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Genomic and dietary discontinuities during the Mesolithic and Neolithic in Sicily

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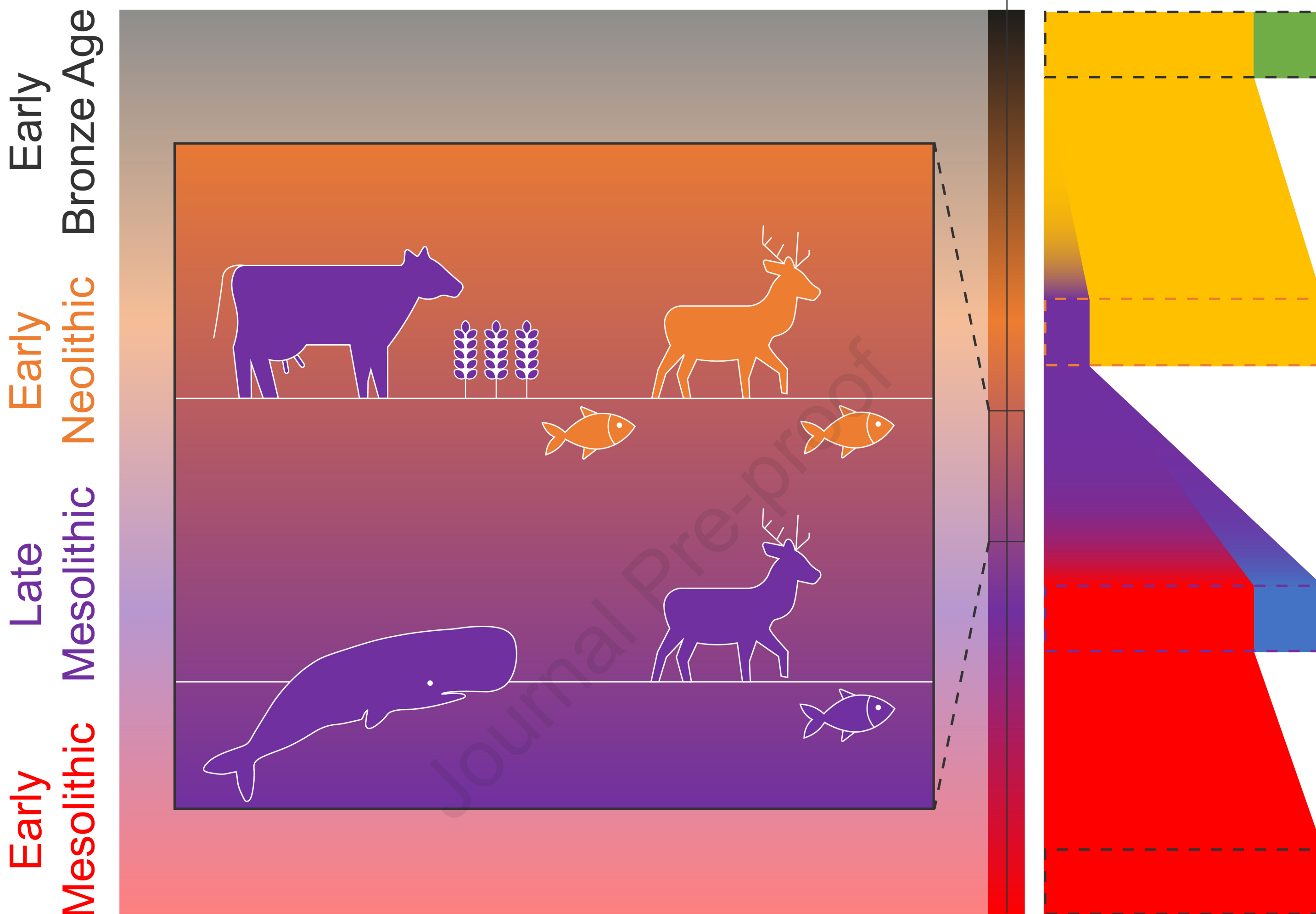
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- Incoming steppe-related ancestry
- Incoming Neolithic ancestry
- Incoming Eastern Hunter-Gatherer ancestry
- Local Early Mesolithic ancestry

1 **Genomic and dietary discontinuities during the Mesolithic and Neolithic in** 2 **Sicily**

3
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42

43 **Summary**

44 Sicily is a key region for understanding the agricultural transition in the Mediterranean, due to its
45 central position. Here, we present genomic and stable isotopic data for 19 prehistoric Sicilians
46 covering the Mesolithic to Bronze Age periods (10,700-4,100 yBP). We find that Early
47 Mesolithic hunter-gatherers (HGs) from Sicily are a highly drifted lineage of the Early Holocene
48 western European HGs, while Late Mesolithic HGs carry ~20% ancestry related to northern and
49 (south)eastern European HGs, indicating substantial gene flow. Early Neolithic farmers are
50 genetically most similar to farmers from the Balkans and Greece, with only ~7% ancestry from
51 local Mesolithic HGs. The genetic discontinuities during the Mesolithic and Early Neolithic
52 match changes in material culture and diet. Three outlying individuals dated to ~8,000 yBP,
53 however, suggest that hunter-gatherers interacted with incoming farmers at *Grotta dell'Uzzo*,
54 resulting in a mixed economy and diet for a brief interlude at the Mesolithic-Neolithic transition.

55

56 **Keywords:** Ancient DNA, isotopes, Sicily, hunter-gatherer, Neolithisation

57

58

59 Introduction

60
61 One of the most impactful changes in human history was the transition in subsistence practices
62 from comparably mobile hunting and gathering to sedentary farming. The primary zone of
63 Neolithisation in western Eurasia spanned the Fertile Crescent and eastern Anatolia, while the
64 role of central and western Anatolia, as secondary recomposition areas or as a distinct primary
65 core, is still being debated (Bar-Yosef, 2002; Binder, 2002; Özdoğan, 2008). By ~8,700-8,500
66 yBP, several groups of early farmers with or without knowledge of ceramics had established
67 communities around the Aegean (Douka et al., 2017; Horejs et al., 2015; Perlès, 2001). Some of
68 these developed the later Starčevo-Körös-Criş, Karanovo and Sesklo complexes ~8,100-8,000
69 yBP through the Balkans (Karamitrou-Mentessidi et al., 2015; Lichardus-Itten, 2009; Perlès,
70 2001). Farming practices spread across Europe and Mediterranean northwestern Africa along
71 archaeologically distinct routes (Price, 2000; Whittle, 1996). Early farmers associated with the
72 Neolithic Starčevo-Körös-Criş-complex and the successive Linear Pottery culture
73 (Linearbandkeramik, LBK) followed a continental route out of the Balkan Peninsula along the
74 Danube river into central Europe and from there further north and west (so-called
75 Danubian/Continental Route). In parallel, agricultural practices and pottery spread westwards out
76 of Greece and the Balkans along the Mediterranean coastline (so-called Mediterranean Route).
77 Since ~8,100-8,000 yBP, the Neolithisation process in the Mediterranean region was shaped by
78 the succession of various local, Neolithic horizons (Guilaine, 2007; Leppard, 2021). Interactions
79 between the various farming and local hunter-gatherer groups, as well as cultural drift resulted in
80 a complex Neolithic mosaic, involving the *Impressa* and Cardial horizons in the eastern and
81 western Mediterranean, respectively (Binder et al., 2017; Guilaine and Manen, 2007; Manen et
82 al., 2019; Zilhão, 2014).

83 Ancient DNA (aDNA) studies have contributed substantially to the understanding of the
84 Neolithisation of Europe. The general picture that has emerged is that large-scale expansions of
85 early farmers facilitated, and even originated, the agricultural transition in Europe (Haak et al.,
86 2015; Hofmanová et al., 2016; Kılınç et al., 2016; Lazaridis et al., 2016, 2014; Mathieson et al.,
87 2015; Olalde et al., 2015; Omrak et al., 2016; Skoglund et al., 2014, 2012). Nearly all of the
88 farmer ancestry in European early farmer (EEF) groups, including those associated with the
89 Mediterranean Route, represents a subset of the genomic diversity found among early farmers

90 from northwestern Anatolia (*Barcin*) and the northern Aegean (*Revenia*) (Hofmanová et al.,
91 2016; Kılınç et al., 2016; Lazaridis et al., 2017, 2016, 2014; Mathieson et al., 2015). However,
92 early farmers from *Diros* in Peloponnese Greece might have harboured an ancestral component
93 that placed them outside of the genetic diversity found in those from *Barcin* (Mathieson et al.,
94 2018).

95 Moreover, aDNA studies have also indicated that the underlying Neolithisation demographic
96 processes likely differed among regions within Europe (González-Fortes et al., 2017; Lipson et
97 al., 2017b; Mathieson et al., 2018; Rivollat et al., 2020; Skoglund et al., 2014). Early farming in
98 central, western and northern Europe along the Continental Route contained characteristic
99 elements of the Near Eastern Neolithic, including domesticated animals and plants. The early
100 farmers in these regions carried only a very minor genomic contribution from local European
101 HGs (Haak et al., 2015; Hofmanová et al., 2016; Mathieson et al., 2015; Skoglund et al., 2012).
102 In contrast, there is archaeological evidence for a more gradual appearance of agricultural
103 elements along the Mediterranean Route (Isern et al., 2017; Mulazzani et al., 2016; Sánchez et
104 al., 2012). Notably, the contribution of Mesolithic forager ancestry to EEF varied regionally and
105 was higher in some communities in the Balkans, southern France and Iberia, but not in Italy
106 (Antonio et al., 2019; Fregel et al., 2018; Lipson et al., 2017b; Mathieson et al., 2018; Olalde et
107 al., 2019; Rivollat et al., 2020; Valdiosera et al., 2018; Villalba-Mouco et al., 2019). It is
108 important to note, however, that the majority of EEF genetic data comes from groups that spread
109 along the Continental Route. For the Mediterranean Route, the main uncertainties revolve around
110 the expansion of the *Impressa* Ware culture in Italy. Recently, it was shown that some Early
111 Neolithic farmers from peninsular Italy might retain an additional ancestral component related to
112 early farmers from Iran (*Ganj Dareh*) and/or HGs from the Caucasus (CHG) (Antonio et al.,
113 2019). This raises the possibility that they descended from a different group compared to the
114 known western Mediterranean and central European farmers (Antonio et al., 2019; Mathieson et
115 al., 2018).

116 The island of Sicily marks a central position in the Mediterranean, and features some of the
117 earliest evidence for farming, starting as early as ~8,000 cal BP (Binder et al., 2017; Mannino et
118 al., 2015) (calibrated radiocarbon years before present) or even earlier (~8,200 cal BP) (García-
119 Puchol et al., 2017). However, to date no ancient genomes are available for Late Mesolithic and
120 Early Neolithic individuals from Sicily. As such, the demographic processes underlying the

121 initial emergence of farming practises, as well as the origins of the early farmer groups along the
122 European and North African Mediterranean coastlines, remain unknown.

123 *Grotta dell'Uzzo* in northwestern Sicily is a unique site for understanding human prehistory in
124 the Central Mediterranean. The cave stratigraphy at *Grotta dell'Uzzo* covers the late Upper
125 Palaeolithic, a continuous occupation during the Mesolithic, and up to the Middle Neolithic, with
126 traces of later occupation (STAR Methods) (Mannino et al., 2015). This provides direct and
127 unprecedented insights into the cultural, subsistence and dietary changes that took place in the
128 transition from hunting and gathering to farming (Mannino et al., 2015, 2007; Tagliacozzo,
129 1993). In addition, two *Impressa* Ware horizons associated with elements of Early Neolithic
130 farming appeared rapidly in a timeframe of ~500 years. The first horizon of *Impressa* Wares
131 appeared 8,000-7,700 cal BP followed by the Impressed Ware of the Stentinello group
132 (Stentinello/Kronio) around 7,800-7,500 cal BP (Binder et al., 2017; Guilaine, 2018; Mannino et
133 al., 2015; Natali and Forgia, 2018). The continuous stratigraphy across the different Mesolithic
134 and Early Neolithic material horizons with a large set of radiocarbon (^{14}C) dates is a unique
135 feature in the context of Mediterranean Mesolithic-Neolithic sites and allows us to investigate 1)
136 the genomic structure of the Mesolithic Sicilian foragers, and 2) the demographic processes
137 underlying the transition from foraging to farming directly.

138

139 **Results**

140

141 To investigate the biological processes underlying the transition from foraging to
142 agropastoralism in Sicily, we jointly analysed ancient genome-wide data and stable isotopic data
143 for dietary inferences for a chronological transect of 19 individuals from *Grotta dell'Uzzo* in
144 northwestern Sicily. We obtained direct ^{14}C dates on the skeletal elements that were used for
145 genetic analysis and determined carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values from the same
146 bone collagen for dietary reconstruction (Table S1, S2, Data S1.1). We extracted DNA from
147 bone and teeth in dedicated clean room facilities, built DNA libraries and enriched for ~1240k
148 single nucleotide polymorphisms (SNPs) in the nuclear genome, and independently for the
149 complete mitogenome (Fu et al., 2015) using in-solution hybridisation enrichment techniques (Q.
150 Fu et al., 2013). All libraries were checked for endogenous human aDNA content, aDNA
151 damage patterns, and nuclear and mitogenome contamination. We restricted our analyses to

152 individuals with evidence of authentic human aDNA, and removed ~300k SNPs on CpG islands
153 to minimize the effects of residual post-mortem DNA deamination (Seguin-Orlando et al., 2015).
154 The final data set includes 868,755 intersecting autosomal SNPs for which our newly reported
155 individuals cover 53,352-796,174 SNP positions with an average read depth per target SNP of
156 0.09-9.39X (Data S1.1). We compared our data to a global set of contemporary (Lazaridis et al.,
157 2014; Mallick et al., 2016; Patterson et al., 2012) and ancient individuals from Europe, Asia and
158 Africa (Allentoft et al., 2015; Antonio et al., 2019; Brace et al., 2019; Broushaki et al., 2016;
159 Brunel et al., 2020; Catalano et al., 2020; Damgaard et al., 2018; Feldman et al., 2019; Fernandes
160 et al., 2020; Fregel et al., 2018; Fu et al., 2016, 2014; Gamba et al., 2014; Günther et al., 2015;
161 Hofmanová et al., 2016; Jones et al., 2017, 2015; Keller et al., 2012; Kılınç et al., 2016;
162 Lazaridis et al., 2017, 2016, 2014; Lipson et al., 2017b; Llorente et al., 2015; Mallick et al.,
163 2016; Marcus et al., 2020; Mathieson et al., 2018; Meyer et al., 2012; Mittnik et al., 2018; Olalde
164 et al., 2019, 2018, 2015; Omrak et al., 2016; Raghavan et al., 2014; Rivollat et al., 2020; Saag et
165 al., 2017; Sikora et al., 2017; Skoglund et al., 2014; Valdiosera et al., 2018; Villalba-Mouco et
166 al., 2019). Here, we provide population genomic and dietary isotope analyses for 19 individuals
167 that cover a time transect of over 6,000 years, from the Early Mesolithic (EM; ~10,700 cal BP)
168 to the Early Bronze Age (EBA; ~4,100 cal BP) (Data S1.1). An Epigravettian HG individual
169 (*OrienteC*) from the *Grotta d'Oriente* on Favignana island in western Sicily (14,200–13,800 cal
170 BP, ¹⁴C date on charcoal from the deposit) is co-analysed with our data (Catalano et al., 2020;
171 Mathieson et al., 2018).

172

173 **Genetically-distinct groups of prehistoric Sicilians**

174 The newly generated ¹⁴C dates confirm that the prehistoric Sicilians in our time transect can be
175 attributed to five groups that correspond to different archaeological periods (Early Mesolithic,
176 Castelnovian Late Mesolithic, Early Neolithic, Middle Neolithic and Early Bronze Age) attested
177 at *Grotta dell'Uzzo* (Fig. 1A, STAR Methods). When analysed in conjunction with genetic data
178 from published ancient and present-day Europeans, the Uzzo individuals are clustered into four
179 groups based on the principal component analysis (PCA, Fig. 1C).

180 The two oldest groups fall within a cluster of western European Mesolithic hunter-gatherers
181 (WHG), with a subtle distinction in their genetic ancestry, as shown by both PCA positioning
182 and pairwise outgroup- f_3 statistics (Fig. 1B). The first group contains the two oldest individuals

183 (one directly dated to 10,750-10,580 cal BP, Fig. 1A) from *Grotta dell'Uzzo*, who produced a
184 lithic industry that was typologically and stylistically similar to the preceding Epigravettian
185 tradition (STAR Methods (Lo Vetro and Martini, 2016)), and closely associated to the previously
186 published Epigravettian *OrienteC* (14,200–13,800 cal BP) (Catalano et al., 2020; Mathieson et
187 al., 2018). These three individuals all carried mitogenome lineages that fall within the
188 U2'3'4'7'8'9 branch (Data S1.1), which was closely related to an Epigravettian-associated
189 Sicilian from *San Teodoro* and also reported for an older Gravettian-associated *Paglicci108* from
190 the Italy peninsular (Modi et al., 2021; Posth et al., 2016). They also shared a large amount of
191 genetic drift with each other, compared to other individuals in the WHG cluster (Data S5.3,
192 Figure S3). We labelled this group Sicily Early Mesolithic (Sicily EM, n=3).

193 The second, chronologically younger HG group includes nine individuals dated to ~8,650-7,790
194 cal BP. Seven of them correspond archaeologically to the Late Mesolithic and probably for part
195 of the Castelnovian, a variety of the Late Mesolithic blade-and-trapeze horizon in southern
196 France, Italy and Dalmatia, as well as Sicily (Clark, 1958). In the western Mediterranean, the
197 Castelnovian has strong chronological and stylistic as well as technical connections with the
198 Iberian Geometric Mesolithic and with the upper Capsian in the Maghreb (Binder et al., 2012;
199 Marchand and Perrin, 2017), but the blade-and-trapeze horizon also extends eastwards into the
200 Pontic Region and further into the Eurasian land mass (Biagi and Starnini, 2016; Gronenborn,
201 2017). The other two younger individuals (*UZZ71* and *UZZ88*, dated to 7,960-7,790 cal BP)
202 overlap with the supposed earliest emergence of Neolithic aspects at *Grotta dell'Uzzo* (Archaic
203 *Impressa*, STAR Methods). These two individuals fall within the diversity of the foragers
204 attributed to the LM Castelnovian in PC space (Fig. 1C) and pairwise outgroup- f_3 statistics (Fig.
205 1B). Moreover, the mitogenome haplogroups carried by these individuals are all typical for
206 European Late Mesolithic WHG (Bramanti et al., 2009; Posth et al., 2016), falling in
207 haplogroups U4 and U5, different from the first group (Data S5.2). As a consequence, we
208 grouped *UZZ71* and *UZZ88* with the Sicily LM HG individuals, and labelled this group as Sicily
209 Late Mesolithic (Sicily LM, n=9).

210 The third group contains individuals directly dated to ~7,430-6,660 cal BP, overlapping
211 chronologically with Early Neolithic to Middle Neolithic farmer horizons at *Grotta dell'Uzzo*,
212 characterised by *Impressed Wares* (Sicily EN, n=7). In PC space, these individuals group with
213 early farmers from southeastern Europe and Anatolia, and not with the preceding Sicilian HGs

214 (Fig. 1C). All the farmer individuals with sufficient coverage on the mitogenome carried
215 haplogroups characteristic for European early farmers: U8b1b1 (n=2), N1a1a1 (n=1), J1c5 (n=1),
216 K1a2 (n=1) and H (n=1) (Data S1.1) (Brandt et al., 2013). They showed a subtle distinction in
217 PC space from the Middle Neolithic farmers from *Fossato di Stretto Partanna*, Sicily (Sicily
218 MN, 6,940-6,660 cal BP), which are contemporaneous with the Middle Neolithic individual
219 (*UZZ61*) from *Grotta dell'Uzzo* (Fernandes et al., 2020).

220 The fourth and youngest group includes one individual (*UZZ57*) dated to 4,150-3,970 cal BP and
221 is attributed to the Early Bronze Age (Uzzo EBA). This individual is displaced from the Early
222 Neolithic towards the direction of individuals associated with the Bell Beaker phenomenon and
223 other Late Neolithic and BA groups that carry the so-called “steppe”-related ancestry. This
224 ancestry was characteristic for the steppe-nomads from western Eurasia, and spread across
225 Europe during the Bronze Age (Haak et al., 2015). A similar shift was also found in published
226 Early Bronze Age individuals from Sicily (Fernandes et al., 2020). This individual *UZZ57*
227 carried the Y-haplogroup R1b1a1b1a1a2, commonly found in Bronze Age Europe, and also
228 previously reported in Sicilian Bronze Age individuals (Data S1.4, Data S5.2) (Fernandes et al.,
229 2020).

230

231 **Genomic and dietary transitions in Sicily during the Mesolithic and Early Neolithic**

232 Our Mesolithic time transect of 11 individuals, spanning around 3,000 years, provides a unique
233 opportunity to explore changes in genomic substructure over time. A more direct comparison of
234 the ancestries in the Sicily EM and LM HGs with f_4 -cladality statistics of the form $f_4(\text{Chimp}, X;$
235 *Sicily EM HG, Sicily LM HG*) for various West-Eurasian HGs (X) reveals a pattern that is linked
236 to geography (Fig. 2A, Data S2.2). Here, significantly negative f_4 -values show that Sicily EM
237 HGs share more alleles with HGs from (south-)western Europe, including WHGs from the
238 Villabruna cluster, as well as Iberian Upper Palaeolithic and Mesolithic HGs carrying
239 Magdalenian-associated ancestry (Fu et al., 2016; Villalba-Mouco et al., 2019). In contrast, the
240 Sicily LM HGs share significantly more alleles with Upper Palaeolithic and Mesolithic HGs
241 from northern Europe, (south-)eastern Europe and Russia (Data S2.2). This indicates a change in
242 genetic affinities on Sicily during the Mesolithic.

243 The difference in affinity to West-Eurasian HGs between Sicily EM and LM HGs could be
244 explained by residual, (Magdalenian-associated) GoyetQ2-like ancestry present Sicily EM HGs,

245 or alternatively, by the small proportion of Eastern Hunter-gatherer (EHG)-related ancestry in
246 Sicily LM HGs, or by both. As such, we characterised the Sicily EM and LM genetic ancestries
247 more explicitly using *qpWave*- and *qpAdm*-based admixture models (Lazaridis et al., 2016). We
248 found that the ancestry of Sicily EM HGs can be modelled as a clade with *Continenza* HGs from
249 peninsular Italy with regards to the outgroup set used ($P_{wave} = 0.191$, see Methods), to the
250 exclusion of all other tested West-Eurasian HGs, including ~14,000 yBP *Villabruna* from
251 northern Italy ($P_{wave} = 5.98E-05$). Subsequent two-way *qpAdm* admixture models that tested for a
252 mixture of various proxies for WHG ancestry and Magdalenian-related ancestry were rejected
253 for the Sicily EM HG gene pool (Data S2.5). The admixture graphs based on *qpGraph* modelling
254 also fitted the Sicily EM HGs as a sister branch of *Villabruna*, with potential contribution to
255 Magdalenian-related ancestries (Fig. S7-9).

256 Subsequently, we investigated the degree of genetic continuity between the Sicily EM and LM
257 HGs, and explicitly tested whether the latter derive distinct ancestry from an EHG-related source
258 with *qpWave* and *qpAdm*-based ancestry models. We found that neither the ancestry in Sicily
259 EM HGs nor Italian HGs from *Continenza* or *Villabruna* can provide a full fit to the ancestry of
260 the Sicily LM HGs (max. P_{wave} -value: $1.90E-04$, Data S2.5). Instead, a dual ancestry of
261 $80.8 \pm 1.3\%$ Sicily EM HGs and $19.2 \pm 1.3\%$ EHG resulted in a supported model ($P_{Adm} = 0.135$,
262 Fig 3A, Data S2.5). Notably, only Sicily EM HGs can be used as a proxy for the WHG-related
263 ancestry in Sicily LM HGs. All other models with West-Eurasian HGs, including *Continenza*
264 and *Villabruna* HGs from peninsular Italy, were rejected at $p < 0.05$ (Data S2.5). This indicates
265 that the WHG-related ancestry in Sicily LM HGs most likely derived from the preceding local
266 Sicilian foragers. The admixture between Sicily EM HGs and EHG was dated to 20 ± 5
267 generations ago, corresponding to ~8,800 years ago, which coincides with the beginning of Late
268 Mesolithic in *Grotta dell'Uzzo* (Data S5.3, Table S4).

269 We further investigated the observed affinity of Sicily LM HGs to HGs in northern and
270 (south-)eastern Europe as indicated by the f_4 -cladality statistics in more detail (Fig 2B).
271 Congruent with the observed affinities, we found that in the two-way admixture model the EHG-
272 related ancestry in Sicily LM HGs can be approximated by the ancestry found in HGs from
273 Scandinavia (SHG), Latvia, Ukraine and Romania Iron Gates (Data S2.5). This confirms a minor
274 contribution of non-local ancestry, alongside the persistent local ancestry in Sicily during the
275 Mesolithic.

276 Of note, we found that the global nucleotide diversity (π) for the Sicily EM HGs is ~25% lower
277 compared to the subsequent Sicily LM HGs (95% confidence intervals 0.161-0.170 and 0.217-
278 0.223, respectively, Fig. S4). Furthermore, we detected an extremely large amount (>350 cM) of
279 runs of homozygosity (ROH) segments in Sicily EM HGs, especially the shortest 4-8 cM
280 segments that represent background relatedness (Ringbauer and Novembre, 2020). The amount
281 of short ROH segments is much larger compared to all other European Upper Paleolithic or
282 Mesolithic HGs, including the later Sicily LM HGs, and contemporaneous *Continenza* HGs and
283 *Villabruna* from peninsular Italy (Fig. S5). Taken together, these results suggest a small effective
284 population size in the Sicily EM HGs that could result from a population bottleneck (Data S5.3),
285 and an effective population size increase in the Late Mesolithic, potentially due to the influx of
286 non-local ancestry.

287
288 The Sicilian early farmers (Sicily EN) fall closest to European Early Farmers (EEF) and not with
289 the preceding local Sicilian HGs in PC space (Fig. 1C). Using an outgroup- f_3 statistic of the form
290 $f_3(Mbuti; Sicily EN, X)$, we explored which of the other contemporaneous ancient groups show
291 the highest genetic affinity to Sicily EN (Fig. 2B). Congruent with the PCA results, the Sicilian
292 early farmers share most genetic drift with various EN farmers from the Balkans and Greece, as
293 well as central Europe. In contrast, Sicily EN farmers have less genomic affinity with individuals
294 from the western Mediterranean coast such as France, Iberia and northwestern Africa (Fig. 2B,
295 Data S3.1), who carried a higher proportion of HG ancestry as a result of admixture with local
296 HG groups (Lipson et al., 2017b; Olalde et al., 2019; Rivollat et al., 2020; Villalba-Mouco et al.,
297 2019). This supports the finding of a major turnover of genetic ancestry during the Mesolithic-
298 Neolithic transition in Sicily, similar to what has been reported for EN farmers from peninsular
299 Italy (Antonio et al., 2019) and many other regions in Europe (Günther et al., 2015; Hofmanová
300 et al., 2016; Kılınç et al., 2016; Lazaridis et al., 2016, 2014; Lipson et al., 2017b; Mathieson et
301 al., 2015; Olalde et al., 2015; Omrak et al., 2016; Skoglund et al., 2012, 2014).

302 To explore this further, we used f_4 -admixture statistics of the form $f_4(Chimp, Sicily LM HG;$
303 $Anatolia EN Barcin, Sicily EN)$ to test whether the Sicily EN farmers retained an excess of
304 shared alleles with the preceding Sicily LM HGs, when using Anatolia EN *Barcin* as a baseline
305 for EEF ancestry. The statistic was significantly positive, suggesting excess local HG ancestry in
306 Sicily EN farmers ($z = 5.051$, Data S3.2). Indeed, with *qpAdm*-based admixture models we

307 estimate that local Sicilian LM HGs contributed $7.5\pm 0.9\%$ of the ancestry to the Sicilian EN
308 farmer gene pool (Fig. 3A, Data S3.3). Of note, the local HG admixture signal is significantly
309 lower when compared to previously published Sicily MN farmers from *Fossato di Stretto*
310 *Partanna* (Fernandes et al., 2020) ($f_4(\text{Chimp}, \text{Sicily LM HG}; \text{Sicily EN}, \text{Sicily MN})$: $z = 5.381$,
311 Data S3.2), which carried an estimated $11.9\pm 0.9\%$ local Sicily LM HG ancestry (Data S3.3).
312 Overall, this suggests a subtle, yet detectable, contribution and potential resurgence of local HG
313 ancestry in Sicilian farmers during the Neolithic. Importantly, the published Sicily MN farmers
314 are contemporaneous with the youngest farmer individual *UZZ61* (6,830-6,660 cal BP) in our
315 Sicily EN group, which indicates that the resurgence may have taken place elsewhere in Sicily
316 (e.g., at *Fossato di Stretto Partanna*) by the mid-7th-millennium BP, but not yet in *Grotta*
317 *dell'Uzzo*.

318 The Early Bronze Age individual *UZZ57* shows a shift in PC space towards individuals that are
319 associated with the Late Neolithic Bell Beaker phenomenon and EBA groups that carry steppe-
320 related ancestry (Fig. 1C), similar to what has been observed in other EBA individuals from
321 Sicily (Fernandes et al., 2020). This is also confirmed by *qpAdm*, in which individual *UZZ57*
322 could be modelled as a two-way mixture between local Sicily EN ancestry and 'steppe ancestry'
323 represented by Yamnaya Samara (Fig. 3A). The steppe ancestry contribution in *UZZ57* was
324 estimated to $21.0\pm 3.5\%$, which falls within the range of other published Sicily EBA groups (Data
325 S3.4).

326

327 **Did Sicilian Late Mesolithic foragers adopt some aspects of early farming?**

328 To shed further light on the processes underlying the Mesolithic-Neolithic transition in Sicily we
329 jointly analysed the stable isotope data for dietary inference ($\delta^{13}\text{C}/\delta^{15}\text{N}$) and the ancestry profile
330 for each individual in our time transect (Data S5.1, Figure S2, Table S3). We find that
331 individuals from different time periods carrying different genetic ancestries also consumed
332 isotopically different diets (Fig. 3B). The isotopic data show that the Early Mesolithic HGs from
333 *Grotta dell'Uzzo* relied mainly on hunting terrestrial game with substantial contributions of plant
334 foods but limited consumption of marine resources (Mannino et al., 2015). In contrast, the diet of
335 the Sicily LM HGs carrying EHG ancestry was characterized by a significantly higher intake of
336 marine-based protein. The isotopic values for the Sicilian EN farmers are congruent with them
337 having a terrestrial-based farming diet. Overall, the isotopic and ancestry profiles per individual

338 show that diets correspond broadly with the assigned genomic cluster and attested subsistence
339 per archaeological time period.
340 However, two individuals (*UZZ71*, *UZZ88*) chronologically overlap with the period when the
341 *Impressa* Ware made its appearance at the site (Mannino et al., 2015). The two oldest individuals
342 (*UZZ71* and *UZZ88*), genetic females dated to ~7,960-7,790 cal BP, fall fully within the genomic
343 diversity of the Late Mesolithic HGs associated with the Castelnovian *sensu lato*, despite
344 postdating them by ~200 years (Fig. 1C, Data S5.1). Both these individuals show isotope values
345 that are different from the preceding Late Mesolithic HGs, as well as from the later Sicily EN
346 farmers associated with Stentinello/Kronio pottery (Fig. 3B, Data S5.1). The dietary profile of
347 individual *UZZ71* ($\delta^{13}\text{C} = -18.9\%$, $\delta^{15}\text{N} = 14.5\%$) indicates an intake of freshwater protein,
348 similarly to what has been reported for Mesolithic HG from the Iron Gates on the Balkan
349 Peninsula (Bonsall et al., 2015; Borić and Price, 2013). On the other hand, individual *UZZ88*
350 shows an isotopic composition ($\delta^{13}\text{C} = -19.2\%$, $\delta^{15}\text{N} = 7.1\%$) that suggests a terrestrial-based
351 farming diet with very low levels of animal protein consumption (EN farmers analysed from
352 *Grotta dell'Uzzo*): mean $\delta^{13}\text{C} = -19.4 \pm 0.5\%$, mean $\delta^{15}\text{N} = 9.1 \pm 1.2\%$). The observed
353 combination of HG ancestry profile and terrestrial farming diet for *UZZ88* can be explained in
354 two ways: agro-pastoralism had strongly influenced local subsistence practices and/or some
355 foragers had become part of the incoming farming groups. Conversely, *UZZ77*, an individual
356 whose genetic makeup is typical of the incoming farmers, has a dietary profile ($\delta^{13}\text{C} = -18.8\%$,
357 $\delta^{15}\text{N} = 12.5\%$) more similar to that of the Mesolithic terrestrially-based foragers. The combined
358 genetic and isotopic data for *UZZ88* and *UZZ77* point to some degree of interaction between
359 local hunter-gatherers and incoming farmers, which is also compatible with the small proportion
360 of HG ancestry present in Sicily after the introduction of farming, as also attested at the MN site
361 of *Fossato di Stretto Partanna* (Fernandes et al., 2020).

362

363 Discussion

364 The Apennine Peninsula (today's Italy) has long been viewed as one of the refugia during the
365 LGM (Feliner, 2011; Schmitt, 2007), ~25,000-18,000 years ago, from where Europe was
366 repopulated (Fu et al., 2016; Posth et al., 2016). The earliest evidence for the presence of *Homo*
367 *sapiens* in Sicily dates to ~19,000-18,000 cal BP, following the time when a land bridge
368 connected the island to peninsular Italy (Antonioli et al., 2016; Di Maida et al., 2019). Although

369 there are many sites in peninsular Italy and Sicily with evidence of Late Upper Palaeolithic
370 occupation, forager populations seemed to have decreased during the Mesolithic (Biagi, 2003),
371 congruent with the observation that EM HGs from *Grotta dell'Uzzo* produced a lithic industry
372 derived from the Epigravettian tradition (STAR Methods)(Lo Vetro and Martini, 2016). The
373 profoundly reduced population genomic diversity (Figure S4), large quantity of short ROH tracts
374 in the Sicily EM HGs (Figure S5), together with a high level of shared genetic drift with
375 Mesolithic foragers from *Continenza* (Figure S3, Data S2.1), hint at a population bottleneck that
376 affected foragers in Sicily and potentially also central Italy.

377 Some Late Epigravettian sites in Sicily contain rock panels with engraved animal figures that are
378 similar to those of the Franco-Cantabrian, including Magdalenian (Mussi, 2001). Here, we
379 showed that compared to the ~14,000 yBP Epigravettian-associated HG *Villabruna* in northern
380 Italy, the Sicily EM HGs have a higher genetic affinity to Iberian HGs associated with the
381 Magdalenian and Azilian, such as *El Mirón* and *Balma Guilanyà* (Data S2.2). *Antonio et al.*
382 reported similar affinities for Mesolithic HGs from *Continenza* (Antonio et al., 2019). Compared
383 to *Villabruna*, no extra Magdalenian-related ancestry has been found in *Continenza* or *Grotta*
384 *dell'Uzzo* (Data S2.2) (Antonio et al., 2019), while Iberian HGs including *El Mirón* and *Balma*
385 *Guilanyà* have been suggested to carry Epigravettian-related ancestry (Figure S6) (van de
386 Loosdrecht, 2021; Villalba-Mouco et al., 2019). This suggests the Epigravettian-related ancestry
387 in Iberian HGs was likely derived from southern/central Italy. Both archaeological and genomic
388 results suggest a deep connection between the Epigravettian of southern Italy and the
389 Magdalenian and Azilian in Iberia (van de Loosdrecht, 2021), which warrants further
390 investigation.

391 Compared to Sicily EM HGs, Sicily LM HGs derived ~18-21% of their ancestry from an EHG-
392 related source, providing evidence for shifting ancestry during the Mesolithic (Figure 3A). After
393 the LGM, foragers associated with Epigravettian assemblages expanded in both Italy and
394 southeastern Europe (Djindjian, 2016; Maier, 2015). Similar to southern Italy, the Balkans were
395 also a glacial refugium. Currently, there are no genomes available for Epigravettian foragers
396 from the Balkans. However, the Mesolithic HGs from this region are among the oldest HGs
397 carrying EHG-related ancestry in southeastern Europe (Figure S6C) and suggest the Balkans as a
398 candidate region for the excess EHG ancestry found in LM Sicily HGs. From the start of the
399 Early Holocene, ~11,700 yBP onwards, an EHG/Anatolia HG (AHG) mixture can be found

400 among HGs from Scandinavia, the Baltic, Ukraine and the Balkans (Figure S6) (van de
401 Loosdrecht, 2021). This underlines previous reports for a long-standing interaction sphere of
402 HGs with EHG and AHG-related ancestry from northern and eastern Europe towards the Near
403 East and the Caucasus (Feldman et al., 2019; Fu et al., 2016; Mathieson et al., 2018). This
404 population may well have expanded into Sicily in the course of the westward shift of the blade-
405 and-trapeze horizon into central and southern Europe, which seems to have begun after the
406 climatic anomaly around 9,300 yBP (Gronenborn, 2017; van de Loosdrecht, 2021).

407 In contrast, the ancient genome-wide data for the Sicily EN farmers point to a near-complete
408 genetic turnover during the transition from foraging to farming. The preceding Late Mesolithic
409 HGs have contributed at most ~7% ancestry to the EN farmers from *Grotta dell'Uzzo* (Figure
410 3A). This indicates that the transition to agriculture involved population replacement of local
411 foragers by early farmers to a large extent during the Early Neolithic, similar to previous results
412 for early farmers from *Ripabianca* and *Continenza* in peninsular Italy and other regions in
413 Europe (Antonio et al., 2019; Bramanti et al., 2009; Günther et al., 2015; Hofmanová et al.,
414 2016; Kılınç et al., 2016; Lazaridis et al., 2017, 2016, 2014). However, the distinct diets and the
415 intermediate ^{14}C dates of a few individuals from the period around the beginning of the Neolithic
416 provide tentative evidence that HGs and farmers initially exchanged their subsistence practices in
417 Sicily, as was hypothesized by Tusa (Tusa, 1996, 1985). We observed individuals with HG
418 ancestry and a farming/fishing diet, while one individual with farmer ancestry had a terrestrially-
419 based forager diet (Figure 3B). In the absence of strontium isotope analyses on each of these
420 individuals, we cannot exclude that one or more of them were not locals, although this seems
421 unlikely on genetic grounds in the case of *UZZ71* and *UZZ88*, who have the same genetic
422 makeup as the LM hunter-gatherers from *Grotta dell'Uzzo*. This may lead to the question of
423 whether a mixed forager/fishing/farming economy may have become established at *Grotta*
424 *dell'Uzzo* for up to a couple of centuries after the introduction of agro-pastoralism. This
425 possibility is compatible with the zooarchaeological evidence from the site, which indicates that
426 fishing may have been more commonly practiced in the Early Neolithic than in the Mesolithic
427 (STAR Methods).

428 Although rather rare, cases of HGs adopting elements of farming have been reported before in
429 the Balkans, such as at the Iron Gates in Serbia and Romania, *Malak Preslavets* in Bulgaria, and
430 very recently for the French Mediterranean coast (Bonsall et al., 2015; Forenbaheer and Miracle,

2006; Gronenborn, 2017; Lipson et al., 2017b; Mathieson et al., 2018; Perlès, 2001; Rivollat et al., 2020). Also, the few available ancestry profiles for Early Neolithic farmers in the Maghreb showed a strong population genomic continuity with the ~15,000 yBP Iberomaurusian foragers from this region (Fregel et al., 2018; van de Loosdrecht et al., 2018). Taken together, these cases provide joint evidence of generally heightened interaction between HGs with early farmers in central and western Mediterranean regions, such as north-western Sicily (Isern et al., 2017; Mulazzani et al., 2016; Rivollat et al., 2020; Sánchez et al., 2012; van de Loosdrecht, 2021). Future research could explore the possibility that in Mediterranean coastal regions, acculturation of local foragers played a more significant role in the process of Neolithisation compared to regions along the Continental Route (van de Loosdrecht, 2021). The expansion routes into the central and western Mediterranean form an integral part of archaeological discourse on the Mediterranean Neolithic transition. Congruent with previous results for EN farmer groups in Iberia, we show that the Sicilian EN farmers also shared genetic affinity with EN groups from the Balkans, as well as groups in central Europe associated with the Continental Route, rather than North African groups from the southern Mediterranean (Figure 2B, Data S3.1, Data S5.5, Figure S10) (Haak et al., 2015; Olalde et al., 2015; Villalba-Mouco et al., 2019). It is therefore most parsimonious that the majority of early farmers in Sicily and Iberia descended from groups that expanded along a northern Mediterranean route, which share the same origin with the Continental Route in the Balkans and did not cross the Strait of Gibraltar and/or Sicily (van de Loosdrecht, 2021). Overall, our study presents genetic and dietary transitions over a 6,000 years time transect from the same archaeological site. The genomic data from individuals from *Grotta del'Uzzo* show evidence for at least three genetic incursions during the Late Mesolithic, Early Neolithic and Early Bronze Age, with the most significant population shift happening during the Mesolithic-Neolithic transition. Combining genomic and isotopic evidence, we reveal that during the earliest Neolithic phase, resident HGs and incoming farmers were not only genetically interacting, but also may have affected each others' subsistence practices. It is important to note that the analysis of genomic ancestry alone may not detect acculturation. In this study and many previous reports for forager-farmer interactions, the acculturation of foragers could be detected only because of the joint analyses of genomic ancestry, stable isotope data and precise AMS radiocarbon dates together with archaeological context descriptions (Lipson et al., 2017b; Mathieson et al., 2018;

462 Rivollat et al., 2020; van de Loosdrecht, 2021). Hence, multi-disciplinary approaches form the
463 most powerful research strategy to obtain a comprehensive understanding of the transition from
464 foraging to sedentary farming in the Mediterranean (van de Loosdrecht, 2021).

465

466 **Limitations of the study**

467 An important merit of our study is to provide a view on genetic and dietary change in the early to
468 middle Holocene at a single site in the centre of the Mediterranean. Our sampling strategy
469 succeeded in covering different phases of the Mesolithic and Neolithic, enabling us to detect key
470 transitions in genomes and diet. However, the nature of prehistoric bone assemblages, especially
471 when spread out across at least five millennia makes it difficult to have at our disposal more than
472 a few specimens for each phase. The transition from the Mesolithic to the Neolithic is a key time
473 for our study, which has shown it to have been a short-term phase, likely lasting less than the age
474 ranges detectable by means of radiocarbon dating. This implies that in archaeological terms, and
475 particularly for a cave site with a complex stratigraphy and palimpsest-like deposits, we are
476 dealing with a “needle in a haystack” scenario. Our interpretation of what may have happened
477 around the time of contact between hunter-gatherers and early farmers thus relies mainly on
478 genetic and isotopic data from three individuals (i.e. *UZZ71*, *UZZ77* and *UZZ81*). Nevertheless,
479 our reconstructions are not only based on the genetic and isotope data presented here, but also on
480 published isotope data (Mannino et al., 2015), as well as on a considerable amount of
481 archaeological, zooarchaeological and archaeobotanical research undertaken on *Grotta dell’Uzzo*
482 (Costantini et al., 1987; Piperno et al., 1980a, 1980b; Tagliacozzo, 1993; Tusa, 1996, 1985).
483 Another limitation that this kind of investigation has to contend with is the dearth of sites and
484 deposits dating to the Mesolithic-Neolithic transition, which in the Mediterranean are represented
485 by less than a handful of contexts (Biagi, 2003; Biagi and Starnini, 2016; Binder et al., 2012).

486

487

488

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502
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 504 C.C., V.S., and R.DiS. provided the ancient human remains and, together with D.G., and D.B.,
 505 input for the archaeological interpretation. M.vdL., C.F. and H.F. performed laboratory work
 506 with the help of F.A., M.B., R.R., R.S., A.W. and G.B.. M.vdL. and H.Y. conducted the
 507 population genetic analyses with the help of V.V-M., A.B.R., A.C., K.P., C.J. and W.H.. S.T.
 508 and H.F. performed the AMS radiocarbon dating analysis, and M.Ma. the isotope analysis.
 509 M.vdL., H.Y., M.Ma., W.H., C.P., C.J., K.P. and J.K. wrote the paper with input from all co-
 510 authors.

511
 512 **Declaration of Interests:** The authors declare no competing interests.

513
 514 **Figure legends**

515 **Figure 1. Chronology and genomic structure of prehistoric Sicilians.** (A) Calibrated date
 516 ranges (2-sigma) of the prehistoric Sicilians determined from direct radiocarbon (^{14}C)
 517 measurements, or stratigraphy (str.) in the case of *UZZ96* and *UZZ33*, with correction for marine
 518 reservoir effect for some individuals (STAR Methods). The individuals are coloured according to
 519 their assigned genetic group. Individuals *UZZ71*, -88 and -77 may be contemporaneous with the
 520 early *Impressa* Ware phase at the site (marked by *). (B) Heat plot showing three genetic groups
 521 among the prehistoric Sicilians, including previously published OrienteC individual from Sicily.
 522 Genetic distances were measured with pairwise outgroup statistics of the form $f_3(\text{Mbuti}; \text{Ind1},$
 523 $\text{Ind2})$ (Data S1.2). (C) PCA plot of 43 modern West Eurasian groups (grey crosses), on which

524 the newly reported prehistoric Sicilians (colour-filled symbols with black outlines) together with
 525 relevant previously published individuals are projected: from Sicily (filled symbols with no
 526 outline), and from other regions (open symbols).

527 **Figure 2. Genomic affinity of the prehistoric Sicilians.** (A) Comparing the ancestry in Sicily
 528 EM and LM HGs to various West Eurasian HGs (X), as measured by $f_4(\text{Chimp}, X; \text{Sicily EM HG},$
 529 $\text{Sicily LM HG})$. Warmer colours indicate that X shares more genetic drift with Sicily EM HGs
 530 than with Sicily LM HGs, and cooler colours the opposite. Point sizes reflect $|z|$ -scores. (B) Early
 531 Neolithic Sicilian farmers show the highest genetic affinity to contemporaneous farmers from the
 532 Balkans (Croatia and Serbia) and Middle Neolithic Sicily, as measured by $f_3(\text{Mbuti}; \text{Sicily EN},$
 533 $X)$. Warmer colours indicate higher levels of allele sharing. For standard errors, see Data S2.2
 534 and 3.1.

535 **Figure 3. Genomic and dietary discontinuities at Grotta dell'Uzzo, Sicily, during the**
 536 **Mesolithic and Early Neolithic.** (A) Genomic profiles determined from $qpAdm$ -based ancestry
 537 models. The length of coloured bars showed the estimated proportion of each ancestry, with
 538 standard errors. (B) Carbon and nitrogen stable isotope ratios for diet reconstruction. For
 539 European ecosystems, carbon stable isotopes are mostly used to distinguish terrestrial from
 540 marine foods. Nitrogen isotopes ratios incrementally increase in organisms at every trophic level
 541 of food chain, and can therefore give an indication of the amount and trophic level of the
 542 consumed protein (herbivorous, carnivorous, omnivorous). Coloured symbols indicate the
 543 individuals' assigned genetic group. Individuals $UZZ88$, $UZZ71$ and $UZZ77$ have outlier diets
 544 (outlined) and are contemporaneous to the earliest *Impressa* Ware phase (marked with*).

545
 546 **Data S1.** The metadata for newly reported individuals, genetic grouping, biological relatedness
 547 and uniparentally-inherited markers, related to Figure 1.

548 **Data S2.** Genetic analysis of Sicilian hunter-gatherers, related to Figure 2.

549 **Data S3.** Genetic analysis of Sicilian early farmers and Bronze Age individuals, related to Figure
 550 2 and 3.

551 **Data S4.** Details of Y-chromosome haplogroup assignments of four male individuals, related to
 552 STAR Methods.

553

554

555 **STAR Methods**

556

557 RESOURCE AVAILABILITY**558 Lead contact**

559 Further information and requests for resources and reagents should be directed to and will be
560 fulfilled by the lead contact, Johannes Krause (krause@eva.mpg.de).

561 Materials availability

562 This study did not generate new unique reagents.

563 Data and code availability

- 564 ● Genomic data newly generated in this study (BAM format) are available through the
565 European Nucleotide Archive (ENA), with accession number: PRJEB50762. The accession
566 number is also listed in the key resources table.
- 567 ● This paper does not report original code.
- 568 ● Any additional information required to reanalyze the data reported in this paper is available
569 from the lead contact upon request.

571 EXPERIMENTAL MODEL AND SUBJECT DETAILS**573 *Grotta dell'Uzzo: Archaeology and stratigraphic sequence*****574 *The site, its burial ground and human remains***

575 *Grotta dell'Uzzo* is a large shelter-like cave located in northwestern Sicily, along the eastern
576 cliffs of the San Vito lo Capo peninsula (Fig. S1). The site was visited hastily in 1927 by the
577 French archaeologist Raymond Vaufray, who did not realize its importance. The discovery of the
578 deposit and its stratification was made in the early 1970s by Giovanni Mannino (Mannino,
579 1973), who excavated a small test trench in the cave, exposing a sequence of in situ Mesolithic
580 deposits (identified as Epipaleolítico). Prehistoric deposits were excavated during the 1970s,
581 1980s and in 2004 in a number of trenches both inside and outside the overhang of the cave (Fig.
582 S1). This revealed that the site was occupied from at least the late Upper Palaeolithic through the
583 Mesolithic and into the Neolithic (Conte and Tusa, 2012; Piperno et al., 1980a; Piperno and
584 Tusa, 1976; Tagliacozzo, 1993). The cave was also occupied during the Bronze Age and
585 throughout history, and until recently was used by shepherds as a stable for sheep.
586 This long stratigraphic sequence covering the transition from hunter-gatherer to agro-pastoral
587 economies make *Grotta dell'Uzzo* a key site for understanding Mediterranean prehistory

588 (Mannino et al., 2015, 2007; Piperno et al., 1980b; Tagliacozzo, 1993; Tusa, 1996, 1985). It is a
589 unique site, given that Mediterranean sites with such continuous and intact sequences covering
590 the late Mesolithic to the early Neolithic are rare, possibly as a consequence of a decrease in
591 hunter-gatherer populations at the end of the Mesolithic (Biagi, 2003).

592 Another important feature of this cave site is that during the Mesolithic it was used as a burial
593 ground. A total of 11 burials and 13 inhumated individuals (six males, four females and three
594 infants) have been recovered at *Grotta dell'Uzzo* in the course of excavations in the 1970s, 1980s
595 and 2004, close to the walls of the 'inner part' of the cave (Borgognini Tarli et al., 1993; Conte
596 and Tusa, 2012; Di Salvo et al., 2012). Studies on the dental pathologies of the inhumated
597 humans established that plant foods were an important component of the diet of the Mesolithic
598 hunter-gatherers (Silvana et al., 1985). On the other hand, isotopic and zooarchaeological
599 investigations show that the occupants of *Grotta dell'Uzzo* relied heavily on animal protein,
600 which through time originated increasingly from marine ecosystems (Mannino et al., 2015;
601 Tagliacozzo, 1993).

602 Human remains at the cave were, however, also found scattered through the deposits of *Grotta*
603 *dell'Uzzo*. Radiocarbon dating ascertained that these remains were not only Mesolithic but dated
604 to all the main phases of cave occupation, including the so-called Mesolithic-Neolithic transition
605 phase and Neolithic phases (Mannino et al., 2015). As part of the same study, 70 human bones
606 were sampled, of which 57 were recovered from the burials and 13 commingled within the
607 deposits. In total, only 33 bones yielded collagen extracts and 10 of these were from the bones
608 recovered outside of the burials. Only 40% of the bones from the burials yielded collagen
609 extracts and not all of these met the quality criteria established by van Klinken (van Klinken,
610 1999), which is indicative of the poor state of preservation of the human skeletal remains from
611 the burials (Mannino et al., 2015). On the other hand, 77% of the commingled bones yielded
612 collagen extracts, all of which are well preserved. For this reason, and because our aim was to
613 obtain genetic and further isotopic information on the main periods of cave occupation, we
614 decided to target the loose human remains, many of which have been directly dated within the
615 remit of this project.

616

617 ***Cultural succession at Grotta dell'Uzzo from the Mesolithic to Early Neolithic***

618 *Mesolithic*

619 The lithic industries from the two oldest two phases of the Mesolithic at *Grotta dell'Uzzo* have
620 not been studied in detail, but they are contemporary to the occurrence in Sicily of facies of
621 Epigravettian tradition across the island, followed by Sauveterrian-like facies (Lo Vetro and
622 Martini, 2016). In north-western Sicily, microlithic industries of Epigravettian tradition (labelled
623 as *Epigravettiano indifferenziato*) have been identified at *Grotta dell'Uzzo* in the Mesolithic
624 phases I and II (Guerreschi and Fontana, 2012), as well as at *Grotta dell'Isolidda* (Lo Vetro and
625 Martini, 2016) and *Grotta di Cala Mancina* (Lo Vetro and Martini, 2012) on the western coast of
626 the San Vito lo Capo peninsula. These industries demonstrate strong techno-cultural affinities
627 between the Late Epigravettian and early Holocene hunter-gatherers of Sicily. On the other hand,
628 Sauveterrian industries have not been clearly identified at *Grotta dell'Uzzo*, but Sauveterrian-like
629 facies have been retrieved from the nearby site of *Grotta dell'Isolidda* (Lo Vetro and Martini,
630 2012) and at the westernmost end of Sicily on the island of Favignana at *Grotta d'Oriente* (Lo
631 Vetro and Martini, 2012).

632 Levels 14 to 11 in both Trench F and Trench M have previously been defined as the so-called
633 'Mesolithic-Neolithic transition phase' (Costantini et al., 1987; Mannino et al., 2006, 2015,
634 2007; Piperno et al., 1980a; Piperno and Tusa, 1976; Tagliacozzo, 1993; Tusa, 1985), because
635 this was an essentially Mesolithic phase with some Neolithic elements in its upper spits. A recent
636 study of the lithic industry from these layers assigns this phase of cave occupation to the blade-
637 and-trapeze techno-complex of the western Mediterranean Castelnovian tradition (Collina,
638 2015). The oldest date available for the lowermost spits of this phase obtained on charcoal from
639 spits 14 and 13 of Trench F attributes this part to 9,000-8,580 cal BP (P-2734: $7,910 \pm 70$ BP
640 (Piperno, 1985)), which is one of the oldest chronological attributions for a blade-and-trapeze
641 industry (Castelnovian *sensu lato*). The most recent reassessment of the radiocarbon chronology
642 for *Grotta dell'Uzzo*, based on Bayesian modelling of the sequence of dates available for Trench
643 F, suggests that the phase associated with the Castelnovian facies may have spanned ~8,770-
644 7,850 cal BP (Mannino et al., 2015). The following phase is the Neolithic phase I, which
645 according to the above-mentioned Bayesian model may have spanned ~8,050-7,400 cal BP
646 (Mannino et al., 2015).

647 The blade-and-trapeze Castelnovian (*sensu lato*) complex of the ninth millennium BP is in
648 technical continuity with the Neolithic complexes of the following Impressed Ware and
649 Stentinello/Kronio culture of the VI millennium BCE. The production of trapezes constitutes the

650 defining element of the lithic techno-complexes between the VII and VI millennia BCE. This
651 was achieved through a notable standardization of the production processes, particularly through
652 the application of pressure by different modalities (Collina, 2015). Nevertheless, the variability
653 in some technical behaviours (e.g., bladelet fracturing techniques, presence/absence of the
654 microburin technique, façonnage processes of the trapeze truncations) is linked with a break and
655 discontinuity in the Mesolithic-Neolithic technical traditions (Collina, 2015).

656

657 *Early Neolithic*

658 The early Neolithic in Sicily has been defined based on sites in the western part of the island
659 (i.e., *Grotta dell'Uzzo*, *Grotta del Kronio*) and is characterized by three main cultural horizons,
660 which in chronological order are: 'Archaic Impressed Ware' (*ceramiche impresse arcaiche*),
661 'Advanced Impressed Ware' (*ceramiche impresse evolute*) of facies Stentinello I and 'Advanced
662 Impressed Ware' (*ceramiche impresse evolute*) of facies Stentinello II (Natali and Forgia, 2018).
663 The chronology of these horizons is largely based on the dating at *Grotta dell'Uzzo*, which for
664 this part of the sequence does not see full consensus between the different scholars who worked
665 on the site, depending on whether the beginning of the Neolithic is taken to coincide with Spit 12
666 of Trench F, as proposed by Tiné and Tusa (Tiné and Tusa, 2012), or with Spit 10 of Trench F,
667 as proposed by Tagliacozzo (Tagliacozzo, 1993) and Collina (Collina, 2015).

668 The early Neolithic witnessed the introduction of agro-pastoralism, with domestic cereals and
669 animals playing a role in the local economy from the very inception of this cultural phase
670 (Costantini et al., 1987; Tagliacozzo, 1993). However, it should be noted that hunting was still
671 practiced and fishing actually increased following the introduction of farming, with a focus on
672 species such as grouper that could be caught onshore. The early Neolithic was, thus, a phase with
673 a very mixed economy based on a combination of hunting, fishing and agro-pastoralism.

674 In the course of the middle and late Neolithic, the subsistence economy became increasingly less
675 reliant on wild resources and more focussed on domesticates (Tagliacozzo, 1993). This tendency
676 continued through the Copper Age and Bronze Age, when pastoralism seems to have played a
677 more pronounced role within an almost terrestrially based agro-pastoral economy (Tusa, 1999).
678 The deposits at *Grotta dell'Uzzo* do not allow us to ascertain whether this site was occupied
679 continuously from the Neolithic through the Copper Age, when the Bell Beaker Culture
680 (*Campaniforme*) dominated western Sicily, and into the Bronze Age. Nevertheless, pottery

681 fragments attributable to the Rodi-Tindari-Vallelunga and Thapsos-Milazzese cultures suggest
682 that the cave was also frequented in the Early and possibly Middle Bronze Age.

683

684 **METHOD DETAILS**

685 **Ancient DNA processing**

686 All pre-amplification laboratory work was performed in dedicated clean rooms (Gilbert et al.,
687 2005) at the Max Planck Institute (MPI) for the Science of Human history (SHH) in Jena and
688 MPI for Evolutionary Anthropology (EVA) in Leipzig, Germany. At the MPI-SHH the
689 individuals were sampled for bone or tooth powder, originating from various skeletal elements
690 (e.g., petrous, molars, teeth, humerus, phalange, tibia, see Data S1.1). The outer layer of the
691 skeletal elements was removed with high-pressured powdered aluminium oxide in a sandblasting
692 instrument, and the element was irradiated with ultraviolet (UV) light for 15 minutes on all sides.
693 The elements were then sampled using various strategies, including grinding with mortar and
694 pestle or cutting and followed by drilling into denser regions (Data S1.1). Subsequently, for each
695 individual 1-8 extracts of 100uL were generated from ~50mg powder per extract, following a
696 modified version of a silica-based DNA extraction method (Dabney et al., 2013) described
697 earlier (Villalba-Mouco et al., 2019) (Data S1.1). At the MPI-SHH, 20uL undiluted extract
698 aliquots were converted into double-indexed double stranded (ds-) libraries following established
699 protocols (Meyer et al., 2012; Meyer and Kircher, 2010), some of them with a partial uracil-
700 DNA glycosylase ('ds UDG-half') treatment (Rohland et al., 2015) and others without ('ds non-
701 UDG').

702 At the MPI-EVA, 30uL undiluted extract aliquot was converted into double-indexed single-
703 stranded (ss-) libraries (Gansauge et al., 2017) with minor modifications detailed in (Slon et al.,
704 2017), without UDG treatment ('ss non-UDG') (Data S1.1). At the MPI-SHH, all the ds- and ss-
705 libraries were shotgun sequenced to check for aDNA preservation, and subsequently enriched
706 using in-solution capture probes following a modified version of (Q. Fu et al., 2013) (described
707 in (Feldman et al., 2019)) for ~1240k single nucleotide polymorphisms (SNPs) in the nuclear
708 genome (Fu et al., 2015) and independently for the complete mitogenome. Then the captured
709 libraries were sequenced on an Illumina HiSeq4000 platform using either a single end (1x75bp
710 reads) or paired end configuration (2x50bp reads).

711 The sequenced reads were demultiplexed according to the expected index pair for each library,
712 allowing one mismatch per 7 bp index, and subsequently processed using EAGER v1.92.21
713 (Peltzer et al., 2016). We used AdapterRemoval v2.2.0 (Schubert et al., 2016) to clip adapters
714 and Ns stretches of the reads. We merged paired end reads into a single sequence for regions
715 with a minimal overlap of 30 bp, and single end reads smaller than 30 bp in length were
716 discarded. The reads obtained from the nuclear capture were aligned against the human reference
717 genome (hg19), and those from the mitogenome captured against the revised Cambridge
718 Reference Sequence (rCRS). For mapping we used the Burrows-Wheeler Aligner (BWA
719 v0.7.12) *aln* and *samse* programs (Li and Durbin, 2009) with a lenient stringency parameter of ‘-
720 n 0.01’ that allows more mismatches, and ‘-l 16500’ to disable seeding. We excluded reads with
721 Phred-scaled mapping quality (MAPQ) <25. Duplicate reads, identified by having identical
722 strand orientation, start and end positions, were removed using DeDup v.0.12.1 (Peltzer et al.,
723 2016).

725 **Isotope analyses and radiocarbon dating**

726 For the present research, we have undertaken collagen extraction for isotope analysis and
727 radiocarbon dating of all specimens that have been genetically-typed. The isotopic and elemental
728 data obtained by analyzing the collagen extracts from the *Grotta dell’Uzzo* humans are shown in
729 Table S1, whilst the results of the radiocarbon dating are listed in Table S2.

730 In total, 22 samples were pretreated using the method proposed by Talamo and Richards
731 (Talamo and Richards, 2011), which is based on the pretreatment originally established by
732 Longin (Longin, 1971) and modified by Brown *et al.* (Brown et al., 1988). Two samples (R-EVA
733 3521,3523) were extracted using the method for small samples in Fewlass *et al.* (Fewlass et al.,
734 2019). All of the sampled specimens yielded extracts, which can be considered well-preserved
735 collagen according to the quality criteria established by van Klinken (van Klinken, 1999). All
736 individuals can, thus, be used for isotopic dietary reconstructions and AMS radiocarbon dating.

738 ***Direct AMS ¹⁴C bone dates***

739 We obtained a direct ¹⁴C date from 19 skeletal element and 17 of them were used in genetic
740 analysis (Table S2). All bone samples were pretreated at the Department of Human Evolution at
741 the Max Planck Institute for Evolutionary Anthropology (MPI-EVA), Leipzig, Germany, using

742 the method described in (Talamo and Richards, 2011). For each skeletal element, 200-500mg of
743 bone/tooth powder was decalcified in 0.5M HCl at room temperature ~4 hours until no CO₂
744 effervescence was observed. To remove humic acids, in a first step 0.1M NaOH was added for
745 30 minutes, followed by a final 0.5M HCl step for 15 minutes. The resulting solid was
746 gelatinized following a protocol of (Longin, 1971) at pH 3 in a heater block at 75°C for 20h. The
747 gelatin was then filtered in an Eeze-Filter™ (Elkay Laboratory Products (UK) Ltd.) to remove
748 small (> 80 um) particles, and ultrafiltered (Brown et al., 1988) with Sartorius “VivaspinTurbo”
749 30 KDa ultrafilters. Prior to use, the filter was cleaned to remove carbon containing humectants
750 (Brock et al., 2007). The samples were lyophilized for 48 hours. In order to monitor
751 contamination introduced during the pre-treatment stage, a sample from a cave bear bone, kindly
752 provided by D. Döppes (MAMS, Germany), was extracted along with the batch from *Grotta*
753 *dell’Uzzo* (Korlević et al., 2018). In marine environments the radiocarbon is older than the true
754 age, usually by ~400 years (marine reservoir effect). Dates were calibrated with the OxCal 4.4
755 software (Bronk Ramsey, 2009) using the IntCal20 curve (Reimer et al., 2020) and, in addition,
756 the Marine20 curve (Heaton et al., 2020) for individuals that had clearly consumed marine
757 protein. The estimation of the amount of marine protein consumed is based on calculations made
758 for specimen S-EVA 8010 (40±10% marine) by Mannino et al. (Mannino et al., 2015). The
759 individuals for which a correction was necessary are *UZZ4446* (40±10% marine), *UZZ81*
760 (45±10% marine), *UZZ69*, *UZZ79* and *UZZ80* (50±10% marine). Corrections were made using
761 the reservoir correction estimated for the Mediterranean Basin by Reimer and McCormac
762 (Reimer and McCormac, 2002), which is $\Delta R = 58 \pm 85$ 14C yr.

763

764 *Isotope analysis*

765 For 19 individuals we determined the carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values for
766 dietary inference (Table S1). To assess the preservation of the collagen yield, C:N ratios,
767 together with isotopic values are evaluated following the limits of van Klinken 1999 (van
768 Klinken, 1999). The details for Isotope analysis are provided in Data S5.1.

769

770 **QUANTIFICATION AND STATISTICAL ANALYSIS**

771 **aDNA authentication and quality control**

772 We assessed the authenticity and contamination levels in our ancient DNA libraries (unmerged
773 and merged per-individual) in several ways. First, we checked the cytosine deamination rates at
774 the end of the reads (Briggs et al., 2007) using DamageProfiler v0.3 ([https://github.com/apeltzer/](https://github.com/apeltzer/DamageProfiler)
775 [DamageProfiler](https://github.com/apeltzer/DamageProfiler)). After merging the libraries for each individual, we observed 21-52% C>T
776 mismatch rates at the first base in the terminal nucleotide at the 5'-end, an observation that is
777 compatible with the presence of authentic ancient DNA molecules.

778 Second, we tested for contamination of the nuclear genome in males based on the X-
779 chromosomal polymorphism rate. We determined the genetic sex by calculating the X-rate
780 (coverage of X-chromosomal SNPs/ coverage of autosomal SNPs) and Y-rate (coverage of Y-
781 chromosomal SNPs/ coverage of autosomal SNPs) (Fu et al., 2016). Six individuals for which
782 the libraries showed a Y-rate ≥ 0.49 we assigned the label 'male' and 14 individuals with Y-rates
783 0.07 as 'female'. The individual *UZZ26.cont* with an intermediate Y-rate of 0.17 we excluded
784 from further genetic analyses. Then we tested for heterozygosity of the X-chromosome using
785 ANGSD v0.910 (≥ 200 X-chromosomal SNPs, covered at least twice)(Korneliussen et al., 2014).
786 Based on new Method1, we found a nuclear contamination of 0.9-4.4% for five male individuals
787 (Data S1.1) and 18.5% in individual *UZZ99*, which was also excluded from further analyses.
788 Third, we obtained two mtDNA contamination estimates for genetic males and females, using
789 ContaMix v1.0.10 (Qiaomei Fu et al., 2013) and Schmutzi v1.0 (Renaud et al., 2015). Before
790 running Schmutzi, we realigned the reads to the rCRS using CircularMapper v1.93.4 filtering
791 with MAPQ < 30. After removing duplicate reads, we downsampled to ~30,000 reads per
792 library. With Schmutzi we found low contamination estimates of 1-3% for all individuals with
793 sufficient coverage (Data S1.1). ContaMix returned estimates in the range of 0.0-5.6% for all
794 individuals except for *UZZ69* (3.7-10.6%) and the lower coverage individual *UZZ096* (0.3-
795 13.5%).

796

797 **Dataset**

798 For genotyping we extracted reads with high mapping quality (MAPQ ≥ 37) to the autosomes
799 using samtools v1.3. The DNA damage plots indicated that misincorporations could extend up to
800 10 bp from the read termini in non-UDG treated and up to 3bp in UDG-half treated libraries. We
801 hence clipped the reads accordingly, thereby removing G>A transitions from the terminal read
802 ends in ds-libraries and C>T transitions in both ss- and ds-libraries. For each individual, we

803 randomly chose a single base per SNP site as a pseudo-haploid genotype with our custom
804 program ‘pileupCaller’ (<https://github.com/stschiff/sequenceTools>). We intersected our data
805 with a global set of high-coverage genomes from the Simon Genome Diversity Project (SGDP)
806 for ~1240k nuclear SNP positions (Mallick et al., 2016), including previously reported ancient
807 individuals (Allentoft et al., 2015; Antonio et al., 2019; Brace et al., 2019; Broushaki et al., 2016;
808 Brunel et al., 2020; Catalano et al., 2020; Damgaard et al., 2018; Feldman et al., 2019; Fernandes
809 et al., 2020; Fregel et al., 2018; Fu et al., 2016, 2014; Gamba et al., 2014; Günther et al., 2015;
810 Hofmanová et al., 2016; Jones et al., 2017, 2015; Keller et al., 2012; Kılınç et al., 2016;
811 Lazaridis et al., 2017, 2016, 2014; Lipson et al., 2017b; Llorente et al., 2015; Mallick et al.,
812 2016; Marcus et al., 2020; Mathieson et al., 2018; Meyer et al., 2012; Mittnik et al., 2018; Olalde
813 et al., 2019, 2018, 2015; Omrak et al., 2016; Raghavan et al., 2014; Rivollat et al., 2020; Saag et
814 al., 2017; Sikora et al., 2017; Skoglund et al., 2014; Valdiosera et al., 2018; Villalba-Mouco et
815 al., 2019). To minimize the effects of residual ancient DNA damage, we removed ~300k SNPs
816 on CpG islands from the data set. CpG dinucleotides, where a cytosine is followed by a guanine
817 nucleotide, are frequent targets of DNA methylation (Kennett et al., 2017). Post-mortem cytosine
818 deamination was shown to occur more frequently at methylated than unmethylated CpGs
819 (Seguin-Orlando et al., 2015) resulting in excess of CpG → TpG conversions. The final data set
820 includes 868,755 intersecting autosomal SNPs for which our newly reported individuals cover
821 53,352-796,174 SNP positions with an average read depth per SNP of 0.09-9.39X (Data S1.1).
822 For principal component analyses (PCA) we intersected our data and published ancient genomes
823 with a panel of worldwide present-day populations, genotyped on the Affymetrix Human Origins
824 (HO) (Lazaridis et al., 2014; Patterson et al., 2012). After filtering out CpG dinucleotides this
825 data set includes 441,774 SNPs.

826

827 **Biological relatedness and individual assessment**

828 We determined pairwise mismatch rates (PMRs) (Kennett et al., 2017; Kılınç et al., 2016) for
829 pseudo-haploid genotypes to check for genetic duplicate individuals and first-degree relatives. If
830 two samples show similar levels of PMR for inter- and intra-individual library comparisons, then
831 this indicates a genetic duplicate. Moreover, the expected PMR for two first-degree related
832 individuals falls approximately in the middle of the baseline values for comparison between
833 genetically unrelated and identical individuals (van de Loosdrecht et al., 2018). We found a

834 genetic triplicate (UZZ44, -45, -46) and quintuplicate (UZZ50-54) (Data S1.4). After
835 confirmation from uniparental marker analyses for similar haplotypes and an absence of
836 detectable (cross-)contamination for each of the libraries within these library sets, we merged the
837 sets into *UZZ4446* and *UZZ5054*, respectively (Data S1.1). In addition, *UZZ79* and *UZZ81*
838 showed an elevated PMR indicative of a close biological relationship (Data S1.4). We therefore
839 remove from *UZZ81* the group-based *f*-statistics and DATES analysis.

840

841 **Mitogenome haplogroup determination**

842 We could reconstruct the mitochondrial genomes for 17 individuals (Data S1.1). To obtain an
843 automated mitochondrial haplogroup assignment we imported the consensus sequences from
844 Schmutzi into HaploGrep2 v2.1.1 (available via: [https://haplogrep.i-](https://haplogrep.i-med.ac.at/category/haplogrep2/)
845 [med.ac.at/category/haplogrep2/](https://haplogrep.i-med.ac.at/category/haplogrep2/)) (Weissensteiner et al., 2016) based on phylotree (mtDNA tree
846 build 17, available via <http://www.phylotree.org/>) (van Oven and Kayser, 2009). In parallel, we
847 manually haplotyped the reconstructed mitogenomes, based on a procedure described in (Posth
848 et al., 2016). We imported the bam.files for the merged libraries into Geneious v.9.0.5
849 (<http://www.geneious.com>) (Kearse et al., 2012). After reassembling the reads against the
850 revised Cambridge Reference Sequence (rCRS) we called SNP variants with a minimum variant
851 frequency of 0.7 and 2.0X coverage.

852 Using phylotree, we double-checked whether the called variants matched the expected diagnostic
853 ones based on the automated HaploGrep assignment. We did not consider known unstable
854 nucleotide positions 309.1C(C), 315.1C, AC indels at 515-522, 16093C, 16182C, 16183C,
855 16193.1C(C) and 16519. We extracted the consensus sequences based on a minimum of 75%
856 base similarity. Using this approach, we identified a total of twelve lineage-specific and private
857 variants in the high coverage *UZZ5054* mitogenome. Four of the lineage-specific variant
858 positions were covered by only one or two reads in the low coverage *UZZ96* and *OrienteC*
859 genomes, and hence fell initially below our frequency threshold for variant detection. However,
860 since these variants were covered by a large number of reads in the closely related *UZZ5054*
861 mitogenome, for *UZZ96* and *OrienteC* we based the variant calls at these positions on the few
862 reads available and adjusted their consensus sequences accordingly (Data S1.3).

863

864 **Y-chromosome haplogroup determination**

865 To assign Y haplogroups, for each individual, we assembled pileups of every covered site,
866 filtered for sites found on the ISOGG SNP list v14.48
867 (https://isogg.org/tree/ISOGG_YDNA_SNP_Index.html). For each individual we manually
868 inspected this list to determine to which Y haplogroup our individuals most likely belonged,
869 using the script published in Rohrlach *et al.* 2021 (Rohrlach et al., 2021). The output CSV files
870 with ancestral and derived alleles coverage on ISOGG SNPs are provided in Data S4.

871

872 **Principal component analysis (PCA)**

873 We computed principal components from individuals from 43 modern West Eurasian groups in
874 the Human Origin panel (Lazaridis et al., 2014; Patterson et al., 2012) using the *smartpca*
875 program in the EIGENSOFT package v6.0.1 (Patterson et al., 2006) with the parameter
876 ‘numeroutlieriter:0’. Ancient individuals were projected using ‘lsqproject:YES’ and
877 ‘shrinkmode:YES’.

878

879 ***f*-statistics**

880 We performed *f*-statistics on the 1240k data set using ADMIXTOOLS 5.1 (Patterson et al.,
881 2012). For f_3 -outgroup statistics (Reich et al., 2009) we used *qp3Pop* and for f_4 -statistics *qpDstat*
882 with *f4mode:YES*. Standard errors (SEs) were determined using a weighted block jackknife over
883 5Mb blocks. F_3 -outgroup statistics of the form $f_3(O;A,B)$ test the null hypothesis that *O* is a true
884 outgroup to *A* and *B*. The strength of the f_3 -statistic is a measure for the amount of genetic drift
885 that *A* and *B* share after they branched off from a common ancestor with *O*, provided that *A* and
886 *B* are not related by admixture. F_4 -statistics of the form $f_4(X,Y;A,B)$ test the null hypothesis that
887 the unrooted tree topology $((X,Y)(A,B))$, in which (X,Y) form a clade with regard to (A,B) , reflects
888 the true phylogeny. A positive value indicates that either *X* and *A*, or *Y* and *B*, share more drift
889 than expected under the null hypothesis. A negative value indicates that the tree topology under
890 the null-hypothesis is rejected into the other direction, due to more shared drift between *Y* and *A*,
891 or *X* and *B*.

892

893 **Multidimensional scaling (MDS)**

894 We performed MDS using the R package *cmdscale*. Euclidean distances were computed from the
895 genetic distances among West-Eurasian HG, as measured by $f_3(Mbuti; HG1, HG2)$ for all

896 possible pairwise combinations (Fu et al., 2016). The two dimensions are plotted. We restricted
897 the analyses to individuals with >30,000 autosomal SNPs covered. Relevant previously
898 published West Eurasian HGs were pooled in groups according to their geographical or temporal
899 context, following their initial publication labels.

900

901 **Nucleotide diversity**

902 We determined the nucleotide diversity (π) from pseudo-haploid genotypes by calculating the
903 proportion of nucleotide mismatches for overlapping autosomal SNPs covered by at least one
904 read in both individuals. We hence determined π from all possible combinations of individual
905 pairs, rather than from all possible chromosome pairs, within a given group. We filtered out
906 individual pairs that shared less than 30,000 SNPs covered. We calculated an average over all the
907 individual pairs within a group and determined standard errors from block jackknives over 5Mb
908 windows and 95% confidence intervals (95CIs) from 1,000 bootstraps.

909

910 **HapROH**

911 The ROH segments were detected using HapROH (Ringbauer et al., 2021), for selected ancient
912 individuals with >400k SNPs covered in pseudo-haploid genotyping.

913

914 **Inference of mixture proportions**

915 To characterize the ancestry of the ancient Sicilians we used the *qpWave* (Haak et al., 2015) and
916 *qpAdm* (Lazaridis et al., 2016) programs from the Admixtools v5.1 package, with the ‘allsnps:
917 YES’ option. *qpWave* tests whether a set of *Left* populations is consistent with being related via
918 as few as N streams of ancestry to a set of *Outgroup* populations. *qpAdm* tries to fit a *Target* as a
919 linear combination of the *Left/Source* populations, and estimates the respective ancestry
920 proportions that each of the *Left* populations contributed to the *Target*. Both *qpWave* and *qpAdm*
921 are based on f_4 -statistics of the form $f_4(X, O1; O2, O3)$, where *O1*, *O2*, *O3* are all the triplet
922 combinations of the *Outgroup* populations, and *X* is a *Target* or *Left/Source* population. Since
923 missing data may inflate the P-values for this test, we required a test result to be smaller (less
924 extreme) than $P = 0.1$ in order to reject the null-hypothesis of a full ancestry fit between the
925 *Target* and the *Left/Source* population(s). Prior to running *qpAdm* we used *qpWave* to check
926 whether the pairs of *Left/Source* populations are not equally related to the *Outgroups*.

927 For the modeling of the HGs we used the *Outgroup* set: Mbuti, *Mota*, Iberomaurusian, CHG,
 928 Natufian, *Mal'ta*, *AfontovaGora3*, *GoyetQ116*, *Ust Ishim*, *Kostenki14*, *Vestonice16*, *Villabruna*,
 929 Karitiana, Papuan, Onge. For the modeling of the early farmers, we extended the above OG set
 930 with EHG and Pinarbasi (AHG) to differentiate more strongly between the European HG and
 931 EEF ancestry on one hand, and any underlying WHG-EHG/AHG admixture structure in
 932 European HGs. For a generalised European HG ancestry to model the European early farmers,
 933 we combined the following HG into one gene pool: Ukraine (*I5876*), Iron Gates (*I5771*), Sicily
 934 (*UZZ69*), peninsular Italy (*R15*), Iberia (*LaBranca1*, *CMS001*), Germany (*BOT005*, *Falkenstein*),
 935 Luxembourg (*Loschbour*), Hungary (*I1507*), France (*PER3023*, *Ranchot*), England (*I3025*).

936

937 **Admixture dating**

938 The admixture event in Sicily LM HGs was dated using an ancestry covariance pattern-based
 939 DATES 753 program (Chintalapati et al., n.d.), with Sicily EM HGs and EHG as two ancestors.
 940 The bin size for covariance calculation was 0.1cM and exponential fitting started at 0.5cM. The
 941 standard error was determined using jackknife and a generation time of 29 years was used for
 942 admixture date calculation.

943

944 **Phylogeny modelling**

945 We used the qpGraph program (Patterson et al., 2012) to construct a phylogeny of ancestry
 946 lineages found among Palaeolithic and Mesolithic West-Eurasian HG to clarify the genetic
 947 history of Sicily EM HGs. For our modelling we used the parameters 'useallsnps: YES', 'hires:
 948 YES' to improve the resolution and used Mbuti.DG as the outgroup. We started from a published
 949 skeleton graph with six populations: 1) Mbuti, 2) *Ust Ishim*, 3) *Kostenki14*, 4) *GoyetQ116-1*, 5)
 950 *Mal'ta*, 6) *Villabruna* (Fu et al., 2016), then added Sicily EM HGs, *GoyetQ2* or *ElMiron* on the
 951 graph (Data S5.4). After getting the best fitted model with Sicily EM HGs, we further added
 952 *GoyetQ2*, *ElMiron* and *Loschbour* on the model to examine the relationship between *Villabruna*,
 953 Sicily EM HGs with Magdalenians and WHG.

954

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A**Genetic group**

- Sicily EM
- Sicily LM
- Sicily EN
- Uzzo EBA

- UZZ87
- UZZ74
- UZZ75
- UZZ34
- UZZ33 (str.)
- UZZ77*

- UZZ88*
- UZZ71*

- UZZ40
- UZZ4446
- UZZ79
- UZZ80
- UZZ81
- UZZ69
- UZZ82

● UZZ5054

● UZZ96 (str.)

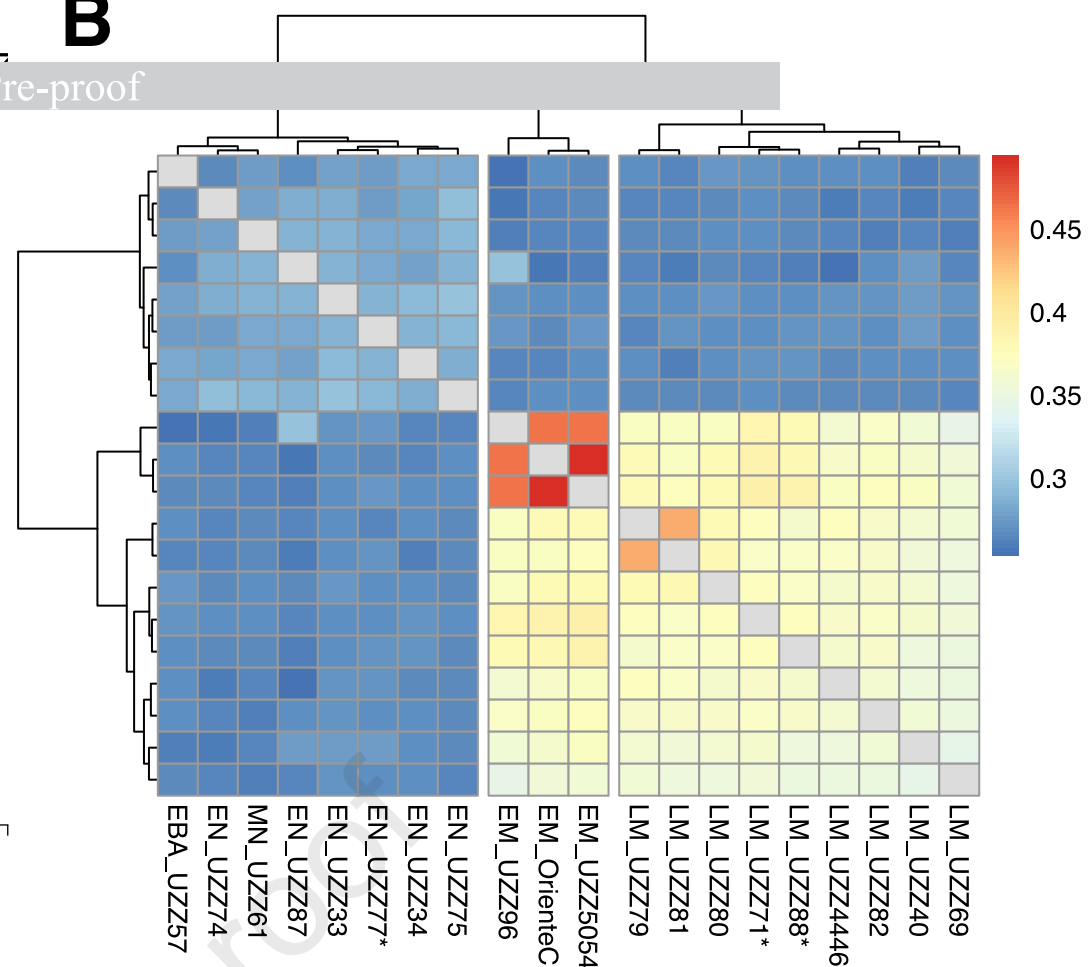
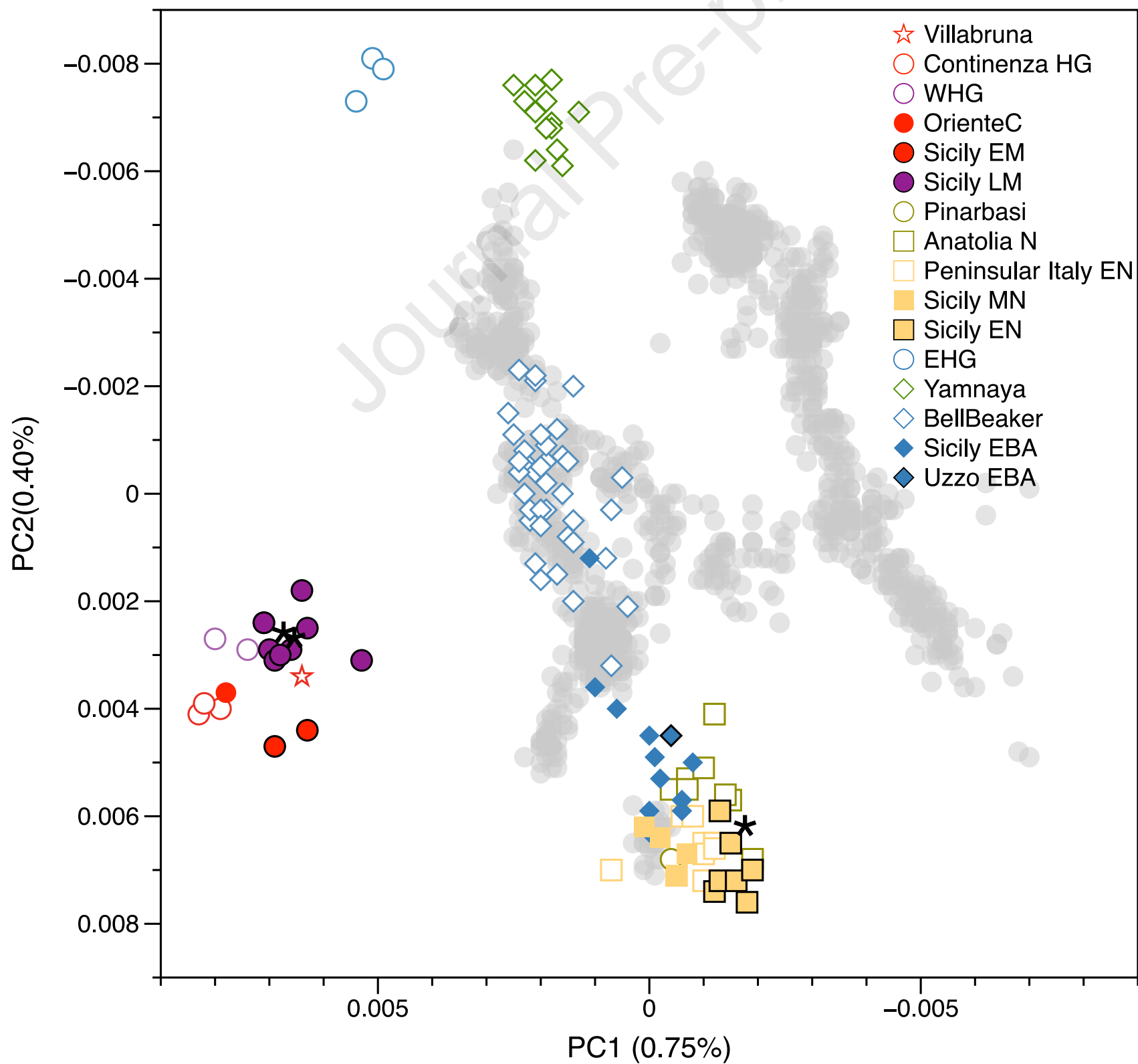
10,000

5,000

Calibrated BP (years)

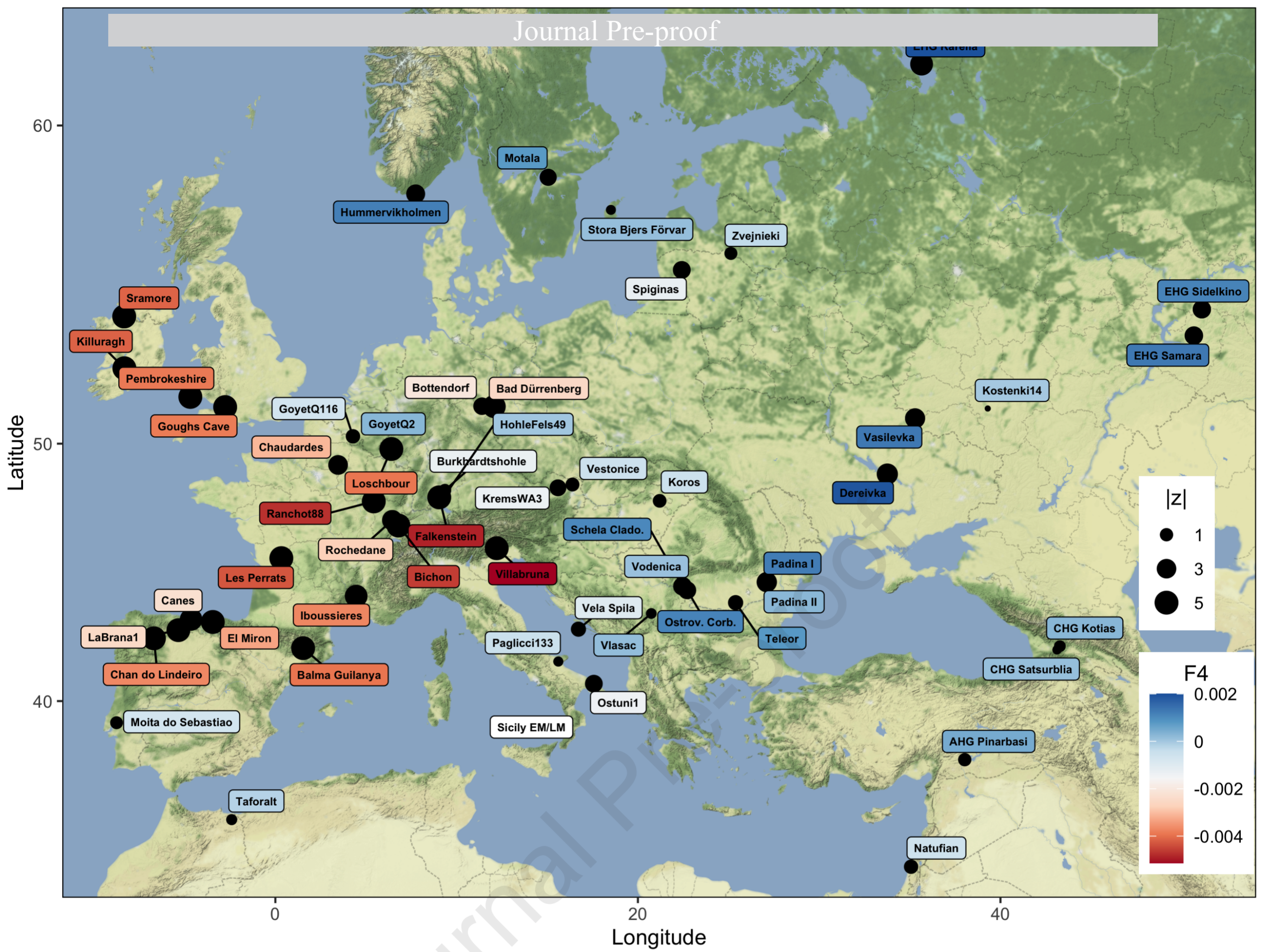
B

Journal Pre-proof

**C**

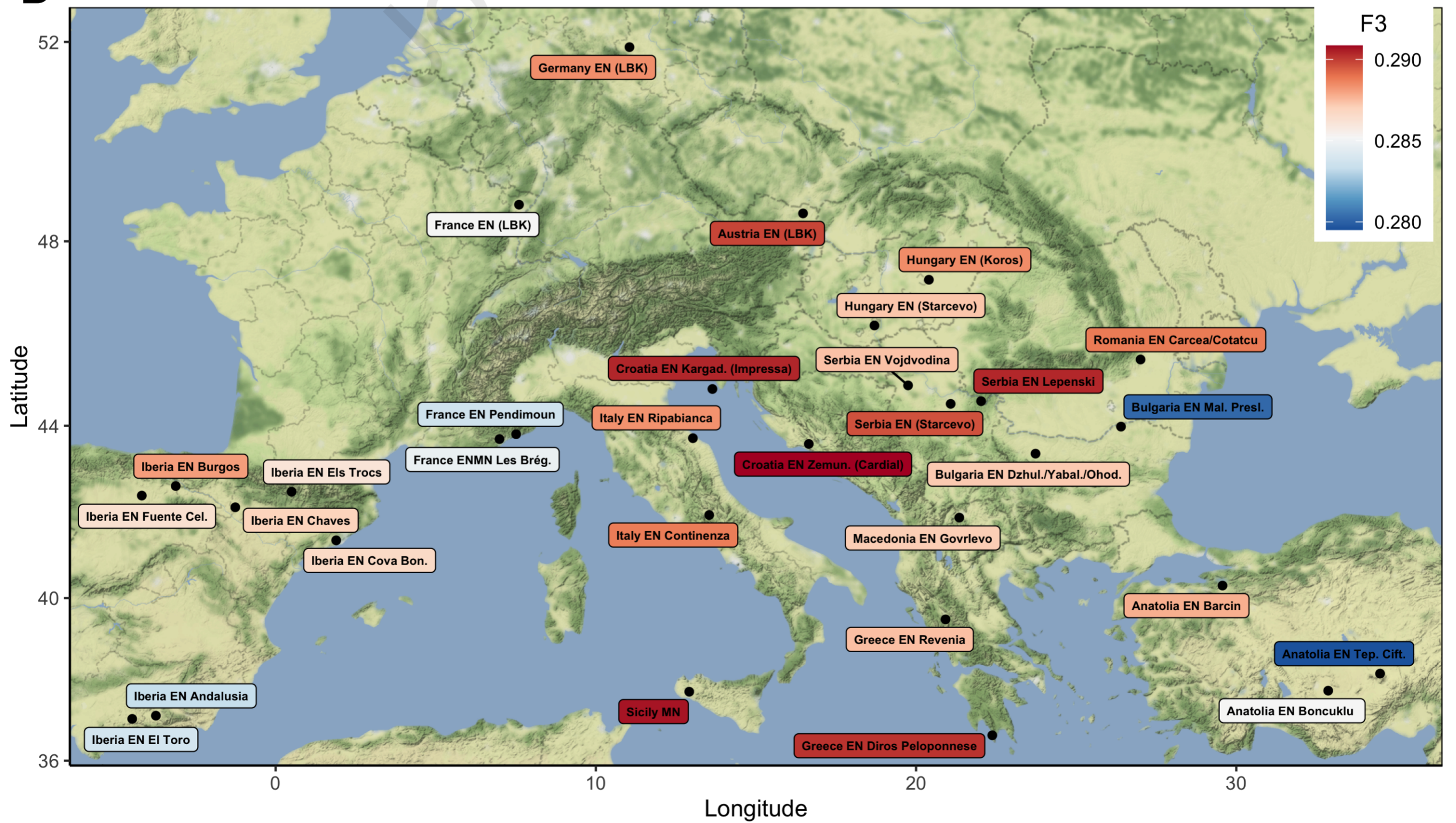
A

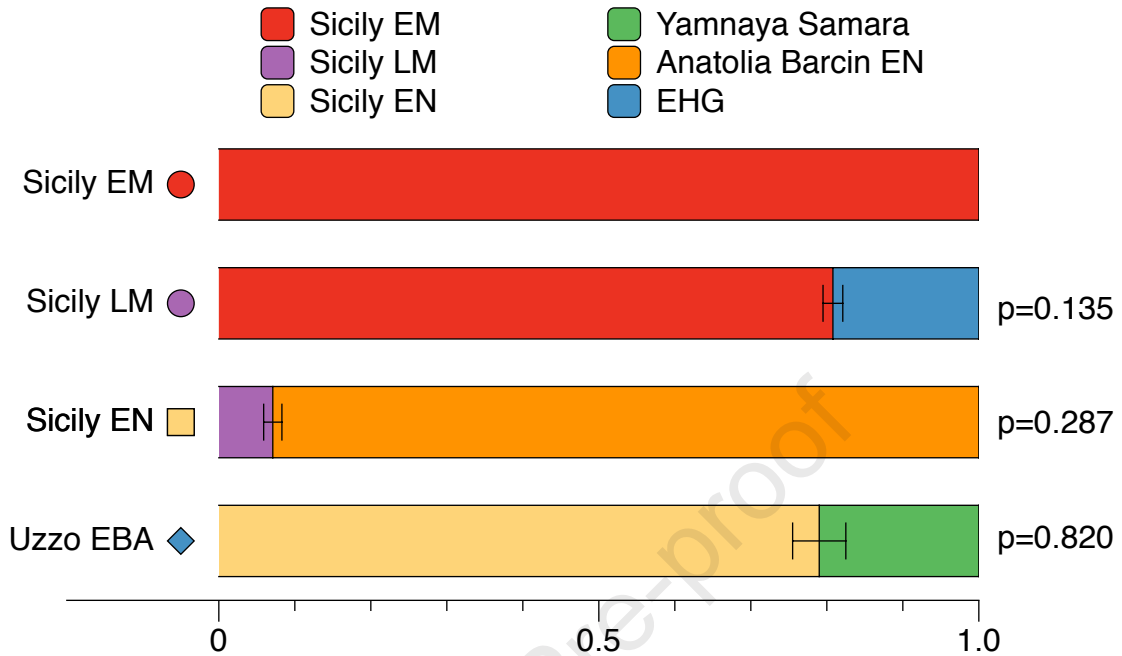
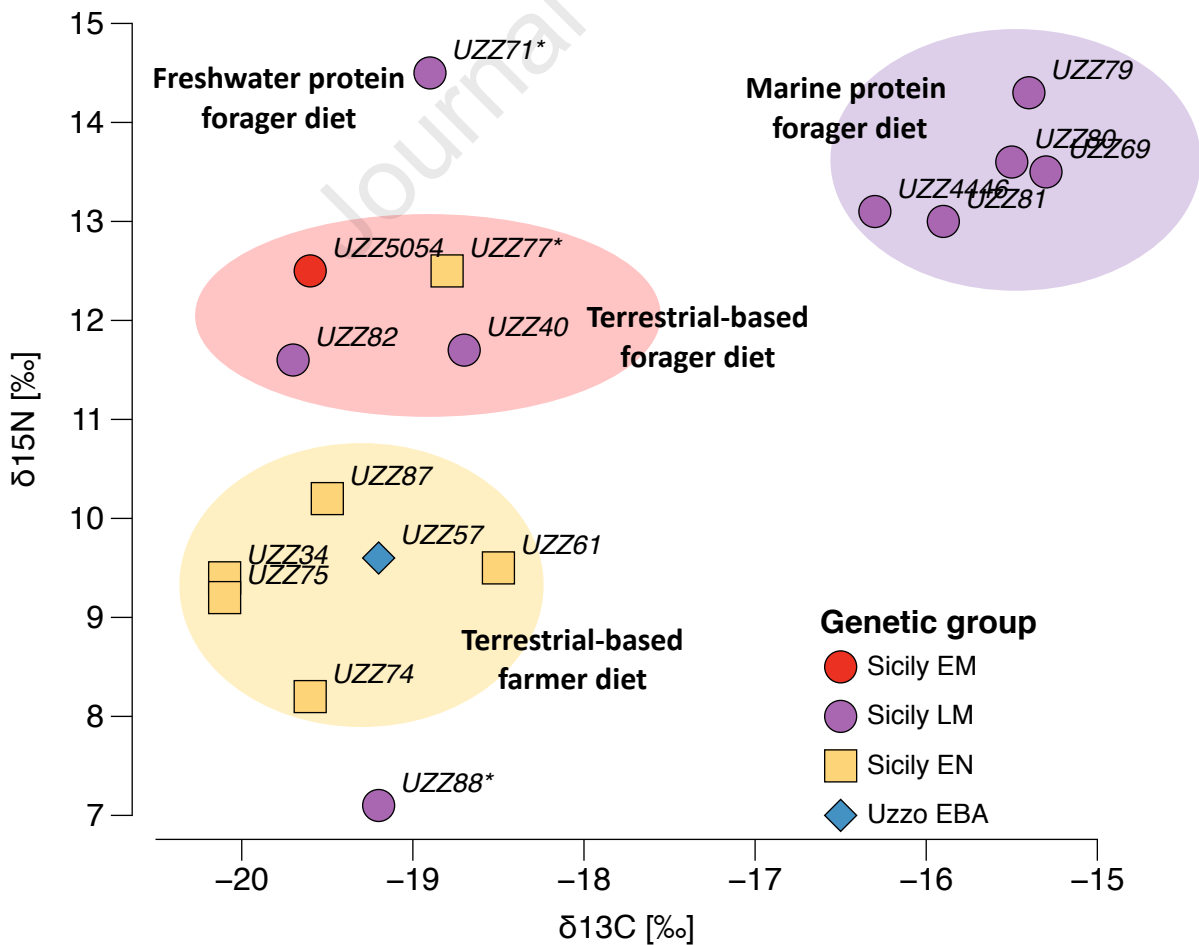
f4(Chimp, X; Sicily EM, Sicily LM)



B

f3(Mbuti; Sicily EN, X)



A**B**

Highlights

1. Genetic transition between Early Mesolithic and Late Mesolithic hunter-gatherers.
2. A near-complete genetic turnover during the Mesolithic-Neolithic transition.
3. Exchange of subsistence practices between hunter-gatherers and early farmers.

Journal Pre-proof

KEY RESOURCES TABLE

The table highlights the reagents, genetically modified organisms and strains, cell lines, software, instrumentation, and source data **essential** to reproduce results presented in the manuscript. Depending on the nature of the study, this may include standard laboratory materials (i.e., food chow for metabolism studies, support material for catalysis studies), but the table is **not** meant to be a comprehensive list of all materials and resources used (e.g., essential chemicals such as standard solvents, SDS, sucrose, or standard culture media do not need to be listed in the table). **Items in the table must also be reported in the method details section within the context of their use.** To maximize readability, the number of **oligonucleotides and RNA sequences** that may be listed in the table is restricted to no more than 10 each. If there are more than 10 oligonucleotides or RNA sequences to report, please provide this information as a supplementary document and reference the file (e.g., See Table S1 for XX) in the key resources table.

Please note that ALL references cited in the key resources table must be included in the references list. Please report the information as follows:

- **REAGENT or RESOURCE:** Provide full descriptive name of the item so that it can be identified and linked with its description in the manuscript (e.g., provide version number for software, host source for antibody, strain name). In the experimental models section (applicable only to experimental life science studies), please include all models used in the paper and describe each line/strain as: model organism: name used for strain/line in paper: genotype. (i.e., Mouse: OXTR^{f/f}: B6.129(SJL)-Oxtr^{tm1.1Wsy/J}). In the biological samples section (applicable only to experimental life science studies), please list all samples obtained from commercial sources or biological repositories. Please note that software mentioned in the methods details or data and code availability section needs to also be included in the table. See the sample tables at the end of this document for examples of how to report reagents.
- **SOURCE:** Report the company, manufacturer, or individual that provided the item or where the item can be obtained (e.g., stock center or repository). For materials distributed by Addgene, please cite the article describing the plasmid and include “Addgene” as part of the identifier. If an item is from another lab, please include the name of the principal investigator and a citation if it has been previously published. If the material is being reported for the first time in the current paper, please indicate as “this paper.” For software, please provide the company name if it is commercially available or cite the paper in which it has been initially described.
- **IDENTIFIER:** Include catalog numbers (entered in the column as “Cat#” followed by the number, e.g., Cat#3879S). Where available, please include unique entities such as RRIDs, Model Organism Database numbers, accession numbers, and PDB, CAS, or CCDC IDs. For antibodies, if applicable and available, please also include the lot number or clone identity. For software or data resources, please include the URL where the resource can be downloaded. Please ensure accuracy of the identifiers, as they are essential for generation of hyperlinks to external sources when available. Please see the Elsevier [list of data repositories](#) with automated bidirectional linking for details. When listing more than one identifier for the same item, use semicolons to separate them (e.g., Cat#3879S; RRID: AB_2255011). If an identifier is not available, please enter “N/A” in the column.
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TABLE FOR AUTHOR TO COMPLETE

Please upload the completed table as a separate document. **Please do not add subheadings to the key resources table.** If you wish to make an entry that does not fall into one of the subheadings below, please contact your handling editor. **Any subheadings not relevant to your study can be skipped.** (NOTE: For authors publishing in Cell Genomics, Cell Reports Medicine, Current Biology, and Med, please note that references within the KRT should be in numbered style rather than Harvard.)

Key resources table

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological samples		
Ancient skeletal element	This study	UZZ26
Ancient skeletal element	This study	UZZ33
Ancient skeletal element	This study	UZZ34
Ancient skeletal element	This study	UZZ40
Ancient skeletal element	This study	UZZ44
Ancient skeletal element	This study	UZZ45
Ancient skeletal element	This study	UZZ46
Ancient skeletal element	This study	UZZ50
Ancient skeletal element	This study	UZZ51
Ancient skeletal element	This study	UZZ52
Ancient skeletal element	This study	UZZ53
Ancient skeletal element	This study	UZZ54
Ancient skeletal element	This study	UZZ57
Ancient skeletal element	This study	UZZ61
Ancient skeletal element	This study	UZZ69
Ancient skeletal element	This study	UZZ71
Ancient skeletal element	This study	UZZ74
Ancient skeletal element	This study	UZZ75
Ancient skeletal element	This study	UZZ77
Ancient skeletal element	This study	UZZ79
Ancient skeletal element	This study	UZZ80
Ancient skeletal element	This study	UZZ81
Ancient skeletal element	This study	UZZ82
Ancient skeletal element	This study	UZZ87
Ancient skeletal element	This study	UZZ88
Ancient skeletal element	This study	UZZ96
Ancient skeletal element	This study	UZZ99
Chemicals, peptides, and recombinant proteins		
D1000 ScreenTapes	Agilent Technologies	Cat# 5067-5582
D1000 Reagents	Agilent Technologies	Cat# 5067-5583
PfuTurbo Cx Hotstart DNA Polymerase	Agilent Technologies	Cat# 600412
Herculase II Fusion DNA Polymerase	Agilent Technologies	Cat# 600679
1x Tris-EDTA pH 8.0	AppliChem	Cat# A8569,0500
Sodiumhydroxide Pellets	Fisher Scientific	Cat# 10306200
Sera-Mag Magnetic Speed-beads Carboxylate-Modified (1 mm, 3EDAC/PA5)	GE LifeScience	Cat# 65152105050250
0.5 M EDTA pH 8.0	Life Technologies	Cat# AM9261

10x Buffer Tango	Life Technologies	Cat# BY5
GeneRuler Ultra Low Range DNA Ladder	Life Technologies	Cat# SM1211
Isopropanol	Merck	Cat# 1070222511
Ethanol	Merck	Cat# 1009832511
USER enzyme	New England Biolabs	Cat# M5505
Uracil Glycosylase inhibitor (UGI)	New England Biolabs	Cat# M0281
Bst DNA Polymerase2.0, large frag.	New England Biolabs	Cat# M0537
BSA 20mg/mL	New England Biolabs	Cat# B9000
T4 Polynucleotide Kinase	New England Biolabs	Cat# M0201
T4 DNA Polymerase	New England Biolabs	Cat# M0203
PEG-8000	Promega	Cat# V3011
20% SDS	Serva	Cat# 39575.01
Proteinase K	Sigma Aldrich	Cat# P2308
Guanidine hydrochloride	Sigma Aldrich	Cat# G3272
3M Sodium Acetate (pH 5.2)	Sigma Aldrich	Cat# S7899
Water	Sigma Aldrich	Cat# 34877
Tween-20	Sigma Aldrich	Cat# P9416
5M NaCl	Sigma Aldrich	Cat# S5150
Denhardt's solution	Sigma Aldrich	Cat# D9905
ATP 100 mM	Thermo Fisher Scientific	Cat# R0441
1 M Tris-HCl pH 8.0	Thermo Fisher Scientific	Cat# 15568025
dNTP Mix	Thermo Fisher Scientific	Cat# R1121
SSC Buffer (20x)	Thermo Fisher Scientific	Cat# AM9770
GeneAmp 10x PCR Gold Buffer	Thermo Fisher Scientific	Cat# 4379874
Dynabeads MyOne Streptavidin T1	Thermo Fisher Scientific	Cat# 65602
Salmon sperm DNA	Thermo Fisher Scientific	Cat# 15632-011
Human Cot-I DNA	Thermo Fisher Scientific	Cat#15279011
0.5M HCl	Carl Roth	Cat# 9277.1
HNO ₃	Merck	Cat# 1.00456.2500
Critical commercial assays		
High Pure Viral Nucleic Acid Large Volume Kit	Roche	Cat# 5114403001
HiSeq 4000 SBS Kit (50/75 cycles)	Illumina	Cat# FC-410-1001/2
DyNAmo Flash SYBR Green qPCR Kit	Thermo Fisher Scientific	Cat# F415L
MinElute PCR Purification Kit	QIAGEN	Cat# 28006
Quick Ligation Kit	New England Biolabs	Cat# M2200L
Oligo aCGH/Chip-on-Chip Hybridization Kit	Agilent Technologies	Cat# 5188-5220
Deposited data		
Raw and analyzed data (European nucleotide archive)	This study	ENA: PRJEB50762

Software and algorithms		
EAGER 1.92.21	Peltzer et al. 2016	https://eager.readthedocs.io/en/latest/
AdapterRemoval 2.2.0	Schubert et al, 2016	https://github.com/MikkelSchubert/adaptremoval
BWA 0.7.12	Li and Durbin, 2009	http://bio-bwa.sourceforge.net/
DeDup 0.12.1	Peltzer et al. 2016	https://github.com/apeltzer/DeDup
DamageProfiler v0.3	Jónsson et al., 2013	https://github.com/apeltzer/DamageProfiler
bamUtil 1.0.13	https://github.com/statgen/bamUtil	https://github.com/statgen/bamUtil
CircularMapper v1.93.4	Peltzer et al. 2016	https://github.com/apeltzer/CircularMapper
Schmutzi v1.0	Renaud et al., 2015	https://github.com/graubaud/schmutzi
ContaMix v1.0.10	Fu et al., 2013	https://doi.org/10.1016/j.cub.2013.02.044
HaploGrep2 v2.1.1	Weissensteiner et al., 2016	https://haplogrep.imed.ac.at/category/haplogrep2/
SAMtools 1.3	Li et al., 2009	http://www.htslib.org/doc/samtools.html
pileupCaller v1.4.0	https://github.com/stschiff/sequenceTools	https://github.com/stschiff/sequenceTools
ANGSD 0.910	Korneliussen et al., 2014	http://www.popgen.dk/angsd/index.php/ANGSD
EIGENSOFT 6.0.1	Patterson et al., 2006	https://github.com/DReichLab/EIG
ADMIXTOOLS v5.1	Patterson et al., 2012	https://github.com/DReichLab/AdmixTools
DATES 753	Chintalapati et al., unpublished	https://github.com/priyamoorthy/DATES
HapROH 0.1	Ringbauer et al., 2021	https://pypi.org/project/hapROH/
OxCal 4.4	Bronk Ramsey, 2009	https://c14.arch.ox.ac.uk/oxcal/OxCal.html
Geneious v9.0.5	http://www.geneious.com	http://www.geneious.com