

Lasting Lower Rhine–Meuse forager ancestry shaped Bell Beaker expansion

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Ancient DNA studies revealed that, in Europe from 6500 to 4000 BCE, descendants of western Anatolian farmers mixed with local hunter-gatherers resulting in 70–100% ancestry turnover¹, then steppe ancestry spread with the Corded Ware complex 3000–2500 BCE². Here we document an exception in the wetland, riverine and coastal areas of the Netherlands, Belgium and western Germany, using genome-wide data from 112 people 8500–1700 BCE. A distinctive population with high (approximately 50%) hunter-gatherer ancestry persisted 3,000 years later than in most European regions, reflecting incorporation of female individuals of Early European Farmer ancestry into local communities. In the western Netherlands, the arrival of the Corded Ware complex was also exceptional: lowland individuals from settlements adopting Corded Ware pottery had hardly any steppe ancestry, despite a Y-chromosome characteristic of people associated with the early Corded Ware complex. These distinctive patterns may reflect the specific ecology that they inhabited, which was not amenable to full adoption of the early Neolithic type of farming introduced with Linearbandkeramik³, and resulted in distinct communities where transfer of ideas was accompanied by little gene flow. This changed with the formation of Lower Rhine–Meuse Bell Beaker users by fusion of local people (13–18%) and Corded Ware associated migrants of both sexes. Their subsequent expansion then had a disruptive impact across a much wider part of northwestern Europe, especially in Great Britain where they were the main source of a 90–100% replacement of local Neolithic ancestry.

Whole-genome ancient DNA (aDNA) analysis has illuminated long-standing debates about cultural and demographic transformations in Holocene Europe. Two major prehistoric events have been characterized: the spread of genetic ancestry originating from western Anatolian farmers into Europe associated with the introduction of farming in the Early Neolithic⁴, and the spread of ancestry characteristic of Yamnaya steppe pastoralists during the third millennium BCE^{2,5–7}, mediated by the dispersal of the Corded Ware (CW) and Bell Beaker (BB) complexes. However, the demographic processes at the regional level are still not clearly understood and have been shown to follow variable patterns. For example, while the spread of Anatolian ancestry in central Europe was primarily propelled by the expansion of Linearbandkeramik (LBK) farmers^{1,4,5}, in the Baltic region and Scandinavia adoption of the farming lifestyle took place much later and, in some cases, there was even a return to hunting, gathering and fishing^{8–10}.

Here we focus on the unique trajectory of communities from water-rich environments in the wider Lower Rhine–Meuse area in western and central Netherlands, Belgium, and northern and northwestern Germany. Around 5500 BCE, the southern part of this region witnessed the arrival of LBK-associated farmers, who settled across the fertile loess soils in the south of the Netherlands and parts of Belgium, Germany and France. Within these communities, there is evidence of contact with hunter-gatherer groups, as documented by Limburg and La Hoguette pottery¹¹, although the origin of these ceramics and the importance¹² of these contacts are debated³. Once established, these LBK communities developed into regional variants such as the Blicquy, Rössen, Villeneuve-Saint-Germain, Bischheim and the later southern Michelsberg groups.

North of the loess, large rivers such as the Scheldt, Meuse and Rhine created a dynamic landscape that included fertile soils favoured by

A list of affiliations appears at the end of the paper.

farmers, alongside coastlines, beach barriers, river delta wetlands and forested river dunes that continued to support hunting, gathering and fishing practices after the full adoption of farming around 4200 BCE^{3,13–16}. This contrasts with other areas of Europe (with the exception of northern Scandinavia, the Baltic region and the eastern European taiga), where farming practices quickly became dominant⁸. In the Lower Rhine–Meuse area, the wetland communities of the Swifterbant (fifth millennium BCE) and Hazendonk cultures (4000–3500 BCE) settled on elevated areas (river and coastal dunes, crevasse splays and river levees) in a region dominated by water courses and peat bogs. They relied mostly on hunting, gathering and fishing, but also practiced farming. Around 3500 BCE, the Vlaardingen culture succeeded the Swifterbant/Hazendonk tradition, while remaining settled in approximately the same region¹⁷. Simultaneously, farmers associated with the Funnelbeaker culture (*Trechterbekercultuur* (TRB) in Dutch) settled on the Frisian–Drenthian plateau in the northeast and its surrounding sandy uplands, in regions where no evidence of earlier habitation, neither burials or settlements, has been found. The Swifterbant, Hazendonk and Vlaardingen settlements were all located near water streams, while TRB farmers settled mostly on forested sandy plateaus and their fringes, as did the Michelsberg communities to the south.

A mixed subsistence strategy of hunting, gathering and farming persisted in the western/central Netherlands until the third millennium BCE, when a more intense farming-based economy emerged in association with the Late Vlaardingen complex and the introduction of the ard plough around 3000 BCE¹⁸. The spread of CW influence to the wider Lower Rhine–Meuse area was more complex than in many other areas of central and eastern Europe. In the uplands, where skeletal material tends to be poorly preserved and no aDNA data are available, the complete CW package emerged as marked by the construction of CW burial mounds, the general absence of settlements and sparse pottery finds¹⁹. By contrast, in wetland areas along the coast, the Rhine–Meuse delta²⁰ and other low-lying regions²¹, CW-associated pottery was incorporated into Vlaardingen settlement contexts, but the characteristic CW-style burials were not^{20,22,23}.

The arrival of the BB complex around 2500 BCE marked another major cultural transition, as settlements spread across the wetlands and coastal areas, replacing Vlaardingen and CW settlements, although generally not using the same sites²¹. The BB economy was similar to the previous CW one and consisted of predominantly farming mixed with low-intensity hunting and gathering. In the sandy uplands, there was a continuation of the barrow ritual, but with distinct BB characteristics and material culture replacing the CW repertoire^{19,24}. BB groups were also well attested south of the Rhine, as evident in BB burial mounds on the sandy soils of the southern Netherlands and Belgium^{25–27}. BB settlement sites remain just as elusive in this area as CW settlements. However, the presence of ploughland dated to the Late Neolithic suggests that the lack of settlement evidence is not the result of nomadism but rather of settlements in lower lying places where there is little chance for detection by archaeologists²¹.

Archaeogenetic data have the potential to deepen our understanding of the nature of the dynamic changes in the Lower Rhine–Meuse region. We generated genome-wide data using in-solution enrichment for more than a million single-nucleotide polymorphisms (SNPs) from 44 individuals dated between 8500 and 1700 BCE, sampling cultural contexts that fill gaps in the aDNA record of this region (Fig. 1a,b and Supplementary Tables 1 and 2). The mean number of SNPs covered from a core set of 1.15 million autosomal targets is 492,551, with a mean coverage of 1.09. Together with 69 published individuals^{1,6,28–31}, the time-transect includes 112 individuals. We also report 14 new direct radiocarbon dates on newly analysed individuals (Supplementary Table 16).

Late persistence of forager ancestry

We report six new Mesolithic individuals who traced all of their ancestry from Mesolithic western hunter-gatherers (WHGs) (Supplementary Table 5), matching previous genetic results from Mesolithic hunter-gatherers from the region²⁸. Based on principal component analysis (PCA) (Fig. 1c), Neolithic individuals from the Lower Rhine–Meuse area fall along the central/western European Neolithic cline, but much closer to WHG than most European Neolithic farmers. This suggests elevated WHG-related ancestry, which we confirmed through modelling using qpAdm (Supplementary Table 6). We found that the earliest Neolithic individuals (4400–3800 BCE), associated with the Swifterbant culture, are genetically highly heterogeneous, with a mother and her daughter (I12093–I12094; Nieuwegein het Klooster) entirely descending from hunter-gatherer populations, one individual (I38442 from Angeren Kampsepad) with 84% of such ancestry; three individuals (I12091–I17968 from Nieuwegein het Klooster and I33739 from Zoelen de Beldert) with 60–63%; and four individuals (SWA001, SWA002 and SWA004 from Swifterbant-S2 and I33738 from Zoelen de Beldert) with 37–45% (Extended Data Fig. 2 and Supplementary Table 6). These results differ from the overall patterns of hunter-gatherer and farmer admixture elsewhere in central and western Europe, where the arrival of a farming economy generally reduced local WHG ancestry to less than 30%. However, the results perhaps make more sense in light of the equally limited economic transformation, which combined farming with continued core reliance on the rich wild resources from the Lower Rhine–Meuse wetlands and river valleys. Genetic mixing of local groups with high WHG ancestry continued for the next approximately 1,500 years, with stable proportions of around 40–50% WHG and 50–60% Early European Farmer (EEF) ancestry. Rare exceptions include one Middle Neolithic individual from the island of Baltrum (BLR001) and one individual from the Blätterhöhle cave (I15651), both with over 75% hunter-gatherer ancestry. The fact that this relatively high WHG ancestry extended not only to the Lower Rhine–Meuse wetlands, but also to further along the Rhine and Meuse rivers and the northern coast is consistent with archaeological evidence of continued cultural engagement of people across this region³². Three individuals from Tiel Medel de Roeskamp who can be indirectly dated to around 3700 BCE (Supplementary Information 2 and Supplementary Table 14) deviate from this pattern of high WHG ancestry, with only around 20% (Extended Data Fig. 2), possibly representing new arrivals from neighbouring parts of northwest Europe with lower WHG-associated ancestry. Their distinct genetic profile, in combination with parallels in pottery and lithic technology³², suggests an origin to the southeast among contemporaneous fully Neolithic communities in that region such as Bischheim groups. As such, the Tiel Medel de Roeskamp settlement represents a regional outlier, both in ancestry and material culture, and highlights that the Lower Rhine–Meuse area was not isolated, but part of a dynamic frontier characterized by mobility, encounter and interaction across cultural boundaries.

Compared with other regions of central, southern and western Europe where farming was practiced, the Lower Rhine–Meuse area stands out for its long survival of high proportions of WHG-related ancestry on a population scale (as opposed to isolated cases^{33–35}) until the BB transition, halfway through the third millennium BCE (Fig. 2). To identify other instances in which WHG ancestry on a population scale endured in such high proportions to the dawn of the Bronze Age, it is necessary to go to parts of the Baltic coast where populations with high EEF ancestry never made a substantial impact⁹, and to Scandinavia where hunter-gatherers with full WHG ancestry persisted until the early third millennium BCE alongside EEF-ancestry-rich farmers¹⁰ (Fig. 2 and Supplementary Table 7).

The unique ancestry makeup of Lower Rhine–Meuse Neolithic groups is also evident from their EEF–WHG admixture time estimates

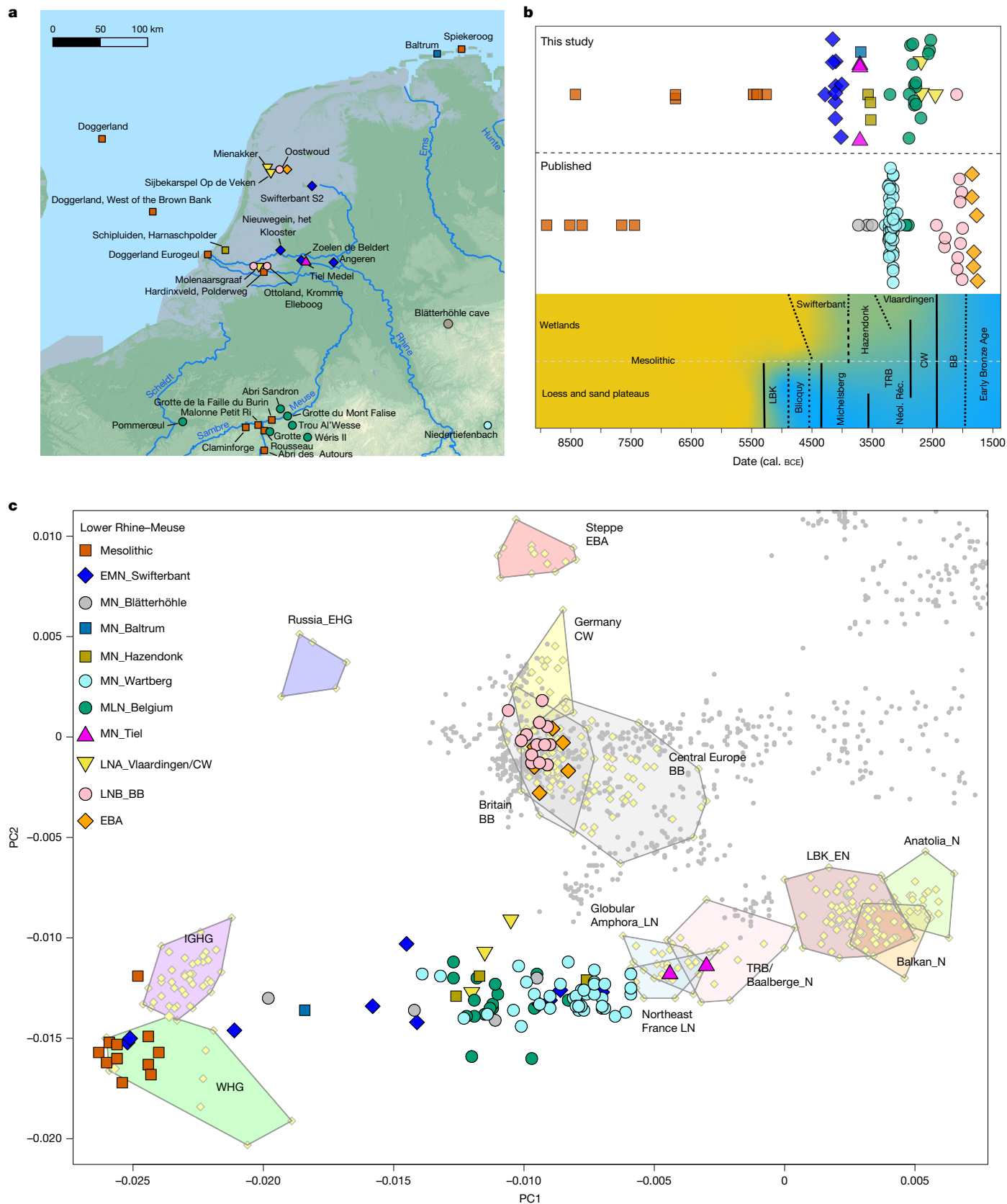


Fig. 1 | See next page for caption.

(Extended Data Fig. 4), which point to ongoing admixture well into the fourth millennium BCE, in contrast to other European regions (Supplementary Table 15). The Tiel Medel de Roeskamp individuals

represent a deviation from this pattern with older admixture dates, again highlighting their likely recent origin outside the Lower Rhine-Meuse area.

Fig. 1 | Overview of ancient individuals analysed in this study. a, Map showing archaeological sites with genome-wide data in the Lower Rhine–Meuse area and adjacent regions. The elevation map was downloaded from <https://www.mapsforeurope.org/datasets/euro-dem>. **b**, Chronological placement of the individuals from the Lower Rhine–Meuse region included in this study. Bottom, the local chronology of archaeological cultures. The black lines indicate the degree of changes; the dashed lines represent a gradual change in material culture; and the solid lines indicate a more abrupt change in material culture.

Female-mediated early farming ancestry

We find that the EEF ancestry proportions in Lower Rhine–Meuse area Neolithic people were significantly higher on chromosome X than the autosomes (normally distributed Z score = 5; Supplementary Table 8), indicating a higher ancestral contribution from women with EEF ancestry. Independent confirmation is provided by analysis of the two uniparentally inherited parts of the genome (Supplementary Table 13). Among the Early and Middle Neolithic men ($n = 43$ excluding close relatives), we observed only Y-chromosome lineages common in Mesolithic hunter-gatherers (haplogroups I2a, R1b-V88 and C1a2). By contrast, the maternally transmitted mitochondrial lineages are predominantly of Neolithic farmer origin (50 out of 71), based on their absence in sampled European Mesolithic individuals^{4,6,9,10,28,35–37}. For example, the earliest individual with EEF ancestry, a female individual associated with the Swifterbant culture and dated to around 4342–4171 calibrated years BCE (cal. BCE) (I17968, Nieuwegein het Klooster) at the start of the transition to farming in the region^{14,16}, has only 37% EEF ancestry in her autosomes but farmer-associated mitochondrial haplogroup H+152. A previous study³⁶ reported similar sex-biased admixture in Neolithic farmers of Iberia and in Funnel Beaker farmers of northern Europe. A plausible scenario is that in all three regions, hunter-gatherer communities incorporated farmer women, who plausibly mediated the exchange of ideas and technologies related to farming. This scenario of sex-biased admixture of Neolithic ancestry contrasts with one of almost complete displacement of local ancestry by incoming farmers and migration of entire groups, a process that occurred in other parts of Early Neolithic Europe³⁸.

The Middle Neolithic populations of the Lower Rhine–Meuse region were highly genetically interconnected, as reflected in large segments (>12 cM) of the genome being identical by descent (IBD), which is expected to be observed only for individuals who share common ancestors in the last dozens of generations³⁹ (Supplementary Table 14). We also find several cases of IBD segments over 20 cM, suggesting even closer relationships between sites such as Blätterhöhle, Niedertiefenbach and Abri Sandron, as well as between sites in the Lower Rhine–Meuse area and nearby areas of central Europe and Northern France (Fig. 4a). A notable case is a relationship (~50 cM in IBD) between an individual from Blätterhöhle, modern western Germany, and a father–daughter pair from Mont-Aimé³⁴ in modern northern France, who are also clear ancestry outliers exhibiting more hunter-gatherer ancestry than other individuals from Mont-Aimé.

CW using groups with minimal steppe DNA

In many areas of Europe, the emergence of the CW complex is associated with large-scale demographic change due to the arrival of groups carrying steppe ancestry. The ancestry change in three sampled individuals from Vlaardingen/CW contexts in the Western Netherlands is far smaller. These individuals were buried within settlements with CW complex material goods, but not the typical CW single grave burials, which are overall absent from the Vlaardingen culture region. One female (I12896 from Molenaarsgraaf-24A) has no steppe-related ancestry at all and instead shares ancestry with local late Neolithic farmers of the region (Fig. 3 and Supplementary Table 9). However, the other two individuals (I12902 and I33741) from Opmeer Mienakker and Sijbekarspel op de Veken, north of the Rhine River delta, can be modelled

The colour gradient indicates the general reliance on hunting and gathering (yellow) to farming (blue). Néol. Réc. refers to Néolithique Récent. **c**, PCA with the ancient individuals projected onto the principal components computed on present-day individuals from West Eurasia. EMN, Early-Middle Neolithic; MLN, Middle–Late Neolithic; EN, Early Neolithic; MN, Middle Neolithic; LN, Late Neolithic; LNA, Late Neolithic A; LNB, Late Neolithic B; N, Neolithic; EBA, Early Bronze Age; IGHG, Iron Gates hunter-gatherers; EHG, Eastern hunter-gatherers.

as a mixture of 12–16% ancestry associated with the main cluster of CW groups, and 84–88% derived from Lower Rhine–Meuse area Neolithic populations with high hunter-gatherer ancestry, similar to Late Neolithic Belgium or Hazendonk (Fig. 3 and Supplementary Table 10). Despite a low steppe ancestry proportion in the autosomes, the male I12902 from Opmeer Mienakker carries Y haplogroup R1b-U106, also known in one early CW-associated individual from Bohemia⁷. Furthermore, one of his bones yields a date of 2852–2574 cal. BCE; one of the earliest CW complex associated dates in Europe outside of Bohemia and the Baltic region⁴⁰. These results suggest that the male ancestor who brought this Y haplogroup to the Lower Rhine–Meuse region was part of the early CW expansion.

While limited to three people, the IBD analysis for the Vlaardingen/CW individuals revealed two additional notable signals. First, the two individuals with around 11% CW ancestry, excavated at nearby sites, have an IBD match that represents approximately a seventh-degree relationship (Supplementary Table 14), hinting at a small community size. Second, the geographical range of their IBD links extends much further east than previous groups (Extended Data Fig. 3). Among their closest connections, we found a Yamnaya-associated individual from Samara in far eastern Europe⁴¹ (ID: I6733) and CW-associated individuals from present-day Poland⁴² (ID: pcw362) and Estonia⁴³ (ID: NEO306), with whom Vlaardingen/CW individuals share one IBD segment of around 19 cM long that was very unlikely to survive for more than a handful of generations. We also detected connections to other Lower Rhine–Meuse area Late Neolithic individuals (Supplementary Table 14), providing direct evidence of a major local ancestry component in Vlaardingen/CW individuals. These patterns reflect their dual sources of ancestry: a minor component (potentially completely along the male line) from central/eastern CW groups (and through them to Yamnaya steppe pastoralists) and a major component from the local Neolithic population. Although our individuals do not represent the initial generation of admixture between CW-related and local groups, patterns from nearby northeastern France could serve as a good model for this interaction. There, around 2500 BCE, a man with ancestry similar to CW-associated individuals (including nearby CBV95⁴⁴ buried with an All-Over Ornamented CW type Beaker) fathered a child with a local woman⁴⁵. His son did the same, rapidly reducing steppe ancestry to levels comparable to those seen in the Vlaardingen/CW individuals I12902 and I33741.

BB users had local admixture

With the advent of the BB complex in the Lower Rhine–Meuse delta after 2500 BCE, we see a strong difference in genetic ancestry compared with the previous CW/Vlaardingen individuals. All 13 available BB-associated individuals appear genetically close to eastern European CW-associated groups, but not to the preceding Vlaardingen/CW individuals in the PCA (Fig. 1c). They can be modelled with around 82% ancestry from the main cluster of eastern European CW-associated individuals (Fig. 3 and Supplementary Table 10), and their remaining ancestry from a Wartberg Neolithic-related group (Supplementary Table 11), representing the Neolithic population from the Lower Rhine–Meuse area with the lowest level of hunter-gatherer ancestry, or as a mixture between Middle and Late Neolithic groups from outside the Lower Rhine–Meuse area (for example, Poland Globular Amphora, Czechia TRB, Germany Baalberge, Iberia Neolithic–Chalcolithic) and Late Neolithic populations

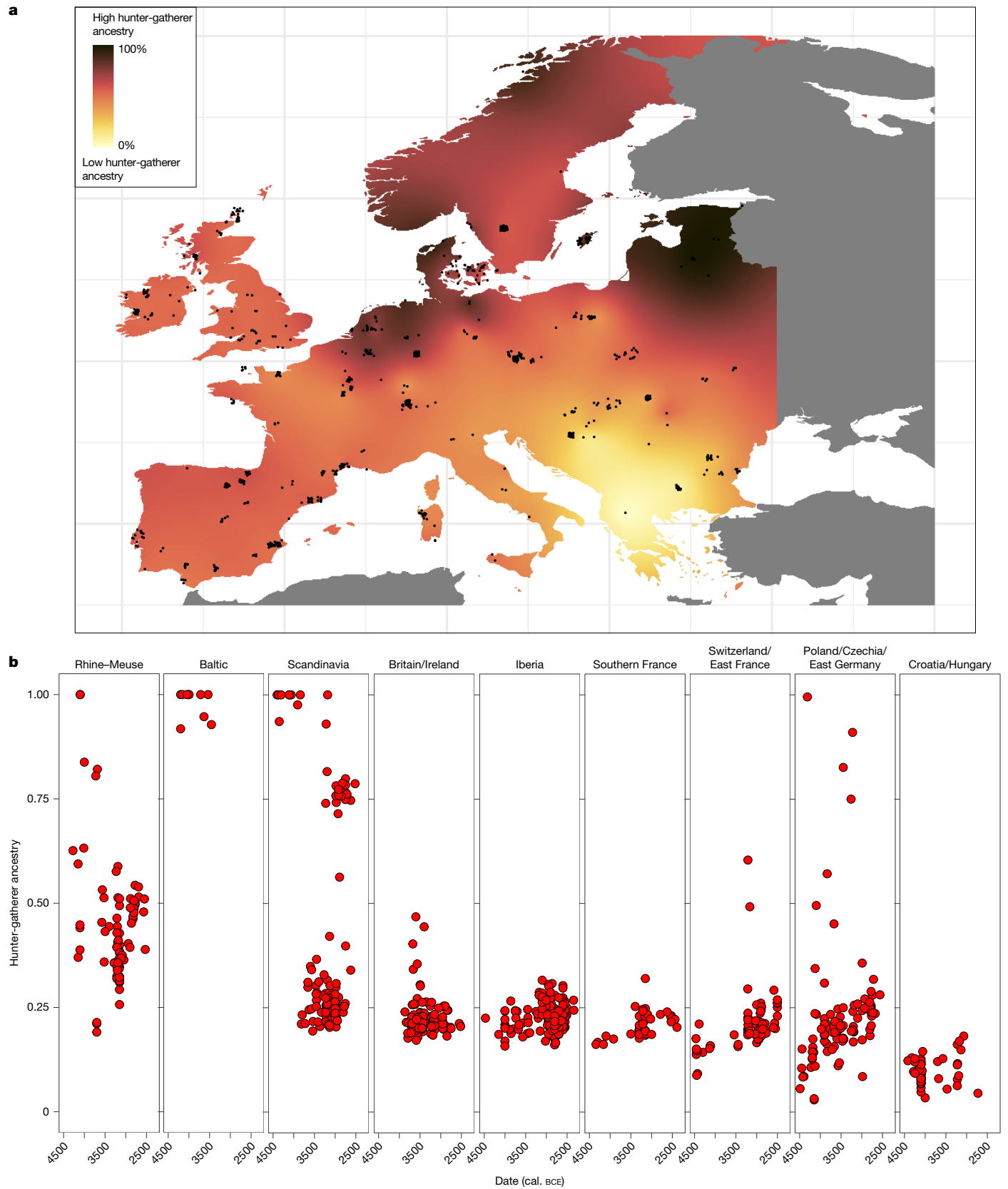


Fig. 2 | Hunter-gatherer ancestry proportions across Europe between 4500 and 2500 BCE. **a**, Spatial kriging of hunter-gatherer ancestry. The colours represent the predicted ancestry proportion at each point in the grid. Map data are from the

R package maps. **b**, Hunter-gatherer ancestry levels in individuals from different European regions. Ancestry proportions were estimated using qpAdm (Supplementary Tables 6 and 7).

from Belgium. All of these scenarios point to an approximately 82–87% (but not 100%) ancestry change associated with the arrival of the BB complex in the Lower Rhine–Meuse region (Supplementary Table 10). A contribution of local farmers, with their distinctive signature of high hunter-gatherer ancestry, is essential to model the formation of Lower Rhine–Meuse delta BB-associated individuals. Even at 13–18%, we can be confident that this local admixture occurred: models lacking this unique Lower Rhine–Meuse farmer genetic contribution are rejected with strong statistical significance (Supplementary Table 10). This suggests that the observed mixture between CW culture associated groups and European farmers that formed the genetic profile of Lower Rhine–Meuse BB must have occurred, at least in part, in the region itself. In the context of these genetic results, it is notable that radiocarbon dates suggest that the Lower Rhine–Meuse area was one of the earliest places where the BB cultural phenomenon arose⁴⁶. Although the earliest appearance of BB cultural material has been located in Iberia⁴⁷, our results show that the earliest formation of BB-associated groups that were influenced not just culturally but also genetically by CW users may have occurred in western Europe including the Lower Rhine–Meuse area.

As there are possibly several centuries between the analysed CW/Vlaardingen and BB populations, we need to consider the option that the considerable change in genetic ancestry could have been a more gradual process, rather than a sudden change. However, what is different compared with the previous ancestry changes in our time transect, is that it involved both sexes this time. Among BB men, all yielded R1b-L151 haplogroups, which were absent in earlier Neolithic European populations, except for early CW-associated individuals from Czechia in central Europe⁷. All nine available BB-associated men from Oostwoud Tuithoorn and Ottoland Kromme Elleboog belonged to the derived R1b-L151-P312 lineage (Supplementary Table 1), the major lineage among BB groups across Europe⁶. Three P312 individuals could be further subtyped to DF19, a minor P312 subtype today mostly present in central/northern European populations (<https://www.yfull.com/tree/R-DF19/>). At Molenaarsgraaf, the only man with enough resolution to determine an L151 subtype belonged to R1b-L151-U106 (I13025), matching the Vlaardingen/CW-associated male individual from Opmeer Mienakker, referred to above, and suggesting a similar CW-related source for the patrilineal ancestry in both Vlaardingen/CW and BB men in the Lower Rhine–Meuse area. This would be consistent with the hypothesis that, even if there was limited local continuity within the lowlands, the same male lineages that were associated with the arrival of CW pottery to the region (in the Vlaardingen/CW context) were at least partially associated with subsequent BB emergence. This suggests that the BB-associated population in the Lower Rhine–Meuse area could have emerged from sustained influx of ‘classic’ CW-related groups to the region (such as those documented in the uplands to the east, where skeletal preservation is absent but classic CW burial features are present), who mixed with the local Vlaardingen or other Lower Rhine–Meuse Neolithic populations who had high hunter-gatherer ancestry.

Further evidence for a major influx from outside regions during the BB period comes from inspection of IBD networks, which, after this point, expand thousands of kilometres further to the east and northeast compared to the CW/Vlaardingen period (Fig. 4b). These show strong links to CW- and BB-associated individuals from Bohemia, as well as evidence of distant Early Bronze Age relatives from England and Scotland (Supplementary Table 14), corroborating findings of a shared origin between these groups located on opposite shores of the North Sea⁶. The BB horizon is the first period in our time transect when people of the Lower Rhine–Meuse region became intensively integrated within a much wider European IBD network, in contrast to the previous more regional patterns—yet another indication for the high level of mobility that has become evident from isotope studies⁴⁸.

After this period of considerable demographic change, Early Bronze Age individuals from the Lower Rhine–Meuse area had similar ancestry to BB predecessors (Figs. 1c and 3), with around 3% additional

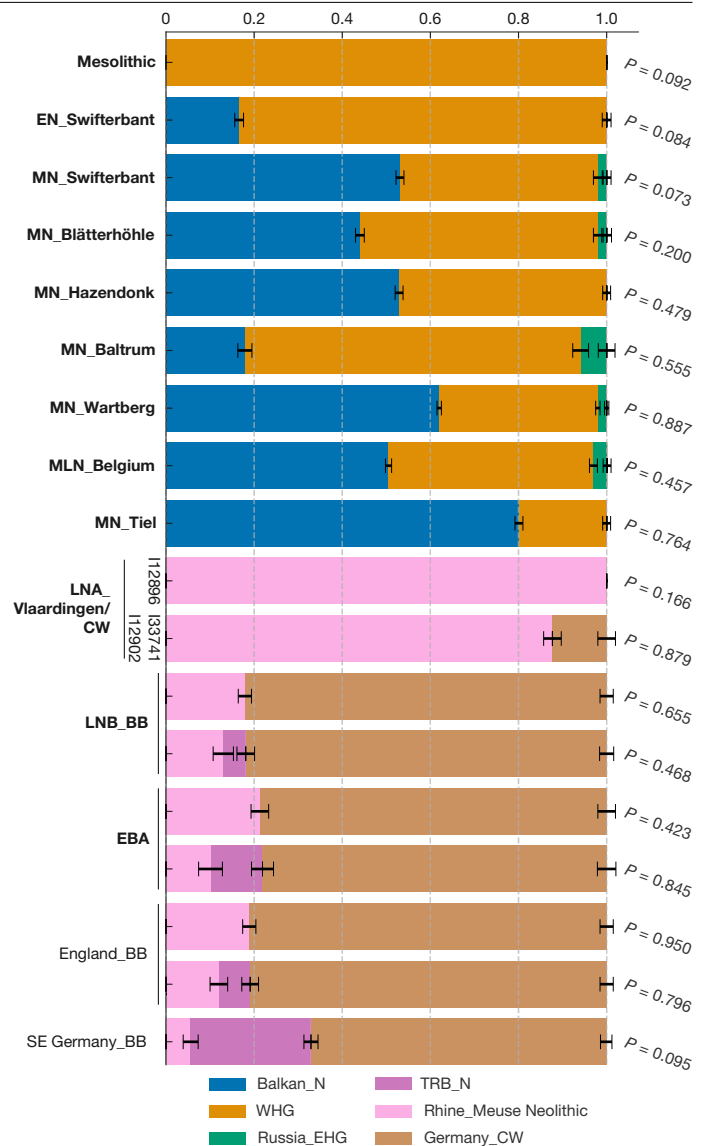


Fig. 3 | Admixture proportions for Lower Rhine–Meuse populations and other relevant groups. Admixture proportions were estimated using qpAdm (Supplementary Tables 5, 6 and 10). Groups from the Rhine–Meuse region are shown in bold. The error bars indicate the s.e. of estimates from 5-cM-block jackknife analysis. P-values for the fit of each qpAdm model to the genetic data are provided. SE, southeast.

Neolithic-related ancestry (Supplementary Table 10), potentially reflecting small-scale admixture with neighbouring populations. Local continuity from the BB period to the Middle Bronze Age is also reflected in the abundant familial links connecting Early Bronze Age individuals with both earlier BB individuals and later Middle Bronze Age ones (Supplementary Table 14), with pairs sharing up to 100 cM IBD as expected for approximately sixth-degree relationships.

Lower Rhine–Meuse expansion to Britain

The study identifies the Lower Rhine–Meuse region as the likely origin of a secondary expansion of BB users who had a greater demographic impact than the postulated initial Iberian expansion.

To document this, we used our statistical modelling framework to re-examine the genetic evidence of the arrival of BB users in Britain. Previous work proposed an origin of British BB-associated groups in the Lower Rhine–Meuse based on Y-chromosome data⁷, and showed

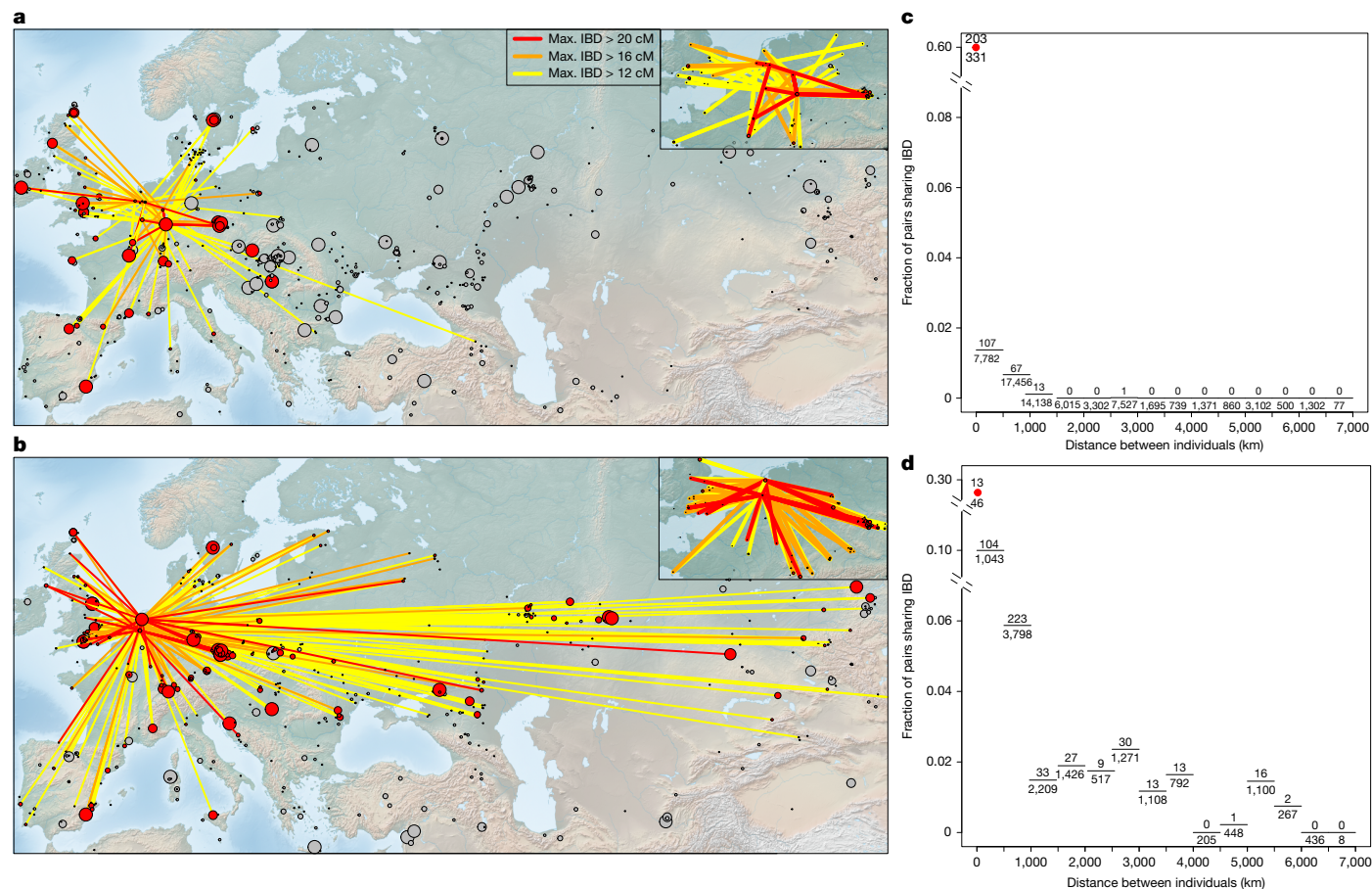


Fig. 4 | Genetic connections of Lower Rhine–Meuse groups. a, b, IBD connections of Lower Rhine–Meuse Early, Middle and Middle–Late Neolithic individuals ($n = 35$) (a) and Lower Rhine–Meuse BB-associated individuals ($n = 11$) (b). Sites are represented by circles; the size is proportional to the number of individuals amenable to IBD calling. The grey circles indicate archaeological sites between 5500 and 2500 BCE (top) and between 3000 and

1500 BCE (bottom) with no IBD connections to Lower Rhine–Meuse individuals. **c, d,** Decay of IBD sharing, with the geographical distance for Lower Rhine–Meuse Early, Middle and Middle–Late Neolithic individuals and Lower Rhine–Meuse BB-associated individuals (d). Pairs were considered to share IBD if they share at least one segment of >12 cM. Maps were drawn using public-domain Natural Earth data using the `rnatuarearth` package in R.

a minimum of around 90% ancestry change⁶, but had not been able to distinguish models in which the EEF ancestry came from Britain itself or elsewhere. We analysed 28 BB-associated individuals from Great Britain from the main homogeneous cluster (Supplementary Tables 3 and 4) and obtained the same result as for Rhine–Meuse delta BB individuals (Table 1 and Supplementary Table 10). Both require around 12–19% ancestry from Lower Rhine–Meuse Neolithic populations with high levels of hunter-gatherer ancestry, plus ancestry from the main CW genetic cluster (Fig. 3). This is consistent with no contribution at all from British Neolithic farmers. However, in an outlier subset of four BB-associated individuals from Britain (including the high-status ‘Amesbury Archer’) with lower proportions of steppe ancestry than the main cluster (Extended Data Fig. 1 and Supplementary Table 3), models featuring CW-complex-associated groups and Lower Rhine–Meuse farmers provide a poor fit (Supplementary Table 10). We cannot rule out the possibility that some of the ancestry of these outliers could derive from local British Neolithic populations, but it could also plausibly come from separate migratory streams into Britain, such as the one suggested for the Amesbury Archer, whose isotopic genetic signatures indicate an origin in the Alps⁴⁹. By the Early Bronze Age, when ancestry proportions in Britain stabilized, we estimate around 92% Lower Rhine–Meuse BB ancestry and at most 8% local British Neolithic ancestry, but possibly as little as 0% (Supplementary Table 12), providing new information about the magnitude of the demographic transition associated with the BB transition in Britain.

Discussion

A notable finding in our study is that the long-term persistence of high hunter-gatherer genetic ancestry proportions was not limited to the previously reported Blatterhöhle cave¹ and Wartberg culture²⁹ in the Rhine region, but also occurred in the core wetlands of the Netherlands and the inland regions of the Meuse. In the context of archaeological evidence, this suggests the co-existence of two distinct but interdigitated Neolithic spheres in the entire Lower Rhine–Meuse region, persisting well into the third millennium BCE. One of these consisted of communities centred around water, not only those in the wetland core but also connected to it through waterways, and practicing a semi-agrarian lifestyle³. Water links were central for these communities, and connections to people living along the waterways were often more important than connections to physically closer neighbours. Surrounding the waterways, the other sphere consisted of early full-blown farming communities that preferred the fertile loess soils and kept to their culturally specific traditions of settlement, housing, material culture and burial. This supports the frontier mobility model proposed previously³⁰, albeit in a more geographically restricted context. These communities exchanged ideas, with women introducing EEF genetic ancestry and probably also new technological knowledge in the more hunting–gathering–practicing communities but their distinct cultures persisted for millennia.

The very high proportion of WHG ancestry was observed from the earliest Neolithic Swifterbant communities to the period of the

Table 1 | Modelling ancestry

	Lower Rhine–Meuse BB	British BB
P value for models with northern Iberian farmers	0.00079	0.0072
P value for models with northeast French farmers	0.00015	0.00077
P value for models with German Baalberge farmers	0.000015	0.000085
P value for models with Globular Amphora farmers	0.0012	0.0071
P value for models with TRB farmers	0.00000018	0.00000042
P value for models with Middle–Late Neolithic Belgium (Lower Rhine–Meuse)	0.0605	0.0057
P value for models with Middle Neolithic Wartberg (Lower Rhine–Meuse)	0.65	0.95
Proportion of ancestry from Late Neolithic Wartberg (Lower Rhine–Meuse) (%)	17.9	18.9
Minimum proportion of ancestry from Middle–Late Neolithic Belgium, allowing three-way qpAdm models with CW and other farmer sources outside the Lower Rhine Meuse area (%)	10.9	9.3

We modelled the ancestry of Lower Rhine–Meuse BB-associated individuals and the main group of British BB-associated individuals using qpAdm models involving a CW group from present-day Germany and different Neolithic populations from within and outside the Lower Rhine–Meuse area. Further details are provided in Supplementary Table 10.

introduction of the CW complex. CW pottery is present in the Rhine–Meuse delta, but other aspects of this culture are lacking, in particular the characteristic burial rituals^{19,20,24}. This is matched by limited population influx and high retention of the genetic ancestry of previously established groups.

The BB complex related communities harbour evidence of a break with the previously established pattern, as they show a profound change in genetic ancestry. This was introduced by new incoming people of both sexes with CW related ancestry. Admixture with local Lower Rhine–Meuse delta populations did occur, but was limited to 13–18%. Owing to the uncertainty of the radiocarbon-dated individuals in our transect, we need to consider a potentially slightly larger time-gap between the three analysed Vlaardingen/CW-associated individuals and the 13 BB-associated individuals. Thus, the time course and exact location in the region where people with a CW-associated genetic profile and a Lower Rhine–Meuse Neolithic genetic profile came together remains unclear. However, the homogeneity of ancestry within the three BB-associated sites that we sampled shows that the mixture had largely taken place by that time (around 2400–1900 BCE).

The evidence for a large-scale demographic change in the Lower Rhine–Meuse region by the time of the spread of Beaker users is important in light of the evidence from Britain, where Beaker users spread at around the same time. As the British Neolithic populations encountered by Beaker users practiced cremation and therefore did not yield samples amenable for aDNA analysis, it has been unclear whether there was a sharp population break or a period of extended co-existence⁵¹. In the Lower Rhine–Meuse region, we do not have this issue, as cremation was rarely practised by previous groups, yet the genetic turnover seems to have been similarly profound as in Britain, with the great majority of local BB burials being consistent with no local British Neolithic ancestry and the contribution of the local British Neolithic population by the Early Bronze Age estimated at $\leq 9\%$. Although we do not know what triggered this large-scale mobility, it is clear that the genetic legacy of local populations both in the Lower Rhine–Meuse area and Britain collapsed relatively rapidly.

Despite the evidence of a cultural break, in both the Lower Rhine–Meuse area and Britain, local cultural traditions and knowledge

remained intact for some time between 2450 and 2200 BCE^{49,52,53}. British archaeologists stress that continuity is witnessed in the building and use of Late Neolithic monuments like Stonehenge, Avebury, Woodhenge and Silbury Hill, and that culturally substantial changes only occur in the twenty-third century BCE^{52,54}. Similarly, in the Lower Rhine–Meuse area, BB groups used the same areas, although not the exact same settlement sites as their Vlaardingen/CW predecessors. They continued to settle in river valleys, on crevasse splays and along river dunes in a way that was oriented explicitly towards a hunting–farming mixed economy. This indicates that the newcomers with their distinct genetic ancestry came from a similar landscape elsewhere or were in close contact with the local communities to learn how to handle this specific type of landscape.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41586-026-10111-8>.

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Methods

Sampling, extraction, library preparation, capture and sequencing

Our initial selection for aDNA analysis comprised 116 ancient individuals from the Lower Rhine–Meuse area for aDNA analysis (Supplementary Table 2), including five previously reported individuals^{1,6,31} for whom we generated additional data. We also selected ten previously reported^{6,36} individuals from relevant contexts outside the Lower Rhine–Meuse area and generated additional data (Supplementary Tables 2–4). We performed laboratory work in dedicated clean rooms. We removed the outer layer of teeth and long bones and collected powder from beneath the cleaned surface. This process minimized the risk of exogenous DNA contamination, and low-speed drilling was used to prevent heat-induced DNA damage⁵⁵. In the case of temporal bones, we removed cochleae through sandblasting⁵⁶ and then milled them. We incubated the resulting powder in lysis buffer and cleaned and concentrated the DNA from one-fifth of the lysate. We did this either manually or using an automated protocol with silica magnetic beads⁵⁷ and Dabney binding buffer^{58,59} for manual extraction. The samples from Trou Al'Wesse, Abri Sandron and Grotte du Mont Falise were prepared and extracted following the method outlined previously⁶⁰.

We built 254 libraries (Supplementary Table 2) using two different protocols. Double-stranded barcoded libraries were prepared with truncated adapters from the extract and subjected to partial (half) uracil–DNA–glycosylase (UDG) treatment before blunt-end repair to substantially reduce the characteristic damage pattern of aDNA^{61,62}. Single-stranded libraries were prepared using automated protocols described previously⁶³. A fraction was subjected to USER treatment⁶³.

DNA libraries were enriched for human DNA using probes that target 1,233,013 (1240k capture)⁶⁴ or 1,352,535 (Twist BioScience)⁶⁵ nuclear SNPs and the mitochondrial genome. We performed two rounds of capture for the 1240k reagent and one for the Twist BioScience reagent. Captured libraries were sequenced on the Illumina HiSeq X10 instrument with 2 × 101 cycles and 2 × 7 cycles to read out the two indices⁶⁶ or on the Illumina NextSeq 500 instrument with 2 × 76 cycles and 2 × 7 cycles to read out the two indices.

For three previously reported individuals (I4075, I0103 and I0104), we generated shotgun data (Supplementary Table 2) from the same libraries that were 1240k captured in the original publications^{6,36}.

Bioinformatics: demultiplexing, adapter removal, mapping and PCR duplicate removal

Reads for each sample were extracted from the raw sequencing data based on sample-specific indices introduced during wet-laboratory processing, permitting up to one mismatch. Adapters were removed and paired-end sequences were merged into single-ended sequences with a required 15-base-pair overlap (allowing one mismatch with high-quality bases or three mismatches with low-quality bases), using a modified version of SeqPrep v.1.1 (<https://github.com/jstjohn/SeqPrep>). This process was applied by selecting the highest-quality base in the overlapping region. Reads that could not be merged were discarded before aligning to the human reference genome (hg19) and the RSRV version of the mitochondrial genome using the same command in bwa (v.0.7.15)⁶⁷. We removed duplicates based on the alignment coordinates and orientation of the aligned reads. Aligned sequences from different libraries of the same sample were merged accordingly into a single BAM file. The computational pipelines are available at GitHub (<https://github.com/dReichLab/ADNA-Tools>, <https://github.com/dReichLab/adna-workflow>).

Evaluation of authenticity

We established aDNA authenticity using several criteria. Libraries with a deamination rate below 3% at the terminal nucleotide were excluded from further analysis. We computed the ratio of Y-chromosome to

X- and Y-chromosome reads. Libraries with ratios above 0.03 and below 0.32 were excluded from further analysis. We estimated mismatch rates to the consensus mitochondrial sequence using contamMix (v.1.0.1051)⁶⁸, and performed X-chromosome contamination estimates using ANGSD⁶⁹ in male individuals with sufficient coverage. Libraries with evidence of contamination were excluded from further analysis. Finally, individuals without a minimum of 20,000 targeted 1240k SNPs with at least one overlapping sequence were discarded from population genetic analysis. After applying these filters, 122 libraries from 59 individuals remained (Supplementary Table 2); we merged data from the libraries to increase sequencing coverage. Of these 59 individuals, 44 were newly reported individuals from the Lower Rhine–Meuse area, five previously reported from the same area and 10 previously reported from other areas.

Analysis datasets

In addition to the 49 individuals with newly generated data from the Lower Rhine–Meuse area, we also included data from 63 previously published individuals^{1,6,28–31} from the region, for a total of 112 individuals from the Lower Rhine–Meuse region and adjacent areas between 8500–1700 BCE (Fig. 1 and Supplementary Table 1). The time–transect dataset includes three new Mesolithic individuals from Belgium, two from the Netherlands and one from northwest Germany, as well as published data from three individuals from now submerged areas of Doggerland²⁸; ten Early–Middle Neolithic individuals from semi-agrarian Swifterbant contexts (4600–4000 BCE) (Netherlands)—the first data from this unique culture; the first three Middle Neolithic individuals from Late Swifterbant or Hazendonk archaeological contexts (Netherlands); three likely Middle Neolithic individuals from Tiel (Netherlands) and one Middle Neolithic individual from Baltrum island (northwest Germany); four published Middle Neolithic individuals from Blätterhöhle cave (3500–3000 BCE)¹ (northwest Germany); 40 published Middle Neolithic individuals from a Wartberg context (3500–2800 BCE)²⁹ (Niedertiefenbach, northwest Germany); 18 Late Neolithic individuals buried in caves from the Ardennes region (3300–2500 BCE) (Belgium); three Late Neolithic individuals from Vlaardingen/CW contexts, including the first data from this culture from the Lower Rhine–Meuse area (3000–2500 BCE) (Netherlands); 13 Late Neolithic individuals from BB contexts (2500–2000 BCE) (Netherlands); and six individuals from an Early Bronze Age context (2000–1700 BCE) (Netherlands).

To aid the analysis of the Lower Rhine–Meuse area individuals, the analysis dataset was further complemented by previously published data from ancient individuals from other regions (Extended Data Fig. 1 and Supplementary Tables 3 and 4). For genome-wide analyses, we assembled two datasets. The HO dataset included the ancient individuals, and 1,036 present-day West Eurasian individuals genotyped on the Affymetrix Human Origins Array^{4,70,71}. We retained 591,642 SNPs shared between the 1240k capture and the Human Origins Array. The HOIII dataset included only the ancient individuals and 1,233,013 SNPs in common between 1240k and Twist reagents. In both datasets, we randomly sampled one allele at each SNP position for each individual, discarding the first and the last two nucleotides of each sequence.

Haplogroup assignment of uniparentally inherited markers

We created consensus mitochondrial haplotypes with samtools and bcftools. We restricted to sequences with a mapping quality of more than 30 and a base quality of more than 30. We then called haplogroups with Haplogrep³⁷² (Supplementary Table 1). We called Y-chromosome haplogroups (Supplementary Table 1) following the methodology described previously⁷³, based on the YFull v.8.09 phylogeny (<https://www.yfull.com/>). Haplogroups found in Neolithic individuals were classified as either ‘hunter-gatherer related’ if they were already present among Mesolithic hunter-gatherers (mitochondrial haplogroups U5, U4'9, U2, U* and K1e; Y-chromosome haplogroups I2a, C1a and R1b-V88) or ‘Neolithic related’ if they were most likely introduced by

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incoming EEF populations (all mitochondrial and Y-chromosome haplogroups except for those mentioned above) (Supplementary Table 13). Using this approach, we understand that we might be underestimating the number of lineages contributed by Neolithic farmers, both in the mtDNA and Y chromosome, as some lineages considered to be Mesolithic hunter-gatherer related, based on their presence during the Mesolithic period, might have been incorporated by farmer populations during their path from Anatolia to the Lower Rhine–Meuse area.

Molecular sex determination

Genetic sex was determined by calculating the ratio of reads mapped to Y-chromosome SNP positions to the total reads mapped to sex-chromosome SNP positions. Individuals with a ratio of <0.03 were classified as female, while those with a ratio >0.32 were classified as male (Supplementary Table 1).

Biological relatedness

To estimate close biological relatedness up to the third degree, mismatch rates were computed between all possible pairs of Lower Rhine–Meuse area individuals, randomly sampling one read for each individual at each of the 1.15 million autosomal SNPs. Mismatch rates were converted to relatedness coefficients as described previously⁷⁴ using three different baseline mismatch rate values to account for the different ancestral backgrounds found in the dataset. If both individuals in the pair had fully Mesolithic hunter-gatherer ancestry, we use a baseline mismatch rate of 0.225. If at least one individual has EEF ancestry and both lack steppe-associated ancestry, we use a baseline mismatch rate of 0.252. If at least one individual has steppe-associated ancestry, we use a baseline mismatch rate of 0.258. Close kinship relationships are annotated in Supplementary Table 1.

IBD

We called IBD segments between the Lower Rhine–Meuse delta individuals with high-quality data ($n = 59$) and all the previously published ancient individuals from Eurasia with high-quality data ($n = 7,034$). We followed the same procedure described previously³⁹, which involves imputing and phasing the aligned sequenced data with GLIMPSE⁷⁵ using haplotypes in the 1000 Genome Project as the reference panel⁷⁶, and detecting IBD segments with ancIBD (<https://github.com/hringbauer/ancIBD>). Pairs of individuals connected by IBD are displayed in Supplementary Table 14. Three individuals from the site of Tiel Medel de Roeskamp have uncertain chronology. The site has a Middle Neolithic Swifterbant occupation but also a Bronze Age occupation phase and the sampled individuals were not amenable to radiocarbon dating. We therefore used their IBD connections to estimate an approximate chronology. Their largest IBD sharing is with I33738, a Middle Neolithic Swifterbant individual from Zoelen de Beldert (Netherlands) dated to 4200–3800 BCE, with whom one of Tiel Medel-de Roeskamp individuals shares four IBD segments longer than 8 cM (the longest being 20.5 cM), for a total share of 53 cM (Supplementary Table 14). The second and third largest IBD sharing are with a Neolithic individual from Hazleton North (England)⁷⁴ who lived 3750–3500 BCE (3 IBD segments for a total of 39 cM) and with a Neolithic individual from Gurgy les Noisats⁷⁷ dated to 4836–4606 cal. BCE (5855 ± 40 BP, Lyon-4446, SacA-8629) (2 IBD segments for a total of 33 cM). On the basis of these IBD results, a Bronze Age chronological attribution is extremely implausible for these individuals, and we therefore approximate their date to the range 3800–3600 BCE, therefore within the Middle Neolithic. This chronology fits well with their lack of steppe-associated ancestry in the autosomal genome, which already suggested a pre-2500 BCE date.

Runs of homozygosity

We called runs of homozygosity using hapROH⁷⁸ for individuals with more than 300,000 available SNPs from the 1240k capture panel (Supplementary Table 1).

PCA

We ran PCA on the HO dataset using the smartpca software from the EIGENSOFT package⁷⁹. We computed PCs on 1,036 present-day West Eurasians genotyped on the Affymetrix Human Origins Array. Ancient individuals were projected onto those PCs using lsqproject:YES and shrinkmode:YES.

qpAdm

We used qpAdm⁵ to estimate ancestry proportions. We set the parameters allsnps: YES and inbreed: YES to account for the use of pseudo-haploid data (Supplementary Information 4).

We ran each qpAdm model with four different setups:

- (1) Using all 1240k autosomal SNPs.
- (2) Using 469k autosomal SNPs reported to greatly reduced the bias when co-analysing 1240k data with Twist and shotgun data⁶⁵.
- (3) Using 711k autosomal SNPs with reduced bias identified using an approach (<https://github.com/rmnfournier/compatibility-panel>) to filter out biased SNPs⁸⁰.
- (4) Using all 1240k autosomal SNPs, but featuring only Twist or shotgun data in the target, source and outgroup populations (Supplementary Table 4).

Throughout this Article, we use terms such as WHG, eastern hunter-gatherers and EEF as genetic shorthand for ancestry components maximized in western European hunter-gatherers, eastern European hunter-gatherers and Neolithic farmers of Anatolian origin, respectively. These labels refer solely to patterns of shared genetic ancestry and do not imply any specific subsistence strategy, cultural affiliation or social identity for individuals in whom these components are detected.

Admixture date estimates

We used DATES⁸¹ to estimate admixture dates leveraging linkage disequilibrium decay (Supplementary Table 15 and Extended Data Fig. 4). We used the same ancestral population as in qpADM modelling. For Neolithic groups/individuals without steppe ancestry, we used Balkan_N + WHG to study EEF–WHG admixture. To study CW–European Neolithic admixture, we used MN_Wartberg + Germany_CordedWare for Lower Rhine–Meuse BB, Lower Rhine–Meuse EBA and England BB; MLN_Belgium + Germany_CordedWare for Vlaardingen/CordedWare; and GlobularAmphora_LN + Germany_CordedWare for SEGermany_BB. To convert the number of generations since admixture given by DATES into years, we assumed 28 years per generation⁸². We used the following parameters: binsize: 0.001; seed: 77; maxdis: 1; qbin: 10; jackknife: YES; affit: YES; runoff: YES; lovalfit: 0.45 and minparentcount: 1. We considered the earliest, the most recent and the mean possible chronological dates for each group when estimating admixture dates (Supplementary Table 15). The estimates obtained for Vlaardingen/CordedWare group were considered to be invalid, as the s.e. was higher than the estimated number of generations.

Radiocarbon chronology

The chronology for each site is described in Supplementary Information 2. All dates were obtained from the original excavation reports, follow-up publications or from direct consultation with the excavators. These have been supplemented by 14 new measurements. Full laboratory codes, pretreatment steps and quantitative quality indicators are reported in Supplementary Table 16. All reported ages were calibrated with the IntCal20 calibration curve using OxCal (v.4.4.4)⁸³.

Several of the dates are potentially susceptible to marine or freshwater reservoir effect (FRE). However, owing to the dynamic hydrological regime of the Rhine Meuse lowlands, it is often impossible to accurately estimate the source of the FRE, and there is currently no consensus on the correction factor to use for the region^{16,84–86}. Thus, all reported radiocarbon dates have not included an FRE correction factor and we

address a potential bias qualitatively in the site descriptions (Supplementary Information 2).

Ethics

The individuals studied here were all analysed with the goal of minimizing damage to their skeletal remains, with permission from local authorities in each location from which they came. Every sample is represented by stewards, such as archaeologists or museum curators, who are either authors or thanked in the Acknowledgments. Open science principles require making all data used to support the conclusions of a study maximally available, and we support these principles here by making fully publicly available not only the digital copies of molecules (the uploaded sequences) but also the molecular copies (the aDNA libraries themselves, which constitute molecular data storage). Those researchers who wish to carry out deeper sequencing of libraries published in this study should send a request to the corresponding author D.R. We commit to granting reasonable requests as long as the libraries remain preserved in our laboratories, with no requirement that we be included as collaborators or co-authors on any resulting publications.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Genotype data for individuals included in this study can be obtained from the Harvard Dataverse repository (<https://reich.hms.harvard.edu/datasets>). The DNA sequences reported in this paper have been deposited in the European Nucleotide Archive under accession number PRJEB105335. Other newly reported data, such as radiocarbon dates and archaeological context information, are included in the Article and its Supplementary Information.

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Author contributions I.O., E.A., Q.B., H.F. and D.R. wrote the manuscript with the input of all of the other authors. M.B.R., R.P., W.H., M.P. and D.R. supervised parts of the study. I.O., I.L., N.P. and M.R. analysed genetic data. E.A., Q.B. and H.F. edited archaeological information. E.A., L.A., S.B., M.-F.D., A.F., D.F., F.G., J.F.K., L.M.K., C.v.d.L., J.v.d.L., K.L., L.L.K., R.L., R.M., P.N., D.C.M.R., M.R., L.S., J.R.S., T.t.A., M.T. and C.J.E. sampled anthropological remains and/or contributed to the creation of the archaeological supplement. G.S., M.M., A.M. and S.M. processed bioinformatic data. K.C., O.C., T.F., L.I., J.O., I.P., L.Q., J.N.W., C.J.E. and N.R. carried out wet laboratory work.

Competing interests The authors declare no competing interests.

Additional information

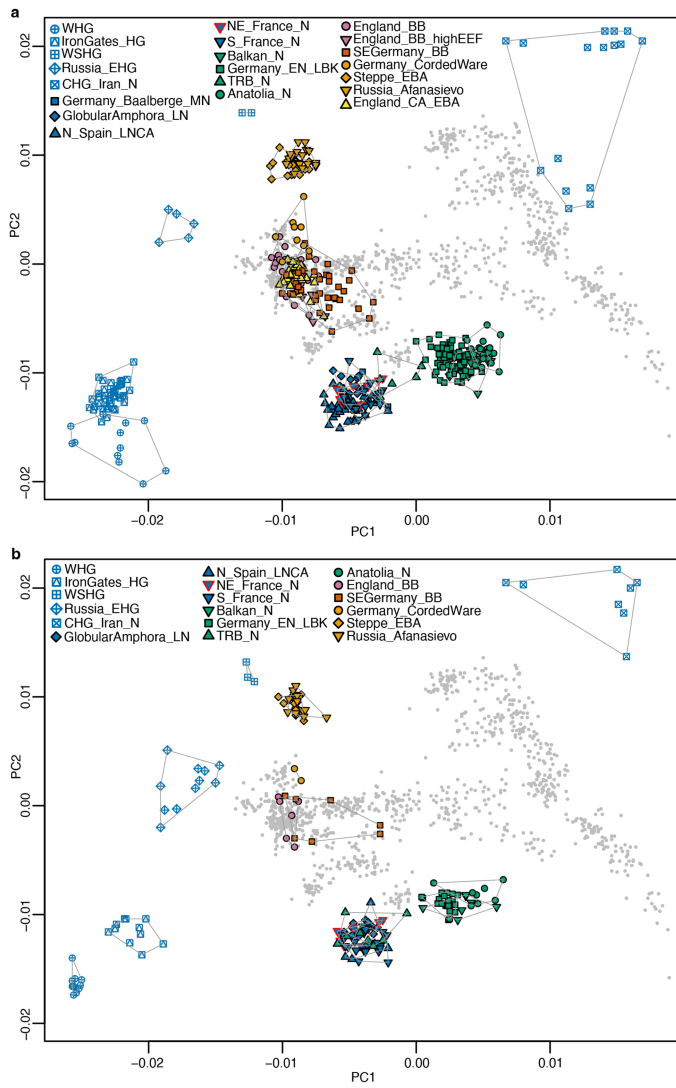
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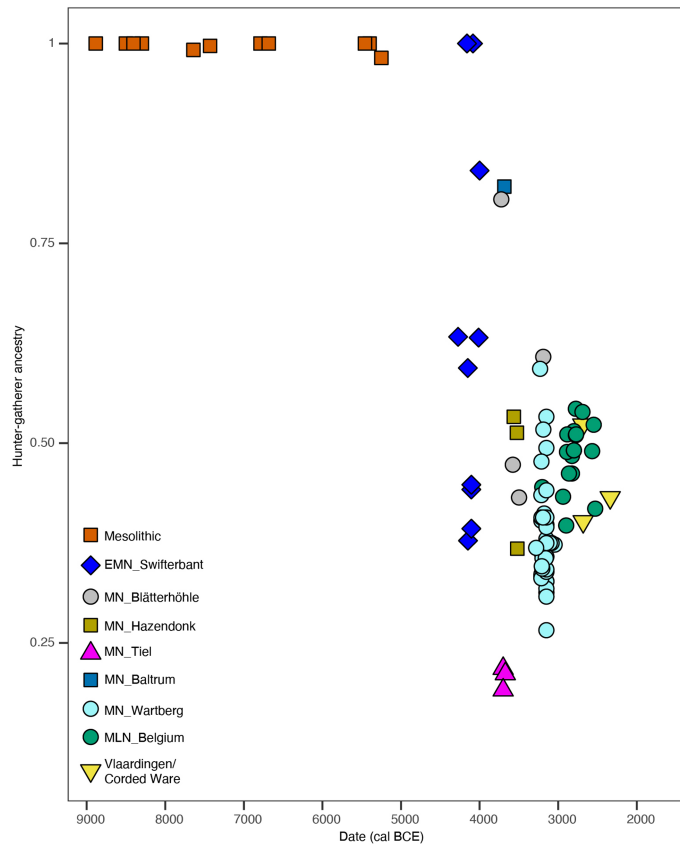
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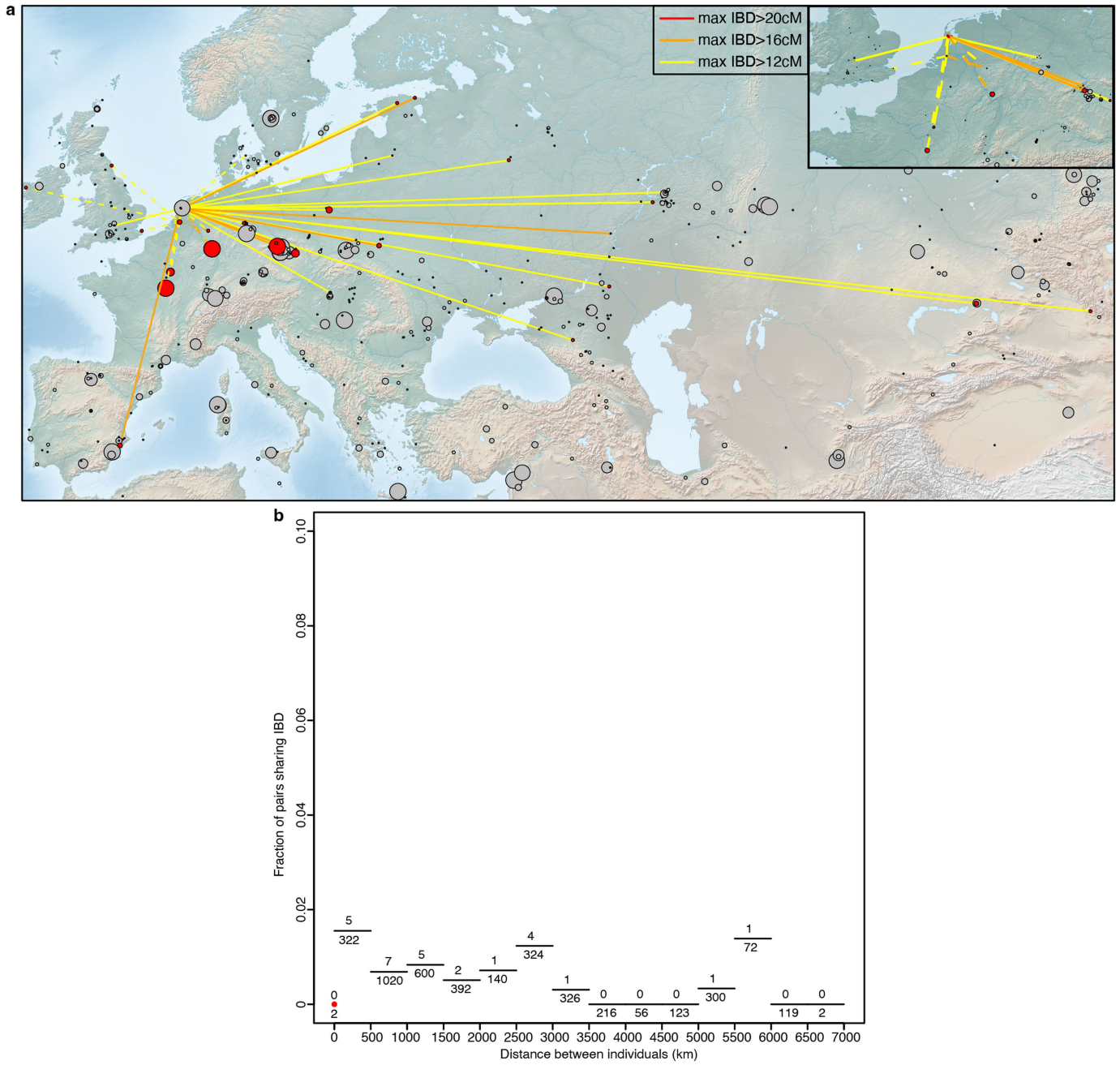
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Extended Data Fig. 1 | Genetic structure of relevant ancient groups used in *qpAdm* analysis. PCA of sources and outgroups used under *qpAdm*: **a**, setup 1-3; and **b**, setup 4 (Supplementary Tables 3, 4).

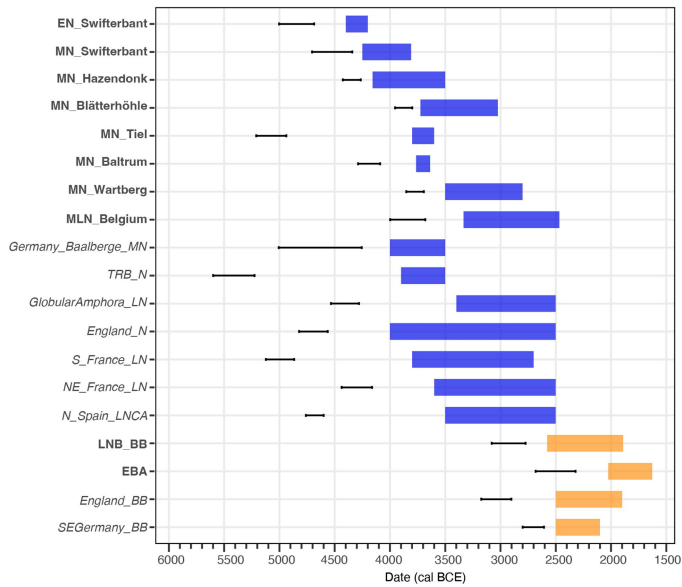


Extended Data Fig. 2 | Hunter-gatherer ancestry proportions across time in the Lower Rhine-Meuse area. Ancestry proportions were estimated using *qpAdm* (Supplementary Table 6).



Extended Data Fig. 3 | Genetic connections of Lower Rhine-Meuse CW/Vlaardingen individuals (n = 3). **a**, IBD sharing of Lower Rhine-Meuse CW/Vlaardingen individuals. Sites are represented by circles with size proportional to the number of individuals amenable to IBD calling. Grey circles indicate archaeological sites between 3000-2000 BCE with no IBD connections to CW/Vlaardingen individuals. The map was drawn using public-domain Natural

Earth data with the `rnaturalearth` package in R⁸⁷. **b**, Decay of IBD sharing with geographic distance for Lower Rhine-Meuse CW/Vlaardingen individuals. Pairs were considered to share IBD if they share at least one segment of >12 cM. Dotted lines represent IBD connections involving at least one individual without steppe-related ancestry.



Extended Data Fig. 4 | Admixture time estimates using DATES⁸¹. Boxes represent the chronological range for each population. Confidence intervals represent admixture date ranges, using 28 years per generation and the average date of the chronological range. We tested Balkan_N + WHG admixture for groups in blue, and MN_Wartberg+Germany_CordedWare admixture for groups in orange. In bold, groups from the Lower Rhine-Meuse region.

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Data collection BWA version 0.7.15 and other bioinformatics tools and data workflows (<https://github.com/DReichLab/ADNA-Tools> and <https://github.com/DReichLab/adna-workflow>). A detailed description of the data preprocessing steps is given in the Methods section of the manuscript.

Data analysis Relevant published software we used (including version):
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Sample size	The sample size and geographic distribution is determined by accessibility of relevant osteological remains with sufficient aDNA preservation; it is not something we can choose a priori. We report new ancient DNA data from contexts where ancient DNA has not previously been reported, analyzing all samples with sufficient aDNA preservation. Although even more powerful inferences could have been made if sample sizes were larger, we can make many meaningful new inferences with the available samples.
Data exclusions	We excluded samples that did not fall within the geographic scope of the study. After collecting genetic data, we excluded individuals from the analysis dataset as described in the Methods section entitled "Evaluation of authenticity". Specifically: "We established aDNA authenticity using several criteria. Libraries with a deamination rate below 3% at the terminal nucleotide were excluded from further analysis. We computed the ratio of Y-chromosome to X- and Y-chromosome reads. Libraries with ratios above 0.03 and below 0.32 were excluded from further analysis. We estimated mismatch rates to the consensus mitochondrial sequence using contamMix-1.0.1051, and X-chromosome contamination estimates using ANGSD in males with sufficient coverage. Libraries with evidence of contamination were excluded from further analysis. Finally, individuals without a minimum of 20,000 targeted 1240k SNPs with at least one overlapping sequence were discarded from population genetic analysis. After applying these filters, 86 libraries from 42 individuals remained, and we merged data from the libraries to increase sequencing coverage."
Replication	Only a single library can be made from each extract aliquot so no replication from the same extract is possible. For the individuals with more than one library, we confirmed in all cases that the libraries were from the same individuals. Another measure of replication also derives from the fact that the ancestry distributions in individuals from the same periods tended to be very similar. As a result of this, key findings in this study are not dependent on single samples.
Randomization	Historical studies are retrospective rather than prospective -- and the actual trajectory of human history has occurred only once -- so randomization of the data into independent processes is not possible. The manuscript discusses a caveat about possible biases due to non-random sampling.
Blinding	Co-analysis of the genetic and archaeological data was central to the study, so we could not be blind to the sample identity.

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Palaeontology and Archaeology

Specimen provenance	We describe the provenance of all archaeological specimens in the Supplementary Information Section 2 "Archaeological context information about the newly reported and published individuals from the Rhine-Meuse area."
Specimen deposition	The bone and tooth parts that remain after analysis for ancient DNA are under the stewardship of the archaeologists and cultural institutions from which they were sampled. At present, they are either already returned to the sample stewards or they are stored on long-term loan at the ancient DNA laboratories where they were analysed. They can be re-examined upon request to the sample stewards. Researchers who wish to replicate analyses from this study or gather new data on the libraries generated for this study are welcome to make a request for aliquots of those libraries to corresponding author David Reich who will fulfill all reasonable requests
Dating methods	We obtained 12 new accelerator mass spectrometry-based dates on bone, using the standardized methods described at the service laboratories.
<input checked="" type="checkbox"/>	Tick this box to confirm that the raw and calibrated dates are available in the paper or in Supplementary Information.
Ethics oversight	All human skeletons analysed in this study were sampled with written permission of the stewards of the skeletons and every individual is represented by at least one co-author. Researchers who wish to obtain further information about specific individuals should write to the corresponding authors and/or the authors. The individuals studied here were all analyzed with permission from local authorities in each location from which they came. Every sample is represented by stewards, such as archaeologists or museum curators, who are either authors or thanked in the Acknowledgments.

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Plants

Seed stocks	N/A
Novel plant genotypes	N/A
Authentication	N/A