A Glimpse into Darkness – Population Genetics of the European Middle Ages

Joscha Gretzinger and Stephan Schiffels

Introduction

The last ten years have seen the rise of archaeogenetics from a rather obscure niche science, discredited by failures and untenable assertions, to an outstanding academic discipline at the crossroads of life sciences and the humanities (Hagelberg et al. 2015). Nowadays, ancient DNA (aDNA) grants us insights into the relationship between archaic and modern humans (Green et al. 2010; Meyer et al. 2012; Prüfer et al. 2014; Fu et al. 2015), the settlements of the Americas (Rasmussen et al. 2015a; Skoglund et al. 2015; Posth et al. 2018; Moreno-Mayar et al. 2018) and Oceania (Lipson et al. 2018; Pugach et al. 2020; Larena et al. 2021; Choin et al. 2021), the spread of the Neolithic revolution (Malmström et al. 2009; Keller et al. 2012; Brandt et al. 2013; Sikora et al. 2014; Cassidy et al. 2016; Lazaridis et al. 2016; Omrak et al. 2016; Lipson et al. 2017; Olalde et al. 2018; Brace et al. 2019; Cassidy et al. 2020) and the Indo-European languages (Allentoft et al. 2015; Haak et al. 2015), as well as many more highly debated archaeological controversies (Nielsen et al. 2017). European prehistory in particular has profited from extensive archaeogenetic research, with dozens of publications so far (Marciniak and Perry 2017) studying the Palaeolithic, Mesolithic, Neolithic and Early Bronze Age using genetic analyses (e.g. Malmström et al. 2009; Skoglund et al. 2012; Fu et al. 2014; Allentoft et al. 2015; Haak et al. 2015; Fu et al. 2015, 2016; Cassidy et al. 2016; Lipson et al. 2017; Olalde et al. 2018; Mathieson et al. 2018; Mittnik et al. 2018; Brace et al. 2019; Cassidy et al. 2020; Furtwängler et al. 2020; Saag et al. 2021).

However, while paleogenetic research has extended our knowledge and understanding of European prehistory, shedding light on the first modern humans of the continent during the Ice Age (Fu et al. 2016, 2015), the interaction between Mesolithic hunter-gatherers and incoming farmers from the Near East (Brace et al. 2019; Lipson et al. 2017), and the introduction of new types of technology (Harney et al. 2018), social systems (Mittnik et al. 2019; Cassidy et al. 2020), and also diseases at the end of the Neolithic and the beginning of the Bronze Age (Rasmussen et al. 2015b; Spyrou et al. 2018; Keller et al. 2019; Kılınç et al. 2021), less is known of what happened in the following three millennia. Indeed, only a small fraction of the hundreds of genomes sequenced date to the post-Bronze Age periods in Europe, and even fewer if we restrict ourselves to the regions north of the Alps. So far, only eight articles to our knowledge cover the northern European Middle Ages (Schiffels et al. 2016; Martiniano et al. 2016; Hedenstierna-Jonson et al. 2017; Veeramah et al. 2018; O'Sullivan et al. 2018; Krzewińska et al. 2018; Ebenesersdóttir et al. 2018; Margaryan et al. 2020). Arguably, due to the lack of written sources and the sheer complexity of the archaeological record, archaeogenetic research seems to generate more value in Prehistoric times, whereas in Historic periods highly resolved chronologies and abundancy of historic sources make aDNA analyses appear superfluous.

Yet, lack of interest does not explain the underrepresentation of historic aDNA research. In fact, population genetic research can contribute substantially to the understanding of European history. The European continent experienced substantial cultural transformations between Late Antiquity and the Middle Ages that laid the foundations of the modern political, social, and religious landscape (Halsall 2007). This transformation has commonly been associated with the movement of historic entities, such as the Goths, Anglo-Saxon, Langobards and Huns, and subsequently the collapse of the Roman Empire. However, the use of migration as an explanation for cultural transitions has varied greatly over the past 100 years and remains controversial (Chapman and Hamerow 1997; Burmeister 2000; Shennan 2000). In particular, since the genetic and social composition of groups involved and the exact nature of these "migrations" are unclear, they have been a subject of substantial historical and archaeological debate (Halsall 2007). But detecting movements of people is precisely what archaeogenetic research can substantially help with, so it is evident that aDNA research would be a valuable complementary science for medieval archaeology and historical sciences. Instead, methodological issues and limitations have so far delayed historic aDNA research, especially in the northern regions of Europe. These limitations arise from the complexity of the European gene pool and its long-shared history of admixture and migration.

Background

With the advent of the Next Generation technologies, the years 2012–2020 have seen the publication of complete prehistoric European genomes, accompanied by thousands of genomes from present-day populations across the globe

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(Sudmant et al. 2015; Marciniak and Perry 2017). These genomes enabled the reconstruction of the processes that lead to the formation of the present-day European gene pool: the genome of the exceptionally well-preserved Copper Age Tyrolean Iceman ("Ötzi") dated to about 5,300 calibrated years before present (cal. BP) was sequenced as the first ancient European genome (Keller et al. 2012). Surprisingly, this individual exhibited strong genetic affinities to present-day Sardinians (Sikora et al. 2014). Subsequently, a genomic sequence from a 5,000-year-old agriculturalist from Sweden was also demonstrated to possess strong genetic affinities to Sardinians, in contrast to contemporaneous hunter-gatherers that originate from the same area (Skoglund et al. 2012). Based on these observations, Skoglund and Sikora proposed in their publications a two-way mixture model for the origin of the European gene pool, with the indigenous European hunter-gatherers becoming progressively more admixed with an incoming farmer population immigrating from the Near East through south-eastern Europe during the Neolithic 8,000–6,000 years BP (Omrak et al. 2016), subsequently forming a population called Early European farmers (EEF). Consequently, the strong affinity of these two ancient genomes to present-day Sardinians results from the uniquely high proportion of early farmer ancestry in the Sardinians' genomes.

Shortly afterwards, Raghavan and colleagues published the genome of the 24,000-year-old "MA-1 boy" (from Mal'ta in southern Siberia; Raghavan et al. 2014). This individual belonged to an ancient north Eurasian (ANE) population, which was found to be deeply ancestral to yet another genetic component that eventually made its way into modern Europeans (Lazaridis et al. 2014). From 2015 to 2016, the number of Eurasian ancient genomic sequences exploded from 15 to over one hundred. Data produced using WGS as well as SNP capture has broadened and refined these previous hypotheses (Haak et al. 2015; Allentoft et al. 2015; Mathieson et al. 2015; Lazaridis et al. 2016). Based on these findings, it was demonstrated that ANE ancestry was transmitted to eastern, central and northern Europe by people of the Yamnaya culture in the form of a substantial migration and then by the "Corded Ware" people that emerged from admixture between the Yamnaya and Middle Neolithic Europeans (Haak et al. 2015). As a consequence of the massive Yamnaya-related westward migration 4,500 years ago (probably accompanied by the spread of the Indo-European languages), a fundamental replacement and homogenisation of European genetic diversity took place at the end of the Neolithic. Relevant to historical aDNA research, studies of the Late Neolithic have demonstrated that populations associated with the Corded Ware culture in the Baltics genetically resembled Corded Ware populations from central Europe (Haak et al. 2015; Mittnik et al. 2018), displaying homogeneity across the European gene pool. Further, individuals associated with the Late Neolithic Bell Beaker culture in Britain trace ~90% of their ancestry to the continent (Olalde et al. 2018), closely resembling Bell Beaker populations there. This demonstrates that the pronounced genetic substructure that had previously characterised western Eurasia collapsed into the present-day very low level of genetic differentiation by the Early Bronze Age (Haak et al. 2015). However, most established and frequently used methods in ancient population genetics were conceptualised to infer genetic affinities, admixture events, and ancestry proportions in the strongly differentiated populations of pre-Bronze Age Europe, based on the often sparsely covered, damaged genome sequences recovered from archaeological material. Thus, while these methods (*outgroup-F_3* (Patterson et al. 2012), *qpAdm* (Haak et al. 2015), and *PCA* (Patterson et al. 2006)) work markedly well in the context of Stone Age European genomes as well as in less homogenous regions of the globe, often also on highly degraded and badly preserved material, these current population genetic approaches struggle to differentiate the highly homogenised and closely related populations of post-Bronze Age Europe.

As a result, less is known about younger prehistoric and historic migrations in Europe, despite the better aDNA preservation. After the population genetic changes and shifts during the early Neolithic and Bronze Age periods, the genetic composition of populations in most parts of Europe had already become similar to the modern-day groups of those same regions (Haak et al. 2015; Günther and Jakobsson 2016). This observation does not preclude later migrations and admixture events, but it elucidates that the populations involved were not as highly differentiated as during the Mesolithic and Neolithic, when populations were almost as different from each other as modern-day continental groups (genetic differentiation as measured by F_{ST} between eastern European hunter-gatherers and early European farmers is 9%, compared with 11% between present-day English and Han Chinese; Haak et al. 2015; Allentoft et al. 2015).

Nowadays, European populations exhibit only low levels of genetic differentiation, with existing differences characterised by a strong continent-wide correlation between geographic and genetic distance (Lao et al. 2008; Novembre et al. 2008; O'Dushlaine et al. 2010a). For example, mean heterozygosity and haplotype diversity (HD) is larger, and mean linkage disequilibrium (LD) smaller, in southern compared to northern Europe (Lao et al. 2008; O'Dushlaine et al. 2010b). Both parameters clearly exhibit a clinal distribution that demonstrates spatial continuity of genetic diversity in Europe (Lao et al. 2008). In addition to this broad geographic pattern, several small and large-scale migrations have formed and contributed to the European subpopulations (Ralph and Coop 2013; Busby et al. 2015). Based on comparisons of modern European DNA, sources of these migrations originated from both within as well as outside of Europe. However, associating admixture events with particular historical migrations is exceedingly difficult, but (for instance) effects of the migration period have been suggested based on modern-day population-genetic data, especially in eastern Europe (Ralph and Coop 2013; Busby et al. 2015). Arguably, these migration and admixture events contributed in subtle ways to the genetic

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pattern observed today in modern Europeans. It is also likely that the increasing population size and density in Europe made later migrations less influential on demography, since the relative fraction of migrants was decreasing (Günther and Jakobsson 2016). Therefore, to study such migrations within continental Europe, it is necessary to look at the "fine-scale structure", a term used to describe areas where F_{ST} between populations tends to be below 1% (Novembre and Peter 2016). As previously stated, current methodological approaches are often insufficient to study such subtle population stratification based on the ancient and present-day reference data provided. Nevertheless, the last five years have seen initial pioneer studies on the topic of European medieval population genetics. Applying established methods of present-day population genomics and/or novel tools, these gained first insights into northern European population genetics during the Middle Ages. Here we highlight three approaches to the possible detection of population stratification in the context of strong genetic population homogeneity.

First, the usage of large reference datasets can facilitate population stratification techniques. Subtle genetic differences become more perceptible as the size of a dataset increases (Novembre and Peter 2016). For example, Principal Component Analysis (PCA) is now one of the most frequently used tools for characterisations of population structure and inference of admixture (Lazaridis et al. 2014; Haak et al. 2015). Patterson and colleagues have shown that structure reveals itself in a PCA approach "like a phase change in physics"; namely "if the product of the number of genetic markers (m) and individuals (n) is greater than $1/F_{ST}^2$ then structure will be evident" (Patterson et al. 2006). While current archaeogenetic methods often use the same dataset of modern reference individuals ("Human Origins dataset"; Lazaridis et al. 2014; Haak et al. 2015), this collection only contains small sample sizes per population, making it inadequate to study fine-scale population genetics affinities in an intra-regional context. For example, the use of a large reference dataset including 2,597 present-day Scandinavians and British-Irish Islanders enabled Ebenesersdóttir and colleagues to use established methods (supervised *ADMIXTURE* (Alexander et al. 2009), F_{ST} (e.g. Holsinger and Weir 2009), F_4 statistics (Reich et al. 2009)), commonly used in aDNA studies, in a fine-structure context comparing closely related ancestries in modern and ancient Icelanders. Based on their observations, they concluded that ancient Icelanders were a population of Norse, Gaelic, and admixed individuals, carrying around 56% Scandinavian and 44% British-Irish ancestry (Ebenesersdóttir et al. 2018).

Second, fine-structure methods developed for the analysis of present-day genomes can be borrowed. While these methods (often haplotype- or identity-by-descent-based (IBD)) have already been established for the analysis of present-day populations for quite some time, providing insights into the formation of the British (Leslie et al. 2015; Gilbert et al. 2019), US American (Han et al. 2017), Estonian (Pankratov et al. 2020), Japanese (Sakaue et al. 2020) etc. gene pools, their application in the context of ancient DNA is still rare and challenging. Due to the highly degraded nature of ancient DNA molecules, the quality of resulting genotype data is much lower than that of modern DNA samples. In particular, due to the often bad preservation of the DNA within the skeletal material, genome quality for calling diploid genotypes (i.e. with enough resolution to separate a person's paternally and maternally inherited genotype in a specific genetic location) is typically not sufficient. However, diploid genotypes are essential for phasing and identification of IBD and/or haplotype blocks on which methods like *fineSTRUCTURE* (Leslie et al. 2015) or *Chromopainter* (Lawson et al. 2012) depend. While, in theory, better preserved samples could be sequenced to such high coverage that their error rates compete with those of high-coverage sequences from extant humans, this is an expensive and, for most research laboratories, unacceptable financial cost. Recently, imputation (the statistical inference of unobserved genotypes based on observed genotypes) has found its way into ancient DNA research. Newly published algorithms enable the identification of diploid genotypes and subsequent phasing of the genome-wide data even for medium- to low-coverage ancient DNA data. Although large-scale imputation and subsequent haplotype-based genetic analyses of ancient DNA data are still in the early stages of development, first results seem promising and demonstrate the applicability of those methods. For example, Cassidy and colleagues used imputed Neolithic Irish genomes from several megalithic burial complexes to uncover deep kin relationships between passage tomb inhumations separated by more than 150 km, as well as evidence for a social stratum already established during the Neolithic, using fine-scale haplotypic structure (Cassidy et al. 2020).

Finally, the advent of whole genome sequencing (WGS) has also enabled a metric that is especially sensitive to recent demographic history: the estimated time to the most recent common ancestor (MRCA) of shared doubletons (variants that are present exactly twice in the entire data set) (Mathieson and McVean 2014; Novembre and Peter 2016). Such doubleton-based metrics had already demonstrated their utility to infer fine-scale population structure in various large-scale sequencing studies (Genome of the Netherlands Consortium 2014; UK10K Consortium et al. 2015). In fact, besides doubletons, there are many mutations of higher—but still low—allele frequency, which are not only shared among pairs of individuals but among three or more samples (here referred to as "rare variants"). Whereas common variants are invariably old (because it takes substantial time for alleles to increase in frequency even in the occasional cases when they are selectively advantageous), the vast majority of rare variants is relatively young (Jobling et al. 2013). This has two main consequences: first, there has been less time for purifying selection to act on them, so they are enriched for deleterious variants in comparison to common variants; second, there has been less time for them to spread geographically since the alleles arose, so they tend to be confined to a single

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population or a group of nearby populations (Jobling et al. 2013). As a consequence, whereas common variants (that can be assayed by SNP technologies) represent gene flow patterns time-averaged over several millennia (Novembre and Ramachandran 2011), rare variants identified with WGS enabled the reconstruction of demographic patterns on the timescale of centuries, shifting the focus from ancient population movements to events during the timeframe of the historical record. Studies conducted by Schiffels and colleagues were the first to introduce this concept of "rare allele sharing" (RAS) to the field of paleogenetics by investigating the Anglo-Saxon settlement of post-Roman Britain (Schiffels et al. 2016). Meanwhile RAS has been used to study the effects of the Crusades on the present-day Levantine populations, which found no evidence for different amounts of European ancestry between Christian and Muslim Lebanese but introgression of African and/or eastern Asian ancestry into Lebanese Muslims (Haber et al. 2019), as well as to reconstruct the spread of Paleo-Eskimo ancestry into North America (Flegontov et al. 2019).

In the near future, novel methods will be introduced, and more complex analyses of ancient DNA based on RAS, IBD, and haplotype structure performed. And while the focus of aDNA research will also shift to more recent time periods, there are already a number of paleogenetic studies providing insights into the population genetics of early medieval Europe. In the following section, three cases will be discussed in which ancient DNA was applied to the historic periods of north-western Europe.

The migration period in Germany

In 2018 Veeramah and colleagues conducted the first population-level analysis of people from the Early Middle Ages (Veeramah et al. 2018). By sequencing 41 genomes from seven early medieval cemeteries located in present-day Bavaria, mostly dating around 500 AD, they gained insights into the population composition of the ancient Baiuvarii, a presumably Germanic-speaking tribal group that was first mentioned by the Gothic historian Jordanes and which gave its name to the modern state of Bavaria. Interestingly, this population is marked by the comparatively high presence of skeletons with artificially deformed or elongated skulls (ACD), a marker of status, nobility, or affiliation to a certain class or group in several societies world-wide (Tiesler 2014). In early medieval Europe it is most popularly associated with the Huns, although the earliest evidence for ACD appears in Europe in 2nd century AD burials in present-day Romania that predate the proposed Hunnic invasion (Hakenbeck 2009). In eastern and south-eastern Europe in particular it was equally common among males and females and across all age groups, which stands in stark contrast to the Bavarian population, where this phenomenon is mainly restricted to adult females (Veeramah et al. 2018). Veeramah and colleagues were able to show that the presence of ACD was strongly associated with genomic ancestry. While both males and females with normal skulls were found to be a largely homogenous group of individuals with a common northern/central European ancestry, females with deformed skulls sampled from the same cemeteries were very genetically diverse, demonstrating a wide range of both northern and southern/south-eastern European ancestry, and even some samples with eastern Asian ancestry. This is consistent with the assumption that adult females with deformed skulls found in medieval Bavaria are likely to have migrated from south-eastern Europe (Hakenbeck 2009). Furthermore, the northern European ancestry found in medieval Bavaria is extremely different to the ancestry found in Bavaria during the Bronze Age, which is more closely related to Bonze Age and present-day French ancestry (Mittnik et al. 2019) (Fig. 1A). This implies that the northern European ancestry entered Bavaria after the Bronze Age, sometime between the Bronze and Middle Ages, and replaced the majority of the preceding gene pool. In terms of population genetic affinities, it shows the greatest similarity to present-day Danes and northern Germans and is basically indistinguishable from Late Bronze Age Danes and early medieval Anglo-Saxons, suggesting a southern Scandinavian origin for this ancestry. Furthermore, this ancestry is found in the Alemannic graveyard of Niederstotzingen in Baden-Württemberg (O'Sullivan et al. 2018), Germany (Fig. 1B), as well as – remarkably – in Langobard cemeteries in Collegno, Italy, and Szolad, Hungary (Amorim et al. 2018) alongside the local gene pool.

We can therefore infer that by the Early Middle Ages southern Scandinavian ancestry had spread not only into southern Germany but as far as northern Italy, which concurs with the historical documented migrations of the Germanic tribes of the Langobards. Similarly, in the Iberian peninsula during the Visigoth period, several individuals show signs of considerable admixture with a northern European source, best approximated by the early medieval Bavarians (Olalde et al. 2019). Summarising, first archaeogenetic results are consistent with the proposed long-distance migration of non-Romanised peoples such as the Goths, Alemanns, and Langobards, although these barbarian populations left no written record. Ancient DNA has been shown to be another form of direct evidence beside archaeological and anthropological remains and can be effectively used to make inferences about group processes, social structures, and migration patterns.

Viking Genetics

The Vikings and their expeditions of discovery fascinated and still fascinate people of all ages and origins, as they feature more frequently in mainstream media than any other historic group or time period. Although the term Viking is by no means intended as an ethnonym, describing a homogenous biological entity, the question of how the Viking groups were composed in terms of different ancestries and how the seafarers (biologically)

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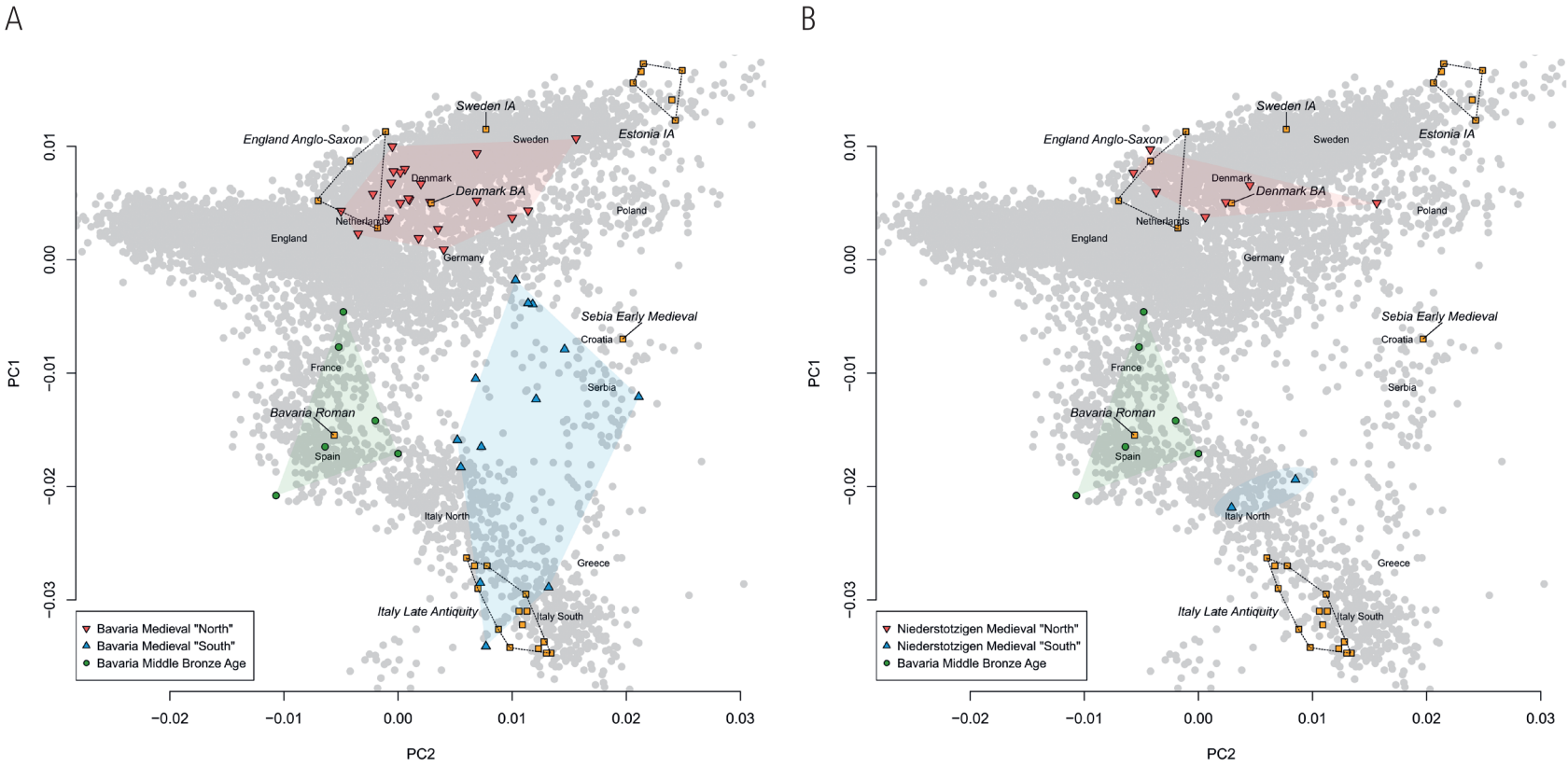

Figure 1. (A) Principal component analysis of 9,470 present-day European individuals (grey dots), with previously published ancient samples projected onto the first two principal components. Individuals from Medieval Bavaria are highlighted. (B) Principal component analysis of 9,470 present-day European individuals (grey dots), with previously published ancient samples projected onto the first two principal components. Individuals from Medieval Niederstotzingen are highlighted.

interacted with the locals they encountered is strongly linked with understanding their export of technologies, beliefs and languages to large parts of the European continent, western Asia, and even North America. The first study of Viking Age Scandinavian genomes was performed in 2017, sequencing a single genome from a richly furnished warrior grave in Birka, one of the most important trading and administrative centres of Viking Sweden (Hedenstierna-Jonson et al. 2017). As the individual was buried with a sword, an axe, a spear, armour-piercing arrows, a battle knife, two shields, and two horses – a mare and a stallion – and prominently placed on an elevated terrace between a hillfort and the town, the individual was identified as a high-ranking officer. Yet, surprisingly, molecular sex determination produced evidence that the deceased was female. Although female burials with weapons as grave goods are attested not only in Viking Age Scandinavia but also other parts of central and northern Europe, the presence of this grave clearly questions the common notion of an exclusively patriarchal Viking society. Unfortunately, insights into the population genetics of Viking Sweden were rather limited. While the female is located in the genetic diversity of present-day Swedish in PCA analysis, descriptive statistics such as outgroup F_3 and F_4 statistics were not able specify closer genetics affinities within northern Europe, generally detecting high similarity to Lithuanians, Icelanders, Norwegians, Swedish and English. We show here that the Birka woman is genetically closer related to modern Danish than to modern Swedes, indicating that Birka also attracted people from southern Scandinavia (Fig. 2A).

Shortly afterwards, in 2018, the first population-level analysis of Viking individuals was conducted by Krzewińska and colleagues (Krzewińska et al. 2018). They sequenced 23 genomes from the town of Sigtuna in eastern central Sweden, dating between the 10th to 12th centuries AD. In congruency with the town being a formal administrative centre with a high level of international contacts, the Viking population of Sigtuna exhibits substantial genetic heterogeneity and diversity, as great as that observed in Roman soldiers in England. Although from fine-scale population genetic analysis it is evident that the majority of individuals fall in the genetic diversity of present-day Swedish, several outlier individuals show excess affinity to north-eastern, especially Baltic populations or to more western European such as British and French (Fig. 2B). Consistently, eight of the tested 16 individuals were confirmed as non-locals using strontium isotope analysis, falling beyond the local range of bioavailable strontium. This demonstrates that the formation of the gene pool of the Viking world was characterised to a high degree by cultural as well as biological reciprocal exchanges between Viking Scandinavia and the rest of the continent.

Margaryan and colleagues impressively verified these results by carrying out the second-largest ancient DNA study so far (Margaryan et al. 2020). By sequencing 442 genomes, most dating to the Viking period, from all over Europe, and novel statistical methods that are able to fill-in ("impute") missing data from reference datasets, they were able to detect substantial gene flow from Scandinavia into the British-Irish Isles, Iceland, Greenland, and the Baltics. On the other hand, this spread of Scandinavian ancestry was followed by introgression of more southern and western as well as in some places north-eastern European ancestry into the Scandinavian peninsula. Summarising, the origins of Viking Age populations in Scandinavia can be traced back to the preceding local Iron Age. However, with the beginning of the Viking Age, Swedish-like ancestry dispersed into the Baltic Sea region and Russia, while Norwegian ancestry was introduced to Ireland, Greenland and Iceland, which is consistent with previous research by Ebenesersdóttir and colleagues (Ebenesersdóttir et al. 2018). Finally, the introgression of up to 40% Danish-like ancestry into present-day English demonstrates the considerably substantial effects of these historic migrations on the modern European gene pool, although it must be added that the majority Danish ancestry found in modern English is likely to have already been introduced during the Anglo-Saxon period and its associated migrations.

The Anglo-Saxon migration

From the late 19th century onwards, the role of migration in the relatively sudden and drastic change from Romano-Britain to Anglo-Saxon Britain has represented one of the most hotly-debated controversies in British archaeology (Härke 2011). The traditional model of the cultural transformation and population change in Britain during the post-Roman period draws primarily on the few written sources (Härke 2011): These texts describe the violent military invasion of Britain by Germanic immigrants from the European continent, starting with the so-called adventus Saxonum ("Arrival of the Saxons") in AD 449 (Laker 2008). According to the Anglo-Saxon chronicle, the Germanic migrants brought their own material culture and language, founding their own ethnic kingdoms according to their respective northern European origin (Härke 2011). Subsequently, the indigenous British population was wiped out as a result of repeated defeats in battle, and a common Anglo-Saxon identity was created (Härke 2011). For most of the 20th century, linguistic and archaeological research seemed to confirm those records and the drastic cultural transition was widely accepted as being the result of mass migration from continental Europe and the near-complete replacement of the indigenous population in England.

However, a new debate on this question has been running since the first half of the 1980s: that instead of the Anglo-Saxon conquest being a "mass migration", it was only a small number of Germanic immigrants (perhaps a male military elite) settling in Britain, with the sudden change to an Anglo-Saxon culture being the result of rapid acculturation and indigenous developments (Higham 1992; Pryor 2004). In consequence, the numerous early Anglo-Saxon cemeteries should represent a culturally homogenous population, consisting of a miniscule

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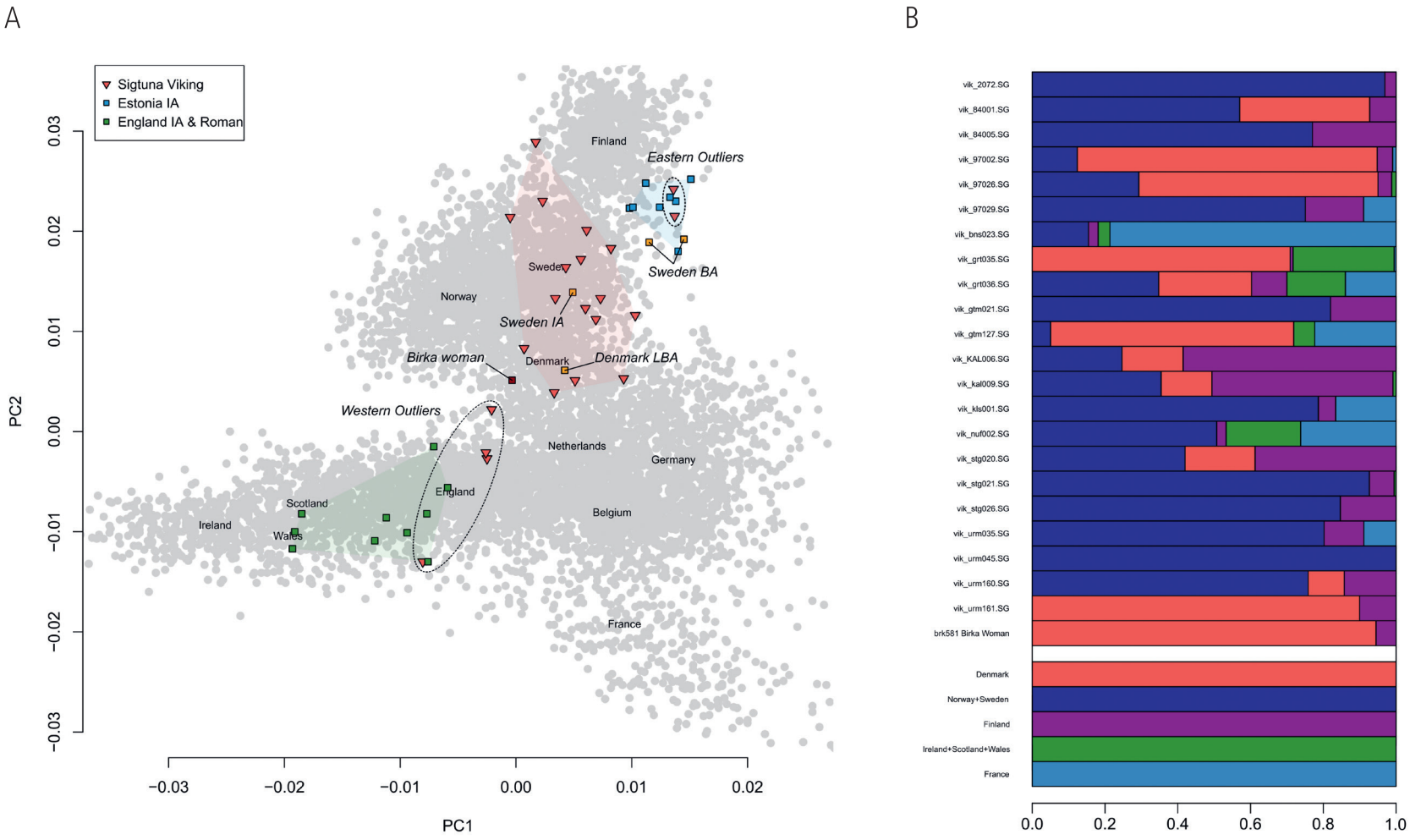

Figure 2. (A) Principal component analysis of 8,063 present-day Western, Central, and Northern European individuals (grey dots), with previously published ancient samples projected onto the first two principal components. (B) Proportions of British-Irish, Northern Scandinavia, Southern Scandinavian, Baltic, and French-related ancestry in Viking Age individuals from Sigtuna and Birka computed with Supervised ADMIXTURE using K=5.

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ruling Germanic elite as well as a majority of native Britons, who had adopted the cultural characteristics of these continental immigrants (Härke 2011). In the light of this new, conflicting explanatory model, the use of mass migration as an explanation for the cultural transition in Post-Roman Britain has substantially declined in popularity. However, according to Heinrich Härke, "Until the beginning of the 21st century, the debate was driven by new thinking rather than new data, but, since then, biological data have had a major impact" (Härke 2011). Indeed, initial genetic studies of uniparental markers of the present-day British population seemed to support the more traditional view, proposing a massive migration from the continent that replaced between 50-100% of the native population (Weale et al. 2002; Capelli et al. 2003).

In contrast, more recent large-scale analyses of present-day autosomal data provide a more modest estimate of the Anglo-Saxon migration impact, not exceeding 40% (Leslie et al. 2015). In 2016, two studies by Schiffels and colleagues and Martiniano and colleagues resolved this issue (Schiffels et al. 2016; Martiniano et al. 2016). They studied 19 (10 and 9 respectively) samples from six different sites in England, ranging from the Iron Age (800 BCE–100 CE) to the Middle Saxon period (660–899 CE). With the exception of one Roman individual (identified as of Near Eastern origin (Martiniano et al. 2016)), all 18 British samples are genetically similar and close to other north-western European populations such as Irish, English or Norwegian (Schiffels and Sayer 2017). To gain deeper insight into the differentiation of the Pre-Anglo-Saxon and Anglo-Saxon populations, Martiniano and colleagues applied an identity-by-state (IBS) approach, detecting strong affinities between the seven Iron Age and Roman period (43–410 CE) samples as well as the extant Celtic-speaking populations of Wales and, to a lesser extent, Ireland and Scotland (Martiniano et al. 2016). In contrast to this genetic continuity, the later Anglo-Saxon genome differs substantially from these populations, in concord with the influx of northern Europe immigrants during the Anglo-Saxon period. In the same year, Schiffels and colleagues developed the novel approach of rare allele sharing (RAS), focusing on rare genetic variation to study fine-scale population affinities. They investigated RAS between ancient samples and a set of extant European reference populations (Finland, Denmark, Netherlands, Britain (represented by Cornwall, Kent and Orkney), Spain, Italy), revealing a substantial stratification based on the ratio of the number of rare alleles shared with Dutch individuals to the number shared with Spanish individuals between Iron Age and Anglo-Saxon samples (Schiffels et al. 2016). Here, the Anglo-Saxon individuals share relatively more rare alleles with extant Dutch than the Iron Age samples. But also, on the individual level, noticeable differences in sharing patterns

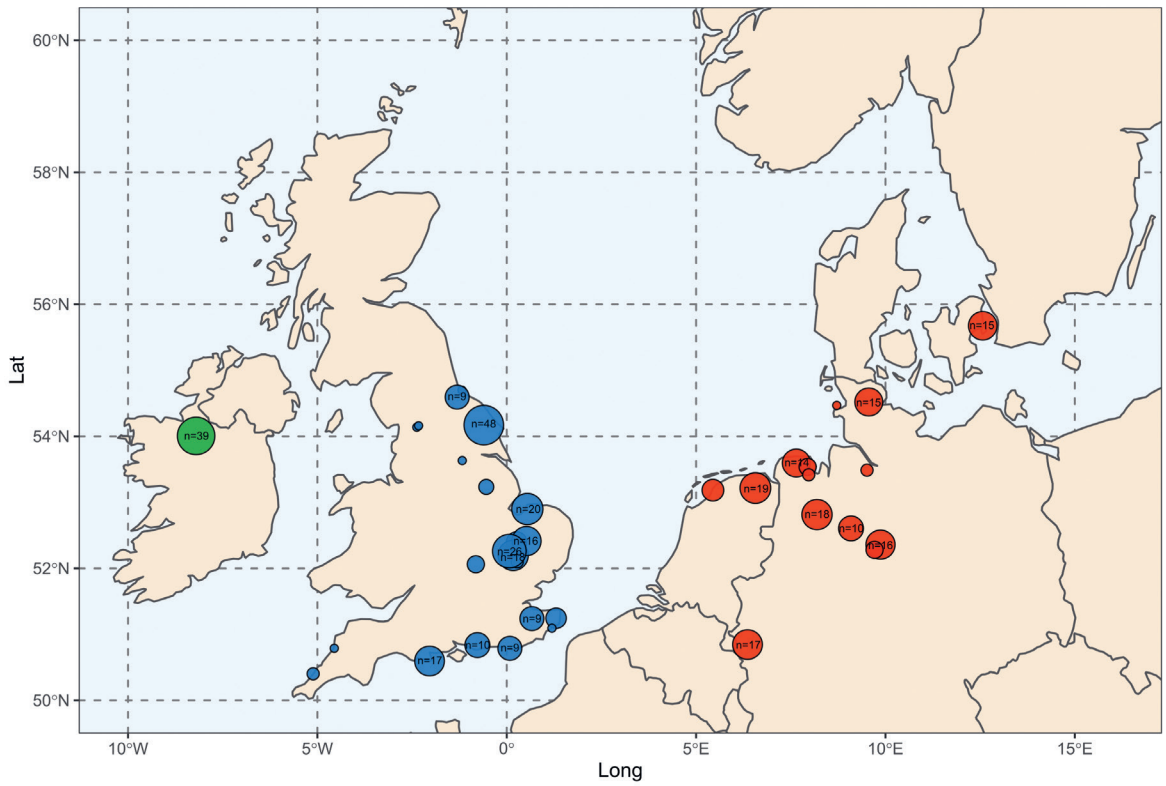

Figure 3. Geographic distribution of sampled sites in Northern Europe. The size of the circles is proportional to the number of sampled individuals (number shown if more than eight).

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are present. In particular, the Early Anglo-Saxon (410–660 CE) population seems diverse, with two samples being closer to the Middle Anglo-Saxon population, one sample exhibiting the same pattern as the Iron Age individuals as well as another sample displaying an intermediate level of rare allele sharing, indicating mixed indigenous and Anglo-Saxon ancestry (Schiffels et al. 2016). With regard to the present-day British population, according to Schiffels and colleagues, today (based on the RAS statistics) the average Anglo-Saxon ancestry proportion in eastern England is only 38% (ranging between 25% to 50%) and 30% in Wales and Scotland (Schiffels et al. 2016), which is close to previous estimates based on modern DNA comparisons.

Nevertheless, in summary, a substantial change in ancestry from the Iron Age through the Early and Middle Anglo-Saxon period associated with a considerable increase of continental ancestry related to northern Europe can be attested. However, there is evidence, especially in the Early Anglo-Saxon period, for a "genetically mixed but culturally homogenous community" (Schiffels et al. 2016; Schiffels and Sayer 2017), in contrast to the earlier claims for a strong, apartheid-like segregation between the "Germanic" immigrants and the indigenous Britons (Thomas et al. 2006) or even total replacement based on historical or outdated Y-chromosome data (Weale et al. 2002). Taken all together, these insights now draw a picture of the Anglo-Saxon Migration as a long-range continuous influx process rather than a sudden and solitary mass-invasion or small elite transfer, resulting in chronological and geographical diversity in the composition and origins of the British population during the last two millennia.

Outlook

Through genomic characterisation, the research presented provided novel insights into the structures and hierarchies of societies from the migration period as well as into demographic events occurring during and after the transition from the Late Antiquity to the Middle Ages. Most noteworthy is the fact that the Early Middle Ages experienced massive shifts in ancestry composition across Europe. In western and southern Europe in particular, this transformation was caused by the introduction of northern European ancestry that shows the highest affinity to present-day Danish and northern Germans. During the migration period it can be found in England, Hungary, Italy, southern Germany, and Iberia where before then it was completely absent. While this clearly demonstrates that the movements of large groups of northern Europeans occurred in the Early Middle Ages that coincide with recorded migrations of Anglo-Saxons, Langobards, Alemanni, and Visigoths geographically and chronologically, this should be in no case misunderstood as a verification of outdated nationalistic archaeological concepts of the 19th and early 20th centuries. Instead, close collaboration between geneticists and archaeologists is necessary to connect the historical, archaeological and biological evidence and reconstruct the interaction between natives and newcomers (Meier and Patzold 2021). Fortunately, good examples demonstrate how archaeogenetics, historical and archaeological science can be brought together as equal partners (e.g. Amorim et al. 2018).

In the context of those recent advances, the authors themselves have initiated a major population genomics project to study the individual, regional, and population-wide genetic transformation at the transition from the Late Antiquity to the Early Middle Ages in England. While previous studies collected only small samples sizes, nearly 500 low-coverage genomes were generated as part of the current project and subsequently combined with genetic information of more than 10,000 modern Europeans. This high number of ancient individuals and their widespread distribution across England allows us now to detect regional differences in interaction and admixture between locals and incomers as well as to estimate better the impact of possible migrations on the native gene pool. Furthermore, to trace back individual ancestry of immigrants, we extended our sampling approach to the continent, collecting reference material of over 150 early medieval individuals from sites in the Netherlands (Groningen and Midlum), northern Germany (Anderten, Dunum, Drantum, Issendorf, Liebenau, Häven, Hiddestorf, Alt-Inden, Schortens, Zetel and Schleswig), and Denmark (Copenhagen) (Fig. 3). While the first genomes from Lower Saxony, Anglia and Frisia constitute a valuable proxy for modelling the flux of ancestry across the North Sea, they also grant us further insights into the population composition and demographic events occurring in northern Europe during the migration period and the beginning of the Middle Ages.

While those analyses are still in progress, we demonstrate the potential of our study using already published genomes in the context of our large-scale high resolution reference panel, to gain extensive and accurate estimates for genetics affinities as well as admixture proportions in England. The main results achieved by this approach comprise two finds. Firstly, the high genetic resemblance of the immigrating Anglo-Saxons to extant as well as ancient continental northern European populations that are linguistically associated with the Germanic languages, in contrast to the pre-Saxon inhabitants that exhibit close genetic ties to the present-day formerly Celtic-speaking populations of Britain as suggested by Martiniano and colleagues (Martiniano et al. 2016) (Fig. 4A). Secondly, despite a distinct increase in ancestry akin to the extant Danish and northern German populations during the Early Anglo-Saxon period, a continuous presence of ancestry identified in Pre-Saxon Iron Age and Roman individuals, indicating persistence and introgression of this population in the immigrating gene pool, as demonstrated by Schiffels and colleagues (Schiffels et al. 2016; Schiffels and Sayer 2017) (Fig. 4B). Our study therefore suggests that the early English population was the outcome of long-term ethnogenetic processes in which the acculturation and assimilation of native Britons into the immigrating Anglo-Saxon society played a key role. Besides

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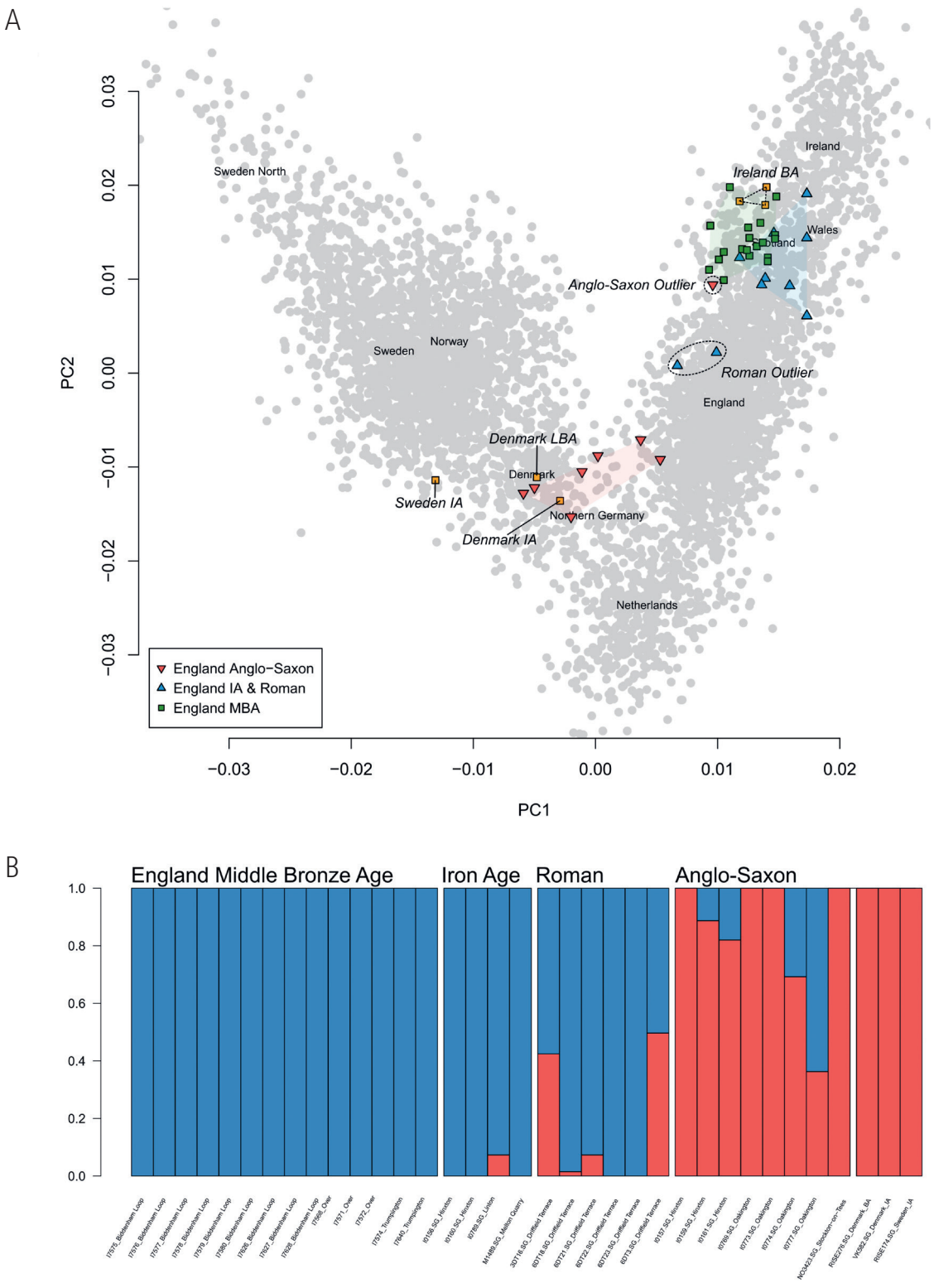

Figure 4. (A) Principal component analysis of 5,381 present-day Scandinavian and British-Irish individuals (grey dots), with previously published ancient samples projected onto the first two principal components. (B) Proportions of modern Danish-related ancestry (in red) and modern Irish/Scottish/Welsh-related ancestry (in blue) in prehistoric English individuals computed with Supervised ADMIXTURE using K=2.

https://doi.org/10.24355/dbbs.084-202301131414-0

these preliminary results, we are aiming to reconstruct the life histories of single Anglo-Saxon individuals, determining the geographical origins of their ancestry components and admixture histories. Combining the individual evidence, we will further describe the Early English gene pool composition between the poles of genetic continuity and replacement and illuminate the relationship between continental immigrants and indigenous Britons on a larger scale than all previous studies.

Methodology

Reference dataset. We compiled a main autosomal reference datasets of microarray SNP data for the purpose of analysing the ancestry of the medieval European genomes. We removed loci and individuals with <95% call rate and pruned for loci on three previously reported long range LD regions on chromosomes 6, 8, and 11 using PLINK (Purcell et al. 2007). Our European reference dataset contained genotypes for 426,164 SNPs (the intersection of several different Affymetrix and Illumina chip types) from 7,680 contemporary individuals sampled from 20 European populations (Genetic Analysis of Psoriasis Consortium et al. 2010; International Multiple Sclerosis Genetics Consortium et al. 2011; Yunusbayev et al. 2012; Genome of the Netherlands Consortium 2014; Kovacevic et al. 2014; Leslie et al. 2015). Published ancient DNA data was merged to this dataset, correcting for reference allele and strand flips.

Principal Components Analysis. We performed PCA using the smartPCA (Patterson et al. 2006) program v.16000 from EIGENSOFT (https://github.com/DReichLab/EIG) on the 1240k-Europe dataset on which ancient individuals were then projected using the options lsq project: YES and shrinkmode: YES.

Model-Based Clustering. ADMIXTURE (Alexander et al. 2009) in supervised mode (https://www.genetics.ucla.edu/software/admixture/download.html) was run with version 1.3.0, following exclusion of variants with minor allele frequency of 0.01 to estimated admixture proportions for the ancient individuals using i) Danish, Norwegian/Swedish, Finnish, French, and Irish/Scottish/Welsh reference populations with K=5 (Fig. 2B), or ii) Danish and Irish/Scottish/Welsh reference populations with K=2 (Fig. 4B).

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Joscha Gretzinger
Max-Planck-Institut für evolutionäre Anthropologie
Deutscher Platz 6
DE 04103 Leipzig
joscha_gretzinger@eva.mpg.de

Stephan Schiffels
Max-Planck-Institut für evolutionäre Anthropologie
Deutscher Platz 6
DE 04103 Leipzig
stephan_schiffels@eva.mpg.de

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