Journal of Human Evolution 79 (2015) 73–92

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

Human paleogenetics of Europe – The known knowns and the known unknowns

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ARTICLE INFO

Article history:
Received 4 February 2014
Accepted 19 June 2014
Available online 13 November 2014

Keywords:
Ancient DNA
Paleolithic
Mesolithic
Neolithic
Archaeology

ABSTRACT

The number of ancient human DNA studies has drastically increased in recent years. This results in a substantial record of mitochondrial sequences available from many prehistoric sites across Western Eurasia, but also growing Y-chromosome and autosomal sequence data. We review the current state of research with specific emphasis on the Holocene population events that likely have shaped the present-day genetic variation in Europe. We reconcile observations from the genetic data with hypotheses about the peopling and settlement history from anthropology and archaeology for various key regions, and also discuss the data in light of evidence from related disciplines, such as modern human genetics, climatology and linguistics.

Introduction

Within the field of ancient DNA (aDNA), considerable focus has been placed on exploring the genetics of ancient hominins and the population history of anatomically modern humans. Despite the controversial early days of aDNA work and inherent pitfalls, especially when working with ancient human samples (Cooper and Poinar, 2000; Pääbo et al., 2004; Gilbert et al., 2005), recent studies on prehistoric individuals have now advanced sufficiently to produce reliable insights into specimens from past populations by applying strict authentication criteria, including 'DNA-free' sampling in the field, dedicated aDNA facilities, a series of decontamination procedures and experimental controls, and a hierarchical framework of independent replication of results (see e.g., Gilbert et al., 2005, 2006; Malmström et al., 2005; Deguilloux et al., 2011a, 2012; Brandt et al., 2013 for more details on this topic). In contrast to modern DNA studies, which can only infer past events from present-day distribution patterns, aDNA studies have the advantage of providing direct genetic evidence at a given point in time (either from a radiocarbon date of the sample itself or its stratigraphic layer and archaeological context). This allows us to directly test hypotheses about the genetic affinity of ancient individuals and/or past populations as a whole.

The temperate and cooler climate zones of the Americas and Europe are the two main areas best studied at this point, due to their natural conditions favorable for DNA preservation. The large number of aDNA laboratories, close and regional collaborations with archaeologists and anthropologists, and significant resources available to study the peopling history of these regions can also be listed as factors. These days, the number of aDNA records amounts to several hundreds of individuals for both America and Europe or Eurasia. The paleogenetic record of Europe has been summarised recently (e.g., Deguilloux et al., 2012; Pinhasi et al., 2012; Lacan et al., 2013), and implications for neighboring fields such as physical anthropology and zooarchaeology (considering domestication events accompanying major cultural transitions) have been discussed (e.g., Vigne, 2011; von Cramon-Taubadel and Pinhasi, 2011; Pinhasi and von Cramon-Taubadel, 2012; Larson and Burger, 2013). However, two more recent studies have substantially solidified the observed population events forming the European genetic landscape, resulting in a four-fold increase of aDNA data available from

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Abbreviations: aDNA, ancient DNA; cal BC, calibrated years Before Christ; LBK, Linear Pottery culture or *Linearbandkeramische Kultur*; mtDNA, mitochondrial DNA; PCA, principal component analysis.

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http://dx.doi.org/10.1016/j.jhevol.2014.06.017
0047-2484/

Europe, which warrants a fresh synthesis of the work to date (Fig. 1A). The first study has provided more data on Mesolithic hunter-gatherers and the complexity surrounding the Meso-Neolithic transition (Bollongino et al., 2013). The second one, a study by our group, has established the first comprehensive genetic transect through time in Central Germany's Mittelelbe-Saale region (Brandt et al., 2013), which can serve as a genetic reference stratigraphy to anchor and assess single site/culture studies in adjacent regions. In short, this detailed chronological study has revealed a series of population events in Central Europe, which in sum could explain most if not all of the genetic diversity observed today:

- The initial peopling event providing a Paleolithic and Mesolithic genetic substratum
- The impact of incoming farmers during the Early Neolithic (event A)
- A period of genetic continuity followed by an assimilation of surrounding hunter-gatherers in peripheral contact zones (events B1 and B2)
- A period of renewed genetic influx during the Late Neolithic with variable regional repercussions (events C and D).

In this review we will use this chronological reference dataset, updated with most recent studies, and discuss parallels and differences to various regions in Europe with specific focus on the more recent ‘Holocene’ population history. We will summarise the current status of uni-parentally inherited markers (i.e., mostly mitochondrial sequence data but also Y-chromosome data) and the first exciting results from genome sequencing efforts, but will also discuss further implications of genetic results in light of linguistic and climatic records.

Setting the scene – The genetics of pre-agricultural Europe

In order to shed light on the peopling of Europe, and especially the process of Neolithisation[1] with associated genetic changes in various regions of Europe, it is of utmost importance to fully understand the genetic substratum, i.e., the prevailing genetic diversity in Europe at the time of the Late Mesolithic. The genetic data available at present consist mostly of mitochondrial DNA (mtDNA) studies, but nuclear genomic data will undoubtedly widen our knowledge about past populations. This will include information about timing, number and mode of admixture events, population structure as well as sex-biased migration patterns, which cannot be inferred from uni-parentally inherited mtDNA. However, the chances of retrieving nuclear data at a sufficiently high level of complexity decrease as we gradually move from cooler and temperate climate zones to warmer and more challenging regions (Burger et al., 1999; Bollongino and Vigne, 2008; Pruvost et al., 2008), such as the Mediterranean coastlines including North Africa and the Near and Middle East, which promise to hold the ultimate answer to many of the questions tackled here. In all likelihood and despite great technological advances (Meyer et al., 2012; Gansauge and Meyer, 2013), aDNA studies in these regions will require intensive screening of many samples in order to find ones with suitable DNA preservation, and will often remain restricted to mtDNA evidence for the majority of specimens (Salamon et al., 2005; Hughey et al., 2013).

To date, 83 mtDNA sequences from 32 hunter-gatherer sites of Central, East, North, and South Europe have been published (Caramelli et al., 2003; Chandler, 2003; Chandler et al., 2005; Bramanti et al., 2009; Malmström et al., 2009; Krause et al., 2010; Hervella et al., 2012; Sanchez-Quinto et al., 2012; Skoglund et al., 2012; Bollongino et al., 2013; Der Sarkissian et al., 2013; Fu et al., 2013; Lazaridis et al., 2014) (Fig. 1A, sites 1–30, 63, 80). However, some of these forager populations, such as the Pitted Ware culture (Malmström et al., 2009; Skoglund et al., 2012) or the Ostorf site in northern Germany (Bramanti et al., 2009) were contemporaneous with Neolithic cultures of the relevant regions and therefore potentially influenced by farming communities. In the latter case, archaeological research has suggested that the Ostorf people were formerly farmers who became fishermen (Lübke et al., 2007). The 57 remaining sequences from confirmed Mesolithic contexts clearly cement the Upper Paleolithic and post-glacial Mesolithic female substratum as predominantly members of mtDNA haplogroup[2] U, e.g., U2, U4, U5a, U5b, and U8 (Bramanti et al., 2009; Krause et al., 2010; Hervella et al., 2012; Sanchez-Quinto et al., 2012; Bollongino et al., 2013; Der Sarkissian et al., 2013; Fu et al., 2013; Lazaridis et al., 2014). In sharp contrast, the genetic lineages of Early Neolithic farmers from Central and Southwest Europe (238 individuals from 30 sites (Fig. 1A, sites 31–58, 81)) are comprised of a wider array of mtDNA lineages with a generally higher diversity (e.g., H, HV, V, K, J, T2, X, W, N1a), in which U lineages are generally less frequent, or in the case of Central Europe very rare or even absent (Fig. 1B and Fig. 2A–C) (Chandler et al., 2005; Haak et al., 2005, 2010; Bramanti, 2008; Lacan et al., 2011a; Gamba et al., 2012; Hervella et al., 2012; Lee et al., 2012; Brandt et al., 2013; Lazaridis et al., 2014), supporting a genetic discontinuity of maternal lineages at the advent of farming (Bramanti et al., 2009; Haak et al., 2010; Brandt et al., 2013).

The wide geographic distribution of haplogroup U in the Upper Paleolithic and Mesolithic ranging from sites in Portugal (Chandler et al., 2005) and the two La Braña individuals (possibly closely related; Sanchez-Quinto et al., 2012) in the far West to the Yuzhny Oleni Ostrov site in Karelia's North (Der Sarkissian et al., 2013), Kostenki in Russia (Krause et al., 2010) and the Mal'ta boy in the Lake Baikal region (Raghavan et al., 2014) is very interesting and argues for a relatively small population size of hunter-gatherer bands, stretching across vast longitudinal space. Associated cultural attributes, such as ornaments and figurines seem to indicate cultural affinities across large geographic distances (Sanchez-Quinto et al., 2012; Olalde et al., 2014).

The finding of U types in pre-agricultural Europeans is consistent with a study of Richards and colleagues (Richards et al., 2000), who, based on coalescence age calculation of modern-day European population data, suggested that haplogroup U was one of the oldest Eurasian branches in the mitochondrial phylogeny and therefore a prime candidate for an expanding lineage during the initial peopling of Eurasia by anatomically modern humans ~42 kya (thousand years ago) (Mellars, 2006). Another interesting aspect is that some of the oldest samples (e.g., Mal'ta and Dolní Věstonice) show basal U haplotypes (Fu et al., 2013; Raghavan et al., 2014), which cannot be attributed to any of the known sub-clades. This not only supports the authenticity of individual results but also matches our expectations about sequence evolution (with the age

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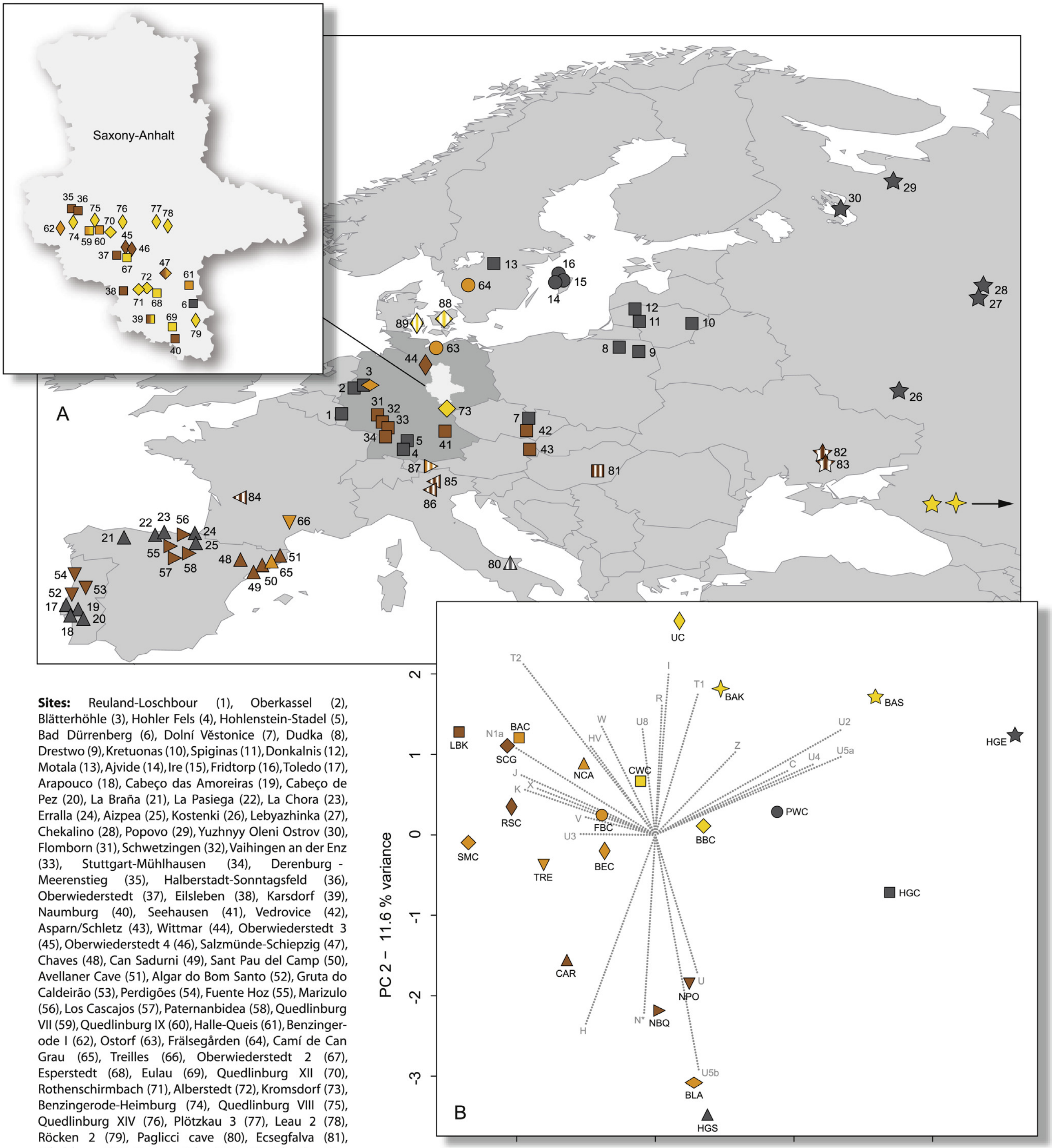
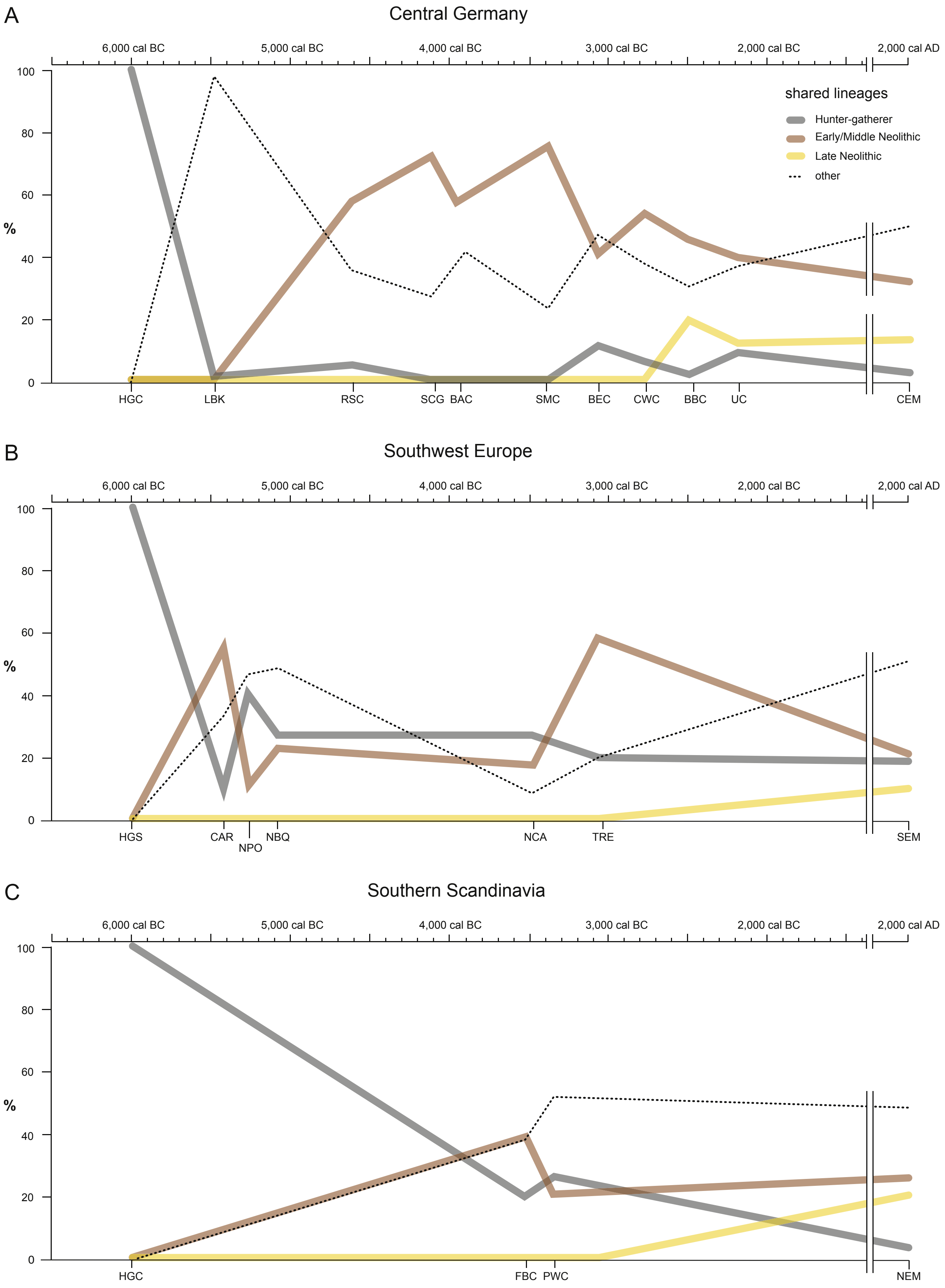
[1] The process of Neolithisation describes the shift from a nomadic or seasonally changing hunter-gatherer-fisher lifestyle to more sedentary subsistence strategies involving agricultural practices, animal and plant husbandry, and accompanying changes in material culture and social organisation.

[2] Human mitochondrial sequence polymorphisms are commonly described as ‘haplotypes’, whereas characteristic polymorphisms, which are shared between individuals, are combined in ‘haplogroups’ (or lineages), following a hierarchical phylogenetic structure and nomenclature, including macro- and sub-haplogroups. Haplogroups commonly found in Europe today include U2–U5,K,R0,HV,V,H,J,T,W,I,X, and N1a (Richards et al., 1998).



Sites: Reuland-Loschbour (1), Oberkassel (2), Blätterhöhle (3), Hohler Fels (4), Hohlenstein-Stadel (5), Bad Dürrenberg (6), Dolní Věstonice (7), Dudka (8), Drestwo (9), Kretuonas (10), Spiginas (11), Donkalnis (12), Motala (13), Ajvide (14), Ire (15), Fridtorp (16), Toledo (17), Arapouco (18), Cabeço das Amoreiras (19), Cabeço de Pez (20), La Braña (21), La Pasiega (22), La Chora (23), Erralla (24), Aizpea (25), Kostenki (26), Lebyazhinka (27), Chekalino (28), Popovo (29), Yuzhnyy Oleni Ostrov (30), Flomborn (31), Schwetzingen (32), Vaihingen an der Enz (33), Stuttgart-Mühlhausen (34), Derenburg - Meerenstieg (35), Halberstadt-Sonntagsfeld (36), Oberwiederstedt (37), Eilsleben (38), Karsdorf (39), Naumburg (40), Seehausen (41), Vedrovice (42), Asparn/Schletz (43), Wittmar (44), Oberwiederstedt 3 (45), Oberwiederstedt 4 (46), Salzmünde-Schiepzig (47), Chaves (48), Can Sadurni (49), Sant Pau del Camp (50), Avellaner Cave (51), Algar do Bom Santo (52), Gruta do Caldeirão (53), Perdigões (54), Fuente Hoz (55), Marizulo (56), Los Cascajos (57), Paternanbidea (58), Quedlinburg VII (59), Quedlinburg IX (60), Halle-Queis (61), Benzingerode I (62), Ostorf (63), Frälsegården (64), Camí de Can Grau (65), Treilles (66), Oberwiederstedt 2 (67), Esperstedt (68), Eulau (69), Quedlinburg XII (70), Rothenschirmbach (71), Alberstedt (72), Kromsdorf (73), Benzingerode-Heimburg (74), Quedlinburg VIII (75), Quedlinburg XIV (76), Plötzkau 3 (77), Leau 2 (78), Röcken 2 (79), Paglicci cave (80), Ecsegfalva (81), Nikolskoye (82), Yasinovataka (83), Prissé-la-Charrière (84), Borgo Nuovo (85), Mezzocorona (86), Tisenjoch (87), Damsbo (88), Bredtoftegård (89).

Figure 1. Location and principal component analysis (PCA) of paleogenetic data published to date. (A) Map showing the location of prehistoric sites from which aDNA data have been published. Symbols indicate populations from Central Europe (squares and diamonds), outhern Scandinavia (circles), South/Southwest Europe (triangles), and East Europe/Asia (stars). Colour shadings denote hunter-gatherer (grey), Early Neolithic (brown), Middle Neolithic (orange), and Late Neolithic/Bronze Age (yellow) samples. (B) The majority of these ancient DNA sequences were pooled into 22 groups according to cultural affiliation or spatial and temporal relations. The mtDNA haplogroup frequencies of these groups were used to perform PCA as described in Brandt et al. (2014). Each haplogroup is superimposed as component loading vector (grey), proportionally to its contribution. Striped colours on the map indicate data that were not included in the PCA due to small samples sizes. Abbreviations: BAC = Baalberge culture, BAK = Bronze Age Kazakhstan, BAS = Bronze Age Siberia, BBC = Bell Beaker culture, BEC = Bernburg culture, BLA = Blätterhöhle, CAR = (Epi)Cardial culture, CWC = Corded Ware culture, FBC = Funnel Beaker culture, HGC = hunter-gatherers Central and North Europe, HGE = hunter-gatherers East Europe, HGS = hunter-gatherers Southwest Europe, LBK = Linear Pottery culture, NBQ = Neolithic Basque Country and Navarre, NCA = Neolithic Catalonia, NPO = Neolithic Portugal, PWC = Pitted Ware culture, RSC = Rössen culture, SCG = Schöningen group, SMC = Salzmünde culture, TRE = Treilles culture, UC = Unetice culture. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).


A
Central Germany
6,000 cal BC
5,000 cal BC
4,000 cal BC
3,000 cal BC
2,000 cal BC
2,000 cal AD
100
80
60
40
20
0
%
shared lineages
Hunter-gatherer
Early/Middle Neolithic
Late Neolithic
other
HGC
LBK
RSC
SCG
BAC
SMC
BEC
CWC
BBC
UC
CEM
B
Southwest Europe
6,000 cal BC
5,000 cal BC
4,000 cal BC
3,000 cal BC
2,000 cal BC
2,000 cal AD
100
80
60
40
20
0
%
HGS
CAR
NPO
NBQ
NCA
TRE
SEM
C
Southern Scandinavia
6,000 cal BC
5,000 cal BC
4,000 cal BC
3,000 cal BC
2,000 cal BC
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100
80
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HGC
FBC
PWC
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of the older samples being closer to the coalescence date and therefore closer to the root of the branch).

Despite the apparent uniformity at the haplogroup level, there is increasing evidence for a Mesolithic population structure in Eurasia, justifying a closer look at the available data. Malyarchuk et al. (2010) studied the modern-day distribution of subhaplogroup U5 in particular and proposed different places of origin during the Upper Paleolithic for each of the sub-clades, with U5b in the West and U5a in the East. This is in accordance with studies that linked sub-haplogroups of U5b, such as U5b1b1 and U5b3, with an expansion after the Last Glacial Maximum from southwestern refugia in Franco-Cantabria and Italy, respectively (Achilli et al., 2005; Pala et al., 2009). So far, final conclusions cannot be drawn from the small number of ancient individuals from each separate aDNA study. However, when taken together it appears that ancient hunter-gatherer samples confirm the hypothesis of different places of origin for each of the U5 sub-clades, showing higher frequencies of U5b in the West (Chandler et al., 2005; Hervella et al., 2012; Sanchez-Quinto et al., 2012), with U5a more common in the (North)east (Bramanti et al., 2009; Krause et al., 2010; Der Sarkissian et al., 2013; Lazaridis et al., 2014), and a mixed composition in Central Europe (Bramanti et al., 2009; Bollongino et al., 2013; Fu et al., 2013). This is also indicated by the separation of distant hunter-gatherer groups from Central, East, and Southwest Europe in the principal component analysis (PCA) (Fig. 1B). Interestingly, sub-clade U4 seems to be most common around the Baltic region and South Scandinavia today and has been proposed to have originated in a Southeast European glacial refugium (Malyarchuk et al., 2008) and is indeed more frequent in central and northeastern hunter-gatherers (Bramanti et al., 2009; Malmström et al., 2009; Der Sarkissian et al., 2013; Lazaridis et al., 2014) (Fig. 1B), which also argues for structured ancient populations during Upper Paleolithic and Mesolithic times. This picture becomes more complex with the observation of non-U lineages in peripheral regions in the far West (haplogroup H and N*) and Northern Russia (haplogroup H and C), while these are absent in Central European foragers. Haplogroup H has been reported with high frequencies (38%) from hunter-gatherers in Portugal and the Basque country (Chandler et al., 2005; Hervella et al., 2012) and one individual from the Yuzhnyy Oleni Ostrov site in Northern Karelia (Der Sarkissian et al., 2013), indicating a widespread and possibly clinal distribution of haplogroup H in Mesolithic Europe. Under this hypothesis it seems to be a question of time when the first H lineage will be reported from Central European hunter-gatherers. In addition, haplogroup N* has been described in Mesolithic individuals from Portugal (Chandler et al., 2005) and one Paleolithic individual from South Italy (Caramelli et al., 2003), suggesting a distribution across Southern Europe during Paleolithic and Mesolithic times. While the data from Portugal have not been published in a peer-reviewed journal and therefore are best viewed cautiously, the reported presence of U5b in this Mesolithic dataset is absolutely plausible, while N* and H have seemingly been confirmed by independent studies (Caramelli et al., 2003; Hervella et al., 2012). N* has also described from the Cardial culture in Northeastern Spain (Gamba et al., 2012), which represents the first farming culture of the Iberian Peninsula. If we accept that N* was already present in Mesolithic Southwestern Europe, this can be likely interpreted as the result of admixture between immigrant farmers and local hunter-gatherers. As such, based on the current state of research, the presence of haplogroups N*, H, U5b, and U4 (albeit at low frequency) and the absence of U2 and U5a, could be interpreted as the genetic Mesolithic substratum of Southwestern Europe. In contrast, East European hunter-gatherers show a different haplogroup composition, which is based on higher frequencies of U2, U4, and U5a than in Central and South Europe, very low frequencies of H, and the absence of U5b and N*. Haplogroup U2 has been identified in Paleolithic individuals from Kostenki (Krause et al., 2010), Motala in Sweden (Lazaridis et al., 2014) and Mesolithic data from the Republic of Karelia in Northwest Russia (Der Sarkissian et al., 2013). In contrast, U2 has been detected only rarely in Central Europe (Bollongino et al., 2013), and has not yet been observed in Southwestern Europe. Therefore, it appears that haplogroup U2 was more frequent in the Mesolithic of North and East Europe than in Central or Southwest Europe. Furthermore, a considerable amount of haplogroup C, common in Asia and the Americas today, has been detected in forager populations of Northwest Russia, which was interpreted as genetic influx from West Siberia during the Mesolithic (Der Sarkissian et al., 2013).

The emerging genome data from a few Mesolithic and early farming individuals (Keller et al., 2012; Sanchez-Quinto et al., 2012; Skoglund et al., 2012; Lazaridis et al., 2014; Olalde et al., 2014; Raghavan et al., 2014) confirms the discontinuity between hunter-gatherers and early farmers by identifying at least two distinct genetic components. Skoglund and colleagues attributed the first component to South/Southeast European farmers, which is best represented by modern-day Sardinians, but also matches genomic data from the famous Tyrolean Iceman (Keller et al., 2012; Skoglund et al., 2012). The second component characterises Northwest European hunter-gatherers and is still present in many modern-day North European populations. Low coverage genome sequencing of two Mesolithic individuals from Iberia confirms this discontinuity in Western Europe (Sanchez-Quinto et al., 2012). Importantly, the first autosomal data not only support the discontinuity seen in the mitochondrial results, and as such critically undermine the idea of an exclusively cultural diffusion of the Neolithic way of life, but also suggest a more complex population structure in pre-agricultural Europe, which in turn will affect our interpretation of the events following the initial Meso-Neolithic transition. In particular, the most recent study by Lazaridis et al. (2014), including high coverage genome data from one Mesolithic individual from Loschbour/Luxembourg plus additional low coverage data from the Swedish hunter-gatherer site Motala and one early farmer of the Linear Pottery culture or *Linearbandkeramische Kultur* (LBK) from Stuttgart-Mühlhausen, is most elucidating, suggesting at least three ancient populations, contributing in various proportions to all modern-day Europeans. The first is an

Figure 2. Shared haplotype analyses. Shared haplotype analyses were performed in three key regions of Europe including Central Germany's Mittelelbe-Saale region (A), Southwestern Europe (B) and Southern Scandinavia (C), following the concept described in (Szécsényi-Nagy et al., 2014). Available Neolithic data from each region were combined with respective hunter-gatherer and modern-day metapopulations (CEM = Central European metapopulation, SEM = South European metapopulation, NEM = North European metapopulation) and placed in chronological order. The modern-day metapopulations are each represented by 500 randomly selected individuals. To estimate the amount of lineages in each region, which were present during the Paleo/Mesolithic and likely have been brought in by incoming farmers or emerged in later Neolithic periods, we traced each lineage of a temporal group back to its earliest match in the chronology and regarded it as an ancestral lineage that appeared in this group for the first time. Colored lines indicate summarised matches with lineages from hunter-gatherers (grey), Early/Middle Neolithic (brown) and Late Neolithic/Early Bronze Age (yellow) cultures. Haplotypes without direct matches in previous cultures/populations were not resolved and defined as others (black dotted line). Since the available data from Mittelelbe-Saale provides a gapless genetic record from the introduction of farming to the Early Bronze Age, we used this genetic reference stratigraphy together with respective Mesolithic data to also evaluate the amount of hunter-gatherer, early farmer and Late Neolithic components in Southwestern Europe and Southern Scandinavia via direct comparison with Mittelelbe-Saale data. Abbreviations are consistent with Figure 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

ancient North Eurasian population, exemplified by the Upper Paleolithic Mal'ta boy from Siberia (Raghavan et al., 2014), the second is a Western hunter-gatherer component (represented by Loschbour and also the two La Braña individuals; Sanchez-Quinto et al., 2012), and the third is an early European farmer component, which is represented by the LBK farmer from Stuttgart, the Iceman (Keller et al., 2012) and a Scandinavian farmer (Skoglund et al., 2012), closely related to modern-day Sardinians. The Scandinavian hunter-gatherers from Motala form their own cluster together with data from Skoglund et al. (2012), explained by the proportion of shared alleles with the ancient North Eurasian population, which is otherwise absent in the Western hunter-gatherer and early European farmer clusters.

The recent study by Lazaridis and colleagues (2014) also reports the first Y-chromosome results for five European hunter-gatherers (Loschbour and four males from Motala). Most interestingly, all five samples can be attributed to Y haplogroup I, which appears to be the predominant haplogroup in European hunter-gatherers and so far parallels the relative antiquity and constraint to one single (but major) branch as seen in mtDNA haplogroup U. This is consistent with population genetic studies that described the highest frequencies of Y haplogroup I in present-day Scandinavian and Southeast European populations, and proposed that I subgroups had been present in Europe since the late Upper Paleolithic and expanded after the Last Glacial Maximum from the Franco-Cantabrian and a Southeast European glacial refugium (Rootsi et al., 2004; Pericic et al., 2005; Karlsson et al., 2006; Lappalainen et al., 2009). However, the available Y data from early farmers do not parallel the diversity indicated by the mitochondrial data and appear, at the moment at least, restricted to only a few haplogroups among which G2a is predominant. G2a is rather rare in modern-day Europeans but was found in one out of three samples from LBK farmers in Central Europe (Haak et al., 2010), five out of six males at an Epicardial site in Spain (Lacan et al., 2011a), 20 out of 22 males at the Mid/Late Neolithic site Treilles in Southern France (Lacan et al., 2011b), and the Tyrolean Iceman (Keller et al., 2012). A recent study of late hunter-gatherers and early farmers from the Carpathian Basin by our group confirms this pattern further, observing predominantly G2a and to a smaller proportion I in nine male individuals (Szécsényi-Nagy et al., 2014).

While the presence of haplogroup I in Neolithic contexts could be interpreted as a signal of hunter-gatherer introgression in farming communities, and therefore represents a Paleolithic legacy, the precise way in which modern-day European Y-chromosome diversity was formed remains elusive. To date, the only other Y-haplogroups observed in early farming sites are haplogroup F in Germany and Hungary (Haak et al., 2010; Szécsényi-Nagy et al., 2014), and E1b in one individual in Spain (Lacan et al., 2011b). The presence of haplogroup F is very surprising, as it is very rare in modern-day European populations and therefore not well studied. It has been reported at a low frequency in Southeast Europe and the Near East (Underhill and Kivisild, 2007), whereas subgroups of F have been primarily found in India (Kivisild et al., 2003). E1b and J2 are common in extant South and Southeast Europeans and were thought to have spread with the Neolithic expansion (Semino et al., 2004), and while E1b has been observed, J2 and other common modern haplogroups, such as N1c (frequent in Siberian and Northeast European populations; Rootsi et al., 2007; Balanovsky et al., 2008) have yet to be observed in prehistoric contexts. Similarly, the most predominant haplogroups in modern-day European populations (R1b in West Europe and R1a in East Europe; Balaresque et al., 2010; Underhill et al., 2010; Myres et al., 2011) have not been found in early farming sites, but instead have been reported from Late Neolithic contexts with a surprisingly matching geographic distribution of the associated archaeological cultural complexes, namely the Bell Beaker complex in Western Europe (R1b; Lee et al., 2012) and the Corded Ware culture in East Europe (R1a; Haak et al., 2008; see also below). Interestingly, the aforementioned Mal'ta boy from Siberia carries a basal R haplogroup and likely predates the split into subgroups R1a, R1b and R2 (frequent in India). Since R is a sister-clade of Q, which is common in Native Americans, this argues for a common origin of RQ in Siberia (Wells et al., 2001; Raghavan et al., 2014). How and when the now frequent R1 subtypes reached Western Eurasia is an important question, which will need to be addressed in future aDNA studies (Underhill et al., 2010; Myres et al., 2011). In light of the population events A–D mentioned above, which contributed substantially to modern-day Central European mtDNA diversity (Brandt et al., 2013), it could be speculated that similar demographic processes had also shaped the European Y-chromosome variability. However, apart from the ‘I versus G2a pattern’, which now has been detected in sufficient numbers and from various sites, the presence/absence of other Y-chromosome haplogroups in prehistoric contexts is clearly of stochastic nature and can only serve as a working hypothesis until more information becomes available.

The importance of the Meso-Neolithic transition

The transition to farming (or the process of Neolithisation) emerged in the Near East's Fertile Crescent about 12,000 years ago and is described as one of if not the most fundamental cultural change in human history (Whittle, 1996; Price, 2000; Whittle and Cummings, 2007). It is deeply linked to the transition from foraging to agriculture and animal domestication alongside a more sedentary lifestyle, which was accompanied by radically new economic strategies and numerous changes in material culture, social life, customs and ideologies (Price, 2000; Whittle and Cummings, 2007). Over the course of the following millennia farming spread across Europe and replaced the foraging lifestyle of indigenous hunter-gatherer populations.

The nature and mode of the transition from a foraging to a farming lifestyle are the matter of longstanding debate in archaeology and adjacent fields (Rowley-Conwy, 2011). Archaeologists have described and discussed two major and largely contemporaneous routes of the expansion of farming, namely the Continental and the Mediterranean route (Price, 2000; Whittle and Cummings, 2007; Rowley-Conwy, 2011). The emergence and dispersal of Neolithic cultures, as well as the speed of the Neolithisation, varied across different regions in Europe in a series of complex interactions and temporal fluctuations (Bocquet-Appel et al., 2009). Traditionally, scholars explained the Neolithic transition either by expansion of early farmers from the Near East, who brought new ideas as well as new genes (demic diffusion) (Childe, 1925; Ammerman and Cavalli-Sforza, 1984; Cavalli-Sforza et al., 1994; Chikhi et al., 1998, 2002) or by adoption of innovative subsistence strategies of indigenous hunter-gatherer populations by a transfer of ideas with little or no genetic influence (cultural diffusion) (Whittle, 1996; Richards et al., 1996, 2000; Semino et al., 2000). Consequently, both the existence and the extent of a Neolithic contribution to the gene pool of present-day Europeans have been intensely debated until recently (Achilli et al., 2004; Dupanloup et al., 2004; Currat and Excoffier, 2005; Balaresque et al., 2010; Soares et al., 2010; Pala et al., 2012; Pinhasi et al., 2012; Olivieri et al., 2013).

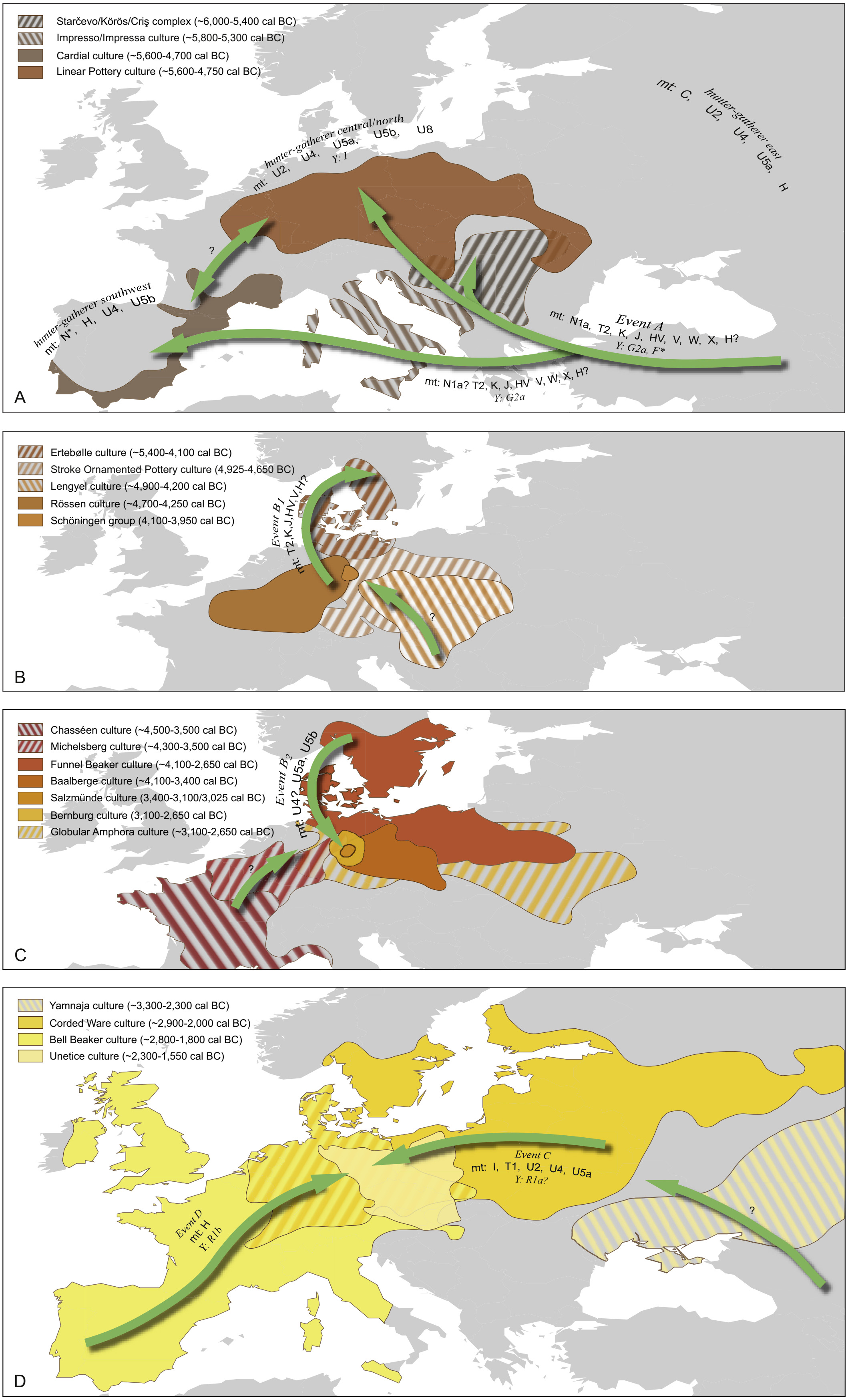
Uni-parentally inherited markers, such as mtDNA and Y-chromosome, have earned their merits in population genetics as they are relatively easy to track through generations, but the true advantage is that the respective modes of inheritance provide us with a uniquely male and female perspective of human evolutionary history (Pakendorf and Stoneking, 2005). It is crucial to investigate these two lines of evidence in parallel to data from the recombining autosomes, as they provide insights into social and demographic parameters, such as sex-biased introgression or mobility, which are important for the reconstruction of past societies (Haak et al., 2008).

Ethnographic and demographic studies have shown that economic factors (status and wealth) and social differentiation drive variation in sex-biased mobility (e.g., Bentley et al., 2009, 2012, and references therein). It is generally assumed that the transition from a foraging to a farming lifestyle brought about drastic changes to the social structure and residence patterns, shifting from bilocality to patrilocality in farming societies, which guaranteed the intergenerational transfer of status, wealth and territory (Marlowe, 2004; Wilkins, 2006; Wilkins and Marlowe, 2006; Rasteiro et al., 2012). Ethnographic research in contact zones between forager and farmer societies has also highlighted the social and economic imbalance between the two societies, often resulting in a 'culture clash', in which the farmers directly compete with hunter-gatherers, and the sustainable practices of farming seem to be an important economic drawing card. As a consequence, mobility under such a demographic scenario is most often uni-directional, with hunter-gatherer women marrying into farmer communities, but never or very rarely the opposite. At the genetic level, we would therefore expect to see a consolidation of farmer Y lineages replacing hunter-gatherer lines, whereas the female hunter-gatherer lineages would contribute to the diversity of farmers. Such a scenario is highly likely in contact zones at the wave-front of an expanding farming culture and would provide a plausible explanation for a slow but steady increase (or comeback) of e.g., mtDNA U lineages in cultural horizons, following the first assimilation and consolidation phases. At the same time, this would also explain the relatively limited diversity of Y lineages in early farming communities.

The early farmers of the LBK in Central Europe

A recent genetic study by our group has substantially extended the dataset for LBK farmers (Brandt et al., 2013), now comprising 109 individuals from 13 sites in Germany, Austria and the Czech Republic (Fig. 1A, sites 31–43). This represents to our knowledge the largest dataset from a single cultural horizon, and can be considered a sample size large enough to be truly representative, allowing for minimal statistical error. The resulting genetic profile is surprisingly consistent with our previous results from this culture (Haak et al., 2005, 2010) and fully confirms the conclusions drawn from the analysis: the haplogroup compositions of the last hunter-gatherers and early LBK farmers are virtually exclusive and a genetic discontinuity during the Meso-Neolithic transition appears to be 'set in stone', as shown by tests for population continuity (Brandt et al., 2013) and coalescent simulations (Bramanti et al., 2009; Haak et al., 2010). Several lines of analytical evidence support affinities of the LBK to modern-day populations of the Near East and reveal that the transition from a foraging to a farming lifestyle in Central Europe in the mid-sixth millennium BC was clearly associated with genetic influx via expanding LBK communities (event A, ~5500 cal BC, Fig. 3A), which brought new genetic elements from regions in Southeast Europe, Anatolia, the Caucasus and the Near East (Haak et al., 2010; Brandt et al., 2013). A shared haplotype analysis shows that only 1.8% of the LBK haplotypes match hunter-gatherers lineages, while the remaining 98.2% have not yet been reported from the Central and Northern European Mesolithic (Fig. 2A). The majority of these lineages (79.8%) can be assigned to haplogroups N1a, T2, K, J, HV, V, W, and X, which appear to be the most characteristic for the LBK period (Fig. 1B) and can thus be defined as the 'mitochondrial Neolithic package' that reached Central Europe in the sixth millennium BC (Brandt et al., 2013). The remaining lineages belong to haplogroup H (16.5%), U3 (0.9%), and U5a (0.9%). If we followed the logic above, then the U haplotypes could likely be interpreted as a Mesolithic legacy. However, the situation is more difficult to decipher in the case of haplogroup H, which has not been observed in Mesolithic Central Europe and Scandinavia but is present in Iberian hunter-gatherers (as shown above). A recent aDNA study by our team has revealed that the distribution of H subgroups in Central Europe changes over the course of the Neolithic, arguing for a more complex evolutionary history of this branch rather than being attributed to a single major event (Brotherton et al., 2013). Haplogroup H is the most common maternal lineage in extant European populations with frequency peaks of over 45% in Western Europe. The origin of H has been attributed to the Near Eastern Upper Paleolithic, from where it branched off from its sister-clades R0 and HV0 upon entering Europe. Most of the subgroups in present-day Europe show late glacial or post-glacial coalescence dates, arguing for a re-expansion during the major warming phases after 15 kya (Achilli et al., 2004; Pereira et al., 2005; Soares et al., 2010). Subgroups H1, H3, and H5 are believed to have spread from a Western refugium in Franco-Cantabria based on largely overlapping dates (11.1 kya, 11.5 kya, 13.9 kya, respectively) (Soares et al., 2010) and the fact that these are the most common types in Western Europe. While haplogroup H has been reported from Iberian Mesolithic individuals, the typing resolution unfortunately does not provide an unambiguous assignment to any of these subgroups (Chandler et al., 2005; Hervella et al., 2012). However, all Middle Neolithic individuals from Treilles in Southern France could be assigned to subgroups H1 and H3 via coding region SNP typing (Lacan et al., 2011b). In contrast, near complete mitochondrial genome sequences from LBK individuals show that only three out of nine fall within subgroup H1. The remaining six individuals carry basal and ancestral H lineages, which are rare today and show affinities to the Caucasus, Anatolia and the Near East, in support of an origin of basal H in this region (Brotherton et al., 2013). Based on these preliminary results, we feel that there is considerable structure within this large branch, which necessitates a higher resolution (complete mtDNA genomes) before we can ascribe certain subgroups to a specific time period in prehistory.

Aside from the haplogroup H conundrum, the overall mtDNA composition among and between extent LBK communities, ranging from the well known archaeological sites Flomborn, Vaihingen and Schwetzingen in Southwest Germany (Haak et al., 2005) to Vedrovice in the Czech Republic (Bramanti, 2008) (Fig. 1A), is surprisingly uniform with non-significant differences both on the haplotype and haplogroup level (Brandt et al., 2014). This suggests that the Neolithic transition in Central Europe driven by the LBK affected large territories and replaced most of the known hunter-gatherer variability with a relatively homogenous and coherent mitochondrial signature. This finding is in accordance with the archaeological hypothesis, which proposed a spread of farmers into Central Europe along a Continental route following the Danubian corridor (Gronenborn, 1999, 2007a; Bánffy, 2000; Price, 2000; Bogucki and Crabtree, 2004; Whittle and Cummings, 2007; Bocquet-Appel et al., 2009; Rowley-Conwy, 2011). Detailed archaeological research has shown that the cultural characteristics of the LBK emerged around 5600 cal BC from Early Neolithic cultures in the Carpathian Basin (Starčevo-Körös–Criş complex, ~6000–5400 cal BC) (Gronenborn, 1999; Bánffy, 2000). Our group is currently investigating Neolithic samples from the Carpathian Basin and the first results indeed hint at a close genetic affinity of LBK farmers with its preceding neighbors (Szécsényi-Nagy et al., 2014).


Starčevo/Körös/Criş complex (~6,000-5,400 cal BC)
Impresso/Impressa culture (~5,800-5,300 cal BC)
Cardial culture (~5,600-4,700 cal BC)
Linear Pottery culture (~5,600-4,750 cal BC)
mt: C, U2, U4, U5a, H
hunter-gatherer east
hunter-gatherer central/north
mt: U2, U4, U5a, U5b, U8
Y: I
?
hunter-gatherer southwest
mt: N*, H, U4, U5b
Event A
mt: N1a, T2, K, J, HV, V, W, X, H?
Y: G2a, F*
mt: N1a? T2, K, J, HV V, W, X, H?
Y: G2a
A
Ertebølle culture (~5,400-4,100 cal BC)
Stroke Ornamented Pottery culture (4,925-4,650 cal BC)
Lengyel culture (~4,900-4,200 cal BC)
Rössen culture (~4,700-4,250 cal BC)
Schöningen group (4,100-3,950 cal BC)
Event B1
mt: T2,K,J,HV,V,H?
?
B
Chasséen culture (~4,500-3,500 cal BC)
Michelsberg culture (~4,300-3,500 cal BC)
Funnel Beaker culture (~4,100-2,650 cal BC)
Baalberge culture (~4,100-3,400 cal BC)
Salzmünde culture (3,400-3,100/3,025 cal BC)
Bernburg culture (3,100-2,650 cal BC)
Globular Amphora culture (~3,100-2,650 cal BC)
Event B2
mt: U4? U5a, U5b
?
C
Yamnaja culture (~3,300-2,300 cal BC)
Corded Ware culture (~2,900-2,000 cal BC)
Bell Beaker culture (~2,800-1,800 cal BC)
Unetice culture (~2,300-1,550 cal BC)
Event C
mt: I, T1, U2, U4, U5a
Y: R1a?
?
Event D
mt: H
Y: R1b
D

Previous studies have singled out haplogroup N1a as a potential mtDNA marker associated with the spread of the first farmers into Central Europe (Haak et al., 2005, 2010). The enlarged dataset of 109 LBK individuals has revealed more N1a individuals, confirming a stable frequency of N1a (11.9%) during the Early Neolithic. The transect through time in Mittelelbe-Saale showed that the frequency of haplogroup N1a decreases during the Early and Middle Neolithic and is absent from the Bernburg culture and the Late Neolithic/Early Bronze Age samples (Brandt et al., 2013). Other associated early farming lineages (e.g., T2, K, J, HV, and V) also decreased in frequency during the Middle and Late Neolithic, which can be explained by the impacts of subsequent migration and expansion events (e.g., B, C and D in Fig. 3A–D; Brandt et al., 2013, see also below). However, the reasons for the almost complete disappearance of N1a (<1% in modern-day Eurasian populations) are not fully understood. Interestingly, N1a has also been found in one individual of the Megalith culture (4340–4076 cal BC) from Southwest France (Deguilloux et al., 2011b) and one individual of the Alföld Linear Pottery culture (Ecsegfalva 23A, 5250–5000 BC; Haak et al., 2005), which can be regarded as a parallel development to the LBK in East Hungary (Alföld region). In addition, data from preceding cultures of the Carpathian Basin confirm the presence of N1a during the Neolithic in this region (Szécsényi-Nagy et al., 2014). Future aDNA studies targeting archaeological cultures south and east of the Carpathian Basin and from Eastern Anatolia are desired to further trace the expansion of early farmers through space and time.

Going West – the Neolithic transition in Southwest Europe via the Mediterranean route

In parallel to the spread of farming along the Continental route, the Neolithic way of life also expanded from the Near East Fertile Crescent to the Iberian Peninsula on a route that followed the coastlines of the northern Mediterranean Sea from the Aegean over the Tyrrhenian and Ligurian Sea to Southern France and Northeastern Spain. From there, farming spread further inland via major river systems, such as the Rhône and Ebro, and along the Mediterranean coastlines into Portugal (Price, 2000; Gronenborn, 2003; Rowley-Conwy, 2011). Additional ways for the distribution of Neolithic elements have been put forward, such as an expansion along the Pyrenees rather than the Mediterranean coasts (Schuhmacher and Sanz González de Lema, 2013) or a parallel route along the southern Mediterranean coastline in North Africa, which is thought to have influenced the southern parts of the Iberian Peninsula (Lewthwaite, 1989; Linstädter, 2008).

The earliest Neolithic of the Iberian Peninsula is mostly connected to the Cardial culture, which was established in the first half of the sixth millennium BC primarily on the Mediterranean coast of Spain and Southern France, concurrent with the appearance of the LBK in Central Europe (Zilhão, 1997, 2001; Price, 2000; Rowley-Conwy, 2011). Early Neolithic sites are known from the Ebro Valley and Portugal from the mid-sixth millennium BC onwards, arguing for a rapid spread along the Iberian Peninsula (Zilhão, 2001; Zapata et al., 2004; Rojo Guerra et al., 2006). Archaeologists have discussed numerous models for the transition from foraging to farming, each suggesting varying impacts of Neolithic encounters or Mesolithic residents (e.g., maritime pioneer colonisation model, mosaic model, dual model, and capillary model) (Vicent-García, 1997; Zilhão, 1997, 2001; Schuhmacher and Sanz González de Lema, 2013, and citations therein). It seems that different areas of the Iberian Peninsula present themselves with varying degrees and densities of Neolithic versus Mesolithic components. Moreover, older radiocarbon dates and questionable contexts of many multiphase archaeological sites complicate the interpretation of archaeological data. However, it has been widely accepted that the complexity of the shift from foraging to farming cannot be covered by oversimplifying models and should be interpreted in the specific context of each region (Férnandez López de Pablo and Gómez Puche, 2009).

Recent aDNA studies have provided direct insights into the mitochondrial and Y-chromosome diversity of Southwestern Europe during the Late Mesolithic and the Neolithic periods (Chandler et al., 2005; Sampietro et al., 2006; Lacan et al., 2011a,b; Gamba et al., 2012; Hervella et al., 2012; Sanchez-Quinto et al., 2012) (Fig. 1A, sites 17–25, 48–58, 65–66). In particular, the growing number of aDNA studies of early farmers from different regions in Iberia, namely Northeast Spain, Northern Spain, and Central Portugal, allow us to draw a more detailed picture of population dynamic processes at the onset of farming in the Iberian Peninsula.

Four Early Neolithic sites of the Cardial and Epicardial culture have been published covering the core region of Neolithisation in Iberia (Lacan et al., 2011a; Gamba et al., 2012) (Fig. 1A, sites 48–51). The composition of mitochondrial lineages comprises both southwestern hunter-gatherer haplogroups (U5b, H, and N*) and haplogroups that are common among Early and Middle Neolithic farmers from Central Europe (T2, K, and X), resulting in an intermediate positioning between these two in the PCA (Fig. 1B). On the haplotype level, 11.1% of the Cardial lineages can be traced back to the pre-Neolithic gene pool of Southwestern Iberia while 55.6% directly match those of early Central European farmers (Fig. 2B). This sharp increase of farmer lineages suggests a fast genetic turnover during the Neolithic transition in Southwest Europe, similar to the scenario in Central Europe, and is also supported by ^{14}C dates ranging in a narrow temporal window (Zilhão, 2001). In contrast, Early Neolithic samples from Central Portugal (Chandler et al., 2005) and Northern Spain (Hervella et al., 2012) harbor a larger number of forager lineages (41.2% and 27.9%, respectively) and fewer shared farming lineages (11.8% and 23.3%, respectively; Fig. 2B), resulting in greater affinities to southwestern hunter-gatherers as shown by the PCA plot (Fig. 1B). Taken together, this suggests that genetic elements of the ‘Neolithic package’, which had reached Central Europe via the Continental route (event A), also arrived in Southwest Europe through the Mediterranean route (Fig. 3A). However, the hunter-gatherer legacy is more dominant in the Iberian Neolithic compared with Central Europe, indicating a Neolithic transition with a larger contribution of the indigenous population combined with a reduced impact of early farmers. This apparent trend seems to be accentuated with growing distance from Northeast Spain, both inland and along the coast, and is consistent with a proposed pioneer colonisation model for Southwest Europe, according to which small farmer groups from the Near East spread along the Mediterranean coastlines (Chandler et al., 2005; Gamba et al., 2012; Hervella et al., 2012).

Figure 3. Summary of population dynamic events during the Neolithic period in Europe. Different shadings and patterns denote the geographic distributions of cultures during the Neolithic period until the Bronze Age: Early Neolithic (A and B), Middle Neolithic (C), and Late Neolithic/Early Bronze Age (D). Striped areas indicate archaeological cultures for which no aDNA data is available so far. Green arrows display potential geographic expansions and their associated mtDNA (mt) and Y chromosomal (Y) haplogroups. The mtDNA variability of indigenous hunter-gatherer populations from Central/North, Southwest, and East Europe is given in the respective regions (A). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

To date, only two studies have focused on later Neolithic periods in Southwestern Europe. The first study analyzed individuals from the Middle Neolithic period in Catalonia, Spain (~3500–3000 cal BC) (Sampietro et al., 2006), and the second one investigated the Treilles culture (~3030–2890 cal BC) in Southeastern France (Lacan et al., 2011b). While the Treilles culture shows a genetic composition comparable with the Cardial culture with 20.7% hunter-gatherer and 58.6% early farmer lineages, the samples from the Middle Neolithic in Northeastern Spain harbor a higher amount of forager (27.3%) and a lower frequency of farming lineages (18.2%), a composition very similar to the Early Neolithic samples from Portugal, Northern Spain, and present-day populations of Southwest Europe (Fig. 2B). As a result, the high abundance of characteristic farmer haplogroups observed in the Treilles culture leads to a positioning closer to the Early and Middle Neolithic cultures from Central Europe in the PCA plot (Fig. 1B). Despite the fact that all individuals from Early and Middle Neolithic Northeast Spain as well as the Treilles culture were sampled in regions where farming was first established in Southwest Europe, the varying amount of early farming lineages between these populations argues for a complex population history through time and across space.

Coalescent simulations suggested that the effect of genetic drift in structured populations must have played an important role between the Early and Middle Neolithic, resulting in a dilution of early farmer lineages from the Near East, and an mtDNA composition of Middle Neolithic individuals similar to present-day Iberians (Gamba et al., 2012). The mitochondrial composition of the Treilles group on the other hand points to more stable conditions in Southern France, in which farming lineages from the Near East persisted for a longer period of time than in neighboring regions of Northeastern Spain. However, Early Neolithic data from Southern and Central Spain and other parts of France would be desirable to test this hypothesis. In conclusion, the spread of farming into and over Southwest Europe and the transition to later Neolithic periods were characterised by several and varying processes at a regional level (Hervella et al., 2012). Despite the ostensible wealth of available aDNA data, we feel that the emerging regional complexity necessitates further detailed investigations both at larger geographic scale and chronological resolution to increase our knowledge about (regional) demographic processes during the Neolithisation and subsequent periods in Southwest Europe.

Population shifts in Southern Scandinavia

The Middle Neolithic period in Central Europe is characterised by the Neolithic expansion into regions outside the former LBK territory, especially North and Northeast Europe. In addition to the abundance of natural resources along the coastlines of the North and Baltic Sea, which did not necessitate a change in subsistence strategy, harsher climatic conditions and less fertile soils north of the preferred loess plains also prevented a rapid spread of agriculture in these regions (Whittle and Cummings, 2007). As a consequence, local hunter-gatherer communities of North Germany, Denmark, and South Sweden (Ertebølle culture, ~5400–4100 cal BC) still retained a foraging lifestyle for more than 1500 years after the emergence of the LBK, despite contacts with Central European farmers (Bogucki and Crabtree, 2004; Whittle and Cummings, 2007; Rowley-Conwy, 2011). There is a considerable debate in the archaeological literature examining whether farming was introduced but failed, after which people reverted back to the original/alternative subsistence strategies (Rowley-Conwy, 2011). However, farming was eventually established in Southern Scandinavia with the emergence of the Funnel Beaker culture complex or Trichterbecher Kultur (~4100–2650 cal BC), which had a clear emphasis on animal husbandry over cultivation of crops, while contemporaneous cultures like the Pitted Ware culture still retained their Mesolithic lifestyle (Bogucki and Crabtree, 2004; Rowley-Conwy, 2011).

Recent studies focusing on Mesolithic/Neolithic hunter-gatherer and farmer communities of Northern Europe have produced useful insights into the population history of the region (Bramanti et al., 2009; Malmström et al., 2009; Skoglund et al., 2012; Lazaridis et al., 2014) (Fig. 1A, sites 13–16, 63–64). Seven individuals from the site of Motala in Southern Sweden represent genuine Mesolithic data from this region (Lazaridis et al., 2014), and show exclusively haplogroup U (U2, U4, U5a), consistent with other data from Central/Northern Europe (as outlined above). In contrast, samples attributed to the Funnel Beaker culture (Bramanti et al., 2009; Malmström et al., 2009) can be characterised by a mixture of typical hunter-gatherer lineages (U5a and U5b) and haplogroups from the ‘Neolithic package’, such as T2, J, and K. This results in an intermediate position of the Funnel Beaker culture between hunter-gatherer populations and the Early/Middle Neolithic cultures on the PCA plot (Fig. 1B). On a more detailed haplotype level, 20% and 40% of the Funnel Beaker samples match hunter-gatherer and early farmer haplotypes, respectively (Fig. 2C), suggesting genetic influence from Central Europe into Funnel Beaker communities in Southern Scandinavia. We therefore proposed a dynamic population or migration event B_2 at ~4100 cal BC (Brandt et al., 2013) (Fig. 3B), which can be considered as delayed extension of the initial farming expansion during the LBK. Genomic sequence data from one Funnel Beaker individual has shown the greatest similarity to present day South(east) European populations, Sardinians in particular, and has supported genetic influx from the South into Southern Scandinavia at the advent of farming (Skoglund et al., 2012). Interestingly, contemporaneous Neolithic foragers of the Pitted Ware culture from the Island of Gotland (Malmström et al., 2009) also show a mixed mtDNA composition of hunter-gatherer and farmer elements comparable to the Funnel Beaker culture, albeit with higher proportions of Mesolithic lineages (26.3%), predominantly consisting of haplogroup U4, and lower amounts of farming lineages of haplogroups T2, K, HV, and V (21.1%) (Fig. 2C). The high U4 frequency in the Pitted Ware culture is in accordance with a proposed eastern Baltic refugium for some of the European hunter-gatherer populations during the Last Glacial Maximum (Malmström et al., 2009), which has been further supported by genomic affinities of three Pitted Ware culture individuals to modern-day Northeast European populations (Skoglund et al., 2012). The presence of farmer lineages in the Pitted Ware culture can be interpreted either as direct gene flow from the south, i.e., Central Europe, or indirectly via admixture between Funnel Beaker and the Pitted Ware groups. However, the amount of hunter-gatherer lineages in both Scandinavian cultures is remarkably higher than in any Early/Middle Neolithic Mittelelbe-Saale culture indicating a stronger contribution of Mesolithic females during the Neolithic transition in Southern Scandinavia. It seems highly plausible to us that the process of Neolithisation was much slower in northern frontier zones and had at least partially relied on Mesolithic subsistence or good relations to hunter-gatherer-fisher neighbors compared with Central Europe. Presumably, subsistence was introduced by small pioneer groups from the former LBK area, using what Rowley-Conwy (2011) describes as ‘lurches of advance’, which encouraged local hunter-gatherer groups of the Ertebølle culture to slowly adopt the new lifestyle. Archaeologists have described contacts of the Ertebølle culture with southern farming communities, such as the LBK and the Rössen culture, which likely introduced new farming techniques and subsistence strategies in Southern Scandinavia resulting in the manifestation of the Funnel Beaker complex about 1500 years later (Behrens, 1973; Beier and Einicke, 1994; Preuss, 1998; Bogucki and Crabtree, 2004; Whittle and Cummings, 2007; Rowley-Conwy, 2011).

The combined genetic data from Central Europe and Scandinavia also reveal a reflux of hunter-gatherer lineages from the North to Central Europe by representatives of the Funnel Beaker culture complex, which becomes evident in increasing frequencies of haplogroups U5a and U5b in Mittelelbe-Saale's Bernburg culture, leading us to propose event B_2 at ~3100 cal BC (Fig. 3C). However, the archaeological record has described a more detailed cultural sequence, in which the Bernburg culture represents only the latest phase of a longer and more complex development (Behrens, 1973; Beier and Einicke, 1994; Preuss, 1998). The Bernburg culture arose from the preceding Walternienburg culture (3325–3100 cal BC), which in turn emerged from the preceding Tiefstich Pottery culture (3650–3325 cal BC), even though all of these represent subtle variations of the Funnel Beaker culture complex (Fig. 4). In fact, the Tiefstich Pottery culture originated from northern Funnel Beaker

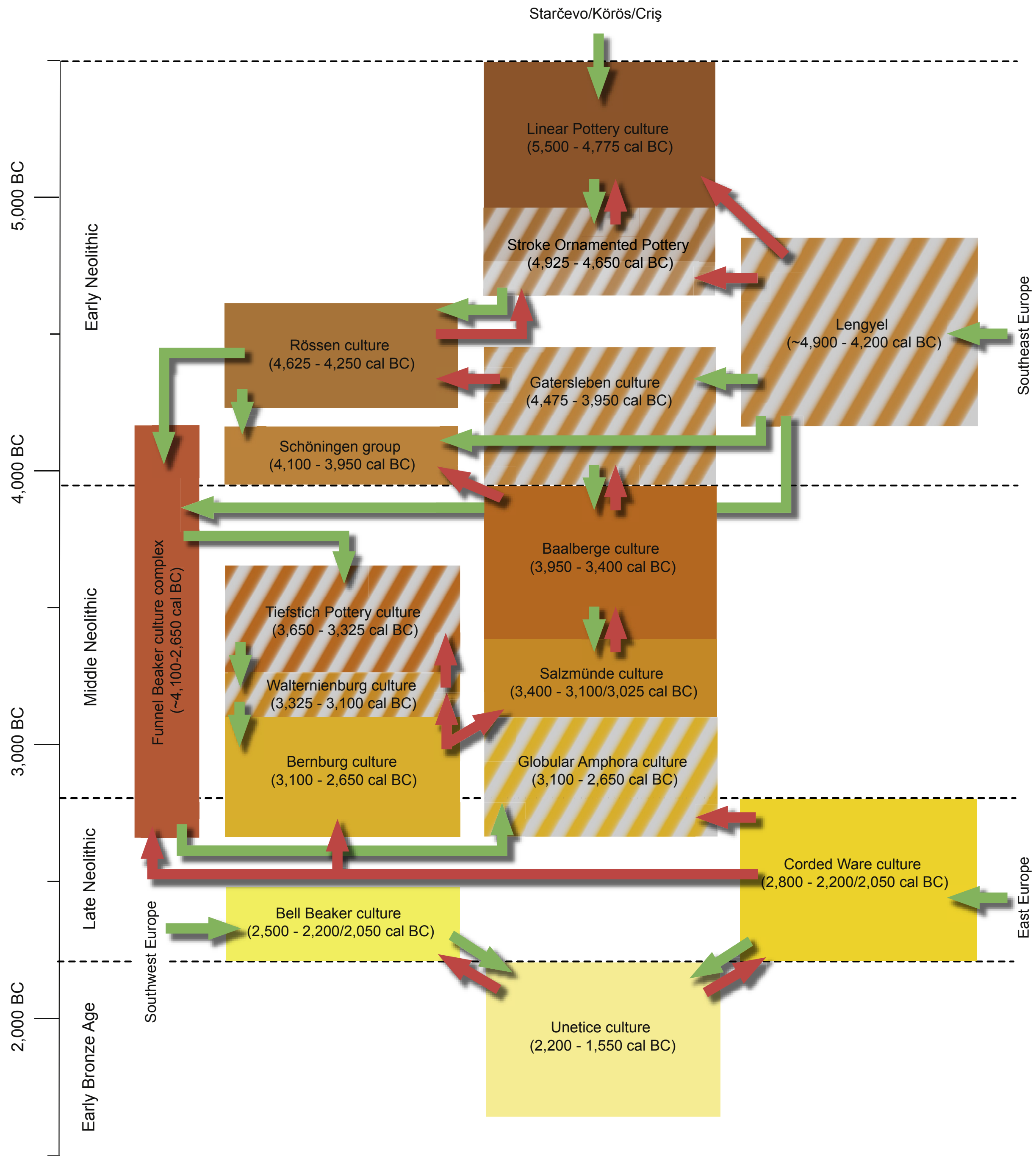


Figure 4. Complexity of cultural interactions in Germany's Mittelelbe-Saale region during the Neolithic. Archaeological cultures of the Mittelelbe-Saale region are placed in chronological order from top to bottom, also including cultures with main distribution outside the Mittelelbe-Saale region, based on contextual importance. Striped fields mark archaeological cultures for which no aDNA data is available so far. Green arrows denote contacts or influences that affected the emergence of a new cultural horizon, whereas red arrows indicate cultural developments that lead to the end of a preceding culture. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

groups of the North German Plain, which were thought to have expanded southwards to Central Europe, even suggesting a migration event from the North at this time (Beier and Einicke, 1994; Preuss, 1998). In the light of this cultural sequence, it is likely that population event B_2 was initiated by earlier Funnel Beaker groups, but penetrated slowly further south reaching Mittelelbe-Saale with the Bernburg culture. Thus, the Early and Middle Neolithic of Central Europe appears to have been, at various times, both a source and sink area for population dynamic events. However, more direct and detailed aDNA evidence from the various geographically and temporally distinct Funnel Beaker groups is desired to confirm and specify the timing of the proposed southern expansion.

Further population shifts in Southern Scandinavia after the initial Neolithic transition become apparent when the prehistoric data is compared to a pooled present-day metapopulation of North Europeans. The modern populations reveal an increase of lineages that match those of Late Neolithic and Early Bronze Age individuals in Central Europe (21%), and which predominantly contain haplogroups H, I, U2, U4, and U5a. Intriguingly, the increase of these haplogroups has been attributed to genetic influx into Central Europe via the Corded Ware and Bell Beaker cultures, corresponding to the migration events C and D (see below) (Brandt et al., 2013) (Fig. 3D). In contrast, the amount of hunter-gatherer and early farming lineages in the North European metapopulation is reduced to 3.4% and 26.6%, respectively (Fig. 2C). This composition suggests that further migration events occurred after the Funnel Beaker culture, which affected the contemporary mitochondrial variability of North Europe in a similar way as the Late Neolithic events C and D contributed to the formation of the Central European diversity. Archaeological studies have shown that the Funnel Beaker and Pitted Ware cultures were replaced by the subsequent Corded Ware culture in the third millennium BC (Bogucki and Crabtree, 2004), virtually skipping the Middle Neolithic. Thus, despite the fact that the aDNA evidence from Late Neolithic and Early Bronze Age North European is limited to only three samples (showing a preserved Mesolithic substratum consisting of haplogroups U4 and U5a (Melchior et al., 2010)), more recent Iron Age samples from Denmark show the presence of haplogroup I, U2 and a high frequency of H (Melchior et al., 2008). It therefore seems highly likely that Pan-European cultural phenomena, such as the Corded Ware and Bell Beaker cultures, leading up to the Bronze Age, also contributed to the formation of the present-day mtDNA diversity in Southern Scandinavia.

Calmer waters? Cultural and genetic diversity in Central Europe after the LBK

During the first half of the fifth millennium BC, the homogenous unity of the LBK in Central Europe disintegrated into several smaller cultural groups with rather regional dispersal. These groups included the Stroke Ornamented Pottery culture (4925–4550 cal BC) in the eastern part, the Lengyel culture (~4900–4200 cal BC) in the southeastern part, and the Rössen culture (~4700–4250 cal BC) in the western part of the former LBK area (Preuss, 1998; Bogucki and Crabtree, 2004; Whittle and Cummings, 2007) (Fig. 3B). The cultural differentiation was seemingly based on a series of local and regional developments, which in turn affected the emergence of other cultural groups during the following millennia. The Lengyel culture emerged in Western Hungary through influences from adjacent cultures in Southeast Europe and spread across Austria, the Czech Republic, Slovakia, and Poland (Preuss, 1998; Bogucki and Crabtree, 2004). Archaeological research describes the Lengyel culture as one of the major horizons, which affected various local cultures in Central Europe, such as Balaton Lasinja, Münchshöfen, Schöningen, Gatersleben, Baalberge and other groups of the Funnel Beaker culture complex. The Chasséen culture (~4500–3500 cal BC) forms a Western European parallel, which emerged from preceding Early Neolithic farming communities of the Cardial/Epicardial around the mid-fifth millennium BC in southeastern France. The Chasséen subsequently expanded northeastwards eventually covering most of present-day France. It is now widely accepted that the Chasséen had influenced the emergence of the Michelsberg culture (4300–3500 cal. BC) in Central Europe, which in turn then replaced the LBK derived Rössen culture in the Paris Basin and Western Germany (Jeunesse, 1998, 2010; Bogucki and Crabtree, 2004; Whittle and Cummings, 2007). Together with the Funnel Beaker culture, which expanded from Southern Scandinavia slightly later, it appears that Central Europe had witnessed several cultural influences from the Southeast, West, and North after the initial Neolithisation (Fig. 3B and C). This led to a complex network of sociocultural interactions between farming communities of the Early and Middle Neolithic period, as exemplified in Central Germany's Mittelelbe-Saale region in Fig. 4.

Genetic data from cultural groups, following the initial Neolithic transition in Central Europe through the LBK, are currently available from the Rössen, Schöningen, Baalberge and Salzmünde cultures (in chronological order) from 10 sites in Central Germany (Fig. 1A, sites 36, 39, 68, 44–47, 59–61) with sample sizes of 17, 29, 19, and 33 individuals, respectively (Brandt et al., 2013; Lee et al., 2013). These data support a genetic continuity of early farmer lineages in its subsequent regional and cultural derivates, which becomes evident in very similar haplogroup compositions including almost exclusively lineages of the genetic 'Neolithic package', and results in a clustering with the LBK individuals in the PCA plot (Fig. 1B). Shared haplotype analyses reveal that the large majority of sequences (Rössen: 58.8%, Schöningen: 72.7%, Baalberge: 57.9%, Salzmünde: 75.9%) predominantly match lineages first observed during the LBK, whereas hunter-gatherer lineages (0.0–5.9%) remain rare (Fig. 2A). These findings argue for a long-lasting continuation of LBK mtDNA diversity during the Early and Middle Neolithic period, despite the split of the vast LBK area into smaller territories. Thus, the cultural changes observed during the first 2500 years of farming in Central Germany can be explained as a process of cultural regionalization of local farming communities, consistent with the complex archaeological framework of cultural relations (Fig. 4), rather than by larger population movements (Brandt et al., 2013). We feel that it is important to mention that the potential occurrence of (repeated) gene-flow during the Early and Middle Neolithic period on a smaller and more regional scale via multiple or continuous migrations from one to another farming culture, followed by admixture with local communities, cannot be entirely excluded. However, the complex pattern of cultural interactions outlined above, and the relative genetic similarity of all LBK successor cultures is challenging to resolve and contrast against the dominant genetic signature, which had been introduced by the LBK to vast regions in Central Europe.

A recent study from the Western German cave site Blätterhöhle (Fig. 1A, site 3) provides new insights into genetic diversity during the Early and Middle Neolithic (Bollongino et al., 2013). Radiocarbon dates from this site revealed a Mesolithic and a Neolithic occupation phase, of which a total of 25 skeletons were analyzed for aDNA and isotopes. Of these, the five Mesolithic samples could be assigned to mtDNA haplogroup U and its subgroups U2, U5a and U5b (consistent with other data from Central and North European foragers), whereas the 20 individuals of the Neolithic occupation phase (~3900–3000 cal BC) revealed a mixed composition, consisting of 12 U (U5 and U5b) lineages and eight lineages assigned to haplogroup J and subgroups of H (H1, H5, H11). Dietary stable isotope analysis could distinguish two distinct groups among the

Neolithic samples: one with terrestrial diet and one with a high freshwater fish diet. Interestingly, individuals with an inferred fisher-hunter-gatherer diet also exclusively belonged to haplogroup U, whereas the non-U lineages were solely observed in Neolithic samples with a terrestrial diet. This was interpreted as evidence for a parallel existence of two societies with seemingly contrasting lifestyles and genetic signatures a long time (~2000 years) after the initial advent of farming in this region. These findings further contribute to our understanding of the complexity of forager–farmer interactions. It is the large temporal gap of 2000 years in the Blätterhöhle example that argues for a scenario in which well-defined cultural boundaries between distinctly perceived societies form the most plausible explanation (Bentley et al., 2009). The presence of hunter-gatherer lineages in Neolithic samples with a Neolithic diet also shows that this boundary was at least semi-permeable, which can also explain the evidence of U lineages in other Middle Neolithic cultures such as Bernburg (as shown above).

The picture becomes more complex when the geographic and chronological location of the Blätterhöhle is considered. The absence of characteristic finds and bioturbation of the layers inside the cave do not allow a classification to a particular archaeological culture. However, the Blätterhöhle site is located in former LBK and Rössen territory and radiocarbon dates of the samples point to a period when the cultural boundaries of the Michelsberg culture and northern Funnel Beaker groups were formed in this region. Therefore, genetic elements of early farmers, such as LBK and Rössen, but also from western emerging cultures, such as Michelsberg and northern expanding groups of the Funnel Beaker culture, could have influenced the genetic composition of the Neolithic Blätterhöhle remains.

Interestingly, the majority of haplogroup H lineages from the Neolithic Blätterhöhle individuals can be assigned to sub-haplogroup H5, which is also present in the LBK dataset, but more frequent in the Rössen culture (Brandt et al., 2013; Lee et al., 2013). Thus, the H5 types could be interpreted as female lineages that were already present in this region at this time. In general, the mtDNA variability observed at this site is very low. Other early farmer haplogroups, such as T2, K, HV or N1a have not been found among the Neolithic individuals, and the absence of subgroup U5a among the many U5 individuals also argues for a limited diversity (see comment on U5 phylogeography above). As a consequence, the mtDNA haplogroup composition at the Blätterhöhle site results in more pronounced affinities to southwestern hunter-gatherers on the PCA plot (Fig. 1B). While a western influence in this region would be supported from a mere archaeological point of view (Chasséen/Michelsberg complex), a seemingly skewed haplogroup composition could also be due to the effects of genetic drift in a small and genetically isolated group. Therefore, a Western influence has to be taken with caution and would require further direct aDNA evidence from these respective neighboring cultures in the West. In more general terms, since the cave site is situated at the border of the former distribution of the Funnel Beaker cultural complex, for which we also observe rising frequencies of U lineages in other Funnel Beaker associated sites in Mittelelbe-Saale (as discussed above), the evidence from the Blätterhöhle supports an increasing assimilation of female hunter-gatherers (or their respective ancestral components) towards the end of the Middle Neolithic around 3500–3000 cal BC.

Bell Beaker and Corded Ware culture interactions and the emergence of the Early Bronze Age

The Late Neolithic in Central Europe is characterised by the appearance of two contrasting Pan-European phenomena: the Corded Ware culture across Eastern Europe and the Bell Beaker complex in Western Europe with an overlapping zone in Central Europe (Fig. 3D). Here, both cultures coexisted for more than 300 years, sometimes even at the same site, and were finally replaced at 2200 cal BC by the emerging Unetice culture of the Bronze Age era. This raises questions about interactions between these contrasting cultural phenomena and their influence on the genesis of the Unetice culture (Beier and Einicke, 1994; Preuss, 1998; Czebreszuk and Szmyt, 2003; Heyd, 2007; Hille, 2012).

Ancient DNA data from the Corded Ware, Bell Beaker, and Unetice culture sites are available from Central Germany (Haak et al., 2008; Lee et al., 2012; Brandt et al., 2013) with sample sizes of 44, 35, and 94 individuals, respectively. In addition, two Bell Beaker samples have been reported from Denmark (Melchior et al., 2010) (Fig. 1A, sites 39, 59, 67–79, 88). The Corded Ware and Unetice cultures have been characterised by a common mtDNA composition consisting of haplogroups I, U2, T1, U4, and U5a, alongside haplogroups derived from early farmers, which indicates a linked maternal ancestry of both cultures at the transition from the Neolithic to the Bronze Age (Brandt et al., 2013). In contrast, the Bell Beaker individuals show a high frequency of diverse H lineages. Intriguingly, these lineages have been shown to be different from those of all preceding Early and Middle Neolithic cultures in Central Europe (Brotherton et al., 2013).

As a consequence, the contrasting mtDNA compositions of the Late Neolithic cultures result in distinct geographic affinities when compared with data from extant populations. The Corded Ware and Unetice individuals show highest similarities to modern-day Eastern Europeans, whereas the Bell Beaker individuals show greater affinities to Southwestern Europeans. In light of the geographic distribution of each culture, this led us to suggest Late Neolithic migration event C (~2800 cal BC) and D (~2500 cal BC) had brought additional genetic diversity to Central Europe (Fig. 3D) (Brandt et al., 2013). Intriguingly, some of the characteristic haplogroups of the Corded Ware and Bell Beaker people, such as U2, U4, U5a and H, appear to match the respective Mesolithic substratum of Eastern and Southwestern Europe. Assuming a pre-agricultural population structure in Europe with a Western and Eastern hunter-gatherer component (as outlined above), it seems highly plausible that Mesolithic mtDNA variability of distant geographic regions spread into Central and potentially also North Europe in the course of migrations, assimilations and acculturation processes during the later Neolithic.

However, despite the contrasting mtDNA signature of the Corded Ware/Unetice and Bell Beaker individuals, a shared haplotype analysis revealed that 20% of the maternal Bell Beaker lineages match those of the preceding Corded Ware culture (Fig. 2A), arguing for a considerable amount of admixture and continuity between both Late Neolithic cultures in the overlapping zone. Bell Beaker individuals from the Kromsdorf site in Thuringia, Germany, are a good example (Lee et al., 2012). These individuals show predominantly characteristic Corded Ware haplogroups, such as I, T1, U2, U5a, of which 50% directly match Corded Ware lineages in Mittelelbe-Saale. Similarly, one of the two Danish Bell Beaker samples (Melchior et al., 2010) shares a U4 lineage identical with the Corded Ware dataset. It appears that the female contribution of lineages attributed to the Corded Ware had a stronger and more lasting impact in this region as individuals of the subsequent Unetice culture, show a high proportion of Corded Ware haplogroups, in particular I and U2. In contrast, the frequency of haplogroup H decreased substantially and none of the Unetice lineages could be linked back to Bell Beaker individuals.

The genetic continuity between Corded Ware and Unetice and the amount of shared lineages between the Corded Ware and Bell Beaker individuals could potentially be interpreted as admixture with sex-biased migration during the Late Neolithic. If we assumed a diffusion of Bell Beaker males into Central Europe and admixture between Corded Ware and Bell Beaker groups, we would expect to see introgression and persistence of preceding Corded Ware female lineages in the Bell Beaker culture, but also the appearance of specific maternal Bell Beaker elements, as indicated by the high amount of shared Corded Ware lineages in the Bell Beaker culture and the increasing frequency and diversity of haplogroup H. In the subsequent Unetice culture we would expect to observe persistence of Corded Ware lineages and a dilution of the mitochondrial Bell Beaker signal, which is apparent from the distinct haplogroup profiles of the Corded Ware/Unetice and Bell Beaker individuals, respectively. Simultaneously, we would also expect to observe male gene flow in the Bell Beaker culture as shown by the example of Y-haplogroup R1b from the site of Thuringia (Lee et al., 2012), in contrast to R1a1a observed from the Corded Ware culture (Haak et al., 2008). R1b is most frequent in Western Europe today and has a proposed origin and current geographic distribution very similar to mtDNA haplogroup H (Myres et al., 2011), whereas Y-haplogroup R1a1a is most frequent in present-day East European, West, South, and Central Asian populations, which strikingly resembles the former geographic distribution of the Corded Ware and preceding Kurgan cultures (Semino et al., 2000; Underhill et al., 2010). Together, these findings suggest that the migration event associated with the Bell Beaker culture (event D) was potentially driven by male diffusion followed by admixture with residential Corded Ware communities, which finally resulted in the formation of the Unetice culture.

The development of two roughly contemporaneous cultural complexes at the dawn of metallurgy with nearly Pan-European, but opposing geographic distribution, is a highly interesting phenomenon in archaeology (Heyd, 2007). The overlapping region in Central Europe will be of key interest in reconstructing the cultural and biological interactions between the two groups. However, more aDNA evidence from geographically distant Corded Ware and Bell Beaker sites (covering the vast eastern and western distribution area) will be needed in order to fully characterise the genetic signature of these important cultural horizons, the proposed contribution of new and old lineages (assuming a distinct Mesolithic substratum in each area), and to estimate the amount of admixture in the overlapping distribution area of Central Europe.

Implications beyond the genetic record

The available wealth of paleogenetic data for Central Europe allows us to start correlating/comparing temporal genetic data with other lines of evidence, such as climatic and linguistic records. Such reconciliations have to remain speculative at the moment, but could serve as starting point or directions for further detailed investigations.

Paleoclimate

The potential impact of Holocene climate fluctuations on the rise and fall of prehistoric societies has been increasingly discussed in the archaeological literature over the past decade (e.g., Weiss and Bradley, 2001; Bonsall et al., 2002; Arbogast et al., 2006; Migowski et al., 2006; Gronenborn, 2007b, 2012; Weninger et al., 2009; Medina-Elizalde and Rohling, 2012). Archaeological research has convincingly shown that the speed and mode of agricultural expansions, and also the success of their lasting establishments, were based on a combination of numerous factors, of which suitable environmental and climatic conditions are widely agreed on (Whittle, 1996; Gronenborn, 1999; Price, 2000; Whittle and Cummings, 2007; Rowley-Conwy, 2011). It is also clear that farming practices remained vulnerable to these factors, especially at the wave-front of the expansion into more climatically unstable northerly latitudes, and also when climatic conditions changed over longer periods of time. This raises the question whether the observed events A–D, as proposed in Brandt et al. (2013) and further explored here, might correlate with changes or fluctuations in environmental conditions observed in climatic records.

Paleoclimatological research has shown that lower levels of solar activity, i.e., when sunspot numbers are minimal, correlate with increasing ^{14}C production during the 11-year sun cycle (Solanki et al., 2004). Accordingly, peaks in the ^{14}C production curve can be generally interpreted as times of weak solar intensity and colder winters in Eurasia (Lockwood et al., 2010; Woollings et al., 2010; Sirocko et al., 2012). Beside the advantage that the ^{14}C production curve is one of the best-dated climate proxies currently available, numerous studies have linked solar intensity to other terrestrial proxies (Burga and Perret, 1998; Haas et al., 1998; Spurk et al., 2002; Blaauw et al., 2004; Magny, 2004), suggesting a relationship between environmental changes and atmospheric ^{14}C levels. We used the ^{14}C production curve published in Kromer and Friedrich (2007) to compare the proposed genetic shifts from our genetic transect data from Central Europe to climatic fluctuations in Europe for the time period ranging from the Late Mesolithic to the Early Bronze Age.

The climate data suggests that periods of extremely cold winters precede the events A, B_1, and B_2, and potentially C/D (Fig. 5). During the Late Mesolithic (~7000–5650 cal BC) the climate was generally stable with warm summers and temperate winters. However, these favorable climate conditions changed between 5650 and 5200 cal

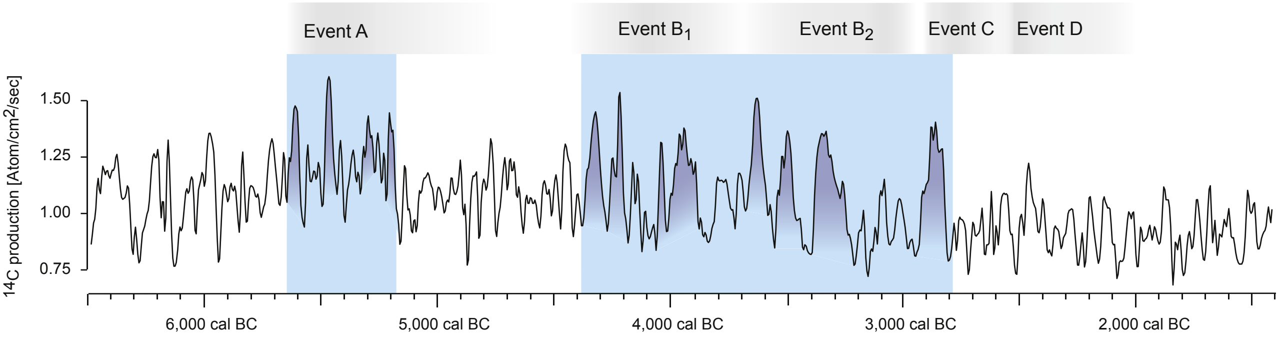


Figure 5. Holocene climate fluctuations. Climate fluctuations inferred from the record of solar induced ^{14}C production (Kromer and Friedrich, 2007) indicate phases of generally stable climate conditions with warm summers and temperate winters (non-shaded areas) and intermittent cooling phases (blue shaded areas). Within these cooling phases, peaks in the ^{14}C production curve suggest decades of extremely cold winters (blue shaded peaks). Clusters of cold decades appear before events A and B, and potentially C/D. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

BC. During this period, the record of solar induced ^{14}C production reaches clear maxima at 5,610, 5,460, 5,300, and 5210 cal BC, pointing to decades of cooler winters around the time of the emergence of the LBK in Western Hungary at ~5600 cal BC and the continuous expansion across Central Europe within the following 500 years (event A). Similarly, the period between 4400 and 2800 cal BC signals a number of climate changes with alternating phases of temperate and extreme cold winters. The latter can be postulated around 4320, 4220, 4040, 3940, 3630, 3490, 3330, and 2860 cal BC. The decades of cold winters between 4320 and 3940 cal BC can be potentially related to the introduction of farming to Southern Scandinavia by expanding Central European farmers, which resulted in the emergence of the Funnel Beaker culture ~4100 cal BC (event B_1). In turn, periods of cold winters around 3630, 3490, and 3330 cal BC occurred in the lead up to the expansion of Funnel Beaker groups into the highly productive loess plains of Central Germany (event B_2), for example with the Bernburg precursors Tiefstich Pottery (~3650 cal BC) and Walternienburg cultures (~3325 cal BC). Hence, it is possible that changing climatic conditions were driving factors of both the Neolithisation of Southern Scandinavia and the southward expansion of FBC groups into Central Europe. Another major cold event is also apparent at 2860 cal BC, contemporaneous with the expansion of the Corded Ware culture in East Europe (event C) and the Bell Beaker culture in Southwest Europe (events D) starting at ~2900 cal BC and ~2800 cal BC, respectively.

Potential reasons for such matching patterns of climatic and genetic data are manifold and we are fully aware that climate fluctuations alone cannot explain the causes of population dynamic events. However, a possible scenario would be that harsher and more challenging climate conditions resulted in a reduction of natural resources, which might have forced prehistoric societies into lifestyles with a higher mobility, and triggered adaptations of cultural practices, leading to advanced stockpiling strategies. Especially the latter would be a plausible scenario for the introduction of farming to Southern Scandinavia, where local societies practiced foraging for a long period of time after farming was already established in Central Europe and then adopted the new subsistence strategies when the climate changed to cooler conditions around 4300 BC.

The matching pattern of cultural shift with marked peaks in climate proxy data has been recognised in archaeological research (Gronenborn, 2009, 2012), and the available data from various disciplines now encourage in depth analyses of genetic, archaeological and climate data, which involves multiple proxies, each informative for the relevant regions under investigation, in order to examine the role of climate fluctuations as potential driving factors for population movements in the past.

The Indo-European language dispersal

The origin and timing of the spread of the Indo-European language family has been heavily debated in archaeology and linguistics. Archaeological and linguistic models have proposed either an expansion of Proto-Indo-European from Anatolia associated with the spread of farming (Renfrew, 1987, 1999), a Near Eastern model with origin south of the Caucasus slightly later and largely decoupled from the spread of farming (Gamkrelidze and Ivanov, 1984), and an origin in the Pontic-Caspian steppes northwest of the Black Sea and dispersal via Kurgan communities (Gimbutas, 1991; Anthony, 2007). While some scholars consider it a 'cardinal sin' to conflate linguistic with archaeological and genetic data (see Lawler, 2008; Soares et al., 2010 paraphrasing Phil Kohl), we rather agree with Balanovsky et al. (2013) in that we can learn more about past populations when we look at linguistic and genetic data in parallel and attempt integrative analyses, than keeping the fields separated. The quantity and quality of data are decisive factors for such questions with wide implications as the search for the origins and the spread of the Indo-European language. A recent example of parallel evolution of (non-Indo-European) languages and genes in the Caucasus (Balanovsky et al., 2011) seems to have met these prerequisites by showing a strong correlation between the two factors language and genes. We believe that the field of human genetics and genomics (including work on ancient human DNA) has made major advances in the last five years, now providing a solid genetic framework against which archaeological and linguistic models can be tested. This includes progress in dating of divergence times of population and/or particular lineages of interest (Soares et al., 2010; Scally and Durbin, 2012; Fu et al., 2013). Consequently, the 'props of the edifice are not as shaky' anymore as they were a decade ago (Sims-Williams, 1998, 2012), which at least holds true for the genetic data. We feel that data gleaned from the most recent aDNA studies now allow a cautious reappraisal (perhaps not a new synthesis) of the issues raised above. We would therefore like to address the potential implications of some of the migration events A–D identified in Brandt et al. (2013) for the origin and spread of the Indo-European language family.

A recent 'glottochronological' study supporting an Anatolian origin of the Proto-Indo-European language and a dispersal across Europe and Asia starting around ~7500–6000 BC, and in favor of Renfrew's model (the 'long chronology'; Heggarty, 2013), has reignited the debate among linguists and anthropologists (Bouckaert et al., 2012). This finding and the date in particular are strikingly concurrent with the expansion of early farmers into Central Europe via the Continental route and would argue for an involvement of early farming cultures such as the LBK (event A). As outlined above, genetic data strongly support a discontinuity between the last Mesolithic hunter-gatherers and early farmers, providing the basis for a substantial genetic changeover. In all likelihood, such a sharp shift must have been accompanied by a common language across a larger territory, not only facilitating the speed at which the spread of farming throughout Europe occurred but also evidenced by the relative homogeneity of the genetic signal carried by the earliest farmers (Skoglund et al., 2012; Brandt et al., 2013). Bouckaert and colleagues go even a step further and provide divergence dates for the subfamilies Celtic, Germanic, Balto-Slavic and Indo-Iranian; all of which emerged between 4000 and 2000 BC (Bouckaert et al., 2012). Considering the temporal overlap and the genetic influx from the East, the Corded Ware culture in association with Kurgan people could be likely interpreted as a key candidate for either the spread of the Germanic or the Balto-Slavic branch of the Indo-European language family (event C). Modern genetic studies also hinted at this possibility based on matching distributions of Y-chromosome variability, in particular R1a1a in Slavic and to a lesser extent in Germanic speaking countries (Soares et al., 2010; Underhill et al., 2010). Similarly, the genetic influx from the southwest associated with the Bell Beaker culture could be correlated with an earlier spread of the Celtic language family across Western Europe than assumed, as recently suggested by linguists (Koch, 2009; Cunliffe and Koch, 2010). Such a coherent cultural package in the West could therefore also be linked with the pattern of high frequencies of mtDNA haplogroup H and Y-haplogroup R1b in modern-day West Europeans, as suggested in Brotherton et al. (2013) and hypothesised by Barry Cunliffe's model of Atlantic Europe, which rests upon a common cultural element emerging during the Megalithic, i.e., Middle Neolithic in Western Europe (Cunliffe, 2001).

Alternatively, if we consider a later spread of Indo-European through steppe cultures (the 'short chronology') (Gimbutas, 1991; Anthony, 2007), this would most likely coincide with an arrival in

Central Europe via the Corded Ware cultural complex and its cultural predecessors further east (Globular Amphora culture and the Yamnaya culture north of the Black sea; Fig. 3D). Event C would in theory provide a good candidate for an accompanying and lasting genetic impact around this time. The remaining temporal framework would then foresee a spread of Celtic during the Celtic Iron Age in Western and Central Europe, superseding/replacing non-Indo-European speakers. However, the repeated replacement with Latin during Roman times (another Indo-European language) shortly after requires that the respective Indo-European-branches in place at the time (Celtic, Latin, Germanic in the barbaric North) must have undergone a rapid dissemination after geographic structuring and emergence from the common root during the Bronze Age, or perhaps early Iron Age at latest.

Seeing the forest for the trees… and the trees for the forest

Another point we would like to address concerns the level of resolution achievable with genetic studies. High-resolution genome data allows not only personal identification and the reconstruction of interpersonal relationship, potentially across several generations and degrees of relatedness, analogous to multi-loci DNA fingerprinting techniques used in forensics, but also the reconstruction of intra-population or infra-group relationships.

This level of ‘genealogical’ resolution is most likely too high for ‘big picture’ population studies, but will be needed to further disentangle the complex succession of cultures as described in the archaeological record as well as in later ‘historic’ periods leading up to the present day. Fig. 4 illustrates the many interactions that have shaped the cultural diversity in Germany's Mittelelbe-Saale region, resulting in an already complex flow chart for a relatively small region and temporal snapshot, and we can only imagine an even higher complexity at a continent wide level and wider temporal windows. However, it shows that a high level resolution and dense temporal sampling is needed to test whether the cultural succession is accompanied by changes in the genetic makeup. Our recent study has highlighted the usefulness of sampling in gapless temporal transects to reconstruct and understand the genetic stratigraphy (Brandt et al., 2013). It is obvious that the patterns of discontinuity versus continuity will not be as clear as the dichotomy between hunter-gatherers and expanding farmers, as we follow the timeline to the present. The archaeological record in Europe lets us expect a very vivid (pre-)history with many episodes allowing for genetic influx and mixing events, resulting in a complicated genetic stratigraphy, which has aptly been described as incremental genetic ‘palimpsest’ (Renfrew, 1998; Richards, 2003). It is also clear that we should not expect a genetic entity (population?) or signature (genealogy?) behind every culture or cultural horizon. The duration of many later periods is certainly not long enough to allow for the formation of a unique signature through concerted effects of genetic drift in isolation. In other words, if we assumed a constant rate of genetic changes over time (Scally and Durbin, 2012), more time is needed to have such changes become fixed in a population and to lead to differentiation without any outside influence or selection pressure. On the other hand, the effects of group size (effective population size) and relative isolation will also play a role. This is of particular interest for older periods of human history, including those of archaic hominins such as Neanderthals and Denisovans, for which we won't be able to produce a dense temporal and geographic resolution. While it is impossible to overcome the taphonomic biases in the paleoanthropological records or issues related to the visibility of Paleolithic and Mesolithic hunter-gatherers in the archaeological record, we can safely say that group sizes and population growth rates were smaller in pre-agricultural societies. As such, genetic changes have had a higher chance of rising to fixation in smaller bands of people, which in combination with relative geographic isolation or limited gene flow can produce a genetic signature distinct from populations or groups in other regions. As a result, the genetic differentiation between these ancestral groups is expected to be more pronounced when compared with more recent periods or modern-day populations. This effect is visible from recent studies on Paleolithic and Mesolithic hunter-gatherers, which form distinct geographic clusters outside modern-day Eurasian variations (Lazaridis et al., 2014; Olalde et al., 2014; Raghavan et al., 2014). Whether we will be able to reconcile observed genetic changes with, for example, climatic fluctuations and/or expanding group sizes will rest on the increasing precision of dating techniques and the availability of new finds to fill critical gaps between the last occurrence and first appearance of certain features (including genetics) in the paleoanthropological and archaeological record (e.g., Higham et al., 2014).

Overall, the duration and geographic spread of an archaeological horizon is not necessarily indicative of its potential to harbor new genetic elements. Even a short-lived horizon could hold the potential of having experienced ‘exotic’ genetic influx, which can affect subsequent layers. A recent study on modern-day autosomal population data has highlighted the power of statistical methods in disentangling recent admixture events with a temporal depth of up to 4000 years (Hellenthal et al., 2014). From an ancient DNA perspective, it is therefore important to study individuals from before, during and after a particular period in order to understand the temporal mechanisms at work, and to render estimates of timing and admixture proportions more precisely. While some scholars might argue that genetics hold the potential to independently test hypotheses put forward by archaeologist and anthropologists, we think that it is important to incorporate the archaeological framework as exemplified in Fig. 4 as a basis for hypothesis testing in future genetic studies.

The expected increase in available ancient human DNA studies with high-resolution data in the near future will finally also allow us to perform intra-population or infra-group analyses, which will help in understanding the internal structure of small and large-scale cultural layers, and whether these were driven by overarching economic factors (potentially vulnerable to climatic fluctuations) and/or by the power of social structures (clans, dynasties, etc.) with a traceable genetic signal, and perhaps a common language.

Acknowledgments

We thank the guest editors of this special issue, George Perry and Ludovic Orlando, for the invitation and the opportunity to prepare this manuscript. Special thanks goes to Harald Meller, Susanne Friederich, Veit Dresely, Robert Ganslmeier, Nicole Nicklisch, Angelina Siebert, Corina Knipper, Eszter Banffy for archaeological and anthropological support, to Frank Sirocko for expert knowledge on paleoclimatological records, and to Alan Cooper, Christina Adler, Laura Weyrich, Bastian Llamas and Julien Soubrier for sharing knowledge and permanent collegial support. This work was supported by the German Research Foundation (awarded to KWA) and by the Australian Research Council (Discovery Project 130102158 awarded to WH). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

References

Achilli, A., Rengo, C., Magri, C., Battaglia, V., Olivieri, A., Scozzari, R., Cruciani, F., Zeviani, M., Briem, E., Carelli, V., Moral, P., Dugoujon, J.M., Roostalu, U., Loogvali, E.L., Kivisild, T., Bandelt, H.J., Richards, M., Villems, R., Santachiara-

Benerecetti, A.S., Semino, O., Torroni, A., 2004. The molecular dissection of mtDNA haplogroup H confirms that the Franco-Cantabrian glacial refuge was a major source for the European gene pool. Am. J. Hum. Genet. 75, 910–918.

Achilli, A., Rengo, C., Battaglia, V., Pala, M., Olivieri, A., Fornarino, S., Magri, C., Scozzari, R., Babudri, N., Santachiara-Benerecetti, A.S., Bandelt, H.J., Semino, O., Torroni, A., 2005. Saami and Berbers—an unexpected mitochondrial DNA link. Am. J. Hum. Genet. 76, 883–886.

Ammerman, A.J., Cavalli-Sforza, L.L., 1984. The Neolithic Transition and the Genetics of Populations in Europe. Princeton University Press, Princeton.

Anthony, D.W., 2007. The Horse, the Wheel, and Language. How Bronze-Age Riders from the Eurasian Steppes shaped the Modern World. Princeton University Press, Princeton and Oxford.

Arbogast, R.-M., Jacomet, S., Magny, M., Schibler, J., 2006. The significance of climate fluctuations for lake level changes and shifts in subsistence economy during the late Neolithic (4300–2400 BC) in Central Europe.Veg. Hist. Archaeobot. 15, 403–418.

Balanovsky, O., Rootsi, S., Pshenichnov, A., Kivisild, T., Churnosov, M., Evseeva, I., Pocheshkhova, E., Boldyreva, M., Yankovsky, N., Balanovska, E., Villems, R., 2008. Two sources of the Russian patrilineal heritage in their Eurasian context. Am. J. Hum. Genet. 82, 236–250.

Balanovsky, O., Dibirova, K., Dybo, A., Mudrak, O., Frolova, S., Pocheshkhova, E., Haber, M., Platt, D., Schurr, T., Haak, W., Kuznetsova, M., Radzhabov, M., Balaganskaya, O., Romanov, A., Zakharova, T., Soria Hernanz, D.F., Zalloua, P., Koshel, S., Ruhlen, M., Renfrew, C., Wells, R.S., Tyler-Smith, C., Balanovska, E., 2011. Parallel evolution of genes and languages in the Caucasus region. Mol. Biol. Evol. 28, 2905–2920.

Balanovsky, O., Utevska, O., Balanovska, E., 2013. Genetics of Indo-European populations: the past, the future. J. Lang. Relationsh. 9, 23–35.

Balaresque, P., Bowden, G.R., Adams, S.M., Leung, H.Y., King, T.E., Rosser, Z.H., Goodwin, J., Moisan, J.P., Richard, C., Millward, A., Demaine, A.G., Barbujani, G., Previdere, C., Wilson, I.J., Tyler-Smith, C., Jobling, M.A., 2010. A predominantly Neolithic origin for European paternal lineages. PLoS Biol. 8 e1000285.

Bánffy, E., 2000. The late Starcevo and the earliest linear pottery groups in western Transdanubia. Doc. Praehist. 27, 173–185.

Behrens, H., 1973. Die Jungsteinzeit im Mittelelbe-Saale-Gebiet, Berlin.

Beier, H.J., Einicke, R., 1994. Das Neolithikum im Mittelelbe-Saale-Gebiet und in der Altmark. Eine Übersicht und ein Abriß zum Stand der Forschung. Beier & Beran, Wilkau-Hasslau.

Bentley, R.A., Layton, R.H., Tehrani, J., 2009. Kinship, marriage, and the genetics of past human dispersals. Hum. Biol. 81, 159–179.

Bentley, R.A., Bickle, P., Fibiger, L., Nowell, G.M., Dale, C.W., Hedges, R.E., Hamilton, J., Wahl, J., Francken, M., Grupe, G., Lenneis, E., Teschler-Nicola, M., Arbogast, R.M., Hofmann, D., Whittle, A., 2012. Community differentiation and kinship among Europe's first farmers. Proc. Natl. Acad. Sci. 109, 9326–9330.

Blaauw, M., van Geel, B., van der Plicht, J., 2004. Solar forcing of climatic change during the mid-Holocene: indications from raised bogs in The Netherlands. Holocene 14, 35–44.

Bocquet-Appel, J.P., Naji, S., Vander Linden, M., Kozlowski, J.K., 2009. Detection of diffusion and contact zones of early farming in Europe from the space-time distribution of 14C dates. J. Archaeol. Sci. 36, 807–820.

Bogucki, P.I., Crabtree, P.J., 2004. Ancient Europe 8000 B.C.–A.D. 1000: Encyclopedia of the Barbarian World. Charles Scribner's Sons, New York.

Bollongino, R., Vigne, J.D., 2008. Temperature monitoring in archaeological animal bone samples in the Near East and area, before, during and after excavation. J. Archaeol. Sci. 35, 873–881.

Bollongino, R., Nehlich, O., Richards, M.P., Orschiedt, J., Thomas, M.G., Sell, C., Fajkosova, Z., Powell, A., Burger, J., 2013. 2000 years of parallel societies in Stone Age Central Europe. Science 342, 479–481.

Bonsall, C., Macklin, M.G., Anderson, D.E., Payton, R.W., 2002. Climate change and the adoption of agriculture in north-west Europe. Eur. J. Archaeol. 5, 7–21.

Bouckaert, R., Lemey, P., Dunn, M., Greenhill, S.J., Alekseyenko, A.V., Drummond, A.J., Gray, R.D., Suchard, M.A., Atkinson, Q.D., 2012. Mapping the origins and expansion of the Indo-European language family. Science 337, 957–960.

Bramanti, B., 2008. Genetic analysis of aDNA from sixteen skeletons of the Vedrovice collection. Anthropologie 46, 153–160.

Bramanti, B., Thomas, M.G., Haak, W., Unterlaender, M., Jores, P., Tambets, K., Antanaitis-Jacobs, I., Haidle, M.N., Jankauskas, R., Kind, C.J., Lueth, F., Terberger, T., Hiller, J., Matsumura, S., Forster, P., Burger, J., 2009. Genetic discontinuity between local hunter-gatherers and central Europe's first farmers. Science 326, 137–140.

Brandt, G., Haak, W., Adler, C.J., Roth, C., Szecsenyi-Nagy, A., Karimnia, S., Moeller-Rieker, S., Meller, H., Ganslmeier, R., Friederich, S., Dresely, V., Nicklisch, N., Pickrell, J.K., Sirocko, F., Reich, D., Cooper, A., Alt, K.W., The Genographic Consortium, 2013. Ancient DNA reveals key stages in the formation of central European mitochondrial genetic diversity. Science 342, 257–261.

Brandt, G., Knipper, C., Nicklisch, N., Ganslmeier, R., Klamm, M., Alt, K.W., 2014. Settlement burials at the Karsdorf LBK site, Saxony-Anhalt, Germany: biological ties and residential mobility. In: Whittle, A., Bickle, P. (Eds.), Early Farmers: The View from Archaeology and Science. Oxford University Press, Oxford (in press).

Brotherton, P., Haak, W., Templeton, J., Brandt, G., Soubrier, J., Adler, C.J., Richards, S.M., Sarkissian, C.D., Ganslmeier, R., Friederich, S., Dresely, V., van Oven, M., Kenyon, R., Van der Hoek, M.B., Korlach, J., Luong, K., Ho, S.Y., Quintana-Murci, L., Behar, D.M., Meller, H., Alt, K.W., Cooper, A., The Genographic Consortium, 2013. Neolithic mitochondrial haplogroup H genomes and the genetic origins of Europeans. Nat. Commun. 4, 1764.

Burga, C.A., Perret, R., 1998. Vegetation und Klima der Schweiz seit dem jüngeren Eiszeitalter. Ott Verlag, Thun.

Burger, J., Hummel, S., Hermann, B., Henke, W., 1999. DNA preservation: a microsatellite-DNA study on ancient skeletal remains. Electrophoresis 20, 1722–1728.

Caramelli, D., Lalueza-Fox, C., Vernesi, C., Lari, M., Casoli, A., Mallegni, F., Chiarelli, B., Dupanloup, I., Bertranpetit, J., Barbujani, G., Bertorelle, G., 2003. Evidence for a genetic discontinuity between Neandertals and 24,000-year-old anatomically modern Europeans. Proc. Natl. Acad. Sci. 100, 6593–6597.

Cavalli-Sforza, L.L., Menozzi, P., Piazza, A., 1994. The History and Geography of Human Genes. Princeton University Press, Princeton.

Chandler, H., 2003. Using ancient DNA to link culture and biology in human populations. Ph.D. Dissertation, University of Oxford.

Chandler, H., Sykes, B., Zilhão, J., 2005. Using ancient DNA to examine genetic continuity at the Mesolithic-Neolithic transition in Portugal. Monografías del Instituto Internacional de Investigaciones Prehistóricas de Cantabria 1. In: Arias, P., Ontanon, R., Garcia-Monco, C. (Eds.), Actas del III Congreso del Neolítico en la Península Ibérica, Santander, pp. 781–786.

Chikhi, L., Destro-Bisol, G., Bertorelle, G., Pascali, V., Barbujani, G., 1998. Clines of nuclear DNA markers suggest a largely Neolithic ancestry of the European gene pool. Proc. Natl. Acad. Sci. 95, 9053–9058.

Chikhi, L., Nichols, R.A., Barbujani, G., Beaumont, M.A., 2002. Y genetic data support the Neolithic demic diffusion model. Proc. Natl. Acad. Sci. 99, 11008–11013.

Childe, V.G., 1925. The Dawn of European Civilisation. Kegan Paul, London.

Cooper, A., Poinar, H.N., 2000. Ancient DNA: do it right or not at all. Science 289, 1139.

Cunliffe, B., 2001. Facing the Ocean: The Atlantic and its People 8000BC– 1500 AD. Cambridge University Press, Cambridge.

Cunliffe, B., Koch, J.T., 2010. Celtic from the West: Alternative Perspectives from Archaeology, Genetics, Language and Literature, First edition. Oxbow Books, Oxford.

Currat, M., Excoffier, L., 2005. The effect of the Neolithic expansion on European molecular diversity. Proc. R. Soc. B 272, 679–688.

Czebreszuk, J., Szmyt, M., 2003. The Northeast Frontier of Bell Beaker. British Archaeological Reports International Series 1155. Archaeopress, Oxford.

Deguilloux, M.F., Ricaud, S., Leahy, R., Pemonge, M.H., 2011a. Analysis of ancient human DNA and primer contamination: one step backward one step forward. Forensic Sci. Int. 210, 102–109.

Deguilloux, M.-F., Soler, L., Pemonge, M.-H., Scarre, C., Joussaume, R., Laporte, L., 2011b. News from the west: ancient DNA from a French megalithic burial chamber. Am. J. Phys. Anthropol. 144, 108–118.

Deguilloux, M.F., Leahy, R., Pemonge, M.H., Rottier, S., 2012. European Neolithization and ancient DNA: an assessment. Evol. Anthropol. 21, 24–37.

Der Sarkissian, C., Balanovsky, O., Brandt, G., Khartanovich, V., Buzhilova, A., Koshel, S., Zaporozhchenko, V., Gronenborn, D., Moiseyev, V., Kolpakov, E., Shumkin, V., Alt, K.W., Balanovska, E., Cooper, A., Haak, W., The Genographic Consortium, 2013. Ancient DNA reveals prehistoric gene-flow from Siberia in the complex human population history of north east Europe. PLoS Genet. 9 e1003296.

Dupanloup, I., Bertorelle, G., Chikhi, L., Barbujani, G., 2004. Estimating the impact of prehistoric admixture on the genome of Europeans. Mol. Biol. Evol. 21, 1361–1372.

Férnandez López de Pablo, J., Gómez Puche, M., 2009. Climate change and population dynamics during the late Mesolithic and the Neolithic transition in Iberia. Doc. Praehist. 36, 67–96.

Fu, Q., Mittnik, A., Johnson, P.L., Bos, K., Lari, M., Bollongino, R., Sun, C., Giemsch, L., Schmitz, R., Burger, J., Ronchitelli, A.M., Martini, F., Cremonesi, R.G., Svoboda, J., Bauer, P., Caramelli, D., Castellano, S., Reich, D., Pääbo, S., Krause, J., 2013. A revised timescale for human evolution based on ancient mitochondrial genomes. Curr. Biol. 23, 553–559.

Gamba, C., Fernandez, E., Tirado, M., Deguilloux, M.F., Pemonge, M.H., Utrilla, P., Edo, M., Molist, M., Rasteiro, R., Chikhi, L., Arroyo-Pardo, E., 2012. Ancient DNA from an Early Neolithic Iberian population supports a pioneer colonization by first farmers. Mol. Ecol. 21, 45–56.

Gamkrelidze, T., Ivanov, V., 1984. Indoevropeyskiy Yazyk I Indoevropeytsy. Izdatel'stvo Tbilisskogo Universiteta, Tbilisi.

Gansauge, M.T., Meyer, M., 2013. Single-stranded DNA library preparation for the sequencing of ancient or damaged DNA. Nat. Protoc. 8, 737–748.

Gilbert, M.T.P., Bandelt, H.-J., Hofreiter, M., Barnes, I., 2005. Assessing ancient DNA studies. Trends Ecol. Evol. 20, 541–544.

Gilbert, M.T.P., Hansen, a.J., Willerslev, E., Turner-Walker, G., Collins, M., 2006. Insights into the processes behind the contamination of degraded human teeth and bone samples with exogenous sources of DNA. Int. J. Osteoarchaeol. 16, 156–164.

Gimbutas, M., 1991. The Civilisation of the Goddess: The World of Old Europe. Harper Collins, New York.

Gronenborn, D., 1999. A variation on a basic theme: the transition to farming in southern central Europe. J. World Prehist. 13, 123–210.

Gronenborn, D., 2003. Migration, acculturation and culture change in western temperate Eurasia, 6500–5000 cal BC. Doc. Praehist. 30, 79–91.

Gronenborn, D., 2007a. Beyond the models: 'Neolithisation' in Central Europe. In: Whittle, A., Cummings, V. (Eds.), Going Over: The Mesolithic-Neolithic Transition in North-West Europe. Oxford University Press, Oxford, pp. 73–98.

Gronenborn, D., 2007b. Climate change and socio-political crises: some cases from Neolithic Central Europe. In: Pollard, T., Banks, I. (Eds.), War and Sacrifice: Studies in the Archaeology of Conflict. Brill, Leiden, pp. 13–32.

Gronenborn, D., 2009. Climate fluctuations and trajectories to complexity in the Neolithic: towards a theory. Doc. Praehist. 36, 97–110.

Gronenborn, D., 2012. Das Ende von IRD 5b: Abrupte Klimafluktuationen um 5100 denBC und der Übergang vom Alt-zum Mittelneolithikum im westlichen Mitteleuropa. In: Kreienbrink, F., Cladders, M., Stäuble, H., Tischendorf, T., Wolfram, S. (Eds.), Siedlungsstrukturen und Kulturwandel in der Bandkeramik. Beiträge der Internationalen Tagung “Neue Fragen zur Bandkeramik oder Alles beim Alten?, Leipzig, September 2010. Arbeits- und Forschungsberichte der Sächsischen Bodendenkmalpflege, Beihefte, Dresden, pp. 241–250.

Haak, W., Forster, P., Bramanti, B., Matsumura, S., Brandt, G., Tänzer, M., Villems, R., Renfrew, C., Gronenborn, D., Alt, K.W., Burger, J., 2005. Ancient DNA from the first European farmers in 7500-year-old Neolithic sites. Science 310, 1016–1018.

Haak, W., Brandt, G., de Jong, H.N., Meyer, C., Ganslmeier, R., Heyd, V., Hawkesworth, C., Pike, A.W., Meller, H., Alt, K.W., 2008. Ancient DNA, Strontium isotopes, and osteological analyses shed light on social and kinship organization of the Later Stone Age. Proc. Natl. Acad. Sci. 105, 18226–18231.

Haak, W., Balanovsky, O., Sanchez, J.J., Koshel, S., Zaporozhchenko, V., Adler, C.J., Der Sarkissian, C.S.I., Brandt, G., Schwarz, C., Nicklisch, N., Dresely, V., Fritsch, B., Balanovska, E., Villems, R., Meller, H., Alt, K.W., Cooper, A., The Genographic Consortium, 2010. Ancient DNA from European early Neolithic farmers reveals their Near Eastern affinities. PLoS Biol. 8 e1000536.

Haas, J.N., Richoz, I., Tinner, W., Wick, L., 1998. Synchronous Holocene climatic oscillations recorded on the Swiss Plateau and at timberline in the Alps. Holocene 8, 301–309.

Heggarty, P., 2013. Europe and Western Asia: Indo-European linguistic history. In: Ness, I. (Ed.), The Encyclopedia of Global Human Migration. Blackwell Publishing Ltd., Oxford, pp. 157–167.

Hellenthal, G., Busby, G.B., Band, G., Wilson, J.F., Capelli, C., Falush, D., Myers, S., 2014. A genetic atlas of human admixture history. Science 343, 747–751.

Hervella, M., Izagirre, N., Alonso, S., Fregel, R., Alonso, A., Cabrera, V.M., de la Rua, C., 2012. Ancient DNA from hunter-gatherer and farmer groups from Northern Spain supports a random dispersion model for the Neolithic expansion into Europe. PLoS One 7 e34417.

Heyd, V., 2007. Families, prestige goods, warriors and complex societies: Beaker groups of the 3rd millennium cal BC along the upper and middle Danube. Proc. Prehist. Soc. 73, 327–379.

Higham, T., Douka, K., Wood, R., Ramsey, C.B., Brock, F., et al., 2014. Nature 512, 306–309.

Hille, A., 2012. Die Glockenbecherkultur in Mitteldeutschland. Veröffentlichungen des Landesamtes für Denkmalpflege und Archäologie Sachsen-Anhalt – Landesmuseum für Vorgeschichte 66. Beier & Beran, Halle.

Hughey, J.R., Paschou, P., Drineas, P., Mastropaolo, D., Lotakis, D.M., Navas, P.A., Michalodimitrakis, M., Stamatoyannopoulos, J.A., Stamatoyannopoulos, G., 2013. A European population in Minoan Bronze Age Crete. Nat. Commun. 4, 1861.

Jeunesse, C., 1998. Pour une origine occidentale de la culture de Michelsberg? In: Biel, J., Schlichterele, H., Strobel, M., Zeeb, A. (Eds.), Die Michelsberger Kultur und ihre Randgebiete - Probleme der Entstehung, Chronologie und des Siedlungswesens. Kolloquium Hemmenhofen. Konrad Theiss, Stuttgart, pp. 29–46.

Jeunesse, C., 2010. Die Michelsberger Kultur. In: Landesmuseum Karlsruhe, Badisches (Ed.), Jungsteinzeit im Umbruch. Die Michelsberger Kultur und Mitteleuropa vor 6000 Jahren, pp. 46–55.

Karlsson, A.O., Wallerström, T., Götherström, A., Holmlund, G., 2006. Y-chromosome diversity in Sweden – a long-time perspective. Eur. J. Hum. Genet. 14, 963–970.

Keller, A., Graefen, A., Ball, M., Matzas, M., Boisguerin, V., Maixner, F., Leidinger, P., Backes, C., Khairat, R., Forster, M., Stade, B., Franke, A., Mayer, J., Spangler, J., McLaughlin, S., Shah, M., Lee, C., Harkins, T.T., Sartori, A., Moreno-Estrada, A., Henn, B., Sikora, M., Semino, O., Chiaroni, J., Rootsi, S., Myres, N.M., Cabrera, V.M., Underhill, P.A., Bustamante, C.D., Vigl, E.E., Samadelli, M., Cipollini, G., Haas, J., Katus, H., O'Connor, B.D., Carlson, M.R., Meder, B., Blin, N., Meese, E., Pusch, C.M., Zink, A., 2012. New insights into the Tyrolean Iceman's origin and phenotype as inferred by whole-genome sequencing. Nat. Commun. 3, 698.

Kivisild, T., Rootsi, S., Metspalu, M., Mastana, S., Kaldma, K., Parik, J., Metspalu, E., Adojaan, M., Tolk, H.V., Stepanov, V., Golge, M., Usanga, E., Papiha, S.S., Cinnioglu, C., King, R., Cavalli-Sforza, L., Underhill, P.A., Villems, R., 2003. The genetic heritage of the earliest settlers persists both in Indian tribal and caste populations. Am. J. Hum. Genet. 72, 313–332.

Koch, J.T., 2009. Tartessian: Celtic in the South-west at the Dawn of History. Acta Palaeohispanica X Palaeohispanica 9, 339–351.

Krause, J., Briggs, A.W., Kircher, M., Maricic, T., Zwyns, N., Derevianko, A., Pääbo, S., 2010. A complete mtDNA genome of an early modern human from Kostenki, Russia. Curr. Biol. 20, 231–236.

Kromer, B., Friedrich, M., 2007. Jahrringchronologien und Radiokohlenstoff: Ein ideales Gespann in der Paläoklimaforschung. Geographische Rundschau 59, 50–55.

Lacan, M., Keyser, C., Ricaut, F.X., Brucato, N., Tarrus, J., Bosch, A., Guilaine, J., Crubezy, E., Ludes, B., 2011a. Ancient DNA suggests the leading role played by men in the Neolithic dissemination. Proc. Natl. Acad. Sci. 108, 18255–18259.

Lacan, M., Keyser, C., Ricaut, F.X., Brucato, N., Duranthon, F., Guilaine, J., Crubezy, E., Ludes, B., 2011b. Ancient DNA reveals male diffusion through the Neolithic Mediterranean route. Proc. Natl. Acad. Sci. 108, 9788–9791.

Lacan, M., Keyser, C., Crubezy, E., Ludes, B., 2013. Ancestry of modern Europeans: contributions of ancient DNA. Cell. Mol. Life Sci. 70, 2473–2487.

Lappalainen, T., Hannelius, U., Salmela, E., von Dobeln, U., Lindgren, C.M., Huoponen, K., Savontaus, M.L., Kere, J., Lahermo, P., 2009. Population structure in contemporary Sweden–a Y-chromosomal and mitochondrial DNA analysis. Ann. Hum. Genet. 73, 61–73.

Larson, G., Burger, J., 2013. A population genetics view of animal domestication. Trends Genet. 29, 197–205.

Lawler, A., 2008. From the Horse's Mouth. Humanities 11–13.

Lazaridis, I., Patterson, N., Mittnik, A., Renaud, G., Mallick, S., Sudmant, P.H., Schraiber, J.G., Castellano, S., Kirsanow, K., Economou, C., Bollongino, R., Fu, Q., Bos, K., Nordenfelt, S., de Filippo, C., Prüfer, K., Sawyer, S., Posth, C., Haak, W., Hallgren, F., Fornander, E., Ayodo, G., Babiker, H.A., Balanovska, E., Balanovsky, O., Ben-Ami, H., Bene, J., Berrada, F., Brisighelli, F., Busby, G.B.J., Cali, F., Churnosov, M., Cole, D.E.C., Damba, L., Delsate, D., van Driem, G., Dryomov, S., Fedorova, S.A., Francken, M., Gallego Romero, I., Gubina, M., Guinet, J.M., Hammer, M., Henn, B., Helvig, T., Hodoglugil, U., Jha, A.R., Kittles, R., Khusnutdinova, E., Kivisild, T., Kučinskas, V., Khusainova, R., Kushniarevich, A., Laredj, L., Litvinov, S., Mahley, R.W., Melegh, B., Metspalu, E., Mountain, J., Nyambo, T., Osipova, L., Parik, J., Platonov, F., Posukh, O.L., Romano, V., Rudan, I., Ruizbakiev, R., Sahakyan, H., Salas, A., Starikovskaya, E.B., Tarekegn, A., Toncheva, D., Turdikulova, S., Uktveryte, I., Utevska, O., Voevoda, M., Wahl, J., Zalloua, P., Yepiskoposyan, L., Zemunik, T., Cooper, A., Capelli, C., Thomas, M.G., Tishkoff, S.A., Singh, L., Thangaraj, K., Villems, R., Comas, D., Sukernik, R., Metspalu, M., Meyer, M., Eichler, E.E., Burger, J., Slatkin, M., Pääbo, S., Kelso, J., Reich, D., Krause, J., 2014. Ancient human genomes suggest three ancestral populations for present-day Europeans. Nature 513, 409–413.

Lee, E.J., Makarewicz, C., Renneberg, R., Harder, M., Krause-Kyora, B., Müller, S., Ostritz, S., Fehren-Schmitz, L., Schreiber, S., Müller, J., von Wurmb-Schwark, N., Nebel, A., 2012. Emerging genetic patterns of the European Neolithic: perspectives from a late Neolithic Bell Beaker burial site in Germany. Am. J. Phys. Anthropol. 148, 571–579.

Lee, E.J., Krause-Kyora, B., Rinne, C., Schütt, R., Harder, M., Müller, J., von Wurmb-Schwark, N., Nebel, A., 2013. Ancient DNA insights from the Middle Neolithic in Germany. Archaeol. Anthropol. Sci. 6, 199–204.

Lewthwaite, J., 1989. Isolating the residuals: The Mesolithic basis of man-animal relationships on the Mediterranean islands. In: Bonsall, C. (Ed.), The Mesolithic in Europe. John Donald Publishers Ltd., Edinburgh, pp. 541–555.

Linstädter, J., 2008. The Epipalaeolithic-Neolithic transition in the Mediterranean region of northwest Africa. Quartär 55, 41–62.

Lockwood, M., Harrison, G.R., Woollings, T., Solanki, S.K., 2010. Are cold winters in Europe associated with low solar activity? Environ. Res. Lett. 5, 24001.

Lübke, H., Lüth, F., Terberger, T., 2007. Fisher or farmers? The archaeology of the Ostorf cemetary and related burials in the light of new information. In: Larssen, L., Lüth, L., Terberger, T. (Eds.), Non-Megalithic Mortuary Practices in the Baltic – New Methods and Research into the Development of Stone Age Society, Bericht der Römisch-Germanischen Kommission 88, Schwerin, pp. 307–338.

Magny, M., 2004. Holocene climate variability as reflected by mid-European lake-level fluctuations and its probable impact on prehistoric human settlements. Quatern. Int. 113, 65–79.

Malmström, H., Stora, J., Dalen, L., Holmlund, G., Götherström, A., 2005. Extensive human DNA contamination in extracts from ancient dog bones and teeth. Mol. Biol. Evol. 22, 2040–2047.

Malmström, H., Gilbert, M.T.P., Thomas, M.G., Brandström, M., Storå, J., Molnar, P., Andersen, P.K., Bendixen, C., Holmlund, G., Götherström, A., Willerslev, E., 2009. Ancient DNA reveals lack of continuity between Neolithic hunter-gatherers and contemporary Scandinavians. Curr. Biol. 19, 1758–1762.

Malyarchuk, B., Derenko, M., Perkova, M., Vanecek, T., 2008. Mitochondrial haplogroup U2d phylogeny and distribution. Hum. Biol. 80, 565–571.

Malyarchuk, B., Derenko, M., Grzybowski, T., Perkova, M., Rogalla, U., Vanecek, T., Tsybovsky, I., 2010. The peopling of Europe from the mitochondrial haplogroup U5 perspective. PLoS One 5 e10285.

Marlowe, F.W., 2004. Marital residence among foragers. Curr. Anthropol. 45, 277–284.

Medina-Elizalde, M., Rohling, E.J., 2012. Collapse of Classic Maya civilization related to modest reduction in precipitation. Science 335, 956–959.

Melchior, L., Gilbert, M.T., Kivisild, T., Lynnerup, N., Dissing, J., 2008. Rare mtDNA haplogroups and genetic differences in rich and poor Danish Iron-Age villages. Am. J. Phys. Anthropol. 135, 206–215.

Melchior, L., Lynnerup, N., Siegismund, H.R., Kivisild, T., Dissing, J., 2010. Genetic diversity among ancient Nordic populations. PLoS One 5 e11898.

Mellars, P., 2006. A new radiocarbon revolution and the dispersal of modern humans in Eurasia. Nature 439, 931–935.

Meyer, M., Kircher, M., Gansauge, M.T., Li, H., Racimo, F., Mallick, S., Schraiber, J.G., Jay, F., Prüfer, K., de Filippo, C., Sudmant, P.H., Alkan, C., Fu, Q., Do, R., Rohland, N., Tandon, A., Siebauer, M., Green, R.E., Bryc, K., Briggs, A.W., Stenzel, U., Dabney, J., Shendure, J., Kitzman, J., Hammer, M.F., Shunkov, M.V., Derevianko, A.P., Patterson, N., Andres, A.M., Eichler, E.E., Slatkin, M., Reich, D., Kelso, J., Pääbo, S., 2012. A high-coverage genome sequence from an archaic Denisovan individual. Science 338, 222–226.

Migowski, C., Stein, M., Prasad, S., Negendank, J.F.W., Agnon, A., 2006. Holocene climate variability and cultural evolution in the Near East from the Dead Sea sedimentary record. Quatern. Res. 66, 371–504.

Myres, N.M., Rootsi, S., Lin, A.A., Jarve, M., King, R.J., Kutuev, I., Cabrera, V.M., Khusnutdinova, E.K., Pshenichnov, A., Yunusbayev, B., Balanovsky, O., Balanovska, E., Rudan, P., Baldovic, M., Herrera, R.J., Chiaroni, J., Di Cristofaro, J., Villems, R., Kivisild, T., Underhill, P.A., 2011. A major Y-chromosome haplogroup R1b Holocene era founder effect in Central and Western Europe. Eur. J. Hum. Genet. 19, 95–101.

Olalde, I., Allentoft, M.E., Sanchez-Quinto, F., Santpere, G., Chiang, C.W.K., DeGiorgio, M., Prado-Martinez, J., Rodriguez, J.A., Rasmussen, S., Quilez, J., Ramirez, O., Marigorta, U.M., Fernandez-Callejo, M., Prada, M.E., Encinas, J.M.V., Nielsen, R., Netea, M.G., Novembre, J., Sturm, R.A., Sabeti, P., Marques-Bonet, T., Navarro, A., Willerslev, E., Lalueza-Fox, C., 2014. Derived immune and ancestral pigmentation alleles in a 7,000-year-old Mesolithic European. Nature 507, 225–228.

Olivieri, A., Pala, M., Gandini, F., Hooshiar Kashani, B., Perego, U.A., Woodward, S.R., Grugni, V., Battaglia, V., Semino, O., Achilli, A., Richards, M.B., Torroni, A., 2013. Mitogenomes from two uncommon haplogroups mark late glacial/postglacial expansions from the Near East and Neolithic dispersals within Europe. PLoS One 8 e70492.

Pääbo, S., Poinar, H., Serre, D., Jaenicke-Despres, V., Hebler, J., Rohland, N., Kuch, M., Krause, J., Vigilant, L., Hofreiter, M., 2004. Genetic analyses from ancient DNA. A. Rev. Genet. 38, 645–679.

Pakendorf, B., Stoneking, M., 2005. Mitochondrial DNA and human evolution. A. Rev. Genome Hum. Genet. 6, 165–183.

Pala, M., Achilli, A., Olivieri, A., Kashani, B.H., Perego, U.A., Sanna, D., Metspalu, E., Tambets, K., Tamm, E., Accetturo, M., Carossa, V., Lancioni, H., Panara, F., Zimmermann, B., Huber, G., Al-Zahery, N., Brisighelli, F., Woodward, S.R., Francalacci, P., Parson, W., Salas, A., Behar, D.M., Villems, R., Semino, O., Bandelt, H.J., Torroni, A., 2009. Mitochondrial haplogroup U5b3: a distant echo of the epipaleolithic in Italy and the legacy of the early Sardinians. Am. J. Hum. Genet. 84, 814–821.

Pala, M., Olivieri, A., Achilli, A., Accetturo, M., Metspalu, E., Reidla, M., Tamm, E., Karmin, M., Reisberg, T., Kashani, B.H., Perego, U.A., Carossa, V., Gandini, F., Pereira, J.B., Soares, P., Angerhofer, N., Rychkov, S., Al-Zahery, N., Carelli, V., Sanati, M.H., Houshmand, M., Hatina, J., Macaulay, V., Pereira, L., Woodward, S.R., Davies, W., Gamble, C., Baird, D., Semino, O., Villems, R., Torroni, A., Richards, M.B., 2012. Mitochondrial DNA signals of late glacial recolonization of Europe from Near Eastern refugia. Am. J. Hum. Genet. 90, 91–924.

Pereira, L., Richards, M., Goios, A., Alonso, A., Albarran, C., Garcia, O., Behar, D.M., Golge, M., Hatina, J., Al-Gazali, L., Bradley, D.G., Macaulay, V., Amorim, A., 2005. High-resolution mtDNA evidence for the late-glacial resettlement of Europe from an Iberian refugium. Genome Res. 15, 19–24.

Pericic, M., Lauc, L.B., Klaric, I.M., Rootsi, S., Janicijevic, B., Rudan, I., Terzic, R., Colak, I., Kvesic, A., Popovic, D., Sijacki, A., Behluli, I., Dordevic, D., Efremovska, L., Bajec, D.D., Stefanovic, B.D., Villems, R., Rudan, P., 2005. High-resolution phylogenetic analysis of southeastern Europe traces major episodes of paternal gene flow among Slavic populations. Mol. Biol. Evol. 22, 1964–1975.

Pinhasi, R., von Cramon-Taubadel, N., 2012. A craniometric perspective on the transition to agriculture in Europe. Hum. Biol. 84, 45–66.

Pinhasi, R., Thomas, M.G., Hofreiter, M., Currat, M., Burger, J., 2012. The genetic history of Europeans. Trends Genet. 28, 496–505.

Preuss, J., 1998. Das Neolithikum in Mitteleuropa. Beier & Beran, Weissbach.

Price, T.D., 2000. Europe's First Farmers. Cambridge University Press, Cambridge.

Pruvost, M., Schwarz, R., Correia, V.B., Champlot, S., Grange, T., Geigl, E.M., 2008. DNA diagenesis and palaeogenetic analysis: Critical assessment and methodological progress. Palaeogeogr. Palaeoclimatol. Palaeoecol. 266, 211–219.

Raghavan, M., Skoglund, P., Graf, K.E., Metspalu, M., Albrechtsen, A., Moltke, I., Rasmussen, S., Stafford Jr., T.W., Orlando, L., Metspalu, E., Karmin, M., Tambets, K., Rootsi, S., Magi, R., Campos, P.F., Balanovska, E., Balanovsky, O., Khusnutdinova, E., Litvinov, S., Osipova, L.P., Fedorova, S.A., Voevoda, M.I., DeGiorgio, M., Sicheritz-Ponten, T., Brunak, S., Demeshchenko, S., Kivisild, T., Villems, R., Nielsen, R., Jakobsson, M., Willerslev, E., 2014. Upper Palaeolithic Siberian genome reveals dual ancestry of Native Americans. Nature 505, 87–91.

Rasteiro, R., Bouttier, P.A., Sousa, V.C., Chikhi, L., 2012. Investigating sex-biased migration during the Neolithic transition in Europe, using an explicit spatial simulation framework. Proc. R. Soc. B 279, 2409–2416.

Renfrew, C., 1987. Archaeology and Language: The Puzzle of Ind-European Origins. Cape, London.

Renfrew, C., 1998. Comments on Cavalli-Sforza and Otte. J. Anthropol. Res. 54, 417–419.

Renfrew, C., 1999. Time depth, convergence theory, and innovation in Proto-Indo-European: 'Old Europe' as a PIE linguistic area. J. Indo-Eur. Stud. 27, 257–293.

Richards, M., 2003. The Neolithic invasion of Europe. A. Rev. Anthropol. 32, 135–162.

Richards, M., Corte-Real, H., Forster, P., Macaulay, V., Wilkinson-Herbots, H., Demaine, A., Papiha, S., Hedges, R., Bandelt, H.J., Sykes, B., 1996. Paleolithic and Neolithic lineages in the European mitochondrial gene pool. Am. J. Hum. Genet. 59, 185–203.

Richards, M., Macaulay, V.A., Bandelt, H.J., Sykes, B.C., 1998. Phylogeography of mitochondrial DNA in Western Europe. Annls. Hum. Genet. 62, 241–260.

Richards, M., Macaulay, V., Hickey, E., Vega, E., Sykes, B., Guida, V., Rengo, C., Sellitto, D., Cruciani, F., Kivisild, T., Villems, R., Thomas, M., Rychkov, S., Rychkov, O., Rychkov, Y., Golge, M., Dimitrov, D., Hill, E., Bradley, D., Romano, V., Cali, F., Vona, G., Demaine, A., Papiha, S., Triantaphyllidis, C., Stefanescu, G., Hatina, J., Belledi, M., Di Rienzo, A., Novelletto, A., Oppenheim, A., Norby, S., Al-Zaheri, N., Santachiara-Benerecetti, S., Scozari, R., Torroni, A., Bandelt, H.J., 2000. Tracing European founder lineages in the Near Eastern mtDNA pool. Am. J. Hum. Genet. 67, 1251–1276.

Rojo Guerra, M.A., Kunst, M., Garrido Pena, R., García- Martínez de Lagrán, I., 2006. La neolitización de la Meseta Norte a la luz del C-14: análisis de 47 dataciones absolutas de dos yacimientos domésticos del Valle de Ambrona, Soria, España. Archivo de Prehistoria Levantina XXVI, pp. 39–100.

Rootsi, S., Magri, C., Kivisild, T., Benuzzi, G., Help, H., Bermisheva, M., Kutuev, I., Barac, L., Pericic, M., Balanovsky, O., Pshenichnov, A., Dion, D., Grobei, M., Zhivotovsky, L.A., Battaglia, V., Achilli, A., Al-Zahery, N., Parik, J., King, R., Cinnioglu, C., Khusnutdinova, E., Rudan, P., Balanovska, E., Scheffrahn, W., Simonescu, M., Brehm, A., Goncalves, R., Rosa, A., Moisan, J.P., Chaventre, A., Ferak, V., Furedi, S., Oefner, P.J., Shen, P., Beckman, L., Mikerezi, I., Terzic, R., Primorac, D., Cambon-Thomsen, A., Krumina, A., Torroni, A., Underhill, P.A., Santachiara-Benerecetti, A.S., Villems, R., Semino, O., 2004. Phylogeography of Y-chromosome haplogroup I reveals distinct domains of prehistoric gene flow in Europe. Am. J. Hum. Genet. 75, 128–137.

Rootsi, S., Zhivotovsky, L.A., Baldovic, M., Kayser, M., Kutuev, I.A., Khusainova, R., Bermisheva, M.A., Gubina, M., Fedorova, S.A., Ilumae, A.M., Khusnutdinova, E.K., Voevoda, M.I., Osipova, L.P., Stoneking, M., Lin, A.A., Ferak, V., Parik, J., Kivisild, T., Underhill, P.A., Villems, R., 2007. A counter-clockwise northern route of the Y-chromosome haplogroup N from Southeast Asia towards Europe. Eur. J. Hum. Genet. 15, 204–211.

Rowley-Conwy, P., 2011. Westward Ho! The spread of agriculture from Central Europe to the Atlantic. Curr. Anthropol. 52, S431–S451.

Salamon, M., Tuross, N., Arensburg, B., Weiner, S., 2005. Relatively well preserved DNA is present in the crystal aggregates of fossil bones. Proc. Natl. Acad. Sci. 102, 13783–13788.

Sampietro, M.L., Gilbert, M.T., Lao, O., Caramelli, D., Lari, M., Bertranpetit, J., Lalueza-Fox, C., 2006. Tracking down human contamination in ancient human teeth. Mol. Biol. Evol. 23, 1801–1807.

Sanchez-Quinto, F., Schroeder, H., Ramirez, O., Avila-Arcos, M.C., Pybus, M., Olalde, I., Velazquez, A.M., Marcos, M.E., Encinas, J.M., Bertranpetit, J., Orlando, L., Gilbert, M.T., Lalueza-Fox, C., 2012. Genomic affinities of two 7,000-year-old Iberian hunter-gatherers. Curr. Biol. 22, 1494–1499.

Scally, A., Durbin, R., 2012. Revising the human mutation rate: implications for understanding human evolution. Nat. Rev. Genet. 13, 745–753.

Schuhmacher, T.X., Sanz González de Lema, S., 2013. “Kontinuität und Wandel”: 20 Jahre später. Zur Frage der Neolithisierung Ost-Spaniens. In: Pastoors, A., Auffermann, B. (Eds.), Pleistocene Foragers. Their Culture and Environment. Festschrift in Honour of Gerd-Christian Weniger for his Sixtieth birthday, Mettmann, pp. 163–186.

Semino, O., Passarino, G., Oefner, P.J., Lin, A.A., Arbuzova, S., Beckman, L.E., De Benedictis, G., Francalacci, P., Kouvatsi, A., Limborska, S., Marcikiae, M., Mika, A., Mika, B., Primorac, D., Santachiara-Benerecetti, A.S., Cavalli-Sforza, L.L., Underhill, P.A., 2000. The genetic legacy of Paleolithic *Homo sapiens* in extant Europeans: a Y chromosome perspective. Science 290, 1155–1159.

Semino, O., Magri, C., Benuzzi, G., Lin, A.A., Al-Zahery, N., Battaglia, V., Maccioni, L., Triantaphyllidis, C., Shen, P., Oefner, P.J., Zhivotovsky, L.A., King, R., Torroni, A., Cavalli-Sforza, L.L., Underhill, P.A., Santachiara-Benerecetti, A.S., 2004. Origin, diffusion, and differentiation of Y-chromosome haplogroups E and J: inferences on the Neolithization of Europe and later migratory events in the Mediterranean area. Am. J. Hum. Genet. 74, 1023–1034.

Sims-Williams, P., 1998. Genetics, linguistics, and prehistory: thinking big and thinking straight. Antiquity 72, 505–527.

Sims-Williams, P., 2012. Bronze- and Iron-Age Celtic Speakers: What don't we know, what can't we know, and what could we know? Language, genetics and archaeology in the twenty-first century. Antiq. J. 92, 427–449.

Sirocko, F., Brunck, H., Pfahl, S., 2012. Solar influence on winter severity in central Europe. Geophys. Res. Lett. 39. L16704.

Skoglund, P., Malmstrom, H., Raghavan, M., Stora, J., Hall, P., Willerslev, E., Gilbert, M.T., Götherström, A., Jakobsson, M., 2012. Origins and genetic legacy of Neolithic farmers and hunter-gatherers in Europe. Science 336, 466–469.

Soares, P., Achilli, A., Semino, O., Davies, W., Macaulay, V., Bandelt, H.J., Torroni, A., Richards, M.B., 2010. The archaeogenetics of Europe. Curr. Biol. 20, R174–R183.

Solanki, S.K., Usoskin, I.G., Kromer, B., Schussler, M., Beer, J., 2004. Unusual activity of the sun during recent decades compared to the previous 11,000 years. Nature 431, 1084–1087.

Spurk, M., Leuschner, H.H., Baillie, M.G.L., Briffa, K.R., Friedrich, M., 2002. Depositional frequency of German subfossil oaks: climatically and non-climatically induced fluctuations in the Holocene. Holocene 12, 707–715.

Szécsényi-Nagy, A., Brandt, G., Keerl, V., Jakucs, J., Haak, W., Möller-Rieker, S., Köhler, K., Mende, B.G., Fecher, M., Oross, K., Paluch, T., Osztás, A., Kiss, V., Pálfi, G., Molnár, E., Sebők, K., Czene, A., Šlaus, M., Novak, M., Pećina- Šlaus, N., Ősz, B., Voicsek, V., Somogyi, K., Tóth, G., Kromer, B., Bánffy, E., Alt, K.W., 2014. Tracing the genetic origin of Europe's first farmers reveals insights into their social organization. bioRxiv. http://dx.doi.org/10.1101/008664.

Underhill, P.A., Kivisild, T., 2007. Use of Y chromosome and mitochondrial DNA population structure in tracing human migrations. A. Rev. Genet. 41, 539–564.

Underhill, P.A., Myres, N.M., Rootsi, S., Metspalu, M., Zhivotovsky, L.A., King, R.J., Lin, A.A., Chow, C.E., Semino, O., Battaglia, V., Kutuev, I., Jarve, M., Chaubey, G., Ayub, Q., Mohyuddin, A., Mehdi, S.Q., Sengupta, S., Rogaev, E.I., Khusnutdinova, E.K., Pshenichnov, A., Balanovsky, O., Balanovska, E., Jeran, N., Augustin, D.H., Baldovic, M., Herrera, R.J., Thangaraj, K., Singh, V., Singh, L., Majumder, P., Rudan, P., Primorac, D., Villems, R., Kivisild, T., 2010. Separating the post-Glacial coancestry of European and Asian Y chromosomes within haplogroup R1a. Eur. J. Hum. Genet. 18, 479–484.

Vicent-García, J.M., 1997. The island filter model revisited. In: Balmuth, M.S., Gilman, A., Prados-Torreira, L. (Eds.), Encounters and Transformations. The Archaeology of Iberia in Transition. Sheffield Academic Press, Sheffield, pp. 1–13.

Vigne, J.D., 2011. The origins of animal domestication and husbandry: a major change in the history of humanity and the biosphere. C. R. Biol. 334, 171–181.

von Cramon-Taubadel, N., Pinhasi, R., 2011. Craniometric data support a mosaic model of demic and cultural Neolithic diffusion to outlying regions of Europe. Proc. R. Soc. B 278, 2874–2880.

Weiss, H., Bradley, R.S., 2001. Archaeology. What drives societal collapse? Science 291, 609–610.

Wells, R.S., Yuldasheva, N., Ruzibakiev, R., Underhill, P.A., Evseeva, I., Blue-Smith, J., Jin, L., Su, B., Pitchappan, R., Shanmugalakshmi, S., Balakrishnan, K., Read, M., Pearson, N.M., Zerjal, T., Webster, M.T., Zholoshvili, I., Jamarjashvili, E., Gambarov, S., Nikbin, B., Dostiev, A., Aknazarov, O., Zalloua, P., Tsoy, I., Kitaev, M., Mirrakhimov, M., Chariev, A., Bodmer, W.F., 2001. The Eurasian heartland: a continental perspective on Y-chromosome diversity. Proc. Natl. Acad. Sci. 98, 10244–10249.

Weninger, B., Clare, L., Rohling, E.J., Bar-Yosef, O., Böhner, U., Budja, M., Bundschuh, M., Feurdean, A., Gebel, H.G., Jöris, O., Linstädter, J., Mayewski, P., Mühlenbruch, T., Reingruber, A., Rollefson, G., Schyle, D., Thissen, L., Todorova, H., Zielhofer, C., 2009. The impact of rapid climate change on prehistoric societies during the Holocene in the Eastern Mediterranean. Doc. Praehist. 36, 7–59.

Whittle, A.W.R., 1996. Europe in the Neolithic: The Creation of New Worlds. Cambridge University Press, Cambridge.

Whittle, A.W.R., Cummings, V., 2007. Going Over: The Mesolithic-Neolithic Transition in North-West Europe. Oxford University Press, Oxford.

Wilkins, J.F., 2006. Unraveling male and female histories from human genetic data. Curr. Opin. Genet. Dev. 16, 611–617.

Wilkins, J.F., Marlowe, F.W., 2006. Sex-biased migration in humans: what should we expect from genetic data? Bioessays 28, 290–300.

Woollings, T., Lockwood, M., Masato, G., Bell, C., Gray, L., 2010. Enhanced signature of solar variability in Eurasian winter climate. Geophys. Res. Lett. 37, 1–6.

Zapata, L., Peña-Chocarro, L., Pérez-Jordá, G., Stika, H.-P., 2004. Early Neolithic agriculture in the Iberian Peninsula. J. World Prehist. 18, 283–325.

Zilhão, J., 1997. Maritime pioneer colonization in the Early Neolithic of the west Mediterranean. Testing the model against the evidence. Porocilo 24, 19–42.

Zilhão, J., 2001. Radiocarbon evidence for maritime pioneer colonization at the origins of farming in west. Mediterranean Europe. Proc. Natl. Acad. Sci. 98, 14180–14185.