Socio-cultural practices affect sexual dimorphism in stature in Early Neolithic Europe

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Abstract

The rules and structure of human culture impact health and disease as much as genetics or the natural environment. Studying the origins and evolution of these patterns in the archaeological record is challenging as it is difficult to tease apart the effects of genetics, culture, and environment. We take a multidisciplinary approach by combining published ancient DNA, skeletal metrics, paleopathology, and dietary stable isotopes to analyze cultural, environmental, and genetic contributions to variation in stature in four geographically defined populations of Early Neolithic Europe: North Central, South Central, Southern (Mediterranean), and Southeastern (Balkan) Europeans. In individuals from Central Europe, female stature is low, despite polygenic scores for height identical to males and to neighboring regions. Dietary and skeletal stress markers indicate environmental stress that is equal in both sexes, but the high stature sexual dimorphism ratio suggests that these stresses were exacerbated in females by cultural factors, likely associated with male preference and sex-biased allocation of resources. In contrast, shorter average stature in Mediterranean Neolithic populations have been previously reported to be associated with genetic differences; however, this is likely an artifact of residual population structure in the genome-wide association studies (GWAS). Instead, we suggest that reduced sexual dimorphism in the region indicates a degree of male vulnerability in response to general environmental stress. We conclude that while population-level stature trends may in some cases reflect genetic factors, differences in sexual dimorphism are largely driven by culture, or the interaction of culture and environment. Our analysis indicates that biological effects of sex-specific inequities can be linked to cultural influences at least as early as 7000 years before present. Understanding these patterns is key to interpreting the evolution of genetic and socio-cultural determinants of health and our results show that culture, more than environment or genetics, drove height disparities in Early Neolithic Europe.

1   Introduction

Human skeletal variation reflects varying combinations of genetic, cultural, and environmental factors. While there are many links between culture and health in the modern world, the history and evolution of these relationships are not always well established. Due to the entanglement of these factors, our ability to draw conclusions about their effects has been limited in archaeological data. With the recent advent of ancient DNA sequencing technology, genetic information from ancient populations has become increasingly available, but attempting to analyze changing patterns of variation based solely on genetic data is equally difficult as genotypes do not necessarily equate to phenotypes due to the effect of environment (Harpak & Przeworski, 2021). Similarly, while it is tempting to predict phenotypic changes in ancient people based on their genetic variation, this is currently challenging as genetic effects are not always transferable across populations (Martin et al., 2019). Our solution is to integrate these complementary fields to construct multidisciplinary analyses with phenotype, genotype, culture, and environment data from ancient human populations. This approach allows us to begin to separate the effects of these variables and reveal the interactions between genes, environment, and culture which are critical in shaping human health and variation.

Many traits of interest, including height, are highly polygenic with thousands of independent genetic variants contributing significantly to heritability. One common approach to addressing the role of genetics in morphological change is to compare patterns of phenotypic variation with genetic ancestry or genome-wide patterns of genetic variation (e.g., Roseman, 2004; Whitlock, 2008; Savell et al., 2016). However, even for highly polygenic traits like height, genome-wide variation may not be directly relevant to a particular trait, leading to spurious associations between genetic effects, ancestry, and environmental confounds. For example, if a population is tall and has a high proportion of ancestry from Neolithic sources, it could be concluded that Neolithic ancestry is associated with "genetic tallness"; however, the effects could equally be non-genetic and related to lifestyle changes associated with agriculture. An alternative approach is to focus only on genetic variation that is known to be associated with a specific trait (e.g., Berg & Coop, 2014; Mathieson et al., 2015). Effect sizes for these trait-related variants estimated from genome-wide association studies (GWAS) of present-day individuals can be combined with genetic data from ancient individuals to calculate polygenic scores (PRS), which can be thought of as estimated genetic values for the phenotype. In European ancestry populations, polygenic scores for height can explain up to 25% of phenotypic variation in present-day individuals (Yengo et al., 2018), and 6-8% of variation in ancient individuals (Cox et al., 2022; Marciniak et al., 2022). On a broad scale, temporal changes in polygenic score over time in Europe are qualitatively consistent with changes in stature as inferred from the skeletal record (Cox et al., 2019) while local deviations from this pattern provide evidence of environmental effects (Cox et al., 2019; Marciniak et al., 2022).

Analyses of human populations over tens of thousands of years involve individuals that are diverse in genetic ancestry, environment, and culture and it is challenging to exclude the possibility

76 of confounding by unmeasured variables. We therefore focus specifically on the European Early
77 Neolithic. One of the most studied periods in prehistory, it represents a fundamental shift in
78 technology, culture, and genetics. In particular, the *Linearbandkeramik* (LBK) culture of Central
79 Europe is one of the most comprehensively documented Early Neolithic cultures, with an abundance
80 of excavated settlements and cemeteries (i.e, Bickle & Whittle, 2013). The Mesolithic hunter-
81 gatherer population in this region made a limited genetic contribution to the LBK population, whose
82 members harbor only traces of hunter-gatherer admixture (Haak et al., 2015; Mathieson et al., 2015;
83 Lipson et al., 2017). Contemporary populations from southeastern Europe have similarly low levels
84 of hunter-gatherer ancestry (Mathieson et al., 2018). In contrast, Neolithic southern European
85 populations associated with the Cardial and Impressed Ware cultures followed a separate migration
86 route, occupied a milder climate zone, and carry more Mesolithc ancestry (Haak et al., 2015; Antonio
87 et al., 2019) (Fig. 1). Individuals in this region tend to be shorter than those from Central Europe
88 and this combination of factors has led to suggestions of a genetic basis for decreased statures in
89 this region (Mathieson et al., 2015; Martiniano et al., 2017).

90   By comparing and contrasting these three closely related archaeological populations, we aim to
91 investigate how differences in environment and genetics combine to produce observed phenotypes.
92 We collected genetic data, skeletal metrics, paleopathology, and dietary stable isotopes, to begin
93 separating the effects of each on Neolithic stature trends. By specifically investigating and control-
94 ling for the effects of genetics in these samples, we are able to provide novel, nuanced interpretations
95 of height variation, gain a better understanding of the aspects of height which are controlled by
96 genetics or environment, and show evidence for sex-specific cultural effects which modify the ge-
97 netically predicted patterns. We illustrate the strengths of leveraging multidisciplinary datasets,
98 and indicate caution when analyzing genotype-phenotype relationships without complete data, es-
99 pecially for traits which are not preserved in the archaeological record and cannot be directly tested.
100 This integrated analysis highlights the role of plasticity in morphology, and establishes culturally
101 mediated disparities at least as early as the European Neolithic.

2 Materials and Methods

103 We collected a combination of genetic, dietary stable isotope, skeletal metric, and paleopathological
104 (stress) data from 1282 individuals from the Central European Early Neolithic associated with the
105 archaeological LBK culture, approximately 7700-6900BP (Figure 2, Supplementary Table 1). We
106 divided these individuals into two regions based on geographical location, those to the north of
107 50°N latitude (North Central) and those to the south (South Central) (Figure 2A-B; North Central
108 n=203, n femur length=131, n isotopes=100, n aDNA=67, n stress=97; South Central n=1107,
109 n femur length=188, n isotopes=670, n aDNA=72, N stress=526). Each individual has at least
110 one of the data types, and while some individuals have multiple data types, the overlaps are small
111 (Supplementary Figure 1).
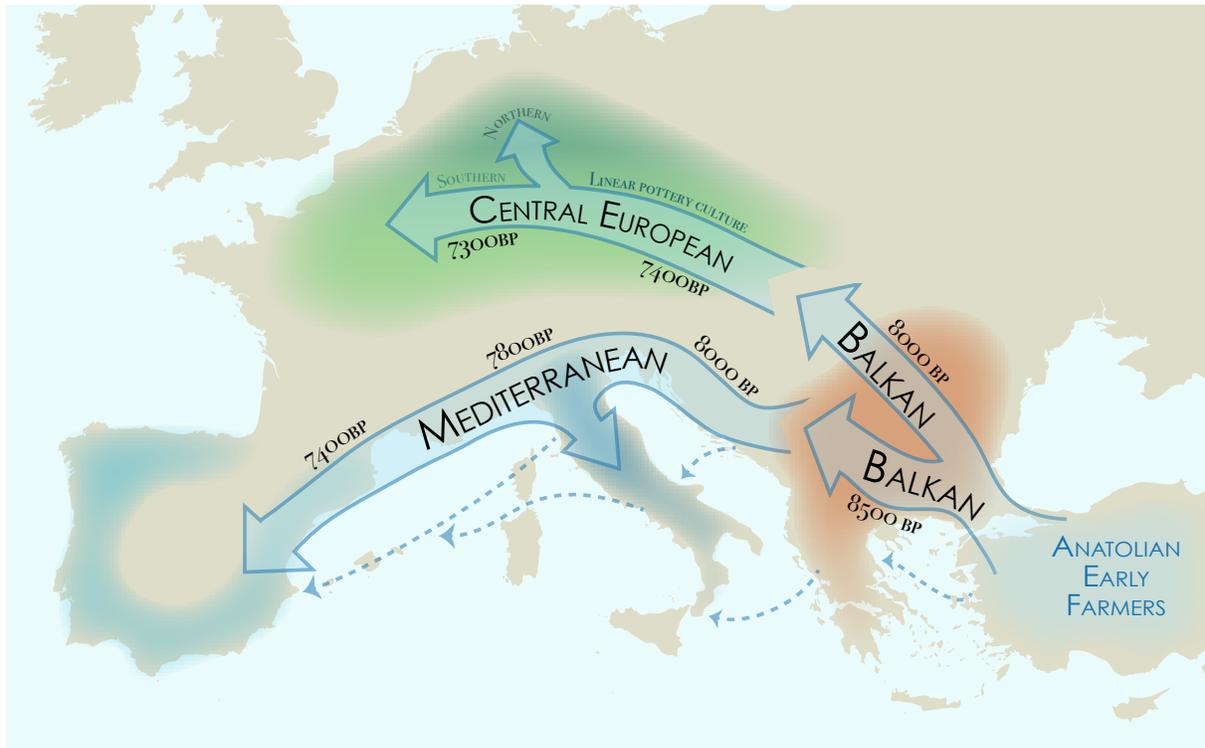
Figure 1: *This schematic illustration highlights the two main migration routes from Anatolia into Europe during the Early Neolithic period. Population movements followed two routes: southern, along the Mediterranean coast (including sea routes, generalized here by dashed blue lines) where they admixed with existing hunter-gatherer populations; or northern, through the Balkans and into Central Europe, with only limited hunter-gatherer admixture. We also analyze patterns within the Linearbandkeramik culture, dividing it into Northern and Southern Central European groups.*

112   To provide wider context, we also compared Central individuals to other Neolithic popula-
113   tions from southern European (Mediterranean) and southeastern European (Balkan) regions, and
114   restricted to individuals dated to between 8000-6000BP. We chose these regions as the Neolithic
115   transition occurs at a similar time and is associated with populations closely related to Central
116   Europe. The acceptable date range for inclusion in the study was expanded from that which defines
117   the LBK as these dates encompass comparable Early Neolithic phases in other parts of Europe while
118   maximizing the number of eligible individuals. There could be a possibility that the later Balkan
119   and Mediterranean individuals were more adapted to Neolithic life than the Central European
120   groups, as these samples cover a longer time period, but we found no statistical within-population
121   differences in our variables between the early and late ranges of our time span (minimum p=0.08).
122   We excluded areas such as Scandinavia and Britain where Neolithic technologies were not gener-
123   ally adopted until a later date. For the final analysis, we included 160 Mediterranean (n femur
124   length=67, n isotopes=26, n aDNA=42) and 135 Balkan (n femur length=12, n isotopes=97, n
125   aDNA=49) individuals (Figure 2). Unfortunately, there is a wide range of recording and reporting
126   used for skeletal stress indicators, and it was not possible to build a statistically powerful dataset in
127   these two populations for comparison; as a result, we did not analyze paleopathology in these pop-
128   ulations. Finally, we collected genetic data from Mesolithic hunter-gatherer (n=25, 14000-7080BP,
129   south of 48°N) and Anatolian Neolithic (n=21) individuals for additional comparison.

2.1   Genetic data

131   We obtained genetic data for a total of 276 individuals (Antonio et al., 2019; Brunel et al., 2020;
132   Childebayeva et al., 2022; Fernandes et al., 2020; Fregel et al., 2018; Fu et al., 2016; Gamba et al.,
133   2014; González-Fortes et al., 2017; Hofmanová et al., 2016; Jones et al., 2015; Lazaridis et al., 2017;
134   Lipson et al., 2017; Marcus et al., 2020; Mathieson et al., 2015, 2018; Nikitin et al., 2019; Olalde et al.,
135   2015, 2019; Rivollat et al., 2020; Valdiosera et al., 2018; Villalba-Mouco et al., 2019). Most data were
136   generated by targeting a set of 1.24 million SNPs (the "1240" capture reagent, Haak et al., 2015; Fu
137   et al., 2016). For those individuals with shotgun sequence data we randomly selected a single allele
138   from each of the 1240k sites. Coverage in our dataset is low (median coverage=0.33; coverage above
139   0.60 n=71), and typically, it is not possible to directly infer diploid genotypes, potentially limiting
140   PRS performance. Cox et al. (2022) showed that imputation of missing genotypes helps to improve
141   polygenic predictions for low coverage ancient samples, and we imputed using the two-stage method
142   described in that paper, restricting to SNPs in the 1240k set.

143   We calculated polygenic scores as described in Cox et al. (2022). Briefly, we used standing
144   height summary statistics generated by *fastGWA* from 456,000 individuals of European ancestry
145   in the UK Biobank (Jiang et al., 2019) for analyses of combined-sex PRS, and summary statistics
146   from male- and female-only UK Biobank GWAS generated by the Neale Lab (Neale Lab, 2018).
147   To test the potential effects of residual population structure in our data, we also computed PRS
148   using additional summary statistics from the Howe et al. (2022) sibling cohort (n=99,997). We

149 intersected the sites from each of these datasets with those on the 1240k array and then further
150 restricted to HapMap3 SNPs (SNPs n=405,000). We computed polygenic scores using both a
151 clumping/thresholding approach (r^2=0.3, p-value cutoff=10^{-6}, 100kb windows in *plink2* (Chang
152 et al., 2015)), and an infinitesimal *LDpred2* model using their pre-computed LD reference panel
153 (Privé et al., 2020). Finally, we computed polygenic scores using the --score command in *plink2*.
154 In order to maximize the possibility of detecting sex-specific effects, we generated sex-specific PRS
155 using three different approaches: 1) calculating PRS for all individuals using the female summary
156 statistics; 2) calculating PRS for all individuals using the male summary statistics; and 3) calculating
157 PRS for males and females separately using their respective summary statistics. While approach
158 3 seems at first to be the best for detecting these effects, observed patterns potentially become
159 difficult to interpret due to differences in scaling between male and female PRS calculated as separate
160 datasets.

161 We computed principal components for both unimputed and imputed data using *smartpca* (Pat-
162 terson et al., 2006), projecting ancient individuals onto principal component axes defined by 777
163 present-day West Eurasian individuals (Lazaridis et al., 2014). We also estimated K=2 ADMIX-
164 TURE (Alexander et al., 2009) components for unimputed ancient individuals after first LD pruning
165 using the command --pairwise-indep 200 25 0.4 in *plink2*.

2.2 Osteology and stable isotope data

167 We aggregated skeletal metric data from both published (Hujić, 2016; Nicklisch, 2017; Ruff, 2018;
168 Meyer et al., 2018; Rosenstock et al., 2019a,b) and unpublished (new n=28) sources. Maximum
169 femur lengths were recorded when available, otherwise we estimated femur length from published
170 stature estimates as described by Cox et al. (2022). Estimated femur lengths correlate highly
171 with stature estimates but decrease the error that results from combining different estimations
172 methods. The method from Ruff et al (2012) provides separate equations for estimating the statures
173 of northern vs. southern Europeans when using the tibia due to differences in body proportions
174 between the regions. There are two Mediterranean samples for which we estimated the length of
175 the femur based on statures which used Ruff et al's southern tibia equation. Ruff et al do not
176 provide regional equations for femur estimation, so for these two individuals, we estimated femur
177 length using the reverse of this region-agnostic femur equation. For individuals without DNA, we
178 relied upon their published sex estimations; sex for unpublished individuals was determined using
179 Acsádi et al. (1970) (see the Supplement for details). Similarly, ages were determined based on
180 the average of the age range reported for each individual in their original publications. Finally, for
181 the paleopathological data in Central Europe, we took data from published sources (Lillie, 2008;
182 Whittle et al., 2013a,b; Ash et al., 2016; Hujić, 2016; Nicklisch, 2017), recorded as presence/absence
183 of linear enamel hypoplasia, porotic hyperostosis, and cribra orbitalia.

184 While affected by many confounding factors such as climate, vegetation, and individual metabolism
185 (Scheibner, 2016), δ^{13}C and δ^{15}N stable isotope data can be used to reconstruct aspects of diet

186 (O'Brien, 2015). Here, carbon values are indicative of dietary plant resources, and of the terrestrial
187 vs marine vs limnic provenance of food, while nitrogen values are mainly associated with dietary
188 protein intake and generally indicate proportions of plant- vs animal-based diets (O'Brien, 2015;
189 Scheibner, 2016). We collected dietary stable isotopes δ^{13}C and δ^{15}N from published (Dürrwächter
190 et al., 2006; Richards et al., 2008; Oelze et al., 2011; Bentley et al., 2013; Bickle et al., 2013b,a;
191 Hofmann et al., 2013; Whittle et al., 2013a,b; Ash et al., 2016; Hujić, 2016; Scheibner, 2016; Meyer
192 et al., 2018; Münster et al., 2018; Knipper, 2020) and unpublished (new n=38) reports. We ex-
193 cluded atomic mass spectrometer (AMS) values derived from radiocarbon dating, as they may not
194 be comparable to isotope-ratio mass spectrometer (IRMS) measurements, as well as values from
195 children below the age of three, due to increased nitrogen values from breastfeeding. Stable isotope
196 values from older children were included in population-wide diet analyses as the isotope ranges fall
197 within those of adults; however, we only included adults with estimated sexes in the sex-based diet
198 analyses. If information on the sampled material was available, we chose values measured from
199 rib collagen, as these samples are most plentiful, though they only reflect the last few years of the
200 individual's life.

201 All previously unpublished osteological data was collected and analyzed by co-authors with
202 permission from the necessary regulating organizations and in accordance with German laws and
203 policies.

2.3 Statistical models

205 We tested the effects of PRS, femur length, and isotope data on stature using linear regression
206 models including sex and geographic region as covariates in combination with other variables as
207 appropriate (e.g., femur $\sim$ sex + region + PRS; δ^{15}N $\sim$ sex + region + femur). We included
208 interaction terms to test the relationships between geographic regions and sex (e.g., femur $\sim$ region
209 * sex) and used t-tests to test within-sex differences between regions. We used logistic regression
210 with the same covariates to test for factors affecting presence/absence of paleopathologies. We
211 carried out all statistical tests using the the base functions in R version 4.0 (R Core Team, 2021).

3 Results

3.1 Distribution of stature, polygenic scores and stable isotope values

214 Polygenic scores are very similar between all populations (pairwise t-test p > 0.9) using the clump-
215 ing/thresholding PRS construction (Figure 3A). PRS constructed with LDPred show Mediterranean
216 individuals to be shorter than the other populations (p=0.002; Supplementary Fig 5). However,
217 PRS constructed using summary statistics derived from between-sibling analysis finds similar ge-
218 netic values in all populations, with both PRS construction methods, so we conclude that apparent
219 lower Mediterranean PRS may be due to population stratification in the GWAS data and may not

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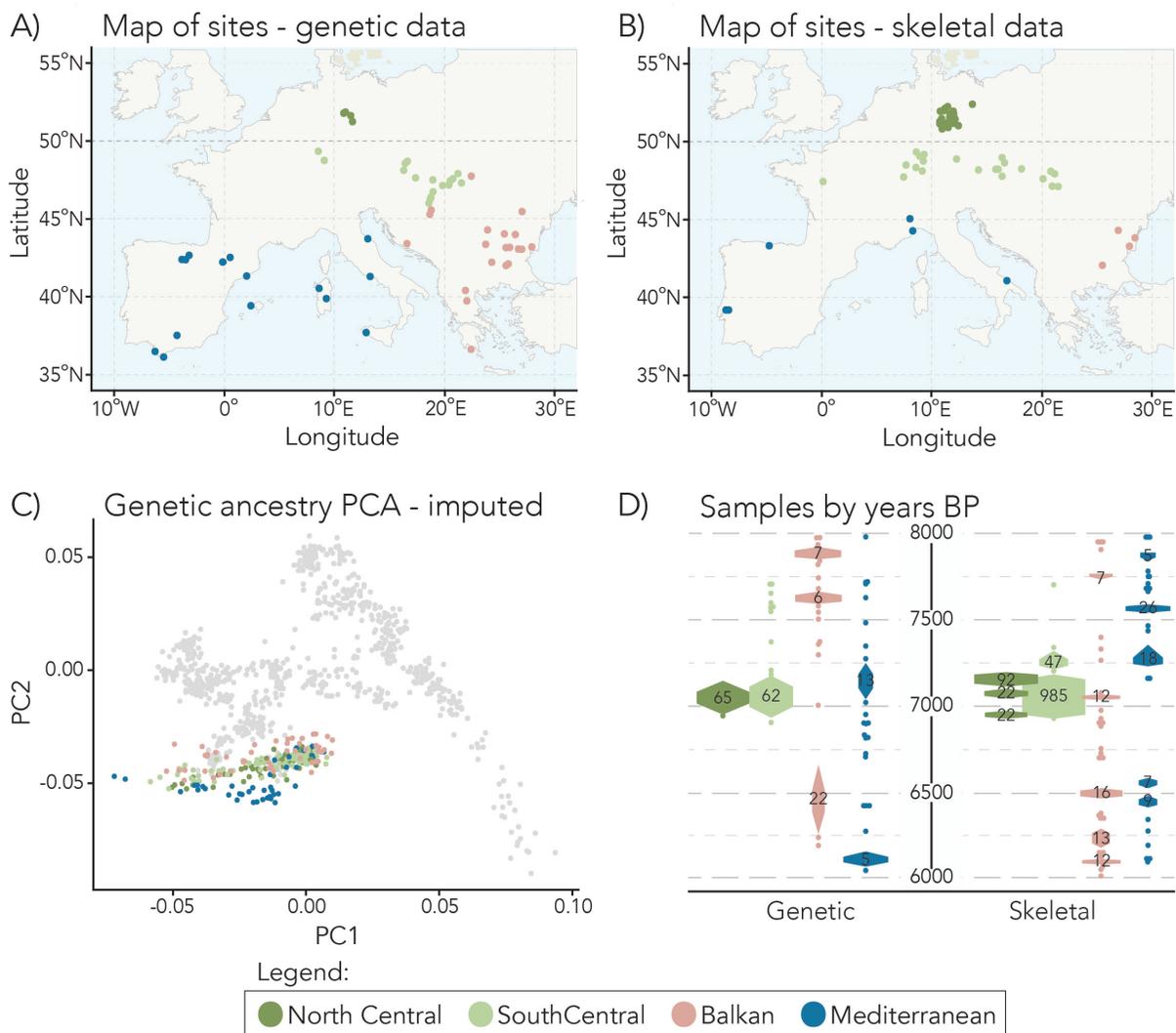
Figure 2: *Upper row: Locations of sites used for genetic (A) and skeletal (B) data in the analysis. The Central European population is split into Northern and Southern groups at 50°N latitude (emphasized). Lower row: (C) imputed genetic data projected into the PCA space of 777 modern Eurasian individuals (grey points). (D) plot of sample numbers by time period in years before present (years BP) for skeletal (right) and genetic (left) data.*

220 reflect a true genetic difference (Figure 5D). Despite the similarities in PRS, observed patterns of
221 femur length vary between sexes and populations. Males show no apparent difference between the
222 Central and Balkan femora (p=0.56), but the Mediterranean male population is significantly shorter
223 (p=5.5×10^{-7}, β=-1.44cm). Conversely, female femora show a different pattern, with no significant
224 difference between Mediterranean, South Central (p=0.97), and Balkan (p=0.54) populations, but
225 substantially shorter values in the North Central (β=-2.0cm, p=9×10^{-07}) (Figure 3B). There are
226 no significant differences between male and female PRS in any population (Fig. 3A), providing no
227 evidence for a genetic basis to this dimorphism.

228 Signatures of δ^{13}C and δ^{15}N indicate different dietary patterns in each of the analyzed groups.
229 Both the Mediterranean and Balkan groups are significantly distinct from the Central in δ^{13}C
230 (p<4×10^{-16}) and δ^{15}N (Balkans: p<7.7×10^{-13}; Mediterranean: 1.2×10^{-122}) values. Generally,
231 the Balkan population is characterized by high δ^{15}N values, while Mediterranean populations show
232 high δ^{13}C relative to the Central Europeans (Figure 3C). The exception to this pattern is a cluster
233 of individuals, classified as Balkan in our analysis, which overlap with the North Central population
234 as well as some of the Mediterranean values. These points represent individuals from present-day
235 Greece and indicate that the diets of these peoples might better be classified as Mediterranean
236 rather than Balkan. Nitrogen values are generally elevated in males compared to females, but this
237 difference is only significant in the Mediterranean (p=0.035).

3.2 Patterns of non-genetic factors in Central Europe

239 The most dramatic observation is the difference in female stature and consequent sexual dimpor-
240 phism in Northern compared to Southern Central Europe. Female femora in Northern Central
241 Europe are significantly shorter than female femora in the South (p=2.7×10^{-6}, β=1.7cm), while
242 male femora are not significantly different (p=0.35) (Figure 3B). On average, male femora from the
243 North are about 13% longer than female femora, Southern Central and Balkan males are about 9%
244 and 11% longer respectively, and Mediterranean males are only 5% longer (Figure 3B). These val-
245 ues are reduced slightly when calculated using estimated statures instead of femora (North Central:
246 10%, South Central: 7%, Balkans: 8%, Mediterranean: 4%), possibly due to error associated with
247 stature estimation (see Cox et al., 2022) and body proportions, or because the relationship between
248 femur length and stature is different between males and females. Where we have both genetic and
249 metric data for the same individuals, there is a qualitative relationship between femur length and
250 PRS; PRS tends to increase as femur lengths increase (Supplementary Figure 3B). However, the
251 effect of PRS on femur length is barely statistically significant (p=0.05), likely due to the small
252 number of individuals in the sample (n=55).

253 Overall, trends in dietary stable isotopes show both males and females in Southern Central
254 Europe to have significantly higher δ^{15}N (Male p=1.3×10^{-9}, β=0.83‰, Female p=5.3×10^{-9},
255 β=0.87‰) and lower δ^{13}C (Male p=0.0003, β=-0.30‰, Female p=8.1×10^{-7}, β=-0.38‰) as
256 compared to the North. However, while males qualitatively have higher nitrogen, the interaction

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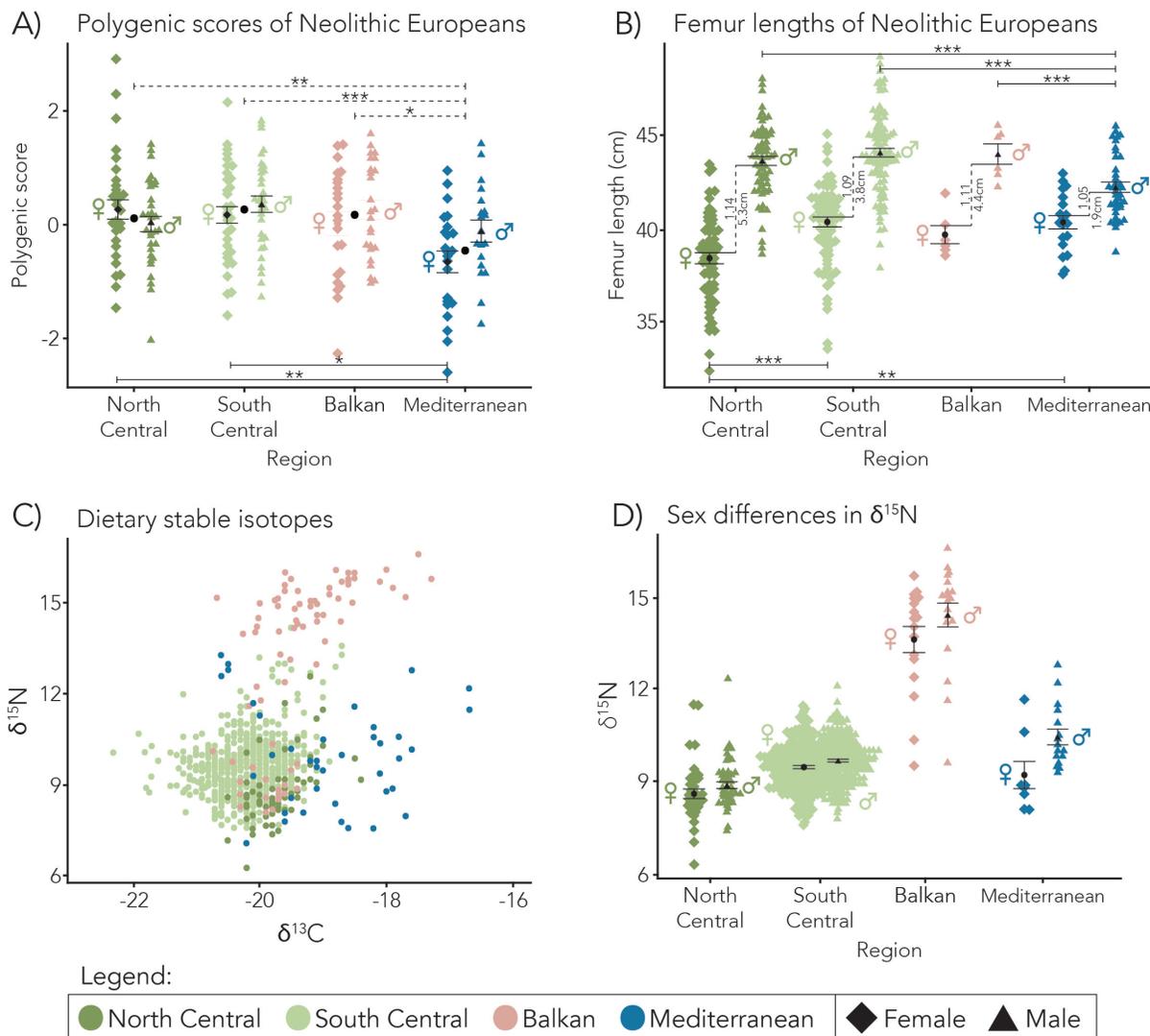
Figure 3: *Solid bars across the tops of plots indicate significant differences between male populations by pairwise t-test; solid bars below plots indicate significant differences between female populations by pairwise t-test; p-values < 0.05 (*), < 0.01 (**) and < 0.001 (***). Black points indicate the mean of each group and vertical bars show mean standard error. A) Polygenic scores for the four populations show similar scores for individuals across all regions. Differences between male and female PRS are not significant. B) Femur length in the four populations. Values to the right of the vertical dotted line are the difference between the mean male and female femora; values to the left of the vertical dotted line are the sexual dimorphism ratios of male/female femur lengths for each population. C) Plot of $\delta^{13}C$ (x-axis) and $\delta^{15}N$ (y-axis) dietary stable isotopes for the four populations. Individuals from the Balkans are distinguished by high nitrogen values, while those in the Mediterranean generally have higher carbon. D) Sex differences in $\delta^{15}N$ values by sex for each population. $\delta^{15}N$ values are slightly higher for males in all our populations but this difference is only significant in the Mediterranean ($p = 0.035$).*
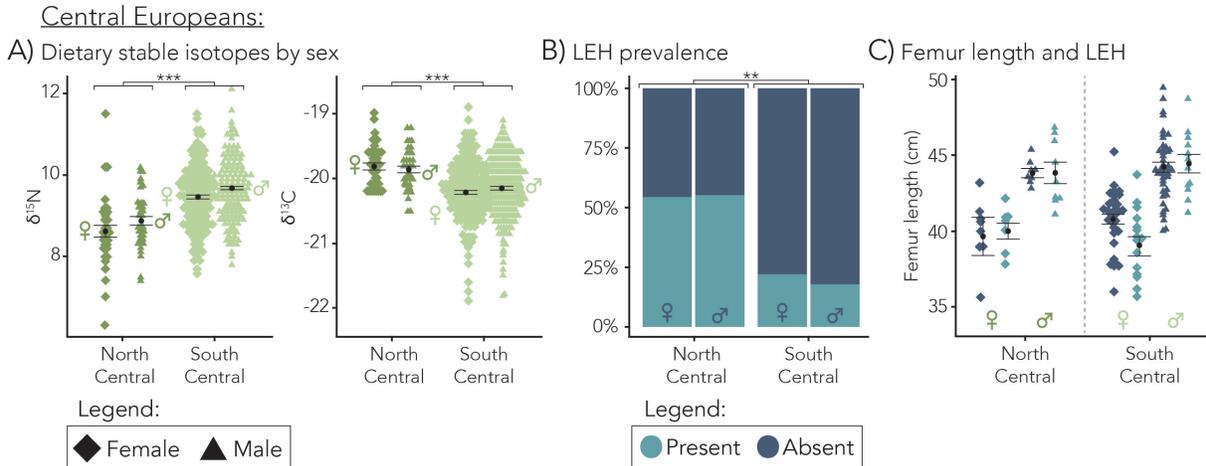
Figure 4: *Evidence of environmental stress in Northern Central Europe. A) Differences in $\delta^{13}C$ (right) and $\delta^{15}N$ (left) values. Overall, the South has higher nitrogen values than the North (p=6.8 × 10^{-13}), and less carbon (p=5.3 × 10^{-15}); within each population, the difference in isotopes between sexes is not significant. B) Proportion of linear enamel hypoplasias. The South has significantly less than the North (p=0.001). C) Presence of linear enamel hypoplasia is significantly associated with shorter femora (p=0.02); differences in prevalence between sexes are not significant.*

effect between sexes is not significant in either region (Figure 4A). There is no difference in carbon values between sexes. For individuals with both stature and stable isotope values, we find no statistically significant relationship between femur length and δ^{15}N or δ^{13}C in either Central group, separately or combined, though the sample is small.

We do, however, find a statistically significant relationship between presence of linear enamel hypoplasias and shorter femora, suggesting that LEH may reflect some underlying variable in childhood that also affects stature (p=0.021, β=-1.0cm)(Figure 4C). Both males and females from the north are more likely to have LEH than individuals living in the south (p=0.002). Indeed, over 50% of the Northern sample have LEH while they are only present in about 20% of the Southern (Figure 4B). There is no significant difference between the number of males and females with LEH in either region. Though the interaction effect between sex and LEH on femur length is not significant, qualitatively the effect of LEH on femur length appears greater in females than in males (Figure 4C). When the sexes are analyzed separately, females with LEH do have significantly shorter femora than those without (p=0.018, β=-1.46), which is not the case for males (p=0.479). We hypothesize that the relationship between LEH and femur length is driven by females but we lack an adequate sample size to detect the interaction effect in the full model. Incidence of cribra orbitalia is also significantly higher in the Northern region than in the Southern (p=1.8 × 10^{-6}), though there is no relationship with femur length. There are no significant trends related to the presence of porotic hyperostosis.

In summary, comparison of Northern and Southern Central Europe identifies no predicted genetic difference in stature, which is consistent with male but not female femur length. This suggests a non-genetic basis for reduced female stature. Stable isotope data and skeletal stress indicators

279 suggest less protein intake and more general stress in the North; however, males and females overall
280 appear equally affected by these variables. Despite a similar number of hypoplasias in both sexes,
281 shorter femora in females suggests increased general stress leading to a female-specific reduction in
282 stature due to other unmeasured environmental or cultural factors.

3.3 Patterns of genetic ancestry in the Mediterranean

284 In contrast to Northern Central Europe, Mediterranean Neolithic males are shorter than other
285 groups, but females are not. PCA indicates that individuals from the Central regions and the
286 Balkans share similar genetic ancestry while those from the Mediterranean are distinct (Figure 2C;
287 unimputed PCA in Supplementary Figure 4A), a known difference due to higher levels of hunter-
288 gatherer ancestry in the Mediterranean (Haak et al., 2015). We therefore additionally compared
289 our samples to Mesolithic individuals of Western Hunter-Gatherer (WHG) ancestry, as well as
290 individuals from early Neolithic Anatolia. These two groups represent source populations for the
291 two largest ancestry components in Europe at this time (Haak et al., 2015; Mathieson et al., 2015).
292   On the PCA plots of these extended data, Neolithic Anatolians cluster with the Central and
293 Balkan groups. While Mediterraneans are near the farmer cluster, they are shifted towards the
294 WHG (Figure 5A; unimputed PCA in Supplementary Figure 4B). ADMIXTURE analysis on all six
295 populations supports this conclusion, showing significantly increased proportions of WHG ancestry
296 in the Neolithic Mediterranean as compared with the other groups (maximum p=0.002 vs the
297 Balkans, Fig. 5C). The average proportion of WHG ancestry in the Mediterranean is 11.4%; in the
298 Balkans, 5.3%; in the South Central, 4.1%; and in the North Central, 1.1%. If there are significant
299 PRS differences between Mediterranean and other populations, they are likely linked to this greater
300 WHG ancestry and reflect genetic differences between WHG and other populations.
301   Computing PRS using clumping/thresholding, we find that the WHG have the lowest PRS of
302 any population in our data (maximum p=0.002 vs Mediterranean), while Anatolians are similar to
303 the Balkan and Central Europeans. Among individuals, proportions of WHG ancestry are strongly
304 associated with decreased PRS (p=1.6×10^{-06}, β=-0.08cm/%). However, when we compute PRS
305 with an infinitesimal LDpred2 model, Mediterranean PRS is intermediate between Neolithic Euro-
306 peans and WHG. When we repeat the LDpred analysis using summary statistics computed from
307 between-sibling GWAS (Howe et al., 2022) we find that the direction of Hunter-Gatherer PRS flips,
308 and they have significantly greater PRS than the other groups (p=0.002) (Supplementary Figure
309 3A). The inconsistency of these results shows that the apparent PRS difference between WHG and
310 Neolithic populations is highly sensitive to the PRS construction and summary statistics. This may
311 indicate uncorrected population stratification in the non-sibling GWAS (Sohail et al., 2019; Berg
312 et al., 2019). We therefore conclude that there is no strong evidence for a genetic difference in
313 stature between Mediterranean and other Neolithic populations.

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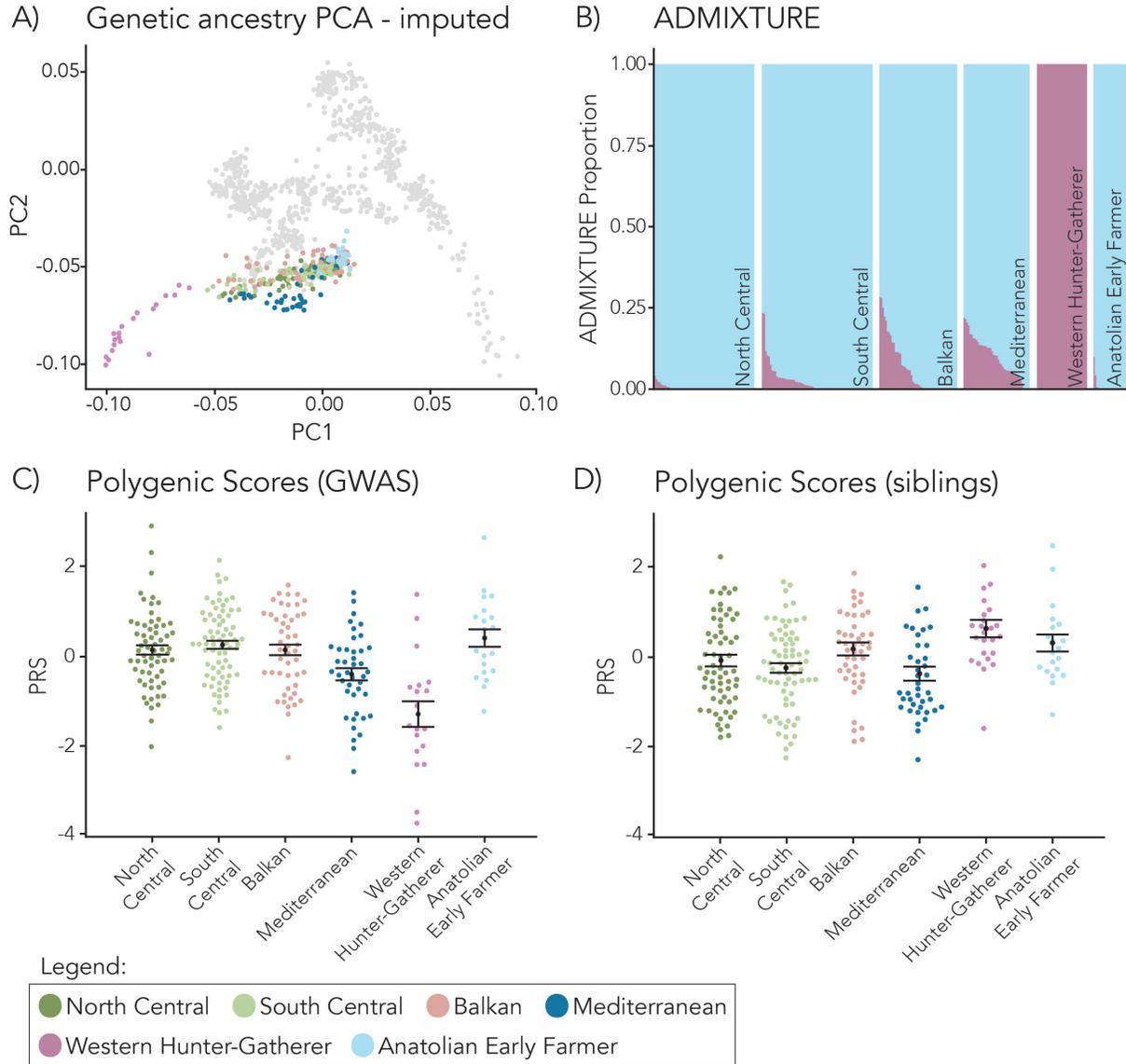
Figure 5: *A) Plot of ancient individuals projected into modern PCA space, including those of Mesolithic Western Hunter-Gatherer (WHG) and Anatolian Early Farmer ancestry. B) ADMIXTURE plot of K=2 ancestry groups showing the increased proportion of WHG ancestry in the Mediterranean individuals. C) Polygenic scores for each region including Mesolithic Hunter-Gatherers and Anatolian Early Farmers. D) Polygenic scores calculated from between-sibling summary statistics.*

4   Discussion

Interpretations of human stature variation through time remain confounded by the difficulty of separating genetic and environmental effects, obscuring trends. Accurately interpreting past stature variation not only allows us to understand these communities, but provides us with insights into the origin and evolution of modern health patterns. Height, while interesting in its own right, can also serve as a model trait for how to incorporate genetics and anthropological data into studies of human morphology and variation. Here, by integrating genetic, cultural, and environmental data, we are able to begin teasing apart the contributions of genetic and non-genetic factors in producing the observed phenotypic variation. We also illustrate the existing limitations of interpreting genetic data.

Overall, the Central and Balkan groups are genetically homogenous with similar levels of WHG admixture and polygenic scores, while Mediterranean individuals have more WHG ancestry (consistent with previous observations: Haak et al. (2015); Mathieson et al. (2015); Lipson et al. (2017)), which may be associated with lower PRS, though this relationship is not robust and may simply reflect residual population stratification. None of our populations show evidence for substantial genetic differences in height between sexes, which is expected given that there is little evidence for sex-specific genetic effects (Randall et al., 2013; Bernabeu et al., 2021; Zhu et al., 2022) (Supplemetary Figure 2). We can therefore largely exclude a genetic contribution to differences in stature between North Central individuals and other groups, while we find no strong evidence for a genetic contribution to shorter Mediterranean femora.

4.1   Sexual dimporphism in Central Europe reflects the effects of culture

Dietary differences between Southern and Northern Central European populations may indicate environmental stress in the north. In the early European Neolithic, the expansion of agriculture is thought to have been largely limited by poor soils and climate, as colder temperatures and decreased daylight made it increasingly difficult to grow early cereals (wheat, barley) and pulses (peas) (Bogaard, 2004; Schier, 2022), resulting in inconsistent, small harvests. The boundary to which these plants could be grown has been estimated to coincide with the northern limits of the LBK culture (Betti et al., 2020), and the majority of our Northern sites are concentrated near this climate edge in areas of fertile loess soils. However, examination of isotope values from herbivorous animals in our study regions (Dürrwächter et al., 2006; Oelze et al., 2011; Bentley et al., 2013; Denaire et al., 2017; Gillis et al., 2020; Knipper, 2020, data from) indicates that baseline values of δ^{15}N are elevated in the South Central region as compared to the North potentially due to differences in climate and the use of manure as fertilizer, and therefore at least some of the difference between Northern and Southern nitrogen values might be attributable to differences in climate and farming practices rather than diet. On the other hand, while remains of cattle and dairy production are documented in Northern LBK sites (Gillis et al., 2017; Salque et al., 2013), there is less archaeological

350 evidence for the presence of other wild or domesticated animals, indicating the people of this region
351 were highly reliant on plant foods (Nicklisch et al., 2016; Münster et al., 2018). Isotopic values
352 from other studies confirm the zooarchaeological evidence and show a higher proportion of plant
353 vs animal foods in the North, particularly domesticated cereal grains (Nicklisch et al., 2016; Oelze
354 et al., 2011). We conclude that our observed differences in Northern and Southern stable isotope
355 values probably reflects both dietary factors and differences in climate or farming practices.

356 It is therefore not surprising that the people living in the Northern Central region exhibit
357 evidence of increased stress due to potentially unreliable and lower quality food resources. Lower
358 protein consumption has been linked to decreased stature (Ghosh, 2016), and could be an indicator
359 of dietary stress. Diet can in some cases affect dimorphism (Gray & Wolfe, 1980), but while males
360 in the Southern Central and Balkan regions have higher nitrogen levels than females, the isotopic
361 signatures of North Central males and females are very similar, suggesting that this factor alone does
362 not explain reduced female stature in the North. Femur length and isotope values for individuals are
363 not significantly associated in our data, an indication that either diet has little effect on Neolithic
364 stature or stable isotopes do not capture the elements of diet relevant to height. Alternatively,
365 it is possible the range of variation in our data is too small to see this effect, or our sample of
366 individuals with both metric and isotopic data is not large enough. In addition, we only analyzed
367 adult samples and while the isotopic values of weaned children in the LBK fall within the range of
368 adults (Münster et al., 2018), it is possible that there could be sex differences in childhood diets
369 affecting femur growth.

370 Paleopathological analysis also indicates increased stress in the Northern population in the form
371 of increased incidence of linear enamel hypoplasia and cribra orbitalia. The causes of LEH formation
372 are varied and their appearance in the bioarchaeological record is generally interpreted as a non-
373 specific indication of childhood stress (Guatelli-Steinberg & Lukacs, 1999). Other archaeological
374 sites have reported a high instance of LEH with high sexual dimorphism ratios in areas of Neolithic
375 Europe, though the cause and meaning of these patterns was not explored (e.g, Lubell et al., 1990,
376 and references therein). It has been suggested that cribra orbitalia might also reflect childhood
377 stress, specifically anaemias, even when seen in adults (McFadden & Oxenham, 2020). Incidence of
378 both these stress indicators is higher in Northern compared to Southern Central Europe but is not
379 different between sexes in either group. The association between shorter femora and presence of
380 LEH appears to be driven by the females, suggesting a moderating factor causing a female-specific
381 effect despite equal incidence of LEH in both sexes.

382 While we see a general increase in stress shared between sexes in North Central Europe, typical
383 population-level stress responses usually show male vulnerability and female buffering effects (Ger-
384 man & Hochberg, 2020; Stini, 1985; Brauer, 1982). Our data indicate an opposite pattern in Central
385 Europe, and no evidence of a variable which acts upon females alone. However, the Northern pop-
386 ulation shows sexual dimorphism that is extreme by present-day standards. In modern samples,
387 the ratio of male to female height is 1.06-1.08 in most global populations (Gaulin & Boster, 1992),

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388 though it is difficult to know how to compare height versus femur length ratios as the transformation
389 from metrics to stature scales differently in males and females. Based on 147 European individuals
390 from the past 100 years (data from Ruff, 2018), we find that the height ratio is very similar to
391 the ratio of femur length—typically within 1%. We therefore conclude that dimporphism ratios
392 in Southern Central (1.09) and Balkan (1.11) Europeans are elevated and the ratio in the North
393 Central region is exceptionally high (1.14). Few modern populations have height dimorphism ratios
394 as high as 1.10, and those that we could find in the literature come from India (Kanwar et al., 2011)
395 and the United Arab Emirates (Abdulrazzaq et al., 2008), both of which are countries known for
396 their cultural preferences and biases for male children.

397   We therefore hypothesize that the effects of high environmental stress in the North were mod-
398 ulated by culture. Other researchers have noted specific situations in which culture buffers males
399 against environmental effects and creates vulnerability in females: there is an association between
400 decreased female stature and polygyny in cultures around the globe (see Kanazawa & Novak, 2005);
401 female height was more influenced by economic conditions during infancy and early childhood than
402 males in lower-class 19th-century Europe (Baten & Murray, 2000); sexual dimorphism ratios in
403 modern Chile decreased after the institution of social and government programs to combat gender
404 inequality (Castellucci et al., 2021); and 20th-century female stature decreased in India during times
405 of environmental stress due to sexually disproportionate investment of scarce resources (Moradi &
406 Guntupalli, 2009). Strontium isotope values from LBK sites identify a large portion of LBK females
407 across the region as being non-local to those sites, though patterns in specific locations vary, broadly
408 indicating patrilocality and the potential for differential cultural treatments of females as compared
409 to males (Bentley et al., 2002, 2012; Hrnčíř et al., 2020). We suggest that culturally mediated
410 differences led to sex-specific stress responses in Neolithic Central Europe, *via* cultural practices
411 which either directly decrease female stature or, more likely, support catch-up growth preferentially
412 in males. Though dimorphism ratios in the South Central and Balkan regions are not as extreme
413 as in the North, they are elevated and also consistent with this pattern of male-bias, but response
414 is likely less exaggerated due to lower environmental stress conditions.

4.2   Mediterranean differences may have both genetic and environmental bases

416 In the Early Neolithic Mediterranean population we see decreased male stature and very low di-
417 morphism ratios (1.05) relative to other Neolithic populations. Mediterranean populations are
418 genetically distinct from other Early Neolithic groups with a higher proportion of WHG ancestry.
419 In some analyses, WHG ancestry proportion correlates with lower PRS for height. However, PRS
420 in the Mediterranean and WHG populations are sensitive to PRS construction method likely due to
421 residual population stratification in the GWAS. These inconsistent results mean that we can neither
422 confirm nor exclude the possibility of a genetic contribution to differences in stature between the
423 Mediterranean and other Early Neolithic populations. Even so, as with Central European popla-
424 tions, genetic effects alone would not explain the reduced dimorphism ratio, so we also need to

425 consider cultural/environmental effects.

426 The dimorphism ratio in the Mediterranean Neolithic is low, though not outside the range of
427 present-day populations (Gaulin & Boster, 1992). In fact, while males are relatively short, the
428 longest average female femur lengths of our data are in the Mediterranean. This reduction in
429 dimorphism is commonly seen in populations where the sexes experience an equal stress burden as
430 males tend to be more sensitive, decreasing their height, while females are biologically buffered and
431 stature remains consistent (German & Hochberg, 2020; Stini, 1985; Brauer, 1982; Garvin, 2012).
432 Although we do not have paleopathological stress data for the Mediterranean individuals in our
433 sample, published values for other Neolithic Mediterranean populations are generally similar to
434 those for South Central Europe (e.g., Papathanasiou, 2011, 2005; Silva & Cunha, 2001, except,
435 Cucina 2002). Dietary isotopes indicate that the Mediterranean diet differs in some aspects, with
436 increased $\delta^{13}C$ values compared to the other Neolithic populations but similar $\delta^{15}N$ values. Our
437 data indicates similar protein intake and low-level stress as other Neolithic populations, but do not
438 suggest any clear hypothesis for the difference in male stature between the Mediterranean and other
439 Neolithic groups. Possible differences in Mediterranean body proportions which are not captured
440 by femur length should also be mentioned as a caveat, though this likely would not be enough to
441 account for the differences in stature compared to the rest of Europe, and would not affect observed
442 dimorphism within the population. One possibility is that the Mediterranean experienced similar
443 levels of environmental stress as other Neolithic groups, but that they did not share the cultural
444 practices which preferentially supported males and increased female vulnerability.

445 4.3   Conclusion

446 By integrating genetic and anthropological data, we are able to begin to understand the contribu-
447 tions of genetics and environment to human variation, allowing us to better interpret the genetic,
448 environmental, and cultural landscapes of Neolithic Europe. Using this approach, we gain a deeper
449 understanding of the relationship between phenotypic plasticity and genetic architecture, which con-
450 strains the mechanisms by which human biology adapts to environment, culture, and genetic drift.
451 Our results are consistent with a model in which sexually dimorphic differences in femur length are
452 culturally and environmentally driven: relatively low dimorphism in the Mediterranean caused by
453 female buffering to environmental stress and less cultural male-preference, and high dimorphism
454 in Northern Central Europe caused by the interaction of relatively high environmental stress and
455 strong cultural male-preference. Some analyses suggest that differences in average femur length
456 between Central/Southeastern Europe and the Mediterranean are associated with differing genetic
457 ancestries, but less robust results, uncertainty about the transferrability of polygenic scores, and
458 questions of residual population stratification prevent us from interpreting this conclusively. In this
459 study we focused on the European Early Neolithic because of relative genetic, cultural, and environ-
460 mental homogeneity but, with more data, these approaches could be extended to other populations,
461 traits, and timescales to further explore the effects of human culture on biological variation.

462   **Data Availability** All data used in this analysis is provided in Supplementary Table 1. Original
463   ancient DNA data files can be downloaded from the resources provided in their cited publications.
464   Previously published osteological data can be found in their cited sources (Supplementary Table 1).
465   **Code Availability** R code used in this analysis is available for download on the Mathieson Lab
466   GitHub: $https://github.com/mathilab/Neolithic_height.git$.

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