

# POPULATION GENOMICS OF STONE AGE EURASIA

Morten E. Allentoft<sup>1,2,\*</sup>§, Martin Sikora<sup>1\*</sup>§, Alba Refoyo-Martínez<sup>1</sup>§, Evan K. Irving-Pease<sup>1</sup>§, Anders Fischer<sup>3,4</sup>§, William Barrie<sup>5</sup>§, Andrés Ingason<sup>6,1</sup>§, Jesper Stenderup<sup>1</sup>, Karl-Göran Sjögren<sup>3</sup>, Alice Pearson<sup>7</sup>, Barbara Mota<sup>8,9</sup>, Bettina Schulz Paulsson<sup>3</sup>, Alma Halgren<sup>10</sup>, Ruairidh Macleod<sup>1,5,11</sup>, Marie Louise Schjellerup Jørkov<sup>12</sup>, Fabrice Demeter<sup>1,13</sup>, Maria Novosolov<sup>1</sup>, Lasse Sørensen<sup>14</sup>, Poul-Otto Nielsen<sup>14</sup>, Rasmus H.A. Henriksen<sup>1</sup>, Tharsika Vimala<sup>1</sup>, Hugh McColl<sup>1</sup>, Ashot Margaryan<sup>15,16</sup>, Melissa Ilardo<sup>17</sup>, Andrew Vaughn<sup>18</sup>, Morten Fischer Mortensen<sup>14</sup>, Anne Birgitte Nielsen<sup>19</sup>, Mikkel Ulfeldt Hede<sup>20</sup>, Peter Rasmussen<sup>14</sup>, Lasse Vinner<sup>1</sup>, Gabriel Renaud<sup>21</sup>, Aaron Stern<sup>18</sup>, Theis Zetner Trolle Jensen<sup>15</sup>, Niels Nørkjær Johannsen<sup>22</sup>, Gabriele Scorrano<sup>1</sup>, Hannes Schroeder<sup>15</sup>, Per Lysdahl<sup>23</sup>, Abigail Daisy Ramsøe<sup>1</sup>, Andrei Skorobogatov<sup>24</sup>, Andrew Joseph Schork<sup>6,25</sup>, Anders Rosengren<sup>6,1</sup>, Anthony Ruter<sup>1</sup>, Alan Outram<sup>26</sup>, Aleksey A. Timoshenko<sup>27</sup>, Alexandra Buzhilova<sup>28</sup>, Alfredo Coppa<sup>29</sup>, Alisa Zubova<sup>30</sup>, Ana Maria Silva<sup>31,59</sup>, Anders J. Hansen<sup>1</sup>, Andrey Gromov<sup>30</sup>, Andrey Logvin<sup>32</sup>, Anne Birgitte Gottfredsen<sup>1</sup>, Bjarne Henning Nielsen<sup>33</sup>, Borja González-Rabanal<sup>34</sup>, Carles Lalueza-Fox<sup>35</sup>, Catriona J. McKenzie<sup>26</sup>, Charleen Gaunitz<sup>1</sup>, Concepción Blasco<sup>36</sup>, Corina Liesau<sup>36</sup>, Cristina Martínez-Labarga<sup>37</sup>, Dmitri V. Pozdnyakov<sup>27</sup>, David Cuenca-Solana<sup>38,39</sup>, David O. Lordkipanidze<sup>40,41</sup>, Dmitri En'shin<sup>42</sup>, Domingo C. Salazar-García<sup>43,44</sup>, T. Douglas Price<sup>45</sup>, Dušan Borčić<sup>29,46</sup>, Elena Kostyleva<sup>47</sup>, Elizaveta V. Veselovskaya<sup>48</sup>, Emma R. Usmanova<sup>49,50</sup>, Enrico Cappellini<sup>15</sup>, Erik Brinch Petersen<sup>51</sup>, Esben Kannegaard<sup>52</sup>, Francesca Radina<sup>53</sup>, Fulya Eylem Yediay<sup>1</sup>, Henri Duda<sup>54</sup>, Igor Gutiérrez-Zugasti<sup>38</sup>, Inna Potekhina<sup>55,56</sup>, Irina Shevnina<sup>32</sup>, Isin Altinkaya<sup>1</sup>, Jean Guilaine<sup>57</sup>, Jesper Hansen<sup>58</sup>, Joan Emili Aura Tortosa<sup>43</sup>, João Zilhão<sup>59,60</sup>, Jorge Vega<sup>61</sup>, Kristoffer Buck Pedersen<sup>62</sup>, Krzysztof Tunia<sup>63</sup>, Lei Zhao<sup>1</sup>, Liudmila N. Mylnikova<sup>27</sup>, Lars Larsson<sup>64</sup>, Laure Metz<sup>65</sup>, Levon Yéppiskoposyan<sup>66,93</sup>, Lisbeth Pedersen<sup>67</sup>, Lucia Sarti<sup>68</sup>, Ludovic Orlando<sup>69</sup>, Ludovic Slimak<sup>65</sup>, Lutz Klassen<sup>52</sup>, Malou Blank<sup>3</sup>, Manuel González-Morales<sup>38</sup>, Mara Silvestrini<sup>70</sup>, Maria Vretemark<sup>71</sup>, Marina S. Nesterova<sup>27</sup>, Marina Rykun<sup>72</sup>, Mario Federico Rolfo<sup>73</sup>, Marzena Szmyt<sup>74</sup>, Marcin Przybyła<sup>75</sup>, Mauro Calattini<sup>68</sup>, Mikhail Sablin<sup>76</sup>, Miluše Dobisiková<sup>77</sup>, Morten Meldgaard<sup>78</sup>, Morten Johannsen<sup>79</sup>, Natalia Berezina<sup>28</sup>, Nick Card<sup>80</sup>, Nikolai A. Saveliev<sup>81</sup>, Olga Poshekhonova<sup>42</sup>, Olga Rickards<sup>37</sup>, Olga V. Lozovskaya<sup>82</sup>, Otto Christian Uldum<sup>79</sup>, Paola Aurino<sup>83</sup>, Pavel Kosintsev<sup>84,85</sup>, Patrice Courtaud<sup>54</sup>, Patricia Ríos<sup>36</sup>, Peder Mortensen<sup>86</sup>, Per Lotz<sup>87,88</sup>, Per Åke Persson<sup>89</sup>, Pernille Bangsgaard<sup>90</sup>, Peter de Barros Damgaard<sup>1</sup>, Peter Vang Petersen<sup>14</sup>, Pilar Prieto Martínez<sup>91</sup>, Piotr Włodarczak<sup>63</sup>, Roman V. Smolyaninov<sup>92</sup>, Rikke Maring<sup>22,52</sup>, Roberto Menduina<sup>61</sup>, Ruben Badalyan<sup>91</sup>, Rune Iversen<sup>51</sup>, Ruslan Turin<sup>24</sup>, Sergey Vasilyev<sup>27</sup>, Sidsel Wählin<sup>23</sup>, Svetlana Borutskaya<sup>28</sup>, Svetlana Skochina<sup>42</sup>, Søren Anker Sørensen<sup>87</sup>, Søren H. Andersen<sup>94</sup>, Thomas Jørgensen<sup>87</sup>, Yuri B. Serikov<sup>95</sup>, Vyacheslav I. Molodin<sup>27</sup>, Vaclav Smrcka<sup>96</sup>, Victor Merz<sup>97</sup>, Vivek Appadurai<sup>6</sup>, Vyacheslav Moiseyev<sup>30</sup>, Yvonne Magnusson<sup>98</sup>, Kurt H. Kjær<sup>1</sup>, Niels Lynnerup<sup>12</sup>, Daniel J. Lawson<sup>99</sup>, Peter H. Sudmant<sup>10,18</sup>, Simon Rasmussen<sup>100</sup>, Thorfinn Korneliussen<sup>1</sup>@, Richard Durbin<sup>7,101</sup>@, Rasmus Nielsen<sup>10,1</sup>@, Olivier Delaneau<sup>8</sup>@, Thomas Werge<sup>1,6,102</sup>@, Fernando Racimo<sup>1</sup>@, Kristian Kristiansen<sup>1,3</sup>@, Eske Willerslev<sup>1,5,101,103</sup>\*@

## Affiliations

<sup>1</sup>Lundbeck Foundation GeoGenetics Centre, Globe Institute, University of Copenhagen, Copenhagen, Denmark. <sup>2</sup>Trace and Environmental DNA (TrEnD) Laboratory, School of Molecular and Life Sciences, Curtin University, Perth, Australia. <sup>3</sup>Department of Historical Studies, University of Gothenburg, Gothenburg, Sweden. <sup>4</sup>Sealand Archaeology, Gl. Roesnaesvej 27, 4400 Kalundborg, Denmark. <sup>5</sup>GeoGenetics Group, Department of Zoology, University of Cambridge, Cambridge, UK. <sup>6</sup>Institute of Biological Psychiatry, Mental Health Services, Copenhagen University Hospital, Roskilde, Denmark. <sup>7</sup>Department of Genetics, University of Cambridge, Cambridge, UK. <sup>8</sup>Department of Computational Biology, University of Lausanne, Switzerland. <sup>9</sup>Swiss Institute of Bioinformatics, University of Lausanne, Switzerland. <sup>10</sup>Department of Integrative Biology, University of California, Berkeley, USA. <sup>11</sup>Research department of Genetics, Evolution and Environment, University College London, London, UK. <sup>12</sup>Laboratory of Biological Anthropology, Department of Forensic Medicine, University of Copenhagen, Copenhagen, Denmark. <sup>13</sup>Muséum national d'Histoire naturelle, CNRS, Université de Paris, Muséum de l'Homme, Paris, France. <sup>14</sup>The National Museum of Denmark, Ny Vestergade 10, Copenhagen, Denmark. <sup>15</sup>Section for Evolutionary Genomics, GLOBE Institute, University of Copenhagen, Copenhagen, Denmark. <sup>16</sup>Centre for Evolutionary Hologenomics, University of Copenhagen, Copenhagen, Denmark. <sup>17</sup>Anthropology Department, University of Utah, USA. <sup>18</sup>Center for Computational Biology, University of California, Berkeley, USA. <sup>19</sup>Department of Geology, Lund University, Lund, Sweden. <sup>20</sup>Tårnby Gymnasium og HF, Kastrup, Denmark. <sup>21</sup>Department of Health Technology, Section of Bioinformatics, Technical University of Denmark, Kongens Lyngby, Denmark. <sup>22</sup>Department of Archaeology and Heritage Studies, Aarhus University, Aarhus, Denmark. <sup>23</sup>Vendsyssel Historiske Museum, DK-9800 Hjørring, Denmark. <sup>24</sup>Terra Ltd., Letchik Zlobin St. 20, Voronezh, 394055, Russian Federation. <sup>25</sup>Neurogenomics Division, The Translational Genomics Research Institute (TGEN), Phoenix, AZ, USA. <sup>26</sup>Department of Archaeology, University of Exeter, Exeter, UK. <sup>27</sup>Institute of Archaeology and Ethnography, Siberian Branch of the Russian Academy of Sciences, Novosibirsk, Russian Federation. <sup>28</sup>Research Institute and Museum of Anthropology, Lomonosov Moscow State University, Mokhovaya str. 11, Moscow, Russian Federation. <sup>29</sup>Department of Environmental Biology, Sapienza University of Rome, Rome, Italy. <sup>30</sup>Peter the Great Museum of Anthropology and Ethnography (Kunstkamera), Russian Academy of Sciences, Saint Petersburg, Russian Federation. <sup>31</sup>CIAS, Department of Life Science, University of

60 Coimbra, Coimbra, Portugal. <sup>32</sup>Kostanay Regional University A. Baitursynov, Kostanay, Kazakhstan.  
61 <sup>33</sup>Vesthimmerlands Museum, Søndergade 44, Aars, Denmark. <sup>34</sup>Grupo EvoAdapta, Departamento de Ciencias  
62 Históricas, Universidad de Cantabria, Santander, Spain. <sup>35</sup>Institute of Evolutionary Biology, CSIC-Universitat Pompeu  
63 Fabra, Barcelona, Spain. <sup>36</sup>Departamento de Prehistoria y Arqueología Department, Universidad Autónoma de Madrid,  
64 Madrid, Spain. <sup>37</sup>Department of Biology, University of Rome "Tor Vergata", Rome, Italy. <sup>38</sup>Instituto Internacional de  
65 Investigaciones Prehistóricas de Cantabria, Universidad de Cantabria, Santander, Spain. <sup>39</sup>Centre de Recherche en  
66 Archéologie, Archeosciences, Histoire (CREAAH), UMR-6566 CNRS, Rennes, France. <sup>40</sup>Georgian National Museum,  
67 Tbilisi, Georgia. <sup>41</sup>Tbilisi State University, Tbilisi, Georgia. <sup>42</sup>IPND, Tyumen Scientific Centre, Siberian Branch of the  
68 Russian Academy of Sciences, Tyumen, Russian Federation. <sup>43</sup>Departament de Prehistòria, Arqueologia i Història  
69 Antiga, Universitat de València, València, Spain. <sup>44</sup>Department of Geological Sciences, University of Cape Town, Cape  
70 Town, South Africa. <sup>45</sup>Laboratory for Archaeological Chemistry, Department of Anthropology, University of  
71 Wisconsin-Madison, Madison, USA. <sup>46</sup>Department of Anthropology, New York University, New York, USA. <sup>47</sup>Institute  
72 of Humanities, Ivanovo State University, Ivanovo, Russian Federation. <sup>48</sup>Institute of Ethnology and Anthropology,  
73 Russian Academy of Sciences, Moscow, Russian Federation. <sup>49</sup>Saryarka Archaeological Institute, Buketov Karaganda  
74 University, Karaganda, Kazakhstan. <sup>50</sup>South Ural State University, Chelyabinsk, Russia. <sup>51</sup>The Saxo Institute,  
75 University of Copenhagen, Copenhagen, Denmark. <sup>52</sup>Museum Østjylland, Stemannsgade 2, Randers, Denmark.  
76 <sup>53</sup>Soprintendenza Archeologia Belle Arti e Paesaggio per la Città Metropolitana di Bari, Via Pier l'Eremita, 25, 70122,  
77 Bari, Italy. <sup>54</sup>UMR 5199 PACEA, CNRS, Université de Bordeaux, 33615 Pessac, France. <sup>55</sup>Institute of Archaeology,  
78 National Academy of Sciences of Ukraine, Kyiv, Ukraine. <sup>56</sup>National University of Kyiv-Mohyla Academy, Kyiv,  
79 Ukraine. <sup>57</sup>Collège de France, 75231 Paris cedex 05, France. <sup>58</sup>Odense City Museums, Overgade 48, Odense, Denmark.  
80 <sup>59</sup>UNIARQ, University of Lisbon, Lisbon, Portugal. <sup>60</sup>ICREA, University of Barcelona, Barcelona, Spain. <sup>61</sup>ARGEA  
81 Consultores SL, C. de San Crispin, Madrid, Spain. <sup>62</sup>Museum Sydøstdanmark, Algade 97, 4760 Vordingborg, Denmark.  
82 <sup>63</sup>Institute of Archaeology and Ethnology, Polish Academy of Sciences, Kraków, Poland. <sup>64</sup>Department of Archaeology  
83 and Ancient History, Lund University, Lund, Sweden. <sup>65</sup>CNRS UMR 5608, Toulouse Jean Jaurès University, Maison  
84 de la Recherche, 5 Allées Antonio Machado, 31058 Toulouse, Cedex 9, France. <sup>66</sup>Institute of Molecular Biology,  
85 National Academy of Sciences, Yerevan, Armenia. <sup>67</sup>HistorieUdvikler, Gl. Roesnaesvej 27, DK-4400 Kalundborg,  
86 Denmark. <sup>68</sup>Department of history and cultural heritage, University of Siena, Siena, Italy. <sup>69</sup>Centre d'Anthropobiologie  
87 et de Génomique de Toulouse, CNRS UMR 5288, Université Paul Sabatier, Toulouse, France. <sup>70</sup>Soprintendenza per i  
88 Beni Archeologici delle Marche, Via Birarelli 18, 60100, Ancona, Italy. <sup>71</sup>Västergötlands museum, Stadsträdgården,  
89 Skara, Sweden. <sup>72</sup>Cabinet of Anthropology, Tomsk State University, Tomsk, Russian Federation. <sup>73</sup>Department of  
90 History, Humanities and Society, University of Rome "Tor Vergata", Rome, Italy. <sup>74</sup>Institute for Eastern Research,  
91 Adam Mickiewicz University in Poznań, Poznań, Poland. <sup>75</sup>Institute of Archaeology, Jagiellonian University, Ul.  
92 Gołębia 11, 31-007, Kraków, Poland. <sup>76</sup>Zoological Institute of Russian Academy of Sciences, Universitetskaya nab. 1,  
93 199034, St. Petersburg, Russian Federation. <sup>77</sup>Department of Anthropology, Czech National Museum, Prague, Czech  
94 Republic. <sup>78</sup>Department of Health and Nature, University of Greenland, Greenland. <sup>79</sup>The Viking Ship Museum,  
95 Vindeboder 12, Roskilde, Denmark. <sup>80</sup>Archaeology Institute, University of Highlands and Islands, Scotland, UK.  
96 <sup>81</sup>Scientific Research Center "Baikal region", Irkutsk State University; 1, K. Marx st., Irkutsk, 664003, Russian  
97 Federation. <sup>82</sup>Laboratory for Experimental Traceology, Institute for the History of Material Culture of the Russian  
98 Academy of Sciences, Dvortsovaya nab., 18, 191186, St. Petersburg, Russian Federation. <sup>83</sup>Soprintendenza  
99 Archeologia, Belle Arti e Paesaggio per la provincia di Cosenza, Cosenza, Italy. <sup>84</sup>Paleoecology Laboratory, Institute of  
100 Plant and Animal Ecology, Ural Branch of the Russian Academy of Sciences, Ekaterinburg, Russian Federation.  
101 <sup>85</sup>Department of History of the Institute of Humanities, Ural Federal University, Ekaterinburg, Russian Federation.  
102 <sup>86</sup>Centre for the Study of Early Agricultural Societies, Department of Cross-Cultural and Regional Studies, University  
103 of Copenhagen, 2300 Copenhagen, Denmark. <sup>87</sup>Museum Nordsjælland, Frederiksgade 9, 3400 Hillerød. <sup>88</sup>Museum  
104 Vestsjælland, Klosterstræde 18, 4300 Holbæk, Denmark. <sup>89</sup>Museum of Cultural History, University of Oslo, P.O. Box  
105 6762. St. Olavs Plass NO-0130 Oslo, Norway. <sup>90</sup>ArchaeoScience, GLOBE Institute, University of Copenhagen,  
106 Copenhagen, Denmark. <sup>91</sup>Department of History, University of Santiago de Compostela, Spain. <sup>92</sup>Lipetsk Regional  
107 Scientific Public Organisation "Archaeological Research", Lipetsk, Russian Federation. <sup>92</sup>Institute of Archaeology and  
108 Ethnography, National Academy of Sciences, Yerevan, Armenia. <sup>93</sup>Russian-Armenian University, Yerevan, Armenia.  
109 <sup>94</sup>Moesgaard Museum, Moesgård Allé 15, Højbjerg, Denmark. <sup>95</sup>Nizhny Tagil State Socio-Pedagogical Institute,  
110 Nizhny Tagil, Russia. <sup>96</sup>Institute for History of Medicine, First Faculty of Medicine, Charles University, Prague, Czech  
111 Republic. <sup>97</sup>Centre for Archaeological Research Toraighyrov University, Pavlodar, Kazakhstan. <sup>98</sup>Malmö Museer,  
112 Malmöhusvägen 6, Malmö, Sweden. <sup>99</sup>Institute of Statistical Sciences, School of Mathematics, University of Bristol,  
113 Bristol, UK. <sup>100</sup>Novo Nordisk Foundation Centre for Protein Research, Faculty of Health and Medical Sciences,  
114 University of Copenhagen, Copenhagen N, Denmark. <sup>101</sup>Wellcome Sanger Institute, Wellcome Genome Campus,  
115 Cambridge, UK. <sup>102</sup>Department of Clinical Medicine, University of Copenhagen, 2200 Copenhagen N, Denmark.  
116 <sup>103</sup>MARUM, University of Bremen, Bremen, Germany.

117  
118 \* Corresponding authors; email: [morten.allentoft@curtin.edu.au](mailto:morten.allentoft@curtin.edu.au), [martin.sikora@sund.ku.dk](mailto:martin.sikora@sund.ku.dk), [ew482@cam.ac.uk](mailto:ew482@cam.ac.uk)  
119 § Joint first authors

120 @ Joint last authors

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## 123 **Summary**

124

125 **The transitions from foraging to farming and later to pastoralism in Stone Age Eurasia (c. 11-**  
126 **3 thousand years before present, BP) represent some of the most dramatic lifestyle changes in**  
127 **human evolution. We sequenced 317 genomes of primarily Mesolithic and Neolithic**  
128 **individuals from across Eurasia combined with radiocarbon dates, stable isotope data, and**  
129 **pollen records. Genome imputation and co-analysis with previously published shotgun**  
130 **sequencing data resulted in >1600 complete ancient genome sequences offering fine-grained**  
131 **resolution into the Stone Age populations. We observe that: 1) Hunter-gatherer groups were**  
132 **more genetically diverse than previously known, and deeply divergent between western and**  
133 **eastern Eurasia. 2) We identify hitherto genetically undescribed hunter-gatherers from the**  
134 **Middle Don region that contributed ancestry to the later Yamnaya steppe pastoralists; 3) The**  
135 **genetic impact of the Neolithic transition was highly distinct, east and west of a boundary**  
136 **zone extending from the Black Sea to the Baltic. Large-scale shifts in genetic ancestry**  
137 **occurred to the west of this “Great Divide”, including an almost complete replacement of**  
138 **hunter-gatherers in Denmark, while no substantial ancestry shifts took place during the same**  
139 **period to the east. This difference is also reflected in genetic relatedness within the**  
140 **populations, decreasing substantially in the west but not in the east where it remained high**  
141 **until c. 4,000 BP; 4) The second major genetic transformation around 5,000 BP happened at a**  
142 **much faster pace with Steppe-related ancestry reaching most parts of Europe within 1,000-**  
143 **years. Local Neolithic farmers admixed with incoming pastoralists in eastern, western, and**  
144 **southern Europe whereas Scandinavia experienced another near-complete population**  
145 **replacement. Similar dramatic turnover-patterns are evident in western Siberia; 5) Extensive**  
146 **regional differences in the ancestry components involved in these early events remain visible**  
147 **to this day, even within countries. Neolithic farmer ancestry is highest in southern and eastern**  
148 **England while Steppe-related ancestry is highest in the Celtic populations of Scotland, Wales,**  
149 **and Cornwall (this research has been conducted using the UK Biobank resource); 6) Shifts in**  
150 **diet, lifestyle and environment introduced new selection pressures involving at least 21**  
151 **genomic regions. Most such variants were not universally selected across populations but**  
152 **were only advantageous in particular ancestral backgrounds. Contrary to previous claims, we**  
153 **find that selection on the FADS regions, associated with fatty acid metabolism, began before**  
154 **the Neolithisation of Europe. Similarly, the lactase persistence allele started increasing in**  
155 **frequency before the expansion of Steppe-related groups into Europe and has continued to**  
156 **increase up to the present. Along the genetic cline separating Mesolithic hunter-gatherers**  
157 **from Neolithic farmers, we find significant correlations with trait associations related to skin**  
158 **disorders, diet and lifestyle and mental health status, suggesting marked phenotypic**  
159 **differences between these groups with very different lifestyles. This work provides new**  
160 **insights into major transformations in recent human evolution, elucidating the complex**  
161 **interplay between selection and admixture that shaped patterns of genetic variation in**  
162 **modern populations.**

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164

## 165 **Introduction**

166 The transition from hunting and gathering to farming represents one of the most dramatic shifts in  
167 lifestyle and diet in human evolution with lasting effects on the modern world. For millions of years  
168 our ancestors relied on hunting and foraging for survival but c.12,000 years ago in the Fertile

169 Crescent of the Near East, plant cultivation and animal husbandry were developed<sup>1-3</sup>. This  
170 ultimately resulted in a more sedentary lifestyle accompanied by increasing population sizes and  
171 higher social complexity. Expanding populations and the adoption of herding, carried farming  
172 practices into Europe and parts of SW Asia in the following millennia, and farming was also  
173 developed independently in other parts of the World. Today, 50% of the Earth's habitable land is  
174 used for agriculture and very few hunter-gatherers remain<sup>4,5</sup>. Understanding the changes to the  
175 human gene pool during this shift from hunter-gathering to farming between the Mesolithic and  
176 Neolithic periods is central to understanding ourselves and the events that led to a major  
177 transformation of our planet.

178  
179 While the Neolithisation process has been studied extensively with ancient DNA (aDNA)  
180 technology, several key questions remain unaddressed. Population movements during the Neolithic  
181 can be traced in the gene pools across the European continent as farming was introduced from the  
182 Near East. Several regional studies have testified to varying degrees of reproductive interaction  
183 with local Mesolithic groups, ranging from genetic continuity<sup>6</sup> to gradual population admixture<sup>7-10</sup>  
184 to almost complete replacement<sup>11</sup>. However, our knowledge of the population structure in the  
185 Mesolithic period and how it was formed is limited, partly because of a paucity of data from  
186 skeletons older than 8,000 years, compromising resolution into subsequent demographic transitions.  
187 Moreover, the spatiotemporal mapping of population dynamics east of Europe, including Siberia,  
188 Central- and North Asia during the same time period remains patchy. In these regions the  
189 'Neolithic' typically refers to new forms of lithic material culture, and/or the presence of  
190 ceramics<sup>12</sup>. For instance, the Neolithic cultures of the Central Asian Steppe possessed pottery, but  
191 retained a hunter-gatherer economy alongside stone blade technology similar to the preceding  
192 Mesolithic cultures<sup>13</sup>. The archaeological record testifies to a boundary, ranging from the eastern  
193 Baltic to the Black Sea, east of which hunter-gatherer societies persist for much longer than in  
194 western Europe<sup>14</sup>. The population genomic implications of this "Great Divide" is, however, largely  
195 unknown. Southern Scandinavia represents another enigma in the Neolithisation debate<sup>15</sup>. The  
196 introduction of farming reached a 1,000-year standstill at the doorstep to Southern Scandinavia  
197 before finally progressing into Denmark around 6,000 BP. It is not known what caused this delay  
198 and whether the transition to farming in Denmark, was facilitated by the migration of people (demic  
199 diffusion), similar to the rest of Europe<sup>11,16,17</sup> or mostly involved cultural diffusion<sup>18,19</sup>. Starting at  
200 around 5,000 BP, a new ancestry component emerged on the eastern European plains associated  
201 with Yamnaya Steppe pastoralists culture and swept across Europe mediated through expansion of  
202 the Corded Ware complex (CWC) and related cultures<sup>20,21</sup>. The genetic origin of the Yamnaya and  
203 the fine-scale dynamics of the formation and expansion of the CWC are largely unresolved  
204 questions of central importance to clarify the formation of the present day European gene pool.

205  
206 Rapid dietary changes and expansion into new climate zones represent shifts in environmental  
207 exposure, impacting the evolutionary forces acting on the gene pool. The Neolithisation can  
208 therefore be considered as a series of large-scale selection pressures imposed on humans from  
209 around 12,000 years ago. Moreover, close contact with livestock and higher population densities  
210 have likely enhanced exposure and transmission of infectious diseases, introducing new challenges  
211 to our survival<sup>22,23</sup>. While signatures of selection can be identified from patterns of genetic diversity  
212 in extant populations<sup>24,25</sup>, this can be challenging in species such as humans, which show very wide  
213 geographic distributions and have thus been exposed to highly diverse and changing local  
214 environments through space and time. In the complex mosaic of ancestries that constitute a modern  
215 human genome any putative signatures of selection may therefore misrepresent the timing and  
216 magnitude of the actual event unless we can use ancient DNA to chart the individual ancestry  
217 components back into the evolutionary past.

218

219 To investigate these formative processes in Eurasian prehistory, we conducted the largest ancient  
220 DNA study to date on human Stone Age skeletal material. We sequenced low-coverage genomes of  
221 317 radiocarbon-dated (AMS) primarily Mesolithic and Neolithic individuals, covering major parts  
222 of Eurasia. We combined these with published shotgun-sequenced data to impute a dataset of  
223 >1600 diploid ancient genomes. Genomic data from 100 AMS-dated individuals from Denmark  
224 supported detailed analyses of the Stone Age population dynamics in Southern Scandinavia. When  
225 combined with genetically-predicted phenotypes, proxies for diet ( $\delta^{13}\text{C}/\delta^{15}\text{N}$ ), mobility ( $^{87}\text{Sr}/^{86}\text{Sr}$ )  
226 and vegetation cover (pollen) we could connect this with parallel shifts in phenotype, subsidence  
227 and landscape. To test for traces of divergent selection in health and lifestyle-related genetic  
228 variants, we used the imputed ancient genomes to reconstruct polygenic risk scores for hundreds of  
229 complex traits in the ancient Eurasian populations. Additionally, we used a novel chromosome  
230 painting technique based on tree sequences, in order to model ancestry-specific allele frequency  
231 trajectories through time. This allowed us to identify many new phenotype-associated genetic  
232 variants with hitherto unknown evidence for positive selection in Eurasia throughout the Holocene.  
233

## 234 **Results/Discussion**

### 235 *Samples and data*

236 In this study we present genomic data from 317 ancient individuals (Fig 1, Extended data fig. 2,  
237 Supplement Table I). A total of 272 were radiocarbon dated within the project, while 39 dates were  
238 derived from literature and 15 were dated by archaeological context. Dates were corrected for  
239 marine and freshwater reservoir effects (Supplementary Note 8) and ranged from the Upper  
240 Palaeolithic (UP) c. 25,700 calibrated years before present (cal. BP) to the mediaeval period (c.  
241 1200 cal. BP). However, 97% of the individuals (N=309) span 11,000 cal. BP to 3,000 cal. BP, with  
242 a heavy focus on individuals associated with various Mesolithic and Neolithic cultures.  
243

244 Geographically, the sampled skeletons cover a vast territory across Eurasia, from Lake Baikal to the  
245 Atlantic coast, from Scandinavia to the Middle East, and they derive from a variety of contexts,  
246 including burial mounds, caves, bogs and the seafloor (Supplementary Notes 6-7). Broadly, we can  
247 divide our research area into three large regions: 1) central, western and northern Europe, 2) eastern  
248 Europe including western Russia and Ukraine, and 3) the Urals and western Siberia. Our samples  
249 cover many of the key Mesolithic and Neolithic cultures in Western Eurasia, such as the  
250 Maglemose and Ertebølle cultures in Scandinavia, the Cardial in the Mediterranean, the Körös and  
251 Linear Pottery (LBK) in SE and Central Europe, and many archaeological cultures in Ukraine,  
252 western Russia, and the trans-Ural (e.g. Veretye, Lyalovo, Volosovo, Kitoi). Our sampling was  
253 particularly dense in Denmark from where we present a detailed and continuous sequence of 100  
254 genomes spanning from the early Mesolithic to the Bronze Age. Dense sample sequences were also  
255 obtained from Ukraine, Western Russia, and the trans-Ural, spanning from the Early Mesolithic  
256 through the Neolithic, up to c. 5,000 BP.  
257

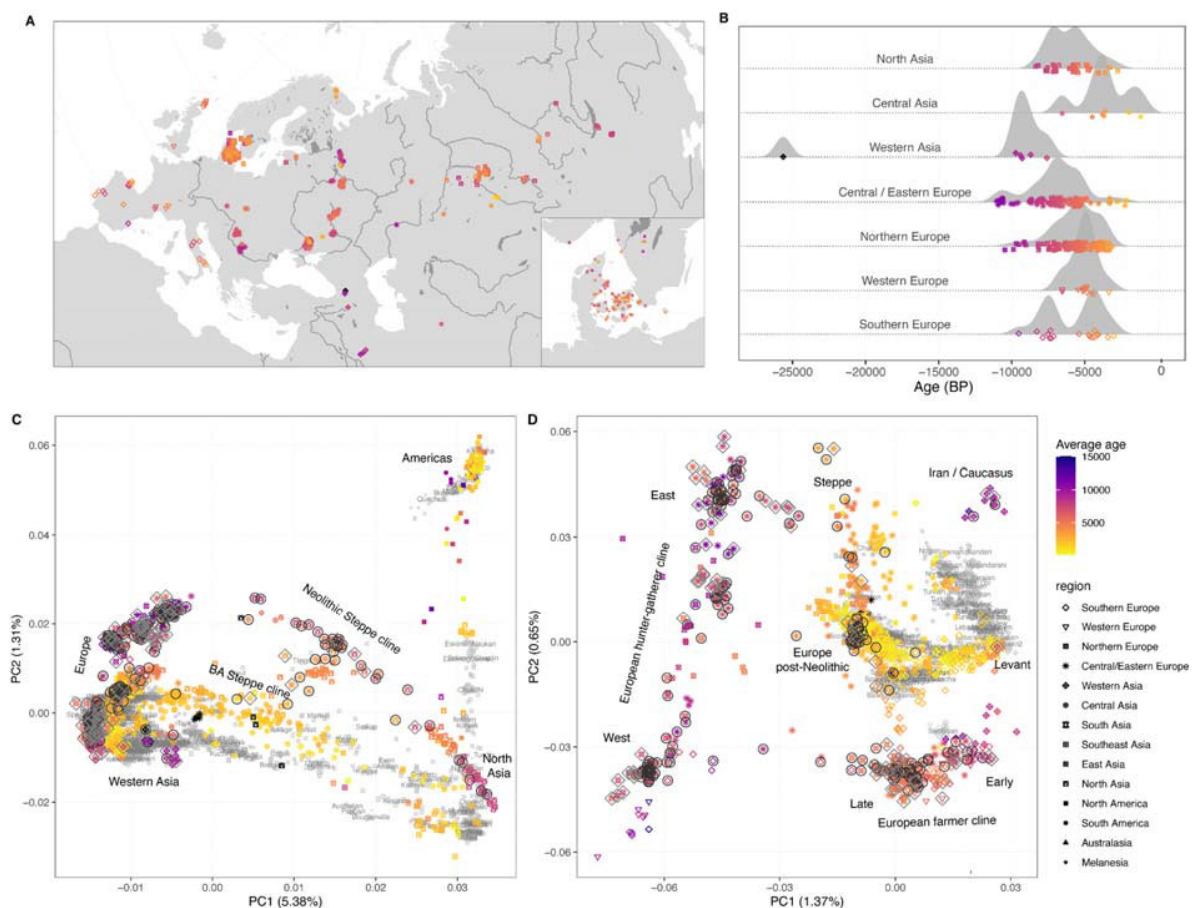
258 We extracted ancient DNA from tooth cementum or petrous bone and shotgun sequenced the 317  
259 genomes to a depth of genomic coverage ranging from 0.01X to 7.1X (mean = 0.75X, median =  
260 0.26X), with 81 individuals having >1X coverage. Using a new imputation method designed for  
261 low-coverage sequencing data<sup>26</sup>, we performed genotype imputation based on the 1,000 Genomes  
262 phased data as a reference panel. We also imputed >1,300 previously published shotgun-sequenced  
263 ancient genomes. This resulted in a “raw” dataset containing 8.5 million common Single Nucleotide  
264 Polymorphisms (SNPs) (>1% MAF and imputation info score > 0.5) from 1,664 imputed diploid  
265 ancient genomes. This number includes 42 high-coverage ancient genomes (Table S2.1,  
266 Supplementary Note 2) that were down-sampled to values between 0.1X and 4X for validation.

267 This demonstrated that 1-fold genome coverage provides remarkably high imputation accuracy  
268 ( $r^2 > 0.95$  at common variants with MAF above 5%) and closely matches what is obtained for  
269 modern samples (Extended Fig. 1A-D). African genomes, however, exhibit lower imputation  
270 accuracy as a result of the poor representation of this ancestry in the reference panel. For European  
271 genomes, this translates into genotyping error rates usually below 5% for the most challenging  
272 genotypes to impute (heterozygous genotypes or with two copies of the non-reference allele;  
273 Supplementary Fig. S2.1-S2.2). Imputation accuracy also depends on minor allele frequency and  
274 genomic coverage (Supplementary Fig. S2.3). We find that coverage values as low as 0.1x and  
275 0.4X are sufficient to obtain  $r^2$  imputation accuracy of 0.8 and 0.9 at common variants  
276 (MAF  $\geq 10\%$ ), respectively. As further validation, we increased genomic coverage to 27.5X, 18.9X  
277 and 5.4X on a previously published trio (mother, father, son) from the Late Neolithic mass burial at  
278 Koszyce in Poland<sup>27</sup>. This allowed for a validation of imputed genotypes and haplotypes using  
279 Mendel's rules of inheritance. We obtained Mendelian error rates from 0.1% at 4X to 0.55% at  
280 0.1X (Extended Fig. 1E). Similarly, we obtained switch error rates between 2% and 6%. Altogether,  
281 our validation analysis showed that ancient European genomes can be imputed confidently from  
282 coverages above 0.4X and highly valuable data can still be obtained with coverages as low as 0.1X  
283 when using specific QC on the imputed data, although at very low coverage a bias arise towards the  
284 major allele (see Supplementary Note 2). We filtered out samples with poor coverage or variant  
285 sites with low MAF in downstream analyses depending on the specific data quality requirements.  
286 For most analyses we use a subset of 1,492 imputed ancient genomes (213 sequenced in this study)  
287 after filtering individuals with very low coverages ( $< 0.1X$ ) and/or low imputation quality (average  
288 genotype probability  $< 0.8$ ) and close relatives. This dataset allows us to characterise the ancient  
289 cross-continental gene pools and the demographic transitions with unprecedented resolution.

290  
291 We performed broad-scale characterization of this dataset using principal component analysis  
292 (PCA) and model-based clustering (ADMIXTURE), recapitulating and providing increased  
293 resolution into previously described ancestry clines in ancient Eurasian populations (Fig. 1;  
294 Extended Data Fig. 2; Supplementary Note 3d). Strikingly, inclusion of the imputed ancient  
295 genomes in the inference of the principal components reveals much higher variance among the  
296 ancient groups than previously anticipated using projection onto a PC-space inferred from modern  
297 individuals alone (Extended Data Fig. 2). This is particularly notable in a PCA of West Eurasian  
298 individuals, where genetic variation among all present-day populations is confined within a small  
299 central area of the PCA (Extended Data Fig. 2C, D). These results are consistent with much higher  
300 genetic differentiation between ancient Europeans than present-day populations reflecting lower  
301 effective population sizes and genetic isolation among ancient groups.

302  
303 To obtain a finer-scale characterization of genetic ancestries across space and time, we assigned  
304 imputed ancient individuals to genetic clusters by applying hierarchical community detection on a  
305 network of pairwise identity-by-descent (IBD)-sharing similarities<sup>28</sup> (Extended Data Fig. 3;  
306 Supplementary Note 3c). The obtained clusters capture fine-scale genetic structure corresponding to  
307 shared ancestry within particular spatiotemporal ranges and/or archaeological contexts, and were  
308 used as sources and/or targets in supervised ancestry modelling (Extended Data Fig. 4;  
309 Supplementary Note 3i). We focus our subsequent analyses on three panels of putative source  
310 clusters reflecting different temporal depths: "deep", using a set of deep ancestry source groups  
311 reflecting major ancestry poles; "postNeol", using diverse Neolithic and earlier source groups; and  
312 "postBA", using Late Neolithic and Bronze Age source groups (Extended Data Fig. 4).

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316  
 317 **Fig 1. Sample overview and broad scale genetic structure.** (A), (B) Geographic and temporal distribution of the 317  
 318 ancient genomes reported here. Age and geographic region of ancient individuals are indicated by plot symbol colour  
 319 and shape, respectively. Random jitter was added to geographic coordinates to avoid overplotting. (C), (D) Principal  
 320 component analysis of 3,316 modern and ancient individuals from Eurasia, Oceania, and the Americas (C), as well as  
 321 restricted to 2,126 individuals from western Eurasia (west of Urals) (D). Principal components were defined using both  
 322 modern and imputed ancient genomes passing all filters, with the remaining low-coverage ancient genomes projected.  
 323 Ancient genomes sequenced in this study are indicated with black circles (imputed genomes passing all filters, n=213)  
 324 or grey diamonds (pseudo-haploid projected genomes, n=104). Genomes of modern individuals are shown in grey, with  
 325 population labels corresponding to their median coordinates.  
 326

### 327 *Deep population structure of western Eurasians*

328 Our study comprises the largest genomic dataset on European hunter-gatherers to date, including  
 329 113 imputed hunter-gatherer genomes of which 79 were sequenced in this study. Among them, we  
 330 report a 0.83X genome of an Upper Palaeolithic (UP) skeleton from Kotias Klde Cave in Georgia,  
 331 Caucasus (NEO283), directly dated to 26,052 - 25,323 cal BP (95%). In the PCA of all non-African  
 332 individuals, it occupies a position distinct from other previously sequenced UP individuals, shifted  
 333 towards west Eurasians along PC1 (Supplementary Note 3d). Using admixture graph modelling, we  
 334 find that this Caucasus UP lineage derives from a mixture of predominantly West Eurasian UP  
 335 hunter-gatherer ancestry (76%) with ~24% contribution from a “basal Eurasian” ghost population,  
 336 first observed in West Asian Neolithic individuals<sup>29</sup> (Extended Data Fig. 5A). Models attempting to  
 337 reconstruct major post-LGM clusters such as European hunter-gatherers and Anatolian farmers  
 338 without contributions from this Caucasus UP lineage provided poor admixture graph fits or were  
 339 rejected in *qpAdm* analyses (Extended Data Fig. 5B,C). These results thus suggest a central role of

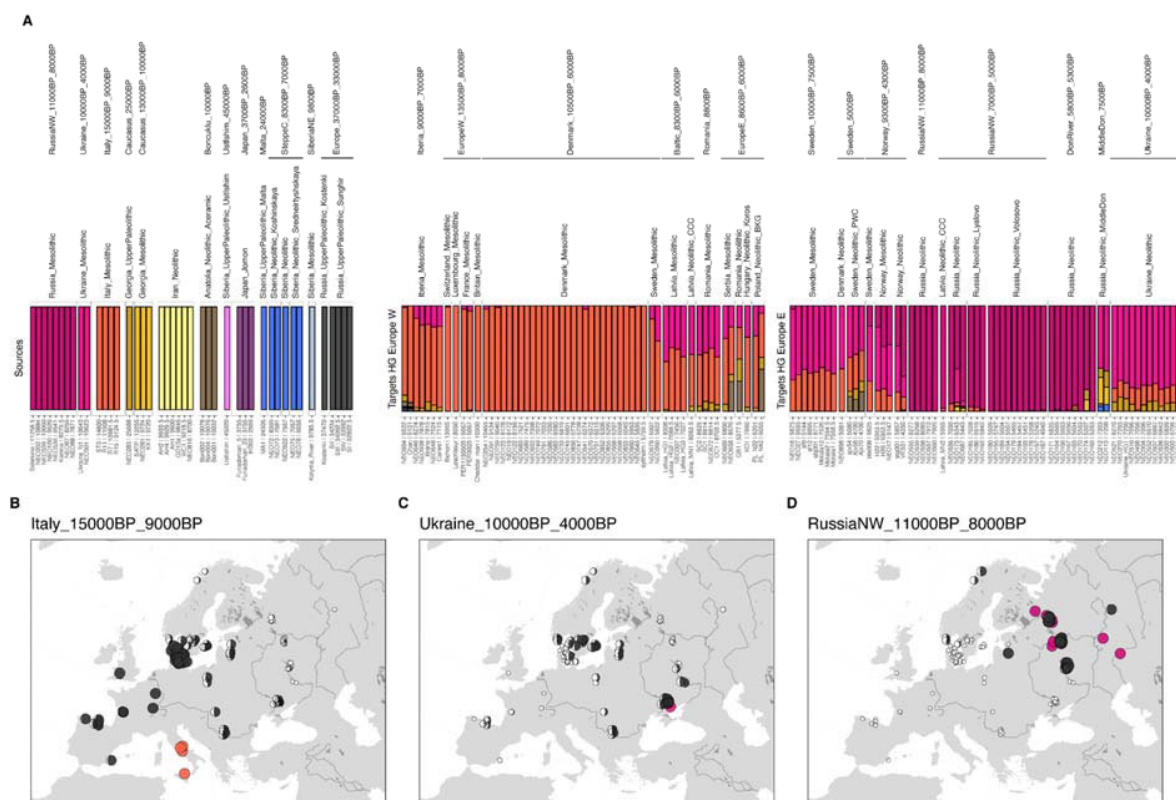
340 the descendants related to this Caucasus UP lineage in the formation of later West Eurasian  
341 populations, consistent with recent genetic data from the nearby Dzudzuana Cave, also in  
342 Georgia<sup>30</sup>.

343  
344 We performed supervised admixture modelling using a set of twelve possible source clusters  
345 representing Mesolithic hunter-gatherers from the extremes of the HG cline, as well as temporal or  
346 geographical outgroups of deep Eurasian lineages (Fig 2A). We replicate previous results of broad-  
347 scale genetic structure correlated to geography in European hunter-gatherers after the LGM<sup>17</sup>, while  
348 also revealing novel insights into their fine-scale structure. Ancestry related to southern European  
349 hunter-gatherers (source: Italy\_15000BP\_9000 BP) predominates in western Europe. This includes  
350 Denmark, where our 28 sequenced and imputed hunter-gatherer genomes derive almost exclusively  
351 from this cluster, with remarkable homogeneity across a 5,000 year transect (Fig. 3A). In contrast,  
352 hunter-gatherer individuals from the eastern and far northern reaches of Europe show the highest  
353 proportions of Russian hunter-gatherer ancestry (source: RussiaNW\_11000BP\_8000BP; Fig. 2B,  
354 D), with genetic continuity until ~5,000 BP in Russia. Ancestry related to Mesolithic hunter-  
355 gatherer populations from Ukraine (source: Ukraine\_10000BP\_4000BP) is carried in highest  
356 proportions in hunter-gatherers from a geographic corridor extending from south-eastern Europe  
357 towards the Baltic and southern Scandinavia. Swedish Mesolithic individuals derive up to 60% of  
358 their ancestry from that source (Fig. 2C). Our results thus indicate northwards migrations of at least  
359 three distinct waves of hunter-gatherer ancestry into Scandinavia: a predominantly southern  
360 European source into Denmark; a source related to Ukrainian and south-eastern European hunter-  
361 gatherers into the Baltic and southern Sweden; and a northwest Russian source into the far north,  
362 before venturing south along the Atlantic coast of Norway<sup>31</sup> (Fig. 2). These movements are likely to  
363 represent post glacial expansions from refugia areas shared with many plant and animal species<sup>32,33</sup>.

364  
365 Despite the major role of geography in shaping European hunter-gatherer structure, we also  
366 document more complex local dynamics. On the Iberian Peninsula, the earliest individuals,  
367 including a ~9,200-year-old hunter-gatherer (NEO694) from Santa Maira (eastern Spain),  
368 sequenced in this study, show predominantly southern European hunter-gatherer ancestry with a  
369 minor contribution from UP hunter-gatherer sources (Fig. 3). In contrast, later individuals from  
370 Northern Iberia are more similar to hunter-gatherers from eastern Europe, deriving ~30-40% of  
371 their ancestry from a source related to Ukrainian hunter-gatherers<sup>34,35</sup>. The earliest evidence for this  
372 gene flow is observed in a Mesolithic individual from El Mazo, Spain (NEO646) that was dated,  
373 calibrated and reservoir-corrected to c. 8,200 BP (8365-8182 cal BP, 95%) but context-dated to  
374 slightly older (8550-8330 BP, see<sup>36</sup>). The younger date coincides with some of the oldest Mesolithic  
375 geometric microliths in northern Iberia, appearing around 8,200 BP at this site<sup>36</sup>. In southern  
376 Sweden, we find higher amounts of southern European hunter-gatherer ancestry in late Mesolithic  
377 coastal individuals (NEO260 from Evensås; NEO679 from Skateholm) than in the earlier  
378 Mesolithic individuals from further inland, suggesting either geographic genetic structure in the  
379 Swedish Mesolithic population or a possible eastward expansion of hunter-gatherers from  
380 Denmark, where this ancestry prevailed (Fig. 3). An influx of southern European hunter-gatherer-  
381 related ancestry in Ukrainian individuals after the Mesolithic (Fig. 3) suggests a similar eastwards  
382 expansion in south-eastern Europe<sup>17</sup>. Interestingly, two herein reported ~7,300-year-old imputed  
383 genomes from the Middle Don River region in the Pontic-Caspian steppe (Golubaya Krinitisa,  
384 NEO113 & NEO212) derive ~20-30% of their ancestry from a source cluster of hunter-gatherers  
385 from the Caucasus (Caucasus\_13000BP\_10000BP) (Fig. 3). Additional lower coverage (non-  
386 imputed) genomes from the same site project in the same PCA space (Fig. 1D), shifted away from  
387 the European hunter-gatherer cline towards Iran and the Caucasus. Our results thus document  
388 genetic contact between populations from the Caucasus and the Steppe region as early as 7,300  
389 years ago, providing documentation of continuous admixture prior to the advent of later nomadic



390 Steppe cultures, in contrast to recent hypotheses, and also further to the west than previously  
 391 reported<sup>17,37</sup>.  
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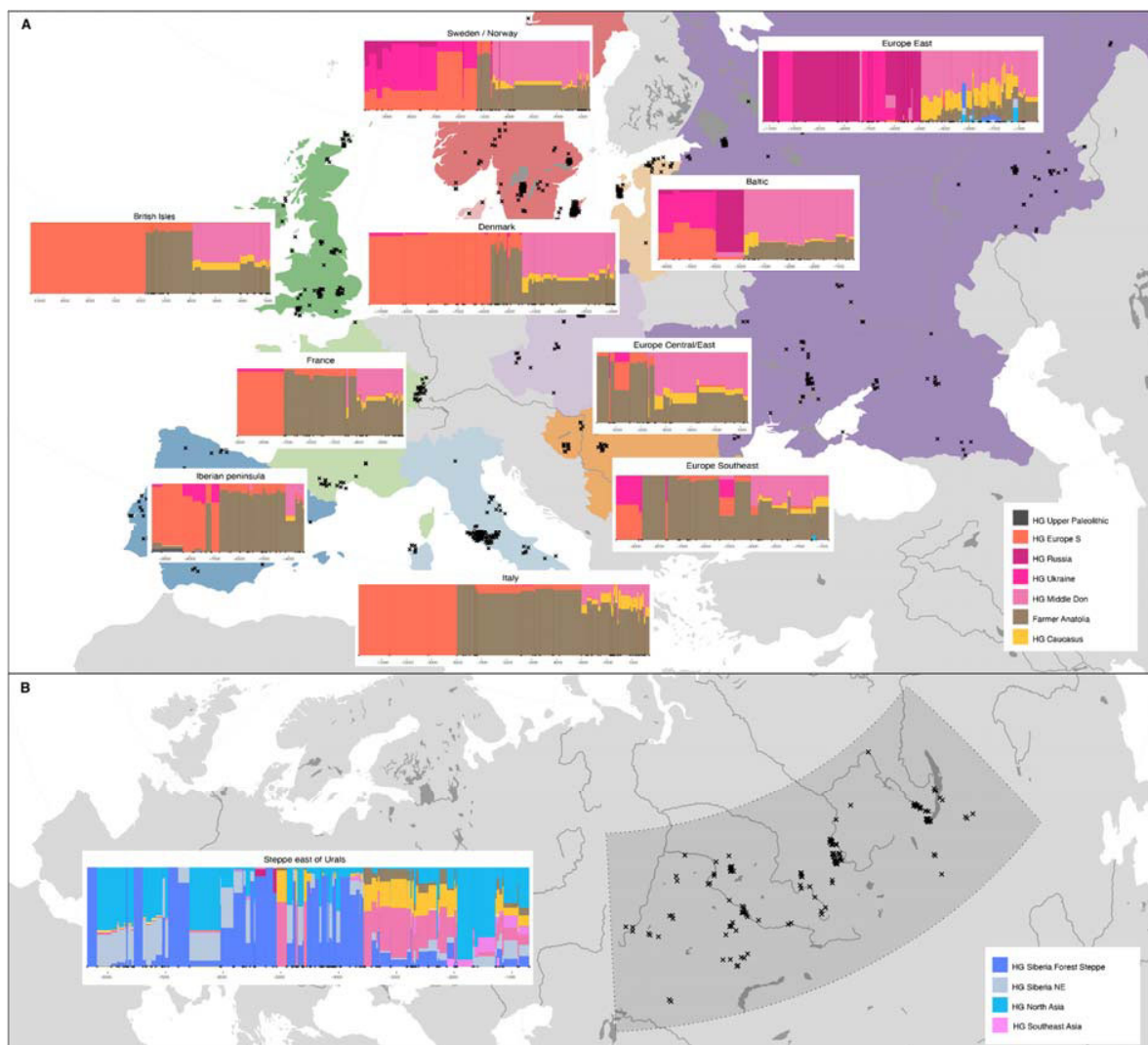
393  
 394 **Fig 2. Genetic structure of European hunter-gatherers** (A) Ancestry proportions in 113 imputed ancient genomes  
 395 representing European hunter-gatherer contexts (right) estimated from supervised non-negative least squares analysis  
 396 using deep Eurasian source groups (left). Individuals from target groups are grouped by genetic clusters. (B)–(D) Moon  
 397 charts showing spatial distribution of ancestry proportions in European hunter-gatherers deriving from three deep  
 398 Eurasian source groups; Italy\_15000BP\_9000BP; Ukraine\_10000BP\_4000BP; RussiaNW\_11000BP\_8000BP (source  
 399 origins shown with coloured symbol). Estimated ancestry proportions are indicated by both size and amount of fill of  
 400 moon symbols.  
 401  
 402

### 403 *Major genetic transitions in Europe*

404 Previous ancient genomics studies have documented multiple episodes of large-scale population  
 405 turnover in Europe within the last 10,000 years<sup>6,11,14,16,17,20,21,34,38–41</sup>. The 317 genomes reported here  
 406 fill important knowledge gaps, particularly in northern and eastern Europe, allowing us to track the  
 407 dynamics of these events at both continental and regional scales.  
 408

409 Our analyses reveal profound differences in the spatiotemporal Neolithisation dynamics across  
 410 Europe. Supervised admixture modelling (“deep” set) and spatiotemporal kriging<sup>42</sup> document a  
 411 broad east-west distinction along a boundary zone running from the Black Sea to the Baltic. On the  
 412 western side of this “Great Divide”, the Neolithic transition is accompanied by large-scale shifts in  
 413 genetic ancestry from local hunter-gatherers to Neolithic farmers with Anatolian-related ancestry  
 414 (Boncuklu\_10000BP; Fig. 3; Extended Data Fig. 4, 6). The arrival of Anatolian-related ancestry in  
 415 different regions spans an extensive time period of over 3,000 years, from its earliest evidence in  
 416 the Balkans (Lepenski Vir) at ~8,700 BP<sup>17</sup> to c. 5,900 BP in Denmark. On the eastern side of this  
 417 divide, no ancestry shifts can be observed during this period. In the East Baltic region (see also<sup>43</sup>),

418 Ukraine and Western Russia local hunter-gatherer ancestry prevails until ~5,000 BP without  
419 noticeable input of Neolithic Anatolian-related farmer ancestry (Fig. 3; Extended Data Fig. 4, 6).  
420 This Eastern genetic continuity is in remarkable congruence with the archaeological record showing  
421 persistence of pottery-using hunter-gatherer-fisher groups in this wide region, and delayed  
422 introduction of cultivation and husbandry by several thousand years (Supplementary Note 5).  
423  
424 From approximately 5,000 BP, an ancestry component appears on the eastern European plains in  
425 Early Bronze Age Steppe pastoralists associated with the Yamnaya culture and it rapidly spreads  
426 across Europe through the expansion of the Corded Ware complex (CWC) and related cultures<sup>20,21</sup>.  
427 We demonstrate that this “steppe” ancestry (Steppe\_5000BP\_4300BP) can be modelled as a  
428 mixture of ~65% ancestry related to herein reported hunter-gatherer genomes from the Middle Don  
429 River region (MiddleDon\_7500BP) and ~35% ancestry related to hunter-gatherers from Caucasus  
430 (Caucasus\_13000BP\_10000BP) (Extended Data Fig. 4). Thus, Middle Don hunter-gatherers, who  
431 already carry ancestry related to Caucasus hunter-gatherers (Fig. 2), serve as a hitherto unknown  
432 proximal source for the majority ancestry contribution into Yamnaya genomes. The individuals in  
433 question derive from the burial ground Golubaya Krinitsa (Supplementary Note 3). Material culture  
434 and burial practices at this site are similar to the Mariupol-type graves, which are widely found in  
435 neighbouring regions of Ukraine, for instance along the Dnepr River. They belong to the group of  
436 complex pottery-using hunter-gatherers mentioned above, but the genetic composition at Golubaya  
437 Krinitsa is different from the remaining Ukrainian sites (Fig 2A, Extended Data Fig. 4). We find  
438 that the subsequent transition of the Late Neolithic and Early Bronze Age European gene pool  
439 happened at a faster pace than during the Neolithisation, reaching most parts of Europe within a  
440 ~1,000-year time period after first appearing in eastern Baltic region ~4,800 BP (Fig. 3). In line  
441 with previous reports we observe that beginning c. 4,200 BP, steppe-related ancestry was already  
442 dominant in samples from France and the Iberian peninsula, while it reached Britain only 400 years  
443 later<sup>11,38,44</sup>. Strikingly, because of the delayed Neolithisation in Southern Scandinavia these  
444 dynamics resulted in two episodes of large-scale genetic turnover in Denmark and southern Sweden  
445 within a 1,000-year period (Fig. 3).  
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**Fig. 3. Genetic transects of Eurasia.** Regional timelines of genetic ancestry compositions within the past 15,000 years in western Eurasia (top) and the Eurasian Steppe belt east of the Urals (bottom). Ancestry proportions in 972 imputed ancient genomes from these regions (covering c. 12,000 BP to 500 BP), inferred using supervised admixture modelling with “deep” hunter-gatherer ancestry source groups. Geographic areas included in timelines are indicated with fill colour (west Eurasia) and grey shading (eastern Steppe region). Excavation locations of the ancient skeletons are indicated with black crosses. Coloured bars within the timelines represent ancestry proportions for temporally consecutive individuals, with the width corresponding to their age difference. Individuals with identical age were offset along the time axis by adding random jitter, ages. We note that the inclusion of only shotgun-sequenced samples may affect the exact timing of events in some regions from where such data are sparse.

460 We next investigated fine-grained ancestry dynamics underlying these transitions. We replicate  
461 previous reports<sup>11,16,17,21,41,45,46</sup> of widespread, but low-level admixture between Neolithic farmers  
462 and local hunter-gatherers resulting in a resurgence of HG ancestry in many regions of Europe  
463 during the middle and late Neolithic (Extended Data Fig. 7). Estimated hunter-gatherer ancestry  
464 proportions among early Neolithic people rarely exceed 10%, with notable exceptions observed in  
465 individuals from south-eastern Europe (Iron Gates), Sweden (Pitted Ware Culture) as well as herein  
466 reported early Neolithic genomes from Portugal (western Cardial), estimated to harbour 27% – 43%  
467 Iberian hunter-gatherer ancestry (Iberia\_9000BP\_7000BP). The latter result, suggesting extensive  
468 first-contact admixture, is in agreement with archaeological inferences derived from modelling the

469 spread of farming along west Mediterranean Europe<sup>47</sup>. Individuals associated with Neolithic  
470 farming cultures from Denmark show some of the highest overall hunter-gatherer ancestry  
471 proportions (up to ~25%), mostly derived from Western European-related hunter-gatherers  
472 (EuropeW\_13500BP\_8000BP) supplemented with marginal contribution from local Danish groups  
473 in some individuals (Extended Data Fig. 7D; Supplementary Note 3f). We estimated the timing of  
474 the admixture using the linkage-disequilibrium-based method DATES<sup>48</sup> at ~6,000 BP. Both lines of  
475 evidence thus suggest that a significant part of the hunter-gatherer admixture observed in Danish  
476 Neolithic individuals occurred already before the arrival of the incoming Neolithic people in the  
477 region (Extended Data Fig. 7), and further imply Central Europe as a key region in the resurgence  
478 of HG ancestry. Interestingly, the genomes of two ~5,000-year-old Danish male individuals  
479 (NEO33, NEO898) were entirely composed of Swedish hunter-gatherer ancestry, and formed a  
480 cluster with Pitted Ware Culture (PWC) individuals from Ajvide on the Baltic island of Gotland  
481 (Sweden)<sup>49–51</sup>. Of the two individuals, NEO033 also displays an outlier Sr-signature (Fig. 4),  
482 potentially suggesting a non-local origin matching his unusual ancestry. Overall, our results  
483 demonstrate direct contact across the Kattegat and Öresund during Neolithic times (Extended Data  
484 Fig. 3, 4), in line with archaeological finds from Zealand (east Denmark) showing cultural affinities  
485 to PWC on the Swedish west coast<sup>52–55</sup>.

486  
487 Further, we find evidence for regional stratification in early Neolithic farmer ancestries in  
488 subsequent Neolithic groups. Specifically, southern European early farmers appear to have provided  
489 major genetic ancestry to mid- and late Neolithic groups in Western Europe, while central European  
490 early farmer ancestry is mainly observed in subsequent Neolithic groups in eastern Europe and  
491 Scandinavia (Extended Data Fig. 7D-F). These results are consistent with distinct migratory routes  
492 of expanding farmer populations as previously suggested<sup>8</sup>. For example, similarities in material  
493 culture and flint mining activities could suggest that the first farmers in South Scandinavia  
494 originated from or had close social relations with the central European Michelsberg Culture<sup>56</sup>.

495  
496 The second continental-wide and CWC-mediated transition from Neolithic farmer ancestry to  
497 Steppe-related ancestry was found to differ markedly between geographic regions. The contribution  
498 of local Neolithic farmer ancestry to the incoming groups was high in eastern, western and southern  
499 Europe, reaching >50% on the Iberian Peninsula (“postNeol” set; Extended Data Fig. 4, 6B, C)<sup>34</sup>.  
500 Scandinavia, however, portrays a dramatically different picture, with a near-complete replacement  
501 of the local Neolithic farmer population inferred across all sampled individuals (Extended Data Fig.  
502 7B, C). Following the second transition, Neolithic Anatolian-related farmer ancestry remains in  
503 Scandinavia, but the source is now different. It can be modelled as deriving almost exclusively from  
504 a genetic cluster associated with the Late Neolithic Globular Amphora Culture (GAC)  
505 (Poland\_5000BP\_4700BP; Extended Data Fig. 4). Strikingly, after the Steppe-related ancestry was  
506 first introduced into Europe (Steppe\_5000BP\_4300BP), it expanded together with GAC-related  
507 ancestry across all sampled European regions (Extended Data Fig. 7I). This suggests that the spread  
508 of steppe-related ancestry throughout Europe was predominantly mediated through groups that were  
509 already admixed with GAC-related farmer groups of the eastern European plains. This finding has  
510 major implications for understanding the emergence of the CWC. A stylistic connection from GAC  
511 ceramics to CWC ceramics has long been suggested, including the use of amphora-shaped vessels  
512 and the development of cord decoration patterns<sup>57</sup>. Moreover, shortly prior to the emergence of the  
513 earliest CWC groups, eastern GAC and western Yamnaya groups exchanged cultural elements in  
514 the forest-steppe transition zone northwest of the Black Sea, where GAC ceramic amphorae and  
515 flint axes were included in Yamnaya burials, and the typical Yamnaya use of ochre was included in  
516 GAC burials<sup>58</sup>, indicating close interaction between the groups. Previous ancient genomic data from  
517 a few individuals suggested that this was limited to cultural influences and not population  
518 admixture<sup>59</sup>. However, in the light of our new genetic evidence it appears that this zone, and

519 possibly other similar zones of contact between GAC and Yamnaya (or other closely-related  
520 steppe/forest-steppe groups) were key in the formation of the CWC through which steppe-related  
521 ancestry and GAC-related ancestry co-dispersed far towards the west and the north<sup>cf. 60</sup>. This  
522 resulted in regionally diverse situations of interaction and admixture<sup>61,62</sup> but a significant part of the  
523 CWC dispersal happened through corridors of cultural and demic transmission which had been  
524 established by the GAC during the preceding period<sup>63,64</sup>.

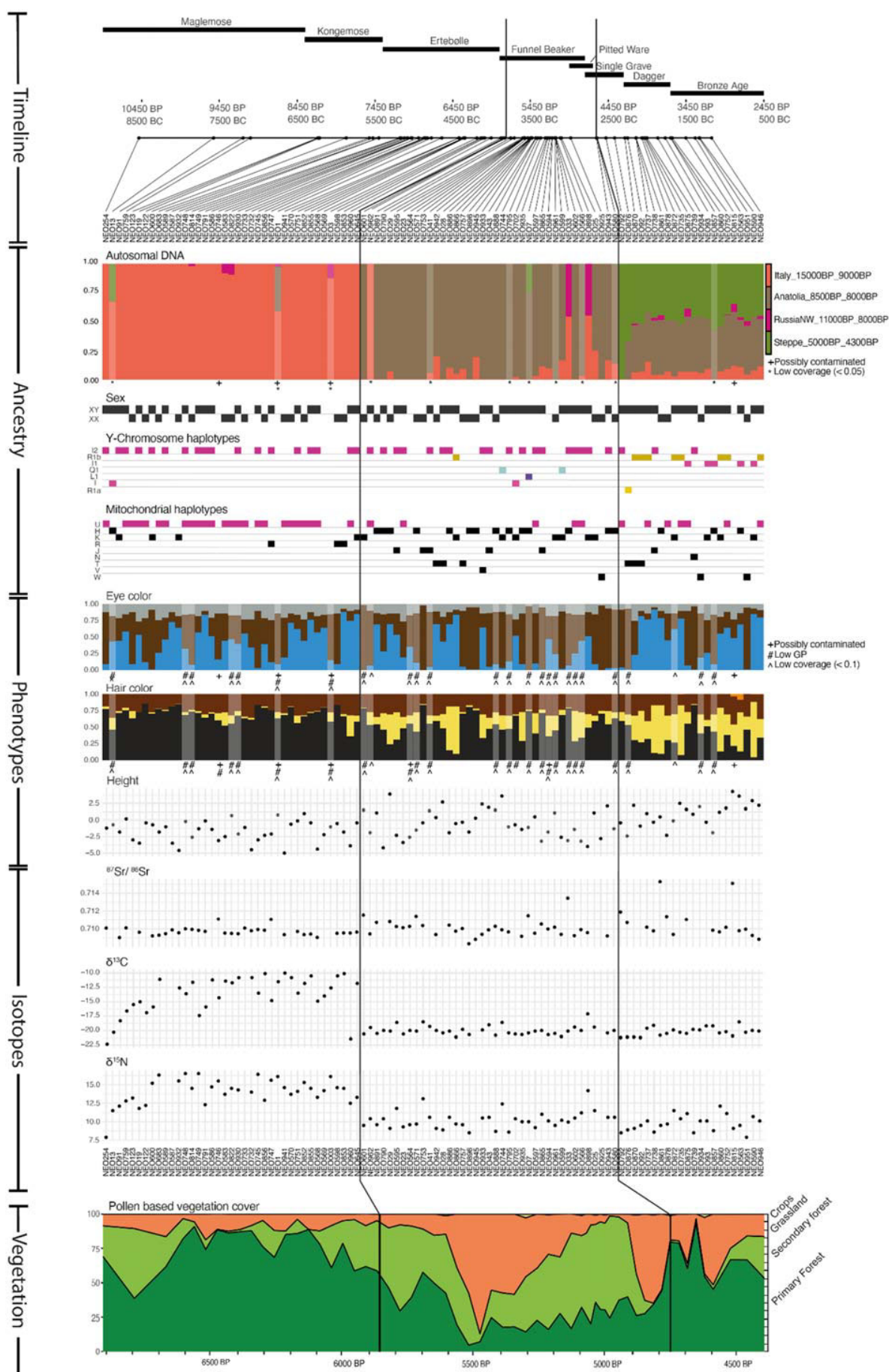
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527 *Fine-scale structure and multiproxy analysis of Danish transect*

528 We present a detailed and continuous sequence of multiproxy data from Denmark, from the Early  
529 Mesolithic Maglemose, via the Kongemose and Late Mesolithic Ertebølle epochs, the Early and  
530 Middle Neolithic Funnel Beaker Culture and the Single Grave Culture, to Late Neolithic and  
531 Bronze Age individuals (Fig. 4). To integrate multiproxy data from as many skeletons as possible  
532 we made use of non-imputed data for the admixture analyses (Supplementary Note S3d) which  
533 were not restricted to the >0.1X coverage cut-off used elsewhere. This provided genetic profiles  
534 from 100 Danish individuals (Fig 4), spanning c. 7,300 years from the earliest known skeleton in  
535 Denmark (the Mesolithic “Koelbjerg Man” (NEO254, 10,648-10,282 cal. BP, 95% probability  
536 interval) and formerly known as the “Koelbjerg Woman”<sup>65</sup>), to a Bronze Age skeleton from Hove Å  
537 (NEO946) dated to 3322-2967 cal. BP (95%). Two temporal shifts in genomic admixture  
538 proportions confirm the major population genetic turnovers (Fig. 4) that was inferred from imputed  
539 data (Fig. 3). The multiproxy evidence, however, unveils the dramatic concomitant changes in all  
540 investigated phenotypic, environmental and dietary parameters (Fig. 4).

541



543

544 **Fig 4. Environmental, dietary, phenotypic and ancestry shifts in Denmark through time.** Two dramatic population  
545 turnovers are evident from chronologically-sorted multiproxy data representing 100 Danish Stone Age and early Bronze  
546 Age skeletons sequenced in this study. The figure shows concomitant changes in several investigated parameters  
547 including (from the top) admixture proportions from non-imputed autosomal genome-wide data, Y-chromosomal and  
548 mitochondrial haplogroups, genetic phenotype predictions (based on imputed data) as well as  $^{87}\text{Sr}/^{86}\text{Sr}$  and  $\delta^{13}\text{C}$  and  
549  $\delta^{15}\text{N}$  isotope data as possible proxies for mobility and diet, respectively. Predicted height values represent differences  
550 (in cm) from the average height of the present-day Danish population, based on genotypes at 310 height-associated loci  
551 (Supplementary Note 4f). Probabilities for the indicated natural eye and hair colours are based on genotypes at 18  
552 pigmentation-associated loci (Supplementary Note 4f) with grey denoting probability of intermediate eye colour  
553 (including grey, green and hazel). Lower panel shows changes in vegetation as predicted from pollen analyses at Lake  
554 Højby in Zealand (Supplementary Note 12). Black vertical lines mark the first presence of Anatolian farmer ancestry  
555 and Steppe-related ancestry, respectively.

556

557

558 During the Danish Mesolithic, individuals from the Maglemose, Kongemose and Ertebølle cultures  
559 displayed a remarkable genetic homogeneity across a 5,000 year transect deriving their ancestry  
560 almost exclusively from a southern European source (source: Italy\_15000BP\_9000BP) that later  
561 predominates in western Europe (Fig. 2). These cultural transitions occurred in genetic continuity,  
562 apparent in both autosomal and uniparental markers, which rules out demic diffusion and supports  
563 the long-held assumption of a continuum of culture and population<sup>e.g. 66–68</sup>. Genetic predictions  
564 indicate blue eye pigmentation with high probability in several individuals throughout the duration  
565 of the Mesolithic (Supplementary Note 4f), consistent with previous findings<sup>11,20,45</sup>. In contrast,  
566 none of the analysed Mesolithic individuals displayed high probability of light hair pigmentation.  
567 Height predictions for Mesolithic individuals generally suggest slightly lower or perhaps less  
568 variable genetic values than in the succeeding Neolithic period. However, we caution that the  
569 relatively large genetic distance to modern individuals included in the GWAS panel make these  
570 scores poorly applicable to Mesolithic individuals (Supplementary Note 4c) and are dependent on  
571 the choice of GWAS filters used. Unfortunately, only a fraction of the 100 Danish skeletons  
572 included were suitable for stature estimation by actual measurement, why these values are not  
573 reported.

574

575 Stable isotope  $\delta^{13}\text{C}$  values in collagen inform on the proportion of marine versus terrestrial protein,  
576 while  $\delta^{15}\text{N}$  values reflect the trophic level of protein sources<sup>69,70</sup>. Both the Koelbjerg Man and the  
577 second earliest human known from Denmark, (Tømmerupgårds Mose – not part of the present  
578 study; see<sup>71</sup>) showed more depleted dietary isotopic values, representing a lifestyle of inland hunter-  
579 fisher-gatherers of the early Mesolithic forest. A second group consisted of coastal fisher-hunter-  
580 gatherers dating to the late half of the Maglemose epoch onwards (Supplementary Figs. S10.1 and  
581 S10.2). During this period global sea-level rise gradually changed the landscape of present-day  
582 Denmark from an interior part of the European continent to an archipelago, where all human groups  
583 had ample access to coastal resources within their annual territories. Increased  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values  
584 imply that from the late Maglemose marine foods gradually increased in importance, to form the  
585 major supply of proteins in the final Ertebølle period<sup>71,cf. 72</sup>. Interestingly, rather stable  $^{87}\text{Sr}/^{86}\text{Sr}$   
586 isotope ratios throughout the Mesolithic indicate limited mobility, in agreement with the evidence  
587 for genetic continuity reported here and modelled in previous work<sup>73,74 Fig. 3</sup>, and/or dietary sources  
588 from homogeneous environments.

589

590 The arrival of Neolithic farmer-related ancestry at c. 5,900 BP in Denmark resulted in a population  
591 replacement with very limited genetic contribution from the local hunter-gatherers. The shift is  
592 abrupt and brings changes in all the measured parameters. This is a clear case of demic diffusion,  
593 which settles a long-standing debate concerning the neolithisation process in Denmark<sup>15,56,75,76</sup>, at  
594 least at a broader population level. The continuing use of coastal kitchen middens well into the

595 Neolithic<sup>77,78</sup> remains, however, an enigma, although this may represent sites where local remnants  
596 of Mesolithic groups survived in partly acculturated form, or it could be middens taken over by the  
597 newcomers. Concomitant shifts in both autosomal and uniparental genetic markers show that the  
598 migration by incoming farmers was not clearly sex-biased but more likely involved nuclear family  
599 units. Diet shifted abruptly to terrestrial sources evidenced by  $\delta^{13}\text{C}$  values around -20 ‰ and  $\delta^{15}\text{N}$   
600 values around 10 ‰ in line with archaeological evidence that domesticated crops and animals were  
601 now providing the main supply of proteins (Supplementary Note 6). Isotope values remained stable  
602 at these levels throughout the following periods, although with somewhat greater variation after c.  
603 4,500 BP. However, five Neolithic and Early Bronze Age individuals have  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values  
604 indicating intake of high trophic marine food. This is most pronouncedly seen for NEO898  
605 (Svinninge Vejle) who was one of the two aforementioned Danish Neolithic individuals displaying  
606 typical Swedish PWC hunter-gatherer ancestry. A higher variability in  $^{87}\text{Sr}/^{86}\text{Sr}$  values can be seen  
607 with the start of the Neolithic and this continues in the later periods, which suggests that the  
608 Neolithic farmers in Denmark consumed food from more diverse landscapes and/or they were more  
609 mobile than the preceding hunter-gatherers (Supplementary Note 11). The Neolithic transition also  
610 marks a considerable rise in frequency of major effect alleles associated with light hair  
611 pigmentation<sup>79</sup>, whereas polygenic score predictions for height are generally low throughout the  
612 first millennium of the Neolithic (Funnel Beaker epoch), echoing previous findings based on a  
613 smaller set of individuals<sup>45,80</sup>.

614  
615 We do not know how the Mesolithic Ertebølle population disappeared. Some may have been  
616 isolated in small geographical pockets of brief existence and/or adapted to a Neolithic lifestyle but  
617 without contributing much genetic ancestry to subsequent generations. The most recent individual  
618 in our Danish dataset with Mesolithic WHG ancestry is “Dragsholm Man” (NEO962), dated to  
619 5,947-5,664 cal. BP (95%) and archaeologically assigned to the Neolithic Funnel Beaker farming  
620 culture based on his grave goods<sup>81,82</sup>. Our data confirms a typical Neolithic diet matching the  
621 cultural affinity but contrasting his WHG ancestry. Thus, Dragsholm Man represents a local person  
622 of Mesolithic ancestry who lived in the short Mesolithic-Neolithic transition period and adopted a  
623 Neolithic culture and diet. A similar case of very late Mesolithic WHG ancestry in Denmark was  
624 observed when analysing human DNA obtained from a piece of chewed birch pitch dated to 5,858–  
625 5,661 cal. BP (95%)<sup>83</sup>.

626  
627 The earliest example of Anatolian Neolithic ancestry in our Danish dataset is observed in a bog  
628 skeleton of a female from Viksø Mose (NEO601) dated to 5,896-5,718 cal. BP (95%) (and hence  
629 potentially contemporaneous with Dragsholm Man) whereas the most recent Danish individual  
630 showing Anatolian ancestry without any Steppe-related ancestry is NEO943 from Stenderup Hage,  
631 dated to 4,818-4,415 cal. BP (95%). Using Bayesian modelling we estimate the duration between  
632 the first appearance of Anatolian ancestry to the first appearance of Steppe-related ancestry in  
633 Denmark to be between 876 and 1100 years (95% probability interval, Supplementary Note 9)  
634 indicating that the typical Neolithic ancestry was dominant for less than 50 generations in Denmark.  
635 From this point onwards the steppe-ancestry was introduced, signalling the rise of the late Neolithic  
636 Corded Ware derived cultures in Denmark (i.e. Single Grave Culture), followed by the later  
637 Neolithic Dagger epoch and Bronze Age cultures. While this introduced a major new component in  
638 the Danish gene pool, it was not accompanied by apparent shifts in diet. Our complex trait  
639 predictions indicate an increase in “genetic height” occurring concomitant with the introduction of  
640 Steppe-related ancestry, which is consistent with Steppe individuals (e.g., Yamnaya) being  
641 genetically taller on average<sup>45</sup> and with previous results from other European regions<sup>80,84</sup>.

642  
643 These major population turnovers were accompanied by significant environmental changes, as  
644 apparent from high-resolution pollen diagrams from Lake Højby in Northwest Zealand



645 reconstructed using the Landscape Reconstruction Algorithm (LRA<sup>85</sup> (Supplementary Note 8).  
646 While the LRA has previously been applied at low temporal resolution regional scale e.g. <sup>86,87</sup>, and at  
647 local scale to Iron Age and later pollen diagrams e.g. <sup>88,89</sup>, this is the first time this quantitative  
648 method is applied at local scale to a pollen record spanning the Mesolithic and Neolithic periods in  
649 Denmark. Comparison with existing pollen records show that the land cover changes demonstrated  
650 here reflect the general vegetation development in eastern Denmark, while the vegetation on the  
651 sandier soils of western Jutland maintains a more open character throughout the sequence  
652 (Supplementary Note 12). We find that during the Mesolithic (i.e. before c. 6,000 BP) the  
653 vegetation was dominated by primary forest trees (*Tilia*, *Ulmus*, *Quercus*, *Fraxinus*, *Alnus* etc.).  
654 The forest composition changed towards more secondary, early successional trees (*Betula* and then  
655 *Corylus*) in the earliest Neolithic, but only a minor change in the relationship between forest and  
656 open land is recorded. From c. 5,650 BP deforestation intensified, resulting in a very open  
657 grassland-dominated landscape. This open phase was short-lived, and secondary forest expanded  
658 from 5,500 to 5,000 BP, until another episode of forest clearance gave rise to an open landscape  
659 during the last part of the Funnel Beaker epoch. We thus conclude that the agriculture practice was  
660 characterised by repeated clearing of the forest with fire, followed by regrowth. This strategy  
661 changed with the onset of the Single Grave Culture, when the forest increased again, but this time  
662 dominated by primary forest trees, especially *Tilia* and *Ulmus*. This reflects the development of a  
663 more permanent division of the landscape into open grazing areas and forests. In contrast, in  
664 western Jutland this phase was characterised by large-scale opening of the landscape, presumably as  
665 a result of human impact aimed at creating pastureland<sup>90</sup>.

666  
667 Finally, we investigated the fine-scale genetic structure in southern Scandinavia after the  
668 introduction of Steppe-related ancestry using a temporal transect of 38 Late Neolithic and Early  
669 Bronze Age Danish and southern Swedish individuals. Although the overall population genomic  
670 signatures suggest genetic stability, patterns of pairwise IBD-sharing and Y-chromosome  
671 haplogroup distributions indicate at least three distinct ancestry phases during a ~1,000-year time  
672 span: i) An early stage between ~4,600 BP and 4,300 BP, where Scandinavians cluster with early  
673 CWC individuals from Eastern Europe, rich in Steppe-related ancestry and males with an R1a Y-  
674 chromosomal haplotype (Extended Data Fig. 8A, B); ii) an intermediate stage until c. 3,800 BP,  
675 where they cluster with central and western Europeans dominated by males with distinct sub-  
676 lineages of R1b-L51 (Extended Data Fig. 8C, D; Supplementary Note 3b) and includes Danish  
677 individuals from Borreby (NEO735, 737) and Madesø (NEO752) with distinct cranial features  
678 (Supplementary Note 6); and iii) a final stage from c. 3,800 BP onwards, where a distinct cluster of  
679 Scandinavian individuals dominated by males with I1 Y-haplogroups appears (Extended Data Fig.  
680 8E). Using individuals associated with this cluster (Scandinavia\_4000BP\_3000BP) as sources in  
681 supervised ancestry modelling (see “postBA”, Extended Data Fig. 4), we find that it forms the  
682 predominant source for later Iron- and Viking Age Scandinavians, as well as ancient European  
683 groups outside Scandinavia who have a documented Scandinavian or Germanic association (e.g.,  
684 Anglo-Saxons, Goths; Extended Data Fig. 4). Y-chromosome haplogroup I1 is one of the dominant  
685 haplogroups in present-day Scandinavians, and we document its earliest occurrence in a ~4,000-  
686 year-old individual from Falköping in southern Sweden (NEO220). The rapid expansion of this  
687 haplogroup and associated genome-wide ancestry in the early Nordic Bronze Age indicates a  
688 considerable reproductive advantage of individuals associated with this cluster over the preceding  
689 groups across large parts of Scandinavia.

690  
691

692 *Hunter-gatherer resilience east of the Urals*

693 In contrast to the significant number of ancient hunter-gatherer genomes from western Eurasia  
694 studied to date, genomic data from hunter-gatherers east of the Urals remain sparse. These regions  
695 are characterised by an early introduction of pottery from areas further east and are inhabited by  
696 complex hunter-gatherer-fisher societies with permanent and sometimes fortified settlements  
697 (Supplementary Note 5; <sup>91</sup>).

698  
699 Here, we substantially expand the knowledge on ancient Stone Age populations of this region by  
700 reporting new genomic data from 38 individuals, 28 of which date to pottery-associated hunter-  
701 gatherer contexts e.g. <sup>92</sup> between 8,300-5,000 BP (Supplementary Table II). The majority of these  
702 genomes form a previously only sparsely sampled <sup>48,93</sup> “Neolithic Steppe” cline spanning the  
703 Siberian Forest Steppe zones of the Irtysh, Ishim, Ob, and Yenisei River basins to the Lake Baikal  
704 region (Fig. 1C; Extended Data Fig. 2A, 3E). Supervised admixture modelling (using the “deep” set  
705 of ancestry sources) revealed contributions from three major sources in these hunter gatherers from  
706 east of Urals: early West Siberian hunter-gatherer ancestry (SteppeC\_8300BP\_7000BP) dominated  
707 in the western Forest Steppe; Northeast Asian hunter-gatherer ancestry (Amur\_7500BP) was  
708 highest at Lake Baikal; and Paleosiberian ancestry (SiberiaNE\_9800BP) was observed in a cline of  
709 decreasing proportions from northern Lake Baikal westwards across the Forest Steppe (Extended  
710 Data Fig. 4, 9). <sup>93</sup>

711  
712 We used these Neolithic hunter-gatherer clusters (“postNeol” ancestry source set, Extended Data  
713 Fig. 4) as putative source groups in more proximal admixture modelling to investigate the  
714 spatiotemporal dynamics of ancestry compositions across the Steppe and Lake Baikal after the  
715 Neolithic period. We replicate previously reported evidence for a genetic shift towards higher  
716 Forest Steppe hunter-gatherer ancestry (SteppeCE\_7000BP\_3600BP) in late Neolithic and early  
717 Bronze Age individuals (LNBA) at Lake Baikal <sup>93,94</sup>. However, ancestry related to this cluster is  
718 already observed at ~7,000 BP in herein-reported Neolithic hunter-gatherer individuals both at Lake  
719 Baikal (NEO199, NEO200), and along the Angara river to the north (NEO843). Both male  
720 individuals at Lake Baikal belonged to Y-chromosome haplogroup Q1, characteristic of the later  
721 LNBA groups in the same region. (Extended Data Fig. 3, 6A). Together with an estimated date of  
722 admixture of ~6,000 BP for the LNBA groups, these results suggest gene flow between hunter-  
723 gatherers of Lake Baikal and the south Siberian forest steppe regions already during the early  
724 Neolithic. This is consistent with archaeological interpretations of contact. In this region, bifacially  
725 flaked tools first appeared near Baikal <sup>95</sup> from where the technique spread far to the west. We find  
726 its reminiscences in Late Neolithic archaeological complexes (Shiderty 3, Borly, Sharbakty 1, Ust-  
727 Narym, etc.) in Northern and Eastern Kazakhstan, around 6,500-6,000 BP <sup>96,97</sup>. Our herein-reported  
728 genomes also shed light on the genetic origins of the early Bronze Age Okunevo culture in the  
729 Minusinsk Basin in Southern Siberia. In contrast to previous results, we find no evidence for Lake  
730 Baikal hunter-gatherer ancestry in the Okunevo <sup>93,94</sup>, suggesting that they instead originate from a  
731 three-way mixture of two different genetic clusters of Siberian forest steppe hunter-gatherers and  
732 Steppe-related ancestry (Extended Data Fig. 4D). We date the admixture with Steppe-related  
733 ancestry to ~4,600 BP, consistent with gene flow from peoples of the Afanasievo culture that  
734 existed near Altai and Minusinsk Basin during the early eastwards’ expansion of Yamnaya-related  
735 groups <sup>20,94</sup>.

736  
737 From around 3,700 BP, individuals across the Steppe and Lake Baikal regions display markedly  
738 different ancestry profiles (Fig. 3; Extended Data Fig. 4D, 9). We document a sharp increase in  
739 non-local ancestries, with only limited ancestry contributions from local hunter-gatherers. The early  
740 stages of this transition are characterised by influx of Yamnaya-related ancestry, which decays over

741 time from its peak of ~70% in the earliest individuals. Similar to the dynamics in western Eurasia,  
742 Yamnaya-related ancestry is here correlated with late Neolithic GAC-related farmer ancestry  
743 (Poland\_5000BP\_4700BP; Extended Data Fig. 9G), recapitulating the previously documented  
744 eastward expansion of admixed Western Steppe pastoralists from the Sintashta and Andronovo  
745 complexes during the Bronze Age<sup>20,48,98</sup>. However, GAC-related ancestry is notably absent in  
746 individuals of the Okunevo culture, providing further support for two distinct eastward migrations  
747 of Western Steppe pastoralists during the early (Yamnaya) and later (Sintashta, Andronovo) Bronze  
748 Age. The later stages of the transition are characterised by increasing Central Asian  
749 (Turkmenistan\_7000 BP\_5000BP) and Northeast Asian-related (Amur\_7500BP) ancestry  
750 components (Extended Data Fig. 9G). Together, these results show that deeply structured hunter-  
751 gatherer ancestry dominated the eastern Eurasian Steppe substantially longer than in western  
752 Eurasia, before successive waves of population expansions swept across the Steppe within the last  
753 4,000 years, including a large-scale introduction of domesticated horse lineages concomitant with  
754 new equestrian equipment and spoke-wheeled chariotry<sup>20,48,98,99</sup>.  
755

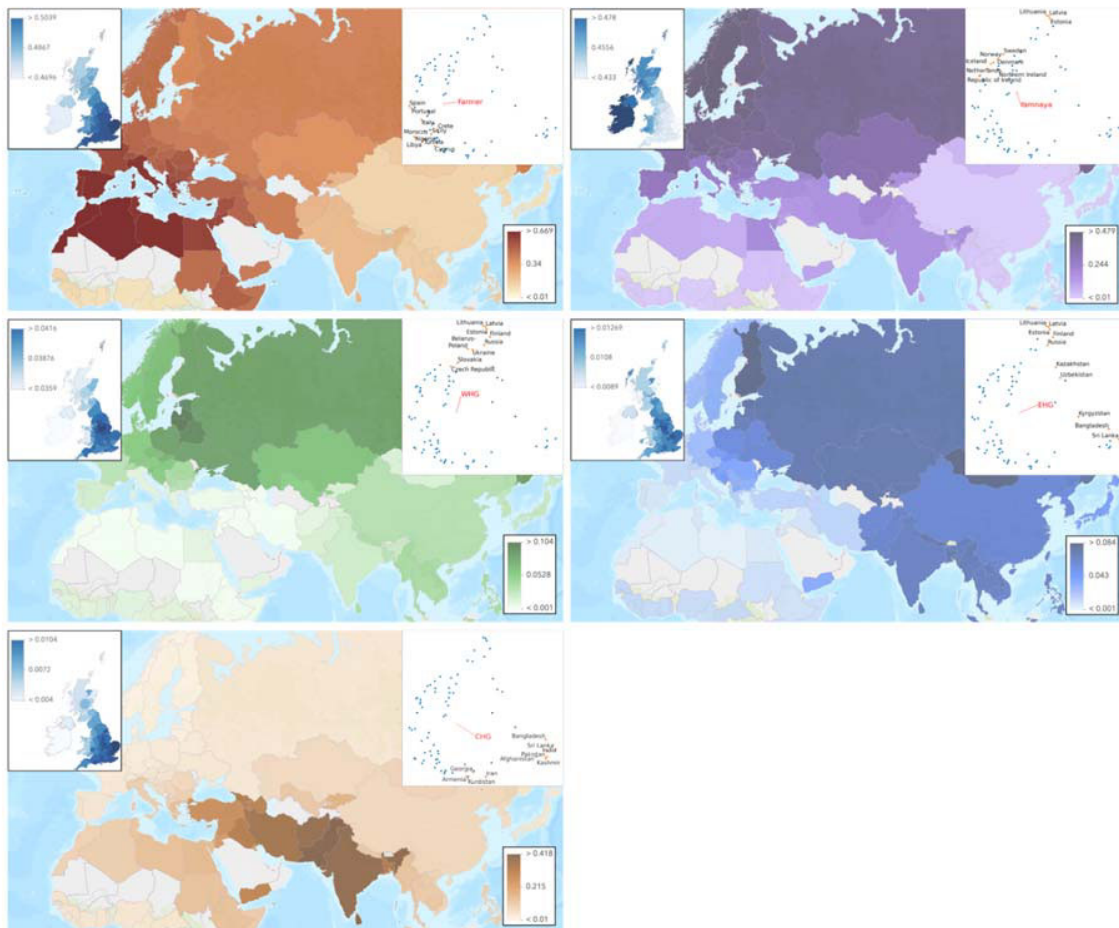
### 756 *Genetic legacy of Stone Age Europeans*

757 To investigate the distribution of Stone Age and Early Bronze Age ancestry components in modern  
758 populations, we used ChromoPainter<sup>100</sup> to “paint” the chromosomes of individuals in the UK  
759 Biobank (<https://www.ukbiobank.ac.uk>) using a panel of 10 ancient donor populations  
760 (Supplementary Note 3h). Painting was done following the pipeline of Margaryan et al.<sup>101</sup> based on  
761 GLOBETROTTER<sup>102</sup>, and admixture proportions were estimated using Non-Negative Least  
762 squares. Haplotypes in the modern genomes are assigned to the genetically closest ancient  
763 population as measured by meiosis events, which favours more recent matches in time. Therefore,  
764 ancestry proportions assigned to the oldest groups (e.g. WHG) should be interpreted as an excess of  
765 this ancestry, which cannot be explained by simply travelling through more recent ancient  
766 populations up to present times.  
767

768 First, we selected non-British individuals from the UK Biobank if their country of birth was  
769 European, African, or Asian. Because many of these individuals are admixed or British, we set up a  
770 pipeline (Supplementary Note 3g) to select individuals of a typical ancestral background for each  
771 country. This resulted in 24,511 individuals from 126 countries, who were then chromosome  
772 painted to assess the average admixture proportions for each ancestry per country.  
773

774 The various hunter-gatherer ancestries are not homogeneously distributed amongst modern  
775 populations (Fig. 5). WHG-related ancestry is highest in present-day individuals from the Baltic  
776 States, Belarus, Poland, and Russia; EHG-related ancestry is highest in Mongolia, Finland, Estonia  
777 and Central Asia; and CHG-related ancestry is maximised in countries east of the Caucasus, in  
778 Pakistan, India, Afghanistan and Iran, in accordance with previous results<sup>103</sup>. The CHG-related  
779 ancestry likely reflects both Caucasus hunter-gatherer and Iranian Neolithic signals, explaining the  
780 relatively high levels in south Asia<sup>104</sup>. Consistent with expectations<sup>105,106</sup>, Neolithic Anatolian-  
781 related farmer ancestry is concentrated around the Mediterranean basin, with high levels in southern  
782 Europe, the Near East, and North Africa, including the Horn of Africa, but is less frequent in  
783 Northern Europe. This is in direct contrast to the Steppe-related ancestry, which is found in high  
784 levels in northern Europe, peaking in Ireland, Iceland, Norway, and Sweden, but decreases further  
785 south. There is also evidence for its spread into southern Asia. Overall, these results refine global  
786 patterns of spatial distributions of ancient ancestries amongst modern populations.  
787

788 The availability of a large number of modern genomes (n=408,884) from self-identified “white”  
789 British individuals who share similar PCA backgrounds <sup>107</sup> allowed us to further examine the  
790 distribution of ancient ancestries at high resolution in Britain (Supplementary Note 3h). Although  
791 regional ancestry distributions differ by only a few percent, we find clear evidence of geographical  
792 heterogeneity across the United Kingdom as visualised by assigning individuals to their birth  
793 county and averaging ancestry proportions per county (Fig. 5, inset boxes). The proportion of  
794 Neolithic farmer ancestry is highest in southern and eastern England today and lower in Scotland,  
795 Wales, and Cornwall. Steppe-related ancestry is inversely distributed, peaking in the Outer  
796 Hebrides and Ireland, a pattern only previously described for Scotland <sup>108</sup>. This regional pattern was  
797 already evident in the Pre-Roman Iron Age and persists to the present day even though immigrating  
798 Anglo-Saxons had relatively less Neolithic farmer ancestry than the Iron-Age population of  
799 southwest Briton (Extended Data Fig. 4). Although this Neolithic farmer/steppe-related dichotomy  
800 mirrors the modern ‘Anglo-Saxon’/‘Celtic’ ethnic divide, its origins are older, resulting from  
801 continuous migration from a continental population relatively enhanced in Neolithic farmer  
802 ancestry, starting as early as the Late Bronze Age <sup>109</sup>. By measuring haplotypes from these  
803 ancestries in modern individuals, we are able to show that these patterns differentiate Wales and  
804 Cornwall as well as Scotland from England. We also found higher levels of WHG-related ancestry  
805 in central and Northern England. These results demonstrate clear ancestry differences within an  
806 ‘ethnic group’ (white British) traditionally considered relatively homogenous, which highlights the  
807 need to account for subtle population structure when using resources such as the UK Biobank  
808 genomes.  
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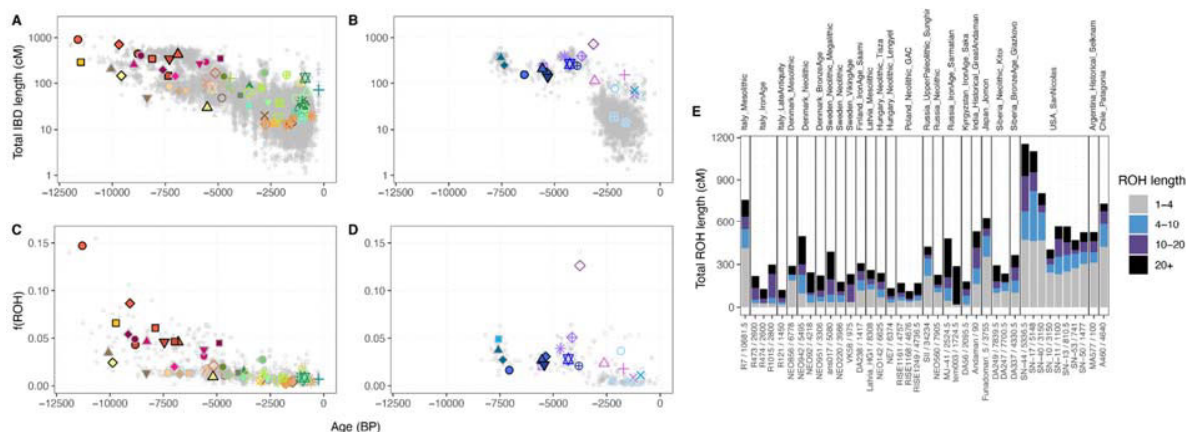
**Fig 5. The genetic legacy of Stone Age ancestry in modern populations.**

From top left clockwise: Neolithic Farmer, Yamnaya, Caucasus hunter-gatherer, Eastern hunter-gatherer, Western hunter-gatherer. Panels show average admixture proportion in modern individuals per country estimated using NNLS (large maps), average per county within the UK (top left insert), and PCA (PC2 vs PC1) of admixture proportions, with the top 10 highest countries by admixture fraction labelled and PCA loadings for that ancestry.

### 817 *Sociocultural insights*

818 We used patterns of pairwise IBD sharing between individuals and runs of homozygosity (ROH)  
819 within individuals (measured as the fraction of the genome within a run of homozygosity  $f(\text{ROH})$ )  
820 to examine our data for temporal shifts in relatedness within genetic clusters. Both measures show  
821 clear trends of a reduction of within-cluster relatedness over time, in both western and eastern  
822 Eurasia (Fig. 6). This pattern is consistent with a scenario of increasing effective population sizes  
823 during this period<sup>110</sup>. Nevertheless, we observe notable differences in temporal relatedness patterns  
824 between western and eastern Eurasia, mirroring the wider difference in population dynamics  
825 discussed above. In the west, within-group relatedness changes substantially during the Neolithic  
826 transition (~9,000 to ~6,000 BP), where clusters of Neolithic farmer-associated individuals show  
827 overall reduced IBD sharing and  $f(\text{ROH})$  compared to clusters of HG-associated individuals (Fig.  
828 6A,C). In the east, genetic relatedness remains high until ~4,000 BP, consistent with a much longer  
829 persistence of smaller localised hunter-gatherer groups (Fig. 6B,D).  
830

831 Next, we examined the data for evidence of recent parental relatedness, by identifying individuals  
 832 harbouring a large fraction of their genomes (> 50cM) in long (>20cM) ROH segments<sup>111</sup>. We only  
 833 detect 39 such individuals out of a total sample of 1,540 imputed ancient genomes (Fig. 6E), in line  
 834 with recent results indicating that close kin mating was not common in human prehistory  
 835 <sup>41,103,111,112</sup>. With the exception of eight ancient American individuals from the San Nicolas Islands  
 836 in California<sup>113</sup>, no obviously discernible spatiotemporal or cultural clustering was observed among  
 837 the individuals with recent parental relatedness. Interestingly, an ~1,700-year-old Sarmatian  
 838 individual from Temyaysovo (tem003)<sup>114</sup> was found homozygous for almost the entirety of  
 839 chromosome 2, but without evidence of ROHs elsewhere in the genome, suggesting an ancient case  
 840 of uniparental disomy. Among several noteworthy familial relationships (see Supplementary Fig.  
 841 S3c.2), we report a Mesolithic father/son burial at Ertebølle (NEO568/NEO569), as well as a  
 842 Mesolithic mother/daughter burial at Dragsholm (NEO732/NEO733).  
 843  
 844



845 **Fig 6. Patterns of co-ancestry.** (A)-(D) Panels show within-cluster genetic relatedness over time, measured either as  
 846 the total length of genomic segments shared IBD between individuals (A, B) or the proportion of individual genomes  
 847 found in a run of homozygosity f(ROH) (C,D). Results for both measures are shown separately for individuals from  
 848 western (A, C) or eastern Eurasia (B, D). Small grey dots indicate estimates for individual pairs (A, B) or individuals  
 849 (C, D), with larger coloured symbols indicating median values within genetic clusters. (E) Distribution of ROH lengths  
 850 for 39 individuals with evidence for recent parental relatedness (>50 cM total in ROHs > 20 cM).  
 851  
 852  
 853

#### 854 *Pathogenic structural variants in ancient vs. modern-day humans*

855  
 856 Rare, recurrent copy-number variants (CNVs) are known to cause neurodevelopmental disorders  
 857 and are associated with a range of psychiatric and physical traits with variable expressivity and  
 858 incomplete penetrance<sup>115,116</sup>. To understand the prevalence of pathogenic structural variants over  
 859 time we examined 50 genomic regions susceptible to recurrent CNV, known to be the most  
 860 prevalent drivers of human developmental pathologies<sup>117</sup>. The analysis included 1442 ancient  
 861 imputed genomes passing quality control for CNV analysis (Supplementary Note 4i) and 1093  
 862 modern human genomes for comparison<sup>118,119</sup>. We identified CNVs in ancient individuals at ten  
 863 loci using a read-depth based approach and digital Comparative Genomic Hybridization<sup>120</sup>  
 864 (Supplementary Table S4i.1; Supplementary Figs. S4i.1-S4i.20). Although most of the observed  
 865 CNVs (including duplications at 15q11.2 and *CHRNA7*, and CNVs spanning parts of the TAR locus  
 866 and 22q11.2 distal) have not been unambiguously associated with disease in large studies, the  
 867 identified CNVs include deletions and duplications that have been associated with developmental  
 868 delay, dysmorphic features, and neuropsychiatric abnormalities such as autism (most notably at  
 869 1q21.1, 3q29, 16p12.1 and the DiGeorge/VCFS locus, but also deletions at 15q11.2 and

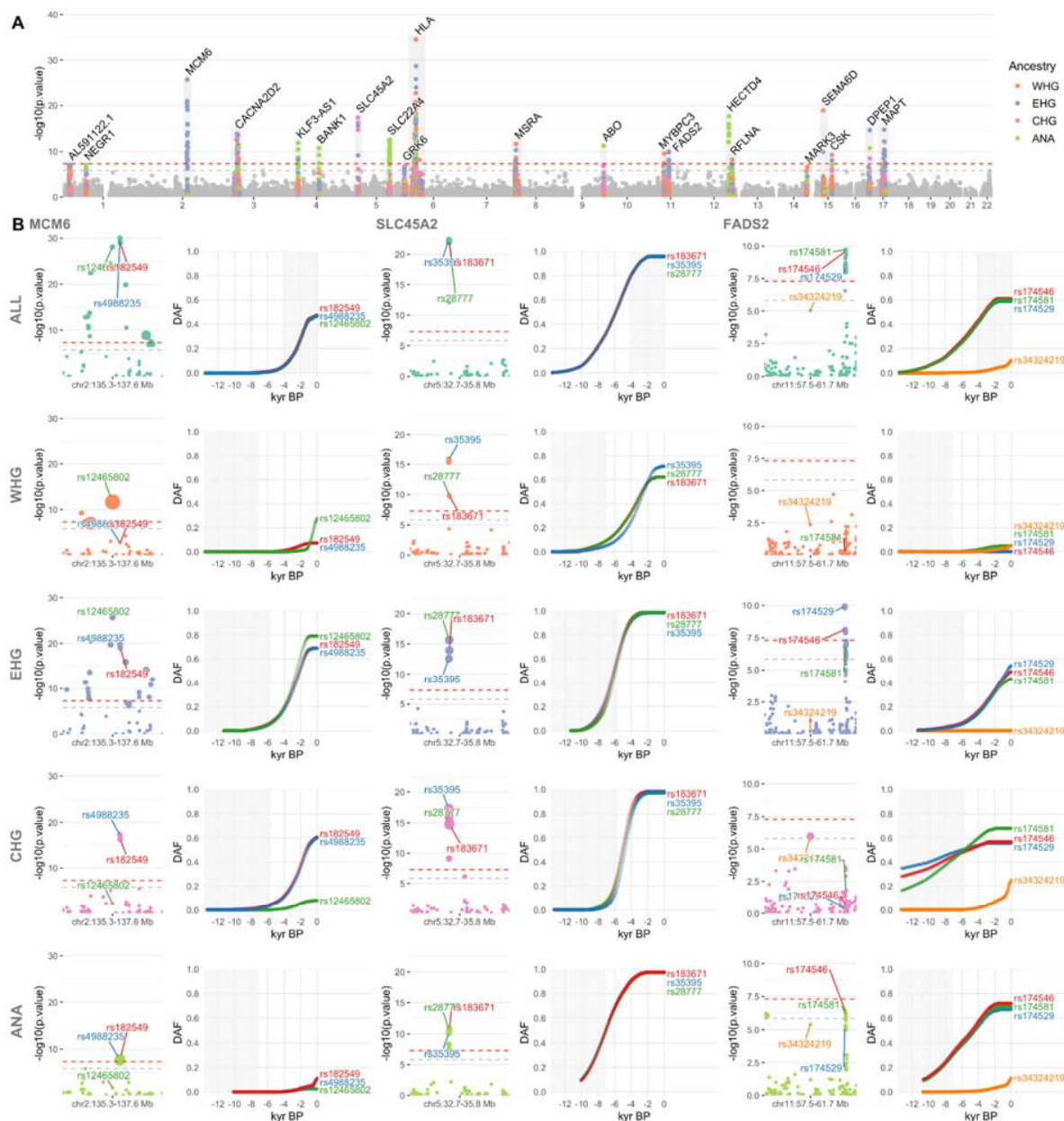
870 duplications at 16p13.11). The individual harbouring the 16p13.1 deletion, RISE586<sup>20</sup>, a 4,000 BP  
871 woman aged 20-30 from the Únětice culture (modern day Czech Republic), had almost complete  
872 skeletal remains, which allowed us to test for the presence of various skeletal abnormalities  
873 associated with the 16p13.11 microdeletion<sup>121</sup>. RISE586 exhibited a hypoplastic tooth,  
874 spondylolysis of the L5 vertebrae, incomplete coalescence of the S1 sacral bone, among other  
875 minor skeletal phenotypes. The skeletal phenotypes observed in this individual are relatively  
876 common (~10%) in European populations and are not specific to 16p13.1 thus do not indicate  
877 strong penetrance of this mutation in RISE586<sup>122–125</sup>. However, these results do highlight our  
878 ability to link putatively pathogenic genotypes to phenotypes in ancient individuals. Overall, the  
879 carrier frequency in the ancient individuals is similar to that reported in the UK Biobank genomes  
880 (1.25% vs 1.6% at 15q11.2 and *CHRNA7* combined, and 0.8% vs 1.1% across the remaining loci  
881 combined)<sup>126</sup>. These results suggest that large, recurrent CNVs that can lead to several pathologies  
882 were present at similar frequencies in the ancient and modern populations included in this study.  
883

#### 884 *Ancestry-stratified patterns of natural selection in the last 13,000 years*

885  
886 The Neolithic transition led to a fundamental change in lifestyle, diet and exposure to pathogens  
887 that imposed drastically new selection pressures on human populations. To detect genetic candidate  
888 targets of selection, we used a set of 1,015 imputed ancient genomes from West Eurasia that were  
889 fitted to a four-way admixture model of demographic history in this region (Supplementary Note 3i)  
890 and identified phenotype-associated variants with evidence for directional selection over the last  
891 13,000 years, with a special focus on the Neolithic transition (Supplementary Note 4a). We adapted  
892 CLUES<sup>127</sup> to model time-series data (Supplementary Note 4a) and used it to infer allele frequency  
893 trajectories and selection coefficients for 33,323 quality-controlled phenotype-associated variants  
894 ascertained from the GWAS Catalogue<sup>128</sup>. An equal number of putatively neutral, frequency-paired  
895 variants were used as a control set. To control for possible confounders, we built a causal model to  
896 distinguish direct effects of age on allele frequency from indirect effects mediated by read depth,  
897 read length, and/or error rates (Supplementary Note 4b), and developed a mapping bias test used to  
898 evaluate systematic differences between data from ancient and present-day populations  
899 (Supplementary Note 4a). Because admixture between groups with differing allele frequencies can  
900 confound interpretation of allele frequency changes through time, we also applied a novel  
901 chromosome painting technique, based on inference of a sample's nearest neighbours in the  
902 marginal trees of a tree sequence (Supplementary Note 3i). This allowed us to accurately assign  
903 ancestral path labels to haplotypes found in both ancient and present-day individuals. By  
904 conditioning on these haplotype path labels, we could infer selection trajectories while controlling  
905 for changes in admixture proportions through time (Supplementary Note 4a).  
906

907 Our analysis identified no genome-wide significant ( $p < 5e-8$ ) selective sweeps when using  
908 genomes from present-day individuals alone (1000 Genomes Project populations GBR, FIN and  
909 TSI), although trait-associated variants were enriched for signatures of selection compared to the  
910 control group ( $p < 2.2e-16$ , Wilcoxon signed-rank test). In contrast, when using imputed aDNA  
911 genotype probabilities, we identified 11 genome-wide significant selective sweeps in the GWAS  
912 variants, and none in the control group, consistent with selection acting on trait-associated variants  
913 (Supplementary Note 4a, Supplementary Figs. S4a.4 to S4a.14). However, when conditioned on  
914 one of our four ancestral histories—genomic regions arriving in present day genomes through  
915 Western hunter-gatherers (WHG), Eastern hunter-gatherers (EHG), Caucasus hunter-gatherers  
916 (CHG) or Anatolian farmers (ANA)—we identified 21 genome-wide significant selection peaks  
917 (including the 11 from the pan-ancestry analysis) (Fig. 7). This suggests that admixture between  
918 ancestral populations has masked evidence of selection at many trait associated loci in modern  
919 populations.

920



921

922 **Fig 7. Genome-wide selection scan for trait associated variants.** A) Manhattan plot of p-values from selection scan  
 923 with CLUES, based on a time-series of imputed aDNA genotype probabilities. Twenty-one genome-wide significant  
 924 selection peaks highlighted in grey and labelled with the most significant gene within each locus. Within each sweep,  
 925 SNPs are positioned on the y-axis and coloured by their most significant marginal ancestry. Outside of the sweeps,  
 926 SNPs show p-values from the pan-ancestry analysis and are coloured grey. Red dotted lines indicate genome-wide  
 927 significance ( $p < 5e-8$ ), while the grey dotted line shows the Bonferroni significance threshold, corrected for the number  
 928 of tests ( $p < 1.35e-6$ ). B) Detailed plots for three genome-wide significant sweep loci: (i) MCM6, lactase persistence;  
 929 (ii) SLC45A2, skin pigmentation; and (iii) FADS2, lipid metabolism. Rows show results for the pan-ancestry analysis  
 930 (ALL) plus the four marginal ancestries: Western hunter-gatherers (WHG), Eastern hunter-gatherers (EHG), Caucasus  
 931 hunter-gatherers (CHG) and Anatolian farmers (ANA). The first column of each loci shows zoomed Manhattan plots of  
 932 the p-values for each ancestry (significant SNPs sized by their selection coefficients), and column two shows allele

24



933 trajectories for the top SNPs across all ancestries (grey shading for the marginal ancestries indicates approximate  
934 temporal extent of the pre-admixture population).

935

936 *Selection on diet-associated loci*

937

938 We find strong changes in selection associated with lactose digestion after the introduction of  
939 farming, but prior to the expansion of the Yamnaya pastoralists into Europe around 5,000 years ago  
940 <sup>20,21</sup>, settling controversies regarding the timing of this selection <sup>129–132</sup>. The strongest overall signal  
941 of selection in the pan-ancestry analysis is observed at the *MCM6 / LCT* locus (rs4988235;  $p=9.86e-$   
942  $31$ ;  $s=0.020$ ), where the derived allele results in lactase persistence <sup>133,134</sup> (Supplementary Note 4a).  
943 The trajectory inferred from the pan-ancestry analysis indicates that the lactase persistence allele  
944 began increasing in frequency only c. 7,000 years ago, and has continued to increase up to present  
945 times (Fig. 7). Our ancestry-stratified analysis shows, however, that selection at the *MCM6/LCT*  
946 locus is much more complex than previously thought. In the pan-ancestry analysis, this sweep is led  
947 by the lactase persistence SNP rs4988235, whereas in the ancestry-stratified analysis, this signal is  
948 primarily driven by sweeps in two of the ancestral backgrounds (EHG and CHG), each of which  
949 differ in their most significant SNPs (Fig. 7). Conversely, in the WHG background, we find no  
950 evidence for selection at rs4988235, but strong selection at rs12465802 within the last c. 2,000  
951 years. Overall, our results suggest that there were multiple, asynchronous selective sweeps in this  
952 genomic region in recent human history, and possibly targeting different loci.

953

954 We also find strong selection in the *FADS* gene cluster — *FADS1* (rs174546;  $p=2.65e-10$ ;  $s=0.013$ )  
955 and *FADS2* (rs174581;  $p=1.87e-10$ ;  $s=0.013$ ) — which are associated with fatty acid metabolism  
956 and known to respond to changes in diet from a more/less vegetarian to a more/less carnivorous diet  
957 <sup>135–140</sup>. In contrast to previous results <sup>138–140</sup>, we find that much of the selection associated with a  
958 more vegetarian diet occurred in Neolithic populations before they arrived in Europe, but then  
959 continued during the Neolithic (Fig. 7). The strong signal of selection in this region in the pan-  
960 ancestry analysis is driven primarily by a sweep occurring on the EHG, CHG and ANA haplotypic  
961 backgrounds (Fig. 7). Interestingly, we find no evidence for selection at this locus in the WHG  
962 background, and most of the allele frequency rise in the EHG background occurs after their  
963 admixture with CHG (around 8ka, <sup>141</sup>), within whom the selected alleles were already close to  
964 present-day frequencies. This suggests that the selected alleles may already have existed at  
965 substantial frequencies in early farmer populations in the Middle East and among Caucasus Hunter  
966 gatherers (associated with the ANA and CHG and backgrounds, respectively) and were subject to  
967 continued selection as eastern groups moved northwards and westwards during the late Neolithic  
968 and Bronze Age periods.

969

970 When specifically comparing selection signatures differentiating ancient hunter-gatherer and farmer  
971 populations <sup>142</sup>, we also observe a large number of regions associated with lipid and sugar  
972 metabolism, and various metabolic disorders (Supplementary Note 4e). These include, for example,  
973 a region in chromosome 22 containing *PATZ1*, which regulates the expression of *FADS1*, and  
974 *MORC2*, which plays an important role in cellular lipid metabolism <sup>143–145</sup>. Another region in  
975 chromosome 3 overlaps with *GPR15*, which is both related to immune tolerance and to intestinal  
976 homeostasis <sup>146–148</sup>. Finally, in chromosome 18, we recover a selection candidate region spanning  
977 *SMAD7*, which is associated with inflammatory bowel diseases such as Crohn's disease <sup>149–151</sup>.  
978 Taken together these results suggest that the transition to agriculture imposed a substantial amount  
979 of selection for humans to adapt to our new diet and that some diseases observed today in modern  
980 societies can likely be understood as a consequence of this selection.

981

982 *Selection on immunity-associated variants*

983

984 In addition to diet-related selection, we observe selection in several loci associated with  
985 immunity/defence functions and with autoimmune disease (Supplementary Note 4a). Some of these  
986 selection events occurred earlier than previously claimed and are likely associated with the  
987 transition to agriculture and may help explain the high prevalence of autoimmune diseases today.  
988 Most notably, we detect a 33 megabase (Mb) wide selection sweep signal in chromosome 6  
989 (chr6:19.1–50.9 Mb), spanning the human leukocyte antigen (HLA) region (Supplementary Note  
990 4a). The selection trajectories of the variants within this locus support multiple independent sweeps,  
991 occurring at different times and with differing intensities. The strongest signal of selection at this  
992 locus in the pan-ancestry analysis is at an intergenic variant, located between *HLA-A* and *HLA-W*  
993 (rs7747253;  $p=8.86e-17$ ;  $s=-0.018$ ), associated with heel bone mineral density<sup>152</sup>, the derived allele  
994 of which rapidly reduced in frequency, beginning c. 8,000 years ago (Extended Data Fig. 10). In  
995 contrast, the signal of selection at *C2* (rs9267677;  $p=9.82e-14$ ;  $s=0.04463$ ), also found within this  
996 sweep, and associated with educational attainment<sup>153</sup>, shows a gradual increase in frequency  
997 beginning c. 4,000 years ago, before rising more rapidly c. 1,000 years ago. This highlights the  
998 complex temporal dynamics of selection at the HLA locus, which not only plays a role in the  
999 regulation of the immune system, but also has association with many other non-immune-related  
1000 phenotypes. The high pleiotropy in this region makes it difficult to determine which selection  
1001 pressures may have driven these increases in frequencies at different periods of time. However,  
1002 profound shifts in lifestyle in Eurasian populations during the Holocene, including a change in diet  
1003 and closer contact with domestic animals, combined with higher mobility and increasing population  
1004 sizes, are likely drivers for strong selection on loci involved in immune response.

1005

1006 We also identified selection signals at the *SLC22A4* (rs35260072;  $p=1.15e-10$ ;  $s=0.018$ ) locus,  
1007 associated with increased itch intensity from mosquito bites<sup>154</sup>, and find that the derived variant has  
1008 been steadily rising in frequency since c. 9,000 years ago (Extended Data Fig. 11). However, in the  
1009 same *SLC22A4* candidate region as rs35260072, we find that the frequency of the previously  
1010 reported SNP rs1050152 plateaued c. 1,500 years ago, contrary to previous reports suggesting a  
1011 recent rise in frequency<sup>45</sup>. Similarly, we detect selection at the *HECTD4* (rs11066188;  $p=3.02e-16$ ;  
1012  $s=0.020$ ) and *ATXN2* (rs653178;  $p=1.92e-15$ ;  $s=0.019$ ) locus, associated with celiac disease and  
1013 rheumatoid arthritis<sup>155</sup>, which has been rising in frequency for c. 9,000 years (Extended Data Fig.  
1014 12), also contrary to previous reports of a more recent rise in frequency<sup>45</sup>. Thus, several disease-  
1015 associated loci previously thought to be the result of recent adaptation may have been subject to  
1016 selection for a longer period of time.

1017

1018 *Selection on the 17q12.13 locus*

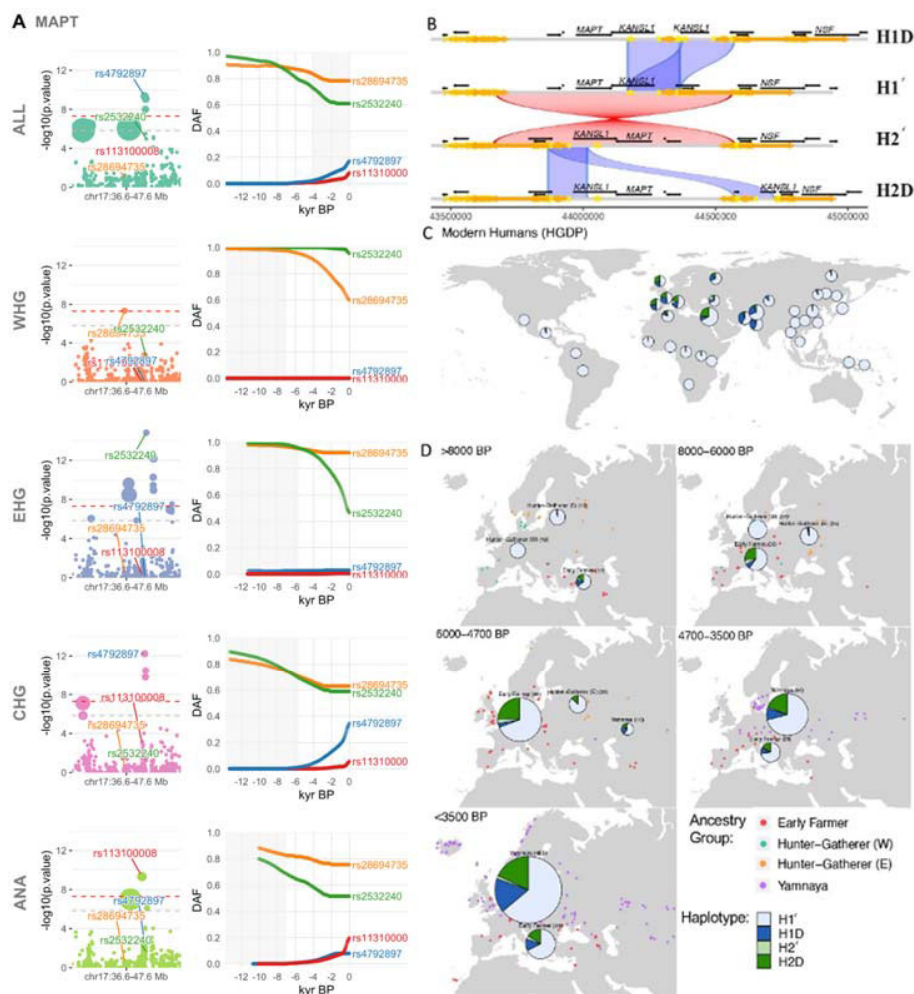
1019

1020 We further detect signs of strong selection in a 12 Mb sweep in chromosome 17 (chr17:36.1–48.1  
1021 Mb), spanning a locus on 17q21.3 implicated in neurodegenerative and developmental disorders  
1022 (Supplementary Note 4a). The locus includes an inversion and other structural polymorphisms with  
1023 indications of a recent positive selection sweep in some human populations<sup>156,157</sup>. Specifically,  
1024 partial duplications of the *KANSL1* gene likely occurred independently on the inverted (H2) and  
1025 non-inverted (H1) haplotypes (Fig. 8B) and both are found in high frequencies (15-25%) among  
1026 current European and Middle Eastern populations but are much rarer in Sub-Saharan African and  
1027 East Asian populations. We used both SNP genotypes and WGS read depth information to  
1028 determine inversion (H1/H2) and *KANSL1* duplication (d) status in the ancient individuals studied  
1029 here (see Supplementary Note 4g).

1030

1031 The H2 haplotype is observed in two of three previously published genomes<sup>158</sup> of Anatolian  
1032 aceramic Neolithic individuals (Bon001 and Bon004) from around 10,000 BP, but data were  
1033 insufficient to identify *KANSLI* duplications. The oldest evidence for *KANSLI* duplications is  
1034 observed in an Iranian early Neolithic individual (AH1 from 9,900 BP<sup>2</sup>) followed by two Georgian  
1035 Mesolithic individuals (NEO281 from 9,724 BP and KK1<sup>6</sup> from 9,720 BP) all of whom are  
1036 heterozygous for the inversion and carry the inverted duplication. The *KANSLI* duplications are  
1037 also detected in two Russian Neolithic individuals: NEO560 from 7,919 BP (H1d) and NEO212  
1038 from 7,390 BP (H2d). With both H1d and H2d having spread to large parts of Europe with  
1039 Anatolian Neolithic Farmer ancestry, their frequency seems unchanged in most of Europe as  
1040 Steppe-related ancestry becomes dominant in large parts of the subcontinent (Extended Data Fig.  
1041 8D). The fact that both H1d and H2d are found in apparently high frequencies in both early  
1042 Anatolian Farmers and the earliest Yamnaya/Steppe-related ancestry groups suggests that any  
1043 selective sweep acting on the H1d and H2d variants would probably have occurred in populations  
1044 ancestral to both.

1045  
1046 We note that the strongest signal of selection observed in this locus is at *MAPT* (rs4792897;  
1047  $p=4.65e-10$ ;  $s=0.03$  (Fig. 8A; Supplementary Note 4a), which codes for the tau protein<sup>159</sup> and is  
1048 involved in a number of neurodegenerative disorders, including Alzheimer's disease and  
1049 Parkinson's disease<sup>160–164</sup>. However, the region is also enriched for evidence of reference bias in  
1050 our imputed dataset—especially around the *KANSLI* gene—due to complex structural  
1051 polymorphisms (Supplementary Note 4i).



1052

1053 **Fig 8. Selection at the *MAPT* / 17q21.31 inversion locus.** A) Results for the pan-ancestry analysis (ALL) plus the four  
1054 marginal ancestries: Western hunter-gatherers (WHG), Eastern hunter-gatherers (EHG), Caucasus hunter-gatherers  
1055 (CHG) and Anatolian farmers (ANA). Grey shading for the marginal ancestries indicates approximate temporal extent  
1056 of the pre-admixture population. B) Haplotypes of the 17q21.31 locus: the ancestral (non-inverted) H1 17q21.31 and  
1057 the inverted H2 haplotype. Duplications of the *KANSL1* gene have occurred independently on both lineages yielding  
1058 H1D and H2D haplotypes. C) Frequency of the 17q21.31 inversion and duplication haplotypes across modern-day  
1059 global populations (Human Genome Diversity Project <sup>119</sup>). D) Change in the frequency of the 17q21.31 inversion  
1060 haplotype through time.

1061

1062 *Selection on pigmentation-associated variants*

1063

1064 Our results identify strong selection for lighter skin pigmentation in groups moving northwards and  
1065 westwards, in agreement with the hypothesis that selection is caused by reduced UV exposure and  
1066 resulting vitamin D deficiency. We find that the most strongly selected alleles reached near-fixation  
1067 several thousand years ago, suggesting that this was not associated with recent sexual selection as  
1068 proposed <sup>165,166</sup> (Supplementary Note 4a).

1069

1070 In the pan-ancestry analysis we detect strong selection at the *SLC45A2* locus (rs35395;  $p=4.13e-23$ ;  
1071  $s=0.022$ ) locus <sup>167,168</sup>, with the selected allele (responsible for lighter skin), increasing in frequency  
1072 from c. 13,000 years ago, until plateauing c. 2,000 years ago (Fig. 7). The dominating hypothesis is  
1073 that high melanin levels in the skin are important in equatorial regions owing to its protection

1074 against UV radiation, whereas lighter skin has been selected for at higher latitudes (where UV  
1075 radiation is less intense) because some UV penetration is required for cutaneous synthesis of  
1076 vitamin D<sup>169,170</sup>. Our findings confirm pigmentation alleles as major targets of selection during the  
1077 Holocene<sup>45,171,172</sup> particularly on a small proportion of loci with large effect sizes<sup>168</sup>.

1078  
1079 Additionally, our results provide unprecedentedly detailed information about the duration and  
1080 geographic spread of these processes (Fig. 7) suggesting that an allele associated with lighter skin  
1081 was selected for repeatedly, probably as a consequence of similar environmental pressures  
1082 occurring at different times in different regions. In the ancestry-stratified analysis, all marginal  
1083 ancestries show broad agreement at the *SLC45A2* locus (Fig. 7) but differ in the timing of their  
1084 frequency shifts. The ANA ancestry background shows the earliest evidence for selection, followed  
1085 by EHG and WHG around c. 10,000 years ago, and CHG c. 2,000 years later. In all ancestry  
1086 backgrounds except WHG, the selected haplotypes reach near fixation by c. 3,000 years ago, whilst  
1087 the WHG haplotype background contains the majority of ancestral alleles still segregating in  
1088 present-day Europeans. This finding suggests that selection on this allele was much weaker in  
1089 ancient western hunter-gatherer groups during the Holocene compared to elsewhere. We also detect  
1090 strong selection at the *SLC24A5* (rs1426654; p=6.45e-09; s=0.019) which is also associated with  
1091 skin pigmentation<sup>167,173</sup>. At this locus, the selected allele increased in frequency even earlier than  
1092 *SLC45A2* and reached near fixation c. 3,500 years ago (Supplementary Note 4a). Selection on this  
1093 locus thus seems to have occurred early on in groups that were moving northwards and westwards,  
1094 and only later in the Western hunter-gatherer background after these groups encountered and  
1095 admixed with the incoming populations.

#### 1096 1097 *Selection among major axes of ancient population variation*

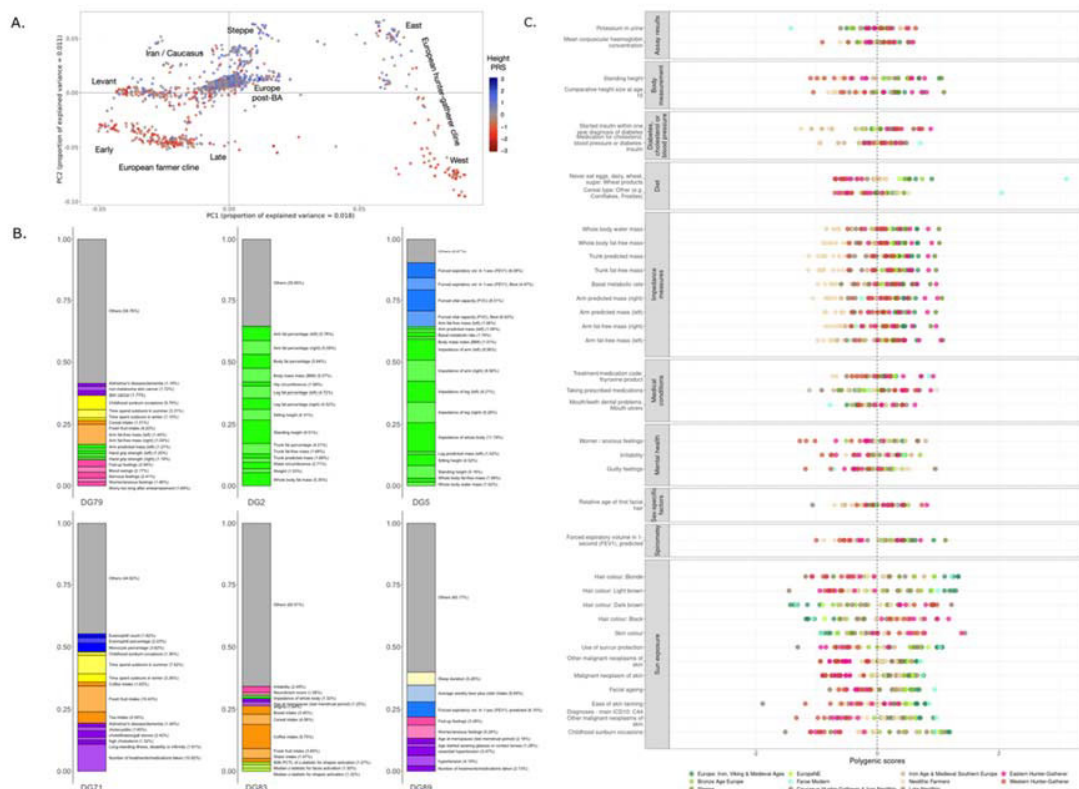
1098  
1099 Beyond patterns of genetic change at the Mesolithic-Neolithic transition, much genetic variability  
1100 observed today reflects high genetic differentiation in the hunter-gatherer groups that eventually  
1101 contributed to modern European genetic diversity<sup>142</sup>. Indeed, a substantial number of loci  
1102 associated with cardiovascular disease, metabolism and lifestyle diseases trace their genetic  
1103 variability prior to the Neolithic transition, to ancient differential selection in ancestry groups  
1104 occupying different parts of the Eurasian continent (Supplementary Note 4d). These may represent  
1105 selection episodes that preceded the admixture events described above, and led to differentiation  
1106 between ancient hunter-gatherer groups in the late Pleistocene and early Holocene. One of these  
1107 overlaps with the *SLC24A3* gene which is a salt sensitivity gene significantly expressed in obese  
1108 individuals<sup>174,175</sup>. Another spans *ROPNI* and *KALRN*, two genes involved in vascular disorders<sup>176–</sup>  
1109<sup>178</sup>. A further region contains *SLC35F3*, which codes for a thiamine transport and has been  
1110 associated with hypertension in a Han Chinese cohort<sup>179,180</sup>. Finally, there is a candidate region  
1111 containing several genes (*CH25H*, *FAS*) associated with obesity and lipid metabolism<sup>181–183</sup> and  
1112 another peak with several genes (*ASXL2*, *RAB10*, *HADHA*, *GPR113*) involved in glucose  
1113 homeostasis and fatty acid metabolism<sup>184–193</sup>. These loci predominantly reflect ancient patterns of  
1114 extreme differentiation between Eastern and Western Eurasian genomes, and may be candidates for  
1115 selection after the separation of the Pleistocene populations that occupied different environments  
1116 across the continent (roughly 45,000 years ago<sup>103</sup>).

#### 1117 1118 *Genetic trait reconstruction and the phenotypic legacy of ancient Europeans*

1119  
1120 When comparing modern European genomes in the UK Biobank to ancient Europeans, we find  
1121 strong differentiation at certain sets of trait-associated variants, and differential contribution of  
1122 different ancestry groups to various traits. We reconstructed polygenic scores for phenotypes in  
1123 ancient individuals, using effect size estimates obtained from GWASs performed using the

1124 >400,000 UK Biobank genomes<sup>107</sup> (<http://www.nealelab.is/uk-biobank>) and looked for  
1125 overdispersion among these scores across ancient populations, beyond what would be expected  
1126 under a null model of genetic drift<sup>194</sup> (Supplementary Note 4c). We stress that polygenic scores and  
1127  $Q_X$  statistic may both be affected by population stratification, so these results should be interpreted  
1128 with caution<sup>195–198</sup>. The most significantly overdispersed scores are for variants associated with  
1129 pigmentation, anthropometric differences and disorders related to diet and sugar levels, including  
1130 diabetes (Fig. 9). We also find psychological trait scores with evidence for overdispersion related to  
1131 mood instability and irritability, with Western Hunter-gatherers generally showing smaller genetic  
1132 scores for these traits than Neolithic Farmers. Intriguingly, we find highly inconsistent predictions  
1133 of height based on polygenic scores in western hunter-gatherer and Siberian groups computed using  
1134 effect sizes estimated from two different - yet largely overlapping - GWAS cohorts (Supplementary  
1135 Note 4c), highlighting how sensitive polygenic score predictions are to the choice of cohort,  
1136 particularly when ancient populations are genetically divergent from the reference GWAS cohort  
1137<sup>198</sup>. Taking this into account, we do observe that the Eastern hunter-gatherer and individuals  
1138 associated with the Yamnaya culture have consistently high genetic values for height, which in turn  
1139 contribute to stature increases in Bronze Age Europe, relative to the earlier Neolithic populations  
1140<sup>45,80,199</sup>.

1141  
1142 We performed an additional analysis to examine the data for strong alignments between axes of  
1143 trait-association<sup>200</sup> and ancestry gradients, rather than relying on particular choices for population  
1144 clusters (Supplementary Note 4e). Along the population structure axis separating ancient East Asian  
1145 and Siberian genomes from Steppe and Western European genomes (Fig. 1), we find significant  
1146 correlations with trait-association components related to impedance, body measurements, blood  
1147 measurements, eye measurement and skin disorders. Along the axis separating Mesolithic hunter-  
1148 gatherers from Anatolian and Neolithic farmer individuals, we find significant correlations with  
1149 trait-association components related to skin disorders, diet and lifestyle traits, mental health status,  
1150 and spirometry-related traits (Fig. 9). Our findings show that these phenotypes were genetically  
1151 different among ancient groups with very different lifestyles. However, we note that the realised  
1152 value of these traits is highly dependent on environmental factors and gene-environment  
1153 interactions, which we do not model in this analysis.  
1154



1155

1156 **Fig. 9** A. First two principal components of a PCA of ancient Western Eurasian samples, coloured by height polygenic  
 1157 scores. B. Top 6 UK Biobank trait-association components from DeGAs that have the highest correlation ( $P < 5e-3$ )  
 1158 with the principal component separating ancient farmers from hunter-gatherer populations (PC1 in Panel A). C. Top UK  
 1159 Biobank traits with highest overdispersion in polygenic scores among ancient populations, out of a total of 320 sets of  
 1160 trait-associated SNPs tested ( $Q_X > 79.4$ ,  $P < 0.05/320$ ).

1161

1162 In addition to the above reconstructions of genetic traits among the ancient individuals, we also  
 1163 estimated the contribution from different ancestral populations (EHG, CHG, WHG, Yamnaya and  
 1164 Anatolian farmer) to variation in polygenic phenotypes in present-day individuals, leveraging the  
 1165 exceptional resolution offered by the UK Biobank genomes<sup>107</sup> to investigate this. We calculated  
 1166 ancestry-specific polygenic risk scores based on the chromosome painting of the >400,000 UKB  
 1167 genomes (Supplementary Note 4h); this allowed us to identify if any of the ancient ancestry  
 1168 components were over-represented in modern UK populations at loci significantly associated with a  
 1169 given trait, and also avoids exporting risk scores over space and time. Working with large numbers  
 1170 of imputed ancient genomes provides high statistical power to use ancient populations as “ancestral  
 1171 sources”. We focused on phenotypes whose polygenic scores were significantly over-dispersed in  
 1172 the ancient populations (Supplementary Note 4c), as well as a single high effect variant, ApoE4,  
 1173 known to be a significant risk factor in Alzheimer’s Disease<sup>(201,202)</sup>. We emphasise that this  
 1174 approach makes no reference to ancient phenotypes but describes how these ancestries contributed  
 1175 to the modern genetic landscape. In light of the ancestry gradients within the British Isles and  
 1176 Eurasia (Fig. 5), these results support the hypothesis that ancestry-mediated geographic variation in  
 1177 disease risks and phenotypes is commonplace. It points to a way forward for disentangling how  
 1178 ancestry contributed to differences in risk of genetic disease – including metabolic and mental  
 1179 health disorders – between present-day populations.

1180

1181 Taken together, these analyses help to settle the famous discussion of selection in Europe relating to  
1182 height <sup>45,80,203</sup>. The finding that steppe individuals have consistently high genetic values for height  
1183 (Supplementary Note 4c), is mirrored by the UK Biobank results, which find that the ‘Steppe’  
1184 ancestral components (Yamnaya/EHG) contributed to increased height in present-day populations  
1185 (Supplementary Note 4h). This shows that the height differences in Europe between north and south  
1186 may not be due to selection, as claimed in many previous studies, but may be a consequence of  
1187 differential ancestry.

1188

1189 Likewise, European hunter gatherers are genetically predicted to have dark skin pigmentation and  
1190 dark brown hair <sup>11,20,21,79,83,168,204,205</sup>, and indeed we see that the WHG, EHG and CHG components  
1191 contributed to these phenotypes in present-day individuals whereas the Yamnaya and Anatolian  
1192 farmer ancestry contributed to light brown/blonde hair pigmentation (Supplementary Note 4h).  
1193 Interestingly, loci associated with overdispersed mood-related polygenic phenotypes recorded  
1194 among the UK Biobank individuals (like increased anxiety, guilty feelings, and irritability) showed  
1195 an overrepresentation of the Anatolian farmer ancestry component; and the WHG component  
1196 showed a strikingly high contribution to traits related to diabetes. We also found that the ApoE4  
1197 effect allele is preferentially found on a WHG/EHG haplotypic background, suggesting it likely was  
1198 brought to western Europe by early hunter-gatherers (Supplementary Note 4h). This is in line with  
1199 the present-day European distribution of this allele, which is highest in north-eastern Europe, where  
1200 the proportion of these ancestries are higher than in other regions of the continent <sup>206</sup>.

1201

## 1202 *Conclusion*

1203

1204 Our study has provided fundamental new insights into one of the most transformative periods of  
1205 human biological and cultural evolution. We have demonstrated that a clear east-west division  
1206 known from Stone Age material culture, extending from the Black Sea to the Baltic and persisting  
1207 across several millennia, was genetically deeply rooted in populations with different ancestries. We  
1208 showed that the genetic impact of the Neolithic transition was highly distinct, east and west of this  
1209 boundary. We have identified a hitherto unknown source of ancestry in hunter-gatherers from the  
1210 Middle Don region contributing ancestry to the Yamnaya pastoralists, and we have documented  
1211 how the later spread of steppe-related ancestry into Europe was very rapid and mediated through  
1212 admixture with people from the Globular Amphora Culture. Additionally, we have observed two  
1213 near-complete population replacements in Denmark within just 1,000 years, concomitantly with  
1214 major changes in material culture, which rules out cultural diffusion as a main driver and settles  
1215 generation-long archaeological debates. Our analyses revealed that the ability to detect signatures of  
1216 natural selection in modern human genomes is drastically limited by conflicting selection pressures  
1217 in different ancestral populations masking the signals. Developing methods to trace selection in  
1218 individual ancestry components allowed us to effectively double the number of significant selection  
1219 peaks, which helped clarify the trajectories of a number of traits related to diet and lifestyle. Our  
1220 results emphasise how the interplay between major ancient selection and admixture events  
1221 occurring across Europe and Asia in the Stone and Bronze Ages have profoundly shaped patterns of  
1222 genetic variation in modern human populations.

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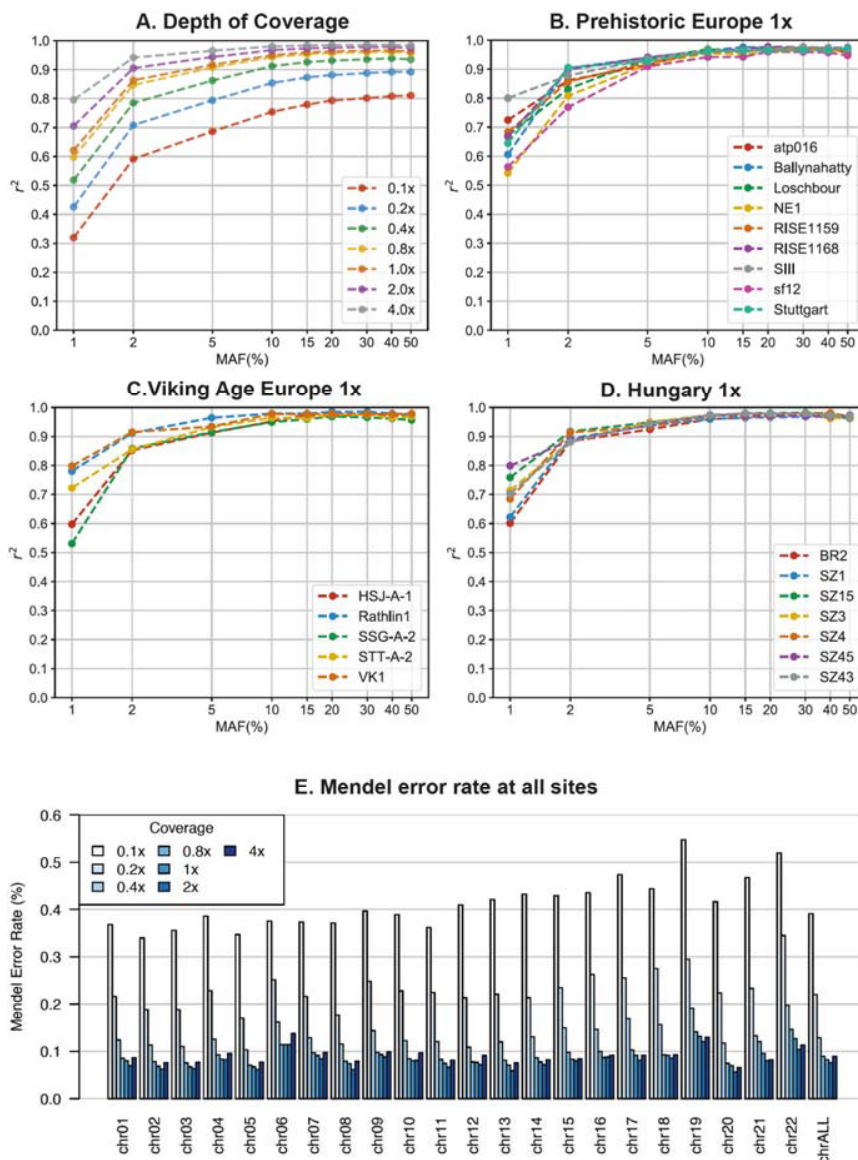
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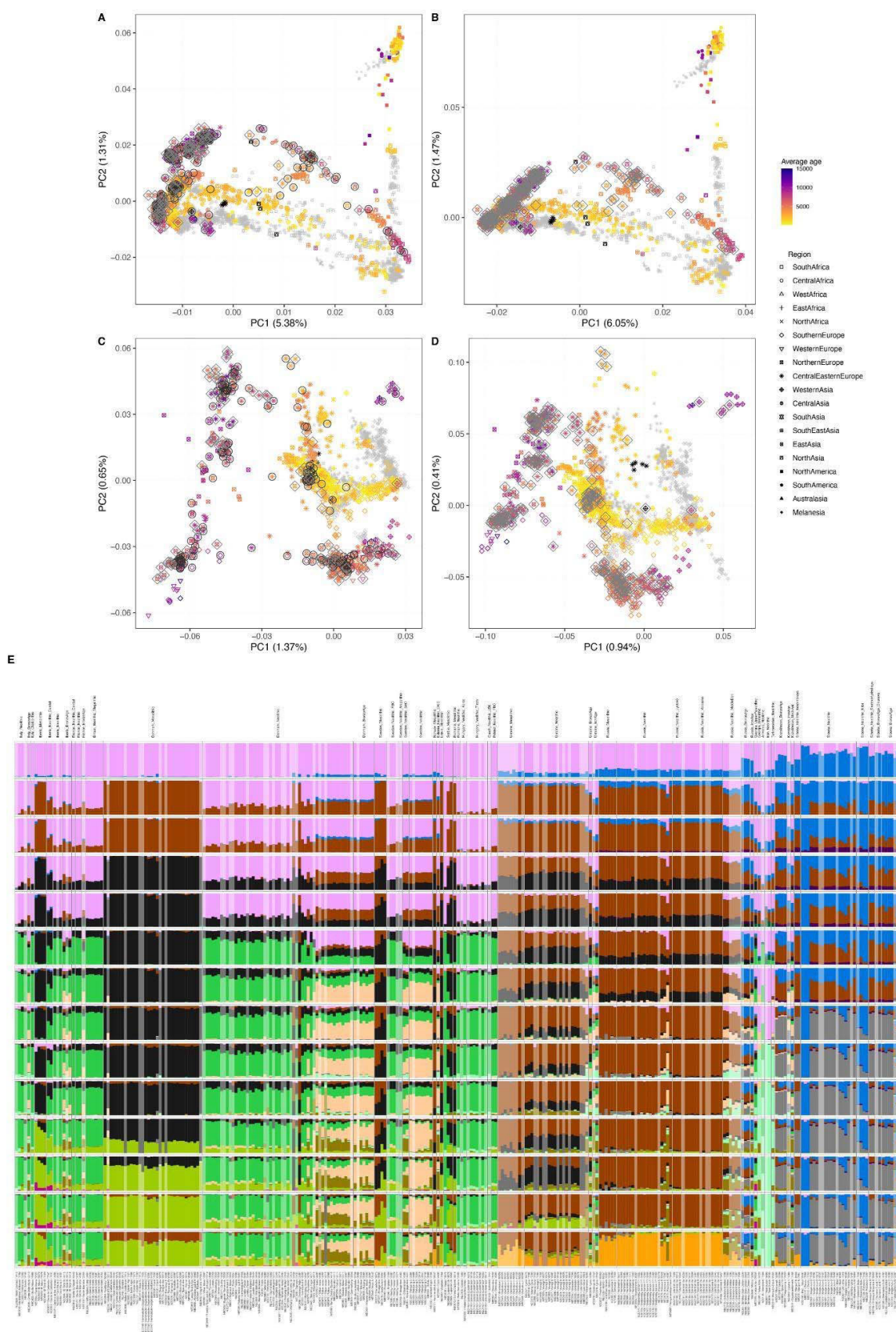
1228

1229 **Extended Data Figures**

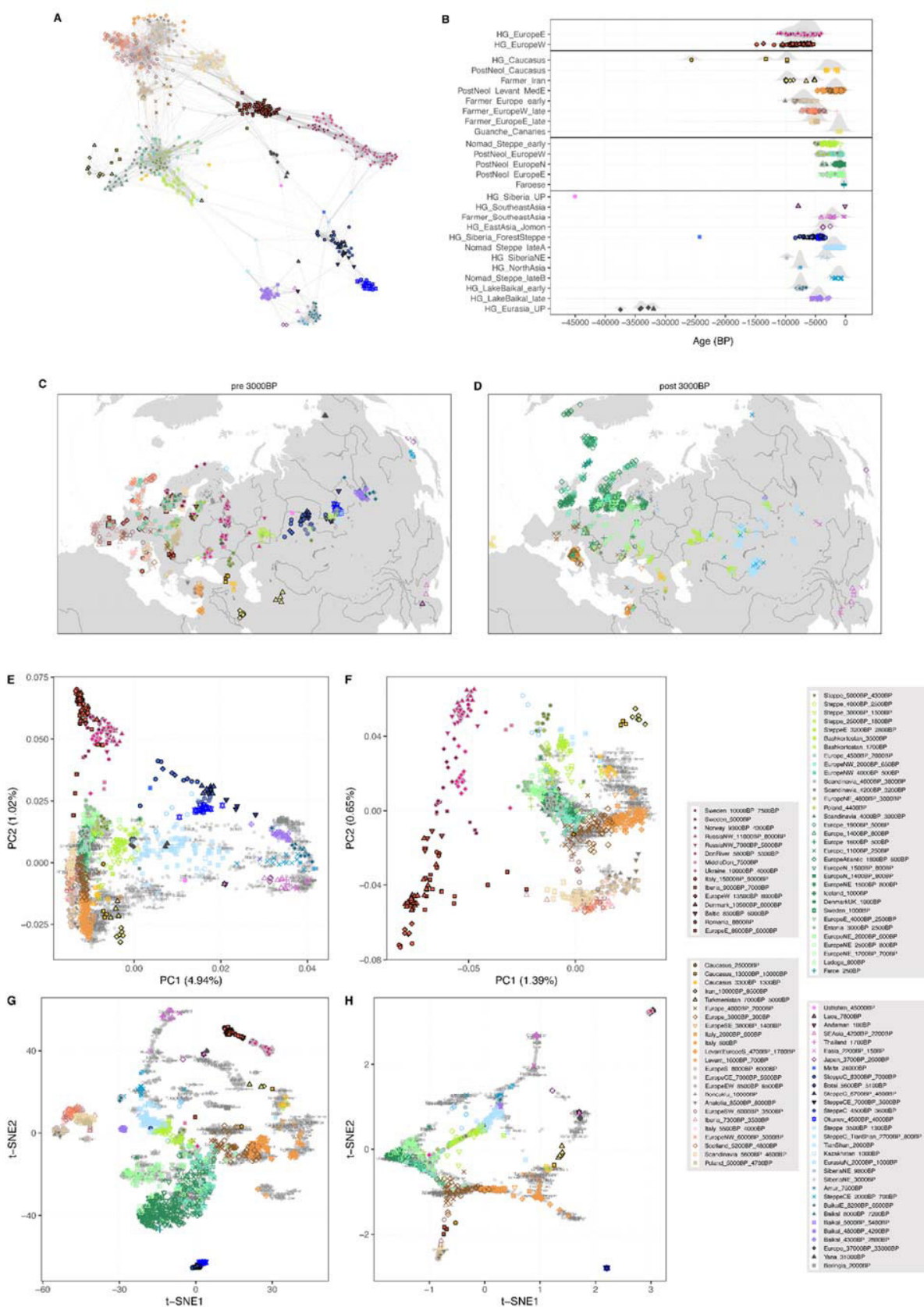


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**Extended Data Fig.1. Imputation accuracy of aDNA.** Panel A shows imputation accuracy across the 42 high-coverage ancient genomes when downsampled to lower depth of coverage values. Panels B-D show imputation accuracy for 1X depth of coverage across 21 high-coverage ancient European genomes. In panels A-D, imputation accuracy is shown as the squared Pearson correlation between imputed and true genotype dosages as a function of minor allele frequency of the target variant sites. Panel E shows imputation accuracy as Mendelian error rates for a re-sequenced Neolithic trio<sup>27</sup> downsampled to a range of low coverage values.

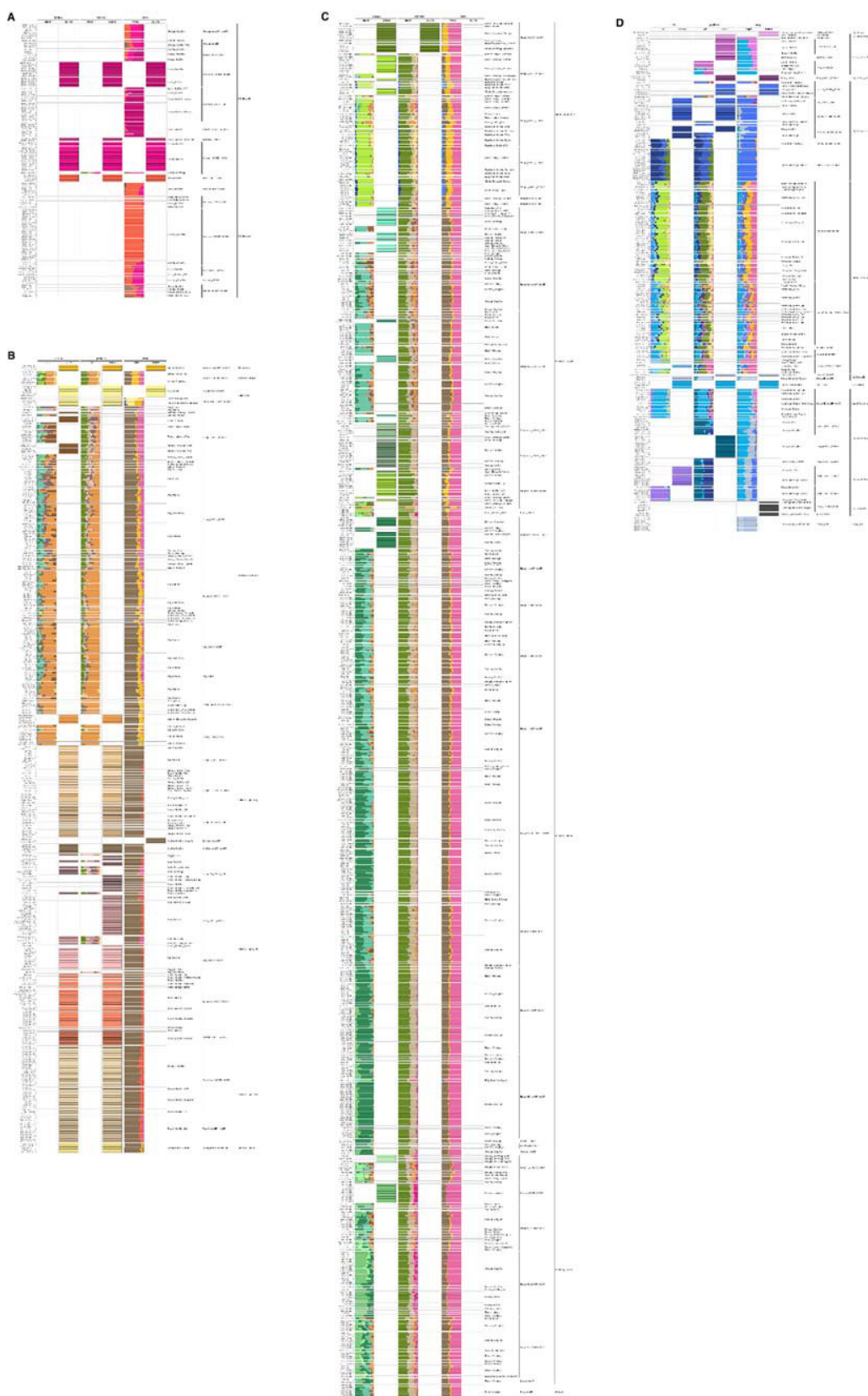


1240 **Extended Data Fig. 2. Genetic structure of the 317 herein-reported ancient genomes.** (A)-(D) Principal component  
1241 analysis of 3,316 modern and ancient individuals from Eurasia, Oceania and the Americas (A, B), as well as restricted  
1242 to 2,126 individuals from western Eurasia (west of Urals) (C, D). Shown are analyses with principal components  
1243 inferred either using both modern and imputed ancient genomes passing all filters, and projecting low coverage ancient  
1244 genomes (A, C); or only modern genomes and projecting all ancient genomes (B, D). Ancient genomes sequenced in  
1245 this study are indicated either with black circles (imputed genomes) or grey diamonds (projected genomes). (E) Model-  
1246 based clustering results using ADMIXTURE for 284 newly reported genomes (excluding close relatives and individuals  
1247 flagged for possible contamination ). Results shown are based on ADMIXTURE runs from K=2 to K=15 on 1,584  
1248 ancient individuals. Low-coverage individuals represented by pseudo-haploid genotypes are indicated with alpha  
1249 transparency.  
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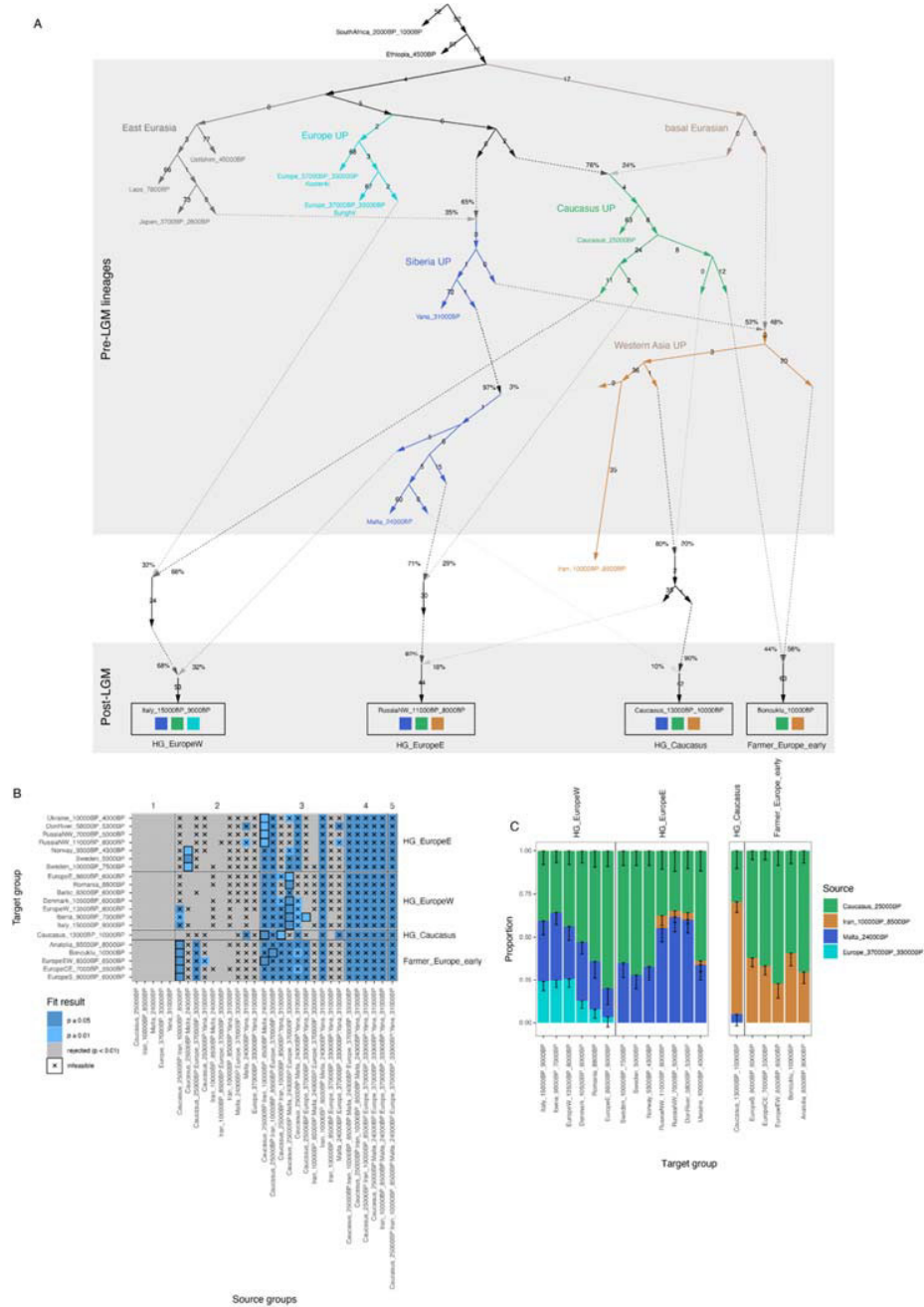


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1252 **Extended Data Fig. 3. Genetic clustering of ancient individuals.** Genetic clusters inferred from pairwise identity-by-  
1253 descent (IBD) sharing of 1,401 ancient Eurasian individuals, indicated using colored symbols throughout (A) Network  
1254 graph of pairwise IBD sharing between 596 ancient Eurasians predating 3,000 BP, highlighting within- and between-  
1255 cluster relationships. Each node represents an individual, and the width of edges connecting nodes indicates the fraction  
1256 of the genome shared IBD between the respective pair of individuals. Network edges were restricted to the 10 highest  
1257 sharing connections for each individual, and the layout was computed using the force-directed Fruchterman-Reingold  
1258 algorithm. (B) Temporal distribution of clustered individuals, grouped by broad ancestry cluster. (C), (D) Geographical  
1259 distribution of clustered individuals, shown for individuals predating 3,000 BP (C) and after 3,000 BP (D). (E)-(H)  
1260 Fine-scale population structure among genetic clusters. Modern individuals are shown in gray, with population labels  
1261 corresponding to their median coordinates. (E), (F) PCA of 3,119 Eurasian (E) or 2,126 west Eurasian (F) individuals.  
1262 (G), (H) t-distributed stochastic neighbour embedding (t-SNE) using the first 12 principal components of the all  
1263 Eurasian panel (E). Shown are embeddings with two different exaggeration factors  $\rho$ , emphasising local (G,  $\rho=1$ ) or  
1264 global (H,  $\rho=30$ ) structure.  
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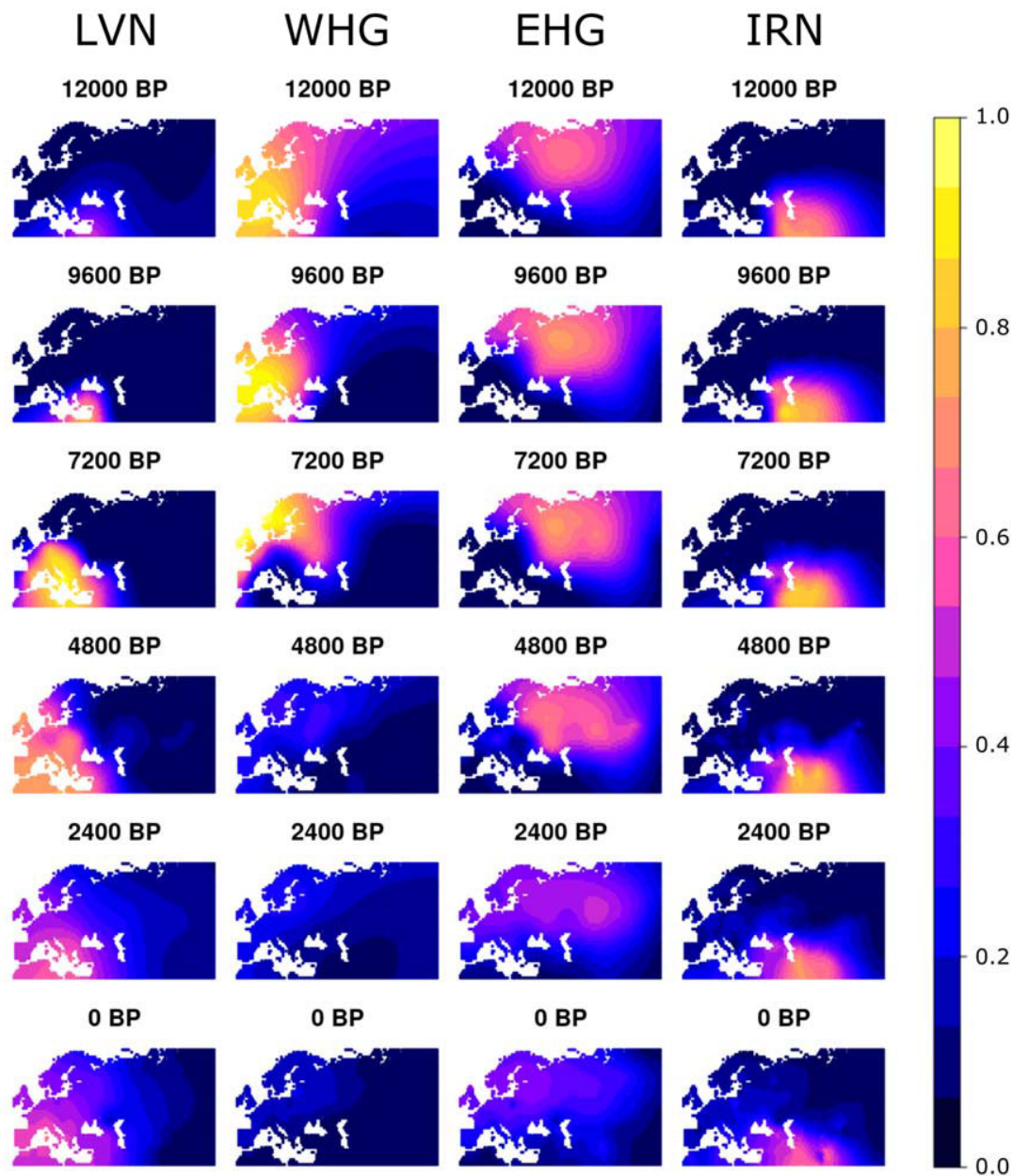
1267 **Extended Data Fig. 4. Admixture modelling.** Supervised admixture modelling using non-negative least squares on  
 1268 IBD sharing profiles. Panels (A)-(D) show estimated ancestry proportions of four global Eurasian clusters,  
 1269 corresponding to (A) European hunter-gatherers before 4,000 BP; (B) Individuals from Europe and Western Asia from  
 1270 around 10,000 BP until historical times, including Neolithic farmers, Caucasus hunter-gatherers and recent individuals  
 1271 with genetic affinity to the Levant; (C) European individuals after 5,000 BP, as well as pastoralist groups from the  
 1272 Eurasian Steppe; (D) Central, East and North Asian individuals with east Eurasian genetic affinities. Column pairs show  
 1273 results of modelling target individuals (left columns) using three panels of increasingly distal source groups (right  
 1274 columns): “postBA”: Bronze Age and Neolithic source groups; “postNeol”, Bronze Age and later targets using Late  
 1275 Neolithic/early Bronze Age and earlier source groups; “deep”, Mesolithic and later targets using deep ancestry source  
 1276 groups. Note that some clusters of individuals can be either sources or targets across distinct panels.



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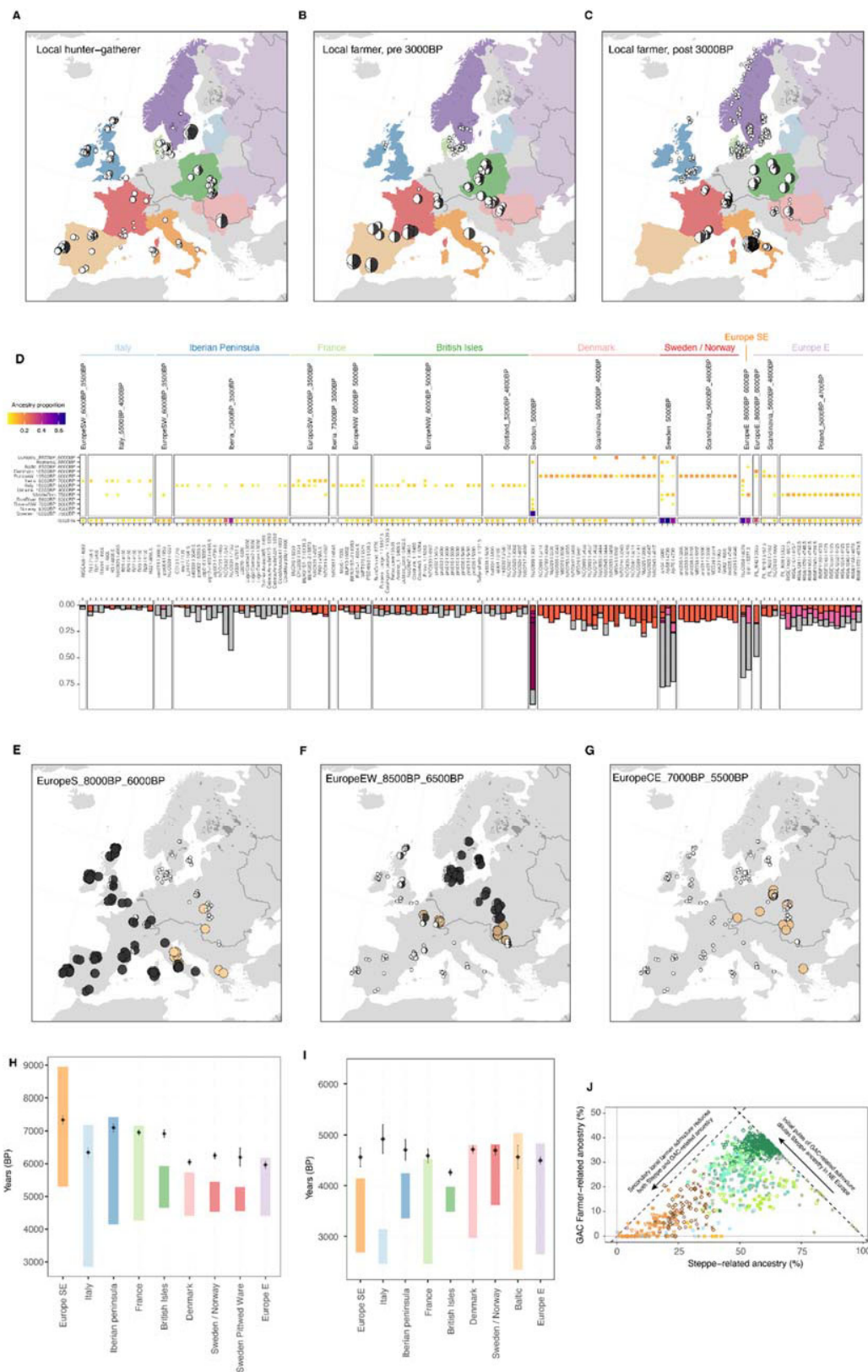
1279 **Extended Data Fig. 5. Deep Eurasian population structure.** (A) Admixture graph fit relating deep Eurasian lineages  
 1280 predating the Last Glacial Maximum (LGM) to later West Eurasian ancestry clusters (worst  $|Z| = 3.65$ ). (B) Rotating  
 1281 outgroup *qpAdm* analysis showing fit results for modelling post-LGM target groups as mixtures of all possible  
 1282 combinations involving one to five source groups. Colours of the individual matrix cells indicate the fit for a particular  
 1283 model, either rejected at  $p < 0.01$  (grey),  $0.01 \leq p < 0.05$  (light blue) or  $p \geq 0.05$  (dark blue). Cells with crosses indicate  
 1284 infeasible models involving negative admixture proportions. (C) Estimated ancestry proportions from *qpAdm* for post-  
 1285 LGM target groups inferred from the model fitting with least number of source groups.



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1288 **Extended Data Fig 6.** Spatiotemporal kriging of four major ancestry clusters over the last 12,000 years of human history.  
 1289 LVN = ancestry maximized in Anatolian farmer populations. WHG = ancestry maximized in western European hunter-  
 1290 gatherers. EHG = ancestry maximized in eastern European hunter-gatherers. IRN = ancestry maximized in Iranian  
 1291 Neolithic individuals and Caucasus hunter-gatherers.

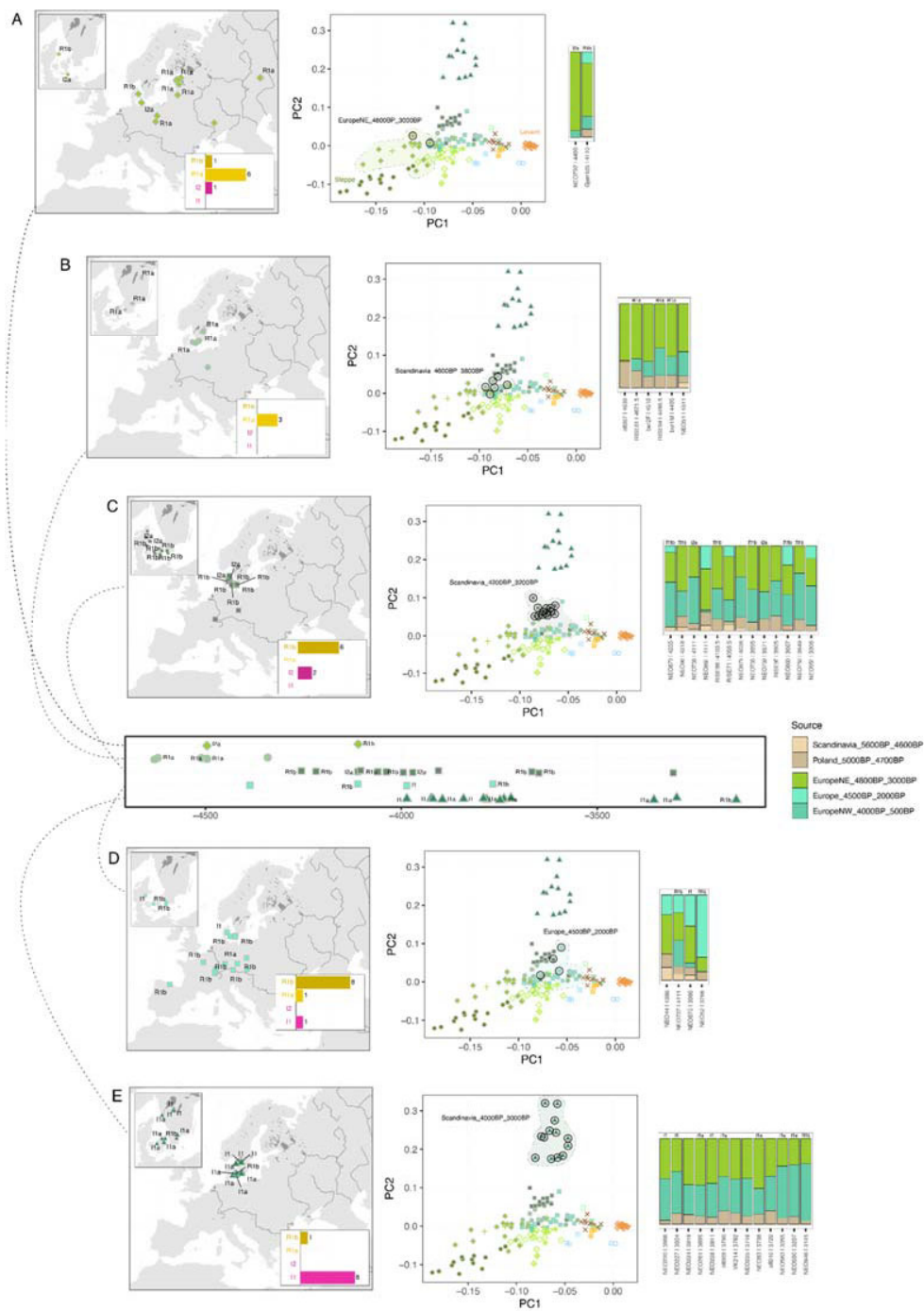




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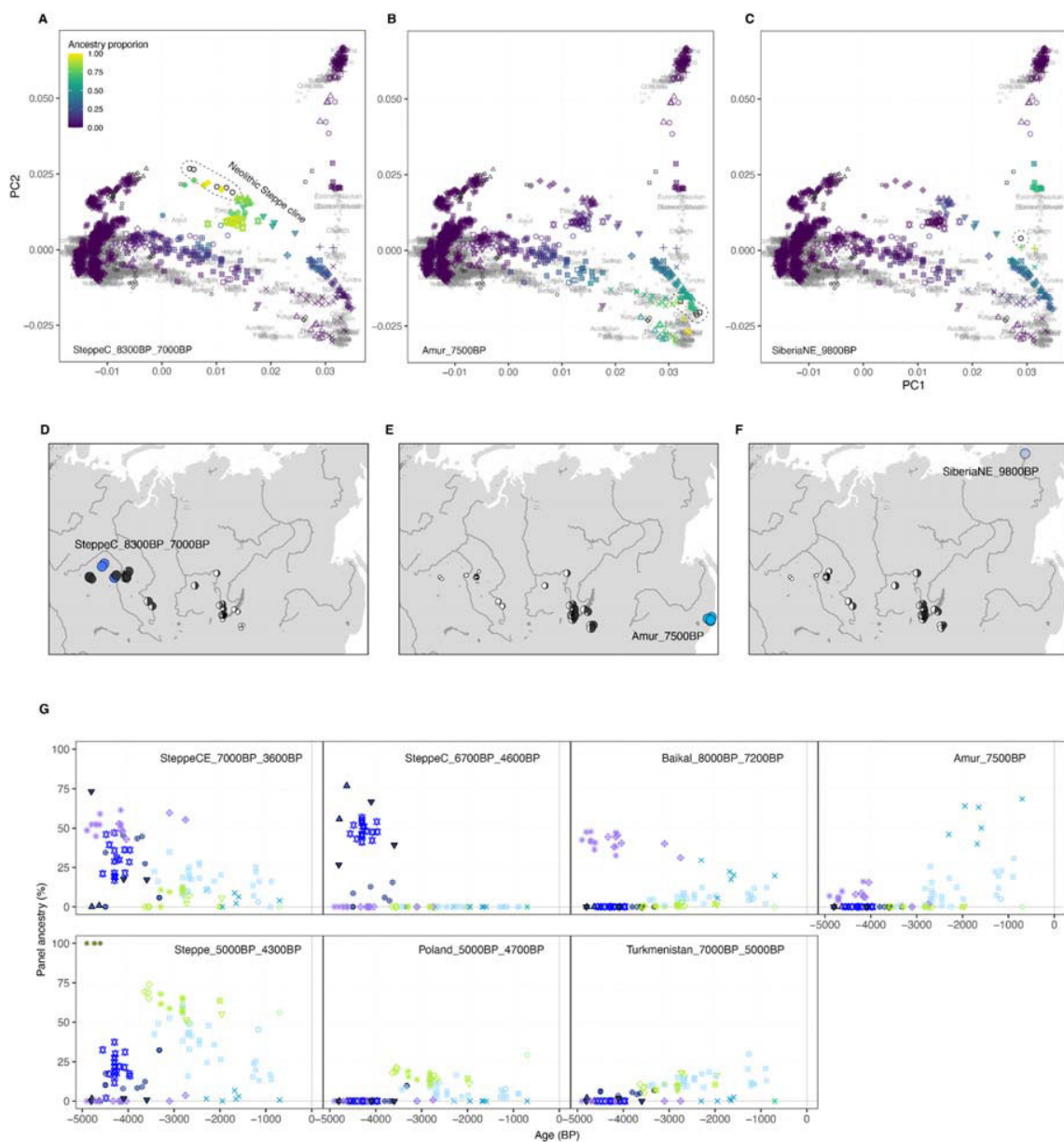
**Extended Data Fig. 7. Genetic transitions in Europe.** (A)-(C) Ancestry proportions contributed from preceding local groups to later individuals during the two major western Eurasian genetic transitions. (A) contribution to individuals

1295 with farmer ancestry from preceding local hunter-gatherer groups; (B,C) contribution to individuals with Steppe-related  
1296 ancestry from preceding local farmer groups. Coloured areas in all maps indicate the geographic extent of individuals  
1297 included in respective regions. (D) Composition of hunter-gatherer ancestry proportions from different source groups in  
1298 individuals with farmer ancestry, shown as heatmap (top) and barplots (bottom). Grey bars represent contributions from  
1299 local hunter-gatherers (E)-(G) Moon charts showing spatial distribution of estimated ancestry proportions of mid- to  
1300 late Neolithic farmer individuals from three clusters of early Neolithic European farmers (locations indicated with  
1301 coloured symbols). Estimated ancestry proportions are indicated by size and amount of fill of moon symbols. (H, I)  
1302 Estimated time of admixture between (H) local hunter-gatherer groups and farmers and (I) eastern European farmers  
1303 with GAC-related ancestry and Steppe pastoralist groups. Black diamonds and error bars represent point estimate and  
1304 standard errors of admixture time, coloured bars show temporal range of included target individuals. The time to  
1305 admixture was adjusted backwards by the average age of individuals for each region. (J) Correlation between estimated  
1306 proportions of Steppe-related and GAC farmer-related ancestries, across west Eurasian target individuals. Symbol shape  
1307 and colour indicate the genetic cluster of respective individuals.  
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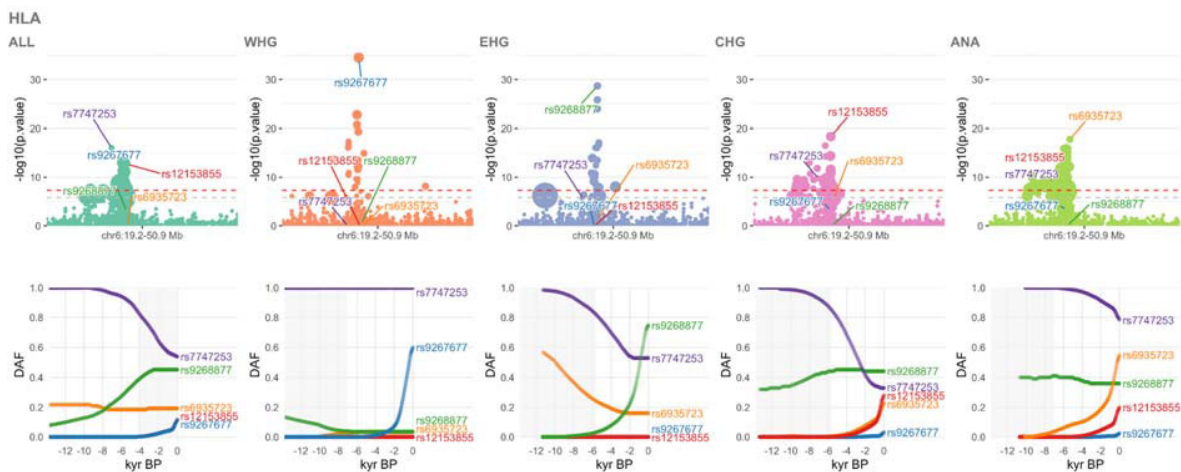
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**Extended Data Fig. 8. Fine-scale structure in Late Neolithic Scandinavians.** (A)-(E) Geographic locations and PCA based on pairwise IBD sharing (middle) of 148 European individuals predating 3,000 BP. Geographic locations are shown for 65 individuals belonging to the five genetic clusters observed in 38 ancient Scandinavians (temporal sequence shown in timeline in centre of plot). Individual assignments and frequency distribution of major Y chromosome haplogroups are indicated by maps and timeline. Plot symbols with black circles indicate the 38 Scandinavian individuals in the PCA panels. Ancestry proportions for the 38 Scandinavian individuals estimated using proximal source groups from outside Scandinavia (“postNeolScand” source set) are shown on the right of the respective cluster results.



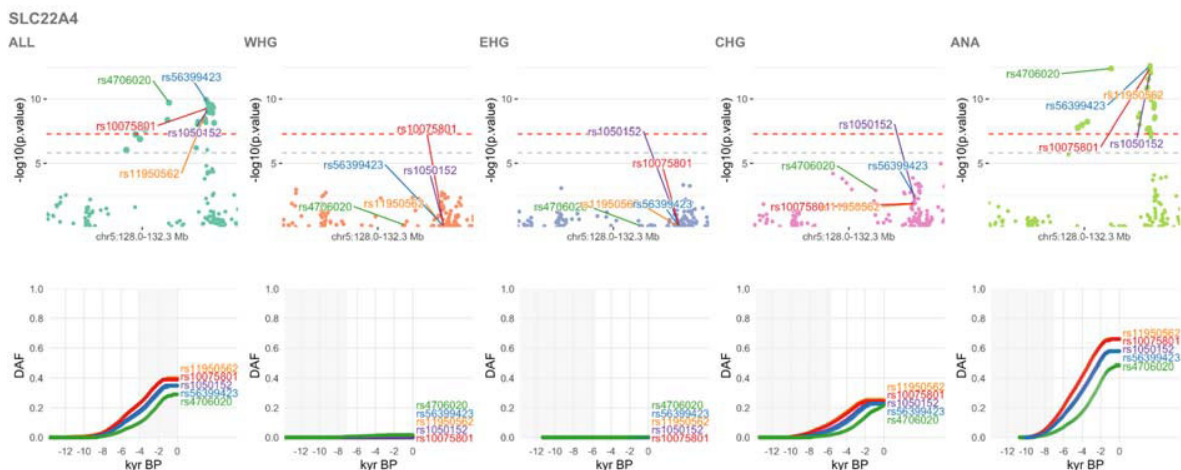
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1319 **Extended Data Fig. 9. Genetic transformations across the Eurasian Steppe.** (A)–(C) Principal component analysis  
 1320 of modern and ancient individuals from Eurasia, Oceania and the Americas, highlighting estimated ancestry proportions  
 1321 from “deep” Siberian ancestry sources (individuals highlighted with dashed line). Present-day individuals are shown in  
 1322 gray, with population labels corresponding to their median coordinates. (D)–(E) Moon charts showing spatial  
 1323 distribution of estimated ancestry proportions of Siberian hunter-gatherers before 5,000 BP from “deep” Siberian  
 1324 ancestry sources (names and locations indicated with coloured symbols). Estimated ancestry proportions are indicated  
 1325 by size and amount of fill of moon symbols. (G) Timelines of ancestry proportions from “postNeol” sources in Central  
 1326 and North Asian ancient individuals after 5,000 BP. Symbol shape and colour indicate the genetic cluster of each  
 1327 individual.  
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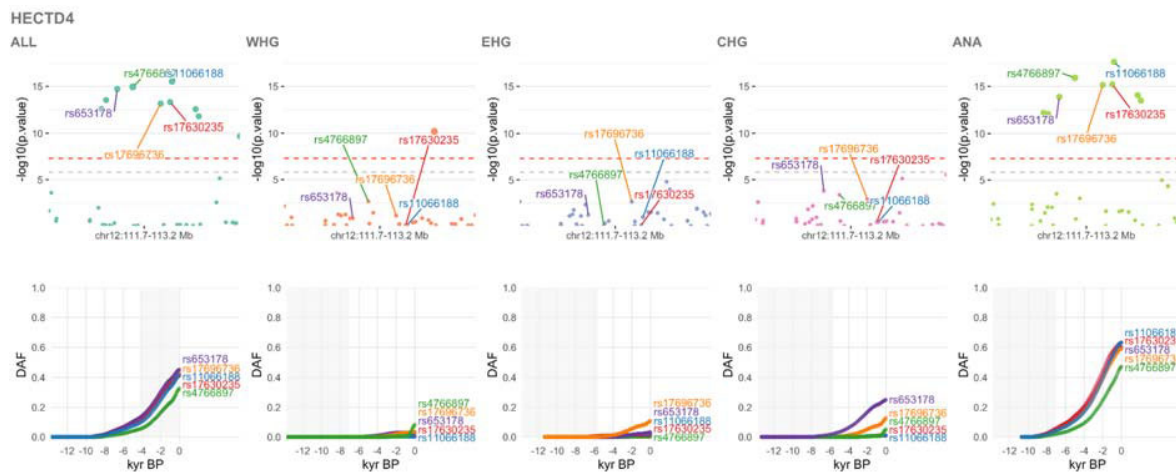
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**Extended Data Fig. 10. Selection at the HLA locus.** Results for the pan-ancestry analysis (ALL) plus the four marginal ancestries: Western hunter-gatherers (WHG), Eastern hunter-gatherers (EHG), Caucasus hunter-gatherers (CHG) and Anatolian farmers (ANA). Row one shows zoomed Manhattan plots of the p-values for each ancestry (significant SNPs sized by their selection coefficients), and row two shows allele trajectories for the top SNPs across all ancestries (grey shading for the marginal ancestries indicates approximate temporal extent of the pre-admixture population).



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**Extended Data Fig. 11. Selective sweep at the *SLC22A4* locus.** Results for the pan-ancestry analysis (ALL) plus the four marginal ancestries: Western hunter-gatherers (WHG), Eastern hunter-gatherers (EHG), Caucasus hunter-gatherers (CHG) and Anatolian farmers (ANA). Row one shows zoomed Manhattan plots of the p-values for each ancestry (significant SNPs sized by their selection coefficients), and row two shows allele trajectories for the top SNPs across all ancestries (grey shading for the marginal ancestries indicates approximate temporal extent of the pre-admixture population).



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1352 **Extended Data Fig. 12. Selective sweep at the *HECTD4* locus.** Results for the pan-ancestry analysis (ALL) plus the  
1353 four marginal ancestries: Western hunter-gatherers (WHG), Eastern hunter-gatherers (EHG), Caucasus hunter-gatherers  
1354 (CHG) and Anatolian farmers (ANA). Row one shows zoomed Manhattan plots of the p-values for each ancestry  
1355 (significant SNPs sized by their selection coefficients), and row two shows allele trajectories for the top SNPs across all  
1356 ancestries (grey shading for the marginal ancestries indicates approximate temporal extent of the pre-admixture  
1357 population).

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1359 **Data availability**

1360 All collapsed and paired-end sequence data for novel samples sequenced in this study will be made  
1361 publicly available on the European Nucleotide Archive, together with trimmed sequence alignment  
1362 map files, aligned using human build GRCh37. Previously published ancient genomic data used in  
1363 this study is detailed in Supplementary Table VII, and are all already publicly available.  
1364 Bioarchaeological data (including Accelerator Mass Spectrometry results) are included in the online  
1365 supplementary materials of this submission.  
1366

1367 **Code availability**

1368 The modified version of CLUES used in this study is available from [https://github.com/standard-](https://github.com/standard-aaron/clues)  
1369 [aaron/clues](https://github.com/standard-aaron/clues). The pipeline and conda environment necessary to replicate the analysis of allele  
1370 frequency trajectories of trait-associated variants in Supplementary Note 4a are available on Github  
1371 at [https://github.com/ekirving/mesoneo\\_paper](https://github.com/ekirving/mesoneo_paper). The pipeline to replicate the analyses for  
1372 Supplementary Note 4c-4e can be found at <https://github.com/albarema/neo>. All other analyses  
1373 relied upon available software which has been fully referenced in the manuscript and detailed in  
1374 the relevant supplementary notes.  
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## 1779 **Acknowledgements**

1780 This publication, the culmination of a research effort lasting over a decade, is dedicated to the memory of Pia  
1781 Bennike, who was part of a small core team that initiated the project. Sadly Pia passed away in 2017 but this  
1782 study, and many others, testifies to her tremendous efforts and knowledge on Danish prehistoric skeletal  
1783 material.

1784  
1785 We are deeply indebted to former and present staff members at the National Museum, the Anthropological  
1786 Laboratory, the regional museums and citizen scientists of Denmark, who for many generations carefully  
1787 collected, recorded and curated the prehistoric skeletal remains that form a key component of this study. We  
1788 are equally thankful to curators of the many other institutions across major parts of Eurasia, who to the  
1789 benefit of following generations curated human skeletal remains and gave us access and permission to  
1790 sample this precious material. We also thank all the former and current staff at the Lundbeck Foundation  
1791 GeoGenetics Centre and the GeoGenetics Sequencing Core, and to colleagues across the many institutions  
1792 detailed below. We are particularly grateful to Line Olsen as project manager for the Lundbeck Foundation  
1793 GeoGenetics Centre project, and to Pernille Selmer Olsen for assisting with sample processing. We thank  
1794 UK Biobank Ltd. for access to the UK Biobank genomic resource. We are thankful to Illumina Inc. for  
1795 collaboration and to L. Speidel for assistance in running *Relate*. EW thanks St. John’s College, Cambridge,  
1796 for providing a stimulating environment of discussion and learning.

1797  
1798 The Lundbeck Foundation GeoGenetics Centre is supported by the the Lundbeck Foundation (R302-2018-  
1799 2155, R155-2013-16338), the Novo Nordisk Foundation (NNF18SA0035006), the Wellcome Trust  
1800 (UNS69906), Carlsberg Foundation (CF18-0024), the Danish National Research Foundation (44113220) and  
1801 the University of Copenhagen (KU2016 programme). This research has been conducted using the UK  
1802 Biobank Resource and the iPSYCH Initiative, funded by the Lundbeck Foundation (R102-A9118 and R155-  
1803 2014-1724). This work was further supported by the Swedish Foundation for Humanities and Social  
1804 Sciences grant (Riksbankens Jubileumsfond M16-0455:1) to KK. M.E.A. was supported by Marie  
1805 Skłodowska-Curie Actions of the EU (grant no. 300554), The Villum Foundation (grant no. 10120) and  
1806 Independent Research Fund Denmark (grant no. 7027-00147B). W.B. is supported by the Hanne and Torkel  
1807 Weis-Fogh Fund (Department of Zoology, University of Cambridge); AP is funded by Wellcome grant  
1808 WT214300, B.S.d.M and O.D. by the Swiss National Science Foundation (SFNS PP00P3\_176977) and  
1809 European Research Council (ERC 679330); M.N. by the Human Frontier Science Program Postdoctoral  
1810 Fellowship (LT000143/2019-L4); R. Macleod by an SSHRC doctoral studentship grant (G101449:  
1811 ‘Individual Life Histories in Long-Term Cultural Change’); G.R. by a Novo Nordisk Foundation Fellowship  
1812 (gNNF20OC0062491); N.N.J. by Aarhus University Research Foundation; H.S. by a Carlsberg Foundation  
1813 Fellowship (CF19-0601); G.S. by Marie Skłodowska-Curie Individual Fellowship ‘PALAEO-ENEO’ (grant

1814 agreement number 751349); A.J. Schork by a Lundbeckfonden Fellowship (R335-2019-2318) and the  
1815 National Institute on Aging (NIH award numbers U19AG023122, U24AG051129, and UH2AG064706);  
1816 A.V.L. and I.V.S. by the Science Committee, Ministry of Education and Science of the Republic of  
1817 Kazakhstan (AP08856317); B.G.R. and MGM by the Spanish Ministry of Science and Innovation (Project  
1818 HAR2016-75605-R); C.M.-L. and O.R. by the Italian Ministry for the Universities (grants '2010-11  
1819 prot.2010EL8TXP\_001 Biological and cultural heritage of the central-southern Italian population trough 30  
1820 thousand Years' and '2008 prot. 2008B4J2HS\_001 Origin and diffusion of farming in central-southern Italy:  
1821 a molecular approach'); D.C.-S. and I.G.Z. by the Spanish Ministry of Science and Innovation (Project  
1822 HAR2017-86262-P). D.C.S.G. acknowledges funding from the Generalitat Valenciana  
1823 (CIDEGENT/2019/061) and the Spanish Government (EUR2020-112213); D.B. was supported by the  
1824 NOMIS Foundation and Marie Skłodowska-Curie Global Fellowship 'CUSP' (grant no. 846856); E.R.U. by  
1825 the Science Committee, Ministry of Education and Science of the Republic of Kazakhstan (AP09261083:  
1826 "Transcultural Communications in the Late Bronze Age (Western Siberia - Kazakhstan - Central Asia)");  
1827 E.C. by Villum Fonden (17649); J.E.A.T. by the Spanish Ministry of Economy and Competitiveness,  
1828 (HAR2013-46861-R) and Generalitat Valenciana (Aico/ 2018/125 and Aico 2020/97). L.Y. acknowledges  
1829 funding by the Science Committee of the Armenian Ministry of Education and Science (Project 21AG-  
1830 1F025), L.V. by ERC Consolidator Grant 'PEGASUS' (agreement no. 681605); M. Sablin by the Russian  
1831 Ministry of Science and Higher Education (075-15-2021-1069); N.C. by Historic Environment Scotland;  
1832 S.V. by the Russian Ministry of Science and Higher Education (075-15-2020-910); V.M. by the Science  
1833 Committee, Ministry of Education and Science of the Republic of Kazakhstan (AR08856925). V.A. is  
1834 supported by a Lundbeckfonden Fellowship (R335-2019-2318); P.H.S. by the National Institute of General  
1835 Medical Sciences (R35GM142916); S.R. by the Novo Nordisk Foundation (NNF14CC0001); R.D. by the  
1836 Wellcome Trust (WT214300); R.N. by the National Institute of General Medical Sciences (NIH grant  
1837 R01GM138634); F. Racimo by a Villum Fonden Young Investigator Grant (no. 00025300). T.W. and V.A.  
1838 are supported by the Lundbeck Foundation iPSYCH initiative (R248-2017-2003).  
1839

## 1840 **Author Information**

1841 These authors contributed equally: Morten E. Allentoft, Martin Sikora, Alba Refoyo-Martínez, Evan K.  
1842 Irving-Pease, Anders Fischer, William Barrie & Andrés Ingason

1843

1844 These authors equally supervised research: Thorfinn Korneliussen, Richard Durbin, Rasmus Nielsen, Olivier  
1845 Delaneau, Thomas Werge, Fernando Racimo, Kristian Kristiansen & Eske Willerslev

1846

### 1847 Affiliations

1848

1849 **Lundbeck Foundation GeoGenetics Centre, GLOBE Institute, University of Copenhagen,**  
1850 **Copenhagen, Denmark**

1851 Morten E. Allentoft, Martin Sikora, Alba Refoyo-Martínez, Evan K. Irving-Pease, Andrés Ingason, Jesper  
1852 Stenderup, Fabrice Demeter, Maria Novosolov, Ruairidh Macleod, Rasmus A. Henriksen, Tharsika Vimala,  
1853 Hugh McColl, Lasse Vinner, Gabriele Scorrano, Abigail Ramsøe, Anders Rosengren, Anthony Ruter, Anne  
1854 Birgitte Gotfredsen, Charleen Gaunitz, Fulya Eylem Yediay, Isin Altinkaya, Lei Zhao, Peter de Barros  
1855 Damgaard, Kurt H. Kjær, Thorfinn Korneliussen, Rasmus Nielsen, Thomas Werge, Fernando Racimo,  
1856 Kristian Kristiansen & Eske Willerslev

1857

1858 **Trace and Environmental DNA (TrEnD) Laboratory, School of Molecular and Life Sciences, Curtin**  
1859 **University, Perth, Australia**

1860 Morten E. Allentoft  
1861  
1862 **GeoGenetics Group, Department of Zoology, University of Cambridge, Cambridge, UK**  
1863 William Barrie, Alice Pearson, Ruairidh Macleod & Eske Willerslev  
1864  
1865 **Department of Historical Studies, University of Gothenburg, Gothenburg, Sweden**  
1866 Anders Fischer, Karl-Göran Sjögren, Bettina Schulz Paulsson, Malou Blank & Kristian Kristiansen  
1867  
1868 **Institute of Biological Psychiatry, Mental Health Services, Copenhagen University Hospital, Roskilde,**  
1869 **Denmark**  
1870 Andrés Ingason, Vivek Appadurai,  
1871  
1872 **The National Museum of Denmark, Ny Vestergade 10, Copenhagen, Denmark**  
1873 Lasse Sørensen, Poul Otto Nielsen, Morten Fischer Mortensen, Peter Rasmussen, Peter Vang Petersen,  
1874  
1875 **Sealand Archaeology, Gl. Roesnaesvej 27, 4400 Kalundborg, Denmark**  
1876 Anders Fischer  
1877  
1878 **Department of Genetics, University of Cambridge, Cambridge, UK**  
1879 Alice Pearson & Richard Durbin  
1880  
1881 **Wellcome Sanger Institute, Wellcome Genome Campus, Cambridge, UK**  
1882 Richard Durbin & Eske Willerslev  
1883  
1884 **Department of Computational Biology, University of Lausanne, Switzerland**  
1885 Bárbara Sousa da Mota & Olivier Delaneau  
1886  
1887 **Swiss Institute of Bioinformatics, University of Lausanne, Switzerland**  
1888 Bárbara Sousa da Mota  
1889  
1890 **Department of Integrative Biology, University of California, Berkeley, USA**  
1891 Alma S. Halgren, Peter H. Sudmant & Rasmus Nielsen  
1892  
1893 **Center for Computational Biology, University of California, Berkeley, USA**  
1894 Andrew Vaughn, Aaron J. Stern, Peter H. Sudmant & Rasmus Nielsen  
1895  
1896 **Laboratory of Biological Anthropology, Department of Forensic Medicine, University of Copenhagen,**  
1897 **Copenhagen, Denmark**  
1898 Marie Louise Schjellerup Jørkov & Niels Lynnerup  
1899  
1900 **Muséum National d'Histoire Naturelle, Paris, France**  
1901 Fabrice Demeter  
1902  
1903 **Research department of Genetics, Evolution and Environment, University College London, London,**  
1904 **UK**  
1905 Ruairidh Macleod  
1906

1907 **Section for Evolutionary Genomics, GLOBE Institute, University of Copenhagen, Copenhagen,**  
1908 **Denmark**  
1909 Ashot Margaryan, Theis Zetner Trolle Jensen, Hannes Schroeder, Enrico Cappellini  
1910  
1911 **Centre for Evolutionary Hologenomics, University of Copenhagen, Copenhagen, Denmark**  
1912 Ashot Margaryan  
1913  
1914 **Anthropology Department, University of Utah, USA**  
1915 Melissa Illardo  
1916  
1917 **Department of Geology, Lund University, Lund, Sweden**  
1918 Anne Birgitte Nielsen  
1919  
1920 **Department of Archaeology and Ancient History, Lund University, Lund, Sweden**  
1921 Lars Larsson  
1922  
1923 **Tårnby Gymnasium og HF, Kastrup, Denmark**  
1924 Mikkel Ulfeldt Hede  
1925  
1926 **Department of Health Technology, Section of Bioinformatics, Technical University of Denmark,**  
1927 **Kongens Lyngby, Denmark**  
1928 Gabriel Renaud  
1929  
1930 **Department of Archaeology and Heritage Studies, Aarhus University, Aarhus, Denmark**  
1931 Niels N. Johannsen, Rikke Maring  
1932  
1933 **Institute of Biological Psychiatry, Mental Health Centre Sct Hans, Copenhagen University Hospital,**  
1934 **Denmark**  
1935 Andrew J. Schork, Anders Rosengren & Thomas Werge  
1936  
1937 **Department of Clinical Medicine, University of Copenhagen, 2200 Copenhagen N, Denmark**  
1938 Thomas Werge  
1939  
1940 **Neurogenomics Division, The Translational Genomics Research Institute (TGEN), Phoenix, AZ, USA**  
1941 Andrew J. Schork  
1942  
1943 **Terra Ltd., Letchik Zlobin St. 20, Voronezh, 394055, Russian Federation**  
1944 Andrey Skorobogatov, Ruslan Turin  
1945  
1946 **Department of Archaeology, University of Exeter, Exeter, UK**  
1947 Alan K. Outram & Catriona J. McKenzie  
1948  
1949 **Institute of Archaeology and Ethnography, Siberian Branch of the Russian Academy of Sciences,**  
1950 **Novosibirsk, Russian Federation**  
1951 Aleksey A. Timoshchenko, Dmitri V. Pozdnyakov, Liudmila N. Mylnikova, Marina S. Nesterova &  
1952 Vyacheslav I. Molodin  
1953

- 1954 **Institute of Ethnology and Anthropology, Russian Academy of Sciences, Moscow, Russian Federation**  
1955 Elizaveta V. Veselovskaya, Sergey Vasilyev  
1956  
1957 **Centre for Egyptological studies, Russian Academy of Sciences, Moscow, Russia**  
1958 Sergey Vasilyev  
1959  
1960 **Research Institute and Museum of Anthropology, Lomonosov Moscow State University, Mokhovaya**  
1961 **str. 11, Moscow, Russian Federation**  
1962 Alexandra Buzhilova, Natalia Berezina, Svetlana Borutskaya  
1963  
1964 **Department of Environmental Biology, Sapienza University of Rome, Rome, Italy**  
1965 Alfredo Coppa, Dušan Borić  
1966  
1967 **Peter the Great Museum of Anthropology and Ethnography (Kunstkamera), Russian Academy of**  
1968 **Sciences, Saint Petersburg, Russian Federation**  
1969 Alisa Zubova & Vyacheslav Moiseyev  
1970  
1971 **CIAS, Department of Life Science, University of Coimbra, Coimbra, Portugal**  
1972 Ana Maria Silva  
1973  
1974 **UNIARQ, University of Lisbon, Lisbon, Portugal**  
1975 Ana Maria Silva & João Zilhão  
1976  
1977 **Kostanay Regional University A. Baitursynov, Kostanay, Kazakhstan**  
1978 Andrey V. Logvin, Irina V. Shevnina  
1979  
1980 **Vesthimmerlands Museum, Søndergade 44, Aars, Denmark**  
1981 Bjarne Henning Nielsen  
1982  
1983 **Museum Nordsjælland, Frederiksgade 9, 3400 Hillerød**  
1984 Per Lotz, Søren Anker Sørensen, Thomas Jørgensen  
1985  
1986 **Museum Vestsjælland, Klosterstræde 18, 4300 Holbæk, Denmark**  
1987 Per Lotz  
1988  
1989 **Vendsyssel Historiske Museum, DK-9800 Hjørring, Denmark**  
1990 Per Lysdahl, Sidsel Wåhlin  
1991  
1992 **Moesgaard Museum, Moesgård Allé 15, Højbjerg, Denmark**  
1993 Søren H. Andersen  
1994  
1995 **Grupo EvoAdapta, Departamento de Ciencias Históricas, Universidad de Cantabria, Santander, Spain**  
1996 Borja González-Rabanal  
1997  
1998 **Museu de Ciències Naturals de Barcelona, Barcelona, Spain**  
1999 Carles Lalueza-Fox  
2000



- 2001 **Institute of Evolutionary Biology, CSIC-Universitat Pompeu Fabra, Barcelona, Spain**  
2002 Carles Lalueza-Fox  
2003
- 2004 **ICREA, University of Barcelona, Barcelona, Spain**  
2005 João Zilhão  
2006
- 2007 **Departamento de Prehistoria y Arqueología Department, Universidad Autónoma de Madrid, Madrid, Spain**  
2008  
2009 Concepción Blasco, Corina Liesau, Patricia Ríos  
2010
- 2011 **Department of Biology, University of Rome "Tor Vergata", Rome, Italy**  
2012 Cristina Martinez-Labarga, Olga Rickards  
2013
- 2014 **Department of History, Humanities and Society, University of Rome "Tor Vergata", Rome, Italy**  
2015 Mario Federico Rolfo  
2016
- 2017 **Instituto Internacional de Investigaciones Prehistóricas de Cantabria, Universidad de Cantabria, Santander, Spain**  
2018  
2019 David Cuenca-Solana, Igor Gutiérrez Zugasti & Manuel González-Morales  
2020
- 2021 **Centre de Recherche en Archéologie, Archeosciences, Histoire (CReAAH), UMR-6566 CNRS, Rennes, France**  
2022  
2023 David Cuenca-Solana  
2024
- 2025 **Georgian National Museum, Tbilisi, Georgia**  
2026 David O. Lordkipanidze  
2027
- 2028 **Tbilisi State University, Tbilisi, Georgia**  
2029 David O. Lordkipanidze  
2030
- 2031 **IPND, Tyumen Scientific Centre, Siberian Branch of the Russian Academy of Sciences, Tyumen, Russian Federation**  
2032  
2033 Dmitri Enshin, Olga Poshekhonova, Svetlana N. Skochina  
2034
- 2035 **Departament de Prehistòria, Arqueologia i Història Antiga, Universitat de València, València, Spain**  
2036 Domingo C. Salazar-García, J.Emili Aura Tortosa  
2037
- 2038 **Department of Geological Sciences, University of Cape Town, Cape Town, South Africa**  
2039 Domingo C. Salazar-García  
2040
- 2041 **Department of Anthropology, New York University, New York, USA.**  
2042 Dušan Borić  
2043
- 2044 **Institute of Humanities, Ivanovo State University, Ivanovo, Russian Federation**  
2045 Elena Kostyleva  
2046
- 2047 **Saryarka Archaeological Institute, Buketov Karaganda University, Karaganda, Kazakhstan**

2048 Emma R. Usmanova  
2049  
2050 **South Ural State University, Chelyabinsk, Russia**  
2051 Emma R. Usmanova  
2052  
2053 **The Saxo Institute, University of Copenhagen, Copenhagen, Denmark**  
2054 Erik Brinch Petersen, Rune Iversen  
2055  
2056 **Museum Østjylland, Stemannsgade 2, Randers, Denmark**  
2057 Esben Kannegaard, Lutz Klassen  
2058  
2059 **Soprintendenza Archeologia Belle Arti e Paesaggio per la Città Metropolitana di Bari, Via Pier**  
2060 **l'Eremita, 25, 70122, Bari, Italy**  
2061 Francesca Radina  
2062  
2063 **Soprintendenza per i Beni Archeologici delle Marche, Via Birarelli 18, 60100, Ancona, Italy**  
2064 Mara Silvestrini  
2065  
2066 **Soprintendenza Archeologia, Belle Arti e Paesaggio per la provincia di Cosenza, Cosenza, Italy**  
2067 Paola Aurino  
2068  
2069 **UMR 5199 PACEA, CNRS, Université de Bordeaux, 33615 Pessac, France**  
2070 Henri Duday, Patrice Courtaud  
2071  
2072 **Institute of Archaeology, National Academy of Sciences of Ukraine, Kyiv, Ukraine**  
2073 Inna Potekhina  
2074  
2075 **National University of Kyiv-Mohyla Academy, Kyiv, Ukraine**  
2076 Inna Potekhina  
2077  
2078 **Collège de France, 75231 Paris cedex 05, France**  
2079 Jean Guilaine  
2080  
2081 **Odense City Museums, Overgade 48, Odense, Denmark**  
2082 Jesper Hansen  
2083  
2084 **Museum Sydøstdanmark, Algade 97, 4760 Vordingborg, Denmark**  
2085 Kristoffer Buck Pedersen  
2086  
2087 **Institute of Archaeology and Ethnology, Polish Academy of Sciences, Kraków, Poland**  
2088 Krzysztof Tunia, Piotr Włodarczyk  
2089  
2090 **CNRS UMR 5608, Toulouse Jean Jaurès University, Maison de la Recherche, 5 Allées Antonio**  
2091 **Machado, 31058 Toulouse, Cedex 9, France**  
2092 Laure Metz & Ludovic Slimak  
2093  
2094 **ARGEA Consultores SL, C. de San Crispín, Madrid, Spain**

- 2095 Jorge Vega, Roberto Menduiña  
2096  
2097 **Institute of Molecular Biology, National Academy of Sciences, Yerevan, Armenia**  
2098 Levon Yepiskoposyan  
2099  
2100 **Russian-Armenian University, Yerevan, Armenia**  
2101 Levon Yepiskoposyan  
2102  
2103 **Institute of Archaeology and Ethnography, National Academy of Sciences, Yerevan, Armenia**  
2104 Ruben Badalyan  
2105  
2106 **HistorieUdvikler, Gl. Roesnaesvej 27, DK-4400 Kalundborg, Denmark**  
2107 Lisbeth Pedersen  
2108  
2109 **Department of history and cultural heritage, University of Siena, Siena, Italy**  
2110 Lucia Sarti, Mauro Calattini  
2111  
2112 **Centre d'Anthropobiologie et de Génomique de Toulouse, CNRS UMR 5288, Université Paul Sabatier,**  
2113 **Toulouse, France**  
2114 Ludovic Orlando  
2115  
2116 **Västergötlands museum, Stadsträdgården, Skara, Sweden**  
2117 Maria Vretemark  
2118  
2119 **Cabinet of Anthropology, Tomsk State University, Tomsk, Russian Federation**  
2120 Marina P. Rykun  
2121  
2122 **Institute for Eastern Research, Adam Mickiewicz University in Poznań, Poznań, Poland**  
2123 Marzena H. Szmyt  
2124  
2125 **Institute of Archaeology, Jagiellonian University, Ul. Gołębia 11, 31-007, Kraków, Poland**  
2126 Marcin Przybyła  
2127  
2128 **Zoological Institute of Russian Academy of Sciences, Universitetskaya nab. 1, 199034, St. Petersburg,**  
2129 **Russian Federation**  
2130 Mikhail Sablin  
2131  
2132 **Department of Anthropology, Czech National Museum, Prague, Czech Republic**  
2133 Miluše Dobisíková  
2134  
2135 **Department of Health and Nature, University of Greenland, Greenland**  
2136 Morten Meldgaard  
2137  
2138 **The Viking Ship Museum, Vindeboder 12, Roskilde, Denmark**  
2139 Morten Johansen, Otto Christian Uldum  
2140  
2141 **Archaeology Institute, University of Highlands and Islands, Scotland, UK**

2142 Nick Card  
2143  
2144 **Laboratory for Experimental Traceology, Institute for the History of Material Culture of the Russian**  
2145 **Academy of Sciences, Dvortsovaya nab., 18, 191186, St. Petersburg, Russian Federation**  
2146 Olga V. Lozovskaya  
2147  
2148 **Scientific Research Center “Baikal region”, Irkutsk State University; 1, K. Marx st., Irkutsk, 664003,**  
2149 **Russian Federation**  
2150 Nikolai A. Saveliev  
2151  
2152 **Paleoecology Laboratory, Institute of Plant and Animal Ecology, Ural Branch of the Russian Academy**  
2153 **of Sciences, Ekaterinburg, Russian Federation**  
2154 Pavel Kosintsev  
2155  
2156 **Department of History of the Institute of Humanities, Ural Federal University, Ekaterinburg, Russian**  
2157 **Federation**  
2158 Pavel Kosintsev  
2159  
2160 **Centre for the Study of Early Agricultural Societies, Department of Cross-Cultural and Regional**  
2161 **Studies, University of Copenhagen, 2300 Copenhagen, Denmark**  
2162 Peder Mortensen  
2163  
2164 **Museum of Cultural History, University of Oslo, P.O. Box 6762. St. Olavs Plass NO-0130 Oslo,**  
2165 **Norway**  
2166 Per Persson  
2167  
2168 **ArchaeoScience, GLOBE Institute, University of Copenhagen, Copenhagen, Denmark**  
2169 Pernille Bangsgaard  
2170  
2171 **Department of History, University of Santiago de Compostela, Spain**  
2172 Pilar Prieto Martinez  
2173  
2174 **Lipetsk Regional Scientific Public Organisation "Archaeological Research", Lipetsk, Russian**  
2175 **Federation**  
2176 Roman V. Smolyaninov  
2177  
2178 **Laboratory for Archaeological Chemistry, Department of Anthropology, University of Wisconsin-**  
2179 **Madison, Madison, USA**  
2180 T. Douglas Price  
2181  
2182 **Nizhny Tagil State Socio-Pedagogical Institute, Nizhny Tagil, Russia**  
2183 Yuri B. Serikov  
2184  
2185 **Institute for History of Medicine, First Faculty of Medicine, Charles University, Prague, Czech**  
2186 **Republic**  
2187 Vaclav Smrcka  
2188

2189 **Centre for Archaeological Research Toraighyrov University, Pavlodar, Kazakhstan**

2190 Victor Merz

2191

2192 **Malmö Museer, Malmöhusvägen 6, Malmö, Sweden**

2193 Yvonne Magnusson

2194

2195 **Institute of Statistical Sciences, School of Mathematics, University of Bristol, Bristol, UK**

2196 Daniel J. Lawson

2197

2198 **Novo Nordisk Foundation Centre for Protein Research, Faculty of Health and Medical Sciences,**

2199 **University of Copenhagen, Copenhagen N, Denmark**

2200 Simon Rasmussen

2201

2202 **MARUM, University of Bremen, Bremen, Germany**

2203 Eske Willerslev

2204

2205 Contributions

2206 M.E.A., M.S., A.R.-M., E.K.I.-P., A.F., W.B., and A.I. contributed equally to this work. M.E.A., M.S.,

2207 T.S.K., R.D., R.N., O.D., T.W., F. Racimo, K.K. and E.W. led the study. M.E.A., M.S., A.F., C.L.-F., R.N.,

2208 T.W., K.K. and E.W. conceptualised the study. M.E.A., M.S., H.S., L.O., T.S.K., R.D., R.N., O.D., T.W., F.

2209 Racimo, K.K. and E.W. supervised the research. M.E.A., L.O., R.D., R.N., T.W., K.K. and E.W. acquired

2210 funding for research. A.F., J.S., K.G.S., M.L.S.J., M.U.H., A.A.T., A.C., A.Z., A.M.S., A.J.H., A.G., A.V.L.,

2211 B.H.N., B.G.R., C.B., C.L., C.M.-L., D.V., D.C.-S., D.L., D.N., D.C.S.-G., D.B., E.K., E.V.V., E.R.U., E.

2212 Kannegaard, F. Radina, H.D., I.G.Z., I.P., I.V.S., J.G., J.H., J.E.A.T., J.Z., J.V., K.B.P., K.T., L.N., L.L.,

2213 L.M., L.Y., L.P., L. Sarti, L. Slimak, L.K., M.G.M., M. Silvestrini, M.V., M.S.N., M.P.R., M.H.S., M.P.,

2214 M.C., M. Sablin, N.C., O.P., O.R., O.V.L., P.A., P.K., P.C., P. Ríos, P. Lotz, P. Lysdahl, P.P., P.B., P.d.B.D.,

2215 P.V.P., P.P.M., P.W., R.V.S., R. Maring, R. Mendiña, R.B., R.T., S.V., S.W., S.B., S.N.S., S.A.S., S.H.A.,

2216 T.D.P., T.J., Y.B.S., V.I.M., V.S., V.M., Y.M. and N.L. were involved in sample collection. M.E.A., M.S.,

2217 A.R.-M., E.K.I.-P., W.B., A.I., J.S., A.P., B.S.d.M., M.I., L.V., A.J. Stern, C.G., F.E.Y., D.J.L., T.S.K., R.D.,

2218 R.N., O.D., F. Racimo, K.K. and E.W. were involved in developing and applying methodology. J.S., C.G.

2219 and L.V. led the DNA laboratory work research component. K.G.S. led bioarchaeological data curation.

2220 M.E.A., M.S., A.R.-M., E.K.I.-P., W.B., A.I., A.P., B.S.d.M., B.S.P., A.S.H., R.A.H., T.V., H.M., A.M.,

2221 A.V., A.B.N., P. Rasmussen, G.R., A. Ramsøe, A.S., A.J. Schork, A. Rosengren, C.J.M., I.A., L.Z.,

2222 R. Maring, V.S., V.A., P.H.S., S.R., T.S.K., O.D. and F. Racimo undertook formal analyses of data. M.E.A.,

2223 M.S., A.R.-M., E.K.I.-P., A.F., W.B., A.I., K.G.S., D.J.L., P.H.S., T.S.K., and F. Racimo drafted the main

2224 text (M.E.A. and M.S. led this). M.E.A., M.S., A.R.-M., E.K.I.-P., A.F., W.B., A.I., K.G.S., A.P., B.S.d.M.,

2225 B.S.P., A.S.H., R. Macleod, R.A.H., T.V., M.F.M., A.B.N., M.U.H., P. Rasmussen, A.J. Stern, N.N.J., H.S.,

2226 G.S., A. Ramsøe, A.S., A. Rosengren, A.K.O., A.B., A.C., A.G., A.V.L., A.B.G., C.J.M., D.C.S.-G., E.

2227 Kostyleva, E.R.U., E. Kannegaard, I.G.Z., I.P., I.V.S., J.G., J.H., J.E.A.T., L.Z., L.Y., L.P., L.K., M.B.,

2228 M.G.M., M.V., M.P.R., M.J., N.B., O.V.L., O.C.U., P.K., P. Lysdahl, P.B., P.W., R.V.S., R. Maring, R.B.,

2229 R.I., S.V., S.W., S.B., S.H.A., T.J., V.S., D.J.L., P.H.S., S.R., T.S.K., O.D. and F. Racimo drafted

2230 supplementary notes and materials. M.E.A., M.S., A.R.-M., E.K.I.-P., A.F., W.B., A.I., G.G.S., A.S.H.,

2231 M.L.S.J., F.D., R. Macleod, L. Sørensen, P.O.N., R.A.H., T.V., H.M., A.M., N.N.J., H.S., A. Ramsøe, A.S.,

2232 A.J. Schork, A. Ruter, A.K.O., B.H.N., B.G.R., D.C.-S., D.C.S.-G., I.G.Z., I.P., J.G., J.E.A.T., L.Z., L.O.,

2233 L.K., M.G.M., P.d.B.D., R.I., S.A.S., D.J.L., P.H.S., T.S.K., R.D., R.N., O.D., T.W., F. Racimo, K.K. and

2234 E.W. were involved in reviewing drafts and editing (M.E.A., A.F., K.G.S., F.D., R. Macleod, H.M. and T.V.

2235 led this). All co-authors read, commented on, and agreed upon the submitted manuscript.

2236

2237 Corresponding authors

2238

2239 Correspondence to Morten E. Allentoft ([morten.allentoft@curtin.edu.au](mailto:morten.allentoft@curtin.edu.au)), Martin Sikora

2240 ([martin.sikora@sund.ku.dk](mailto:martin.sikora@sund.ku.dk)), Eske Willerslev ([ew482@cam.ac.uk](mailto:ew482@cam.ac.uk)).

2241

2242 **Ethics declarations**

2243

2244 Competing interests

2245

2246 The authors declare no competing interests.