patterson, P. Moorjani, N. Rohland, R. Bernardos, S. Mallick, I. Lazaridis, N. Nakatsuka, I. Olalde, M. Lipson, A. M. Kim, L. M. Olivieri, A. Coppa, M. Vidale, J. Mallory, V. Moiseyev, E. Kitov, J. Monge, N. Adamski, N. Alex, N. Broomandkhoshbacht, F. Candilio, K. Callan, O. Cheronet, B. J. Culleton, M. Ferry, D. Fernandes, S. Freilich, B. Gamarra, D. Gaudio, M. Hajdinjak, É. Harney, T. K. Harper, D. Keating, A. M. Lawson, M. Mah, K. Mandl, M. Michel, M. Novak, J. Oppenheimer, N. Rai, K. Sirak, V. Slon, K. Stewardson, F. Zalzala, Z. Zhang, G. Akhatov, A. N. Bagashev, A. Bagnera, B. Baitanayev, J. Bendezu-Sarmiento, A. A. Bissembaev, G. L. Bonora, T. T. Charginov, T. Chikisheva, P. K. Dashkovskiy, A. Derevianko, M. Dobeš, K. Douka, N. Dubova, M. N. Duisengali, D. Enshin, A. Epimakhov, A. V. Fribus, D. Fuller, A. Goryachev, A. Gromov, S. P. Grushin, B. Hanks, M. Judd, E. Kazizov, A. Khokhlov, A. P. Krygin, E. Kupriyanova, P. Kuznetsov, D. Luiselli, F. Maksudov, A. M. Mamedov, T. B. Mamirov, C. Meiklejohn, D. C. Merrett, R. Micheli, O. Mochalov, S. Mustafokulov, A. Nayak, D. Pettener, R. Potts, D. Razhev, M. Rykun, S. Sarno, T. M. Savenkova, K. Sikhymbaeva, S. M.

- Slepchenko, O. A. Soltobaev, N. Stepanova, S. Svyatko, K. Tabaldiev, M. Teschler-Nicola, A. A. Tishkin, V. V. Tkachev, S. Vasilyev, P. Velemínský, D. Voyakin, A. Yermolayeva, M. Zahir, V. S. Zubkov, A. Zubova, V. S. Shinde, C. Lalueza-Fox, M. Meyer, D. Anthony, N. Boivin, K. Thangaraj, D. J. Kennett, M. Frachetti, R. Pinhasi, D. Reich, The formation of human populations in South and Central Asia. *Science*. **365** (2019),  
5 doi:10.1126/science.aat7487.
18. N. Patterson, P. Moorjani, Y. Luo, S. Mallick, N. Rohland, Y. Zhan, T. Genschoreck, T. Webster, D. Reich, Ancient admixture in human history. *Genetics*. **192**, 1065–1093 (2012).
19. J. H. Marcus, C. Posth, H. Ringbauer, L. Lai, R. Skeates, C. Sidore, J. Beckett, A. Furtwängler, A. Olivieri, C. W. K. Chiang, H. Al-Asadi, K. Dey, T. A. Joseph, C.-C. Liu, C. Der Sarkissian, R. Radzevičiūtė, M. Michel, M. G.  
10 Gradoli, P. Marongiu, S. Rubino, V. Mazzarello, D. Rovina, A. La Fragola, R. M. Serra, P. Bandiera, R. Bianucci, E. Pompianu, C. Murgia, M. Guirguis, R. P. Orquin, N. Tuross, P. van Dommelen, W. Haak, D. Reich, D. Schlessinger, F. Cucca, J. Krause, J. Novembre, Genetic history from the Middle Neolithic to present on the Mediterranean island of Sardinia. *Nat. Commun.* **11**, 939 (2020).
20. M. Özdoğan, Archaeological Evidence on the Westward Expansion of Farming Communities from Eastern Anatolia  
15 to the Aegean and the Balkans. *Current Anthropology*. **52**, S415–S430 (2011).
21. M. Lipson, A. Szécsényi-Nagy, S. Mallick, A. Pósa, B. Stégmár, V. Keerl, N. Rohland, K. Stewardson, M. Ferry, M. Michel, J. Oppenheimer, N. Broomandkoshbacht, E. Harney, S. Nordenfelt, B. Llamas, B. Gusztáv Mende, K. Köhler, K. Oross, M. Bondár, T. Marton, A. Osztás, J. Jakucs, T. Paluch, F. Horváth, P. Csengeri, J. Koós, K. Sebők, A. Anders, P. Raczky, J. Regenye, J. P. Barna, S. Fábíán, G. Serlegi, Z. Toldi, E. Gyöngyvér Nagy, J. Dani,  
20 E. Molnár, G. Pálfi, L. Márk, B. Meleg, Z. Bánfai, L. Domboróczki, J. Fernández-Eraso, J. Antonio Mujika-Alustiza, C. Alonso Fernández, J. Jiménez Echevarría, R. Bollongino, J. Orschiedt, K. Schierhold, H. Meller, A. Cooper, J. Burger, E. Bánffy, K. W. Alt, C. Lalueza-Fox, W. Haak, D. Reich, Parallel palaeogenomic transects reveal complex genetic history of early European farmers. *Nature*. **551**, 368–372 (2017).
22. A. G. Nikitin, P. Stadler, N. Kotova, M. Teschler-Nicola, T. D. Price, J. Hoover, D. J. Kennett, I. Lazaridis, N.  
25 Rohland, M. Lipson, D. Reich, Interactions between earliest Linearbandkeramik farmers and central European hunter gatherers at the dawn of European Neolithization. *Sci. Rep.* **9**, 19544 (2019).
23. A. Kousathanas, C. Leuenberger, V. Link, C. Sell, J. Burger, D. Wegmann, Inferring Heterozygosity from Ancient and Low Coverage Genomes. *Genetics*. **205**, 317–332 (2017).

24. H. Ringbauer, J. Novembre, M. Steinrücken, Parental relatedness through time revealed by runs of homozygosity in ancient DNA. *Nat. Commun.* **12**, 5425 (2021).
25. F. C. Ceballos, K. Gürün, N. E. Altınışık, H. C. Gemici, C. Karamurat, D. Koptekin, K. B. Vural, I. Mapelli, E. Sağlıkcan, E. Süreç, Y. S. Erdal, A. Götherström, F. Özer, Ç. Atakuman, M. Somel, Human inbreeding has decreased in time through the Holocene. *Curr. Biol.* **31**, 3925–3934.e8 (2021).
26. T. Günther, H. Malmström, E. M. Svensson, A. Omrak, F. Sánchez-Quinto, G. M. Kılınc, M. Krzewińska, G. Eriksson, M. Fraser, H. Edlund, A. R. Munters, A. Coutinho, L. G. Simões, M. Vicente, A. Sjölander, B. Jansen Sellevold, R. Jørgensen, P. Claes, M. D. Shriver, C. Valdiosera, M. G. Netea, J. Apel, K. Lidén, B. Skar, J. Storå, A. Götherström, M. Jakobsson, Population genomics of Mesolithic Scandinavia: Investigating early postglacial migration routes and high-latitude adaptation. *PLoS Biol.* **16**, e2003703 (2018).
27. C. Aimé, G. Laval, E. Patin, P. Verdu, L. Ségurel, R. Chaix, T. Hegay, L. Quintana-Murci, E. Heyer, F. Austerlitz, Human genetic data reveal contrasting demographic patterns between sedentary and nomadic populations that predate the emergence of farming. *Mol. Biol. Evol.* **30**, 2629–2644 (2013).
28. J. K. Kozłowski, M. Kaczanowska, Gravettian/Epigravettian sequences in the Balkans and Anatolia. *Mediterranean Archaeology and Archaeometry.* **4**, 5–18 (2004).
29. A. Maier, Ed., *The Central European Magdalenian: Regional Diversity and Internal Variability* (Springer, Dordrecht, 2015; <https://link.springer.com/10.1007/978-94-017-7206-8>).
30. H. Buitenhuis, J. Peters, N. Pöllath, M. C. Stiner, N. D. Munro, Ö. Saritaş, in *The Early Settlement at Aşıklı Höyük. Essays in Honor of Ufuk Esin*, M. Özbaşaran, G. Duru, M. Stiner, Eds. (Yayınları, İstanbul, 2018), pp. 281–324.
31. M. Ergun, M. Tengberg, G. Willcox, C. Douché, in *The Early Settlement at Aşıklı Höyük. Essays in Honor of Ufuk Esin*, M. Özbaşaran, G. Duru, M. Stiner, Eds. (Yayınları, İstanbul, 2018), pp. 191–217.
32. A. Bogaard, D. Filipović, A. Fairbairn, L. Green, E. Stroud, D. Fuller, M. Charles, Agricultural innovation and resilience in a long-lived early farming community: the 1,500-year sequence at Neolithic to early Chalcolithic Çatalhöyük, central Anatolia. *Anatolian Studies.* **67** (2017), pp. 1–28.
33. M. M. Lahr, R. A. Foley, Towards a theory of modern human origins: geography, demography, and diversity in recent human evolution. *Am. J. Phys. Anthropol.* **Suppl**, 137–176 (1998).
34. R. Bollongino, O. Nehlich, M. P. Richards, J. Orschiedt, M. G. Thomas, C. Sell, Z. Fajkosová, A. Powell, J. Burger, 2000 years of parallel societies in Stone Age Central Europe. *Science.* **342**, 479–481 (2013).

35. A. Scheu, A. Powell, R. Bollongino, J.-D. Vigne, A. Tresset, C. Çakırlar, N. Benecke, J. Burger, The genetic prehistory of domesticated cattle from their origin to the spread across Europe. *BMC Genet.* **16**, 54 (2015).
36. D. Y. Yang, B. Eng, J. S. Wayne, J. C. Dудар, S. R. Saunders, Improved DNA extraction from ancient bones using silica-based spin columns. *American Journal of Physical Anthropology: The Official Publication of the American Association of Physical Anthropologists.* **105**, 539–543 (1998).
- 5
37. D. E. MacHugh, C. J. Edwards, J. F. Bailey, D. R. Bancroft, D. G. Bradley, The extraction and analysis of ancient DNA from bone and teeth: a survey of current methodologies. *Anc. Biomol.* **3**, 81–102 (2000).
38. C. Gamba, E. R. Jones, M. D. Teasdale, R. L. McLaughlin, G. Gonzalez-Fortes, V. Mattiangeli, L. Domboróczki, I. Kővári, I. Pap, A. Anders, A. Whittle, J. Dani, P. Raczky, T. F. G. Higham, M. Hofreiter, D. G. Bradley, R. Pinhasi, Genome flux and stasis in a five millennium transect of European prehistory. *Nat. Commun.* **5**, 5257 (2014).
- 10
39. M. Kircher, S. Sawyer, M. Meyer, Double indexing overcomes inaccuracies in multiplex sequencing on the Illumina platform. *Nucleic Acids Res.* **40**, e3 (2012).
40. M. P. Verdugo, V. E. Mullin, A. Scheu, V. Mattiangeli, K. G. Daly, P. Maisano Delser, A. J. Hare, J. Burger, M. J. Collins, R. Kehati, P. Hesse, D. Fulton, E. W. Sauer, F. A. Mohaseb, H. Davoudi, R. Khazaeli, J. Lhuillier, C. Rapin, S. Ebrahimi, M. Khasanov, S. M. F. Vahidi, D. E. MacHugh, O. Ertuğrul, C. Koukoulis-Chrysanthaki, A. Sampson, G. Kazantzis, I. Kontopoulos, J. Bulatovic, I. Stojanović, A. Mikdad, N. Benecke, J. Linstädter, M. Sablin, R. Bendrey, L. Gourichon, B. S. Arbuckle, M. Mashkour, D. Orton, L. K. Horwitz, M. D. Teasdale, D. G. Bradley, Ancient cattle genomics, origins, and rapid turnover in the Fertile Crescent. *Science.* **365**, 173–176 (2019).
- 15
41. S. Mallick, H. Li, M. Lipson, I. Mathieson, M. Gymrek, F. Racimo, M. Zhao, N. Chennagiri, S. Nordenfelt, A. Tandon, P. Skoglund, I. Lazaridis, S. Sankararaman, Q. Fu, N. Rohland, G. Renaud, Y. Erlich, T. Willems, C. Gallo, J. P. Spence, Y. S. Song, G. Poletti, F. Balloux, G. van Driem, P. de Knijff, I. G. Romero, A. R. Jha, D. M. Behar, C. M. Bravi, C. Capelli, T. Hervig, A. Moreno-Estrada, O. L. Posukh, E. Balanovska, O. Balanovsky, S. Karachanak-Yankova, H. Sahakyan, D. Toncheva, L. Yepiskoposyan, C. Tyler-Smith, Y. Xue, M. S. Abdullah, A. Ruiz-Linares, C. M. Beall, A. Di Rienzo, C. Jeong, E. B. Starikovskaya, E. Metspalu, J. Parik, R. Villems, B. M. Henn, U. Hodoglugil, R. Mahley, A. Sajantila, G. Stamatoyannopoulos, J. T. S. Wee, R. Khusainova, E. Khusnutdinova, S. Litvinov, G. Ayodo, D. Comas, M. F. Hammer, T. Kivisild, W. Klitz, C. A. Winkler, D. Labuda, M. Bamshad, L. B. Jorde, S. A. Tishkoff, W. S. Watkins, M. Metspalu, S. Dryomov, R. Sukernik, L. Singh, K. Thangaraj, S. Pääbo, J. Kelso, N. Patterson, D. Reich, The Simons Genome Diversity Project: 300 genomes from 142 diverse populations. *Nature.* **538**, 201–206 (2016).
- 20
- 25

42. S. Brace, Y. Diekmann, T. J. Booth, L. van Dorp, Z. Faltyskova, N. Rohland, S. Mallick, I. Olalde, M. Ferry, M. Michel, J. Oppenheimer, N. Broomandkhoshbacht, K. Stewardson, R. Martiniano, S. Walsh, M. Kayser, S. Charlton, G. Hellenthal, I. Armit, R. Schulting, O. E. Craig, A. Sheridan, M. Parker Pearson, C. Stringer, D. Reich, M. G. Thomas, I. Barnes, Ancient genomes indicate population replacement in Early Neolithic Britain. *Nature Ecology & Evolution*. **3**, 765–771 (2019).
43. H. Li, Aligning sequence reads, clone sequences and assembly contigs with BWA-MEM. *arXiv [q-bio.GN]* (2013), (available at <http://arxiv.org/abs/1303.3997>).
44. H. Li, B. Handsaker, A. Wysoker, T. Fennell, J. Ruan, N. Homer, G. Marth, G. Abecasis, R. Durbin, 1000 Genome Project Data Processing Subgroup, The Sequence Alignment/Map format and SAMtools. *Bioinformatics*. **25**, 2078–2079 (2009).
45. M. A. DePristo, E. Banks, R. Poplin, K. V. Garimella, J. R. Maguire, C. Hartl, A. A. Philippakis, G. del Angel, M. A. Rivas, M. Hanna, A. McKenna, T. J. Fennell, A. M. Kernytsky, A. Y. Sivachenko, K. Cibulskis, S. B. Gabriel, D. Altshuler, M. J. Daly, A framework for variation discovery and genotyping using next-generation DNA sequencing data. *Nat. Genet.* **43**, 491–498 (2011).
46. V. Link, A. Kousathanas, K. Veeramah, C. Sell, A. Scheu, D. Wegmann, ATLAS: Analysis Tools for Low-depth and Ancient Samples, , doi:10.1101/105346.
47. J. Koster, S. Rahmann, Snakemake--a scalable bioinformatics workflow engine. *Bioinformatics*. **28** (2012), pp. 2520–2522.
48. Q. Fu, A. Mittnik, P. L. F. Johnson, K. Bos, M. Lari, R. Bollongino, C. Sun, L. Giemsch, R. Schmitz, J. Burger, A. M. Ronchitelli, F. Martini, R. G. Cremonesi, J. Svoboda, P. Bauer, D. Caramelli, S. Castellano, D. Reich, S. Pääbo, J. Krause, A revised timescale for human evolution based on ancient mitochondrial genomes. *Curr. Biol.* **23**, 553–559 (2013).
49. K. Katoh, K. Misawa, K.-I. Kuma, T. Miyata, MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Res.* **30**, 3059–3066 (2002).
50. M. Rasmussen, X. Guo, Y. Wang, K. E. Lohmueller, S. Rasmussen, A. Albrechtsen, L. Skotte, S. Lindgreen, M. Metspalu, T. Jombart, T. Kivisild, W. Zhai, A. Eriksson, A. Manica, L. Orlando, F. M. De La Vega, S. Tridico, E. Metspalu, K. Nielsen, M. C. Ávila-Arcos, J. V. Moreno-Mayar, C. Muller, J. Dortch, M. T. P. Gilbert, O. Lund, A. Wesolowska, M. Karmin, L. A. Weinert, B. Wang, J. Li, S. Tai, F. Xiao, T. Hanihara, G. van Driem, A. R. Jha, F. X. Ricaut, P. de Knijff, A. B. Migliano, I. Gallego Romero, K. Kristiansen, D. M. Lambert, S. Brunak, P. Forster, B.

- Brinkmann, O. Nehlich, M. Bunce, M. Richards, R. Gupta, C. D. Bustamante, A. Krogh, R. A. Foley, M. M. Lahr, F. Balloux, T. Sicheritz-Pontén, R. Villems, R. Nielsen, J. Wang, E. Willerslev, An Aboriginal Australian genome reveals separate human dispersals into Asia. *Science*. **334**, 94–98 (2011).
51. T. 1000 G. P. Consortium, The 1000 Genomes Project Consortium, A global reference for human genetic variation. *Nature*. **526** (2015), pp. 68–74.
52. S. Dimitrieva, P. Bucher, UCNEbase--a database of ultraconserved non-coding elements and genomic regulatory blocks. *Nucleic Acids Res*. **41**, D101–9 (2013).
53. P. Skoglund, J. Storå, A. Götherström, M. Jakobsson, Accurate sex identification of ancient human remains using DNA shotgun sequencing. *Journal of Archaeological Science*. **40**, 4477–4482 (2013).
- 10 54. T. Günther, C. Nettelblad, The presence and impact of reference bias on population genomic studies of prehistoric human populations. *PLoS Genet*. **15**, e1008302 (2019).
55. F. Pouyet, S. Aeschbacher, A. Thiéry, L. Excoffier, Background selection and biased gene conversion affect more than 95% of the human genome and bias demographic inferences. *Elife*. **7** (2018), doi:10.7554/eLife.36317.
56. R. Matthey-Doret, M. C. Whitlock, Background selection and  $F_{ST}$  : Consequences for detecting local adaptation. *Mol. Ecol*. **28**, 3902–3914 (2019).
- 15 57. L. Excoffier, I. Dupanloup, E. Huerta-Sanchez, V. C. Sousa, M. Foll, Robust demographic inference from genomic and SNP data. *PLoS Genet*. **9**, e1003905 (2013).
58. L. Excoffier, N. Marchi, D. A. Marques, R. Matthey-Doret, A. Gouy, V. C. Sousa, fastsimcoal2: demographic inference under complex evolutionary scenarios. *Bioinformatics* (2021), doi:10.1093/bioinformatics/btab468.
- 20 59. O. Delaneau, J.-F. Zagury, M. R. Robinson, J. L. Marchini, E. T. Dermitzakis, Accurate, scalable and integrative haplotype estimation. *Nat. Commun*. **10**, 5436 (2019).
60. S. McCarthy, S. Das, W. Kretschmar, O. Delaneau, A. R. Wood, A. Teumer, H. M. Kang, C. Fuchsberger, P. Danecek, K. Sharp, Y. Luo, C. Sidore, A. Kwong, N. Timpson, S. Koskinen, S. Vrieze, L. J. Scott, H. Zhang, A. Mahajan, J. Veldink, U. Peters, C. Pato, C. M. van Duijn, C. E. Gillies, I. Gandin, M. Mezzavilla, A. Gilly, M. Cocca, M. Traglia, A. Angius, J. C. Barrett, D. Boomsma, K. Branham, G. Breen, C. M. Brummett, F. Busonero, H. Campbell, A. Chan, S. Chen, E. Chew, F. S. Collins, L. J. Corbin, G. D. Smith, G. Dedoussis, M. Dorr, A.-E. Farmaki, L. Ferrucci, L. Forer, R. M. Fraser, S. Gabriel, S. Levy, L. Groop, T. Harrison, A. Hattersley, O. L. Holmen, K. Hveem, M. Kretzler, J. C. Lee, M. McGue, T. Meitinger, D. Melzer, J. L. Min, K. L. Mohlke, J. B. Vincent, M. Nauck, D. Nickerson, A. Palotie, M. Pato, N. Pirastu, M. McInnis, J. B. Richards, C. Sala, V. Salomaa,
- 25

- D. Schlessinger, S. Schoenherr, P. E. Slagboom, K. Small, T. Spector, D. Stambolian, M. Tuke, J. Tuomilehto, L. H. Van den Berg, W. Van Rheenen, U. Volker, C. Wijmenga, D. Toniolo, E. Zeggini, P. Gasparini, M. G. Sampson, J. F. Wilson, T. Frayling, P. I. W. de Bakker, M. A. Swertz, S. McCarroll, C. Kooperberg, A. Dekker, D. Altshuler, C. Willer, W. Iacono, S. Ripatti, N. Soranzo, K. Walter, A. Swaroop, F. Cucca, C. A. Anderson, R. M. Myers, M. Boehnke, M. I. McCarthy, R. Durbin, Haplotype Reference Consortium, A reference panel of 64,976 haplotypes for genotype imputation. *Nat. Genet.* **48**, 1279–1283 (2016).
- 5
61. J. N. Fenner, Cross-cultural estimation of the human generation interval for use in genetics-based population divergence studies. *Am. J. Phys. Anthropol.* **128**, 415–423 (2005).
62. D. Navarro-Gomez, J. Leipzig, L. Shen, M. Lott, A. P. M. Stassen, D. C. Wallace, J. L. Wiggs, M. J. Falk, M. van Oven, X. Gai, Phy-Mer: a novel alignment-free and reference-independent mitochondrial haplogroup classifier. *Bioinformatics.* **31**, 1310–1312 (2015).
- 10
63. A. Ralf, D. M. González, K. Zhong, M. Kayser, Yleaf: Software for Human Y-Chromosomal Haplogroup Inference from Next-Generation Sequencing Data. *Molecular Biology and Evolution.* **35** (2018), pp. 1291–1294.
64. S. Walsh, F. Liu, A. Wollstein, L. Kovatsi, A. Ralf, A. Kosiniak-Kamysz, W. Branicki, M. Kayser, The HirisPlex system for simultaneous prediction of hair and eye colour from DNA. *Forensic Sci. Int. Genet.* **7**, 98–115 (2013).
- 15
65. L. Chaitanya, K. Breslin, S. Zuñiga, L. Wirken, E. Pośpiech, M. Kukla-Bartoszek, T. Sijen, P. de Knijff, F. Liu, W. Branicki, M. Kayser, S. Walsh, The HirisPlex-S system for eye, hair and skin colour prediction from DNA: Introduction and forensic developmental validation. *Forensic Sci. Int. Genet.* **35**, 123–135 (2018).
66. B. P. McEvoy, P. M. Visscher, Genetics of human height. *Econ. Hum. Biol.* **7**, 294–306 (2009).
- 20
67. Y. Chan, R. M. Salem, Y.-H. H. Hsu, G. McMahon, T. H. Pers, S. Vedantam, T. Esko, M. H. Guo, E. T. Lim, L. Franke, G. D. Smith, D. P. Strachan, J. N. Hirschhorn, Genome-wide Analysis of Body Proportion Classifies Height-Associated Variants by Mechanism of Action and Implicates Genes Important for Skeletal Development. *Am. J. Hum. Genet.* **96**, 695–708 (2015).
- 25
68. K. R. Veeramah, A. Rott, M. Groß, L. van Dorp, S. López, K. Kirsanow, C. Sell, J. Blöcher, D. Wegmann, V. Link, Z. Hofmanová, J. Peters, B. Trautmann, A. Gairhos, J. Haberstroh, B. Pääffgen, G. Hellenthal, B. Haas-Gebhard, M. Harbeck, J. Burger, Population genomic analysis of elongated skulls reveals extensive female-biased immigration in Early Medieval Bavaria. *Proc. Natl. Acad. Sci. U. S. A.* **115**, 3494–3499 (2018).
69. M. Nei, W. H. Li., Mathematical model for studying genetic variation in terms of restriction endonucleases. *Proc. Natl. Acad. Sci. U. S. A.* **76**, 5269–5273 (1979).

70. B. L. Browning, S. R. Browning, Detecting identity by descent and estimating genotype error rates in sequence data. *Am. J. Hum. Genet.* **93**, 840–851 (2013).
71. M. Sikora, A. Seguin-Orlando, V. C. Sousa, A. Albrechtsen, T. Korneliussen, A. Ko, S. Rasmussen, I. Dupanloup, P. R. Nigst, M. D. Bosch, G. Renaud, M. E. Allentoft, A. Margaryan, S. V. Vasilyev, E. V. Veselovskaya, S. B. Borutskaya, T. Deviese, D. Comeskey, T. Higham, A. Manica, R. Foley, D. J. Meltzer, R. Nielsen, L. Excoffier, M. Mirazon Lahr, L. Orlando, E. Willerslev, Ancient genomes show social and reproductive behavior of early Upper Paleolithic foragers. *Science*. **358**, 659–662 (2017).
72. F. Racimo, M. Sikora, M. V. Linden, H. Schroeder, C. Lalueza-Fox, Beyond broad strokes: sociocultural insights from the study of ancient genomes. *Nature Reviews Genetics*. **21** (2020), pp. 355–366.
73. E. Fritchot, O. François, LEA: An R package for landscape and ecological association studies. *Methods in Ecology and Evolution*. **6** (2015), pp. 925–929.
74. K. Prüfer, C. de Filippo, S. Grote, F. Mafessoni, P. Korlević, M. Hajdinjak, B. Vernot, L. Skov, P. Hsieh, S. Peyrégne, D. Reher, C. Hopfe, S. Nagel, T. Maricic, Q. Fu, C. Theunert, R. Rogers, P. Skoglund, M. Chintalapati, M. Dannemann, B. J. Nelson, F. M. Key, P. Rudan, Ž. Kućan, I. Gušić, L. V. Golovanova, V. B. Doronichev, N. Patterson, D. Reich, E. E. Eichler, M. Slatkin, M. H. Schierup, A. M. Andrés, J. Kelso, M. Meyer, S. Pääbo, A high-coverage Neandertal genome from Vindija Cave in Croatia. *Science*. **358**, 655–658 (2017).
75. M. Petr, S. Pääbo, J. Kelso, B. Vernot, Limits of long-term selection against Neandertal introgression. *Proc. Natl. Acad. Sci. U. S. A.* **116**, 1639–1644 (2019).
76. K. Wang, M. Li, H. Hakonarson, ANNOVAR: functional annotation of genetic variants from high-throughput sequencing data. *Nucleic Acids Res.* **38**, e164 (2010).
77. X. Huang, A. L. Fortier, A. J. Coffman, T. J. Struck, M. N. Irby, J. E. James, J. E. León-Burguete, A. P. Ragsdale, R. N. Gutenkunst, Inferring Genome-Wide Correlations of Mutation Fitness Effects between Populations. *Mol. Biol. Evol.* **38**, 4588–4602 (2021).
78. S. Gravel, B. M. Henn, R. N. Gutenkunst, A. R. Indap, G. T. Marth, A. G. Clark, F. Yu, R. A. Gibbs, C. D. Bustamante, D. L. Altshuler, R. M. Durbin, G. R. Abecasis, D. R. Bentley, A. Chakravarti, A. G. Clark, F. S. Collins, F. M. De La Vega, P. Donnelly, M. Egholm, P. Flicek, S. B. Gabriel, R. A. Gibbs, B. M. Knoppers, E. S. Lander, H. Lehrach, E. R. Mardis, G. A. McVean, D. A. Nickerson, L. Peltonen, A. J. Schafer, S. T. Sherry, J. Wang, R. K. Wilson, R. A. Gibbs, D. Deiros, M. Metzker, D. Muzny, J. Reid, D. Wheeler, J. Wang, J. Li, M. Jian, G. Li, R. Li, H. Liang, G. Tian, B. Wang, J. Wang, W. Wang, H. Yang, X. Zhang, H. Zheng, E. S. Lander, D. L.



Altshuler, L. Ambrogio, T. Bloom, K. Cibulskis, T. J. Fennell, S. B. Gabriel, D. B. Jaffe, E. Shefler, C. L. Sougnez, D. R. Bentley, N. Gormley, S. Humphray, Z. Kingsbury, P. Koko-Gonzales, J. Stone, K. J. McKernan, G. L. Costa, J. K. Ichikawa, C. C. Lee, R. Sudbrak, H. Lehrach, T. A. Borodina, A. Dahl, A. N. Davydov, P. Marquardt, F. Mertes, W. Nietfeld, P. Rosenstiel, S. Schreiber, A. V. Soldatov, B. Timmermann, M. Tolzmann, M. Egholm, J. Affourtit, D. Ashworth, S. Attiya, M. Bachorski, E. Buglione, A. Burke, A. Caprio, C. Celone, S. Clark, D. Conners, B. Desany, L. Gu, L. Guccione, K. Kao, A. Kebbel, J. Knowlton, M. Labrecque, L. McDade, C. Mealmaker, M. Minderman, A. Nawrocki, F. Niazi, K. Pareja, R. Ramenani, D. Riches, W. Song, C. Turcotte, S. Wang, E. R. Mardis, R. K. Wilson, D. Dooling, L. Fulton, R. Fulton, G. Weinstock, R. M. Durbin, J. Burton, D. M. Carter, C. Churcher, A. Coffey, A. Cox, A. Palotie, M. Quail, T. Skelly, J. Stalker, H. P. Swerdlow, D. Turner, A. De Witte, S. Giles, R. A. Gibbs, D. Wheeler, M. Bainbridge, D. Challis, A. Sabo, F. Yu, J. Yu, J. Wang, X. Fang, X. Guo, R. Li, Y. Li, R. Luo, S. Tai, H. Wu, H. Zheng, X. Zheng, Y. Zhou, G. Li, J. Wang, H. Yang, G. T. Marth, E. P. Garrison, W. Huang, A. Indap, D. Kural, W.-P. Lee, W. F. Leong, A. R. Quinlan, C. Stewart, M. P. Stromberg, A. N. Ward, J. Wu, C. Lee, R. E. Mills, X. Shi, M. J. Daly, M. A. DePristo, D. L. Altshuler, A. D. Ball, E. Banks, T. Bloom, B. L. Browning, K. Cibulskis, T. J. Fennell, K. V. Garimella, S. R. Grossman, R. E. Handsaker, M. Hanna, C. Hartl, D. B. Jaffe, A. M. Kernytsky, J. M. Korn, H. Li, J. R. Maguire, S. A. McCarroll, A. McKenna, J. C. Nemes, A. A. Philippakis, R. E. Poplin, A. Price, M. A. Rivas, P. C. Sabeti, S. F. Schaffner, E. Shefler, I. A. Shlyakhter, D. N. Cooper, E. V. Ball, M. Mort, A. D. Phillips, P. D. Stenson, J. Sebat, V. Makarov, K. Ye, S. C. Yoon, C. D. Bustamante, A. G. Clark, A. Boyko, J. Degenhardt, S. Gravel, R. N. Gutenkunst, M. Kaganovich, A. Keinan, P. Lacroute, X. Ma, A. Reynolds, L. Clarke, P. Flicek, F. Cunningham, J. Herrero, S. Keenen, E. Kulesha, R. Leinonen, W. M. McLaren, R. Radhakrishnan, R. E. Smith, V. Zalunin, X. Zheng-Bradley, J. O. Korbel, A. M. Stutz, S. Humphray, M. Bauer, R. K. Cheetham, T. Cox, M. Eberle, T. James, S. Kahn, L. Murray, A. Chakravarti, K. Ye, F. M. De La Vega, Y. Fu, F. C. L. Hyland, J. M. Manning, S. F. McLaughlin, H. E. Peckham, O. Sakarya, Y. A. Sun, E. F. Tsung, M. A. Batzer, M. K. Konkel, J. A. Walker, R. Sudbrak, M. W. Albrecht, V. S. Amstislavskiy, R. Herwig, D. V. Parkhomchuk, S. T. Sherry, R. Agarwala, H. M. Khouri, A. O. Morgulis, J. E. Paschall, L. D. Phan, K. E. Rotmistrovsky, R. D. Sanders, M. F. Shumway, C. Xiao, G. A. McVean, A. Auton, Z. Iqbal, G. Lunter, J. L. Marchini, L. Moutsianas, S. Myers, A. Tumian, B. Desany, J. Knight, R. Winer, D. W. Craig, S. M. Beckstrom-Sternberg, A. Christoforides, A. A. Kurdoglu, J. V. Pearson, S. A. Sinari, W. D. Tembe, D. Haussler, A. S. Hinrichs, S. J. Katzman, A. Kern, R. M. Kuhn, M. Przeworski, R. D. Hernandez, B. Howie, J. L. Kelley, S. C. Melton, G. R. Abecasis, Y. Li, P. Anderson, T. Blackwell, W. Chen, W. O. Cookson, J. Ding, H. M. Kang, M.

Lathrop, L. Liang, M. F. Moffatt, P. Scheet, C. Sidore, M. Snyder, X. Zhan, S. Zollner, P. Awadalla, F. Casals, Y. Idaghmour, J. Keebler, E. A. Stone, M. Zilversmit, L. Jorde, J. Xing, E. E. Eichler, G. Aksay, C. Alkan, I. Hajirasouliha, F. Hormozdiari, J. M. Kidd, S. C. Sahinalp, P. H. Sudmant, E. R. Mardis, K. Chen, A. Chinwalla, L. Ding, D. C. Koboldt, M. D. McLellan, D. Dooling, G. Weinstock, J. W. Wallis, M. C. Wendl, Q. Zhang, R. M. Durbin, C. A. Albers, Q. Ayub, S. Balasubramaniam, J. C. Barrett, D. M. Carter, Y. Chen, D. F. Conrad, P. Danecek, E. T. Dermitzakis, M. Hu, N. Huang, M. E. Hurles, H. Jin, L. Jostins, T. M. Keane, S. Q. Le, S. Lindsay, Q. Long, D. G. MacArthur, S. B. Montgomery, L. Parts, J. Stalker, C. Tyler-Smith, K. Walter, Y. Zhang, M. B. Gerstein, M. Snyder, A. Abyzov, S. Balasubramanian, R. Bjornson, J. Du, F. Grubert, L. Habegger, R. Haraksingh, J. Jee, E. Khurana, H. Y. K. Lam, J. Leng, X. J. Mu, A. E. Urban, Z. Zhang, Y. Li, R. Luo, G. T. Marth, E. P. Garrison, D. Kural, A. R. Quinlan, C. Stewart, M. P. Stromberg, A. N. Ward, J. Wu, C. Lee, R. E. Mills, X. Shi, S. A. McCarroll, E. Banks, M. A. DePristo, R. E. Handsaker, C. Hartl, J. M. Korn, H. Li, J. C. Nemes, J. Sebat, V. Makarov, K. Ye, S. C. Yoon, J. Degenhardt, M. Kaganovich, L. Clarke, R. E. Smith, X. Zheng-Bradley, J. O. Korbel, S. Humphray, R. K. Cheetham, M. Eberle, S. Kahn, L. Murray, K. Ye, F. M. De La Vega, Y. Fu, H. E. Peckham, Y. A. Sun, M. A. Batzer, M. K. Konkel, J. A. Walker, C. Xiao, Z. Iqbal, B. Desany, T. Blackwell, M. Snyder, J. Xing, E. E. Eichler, G. Aksay, C. Alkan, I. Hajirasouliha, F. Hormozdiari, J. M. Kidd, K. Chen, A. Chinwalla, L. Ding, M. D. McLellan, J. W. Wallis, M. E. Hurles, D. F. Conrad, K. Walter, Y. Zhang, M. B. Gerstein, M. Snyder, A. Abyzov, J. Du, F. Grubert, R. Haraksingh, J. Jee, E. Khurana, H. Y. K. Lam, J. Leng, X. J. Mu, A. E. Urban, Z. Zhang, R. A. Gibbs, M. Bainbridge, D. Challis, C. Coafra, H. Dinh, C. Kovar, S. Lee, D. Muzny, L. Nazareth, J. Reid, A. Sabo, F. Yu, J. Yu, G. T. Marth, E. P. Garrison, A. Indap, W. F. Leong, A. R. Quinlan, C. Stewart, A. N. Ward, J. Wu, K. Cibulskis, T. J. Fennell, S. B. Gabriel, K. V. Garimella, C. Hartl, E. Shefler, C. L. Sougnez, J. Wilkinson, A. G. Clark, S. Gravel, F. Grubert, L. Clarke, P. Flicek, R. E. Smith, X. Zheng-Bradley, S. T. Sherry, H. M. Khouri, J. E. Paschall, M. F. Shumway, C. Xiao, G. A. McVean, S. J. Katzman, G. R. Abecasis, T. Blackwell, E. R. Mardis, D. Dooling, L. Fulton, R. Fulton, D. C. Koboldt, R. M. Durbin, S. Balasubramanian, A. Coffey, T. M. Keane, D. G. MacArthur, A. Palotie, C. Scott, J. Stalker, C. Tyler-Smith, M. B. Gerstein, S. Balasubramanian, A. Chakravarti, B. M. Knoppers, G. R. Abecasis, C. D. Bustamante, N. Gharani, R. A. Gibbs, L. Jorde, J. S. Kaye, A. Kent, T. Li, A. L. McGuire, G. A. McVean, P. N. Ossorio, C. N. Rotimi, Y. Su, L. H. Toji, C. Tyler-Smith, L. D. Brooks, A. L. Felsenfeld, J. E. McEwen, A. Abdallah, C. R. Juenger, N. C. Clemm, F. S. Collins, A. Duncanson, E. D. Green, M. S. Guyer, J. L. Peterson, A. J. Schafer, G. R. Abecasis, D. L. Altshuler, A. Auton, L. D. Brooks, R. M. Durbin, R. A. Gibbs, M. E. Hurles, G. A. McVean, Demographic history and rare

- allele sharing among human populations. *Proceedings of the National Academy of Sciences*. **108**, 11983–11988 (2011).
79. A. P. Ragsdale, A. J. Coffman, P. Hsieh, T. J. Struck, R. N. Gutenkunst, Triallelic Population Genomics for Inferring Correlated Fitness Effects of Same Site Nonsynonymous Mutations. *Genetics*. **203**, 513–523 (2016).
- 5 80. S. Schiffels, K. Wang, MSMC and MSMC2: The Multiple Sequentially Markovian Coalescent. *Methods Mol. Biol.* **2090**, 147–166 (2020).
81. A. Scally, R. Durbin, Revising the human mutation rate: implications for understanding human evolution. *Nat. Rev. Genet.* **13**, 745–753 (2012).
82. H. Akaike, A new look at the statistical model identification. *IEEE Transactions on Automatic Control*. **19** (1974),  
10 pp. 716–723.
83. C. Runnels, A Prehistoric Survey of Thessaly: New Light on the Greek Middle Paleolithic. *Journal of Field Archaeology*. **15**, 277–290 (1988).
84. M. Özdoğan, Anatolia from the Last Glacial Maximum to the Holocene Climatic Optimum: cultural formations and the impact of the environmental setting. *Paléorient*. **23**, 25–38 (1997).
- 15 85. C. Runnels, M. Özdoğan, The Palaeolithic of the Bosphorus Region NW Turkey. *Journal of Field Archaeology*. **28**, 69–92 (2001).
86. J. K. Kozłowski, Gravettian/Epigravettian sequences in the Balkans: environment, technologies, hunting strategies and raw material procurement. *British School at Athens Studies*. **3**, 319–329 (1999).
87. C. Perlès, in *Hunters of the Golden Age. The Mid-Upper Palaeolithic of Eurasia 30,000 - 20,000 BP*, W. Roebroeks, 20 M. Mussi, J. Svoboda, K. Fennema, Eds. (University of Leiden, 2000), vol. 31 of *Analecta Praehistorica Leidensia*, pp. 375–397.
88. E. Adam, Looking out for the Gravettian in Greece. *Paléo*, 145–158 (2007).
89. V. Tourloukis, K. Harvati, The Palaeolithic record of Greece: a synthesis of the evidence and a research agenda for the future. *Quat. Int.* **466**, 48–65 (2018).
- 25 90. P. U. Clark, A. S. Dyke, J. D. Shakun, A. E. Carlson, J. Clark, B. Wohlfarth, J. X. Mitrovica, S. W. Hostetler, A. M. McCabe, The Last Glacial Maximum. *Science*. **325**, 710–714 (2009).
91. K. Lambeck, Late Pleistocene and Holocene sea-level change in Greece and south-western Turkey: a separation of eustatic, isostatic and tectonic contributions. *Geophys. J. Int.* **122**, 1022–1044 (1995).

92. J. Benjamin, A. Rovere, A. Fontana, S. Furlani, M. Vacchi, R. H. Inglis, E. Galili, F. Antonioli, D. Sivan, S. Miko, N. Mourtzas, I. Felja, M. Meredith-Williams, B. Goodman-Tchernov, E. Kolaiti, M. Anzidei, R. Gehrels, Late Quaternary sea-level changes and early human societies in the central and eastern Mediterranean Basin: An interdisciplinary review. *Quat. Int.* **449**, 29–57 (2017).
- 5 93. C. Papoulia, Late Pleistocene to Early Holocene Sea-crossings in the Aegean: direct, indirect and controversial evidence. *Géochronologie des Îles de Méditerranée. CNRS Editions, Paris*, 33–46 (2016).
94. T. Carter, D. A. Contreras, J. Holcomb, D. D. Mihailović, P. Karkanas, G. Guérin, N. Taffin, D. Athanasoulis, C. Lahaye, Earliest occupation of the Central Aegean (Naxos), Greece: Implications for hominin and Homo sapiens' behavior and dispersals. *Sci Adv.* **5**, eaax0997 (2019).
- 10 95. N. V. Esin, N. I. Esin, V. Yanko-Hombach, The Black Sea basin filling by the Mediterranean salt water during the Holocene. *Quat. Int.* **409**, 33–38 (2016).
96. J. K. Kozłowski, The Importance of the Aegean Basin for the Neolithization of South-Eastern Europe. *Journal of the Israel Prehistoric Society.* **35**, 409–424 (2005).
97. T. Carter, Obsidian consumption in the Late Pleistocene–Early Holocene Aegean: contextualising new data from  
15 Mesolithic Crete. *Annual of the British School at Athens.* **111**, 13–34 (2016).
98. C. B. Ramsey, Bayesian Analysis of Radiocarbon Dates. *Radiocarbon.* **51**, 337–360 (2009).
99. P. J. Reimer, W. E. N. Austin, E. Bard, A. Bayliss, P. G. Blackwell, C. B. Ramsey, M. Butzin, H. Cheng, R. Lawrence Edwards, M. Friedrich, P. M. Grootes, T. P. Guilderson, I. Hajdas, T. J. Heaton, A. G. Hogg, K. A. Huguen, B. Kromer, S. W. Manning, R. Muscheler, J. G. Palmer, C. Pearson, J. van der Plicht, R. W. Reimer, D. A.  
20 Richards, E. Marian Scott, J. R. Southon, C. S. M. Turney, L. Wacker, F. Adolphi, U. Büntgen, M. Capano, S. M. Fahrni, A. Fogtmann-Schulz, R. Friedrich, P. Köhler, S. Kudsk, F. Miyake, J. Olsen, F. Reinig, M. Sakamoto, A. Sookdeo, S. Talamo, The IntCal20 Northern Hemisphere Radiocarbon Age Calibration Curve (0–55 cal kBP). *Radiocarbon.* **62**, 725–757 (2020).
100. G. T. Cook, C. Bonsall, R. E. M. Hedges, K. McSweeney, V. Boronean, P. B. Pettitt, A Freshwater Diet-Derived  
25 <sup>14</sup>C Reservoir Effect at the Stone Age Sites in the Iron Gates Gorge. *Radiocarbon.* **43**, 453–460 (2001).
101. C. Bonsall, R. Vasić, A. Boroneanț, M. Roksandic, A. Soficaru, K. McSweeney, A. Evatt, Ü. Agurauja, C. Pickard, V. Dimitrijević, T. Higham, D. Hamilton, G. Cook, New AMS <sup>14</sup>C dates for human remains from Stone Age sites in the Iron Gates reach of the Danube, southeast Europe. *Radiocarbon.* **57**, 33–46 (2015).

102. D. Borić, C. French, V. Dimitrijević, Vlasac revisited: formation processes, stratigraphy and dating. *Documenta Praehistorica*. **35**, 261–287 (2008).
103. D. Borić, in *Beginnings – New Research in the Appearance of the Neolithic between Northwest Anatolia and the Carpathian Basin. Papers of the International Workshop 8th - 9th April 2009, Istanbul. Organized by Dan Ciobotaru, Barbara Horejs und Raiko Krauß.*, R. Krauß, Ed. (Verlag Marie Leidorf GmbH, Rahden/Westf., 2011; <http://orca.cf.ac.uk/id/eprint/32487>), *Menschen – Kulturen – Traditionen: Studien aus den Forschungsclustern des Deutschen Archäologischen Instituts; ForschungsCluster 1*, pp. 157–203.
104. D. Borić, T. D. Price, Strontium isotopes document greater human mobility at the start of the Balkan Neolithic. *Proceedings of the National Academy of Sciences of the United States of America*. **110**, 3298–3303 (2013).
105. Z. Hofmanová, thesis, Mainz (2017).
106. S. Kreutzer, thesis, Mainz (2017).
107. M. Porčić, T. Blagojević, J. Pendić, S. Stefanović, The Neolithic Demographic Transition in the Central Balkans: population dynamics reconstruction based on new radiocarbon evidence. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* (2020), doi:10.1098/rstb.2019.0712.
108. P. Stadler, in *Das Linearbandkeramische Gräberfeld von Kleinhadersdorf. Mitteilungen der Prähistorischen Kommission 82*, C. Neugebauer-Maresch, E. Lenneis, Eds. (Verlag der Österreichischen Akademie der Wissenschaften, Wien, 2015), pp. 149–151.
109. N. Tasić, M. Marić, C. B. Ramsey, B. Kromer, A. Barclay, A. Bayliss, N. Beavan, B. Gaydarska, A. Whittle, *Vinča-Belo Brdo, Serbia: The times of a tell [Dataset]* (Heidelberg Research Data Repository, University of Heidelberg, 2016), vols. 1–75 of *Germania*.
110. D. Baird, in *A Companion to the Archaeology of the Ancient Near East*, D. T. Potts, Ed. (Wiley Online Library, 2012; <https://onlinelibrary.wiley.com/doi/pdf/10.1002/9781444360790#page=469>), vol. 1, pp. 431–465.
111. M. Kartal, Anatolian epi-paleolithic period assemblages: problems, suggestions, evaluations and various approaches. *Anadolu / Anatolia*. **24**, 45–62 (2003).
112. D. Baird, E. Asouti, L. Astruc, A. Baysal, E. Baysal, D. Carruthers, A. Fairbairn, C. Kabukcu, E. Jenkins, K. Lorentz, Others, Juniper smoke, skulls and wolves' tails. The Epipalaeolithic of the Anatolian plateau in its South-west Asian context; insights from Pınarbaşı. *Levantina*. **45**, 175–209 (2013).

113. Ç. Çilingiroğlu, M. Kaczanowska, J. K. Kozłowski, B. Dinçer, C. Çakırlar, D. Turan, Between Anatolia and the Aegean: Epipalaeolithic and Mesolithic Foragers of the Karaburun Peninsula. *J. Field Archaeol.* **45**, 479–497 (2020).
114. Ç. Atakuman, B. Erdoğu, H. C. Gemici, İ. Baykara, M. Karakoç, P. Biagi, E. Starnini, D. Guilbeau, N. Yücel, D. Turan, M. Dirican, Before the Neolithic in the Aegean: The Pleistocene and the Early Holocene record of Bozburun - Southwest Turkey. *The Journal of Island and Coastal Archaeology* (2020), doi:10.1080/15564894.2020.1803458.
115. N. Efstratiou, P. Biagi, E. Starnini, The Epipalaeolithic site of Ouriakos on the island of Lemnos and its place in the Late Pleistocene peopling of the east Mediterranean region. *Adalya*. **17**, 1–13 (2014).
116. J.-P. Bocquet-Appel, O. Bar-Yosef, *The Neolithic Demographic Transition and its Consequences* (Springer Science & Business Media, 2008; <https://play.google.com/store/books/details?id=vMUxhfRImBIC>).
117. O. Bar-Yosef, Climatic Fluctuations and Early Farming in West and East Asia. *Curr. Anthropol.* **52**, S175–S193 (2011).
118. S. Shennan, *The First Farmers of Europe: An Evolutionary Perspective* (Cambridge University Press, 2018; <https://play.google.com/store/books/details?id=4pheDwAAQBAJ>).
119. M. A. Zeder, in *Human Dispersal and Species Movement: From Prehistory to the Present*, N. Boivin, R. Crassard, M. Petraglia, Eds. (Cambridge University Press, 2017; <https://www.cambridge.org/core/books/human-dispersal-and-species-movement/out-of-the-fertile-crescent-the-dispersal-of-domestic-livestock-through-europe-and-africa/519E8E5F0EA170D42EFA8D335B44D002>), pp. 261–303.
120. J.-D. Vigne, F. Briois, A. Zazzo, G. Willcox, T. Cucchi, S. Thiébaud, I. Carrère, Y. Franel, R. Touquet, C. Martin, C. Moreau, C. Comby, J. Guilaine, First wave of cultivators spread to Cyprus at least 10,600 y ago. *Proc. Natl. Acad. Sci. U. S. A.* **109**, 8445–8449 (2012).
121. B. S. Arbuckle, S. W. Kansa, E. Kansa, D. Orton, C. Çakırlar, L. Gourichon, L. Atici, A. Galik, A. Marciniak, J. Mulville, H. Buitenhuis, D. Carruthers, B. De Cupere, A. Demirergi, S. Frame, D. Helmer, L. Martin, J. Peters, N. Pöllath, K. Pawłowska, N. Russell, K. Twiss, D. Würtenberger, Data sharing reveals complexity in the westward spread of domestic animals across Neolithic Turkey. *PLoS One*. **9**, e99845 (2014).
122. D. Baird, A. Fairbairn, E. Jenkins, L. Martin, C. Middleton, J. Pearson, E. Asouti, Y. Edwards, C. Kabukcu, G. Mustafaoglu, N. Russell, O. Bar-Yosef, G. Jacobsen, X. Wu, A. Baker, S. Elliott, Agricultural origins on the Anatolian plateau. *Proc. Natl. Acad. Sci. U. S. A.* **115**, E3077–E3086 (2018).

123. B. Weninger, L. Clare, F. Gerritsen, B. Horejs, R. Krauß, J. Linstädter, R. Özbal, E. J. Rohling, Neolithisation of the Aegean and Southeast Europe during the 6600-6000 calBC period of Rapid Climate Change. *Documenta Praehistorica*. **41** (2014) (available at <https://openresearch-repository.anu.edu.au/bitstream/1885/13435/2/Weninger%20et%20al%20Neolithisation%20of%20the%20Aegean%202014.pdf>).
124. M. Brami, B. Horejs, Eds., *The Central/Western Anatolian Farming Frontier. Proceedings of the Neolithic Workshop held at 10th ICAANE in Vienna* (Austrian Academy of Sciences Press, Vienna, 2019; <https://www.austriaca.at/8415-7>), vol. 12.
125. N. Karul, M. B. Avci, Neolithic communities in the Eastern Marmara region: Aktopraklik C. *Anatolica*. **37**, 1–15 (2011).
126. F. Gerritsen, R. Özbal, Barcın Höyük, a seventh millennium settlement in the Eastern Marmara region of Turkey. *Documenta Praehistorica*. **46**, 58–67 (2019).
127. Ç. Çilingiroğlu, C. Çakırlar, Towards configuring the neolithisation of Aegean Turkey. *Documenta Praehistorica*. **40**, 21–29 (2013).
128. C. Çakırlar, in *Barely surviving or more than enough?*, M. Groot, D. Lentjes, J. Zeiler, Eds. (Sidestone Press, Leiden, 2013), pp. 59–79.
129. B. Horejs, B. Milić, F. Ostmann, U. Thanheiser, B. Weninger, A. Galik, The Aegean in the Early 7th Millennium BC: Maritime Networks and Colonization. *J World Prehist.* **28**, 289–330 (2015).
130. T. H. van Andel, C. N. Runnels, The earliest farmers in Europe. *Antiquity*. **69**, 481–500 (1995).
131. C. Perlès, *The Early Neolithic in Greece: The First Farming Communities in Europe* (Cambridge University Press, 2001; <https://play.google.com/store/books/details?id=Kvy9WI95YC8C>).
132. C. Perlès, A. Quiles, H. Valladas, Early seventh-millennium AMS dates from domestic seeds in the Initial Neolithic at Franchthi Cave (Argolid, Greece). *Antiquity*. **87**, 1001–1015 (2013).
133. K. Douka, N. Efstratiou, M. M. Hald, P. S. Henriksen, A. Karetsou, Dating Knossos and the arrival of the earliest Neolithic in the southern Aegean. *Antiquity*. **91**, 304–321 (2017).
134. E. Weiberg, A. Bevan, K. Kouli, M. Katsianis, J. Woodbridge, A. Bonnier, M. Engel, M. Finné, R. Fyfe, Y. Maniatis, A. Palmisano, S. Panajiotidis, C. N. Roberts, S. Shennan, Long-term trends of land use and demography in Greece: A comparative study. *Holocene*. **29**, 742–760 (2019).

135. P. Halstead, V. Isaakidou, in *Farmers at the Frontier: A Pan European Perspective on Neolithisation*, K. J. Gron, L. Sørensen, P. Rowley-Conwy, Eds. (Oxbow Books, 2020);  
<https://books.google.com/books?hl=en&lr=&id=x3LSDwAAQBAJ&oi=fnd&pg=PA77&dq=Ivanova+et+al.+2018+pioneer+farming&ots=h0aLGSclao&sig=7CXtgushdfsNzi8W0OqkVLiBgjI>), pp. 77–100.
- 5 136. R. Krauß, E. Marinova, H. De Brue, B. Weninger, The rapid spread of early farming from the Aegean into the Balkans via the Sub-Mediterranean-Aegean Vegetation Zone. *Quat. Int.* **496**, 24–41 (2018).
137. M. Ivanova, B. De Cupere, J. Ethier, E. Marinova, Pioneer farming in southeast Europe during the early sixth millennium BC: Climate-related adaptations in the exploitation of plants and animals. *PLoS One.* **13**, e0197225 (2018).
- 10 138. K. Davison, P. Dolukhanov, G. R. Sarson, The role of waterways in the spread of the Neolithic. *J. Archaeol. Sci.* **33**, 641–652 (2006).
139. D. Borić, *Deathways at Lepenski Vir: Patterns in Mortuary Practice* (Serbian Archaeological Society, Belgrade, 2016; <http://orca.cf.ac.uk/id/eprint/96247>).
140. S. Stefanović, *People of the Lepenski Vir: bioanthropological analysis of human skeletal remains (in Serbian)*  
15 (Laboratory for Bioarchaeology, Faculty of Philosophy, Belgrade, 2016).
141. J. Jovanović, C. de Bechedelievre, S. Stefanović, I. Živaljević, V. Dimitrijević, G. Goude, Last hunters - first farmers: new insight into subsistence strategies in the Central Balkans through multi-isotopic analysis. *Archaeological and Anthropological Sciences.* **11**, 3279–3298 (2019).
142. C. de Bechedelievre, J. Jovanović, Z. Hofmanová, G. Goude, S. Stefanović, in *Farmers at the Frontier: A Pan*  
20 *European Perspective on Neolithisation*, K. J. Gron, L. Sørensen, P. Rowley-Conwy, Eds. (Oxbow Books, 2020; [https://books.google.com/books?hl=en&lr=&id=x3LSDwAAQBAJ&oi=fnd&pg=PA45&dq=de+Bechedeli%C3%A8vre+et+al.+2020&ots=h0aLGSdg4r&sig=E4R4R5W6ryrm\\_5W80qmJUg8AFy8](https://books.google.com/books?hl=en&lr=&id=x3LSDwAAQBAJ&oi=fnd&pg=PA45&dq=de+Bechedeli%C3%A8vre+et+al.+2020&ots=h0aLGSdg4r&sig=E4R4R5W6ryrm_5W80qmJUg8AFy8)), pp. 45–76.
143. S. Colledge, J. Conolly, E. Crema, S. Shennan, Neolithic population crash in northwest Europe associated with agricultural crisis. *Quat. Res.* **92**, 686–707 (2019).
- 25 144. C. Neugebauer-Maresch, E. Lenneis, *Das Linearbandkeramische Gräberfeld von Kleinhadersdorf. Mitteilungen der Prähistorischen Kommission 82* (Verlag der Österreichischen Akademie der Wissenschaften, Wien, 2015).
145. B. Boulestin, A. Zeeb-Lanz, C. Jeunesse, F. Haack, R.-M. Arbogast, A. Denaire, Mass cannibalism in the Linear Pottery Culture at Herxheim (Palatinate, Germany). *Antiquity.* **83**, 968–982 (2009).



146. B. Boulestin, A.-S. Coupey, *Cannibalism in the linear pottery culture: The human remains from Herxheim* (Archaeopress, Oxford, 2015; [http://www.academia.edu/download/39064371/Boulestin\\_\\_\\_Coupey\\_-\\_Cannibalism\\_in\\_the\\_Linear\\_Pottery\\_culture.pdf](http://www.academia.edu/download/39064371/Boulestin___Coupey_-_Cannibalism_in_the_Linear_Pottery_culture.pdf)).
147. J. Orschiedt, M. N. Haidle, in *Sticks, Stones, and Broken Bones: Neolithic Violence in a European Perspective*, R. J. Schulting, L. Fibiger, Eds. (Oxford University Press, Oxford, 2012), pp. 121–138.
148. M. Teschler-Nicola, in *Sticks, Stones, and Broken Bones: Neolithic Violence in a European Perspective*, R. J. Schulting, L. Fibiger, Eds. (Oxford University Press, Oxford, 2012), pp. 101–120.
149. H. J. Windl, in *Krisen – Kulturwandel – Kontinuitäten. Zum Ende der Bandkeramik in Mitteleuropa. Beiträge der internationalen Tagung in Herxheim bei Landau (Pfalz) vom 14.-17.06.2007.*, A. Zeeb-Lanz, Ed. (Verlag Marie Leidorf, Rahden, 2009), pp. 191–196.
150. A. Zeeb-Lanz, Ed., *Ritualised Destruction in the Early Neolithic – the Exceptional Site of Herxheim (Palatinate, Germany) Vol. 2* (Generaldirektion Kulturelles Erbe, Direktion Landesarchäologie, Speyer, 2019), vol. 8.2 of *Forschungen zur Pfälzischen Archäologie*.
151. A. Zeeb-Lanz, in *Ritualised Destruction in the Early Neolithic – the Exceptional Site of Herxheim (Palatinate, Germany) Vol. 2*, A. Zeeb-Lanz, Ed. (Generaldirektion Kulturelles Erbe, Direktion Landesarchäologie, Speyer, 2019), vol. 8.2 of *Forschungen zur Pfälzischen Archäologie*, pp. 423–482.
152. C. Budd, M. Lillie, S. Alpaslan-Roodenberg, N. Karul, R. Pinhasi, Stable isotope analysis of Neolithic and Chalcolithic populations from Aktopraklık, northern Anatolia. *Journal of Archaeological Science*. **40**, 860–867 (2013).
153. C. Budd, N. Karul, S. Alpaslan-Roodenberg, A. Galik, R. Schulting, M. Lillie, Diet uniformity at an early farming community in northwest Anatolia (Turkey): carbon and nitrogen isotope studies of bone collagen at Aktopraklık. *Archaeol. Anthropol. Sci.* **10**, 2123–2135 (2018).
154. M. S. Alpaslan-Roodenberg, J. Roodenberg, In the light of new data: The population of the first farming communities in the eastern Marmara region. *Praehistorische Zeitschrift*. **95** (2020), doi:10.1515/pz-2020-0004.
155. S. M. Alpaslan-Roodenberg, A Preliminary Study of the Burials from Late Neolithic-Early Chalcolithic Aktopraklık. *Anatolica*. **37**, 17–43 (2011).
156. I. Lazaridis, A. Mittnik, N. Patterson, S. Mallick, N. Rohland, S. Pfrenkle, A. Furtwängler, A. Peltzer, C. Posth, A. Vasilakis, P. J. P. McGeorge, E. Kouskoumaki, G. Korres, H. Martlew, M. Michalodimitrakis, M. Özsaıt, N. Özsaıt, A. Papathanasiou, M. Richards, S. A. Roodenberg, Y. Tzedakis, R. Arnott, D. M. Fernandes, J. R.

- Hughey, D. M. Lotakis, P. A. Navas, Y. Maniatis, J. A. Stamatoyannopoulos, K. Stewardson, P. Stockhammer, R. Pinhasi, D. Reich, J. Krause, G. Stamatoyannopoulos, Genetic origins of the Minoans and Mycenaeans. *Nature*. **548**, 214–218 (2017).
157. F. Gerritsen, R. Özbal, P. Gerrits, in *Metallurgica Anatolica. Festschrift für Ünsal Yalçın anlässlich seines 65. Geburtstag. Ünsal Yalçın 65. Yaşgünü Armağan Kitabı*, G. Yalçın, O. Stegemeier, Eds. (Bochum/Istanbul, 2020), pp. 35–43.
- 5 158. R. J. Rodden, G. W. Dimpleby, A. C. Western, E. H. Willis, E. S. Higgs, W. J. Clench, Excavations at the Early Neolithic Site at Nea Nikomedeia, Greek Macedonia (1961 season). *Proceedings of the Prehistoric Society*. **28**, 267–288 (1962).
159. R. J. Rodden, Recent discoveries from prehistoric Macedonia: an interim report. *Balkan Studies*. **5**, 109–124 (1964).
160. R. J. Rodden, An Early Neolithic Village in Greece. *Sci. Am*. **212**, 82–93 (1965).
161. G. Pyke, P. Yiouni, *Nea Nikomedeia I: The Excavation of an Early Neolithic Village in Northern Greece 1961-1964. The Excavation and the Ceramic Assemblage* (The British School at Athens, London, 1996), vol. 25 of *Supplementary Volume*.
- 15 162. R. J. Rodden, J. M. Rodden, A European Link with Chatal Huyuk: Uncovering a 7th Millennium Settlement in Macedonia. Part I - Site and Pottery. *The Illustrated London News*, 564–567 (1964).
163. J. L. Angel, in *Die Anfänge des Neolithikums vom Orient bis Nordeuropa. Teil VIIIa Anthropologie*, I. Schwidetzky, Ed. (Böhlau Verlag, Köln/Wien, 1973), vol. 3, pp. 103–112.
164. S. Triantaphyllou, *A Bioarchaeological Approach to Prehistoric Cemetery Populations from Western and Central Greek Macedonia* (Archaeopress, Oxford, 2001; [https://inis.iaea.org/search/search.aspx?orig\\_q=RN:31049032](https://inis.iaea.org/search/search.aspx?orig_q=RN:31049032)), vol. 976 of *BAR International Series*.
- 20 165. I. HersHKovitz, B. M. Rothschild, B. Latimer, O. Dutour, G. Léonetti, C. M. Greenwald, C. Rothschild, L. M. Jellema, Recognition of sickle cell anemia in skeletal remains of children. *Am. J. Phys. Anthropol.* **104**, 213–226 (1997).
- 25 166. D. J. Ortner, *Identification of Pathological Conditions in Human Skeletal Remains* (Academic Press, 2003; <https://play.google.com/store/books/details?id=k4WnC6U2YfoC>).
167. A. Lagia, C. Eliopoulos, S. Manolis, Thalassemia: macroscopic and radiological study of a case. *Int. J. Osteoarchaeol.* **17**, 269–285 (2007).

168. S. Stefanović, D. Borić, in *The Iron Gates in Prehistory: new perspectives*, BAR Int. Series 1893, C. Bonsall, V. Boroneanț, I. Radovanović, Eds. (Archaeopress, Oxford, 2008), pp. 131–169.
169. D. Borić, V. Dimitrijević, When did the “Neolithic package” reach Lepenski Vir? Radiometric and faunal evidence. *Documenta Praehistorica*. **34**, 53–72 (2007).
- 5 170. R. W. Ehrich, in *Ancient Europe and the Mediterranean*, V. Markotić, Ed. (Aris and Phillips, Warminster, 1977), pp. 59–67.
171. J. D. Jovanović, thesis, Belgrade (2017).
172. A. Whittle, L. Bartosiewicz, D. Borić, P. Pettitt, M. Richards, In the beginning: new radiocarbon dates for the Early Neolithic in Northern Serbia and South-East Hungary. *Antaeus*. **25**, 63–117 (2002).
- 10 173. A. T. Clason, Padina and Starčevo: game, fish and cattle. *Palaeohistoria*. **22**, 141–173 (1980).
174. J. Chapman, *Fragmentation in Archaeology. People, Places and Broken Objects in the Prehistory of South Eastern Europe* (Routledge, London/New York, 2000).
175. N. Tasić, D. Srejić, B. Stojanović, *Vinča: Centre of the Neolithic Culture of the Danubian Region* (Project Rastko, Belgrade, 1990; <https://www.bcin.ca/bcin/detail.app?id=388700>).
- 15 176. D. Borić, in *Metals and Societies: Studies in honour of Barbara S. Ottaway*, T. L. Kienlin, B. W. Roberts, Eds. (Verlag Dr. Rudolf Habelt, Bonn, 2009; <http://orca.cf.ac.uk/id/eprint/32490>), *Universitätsforschungen zur prähistorischen Archäologie*, pp. 191–245.
177. O. Nehlich, D. Borić, S. Stefanović, M. P. Richards, Sulphur isotope evidence for freshwater fish consumption: a case study from the Danube Gorges, SE Europe. *Journal of Archaeological Science*. **37**, 1131–1139 (2010).
- 20 178. N. Tasić, M. Marić, C. Bronk Ramsey, B. Kromer, A. Barclay, A. Bayliss, N. Beavan, B. Gaydarska, A. Whittle, Vinča-Belo Brdo, Serbia: The times of a tell. *Germania*. **93**, 1–75 (2015).
179. H. J. Windl, Makabres Ende einer Kultur? *Archäologie in Deutschland*. **1**, 54–57 (1999).
180. E. M. Wild, P. Stadler, A. Häußler, W. Kutschera, P. Steier, M. Teschler-Nicola, J. Wahl, H. J. Windl, Neolithic Massacres: Local Skirmishes or General Warfare in Europe? *Radiocarbon*. **46**, 377–385 (2004).
- 25 181. B. Tiefenböck, M. Teschler-Nicola, in *Das Linearbandkeramische Gräberfeld von Kleinhadersdorf. Mitteilungen der Prähistorischen Kommission* 82, C. Neugebauer-Maresch, E. Lenneis, Eds. (Verlag der Österreichischen Akademie der Wissenschaften, Wien, 2015), pp. 297–392.

182. I. Mateiciucová, in *Das Linearbandkeramische Gräberfeld von Kleinhadersdorf*, C. Neugebauer-Maresch, E. Lenneis, Eds. (Verlag der Österreichischen Akademie der Wissenschaften, 2015), vol. 82 of *Mitteilungen der Prähistorischen Kommission*, pp. 111–122.
183. P. Bickle, D. Hofmann, R. A. Bentley, R. Hedges, J. Hamilton, F. Lainghas, G. Nowell, D. G. Pearson, A. Whittle, in *Das Linearbandkeramische Gräberfeld von Kleinhadersdorf. Mitteilungen der Prähistorischen Kommission* 82, C. Neugebauer-Maresch, E. Lenneis, Eds. (Verlag der Österreichischen Akademie der Wissenschaften, Wien, 2015), pp. 173–177.
184. H. Brink-Kloke, *Das linienbandkeramische Gräberfeld von Essenbach-Ammerbreite*, Ldkr. Landshut, Niederbayern. *Germania*. **68**, 427–481 (1990).
185. N. Nieszery, *Linearbandkeramische Gräberfelder in Bayern* (Verlag Marie Leidorf, Rahden, 1995).
186. H. Dietrich, C. Kociumaka, Jungsteinzeitliche Befunde aus Steinheim: Stadt und Landkreis Dillingen ad Donau, Schwaben. *Das Archäologische Jahr in Bayern* 2000, 32–35 (2001).
187. J. Pechtl, *Zeit und Umwelt. Ein Forschungsprojekt zur ersten bäuerlichen Kultur in Bayerisch-Schwaben. Denkmalpflege Informationen*. **161**, 14–17 (2015).
188. F. Haack, in *Ritualised Destruction in the Early Neolithic - The Exceptional Site of Herxheim (Palatinate, Germany)*, A. Zeeb-Lanz, Ed. (Generaldirektion Kulturelles Erbe Rheinland-Pfalz, Speyer, 2016), *Forschungen zur Pfälzischen Archäologie* 8.1, pp. 19–118.
189. A. Zeeb-Lanz, Ed., *Ritualised Destruction in the Early Neolithic – the Exceptional Site of Herxheim (Palatinate, Germany) Vol. 1* (Generaldirektion Kulturelles Erbe, Direktion Landesarchäologie, Speyer, 2016), vol. 8.1 of *Forschungen zur Pfälzischen Archäologie*.
190. R. Turck, in *Ritualised Destruction in the Early Neolithic – the Exceptional Site of Herxheim (Palatinate, Germany) Vol. 2*, A. Zeeb-Lanz, Ed. (Generaldirektion Kulturelles Erbe, Direktion Landesarchäologie, Speyer, 2019), vol. 8.2 of *Forschungen zur Pfälzischen Archäologie* , pp. 313–421.
191. K. Riedhammer, in *Ritualised Destruction in the Early Neolithic – the Exceptional Site of Herxheim (Palatinate, Germany)*, Vol. 2, A. Zeeb-Lanz, Ed. (Generaldirektion Kulturelles Erbe, Direktion Landesarchäologie, Speyer , 2019), vol. 8.2 of *Forschungen zur Pfälzischen Archäologie*, pp. 285–304.
192. J. Hoefs, *Stable Isotope Geochemistry* (Springer-Verlag Berlin Heidelberg, Berlin, 2009).

193. E. Cristiani, A. Radini, D. Borić, H. K. Robson, I. Caricola, M. Carra, G. Mutri, G. Oxilia, A. Zupancich, M. Šlaus, D. Vujević, Dental calculus and isotopes provide direct evidence of fish and plant consumption in Mesolithic Mediterranean. *Scientific Reports*. **8**, 8147 (2018).
194. M. P. Richards, R. E. M. Hedges, Stable Isotope Evidence for Similarities in the Types of Marine Foods Used by Late Mesolithic Humans at Sites Along the Atlantic Coast of Europe. *Journal of Archaeological Science*. **26** (1999), pp. 717–722.
195. M. J. Schoeninger, M. J. DeNiro, Carbon isotope ratios of apatite from fossil bone cannot be used to reconstruct diets of animals. *Nature*. **297**, 577–578 (1982).
196. S. H. Ambrose, Effects of diet, climate and physiology on nitrogen isotope abundances in terrestrial foodwebs. *J. Archaeol. Sci.* **18**, 293–317 (1991).
197. M. L. Fogel, N. Tuross, D. W. Owsley, Nitrogen isotope tracers of human lactation in modern and archaeological populations. *Carnegie Institution of Washington Yearbook*. **88**, 111–117 (1989).
198. B. T. Fuller, J. L. Fuller, D. A. Harris, R. E. M. Hedges, Detection of breastfeeding and weaning in modern human infants with carbon and nitrogen stable isotope ratios. *Am. J. Phys. Anthropol.* **129**, 279–293 (2006).
199. P. Bickle, Stable isotopes and dynamic diets: The Mesolithic-Neolithic dietary transition in terrestrial central Europe. *Journal of Archaeological Science: Reports*. **22**, 444–451 (2018).
200. C. Bonsall, R. Lennon, K. McSweeney, C. Stewart, D. Harkness, V. Boronean, L. Bartosiewicz, R. Payton, J. Chapman, Mesolithic and Early Neolithic in the Iron Gates: A Paiaeodietary Perspective. *Journal of European Archaeology*. **5**, 50–92 (1997).
201. C. Bonsall, V. Boronean, I. Radovanović, *The Iron Gates in prehistory: new perspectives* (Archaeopress, Oxford, 2008), vol. 1893 of *BAR International Series*.
202. C. Bonsall, A. Boronean, A. Simalsik, T. Higham, in *Southeast Europe and Anatolia in prehistory. Essays in honor of Vassil Nikolov on his 65th anniversary*, K. Bacvarov, R. Gleser, Eds. (Verlag Dr. Rudolf Habelt, Bonn, 2016), vol. 293 of *Universitätsforschungen zur Prähistorischen Archäologie*, pp. 41–50.
203. D. Borić, Lepenski Vir chronology and stratigraphy revisited. *Starinar*, 9–60 (2019).
204. A. Papathanasiou, Stable isotope analysis in Neolithic Greece and possible implications on human health. *Int. J. Osteoarchaeol.* **13**, 314–324 (2003).
205. A. Papathanasiou, in *Human Bioarchaeology of the Transition to Agriculture*, R. Pinhasi, J. Stock, Eds. (John Wiley & Sons, Ltd Chichester, Hoboken, 2011; <https://www.academia.edu/download/44884601/c05.pdf>), pp. 87–106.

206. P. Vaiglova, A. Bogaard, M. Collins, W. Cavanagh, C. Mee, J. Renard, A. Lamb, A. Gardeisen, R. Fraser, An integrated stable isotope study of plants and animals from Kouphovouno, southern Greece: a new look at Neolithic farming. *J. Archaeol. Sci.* **42**, 201–215 (2014).
207. A. Papathanasiou, Stable Isotope Analyses in Neolithic and Bronze Age Greece: An Overview. *Hesperia Supplements*. **49**, 25–55 (2015).
208. H. Ringbauer, J. Novembre, M. Steinruecken, Detecting runs of homozygosity from low-coverage ancient DNA. *bioRxiv* (2020) (available at <https://www.biorxiv.org/content/10.1101/2020.05.31.126912v1.abstract>).
209. F. C. Ceballos, K. Gürün, N. Ezgi Altınışık, H. C. Gemici, C. Karamurat, D. Koptekin, K. B. Vural, E. Sürer, Y. S. Erdal, A. Götherström, F. Özer, Ç. Atakuman, M. Somel, Human inbreeding has decreased in time through the Holocene. *bioRxiv* (2020), doi:10.1101/2020.09.24.311597.
210. S. Gazal, M. Sahbatou, H. Perdry, S. Letort, E. Génin, A.-L. Leutenegger, Inbreeding coefficient estimation with dense SNP data: comparison of strategies and application to HapMap III. *Hum. Hered.* **77**, 49–62 (2014).
211. G. González-Fortes, E. R. Jones, E. Lightfoot, C. Bonsall, C. Lazar, A. Grandal-d’Anglade, M. D. Garralda, L. Drak, V. Siska, A. Simalcsik, A. Boroneanț, J. R. Vidal Romaní, M. Vaqueiro Rodríguez, P. Arias, R. Pinhasi, A. Manica, M. Hofreiter, Paleogenomic Evidence for Multi-generational Mixing between Neolithic Farmers and Mesolithic Hunter-Gatherers in the Lower Danube Basin. *Curr. Biol.* **27**, 1801–1810.e10 (2017).
212. A. Mittnik, K. Massy, C. Knipper, F. Wittenborn, R. Friedrich, S. Pfrengle, M. Burri, N. Carlich-Witjes, H. Deeg, A. Furtwängler, M. Harbeck, K. von Heyking, C. Kociumaka, I. Kucukkalipci, S. Lindauer, S. Metz, A. Staskiewicz, A. Thiel, J. Wahl, W. Haak, E. Pernicka, S. Schiffels, P. W. Stockhammer, J. Krause, Kinship-based social inequality in Bronze Age Europe. *Science*. **366**, 731–734 (2019).
213. I. Olalde, S. Brace, M. E. Allentoft, I. Armit, K. Kristiansen, T. Booth, N. Rohland, S. Mallick, A. Szécsényi-Nagy, A. Mittnik, E. Altena, M. Lipson, I. Lazaridis, T. K. Harper, N. Patterson, N. Broomandkoshbacht, Y. Diekmann, Z. Faltyskova, D. Fernandes, M. Ferry, E. Harney, P. de Knijff, M. Michel, J. Oppenheimer, K. Stewardson, A. Barclay, K. W. Alt, C. Liesau, P. Ríos, C. Blasco, J. V. Miguel, R. M. García, A. A. Fernández, E. Bánffy, M. Bernabò-Brea, D. Billoin, C. Bonsall, L. Bonsall, T. Allen, L. Büster, S. Carver, L. C. Navarro, O. E. Craig, G. T. Cook, B. Cunliffe, A. Denaire, K. E. Dinwiddy, N. Dodwell, M. Ernée, C. Evans, M. Kuchařík, J. F. Farré, C. Fowler, M. Gazenbeek, R. G. Pena, M. Haber-Uriarte, E. Haduch, G. Hey, N. Jowett, T. Knowles, K. Massy, S. Pfrengle, P. Lefranc, O. Lemercier, A. Lefebvre, C. H. Martínez, V. G. Olmo, A. B. Ramírez, J. L. Maurandi, T. Majó, J. I. McKinley, K. McSweeney, B. G. Mende, A. Modi, G. Kulcsár, V. Kiss, A. Czene, R. Patay, A. Endrődi,

- K. Köhler, T. Hajdu, T. Szeniczey, J. Dani, Z. Bernert, M. Hoole, O. Cheronet, D. Keating, P. Velemínský, M. Dobeš, F. Candilio, F. Brown, R. F. Fernández, A.-M. Herrero-Corral, S. Tusa, E. Carnieri, L. Lentini, A. Valenti, A. Zanini, C. Waddington, G. Delibes, E. Guerra-Doce, B. Neil, M. Brittain, M. Luke, R. Mortimer, J. Desideri, M. Besse, G. Brücken, M. Furmanek, A. Hałuszko, M. Mackiewicz, A. Rapiński, S. Leach, I. Soriano, K. T. Lillios, J. L. Cardoso, M. P. Pearson, P. Włodarczak, T. D. Price, P. Prieto, P.-J. Rey, R. Risch, M. A. Rojo Guerra, A. Schmitt, J. Serralongue, A. M. Silva, V. Smrčka, L. Vergnaud, J. Zilhão, D. Caramelli, T. Higham, M. G. Thomas, D. J. Kennett, H. Fokkens, V. Heyd, A. Sheridan, K.-G. Sjögren, P. W. Stockhammer, J. Krause, R. Pinhasi, W. Haak, I. Barnes, C. Lalueza-Fox, D. Reich, The Beaker phenomenon and the genomic transformation of northwest Europe. *Nature*. **555**, 190–196 (2018).
214. I. Olalde, S. Mallick, N. Patterson, N. Rohland, V. Villalba-Mouco, M. Silva, K. Dulias, C. J. Edwards, F. Gandini, M. Pala, P. Soares, M. Ferrando-Bernal, N. Adamski, N. Broomandkoshbacht, O. Cheronet, B. J. Culleton, D. Fernandes, A. M. Lawson, M. Mah, J. Oppenheimer, K. Stewardson, Z. Zhang, J. M. Jiménez Arenas, I. J. Toro Moyano, D. C. Salazar-García, P. Castanyer, M. Santos, J. Tremoleda, M. Lozano, P. García Borja, J. Fernández-Eraso, J. A. Mujika-Alustiza, C. Barroso, F. J. Bermúdez, E. Viguera Mínguez, J. Burch, N. Coromina, D. Vivó, A. Cebrià, J. M. Fullola, O. García-Puchol, J. I. Morales, F. X. Oms, T. Majó, J. M. Vergès, A. Díaz-Carvajal, I. Ollich-Castanyer, F. J. López-Cachero, A. M. Silva, C. Alonso-Fernández, G. Delibes de Castro, J. Jiménez Echevarría, A. Moreno-Márquez, G. Pascual Berlanga, P. Ramos-García, J. Ramos-Muñoz, E. Vijande Vila, G. Aguilera Arzo, Á. Esparza Arroyo, K. T. Lillios, J. Mack, J. Velasco-Vázquez, A. Waterman, L. Benítez de Lugo Enrich, M. Benito Sánchez, B. Agustí, F. Codina, G. de Prado, A. Estalrich, Á. Fernández Flores, C. Finlayson, G. Finlayson, S. Finlayson, F. Giles-Guzmán, A. Rosas, V. Barciela González, G. García Atiénzar, M. S. Hernández Pérez, A. Llanos, Y. Carrión Marco, I. Collado Beneyto, D. López-Serrano, M. Sanz Tormo, A. C. Valera, C. Blasco, C. Liesau, P. Ríos, J. Daura, M. J. de Pedro Michó, A. A. Diez-Castillo, R. Flores Fernández, J. Francès Farré, R. Garrido-Pena, V. S. Gonçalves, E. Guerra-Doce, A. M. Herrero-Corral, J. Juan-Cabanilles, D. López-Reyes, S. B. McClure, M. Merino Pérez, A. Oliver Foix, M. Sanz Borràs, A. C. Sousa, J. M. Vidal Encinas, D. J. Kennett, M. B. Richards, K. Werner Alt, W. Haak, R. Pinhasi, C. Lalueza-Fox, D. Reich, The genomic history of the Iberian Peninsula over the past 8000 years. *Science*. **363**, 1230–1234 (2019).
215. P. Brotherton, W. Haak, J. Templeton, G. Brandt, J. Soubrier, C. Jane Adler, S. M. Richards, C. Der Sarkissian, R. Ganslmeier, S. Friederich, V. Dresely, M. van Oven, R. Kenyon, M. B. Van der Hoek, J. Korfach, K. Luong, S. Y.

- W. Ho, L. Quintana-Murci, D. M. Behar, H. Meller, K. W. Alt, A. Cooper, Genographic Consortium, Neolithic mitochondrial haplogroup H genomes and the genetic origins of Europeans. *Nat. Commun.* **4**, 1764 (2013).
216. M. Coll Macià, L. Skov, B. M. Peter, M. H. Schierup, Different historical generation intervals in human populations inferred from Neanderthal fragment lengths and mutation signatures. *Nat. Commun.* **12**, 5317 (2021).
- 5 217. J. Latreille, K. Ezzedine, A. Elfakir, L. Ambroisine, S. Gardinier, P. Galan, S. Hercberg, F. Gruber, J. Rees, E. Tschachler, C. Guinot, MC1R gene polymorphism affects skin color and phenotypic features related to sun sensitivity in a population of French adult women. *Photochem. Photobiol.* **85**, 1451–1458 (2009).
218. K. Yamaguchi, C. Watanabe, A. Kawaguchi, T. Sato, I. Naka, M. Shindo, K. Moromizato, K. Aoki, H. Ishida, R. Kimura, Association of melanocortin 1 receptor gene (MC1R) polymorphisms with skin reflectance and freckles in  
10 Japanese. *J. Hum. Genet.* **57**, 700–708 (2012).
219. R. M. Harding, E. Healy, A. J. Ray, N. S. Ellis, N. Flanagan, C. Todd, C. Dixon, A. Sajantila, I. J. Jackson, M. A. Birch-Machin, J. L. Rees, Evidence for variable selective pressures at MC1R. *Am. J. Hum. Genet.* **66**, 1351–1361 (2000).
220. L. L. Cavalli-Sforza, A. Moroni, G. Zei, *Consanguinity, Inbreeding, and Genetic Drift in Italy* (Princeton University  
15 Press, 2004; <https://play.google.com/store/books/details?id=wap7N9PFJJ4C>).
221. N. S. Enattah, T. Sahi, E. Savilahti, J. D. Terwilliger, L. Peltonen, I. Järvelä, Identification of a variant associated with adult-type hypolactasia. *Nat. Genet.* **30**, 233–237 (2002).
222. J. Burger, V. Link, J. Blöcher, A. Schulz, C. Sell, Z. Pochon, Y. Diekmann, A. Žegarac, Z. Hofmanová, L. Winkelbach, C. S. Reyna-Blanco, V. Bieker, J. Orschiedt, U. Brinker, A. Scheu, C. Leuenberger, T. S. Bertino, R.  
20 Bollongino, G. Lidke, S. Stefanović, D. Jantzen, E. Kaiser, T. Terberger, M. G. Thomas, K. R. Veeramah, D. Wegmann, Low Prevalence of Lactase Persistence in Bronze Age Europe Indicates Ongoing Strong Selection over the Last 3,000 Years. *Curr. Biol.* (2020), doi:10.1016/j.cub.2020.08.033.
223. J.-H. Park, T. Yamaguchi, C. Watanabe, A. Kawaguchi, K. Haneji, M. Takeda, Y.-I. Kim, Y. Tomoyasu, M. Watanabe, H. Oota, T. Hanihara, H. Ishida, K. Maki, S.-B. Park, R. Kimura, Effects of an Asian-specific  
25 nonsynonymous EDAR variant on multiple dental traits. *J. Hum. Genet.* **57**, 508–514 (2012).
224. D. Shang, X. Zhang, M. Sun, Y. Wei, Y. Wen, Strong association of the SNP rs17822931 with wet earwax and bromhidrosis in a Chinese family. *J. Genet.* **92**, 289–291 (2013).
225. A. Fujimoto, R. Kimura, J. Ohashi, K. Omi, R. Yuliwulandari, L. Batubara, M. S. Mustofa, U. Samakkarn, W. Settheetham-Ishida, T. Ishida, Y. Morishita, T. Furusawa, M. Nakazawa, R. Ohtsuka, K. Tokunaga, A scan for



- genetic determinants of human hair morphology: EDAR is associated with Asian hair thickness. *Hum. Mol. Genet.* **17**, 835–843 (2008).
226. Y. Xue, X. Zhang, N. Huang, A. Daly, C. J. Gillson, D. G. Macarthur, B. Yngvadottir, A. C. Nica, C. Woodwark, Y. Chen, D. F. Conrad, Q. Ayub, S. Q. Mehdi, P. Li, C. Tyler-Smith, Population differentiation as an indicator of recent positive selection in humans: an empirical evaluation. *Genetics*. **183**, 1065–1077 (2009).
227. J. Ohashi, I. Naka, N. Tsuchiya, The Impact of Natural Selection on an ABCC11 SNP Determining Earwax Type. *Mol. Biol. Evol.* **28**, 849–857 (2010).
228. M. Fumagalli, I. Moltke, N. Grarup, F. Racimo, P. Bjerregaard, M. E. Jørgensen, T. S. Korneliussen, P. Gerbault, L. Skotte, A. Linneberg, C. Christensen, I. Brandslund, T. Jørgensen, E. Huerta-Sánchez, E. B. Schmidt, O. Pedersen, T. Hansen, A. Albrechtsen, R. Nielsen, Greenlandic Inuit show genetic signatures of diet and climate adaptation. *Science*. **349**, 1343–1347 (2015).
229. M. T. Buckley, F. Racimo, M. E. Allentoft, M. K. Jensen, A. Jonsson, H. Huang, F. Hormozdiari, M. Sikora, D. Marnetto, E. Eskin, M. E. Jørgensen, N. Grarup, O. Pedersen, T. Hansen, P. Kraft, E. Willerslev, R. Nielsen, Selection in Europeans on Fatty Acid Desaturases Associated with Dietary Changes. *Mol. Biol. Evol.* **34**, 1307–1318 (2017).
230. A. Ameer, S. Enroth, A. Johansson, G. Zaboli, W. Igl, A. C. V. Johansson, M. A. Rivas, M. J. Daly, G. Schmitz, A. A. Hicks, T. Meitinger, L. Feuk, C. van Duijn, B. Oostra, P. P. Pramstaller, I. Rudan, A. F. Wright, J. F. Wilson, H. Campbell, U. Gyllensten, Genetic adaptation of fatty-acid metabolism: a human-specific haplotype increasing the biosynthesis of long-chain omega-3 and omega-6 fatty acids. *Am. J. Hum. Genet.* **90**, 809–820 (2012).
231. E. Marouli, M. Graff, C. Medina-Gomez, K. S. Lo, A. R. Wood, T. R. Kjaer, R. S. Fine, Y. Lu, C. Schurmann, H. M. Highland, S. Rieger, G. Thorleifsson, A. E. Justice, D. Lamparter, K. E. Stirrups, V. Turcot, K. L. Young, T. W. Winkler, T. Esko, T. Karaderi, A. E. Locke, N. G. D. Masca, M. C. Y. Ng, P. Mudgal, M. A. Rivas, S. Vedantam, A. Mahajan, X. Guo, G. Abecasis, K. K. Aben, L. S. Adair, D. S. Alam, E. Albrecht, K. H. Allin, M. Allison, P. Amouyel, E. V. Appel, D. Arveiler, F. W. Asselbergs, P. L. Auer, B. Balkau, B. Banas, L. E. Bang, M. Benn, S. Bergmann, L. F. Bielak, M. Blüher, H. Boeing, E. Boerwinkle, C. A. Böger, L. L. Bonnycastle, J. Bork-Jensen, M. L. Bots, E. P. Bottinger, D. W. Bowden, I. Brandslund, G. Breen, M. H. Brilliant, L. Broer, A. A. Burt, A. S. Butterworth, D. J. Carey, M. J. Caulfield, J. C. Chambers, D. I. Chasman, Y.-D. I. Chen, R. Chowdhury, C. Christensen, A. Y. Chu, M. Cocca, F. S. Collins, J. P. Cook, J. Corley, J. C. Galbany, A. J. Cox, G. Cuellar-Partida, J. Danesh, G. Davies, P. I. W. de Bakker, G. J. de Borst, S. de Denus, M. C. H. de Groot, R. de Mutsert, I. J. Deary,

G. Dedoussis, E. W. Demerath, A. I. den Hollander, J. G. Dennis, E. Di Angelantonio, F. Drenos, M. Du, A. M. Dunning, D. F. Easton, T. Ebeling, T. L. Edwards, P. T. Ellinor, P. Elliott, E. Evangelou, A. -E. Farmaki, J. D. Faul, M. F. Feitosa, S. Feng, E. Ferrannini, M. M. Ferrario, J. Ferrieres, J. C. Florez, I. Ford, M. Fornage, P. W. Franks, R. Frikke-Schmidt, T. E. Galesloot, W. Gan, I. Gandin, P. Gasparini, V. Giedraitis, A. Giri, G. Girotto, S. D. Gordon, P. Gordon-Larsen, M. Gorski, N. Grarup, M. L. Grove, V. Gudnason, S. Gustafsson, T. Hansen, K. M. Harris, T. B. Harris, A. T. Hattersley, C. Hayward, L. He, I. M. Heid, K. Heikkilä, Ø. Helgeland, J. Hernesniemi, A. W. Hewitt, L. J. Hocking, M. Hollensted, O. L. Holmen, G. K. Hovingh, J. M. M. Howson, C. B. Hoyng, P. L. Huang, K. Hveem, M. A. Ikram, E. Ingelsson, A. U. Jackson, J.-H. Jansson, G. P. Jarvik, G. B. Jensen, M. A. Jhun, Y. Jia, X. Jiang, S. Johansson, M. E. Jørgensen, T. Jørgensen, P. Jousilahti, J. W. Jukema, B. Kahali, R. S. Kahn, M. Kähönen, P. R. Kamstrup, S. Kanoni, J. Kaprio, M. Karaleftheri, S. L. R. Kardia, F. Karpe, F. Kee, R. Keeman, L. A. Kiemeny, H. Kitajima, K. B. Kluivers, T. Kocher, P. Komulainen, J. Kontto, J. S. Kooner, C. Kooperberg, P. Kovacs, J. Kriebel, H. Kuivaniemi, S. Küry, J. Kuusisto, M. La Bianca, M. Laakso, T. A. Lakka, E. M. Lange, L. A. Lange, C. D. Langefeld, C. Langenberg, E. B. Larson, I.-T. Lee, T. Lehtimäki, C. E. Lewis, H. Li, J. Li, R. Li-Gao, H. Lin, L.-A. Lin, X. Lin, L. Lind, J. Lindström, A. Linneberg, Y. Liu, Y. Liu, A. Lophatananon, J. 'an Luan, S. A. Lubitz, L.-P. Lyytikäinen, D. A. Mackey, P. A. F. Madden, A. K. Manning, S. Männistö, G. Marenne, J. Marten, N. G. Martin, A. L. Mazul, K. Meidtner, A. Metspalu, P. Mitchell, K. L. Mohlke, D. O. Mook-Kanamori, A. Morgan, A. D. Morris, A. P. Morris, M. Müller-Nurasyid, P. B. Munroe, M. A. Nalls, M. Nauck, C. P. Nelson, M. Neville, S. F. Nielsen, K. Nikus, P. R. Njølstad, B. G. Nordestgaard, I. Ntalla, J. R. O'Connel, H. Oksa, L. M. O. Loohuis, R. A. Ophoff, K. R. Owen, C. J. Packard, S. Padmanabhan, C. N. A. Palmer, G. Pasterkamp, A. P. Patel, A. Pattie, O. Pedersen, P. L. Peissig, G. M. Peloso, C. E. Pennell, M. Perola, J. A. Perry, J. R. B. Perry, T. N. Person, A. Pirie, O. Polasek, D. Posthuma, O. T. Raitakari, A. Rasheed, R. Rauramaa, D. F. Reilly, A. P. Reiner, F. Renström, P. M. Ridker, J. D. Rioux, N. Robertson, A. Robino, O. Rolandsson, I. Rudan, K. S. Ruth, D. Saleheen, V. Salomaa, N. J. Samani, K. Sandow, Y. Sapkota, N. Sattar, M. K. Schmidt, P. J. Schreiner, M. B. Schulze, R. A. Scott, M. P. Segura-Lepe, S. Shah, X. Sim, S. Sivapalaratnam, K. S. Small, A. V. Smith, J. A. Smith, L. Southam, T. D. Spector, E. K. Speliotes, J. M. Starr, V. Steinthorsdottir, H. M. Stringham, M. Stumvoll, P. Surendran, L. M. 't Hart, K. E. Tansey, J.-C. Tardif, K. D. Taylor, A. Teumer, D. J. Thompson, U. Thorsteinsdottir, B. H. Thuesen, A. Tönjes, G. Tromp, S. Trompet, E. Tsafantakis, J. Tuomilehto, A. Tybjaerg-Hansen, J. P. Tyrer, R. Uher, A. G. Uitterlinden, S. Ulivi, S. W. van der Laan, A. R. Van Der Leij, C. M. van Duijn, N. M. van Schoor, J. van Setten, A. Varbo, T. V. Varga, R. Varma, D. R. V. Edwards, S. H. Vermeulen, H. Vestergaard, V. Vitart, T. F. Vogt, D. Vozzi, M. Walker,

- F. Wang, C. A. Wang, S. Wang, Y. Wang, N. J. Wareham, H. R. Warren, J. Wessel, S. M. Willems, J. G. Wilson, D. R. Witte, M. O. Woods, Y. Wu, H. Yaghootkar, J. Yao, P. Yao, L. M. Yerges-Armstrong, R. Young, E. Zeggini, X. Zhan, W. Zhang, J. H. Zhao, W. Zhao, W. Zhao, H. Zheng, W. Zhou, EPIC-InterAct Consortium, CHD Exome+ Consortium, ExomeBP Consortium, T2D-Genes Consortium, GoT2D Genes Consortium, Global Lipids Genetics Consortium, ReproGen Consortium, MAGIC Investigators, J. I. Rotter, M. Boehnke, S. Kathiresan, M. I. McCarthy, C. J. Willer, K. Stefansson, I. B. Borecki, D. J. Liu, K. E. North, N. L. Heard-Costa, T. H. Pers, C. M. Lindgren, C. Oxvig, Z. Kutalik, F. Rivadeneira, R. J. F. Loos, T. M. Frayling, J. N. Hirschhorn, P. Deloukas, G. Lettre, Rare and low-frequency coding variants alter human adult height. *Nature*. **542**, 186–190 (2017).
232. M. Zoledziewska, UK10K Consortium, C. Sidore, C. W. K. Chiang, S. Sanna, A. Mulas, M. Steri, F. Busonero, J. H. Marcus, M. Marongiu, A. Maschio, D. O. Del Vecchio, M. Floris, A. Meloni, A. Delitala, M. P. Concas, F. Murgia, G. Biino, S. Vaccargiu, R. Nagaraja, K. E. Lohmueller, N. J. Timpson, N. Soranzo, I. Tachmazidou, G. Dedoussis, E. Zeggini, S. Uzzau, C. Jones, R. Lyons, A. Angius, G. R. Abecasis, J. Novembre, D. Schlessinger, F. Cucca, The Understanding Society Scientific Group, Height-reducing variants and selection for short stature in Sardinia. *Nature Genetics*. **47** (2015), pp. 1352–1356.
233. E. Rosenstock, J. Ebert, R. Martin, A. Hicketier, P. Walter, M. Groß, Human stature in the Near East and Europe ca. 10,000–1000 BC: its spatiotemporal development in a Bayesian errors-in-variables model. *Archaeol. Anthropol. Sci.* **11**, 5657–5690 (2019).
234. S. L. Cox, C. B. Ruff, R. M. Maier, I. Mathieson, Genetic contributions to variation in human stature in prehistoric Europe. *Proc. Natl. Acad. Sci. U. S. A.* **116**, 21484–21492 (2019).
235. A.-S. Malaspinas, M. C. Westaway, C. Muller, V. C. Sousa, O. Lao, I. Alves, A. Bergström, G. Athanasiadis, J. Y. Cheng, J. E. Crawford, T. H. Heupink, E. Macholdt, S. Peischl, S. Rasmussen, S. Schiffels, S. Subramanian, J. L. Wright, A. Albrechtsen, C. Barbieri, I. Dupanloup, A. Eriksson, A. Margaryan, I. Moltke, I. Pugach, T. S. Korneliussen, I. P. Levkivskyi, J. V. Moreno-Mayar, S. Ni, F. Racimo, M. Sikora, Y. Xue, F. A. Aghakhanian, N. Brucato, S. Brunak, P. F. Campos, W. Clark, S. Ellingvåg, G. Fourmile, P. Gerbault, D. Injie, G. Koki, M. Leavesley, B. Logan, A. Lynch, E. A. Matisoo-Smith, P. J. McAllister, A. J. Mentzer, M. Metspalu, A. B. Migliano, L. Murgha, M. E. Phipps, W. Pomat, D. Reynolds, F.-X. Ricaut, P. Siba, M. G. Thomas, T. Wales, C. M. Wall, S. J. Oppenheimer, C. Tyler-Smith, R. Durbin, J. Dortch, A. Manica, M. H. Schierup, R. A. Foley, M. M. Lahr, C. Bowern, J. D. Wall, T. Mailund, M. Stoneking, R. Nielsen, M. S. Sandhu, L. Excoffier, D. M. Lambert, E. Willerslev, A genomic history of Aboriginal Australia. *Nature*. **538**, 207–214 (2016).

236. A. C. Beichman, T. N. Phung, K. E. Lohmueller, Comparison of single genome and allele frequency data reveals discordant demographic histories. *G3: Genes, Genomes, Genetics*. **7**, 3605–3620 (2017).
237. S. Wahlund, Zusammensetzung von Populationen und Korrelationserscheinungen vom Standpunkt der Vererbungslehre aus betrachtet. *Hereditas*. **11**, 65–106 (1928).
- 5 238. M. de Manuel, M. Kuhlwilm, P. Frandsen, V. C. Sousa, T. Desai, J. Prado-Martinez, J. Hernandez-Rodriguez, I. Dupanloup, O. Lao, P. Hallast, J. M. Schmidt, J. M. Heredia-Genestar, A. Benazzo, G. Barbujani, B. M. Peter, L. F. K. Kuderna, F. Casals, S. Angedakin, M. Arandjelovic, C. Boesch, H. Kühl, L. Vigilant, K. Langergraber, J. Novembre, M. Gut, I. Gut, A. Navarro, F. Carlsen, A. M. Andrés, H. R. Siegismund, A. Scally, L. Excoffier, C. Tyler-Smith, S. Castellano, Y. Xue, C. Hvilsom, T. Marques-Bonet, Chimpanzee genomic diversity reveals ancient admixture with bonobos. *Science*. **354**, 477–481 (2016).
- 10 239. N. Marchi, L. Excoffier, Gene flow as a simple cause for an excess of high-frequency-derived alleles. *Evol. Appl.*, 1–10 (2020).
240. M. Slatkin, Seeing ghosts: the effect of unsampled populations on migration rates estimated for sampled populations. *Mol. Ecol.* **14**, 67–73 (2005).
- 15 241. P. Beerli, Effect of unsampled populations on the estimation of population sizes and migration rates between sampled populations. *Mol. Ecol.* **13**, 827–836 (2004).
242. L. Excoffier, Patterns of DNA sequence diversity and genetic structure after a range expansion: lessons from the infinite-island model. *Mol. Ecol.* **13**, 853–864 (2004).
243. M. Gallego-Llorente, S. Connell, E. R. Jones, D. C. Merrett, Y. Jeon, A. Eriksson, V. Siska, C. Gamba, C. Meiklejohn, R. Beyer, S. Jeon, Y. S. Cho, M. Hofreiter, J. Bhak, A. Manica, R. Pinhasi, The genetics of an early Neolithic pastoralist from the Zagros, Iran. *Sci. Rep.* **6**, 31326 (2016).
- 20

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15

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**Data and materials availability:** Sequences will be made available at the European Nucleotide

20 Archive. ATLAS pipeline commit 6df90e7 is available at:

<https://bitbucket.org/wegmannlab/atlas-pipeline/src/master/>. Other bioinformatic codes will be  
made available upon request.

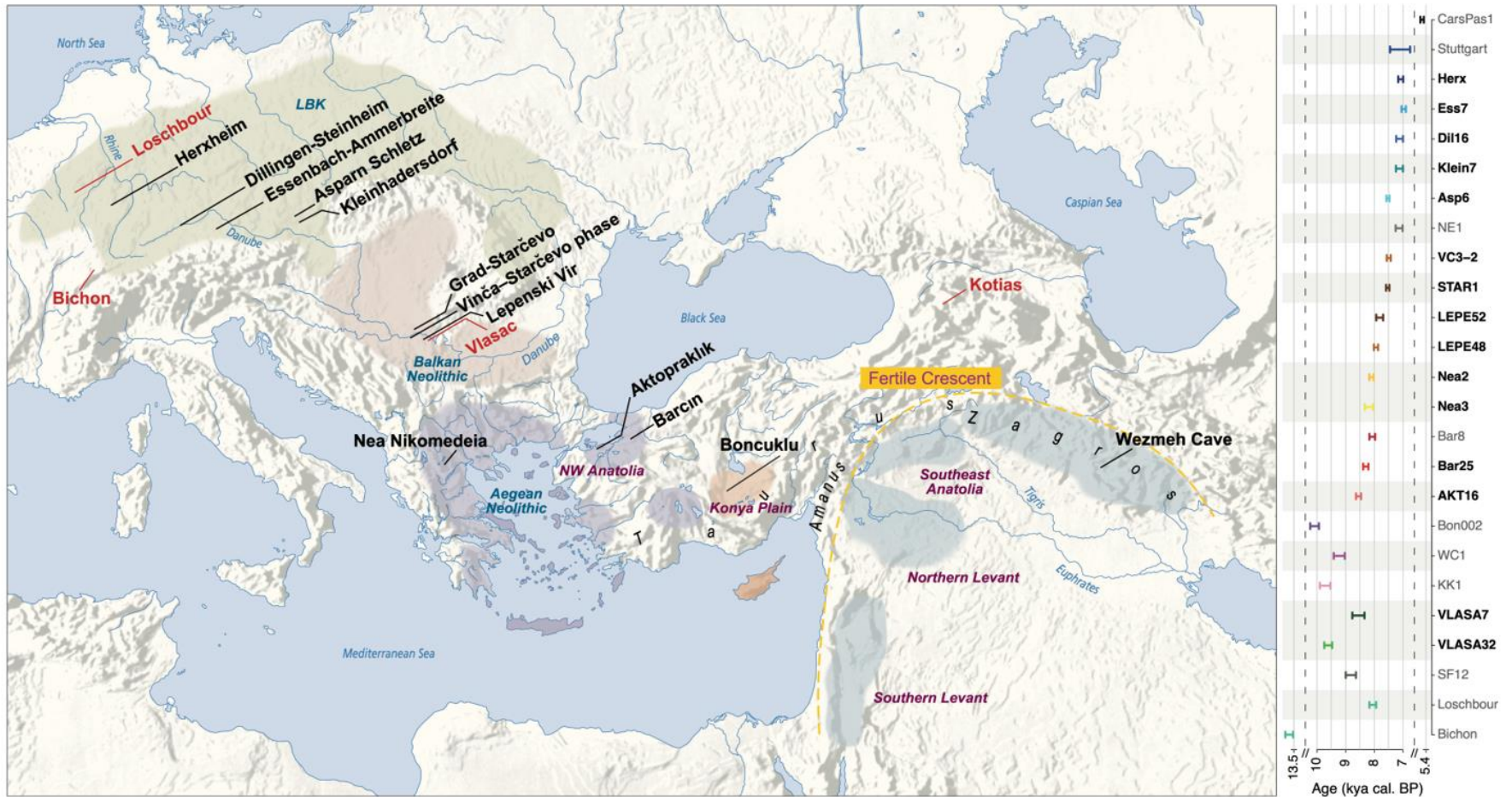
## **Supplementary Materials**

Materials and Methods

Supplementary Text

Supplementary Tables Legend

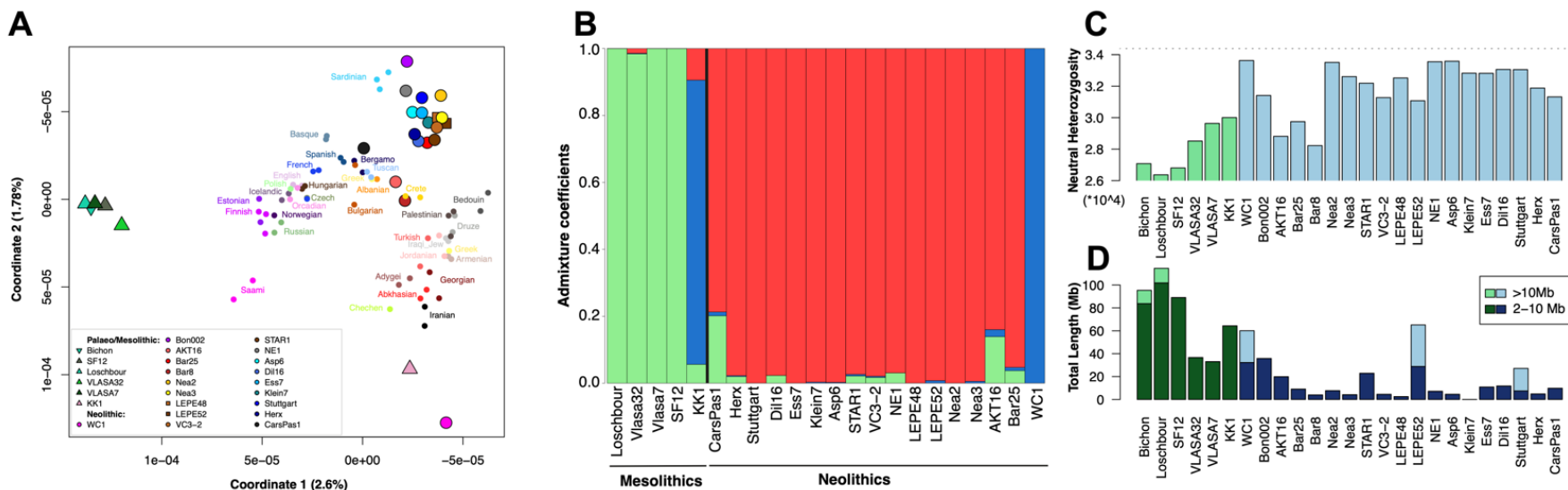
5 Supplementary Tables 1-5



**Fig. 1 - Spatial and temporal distribution of the palaeogenomes analyzed in this study. Left:** Location of Neolithic (black), and Mesolithic or Palaeolithic (red) archaeological sites. Coloured areas represent different chronological phases of Neolithic expansion and cultures (blue) along the Danubian route of Neolithization; geographical areas are indicated in purple. **Right:** Chronological distribution of the 25 genomes analyzed in this



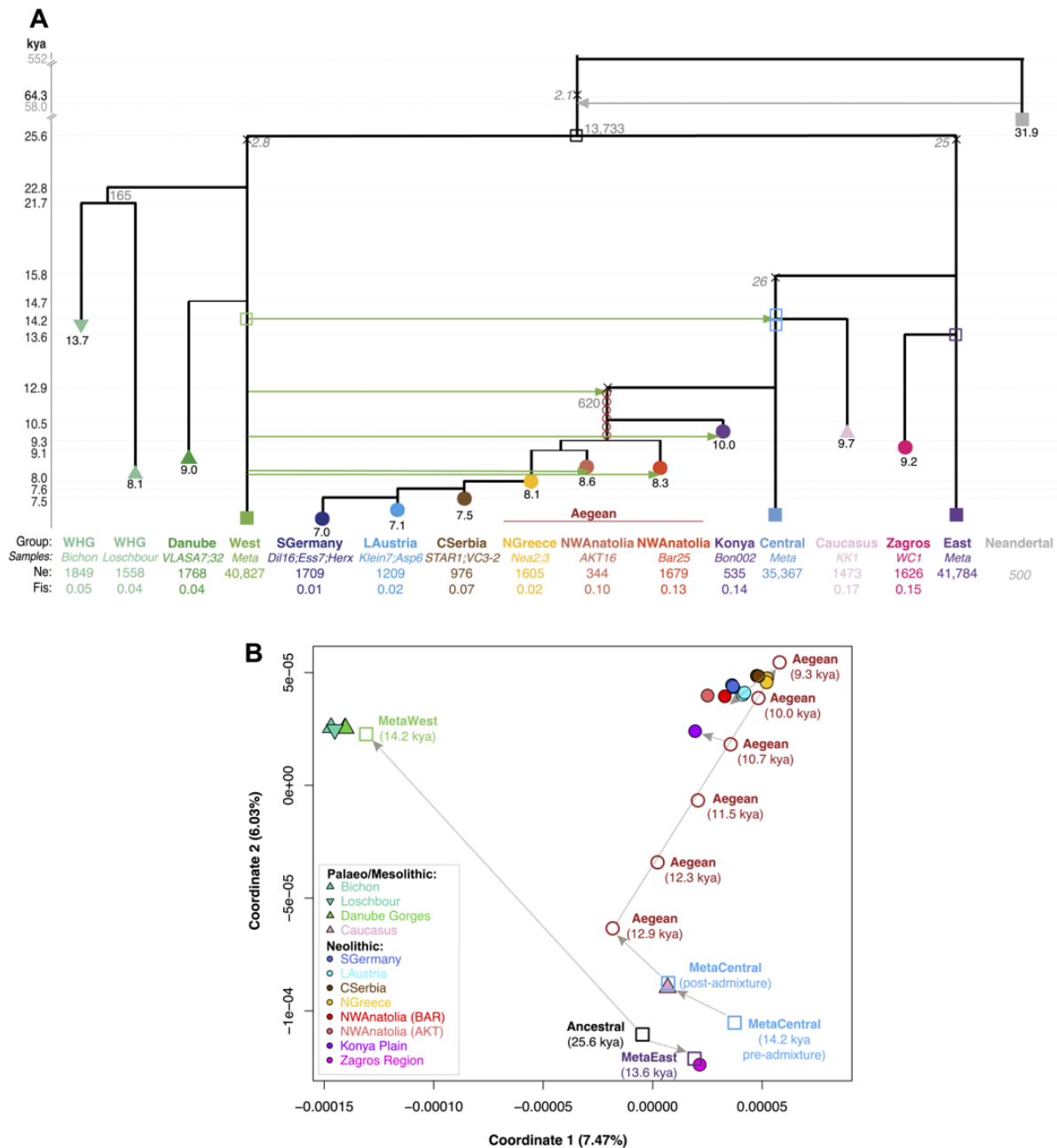
study (see details in Table 1 and Table S2), with the 15 newly-sequenced genomes shown in bold. The chronological interval at 2 sigma (95.4% probability) is shown for each directly-<sup>14</sup>C dated sample, except for Stuttgart and Ess7, for which approximate dates are given based on the archaeological context.



5

**Fig. 2 - Genetic relationships and diversity of high quality ancient genomes.** (A) Multidimensional Scaling (MDS) analysis performed on the neutrally evolving portion of ancient ( $n = 25$ ) and modern ( $n = 65$ , shown as small circles) genomes from Europe and SW Asia. (B) Admixture analyses ( $K = 3$ ) performed on 22 ancient genomes (three genomes with the lowest quality were discarded: Bichon, Bon002, Bar8). (C) Heterozygosity computed at neutral sites in ancient genomes (Palaeolithic and Mesolithic HGs in green, Neolithic individuals in blue); the median heterozygosity observed within

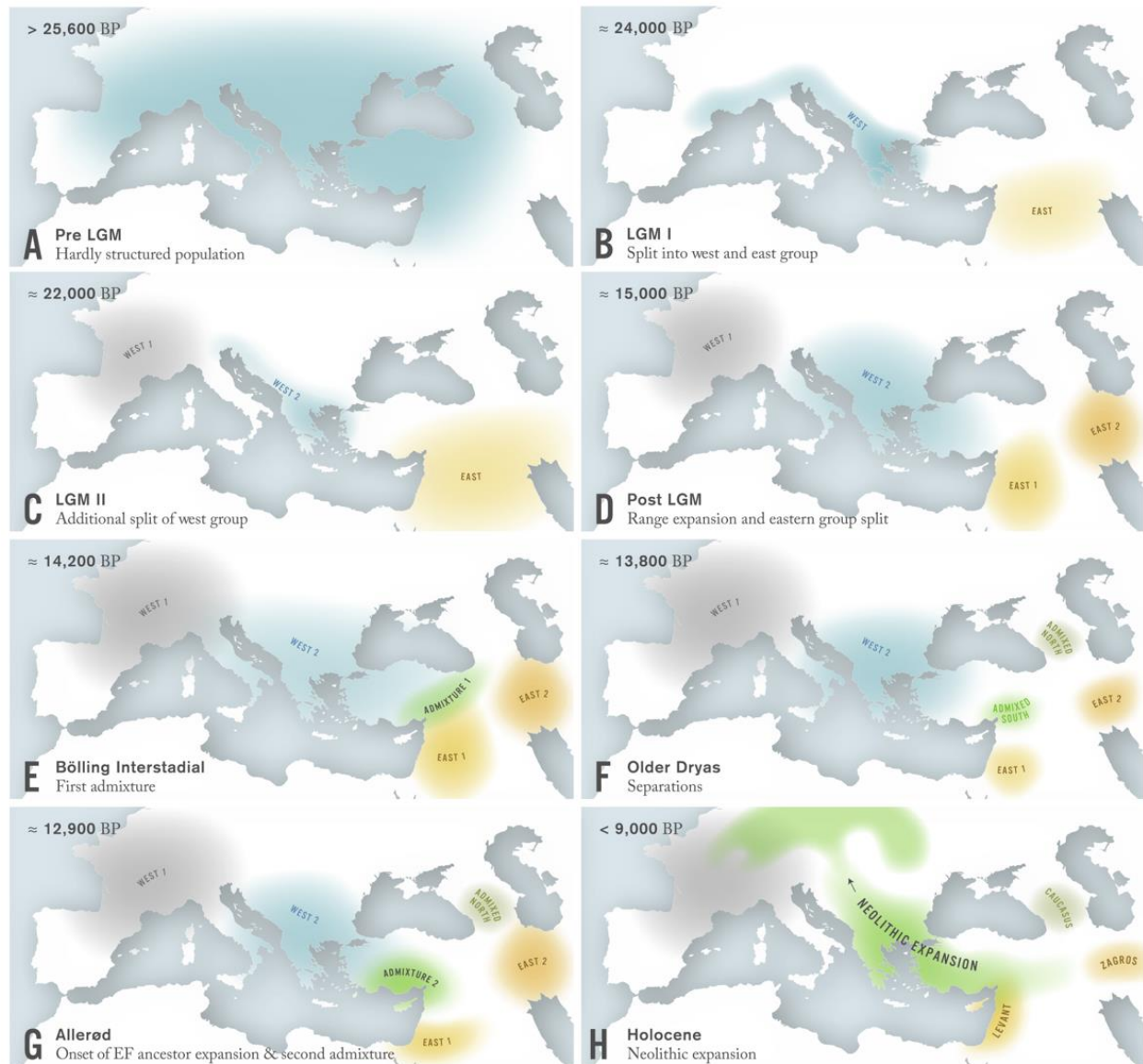
modern genomes is indicated by the dashed line. **(D)** Runs of Homozygosity (ROHs) computed on imputed ancient whole genomes for short ROHs (2-10Mb, dark color) or long ROHs (>10Mb, light color).



**Fig. 3 - Demographic scenario inferred from the sampled genomes. (A)** This demographic history was obtained by compiling the best models of all tested scenarios (see Supp. Text - Demographic inferences with *fastsimcoal2* - Final Model). Times of the events (y-axis) and population ages (shown below their symbol) are indicated in ky BP. Under each population name, we indicate their sampled genomes, their diploid population size and their associated inbreeding coefficient. Empty symbols indicate ancestral populations we simulated after or before key events (admixture or split). The X symbols indicate

bottlenecks that occurred on ancestral branches, modeled as one generation bottleneck through a population of a size indicated in *italic*. Admixture proportions >10% from the *Western* metapopulation populations are represented with green arrows. **(B)** MDS analysis performed on data simulated according to the parameters of the scenario shown in pane A. Empty symbols are for simulated ancestral populations; grey arrows indicate the trajectory of the populations after admixture events and/or episodes of drift.

5



**Fig. 4 - Possible scenario of the population history of SW Asia and Europe between the Last Glacial Maximum (LGM) and the early Neolithic period, i.e. approximately 26,000 to 7,000 years ago.**

Colored shaded areas indicate putative distributions of populations at different time points. See main text for a detailed description. Note that warmer periods (Bölling, Allerød interstadials; Holocene) correspond to population range expansions while colder periods (LGM, Older Dryas) are associated with contractions.

**Table 1 - Archaeological and genetic information on the newly-sequenced genomes.** Mesolithic samples are shown in grey. The samples' ages are based on 14C dating (95.4% probability), except for Ess7 for which an approximate date is given based on the archaeological context (see Supp. Text - Archaeological context of the samples - Essenbach-Ammerbreite).

Individual	Period (culture)	Site	Country	Age (cal. BP)	Mean Depth (X)	Genetic sex	Haplogroups mtDNA	Y
VLASA7	LM	Vlasac	Serbia	8764-8340	15.21	XY	U5a2a	I2
VLASA32	LM	Vlasac	Serbia	9741-9468	12.65	XY	U5a2a	R1b1
AKT16	EN	Aktopraklik	Turkey	8635-8460	12.25	XX	K1a3	–
Bar25	EN	Barcin	Turkey	8384-8205	12.65	XY	N1a1a1	G2a2b2a1
Nea3	EN	Nea Nikomedeia	Greece	8327-8040	11.57	XX	K1a2c	–
Nea2	EN	Nea Nikomedeia	Greece	8173-8023	12.51	XX	K1a	–
LEPE48	TEN	Lepenski Vir	Serbia	8012-7867	10.92	XY	K1a1	C1a2b
LEPE52	E-MN	Lepenski Vir	Serbia	7931-7693	12.37	XY	H3	G2a2b2a1a1c
STAR1	EN (Starčevo)	Grad-Starčevo	Serbia	7589-7476	10.55	XX	T2e2	–
VC3-2	EN (Starčevo)	Vinča-Belo Brdo	Serbia	7565-7426	11.22	XY	HV-16311	G2a2a1a3~
Asp6	EN (LBK)	Asparn-Schletz	Austria	7575-7474	12.11	XY	U5a1c1	G2a2b2a3
Klein7	EN (LBK)	Kleinhadersdorf	Austria	7244-7000	11.30	XX	W1-119	
Dil16	EN (LBK)	Dillingen-Steinheim	Germany	7235-6998	10.60	XY	J1c6	C1a2b
Ess7	EN (LBK)	Essenbach-Ammerbreite	Germany	(7050-6900 BP)	12.34	XY	U5b2c1	G2a2b2a1a1
Herx	EN (LBK)	Herxheim	Germany	7164-6993	11.46	XX	K1a4a1i	–

LM, Late Mesolithic; EN, Early Neolithic; TEN, Transformational/Early Neolithic; E-MN, Early-Middle Neolithic; LBK, Linearbandkeramik